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THE MECHANICS OF ENVIRONMENTAL CONTROL OF BODY FORM IN FISHES

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ABSTRACT

THE relative-growth method has been used in the interpretation of the environmental control of body form in fishes. The relative growth of any body part such as head is characterized by a series of relative-growth stanzas that differ in slope and in the size range over which each is applicable. Five stanzas are described for the salmon during the life of the fish. The four inflections that delimit these stanzas are approximately coincident with the attainment of the eyed-egg stage, with hatching, with ossification, and with sexual maturity. Inflections are demonstrated for more than twenty species of fishes.

Differences in the body form of individuals, groups, or populations of one species are regularly found for all sizes of fish. The relative-growth lines describing such differences are usually parallel within the limits of observational error. This demonstration of parallelism is indirect evidence that inflections, particularly during early development, are important in the control of body form. Direct evidence of the role of inflection in the determination of body form was found in natural populations and experimental lots of rainbow trout. Differences in body proportions of certain mature trout populations are largely dependent on the size at which the fish attain maturity. Body form differences in small trout were produced by controlling temperature during early development. Rainbow trout reared at 46°F. to 20 mm. standard length and then at 60°F. had a higher growth rate, larger size at the subsequent inflection, and larger heads and fins after inflection than did fish reared at 46°F. throughout the experiment, but retained the same growth partition constants. Very early inflections, as well as those at about 30 mm. and at sexual maturity, are probably important in the determination of body form.

The fast-growing individuals of a group have relatively small body parts such as head and fins but a fast-growing group of individuals may have relatively small or relatively large body parts. The relative size of body parts is determined to a large degree by the direction of, degree of, and body size at inflections. Either rate of early development or subsequent growth rate may affect body form through their influence on body size at inflection.

The slope of relative-growth lines was altered experimentally by malnutrition. Relatively large head parts resulted. Differences in the length-weight relationship, found within species, are in part attributable to variation in body size at growth inflection. Body size at inflection plays a major part in the determination of body form in animals other than fishes.

THE MECHANICS OF ENVIRONMENTAL CONTROL OF BODY FORM IN FISHES

INTRODUCTION

MANY facts have been discovered which point to a close correlation between rate of development and the relative size of many body parts of fishes, the proportional dimensions of which are commonly employed by taxonomists in the diagnosis of species and of infraspecific groups. Among these facts are those that relate the body proportions to geographical and ecological distribution of species both in fresh and salt water. Schmidt (1919, 1921, 1930), Hubbs (1922, 1934), Schultz (1927), Rounsefell and Dahlgren (1932), and Tester (1937) are among the many workers who have contributed to this subject. Further evidence which correlates rate of development with body form in fishes has been put forward, on the basis of field observations, by Hubbs (1926). Finally, demonstration that differences in developmental rate can result in differences in meristic characters of fishes has been achieved through direct experiment, notably by Schmidt (1921), Mottley (1937) and Gabriel (1944).

All of these lines of evidence have established that, in general, decreasing the rate of development increases the numbers of meristic parts. Thus, fish which develop in northern waters usually have more vertebrae and scales than do members of the same species which pass their lives in more southern latitudes. There is also a general tendency for the head and fin measurements to be relatively smaller in fish which are held to have a retarded development than in those which develop more rapidly. Accordingly it has been found that northern races of a species have smaller heads, eyes, maxillaries, and fins than do southern races of the same species. These morphological clines are more closely correlated with temperature gradients than with differences in latitude (Jensen, 1944).

In view of the great weight of evidence which has accumulated to indicate the dependence of body form on developmental rate, it is rather disconcerting that in the several studies in which growth in nature has been correlated with body form, a relationship has been found that appears to be diametrically opposed to that adduced from other observations. On this continent, White (1936) showed differences between head and eye measurements of salmon parr, *Salmo salar*, which were negatively correlated with rate of growth. Tester (1937) and Hile (1937) have shown respectively for the Pacific herring, *Clupea pallasii*, and the cisco, *Leucichthys artedi*, that slow-growing members of a year class have longer heads, larger eyes, and longer fins than do the faster-growing members of the same year class in the same locality. The comparison was extended to fish of different populations and different year classes, adding weight to the correlation between body form and growth rate.

The title of White's paper "Age determination of salmon parr by effect of rate of growth on body proportions" and the statement in Hile's summary (p. 125) "The values of certain characters that have been used in the separation of the subspecies show a distinct dependence on growth rate" would seem to indicate that there was no doubt in the minds of these workers as to the causal connection between growth and body form.

Hubbs (personal communication) has recognized this correlation between body form and growth rate for several species. Fast-growing salmonoids, poeciliids, walleyes (*Stizostedion vitreum*), and gizzard shad (*Dorosoma cepedianum*) have been found with relatively small heads, eyes, and fins, and thick terete bodies; a distinct contrast with the relatively large heads, eyes, and fins, and the deep, narrow body form found among very slow-growing fish.

Thus it appears that two processes, rate of development of body parts and rate of growth, are correlated with body form in fishes. These two processes appear to have opposing relationships to body form since relatively small body parts may be associated with either retarded development or with subsequent rapid growth.

The present investigation has been directed toward the assessment of the relative importance of these two processes in the environmental control of body form. Two major lines of attack have been followed:

(1) A relative-growth analysis of ontogenetic growth and of infraspecific differences in body form.

(2) The experimental control of rate of development and rate of growth and an analysis of the resultant effects on body form.

ACKNOWLEDGEMENTS

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The investigation was conducted at the Museum of Zoology, Ann Arbor, Michigan, under the direction of Dr. C. L. Hubbs and completed under Dr. R. M. Bailey. The work was supported in part by the Hinsdale scholarship granted in 1941 and in part by the Associated Fishing Tackle Manufacturer's Trust Fund for fisheries research in the University of Michigan.

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The statistical procedure used in the investigation was outlined by Dr. D. B. DeLury, Ontario Research Foundation.

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This dissertation was submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy in the University of Michigan. The original manuscript, which includes the basic data, is available from University Microfilms, Ann Arbor, Michigan as Publication No. 955, Library of Congress, Card Number Mic A 48-85.

RELATIVE-GROWTH MECHANICS

The relative-growth method of analysis, which was developed by Huxley (1932), consists essentially of plotting the logarithm of some dimension of a body component against the logarithm of a dimension of the whole body over a series of sizes of the organism concerned. Huxley demonstrated that such logarithmic plots almost invariably show a linear relationship over extensive ranges of body size. This linear relation between the logarithms indicates that although body form is rarely constant, the rate of change of body form is generally constant over the greater part of growth. These continuous changes in form can be described by determining the value of the slope, k, in the relative-growth equation, $y = bx^k$ or $\log y = \log b + k \log x$. If the body dimensions considered are of the same order, for example part length against body length, the slope k will approximate one. If area is plotted against length, values approximating two are expected and if volume or weight is plotted against length, k approximates three. In practice, measurements are generally not taken throughout growth of an individual, but rather a series of specimens of different sizes is measured and the resultant data are plotted so that each point represents the end of a particular ontogenetic line of growth. The best line through these end points has been considered representative of the relative growth of an average individual for the body part considered.

The advantages of the relative-growth method of analysis have been recognized by many authors, and may be summarized as follows:

1. It takes cognizance of the multiplicative nature of growth.
2. The increased variance found with increasing body size is reduced to a level comparable with the variance found at small sizes by reducing variance to a percentage basis.
3. Development as a whole may be viewed in one picture.
4. The assessment of rate of change of form as well as change of form is facilitated.
5. A convenient method for the comparison of fish of different sizes but within the same growth stanza, is provided.

Terminology

As a matter of convenience, special terminology has been developed for simple relative growth relating linear dimensions. Variation in relative growth from that in which form is constant has been termed dysharmony by Champy (1924), heterogony by Pézard (1918), and allometry by Huxley and Teissier (1936). More recently Huxley, Needham, and Lerner (1941) have suggested the term heterauxesis for ontogenetic relative growth as distinct from allomorphosis (relative-growth series such as those found in phylogenetic trends). A part growing relatively slowly, $k<1$, is said to show negative heterogony (allometry) or bradyauxesis, whereas a part growing faster than that to which it is related, $k>1$, exhibits positive heterogony (allometry) or tachyauxesis. The special case of a part growing at precisely the same rate as the whole, when $k = 1$, has been termed isogony, isometry, and isauxesis in accordance with this terminology.

Relative Growth in Fishes

Heterauxesis

A few examples of the relative-growth analysis of body form will serve to demonstrate the value of this method of analysis in morphometric investigations.

An extreme form of heterauxesis may be seen in the change of form throughout life in the California ribbon fish, *Trachypterus rex-salmonorum*, reported by Hubbs (1925). Some of Hubbs' data have been plotted in figure 1. The marked bradyauxesis of the head region in contrast with the tachyauxesis of the caudal region is readily apparent.

Tchernavin (1938), Shapiro (1938), and Huggins and Huggins (1942) may be cited as representative of the many authors who have contributed to our knowledge of heterauxesis in growth of fishes. The equilibrium constant, k, was found by them to vary between 0.8 and 1.2. Examination of the literature dealing with relative growth indicates that isometric growth, $k = 1.0$, is rarely observed, although in general the departure from it is only slight during the greater part of growth.

By examination of the relative growth of different body parts

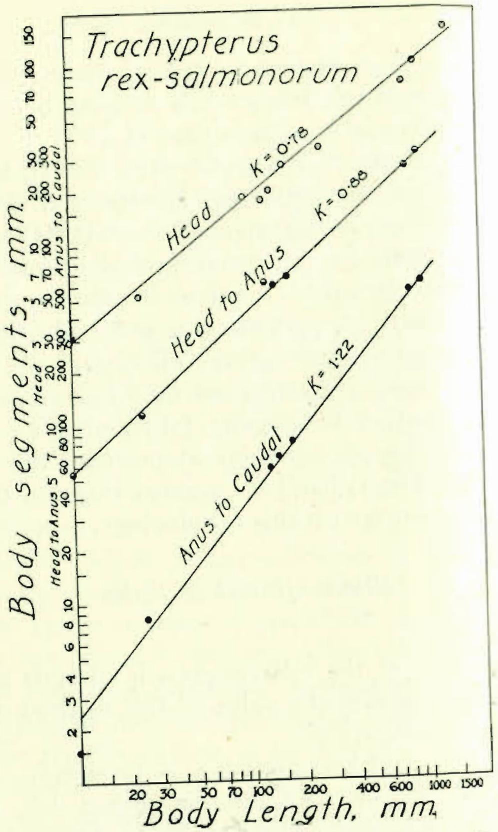

FIGURE 1.—Heterauxesis in *Trachypterus rex-salmonorum*. Data from Hubbs (1925). The head region grows relatively more slowly and the tail region relatively faster than the body as a whole.

of a particular species it has been shown that there is considerable variation in the deviation from isauxesis. Such parts as the eye generally grow much more slowly than the body as a whole. These differences among parts are generally such that a gradient of relative growth may be found along the body axis of a fish with anterior parts generally growing more slowly longitudinally and posterior parts faster than the body as a whole. For the blue marlin, *Makaira nigricans*, Shapiro (1938) has described growth constants of 0.88 for snout length, 0.92 for distance from snout to operculum, 0.90 for distance from snout to maxillary, and 1.10 for the maxillary to tail measurement. Fins, too, showed a graded series of equilibrium constants, 0.98 for pectoral length, 1.15 for first dorsal height, 1.24 for second dorsal height and 1.24 for anal height. A typical series of original measurements has been plotted in figure 2 to show the variation and gradation of relative growth

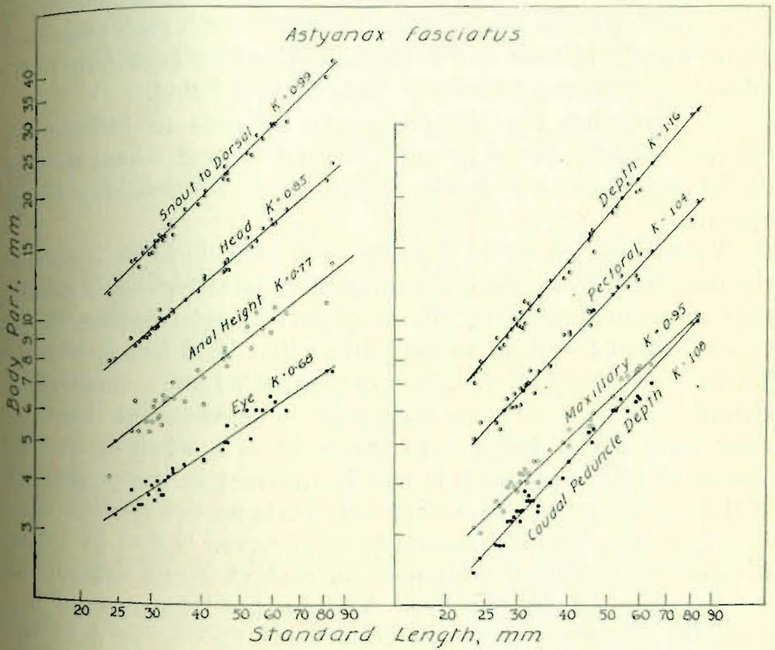

FIGURE 2.—Heterauxesis in *Astyanax fasciatus*. Each point represents one fish.

rates in the characin, *Astyanax fasciatus aeneus*. Growth ratios of 0.68 for eye length, 0.85 for head length, 1.04 for pectoral fin length, 0.99 for snout to dorsal distance, and 0.77 for anal fin height may be seen. Deviations from isauxesis are also apparent in growth of maxillary, body depth, and caudal peduncle depth. It is apparent that, although body form is not the same throughout adult growth, the rate of change of body form is constant over extensive growth periods and subject to precise description.

Growth Inflection

Apart from the gradual changes in body form described above more striking changes in body form of fishes have been recognized. At sexual maturity, the salmonoids in particular show an accentuation of certain characters such as head and fin lengths. So strikingly apparent are the changes in the transition from embryonic to juvenile form that they have been recognized as metamorphoses (Ford 1930, Huxley 1931). Usually fishes exhibit such major form changes early in life, and throughout the long growth period of adult life a relatively constant body form is found.

By extending the relative-growth analysis to include such changes as those found in early life and beyond sexual maturity deviations from the single straight-line relationship become apparent.

A consideration of the body form described in figure 2 indicates the necessity of such deviations from a single straight-line relationship throughout growth. Extrapolation of relative-growth lines to a standard length of 10 mm. infers that head length would be 4.5 mm., anal height 3 mm., and eye length 2.1 mm.—an obviously absurd situation. At some early stage in development these parts must have grown faster than the body as a whole in order to appear at all. That such is true is apparent in the presentation of the relative growth of certain body parts for five species (figures 3 to 7).[1] The essential feature to be observed is that in contrast to figures 1 and 2, all the points for each character measured do not lie on a single straight line. The simplest interpretation is the possibility that the points may be fitted by two straight lines. Such has been the procedure in fitting lines to these relative growth curves. Although straight lines fit the data remarkably well there is some doubt as to whether or not the apparent changes in slope should be drawn as curves or sharp breaks. For simplicity the latter procedure has been followed. Such a proposition of consecutive relative growth stanzas, each fitted by a straight line, facilitates interpretation even though it may only be an approximation.

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[1] Measurements of *Astyanax, Dorosoma, Brycon, Acipenser* and *Leucosomus* were made by the writer on specimens stored in the Fish Division of the Museum of Zoology, Ann Arbor, Michigan. Details of measurement technique are given on page 35.

These changes in the slope of the relative-growth line denote sudden changes in organization and are termed growth *inflections.* The term inflection is used rather than metamorphosis which has been used to describe a whole stanza of growth when body form is changing rapidly and marked heterauxesis is found. Such metamorphosis has been described by Ford (1930) for the stanza from a length of about 25 mm. to about 50 mm. in the Atlantic herring, *Clupea harengus* (see figure 9). Inflections delimit the different relative growth stanzas which are found during the life of the fish.

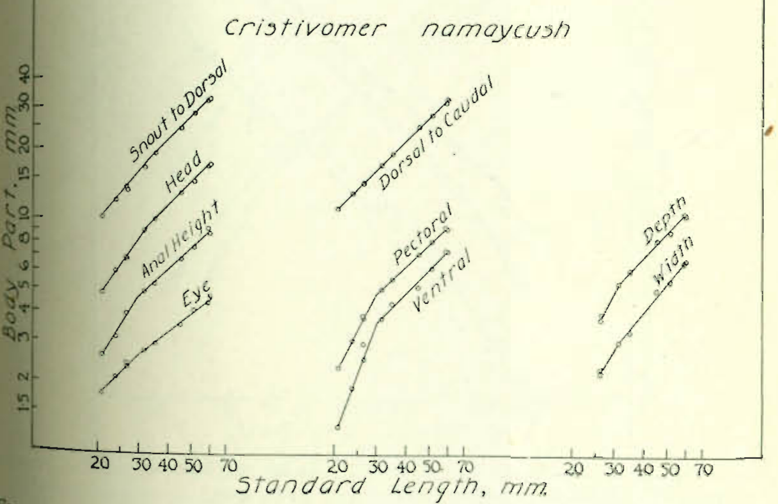


FIGURE 3.—Growth inflection of body parts of lake trout, *Cristivomer namaycush*, reared at Oden hatchery. Each point represents the average measurements for a sample of ten fish. Samples were taken regularly from February to September, 1941.

A clear-cut example of inflection is found in the ontogenetic growth of lake trout, *Cristivomer namaycush*, presented in figure 3 and table 1. The data are the means of measurements for regular samples of hatchery-reared lake trout taken from February to September, 1941, at Oden hatchery, Michigan. Details of sampling and of measurement technique are described on page 34. The interesting feature is the appearance of a growth inflection when the fish reach a length of about 30 mm. Between 20 and 30 mm.

head length, eye length, anal height, pelvic and pectoral fin lengths, body depth and body width all increase rapidly as compared with increase in body length. Beyond 30 mm. these body parts more closely approximate isauxesis. The degree of inflection differs in different body parts. Snout to dorsal and dorsal to caudal measurements do not show appreciable growth inflection; slight inflection is found in head, eye, and body width; strong inflection is apparent in relative growth of body depth and fin lengths.

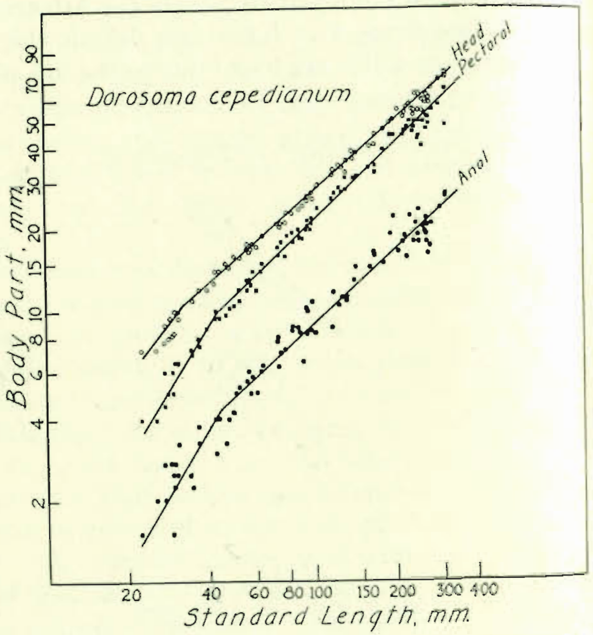


FIGURE 4.—Growth inflection of head, pectoral, and anal fins in *Dorosoma cepedianum*. Each point represents one fish.

Other examples of growth inflection are presented in figures 4 to 7.

The gizzard shad, *Dorosoma cepedianum*, shows inflections in the relative-growth lines of head length, pectoral fin length, and anal fin height (figure 4). Head and eye growth ratios are 1.27 and 1.56 respectively to a length of 34 mm. and 0.86 and 0.72 respectively thereafter. Pectoral and anal fins show growth

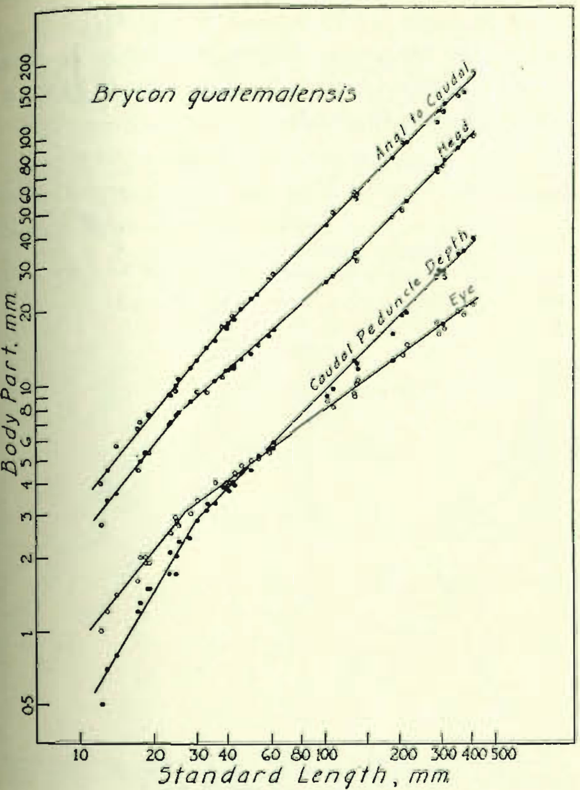


FIGURE 5.—Growth inflection of head, eye, anal to caudal and caudal peduncle depth in *Brycon guatemalensis*. Each point represents one fish. The degree of inflection is stronger in some parts than in others.

constants of 1.58 and 1.66 before inflection and 0.93 and 0.89 thereafter. Hubbs and Whitlock (1929) recognized the dangers involved in using body proportions to describe young gizzard shad since change in form was found to be rapid at small sizes.

In the characin, *Brycon guatemalensis*, the lines for head length and eye diameter shift from the same growth ratio of 1.23 for sizes less than 26 mm. to 1.02 and 0.72 respectively for larger fish (figure 5). Anal to caudal measurements indicate tachyauxesis (1.21) until fish are 38 mm. long, and an equilibrium constant of 0.99 is found thereafter. The caudal peduncle depth shows a comparable shift from tachyauxesis (1.68) to isauxesis (0.98).

The head of the sturgeon, *Acipenser fulvescens*, shows a shift from strong tachyauxesis (2.00) to bradyauxesis (0.84) at a standard length of about 34 mm. (figure 6).

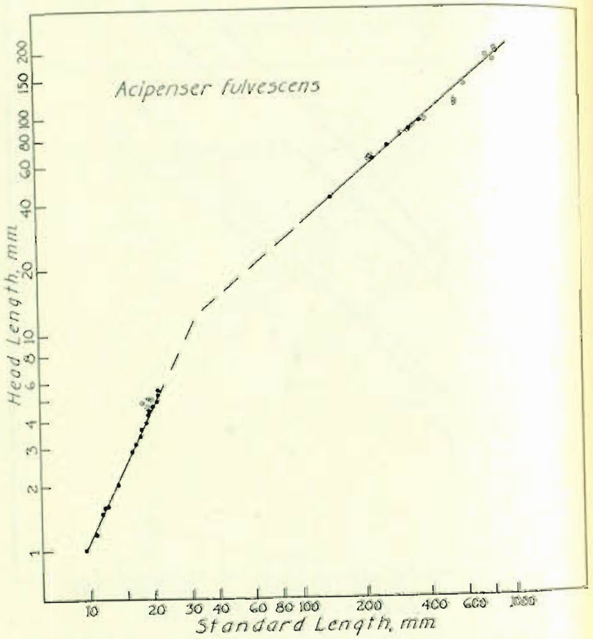


FIGURE 6.—Strong growth inflection of head in *Acipenser fulvescens*. Part of data from Harkness (unpublished). Each point represents one fish.

The data for the fallfish, *Leucosomus corporalis*, demonstrate approximate isauxesis of postorbital length, head length, pectoral fin length, head to dorsal distance, body depth and anal fin height beyond growth inflection (figure 7). Tachyauxesis is apparent in all but postorbital and head to dorsal lengths prior to shifts in growth ratio. The variability in degree of change of slope is worthy of note. The snout shows no obvious inflection and the head very little, whereas pectoral and anal fins show a marked shift. Of further interest is the fact that there are differences in the length at which inflections of different body parts are observed.

Eye diameter and postorbital length shift at a standard length of about 40 mm.; pectoral and anal fins shift from one equilibrium constant to another at a length of about 25 mm. Finally it should be noted that the direction of inflection differs from part to part. Head to dorsal and postorbital lengths increase faster after inflection than before, whereas eye and anal height increase more slowly after inflection than they do before.

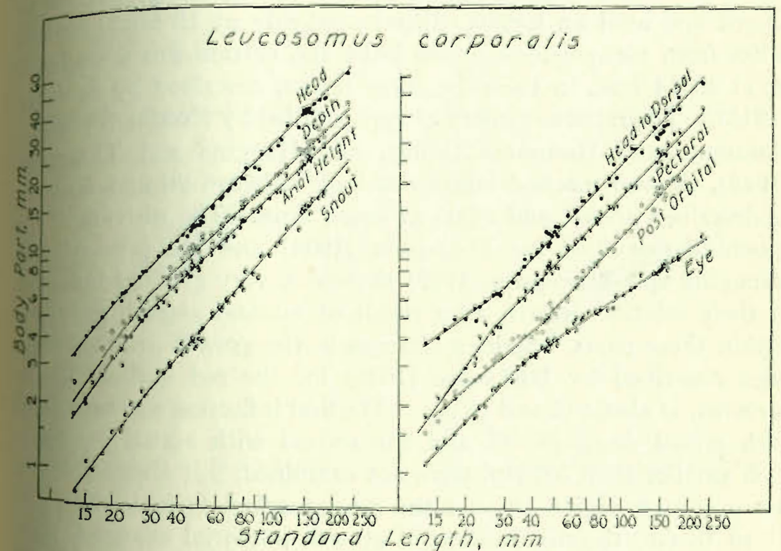


FIGURE 7.—Growth inflection of body parts in *Leucosomus corporalis*. Each point represents one fish. Body parts differ in size at, degree of, and direction of inflection.

In general, definite stanzas of relative growth occur with relatively sudden shifts or inflections from one phase to the next. The species examined are found to demonstrate slight heterauxesis for the major part of the growth period preceded by strong heterauxesis during early growth. The inflections from strong to slight heterauxesis occur between 20 and 45 mm. with considerable variation apparent between species and between body parts within the same species. In addition to this variation in size at inflection, the degree of and direction of inflection from one phase to the next vary markedly from one species to another and from one body part to another within the same species.

Growth inflections in fishes have been recognized by other authors. Doan (1939) described the relative growth of various body parts in the smallmouth bass, *Micropterus dolomieu*. No inflection was found in snout to anal length, snout to dorsal measurement, or dorsal fin length. Head length and eye diameter, however, shifted slope at 9 mm. standard length and pectoral fin length and anal fin height shifted markedly at 12 mm. Sudden shifts from tachyauxesis in the head and certain fins were found at 11 to 14 mm. in the pike, *Esox lucius*, described by Sprenger (1945). The relative growth of gars, studied by Needham (1935a), Hammett and Hammett (1939), and Huggins and Thompson (1942), showed marked inflections both between 20 and 45 mm., as described above, and again at larger sizes. The rostrum of the spoonbill described by Thompson (1934) and the jaws of gars (Huggins and Thompson, 1942) showed a very gradual inflection in their relative growth as a result of marked growth gradients within these parts. Sudden changes in the growth gradient have been described by Desbrosse (1936) for the red barbel, *Mullus barbatus*, at about 12 and 18 cm. The first inflection was associated with gonad development and the second with sexual maturity. Fish smaller than 5.6 cm. were not examined, but above this size the opercular region showed the most marked tachyauxesis. At 11 to 13 cm. the distribution of growth potential changed, there being then two regions of maximum tachyauxesis, the snout and the anterior part of the trunk. Similar changes have been recognized by Hamai (1941) in the carp, *Cyprinus carpio*. Mottley (1936) recognized changes from bradyauxesis to tachyauxesis for several body characters of *Salmo kamloops*, at a length of approximately 26 cm., coincident with the onset of sexual maturity. Similar inflections at sexual maturity in the relative growth of such characters as head and fins have been described for *Salvelinus malma* and *Salmo kamloops* by Martin (1939) and for *Salvelinus fontinalis* by Martin (1939) and Wilder (1944).

Two growth inflections have thus been recognized in many species. One has been shown to occur between 9 and 45 mm., depending on the part and on the species. Needham (1935a) has suggested that the onset of ossification may be responsible for this inflection. The second inflection, found notably among large salmonoid fishes, has been related to the onset of sexual maturity.

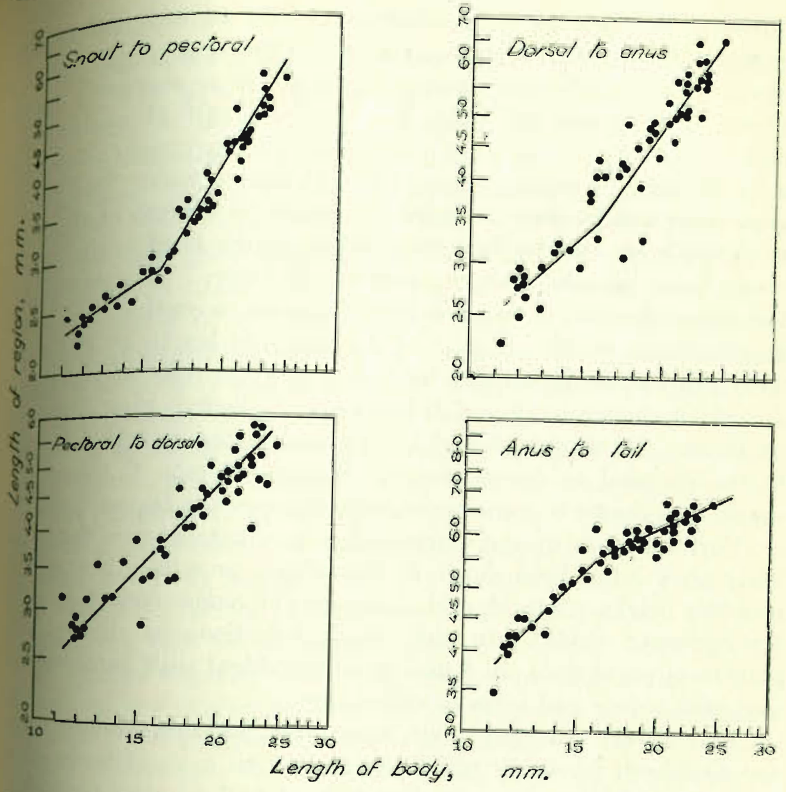


FIGURE 8.—Growth inflection of body regions in *Salmo salar*. Plotted by Fry (unpublished). There is a shift in the relative growth gradient at 16 mm. The earlier inflection mentioned in the text is not illustrated by these data.

The relative-growth picture for the Salmonidae has been extended by measurements of body parts in small fish both before and after hatching. Fry (unpublished) studied changes in the body form during early growth in salmon, *Salmo salar*, which were reared to a length of 25 mm. and sampled regularly during their growth to that size. His findings are presented in figure 8. Two further inflections are recognized at 12 and 16 mm. before the growth inflection found at about 30 mm. The first growth stanza, of which only a glimpse is seen, is featured by an extremely rapid growth of head and eye within the egg at a length of less than 12 mm. Eggs beyond this first phase of development are referred to as eyed eggs. A second stage of growth during which head parts grow more slowly than the body as a whole to a length of 16 mm., is shown more clearly. In the third stage the head again grows much more rapidly than the rest of the body. This growth of the anterior region is so rapid that if it were to continue the head would constitute 70 per cent of the standard length at 100 mm. This third stage is entered into at about the time of hatching. A sudden change in the relative-growth gradient is thus apparent at 16 mm. Between 12 and 16 mm. the fastest growth is found in the pectoral to dorsal region. Beyond 16 mm. the snout to dorsal and dorsal to anus measurements show the fastest growth.

Corroboration of the extreme forms of heterauxesis found in early growth has been shown in the relative growth of postorbital and the pelvic, pectoral, and dorsal fins of *Salmo fario* presented by Sprenger (1945). In this work, inflections in the relative growth of parts were not found to be coincident with hatching but occurred before and after hatching time.

Day (1941) provided snout, operculum, and eye measurements for *Salvelinus fontinalis* which, as plotted on a logarithmic scale, show an inflection from bradyauxesis to tachyauxesis coincident with hatching at 10 to 12 mm.

A relative-growth analysis of change of form throughout the life of a fish thus reveals a number of stanzas of heterauxesis. In the salmon five such stanzas have been recognized. The head growth demonstrates tachyauxesis to the eyed-egg stage, bradyauxesis until about hatching time, tachyauxesis again until the salmon is some 30 mm. long, slight bradyauxesis during the greater part of juvenile growth, and tachyauxesis following the attainment of sexual maturity. Although cases of extreme heterauxesis over an extended period of the life of a fish are probably rare it is perhaps the rule for them to deviate widely from isauxesis in early growth stages.

Possible Mechanisms of Change in Body Form

The mechanics of relative growth has been clearly established as a series of growth stanzas differing in the magnitude of the growth constant with each stanza applicable over a different size range. Differences in body form found among populations, year classes, and individuals of the same genetic group result from deviations from the mean relative-growth pattern for the group. There are two possible mechanisms through which differences in body form can come about. It may be that the slope or degree of heterauxesis of a particular growth stanza is affected, thus bringing about changes in body form directly. On the other hand, differences in body size at the time of inflection from one stanza to the next may bring about differences in body form. If the slopes of each phase of relative growth should remain constant for a species, marked differences in body form could still result from size differences at the time of inflection. If for example the shift from tachyauxesis to bradyauxesis found at say 30 mm. was to occur at a body length of 25 mm., the relative size of the body part considered would be relatively small and continue to be so as compared with fish which shifted slope at greater body lengths. The potential disparity that might result from such a cause would depend on the degree of inflection for the body part under consideration; the sharper the angle of inflection, the greater the possible disparity. Since there is the greatest divergence of relative growth rates from isauxesis in early growth there is an opportunity for slight changes during this period to have a profound effect on the proportionate size of body parts in later life.

In the considerations outlined above, the problem of assessing the factors determining body form has been reduced to terms of relative growth, namely, to determine whether differences in slope and size at time of inflection are both at work in the control of body form, or whether one or the other may predominate. This problem should be solved by an investigation of the relative-growth mechanics involved.

ANALYSIS OF MORPHOLOGICAL DIFFERENCES BY THE RELATIVE-GROWTH METHOD

Differences among Populations

Some of the differences found in nature among fish populations have been examined by the relative-growth method, and the correlations which have been found between body form and growth rate or early rate of development reconsidered in light of this examination. Curves and data found in the literature together with original data have been used in this relative-growth analysis of diversity within species.

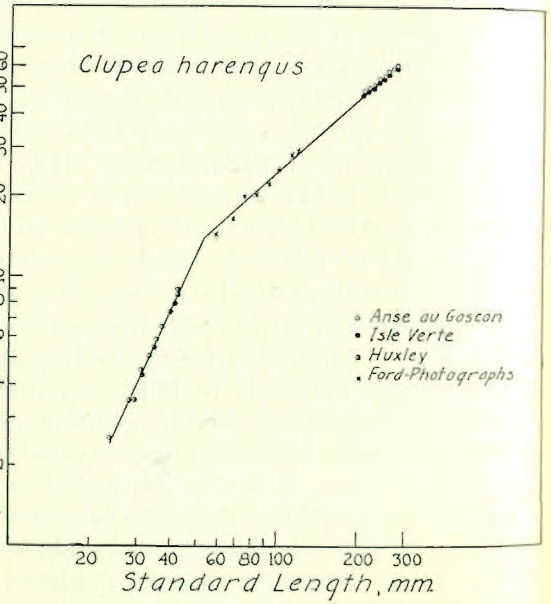


FIGURE 9.—Growth inflection and parallelism of head in *Clupea harengus*. Data from Huxley (1931), Ford (1930) and Jean (1945).

Jean (1945) has compared populations of the Atlantic herring, *Clupea harengus*, taken in the Gulf of St. Lawrence and has shown that the fish from the relatively cold waters of Île Verte, in contrast to those from the warmer waters of Anse au Gascon, were characterized by a slower growth rate and by having smaller heads and more vertebrae. These data are in accord with the hypothesis that fish at higher latitudes (or from colder waters) have relatively smaller heads and other body parts and more vertebrae than do representatives of the same species in more southern latitudes (or warmer waters), but do not conform to the contention that fast-growing fish have relatively small heads. The data on head lengths are presented in figure 9. Jean has demonstrated the parallelism of these relative-growth lines and the difference between them. In order to relate this parallelism to the inflection which is found at about 50 mm. standard length in this species, measurements of photographs presented by Ford (1930) and Huxley's analysis (1931) of Ford's data for small herring are included.

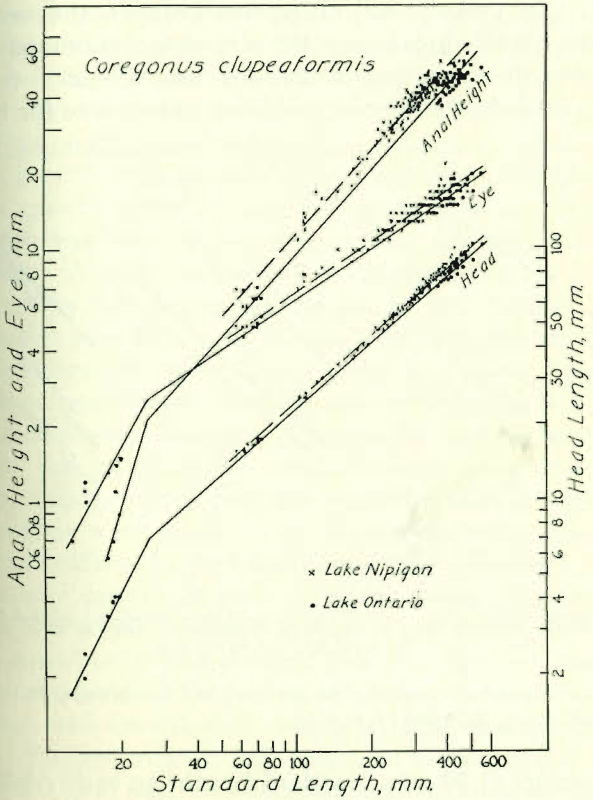


FIGURE 10.—Growth inflection and parallelism of head, eye, and anal height in *Coregonus clupeaformis*. Data from Hart (1930a and b).

Measurements of whitefish, *Coregonus clupeaformis*, as presented by Hart (1930a and b), have been plotted in figure 10. In contrast to the herring described above, the fast-growing whitefish from Lake Ontario were found to have small heads and fins as compared with slower-growing fish from Lake Nipigon. It is apparent, however, that proportional differences between the two populations were equally great over the size range examined since the relative-growth lines remain parallel and distinct throughout growth. An inflection in the relative-growth curve for both head and eye occurs at 30 mm. standard length; an earlier inflection at 8 mm. is also suggested by Hart's data but has not been included here.

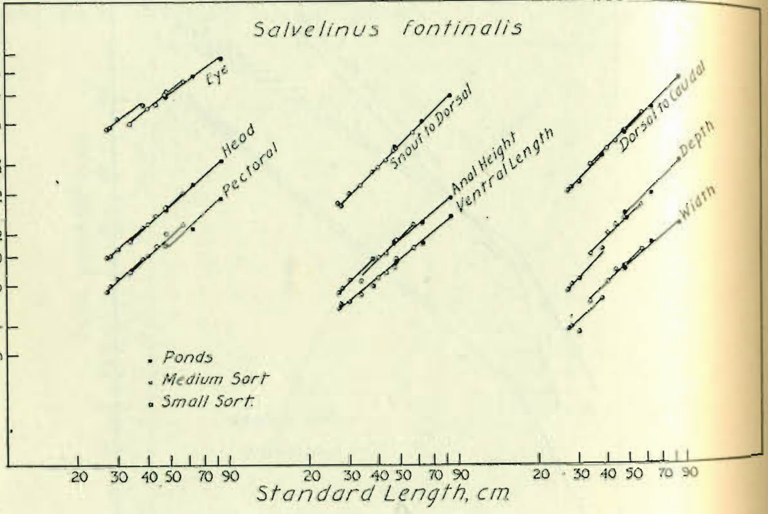


FIGURE 11.—Relative growth of slow, medium, and fast-growing hatchery stocks of brook trout, *Salvelinus fontinalis*.

The data used by White (1936) in the comparison of head size in slow and fast-growing populations of salmon, when plotted on a logarithmic scale, indicate that differences do not result from divergence of slopes. The relative-growth lines are parallel throughout the parr stage. These data on salmon parr, *Salmo salar*, have been extended by Wilder (1940). The striking feature of the comparison again is the fact that relative-growth lines, for head measurements of seven populations, are parallel. Five populations which had diverse rates of growth had virtually the same relative head size. The Beaver river population, in spite of a rapid growth rate, was characterized by a relatively large head size. In these populations there seems to be no correlation between rate of growth and size of head. The eye measurements presented by White, on the other hand, show some divergence of relative growth over and above differences which were established early in growth. This phenomenon will be discussed later.

Relative growth in three lots of brook trout, *Salvelinus fontinalis*, differing in growth rates, is presented in table 2 and figure 11. Since few fish less than 30 mm. were taken, growth inflection is not apparent. Average measurements for each of the samples taken throughout the summer at Oden hatchery have been plotted, and the relative growth of each lot has been followed by drawing straight lines through these points. Those in the small sort had relatively large eyes, heads, pectoral fins, anal fins, and the body was more slender and narrower. Since sorting was carried out on the basis of fish width by screening through trays fitted with closely spaced rods, it is perhaps not surprising that differences in body proportions were found. The interesting feature, however, is the fact that differences were maintained after continued growth. The ontogenetic growth of each group was such that fish with small depth and width continue to have small depth and width, large eyes, large heads, long pectoral fins, and high anal fins after four months of growth. There does not appear to be a divergence of body form with growth rate, but rather the slow-growing fish differ from the fast-growing individuals to a comparable degree over the whole size range. The relative-growth curves of these three lots suggest that the differences in body form resulted from differences established early in development.

Martin (1939) has described north-south form differences in *Cristivomer namaycush* and *Salvelinus alpinus*. Again, although data were limited, the relative-growth ratio was found to be relatively constant for each species and the differences, which were such that southern populations had relatively larger heads, maxillaries, and eyes than northern populations, were largely due to a lateral displacement of the relative-growth lines rather than any change in slope.

This relative-growth analysis has thrown light on the nature of differences among populations of the same species. A feature common to the differences among populations herein described is the constancy of the relative-growth slopes within a species. One case of divergence of relative-growth lines has been found, but this single divergence is overshadowed by cases showing parallelism. This recurrence of parallelism directs attention toward the possible importance of early development, operating through growth inflections, as a factor in the control of the body form of fishes. Thus, in light of this explanation, those exceptions from the general correlation between growth rate and body form which were found in certain populations of *Clupea harengus* and *Salmo salar* are seen not to conflict with the established laws of growth. In general, rapid growth in later life is associated with large size during early development and hence a general correlation between growth rate and body form is to be observed. However in the exceptions to this rule cited above, this more usual correlation was not found, the size relations during early and late development being not so correlated, and the usual relation between body form and growth rate was not observed, although the growth partition constants remained the same.

Differences within Populations

If growth rate were to influence body form directly within one growth stanza this could be accomplished only through a change in the slope of the relative-growth line. Within a population the slow-growing individuals would, under these conditions, have relative-growth lines of different slope from those of faster-growing individuals. Since such differences would be cumulative the relative-growth lines describing slow and fast-growing individuals would continue to diverge, with the result that the variance or spread of points about the line describing any particular body part would increase with growth. However, an examination of figures 2, 4 to 8 and 10 indicates that relative growth is characterized by constancy of scatter among both small and large fish. With such constancy of variance throughout growth, for each

population investigated, little margin is available for variation in slope among individual growth lines. Such evidence contributes to the thesis that differences in body form are established at critical stages of development and remain relatively constant throughout any particular growth stanza.

Asymmetry in Individuals

In a study of halibut, *Hippoglossus hippoglossus*, McCracken (1947) has found that the slopes of the relative-growth lines which describe each pectoral fin are the same, but considerable difference in fin size at a given body length is apparent. The pectoral fin of the eyed side is considerably larger than that of the blind side, and in the size range studied (45 to 200 cm.) the percentage difference between the two is constant. Some critical stage in the early life of the fish, following the symmetrical stage, must bring about a relative difference in fin size which remains constant from then on.

Correlation of Body Form with Meristic Characters

Differences among populations within species have been characterized by the repeated recurrence of correlation between body form and meristic characters. As pointed out above, northern populations commonly have smaller heads and fins, together with a greater number of meristic parts such as vertebrae, scales, and fin rays. This correlation has been referred to by Hubbs (1926) and Tester (1937). Although slow-growing herring, as described by Jean (1945), differed from many slow-growing populations found in other species in having small heads and fins, they also had more vertebrae and thus conformed with the usual correlation between body form and meristic counts.

It is well recognized that somite number and hence number of meristic elements, is modified by rate of early development (Gabriel, 1944). The correlation of body form with meristic characters, indicated throughout the literature, points to a similar predetermination of body form at an early stage of development.

Discussion

In the foregoing relative-growth analyses it has been demonstrated that body-form differences among groups of fish are not always negatively correlated with rate of growth. Relatively small body parts have been found in some examples to be associated with rapid growth and in others with slow growth.

The differences among individuals of one population or among populations of one species seldom result from a change in the growth constant. Variation among populations of the same species has been shown to be such that differences in body form found in later life are also found to be relatively as great at smaller sizes. In the exception to this generalization, found in eye diameter in salmon, the divergence of slopes is superimposed on differences established early in life. The comparable variance of part-length relationships at small and large sizes implies that the relative-growth lines which describe individuals within a population are also parallel.

In discussing the possible growth mechanics involved in effecting morphometric differences it has been pointed out that changes in body form could be brought about either through differences in slope or differences in body size at growth inflection. Since differences in slope have been found to be of little or no importance, there is strong suggestive evidence that body size at growth inflection may play the major role in the fixation of differences in body form.

It is furthermore inferred, from the fact that growth rate is not always correlated with body form, that early development may be an important factor in the direct control of body form. The common correlation between body proportions and number of meristic characters suggests that body form is determined early in life. If inflections can be demonstrated to be important in the mechanics of control of body form, then early development would be expected to be correlated with body form both because of the number and sharpness of inflections at very small sizes.

GROWTH INFLECTION AS IT EFFECTS DIFFERENCES IN BODY FORM

Form Change at Sexual Maturity

The fact that growth inflection may be found coincident with sexual maturity, together with the general recognition that populations and individuals vary in the size at which sexual maturity is reached, suggests an opportunity for the assessment of the importance of inflection in the determination of body form.

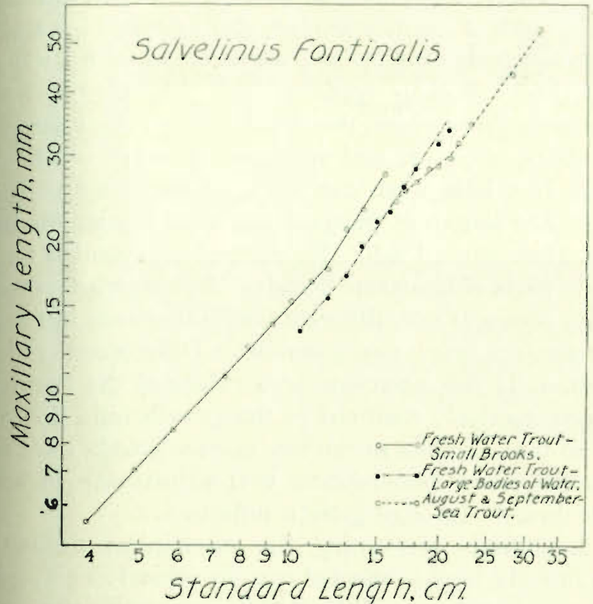


FIGURE 12.—Growth inflection as it effects change in relative maxillary length in *Salvelinus fontinalis*. Taken from Wilder (1944).

Populations of mature trout (*Salvelinus fontinalis*) from small brooks, larger bodies of water, and "sea run" stocks have been compared by Wilder (1944). His presentation of relative maxillary growth of each group is shown in figure 12. It may be seen that the equilibrium constant, *k*, is approximately the same for all three groups both for immature and mature fish. The groups differ in size at maturity, with brook fish attaining that stage at a relatively small size and sea-run stock at a much greater length. These marked differences in size at sexual maturity, and hence at the maturity inflection, resulted in large differences in relative maxillary size among mature groups. In spite of constancy of rate of change of form, gross differences in morphometry resulted directly from differences in body size at growth inflection.

Kennedy's (1943) comparison of dwarf and normal populations of whitefish, *Coregonus clupeaformis*, found within the same lake demonstrated that both groups had the same relative-growth constants. The two populations differed in size at maturity, rate of growth, length of growing season, and number of scales and gill rakers. When body proportions were compared by the relative-growth method it became apparent that although the mature fish differed in body proportions, they followed the same relative-growth pattern. Both slope, *k*, and intercept, *b*, were identical in the two groups (the lines were identical). Equilibrium constants for anal height and length of pectoral fins were greater for immature than for mature normal fish. No data were presented for relative size of body parts of immature dwarfs. Although growth inflection at maturity occurs at very different sizes, differences in the relative-growth constants were not apparent. Differences, which must have occurred in the intercepts or *b* values of the two immature groups, were suddenly removed at the growth inflection at sexual maturity so that *b* values in the two mature groups were identical. This whitefish study demonstrates that adjustments in body form can result directly through growth inflection.

This hypothesis concerning the mechanism through which variation in body form is effected may be offered as an explanation of the data presented by Hile (1937) concerning the correlation between the morphometry and growth rate of the cisco, *Leucichthys artedi*. Hile's data for head length of four Wisconsin populations have been plotted in figure 13 together with data by Fry for head measurements of 3425 Nipissing ciscoes (table 3). The Nipissing line shows an inflection at about 200 mm., coincident with sexual maturity, a change which is considered real in view of the large number of specimens measured. An examination of the points plotted indicates that little divergence in the slope of the relative-growth lines is found among the Wisconsin populations. By using the Nipissing "mature" line as a base, parallel lines were drawn through the points for mature fish from each lake. Since such lines fit the points reasonably well the differences in relative head size may be described by differences in the intercepts, *b*, made by these lines with any *y* axis. The Trout lake population had a slow growth rate and large heads, whereas the Clear lake ciscoes

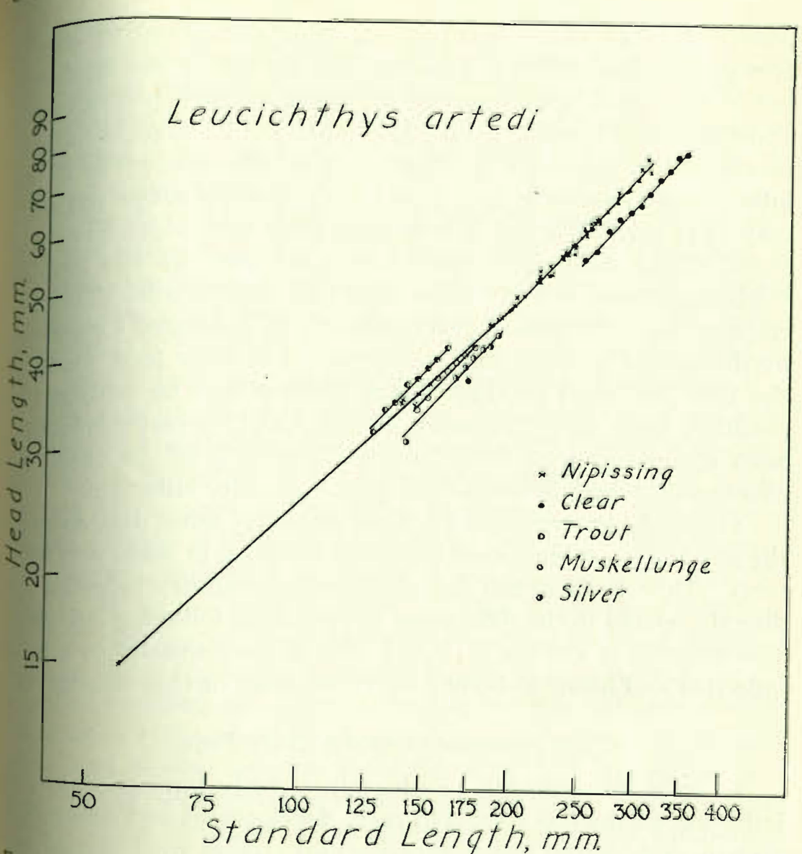


FIGURE 13.—Parallelism of head growth in *Leucichthys artedi*. Data from Hile (1937) and Fry. The lines drawn through the Wisconsin lakes figures have been drawn parallel to the upper slope of the Nipissing data which is for mature fish.

had rapid growth and small heads. Similar differences have been described by Hile for maxillary length, eye diameter, and length of paired and dorsal fins. Such a correlation between body form and rate of growth held for a comparison of populations and for individuals within a single stock. The 1928 year class from Muskellunge lake showed differences in body form which were not related to growth rate. Difference in the environment during development and early growth were the causes suggested. The possibility that differences resulted from differences in size at growth inflection offers a plausible explanation of the mechanics involved. Head measurements of small ciscoes presented by Pritchard (1931), as plotted together with data on larger specimens, reveal growth inflection at 18 mm. Size differences either at this inflection or possibly at that found at the onset of sexual maturity may have resulted in the differences in body form which have been found among ciscoes. It should be noted that the fast growing Nipissing ciscoes did not have relatively small heads. This discrepancy from the general rule can hardly be accounted for entirely by differences in measuring technique. The body form found in the 1928 year class of Muskellunge lake can best be explained as resulting from size differences at some early growth inflection. Such differences may have been sufficiently great to offset the effect of difference in size at the sexual-maturity inflection.

The evidence presented for three species of fishes demonstrates the importance of the sexual-maturity inflection in modifying body form. Differences in fish size at the sexual-maturity inflection are directly related to the differences in body form following inflection. The relation of growth rate and rate of development to size at inflection and hence to body form is discussed further on page 47.

Experimental Control of Body Form

In order to assess the relationship of body form to slope and inflection on the one hand and early development and subsequent growth rate on the other, experimental studies were carried out at the Oden hatchery, Michigan, which has an artesian-well water supply, with a constant temperature of 45°F. throughout the year. Rainbow trout, *Salmo gairdnerii*, were reared under controlled conditions from the day after fertilization and sampled regularly during a 9-month period from December, 1940 to September, 1941. Some were reared on different diets at a constant temperature, and others at different temperatures but on the same diet in order that possible differences in ontogenetic relative-growth mechanics might be traced.

Experimental Methods

1. *Temperature experiment.* Three troughs were held at constant temperatures of 46°F., 53°F., and 60°F., respectively, throughout the 9-month period. Temperature control was effected by means of thermostats in each of the troughs and electric heaters in the reservoir tanks which supplied these troughs. The reservoir tanks were in turn supplied by a head water trough receiving the hatchery water supply at 45°F.

The eggs were hatched in small Clark Williams boxes at each reservoir outlet and, after hatching, the fry were transferred to the small troughs (43 inches long, 13 inches wide, and 7 inches deep). The water flow for each was held constant at 0.2 gallons per minute. Temperatures, taken twice a day at the head of each trough, remained constant throughout the experiment.

The eggs used were a random sample taken from a shipment fertilized at Harrietta hatchery on December 22, 1940, and received at Oden on December 23. Approximately 4,000 eggs were set up at each temperature on December 23 (16 ounces at 240 eggs per ounce). Owing to differential mortality during early development the numbers remaining on March 7 were about 2,500 at 46°F., 1000 at 53°F., and only 25 at 60°F. Due to excessive mortality at 60°F. this part of the experiment was abandoned on March 8 and the remaining fry at this temperature were preserved.

After hatching and prior to feeding each trough was divided longitudinally by a median partition into two halves, and the inlet water was divided between them, in order that fish in one half might be fed more food than those in the other half. The numbers in each trough division at 46°F. were reduced to 500 prior to feeding in order that crowding might be considered comparable with that at 53°F. On March 8, 500 fry, hatched at 46°F., were transferred to one of the 60°F. trough divisions. Thus by March 8 five experimental lots remained, two at 46°F., two at 53°F. and one transferred from 46°F. to 60°F. These fry were reared on a diet of sheep liver fed twice a day until September 20, 1941. Following hatchery procedure, one lot in each trough was fed as much liver as the fish could readily consume. These are referred to as well-fed lots. The two remaining lots at 46°F. and 53°F. were fed one half as much liver by weight as that given the fish in the other division of the same trough. These are referred to as ration-fed lots.

The mortality, apart from sampling, is recorded in table 4.

Mortalities in the 46° and 53° lots were similar, but at 60° the mortality was more than twice as heavy. More than half of this 60° loss occurred during the first month. The possible importance of this differential mortality must be considered as a factor in the selection of fish of certain body form.

2. *Feeding experiment.* In addition to the temperature experiment a feeding experiment was set up to study the effect of different diets in the control of body form. Eyed eggs were received at Oden, from Harrietta hatchery, on February 6, 1941. These eggs were hatched on and about March 1 at 45°F. On March 18, 20,000 of these were transferred to each of eight hatchery rearing troughs and on May 6 the number of fry per trough was reduced to 5,000 to avoid crowding. They were fed sheep liver in accordance with hatchery procedure until May 10. From May 10 to September 20 the same weight of food was given to each of the eight lots of fish but the diet was varied; two lots were given 100 per cent sheep liver, two lots were fed 90 per cent liver and 10 per cent kelp by weight; two lots were reared on 90 per cent liver and 10 per cent beef blood by weight; and two lots were given 50 per cent meal (13.3 per cent skim milk, 13.3 per cent cottonseed meal, 13.3 per cent herring meal and 10 per cent "Red Dog" flour) and 50 per cent beef blood by weight. Temperatures were constant at 45°F. throughout the feeding experiment. The mortality, apart from sampling, is recorded in table 5. Mortality was lowest in the liver fed fish and highest in those receiving meal. The difference in mortality between these extremes was about 50 per cent.

Sampling and Measurements

Samples of about ten fish were taken from each lot regularly (about every two weeks) throughout the experimental period. The standard lengths in millimetres and weight in grams of each sample were measured and the samples were then preserved in 10 per cent formalin (with a small amount of borax added). At the end of the experimental period all samples were transferred to 70 per cent alcohol for storage.

The following measurements were made from one to five years after preservation:

Anal height—Distance from the origin of the anal fin to the tip of the longest ray.

Anal to caudal—Distance from the origin of the anal fin to the structural base of the caudal fin.

Depth—Vertical distance through the body at its deepest part.

Eye—Antero-posterior diameter of the uncompressed eyeball (the eyeball protrudes sufficiently in the small trout so that this measurement was taken with facility).

Dorsal to anal—Distance from the origin of the dorsal fin to the origin of the anal fin.

Dorsal to caudal—Distance from the origin of the dorsal fin to the structural base of the caudal fin.

Head length—From the tip of the snout to the posterior most margin of the operculum.

Pectoral to anal—Distance from the insertion of the pectoral fin to the origin of the anal fin.

Pectoral and pelvic lengths—Distance from the insertion of the fin to the tip of the longest ray.

Snout to dorsal—Distance from the tip of the snout to the origin of the dorsal fin.

Snout to pectoral—Distance from the tip of the snout to the insertion of the pectoral fin.

Standard length—From the tip of the snout to the posterior end of the vertebral column, measured in millimetres.

Weight—Total weight in grams. Average weight of ten fish recorded for small fry (yolk sac was included).

Width—Distance through the body at its widest part.

These measurements were made with needle-pointed dividers and a steel ruler graduated in half millimetres. In view of the small size of most of the fish, each measurement was estimated to 0.1 mm. The well-fed rainbows reared at 46°F., 53°F., and 60°F., and the brook trout, were measured by the writer in 1941. The ration-fed rainbows reared at 46°F. and 53°F., the lake trout, and the rainbows reared on different diets, were measured by N. V. Martin in 1945. Thus, the fish reared on different diets or at different temperatures were handled as a unit at one period and may be compared within the experiment. Fish in different units, however, cannot be compared since there may be differences in the technique of measurement. All measurements were made without reference to the origin of the fish.

Length-weight comparisons for the different well-fed lots in the temperature experiment are based on 11 samples (115 fish) taken from the 46° lot, 11 samples (112 fish) taken from the 53° lot, and 12 samples (125 fish) taken from the 60° transfer lot. Comparisons of body measurements for these fish are based on 12 samples (123 fish) taken from the 46° lot, 15 samples (145) fish taken from the 53° lot and 11 samples (111 fish) from the 60° transfer lot. Ten measurements—standard length, head length, eye diameter, snout to pectoral distance, pectoral length, pectoral to anal distance, anal to caudal distance, body depth, body width, and anal height were made on each fish.

Length-weight comparisons for rainbows reared at different temperatures and on a rationed-liver diet were made on 14 samples (134 fish) taken from the 46° lot and 15 samples (146 fish) taken from the 53° lot. Four body measurements (standard length, head length, eye diameter, and anal height) were made on each fish.

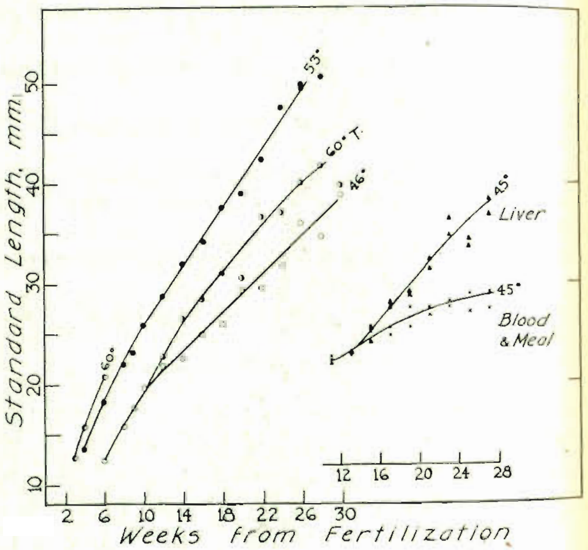


FIGURE 14.—Growth rates of rainbow trout reared at different temperatures and on different diets. Data in tables 6, 7 and 11. The T lot was transferred from 46° to 60° F. after ten weeks.

Length-weight comparisons for rainbows reared in the feeding experiment are based on four diets, two lots on each diet, 9 samples from each lot and a total of 812 fish. Measurements were made on six lots, represented by 49 samples and 493 fish. Ten measurements were made on each fish (standard length, head length, eye diameter, snout to pectoral distance, pectoral length, pectoral to anal distance, anal to caudal distance, body depth, body width and anal height).

Similar sampling was carried out and measurements were taken on the lake trout and the brook trout series reported on pages 13 and 25.

Growth Rates

The growth rates of rainbow trout reared on different diets and at different temperatures are listed in tables 6 to 8 and 11 and are summarized in figure 14. The well-recognized increased rate of growth at higher temperatures is apparent. In spite of differences in growth rate, size at hatching was similar at all three experimental temperatures. Thus, hatching sizes for the 46°, 53°, and 60° lots were 12.5 mm. (8 fish), 13.6 mm. (8 fish), and 12.7 mm. (2 fish), respectively, whereas sizes of these lots on January 25 were 9.5 mm. (7 fish), 13.7 mm. (8 fish) and 15.8 mm. (2 fish) respectively.

Hatching dates for the 46°, 53°, and 60° lots were February 10 (49 days), January 22 (30 days), and January 13 (21 days), respectively, and dates of first feeding for the 46°, 53°, and 60° transfer lots were March 11, February 11, and March 11 respectively.

By July 12, after more than six months growth, 46°, 53°, and 60° transfer lots averaged 36 mm., 50 mm., and 41 mm., respectively, in standard length.

No more than minor differences were apparent in growth rates of fish fed on liver, liver and kelp and liver and blood. The fish reared on blood and meal, however, were only 28 mm. long on July 12 whereas liver fed fish from the same stock averaged about 35 mm. on the same date.

Relative Growth

1. *Effect of temperature.* Comparisons of the body form of the rainbow trout reared at different temperatures are presented in figures 15 and 16 with data for these figures listed by sample averages in tables 7 and 8. The graphical analysis reveals certain morphometric differences between the three lots of fish. Beyond growth inflection, at a body length of about 30 mm., the relative sizes of eye, head, pectoral, anal height, depth and width are

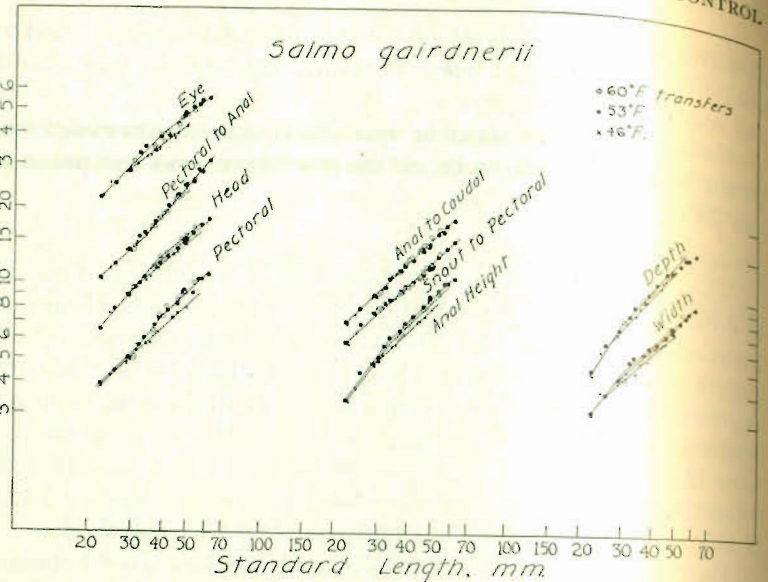


FIGURE 15.—Effect of temperature in the control of body form in well-fed rainbow trout. Data from table 7.

greater in the 53° and 60° transfer lots than in the 46° lot. No differences in snout to pectoral, pectoral to anal, and anal to caudal measurements are apparent. In order that these differences might be understood more fully some of the data have been analysed in accordance with the statistical procedure outlined in appendix I.

Some discussion of the statistical treatment will serve to introduce the comparisons which are made. The treatments compare series of samples of fish taken from two temperatures. All fish taken from one temperature are referred to as one *lot* and each group of fish taken at one time, and thus of the same age, are referred to as a *sample*. Thus, for each temperature, reference is made to one lot, several samples, and many individuals.

If all individuals of a particular lot were to follow exactly the same relative growth pattern, then all points describing a given body part would fall on one line. However, if some fish differ from others in body form there would result a certain spread of points above and below the best line through all points. This dispersion might result from differences in slope among the individual relative-growth lines or from differences in intercept effected at inflection time. By plotting such a series of points for one temperature lot it is apparent that a definite spread about the best line through all points does occur.

Some light is thrown on the nature of this variance about the norm by a consideration of sample slopes within lots. Within each sample different sized fish are taken since some individuals grow faster than others. Thus, a part-length line may be drawn for each sample taken. If the fast-growing fish are of comparable form with the slow-growing fish then the slope of each of these sample lines should be the same as the slope of the line through all points irrespective of sampling time. If, on the other hand, the fast-growing individuals differ in body form from the slow-growing individuals then the sample lines would differ in slope from the best line through all points describing the whole lot and would cut across the line.

The distinction between sample slopes for fish taken at one time and slopes which describe growth from one time to another, is clearly demonstrated on page 59 in a consideration of length-weight relationships. In that section it is pointed out that the slopes of individual age groups often differ widely from the slope of any one year class followed from one year to the next.

For convenience a special terminology is used to refer to these various lines describing samples and lots. The slopes of the individual samples are referred to as "within-times" slopes. The best line through successive sample means is referred to as the "between-times" line. This is the line which most clearly approximates the course of ontogenetic growth. The best line through all points descriptive of one lot of fish, irrespective of time is referred to as the "within-lots" line. This "within-lots" slope is not considered in the statistical analysis since it only approximately describes ontogenetic growth. It is, rather, a combined "within-times" and "between-times" slope which more closely approximates ontogenetic growth as the size range considered is increased. Differences between samples for each temperature lot and differences between lots have been assessed by determining the "within-times" slopes, "between-times" slopes, and the differences among them. The analysis of covariance method described in Fisher (1936) and Snedecor (1946) has been used.

46° (WELL-FED) AND 60° TRANSFER LOTS. These were selected for this statistical analysis since they represent two lots of fish with identical thermal and relative growth histories to a body length of 20 mm., and differences in thermal histories beyond this size. Sixteen samples of fish have been used for this statistical analysis, all of which were larger than 30 mm. standard length and beyond growth inflection. The samples were taken at two-week intervals from June 13 to September 20; eight samples (82 fish) from the 46° (well-fed) lot and eight samples (81 fish) from the 60° transfer lot. Each lot has been examined for "within-times" and "between-times" differences, and the two lots have been compared as to differences in slope and intercept. The statistical treatment for one of the body parts, the head, is outlined in table 9. Other body measurements were treated in a similar manner and the slopes and significance of differences among them are summarized in table 10.

The first point of interest is the fact that "within-times" slopes for each lot do not differ significantly among themselves. For any part considered the "within-times" slopes are similar, with $p>0.05$. Since there is no marked difference among the samples taken from one temperature, the total "within-times" slope may be used in the comparison of "within-times" and "between-times" slopes for each temperature lot. The similarity of "within-times" slopes demonstrates the constancy of variance referred to in section II.

For each temperature lot the "within-times" slope is smaller than the "between-times" slope in eight out of nine body parts. The "within-lots" slope is, of course, intermediate between these. These differences are significant at the 1 per cent level in eye diameter, body width, and anal height for the 46° lot and eye diameter, snout to pectoral distance, and pectoral length for the 60° transfer lot. In addition to pointing out the dangers involved in considering a sample taken at one time to be representative of ontogenetic growth, these differences have further meaning. As pointed out above the sample-slopes are generally less steep than the lot-slopes. From this it may be inferred that fast-growing fish have relatively smaller heads and fins than slow-growing fish of the same stock.

Such a correlation between growth rate and body form is reminiscent of similar correlations described above for large and small sorts of brook trout and those described by Hile for ciscoes and by White for salmon. It is furthermore inferred, from the fact that the "within-times" slopes remain constant, that fast-growing fish have relatively small heads and fins at both small and large sizes. The evidence points toward fixation of body form in this material at a critical stage of development, at a body size of 30 mm. or smaller.

The "between-times" lines for the two lots were compared both as to difference in slope and in adjusted sums of squares (intercepts). This indicates whether or not the two ontogenetic relative-growth lines for each body character are divergent by comparing slopes, k. Further work assessed whether or not the two lines differed significantly in the intercepts made with any y axis.

The head, eye, pectoral, depth, width and anal height lines have slopes that are not significantly different but intercepts that do differ significantly. The snout to pectoral, pectoral to anal, and anal to caudal lines do not show significant differences in intercept, nor do two of them show significant differences in slope. However the snout to pectoral line does show significant differences in slope, a result which seems surprising in view of the fact that the head slopes are similar. The point of major significance in these observations is that body parts showing similar slopes but significant differences in intercepts are also the body parts showing relative-growth inflection at about 30 mm. Those body measurements which do not show such parallelism are the same parts which do not show inflections at this size.

It is apparent then that fish of the same stock reared under identical conditions to a length of 20 mm., but at different temperatures thereafter, developed differences in body form which are of the same order from 31 to 50 mm. The differences occur in those body parts which show growth inflection.

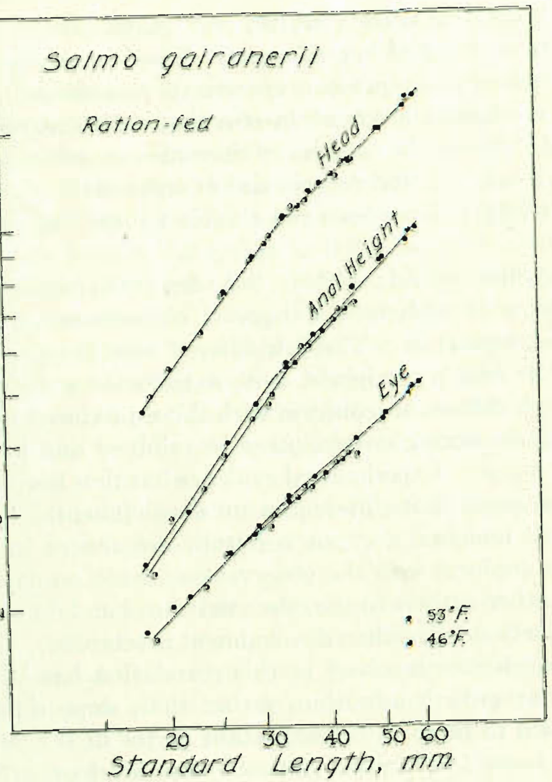
The greater mortality found in the 60° transfer lot can hardly be considered of importance in a selection of fish with different body proportions since body measurements well beyond the 46° lot extremes were found among the 60° fish. As was shown to be true at sexual maturity, another example of difference in body form established with inflection has been found.

In this experiment it was found that the fast-growing 60° transfer fish have relatively large heads and fins as compared with slow-growing 46° fish. This is the direct antithesis of the fact that within each of these lots the fast-growing individuals have relatively small heads and fins. By raising the temperatures prior to the 30 mm. growth-inflection, growth was increased, size at inflection was increased, and large differences in body form resulted. The subject is elaborated further in the discussion on page 47.

46° AND 53° LOTS. These have not been compared statistically, but some differences are apparent in figures 16 and 17. Only in anal height measurements does the 53° well-fed lot show greater differences from the 46° well-fed lot than does the 60° transfer lot. Since the anal height of the 60° lot was significantly different from the 46° lot, the anal height of the 53° lot must also be significantly different. Differences in this character appear both before and after growth inflection. This difference is confirmed by the comparison of 46° and 53° lots of ration-fed fish (figure 16).

Differences in eye diameter, pectoral length, and body width are of the same order in the 53° lot as in the 60° transfer lot and are therefore probably significantly different from the 46° lot. Differences in these characters are not apparent until after growth inflection has occurred. Slight differences are apparent in head and depth measurements beyond growth inflection in the same direction as those found in 60° transfer fish. No differences are apparent over the size range examined in snout to pectoral, pectoral to anal, and anal to caudal measurements. The body form of fish reared at 53° is such that relative sizes of eye, head, pectoral, anal, depth, and width are greater than in fish reared at 46°. Most of these differences appear beyond the 30 mm. inflection, but differences in anal height appear at smaller sizes indicating that they may be associated with some earlier growth inflection. The measurements which have no apparent growth inflection, snout to pectoral, pectoral to anal and anal to caudal, are those that do not show differences in relative size when reared at different temperatures.

BROOK TROUT. Concurrently with the present investigation, Wilder (1944) compared brook trout, *Salvelinus fontinalis*, which



URE: 16.—Effect of temperature in the control of body form in ration-fed rainbow trout. Data in table 8.

re reared at different temperatures. One lot of eggs, from one pair trout, was divided on November 22, 1939, and the two samples re hatched at 5.5°C. and 0.9°C. respectively. The former tched between February 5 and 28, 1940, and absorbed yolk sacs April 19. The latter hatched between May 30 and June 28 d absorbed yolk sacs by August 26. The fish were reared at rmer temperatures after hatching. Samples of fifty fish each, lled on August 19, 1941 and November 12, 1941, at an average ze of 10 cm. were measured in order to compare the morphometry the two lots. The trout hatched at the warmer temperature d larger eyes, maxillaries, head depth, anal height, ventral length, body depth, body width, and caudal peduncle depth than did the trout hatched in cold water. The differences conform with those found in the present investigation although the relative-growth mechanics involved in effecting such differences was not analysed. Since the major environmental differences occurred prior to hatching, difference in size at some early growth inflection is most likely to have been responsible for the differences in body form.

WHITEFISH. Koelz (1929) has described differences in the morphology of whitefish, *Coregonus clupeaformis*, reared in the New York aquarium. The fish differed from the parent lake Erie stock in having larger heads, eyes, maxillaries, snouts, and paired fins. Such differences conform with those produced by raising the temperatures during development in rainbow and brook trout.

DISCUSSION. Experimental evidence has thus been accumulated to demonstrate that differences in developmental rate, as controlled by temperature, can result in differences in body form. The data conform with the observations made on natural populations by other authors to the effect that head and fin measurements are relatively smaller when development is retarded. The relative-growth mechanics involved in this correlation has been analysed and size at growth inflection, rather than slope differences, has been shown to be the most important factor in the determination of body form. Inflections during early development as well as at sexual maturity are effective in the control of body form. Since sharp inflections have been found in many species during early development, there are opportunities for small changes at this stage to produce large differences in body form during later life.

The influence of differences in body size at very early inflections in effecting such variation in body form is as yet not clear, although the importance of such differences in size at the 30 mm.-inflection and again at the sexual-maturity inflection have been described. Earlier inflections have been pointed out but to date no work has been concerned with variation of relative growth at very small sizes. The importance of these early inflections may be inferred by the fact that inflections at larger body sizes are important in the control of body form and those at smaller sizes are judged by analogy to be of at least equal significance. The importance of early inflections is further inferred by the fact that differences in morphometry of rainbow (page 42) and brook trout (page 42) were probably established during very early development.

Although little variation in size at hatching was produced in rainbow trout reared at 46°, 53°, and 61°F., there is evidence in the literature that size differences at hatching do occur:

(1) Gray (1928) was able to reduce wet weight of *Salmo fario* at hatching from 0.132 grams to 0.095 grams by raising developmental temperature from 5°C. to 16°C. Rapid embryonic development was associated with small size at the end of incubation.

(2) Hart (1930) described the size at hatching of whitefish, *Coregonus clupeaformis*, in lake Nipigon and lake Ontario. In the Bay of Quinte, whitefish hatched after 23 weeks (in April) at 12.1 mm. whereas in lake Nipigon hatching occurred after 28 weeks (in May) at 14.3 mm.

(3) Hall (1925) has shown that whitefish reared at low temperatures are 4 to 6 mm. longer than those hatched earlier at higher temperatures.

Inflection has not been demonstrated to be co-incident with hatching. However, the fact that differences in size at hatching can be effected by control of the environment suggests that differences in size at inflection may also occur. Such differences offer a rational explanation of resultant differences in body form. The available evidence indicates that early inflections, as well as those at about 30 mm. and at sexual maturity, play a part in the control of body form.

2. *Effect of diet.* Comparisons of the body form of rainbow trout reared on different diets are presented in figure 17, with data for these comparisons listed by sample averages in tables 11 and 13. The data have not been analysed statistically but certain observations may be made. The slowest-growing lots, reared on blood and meal, did not attain lengths much greater than 30 mm. during the experimental period. Since inflection does not occur until about 30 mm. body length is reached, this study is presumably concerned with differences resulting in one growth stanza. No differences in body form were found among liver-fed fish. The differences in diet, effected by introducing kelp and blood, did not bring about appreciable differences in rate

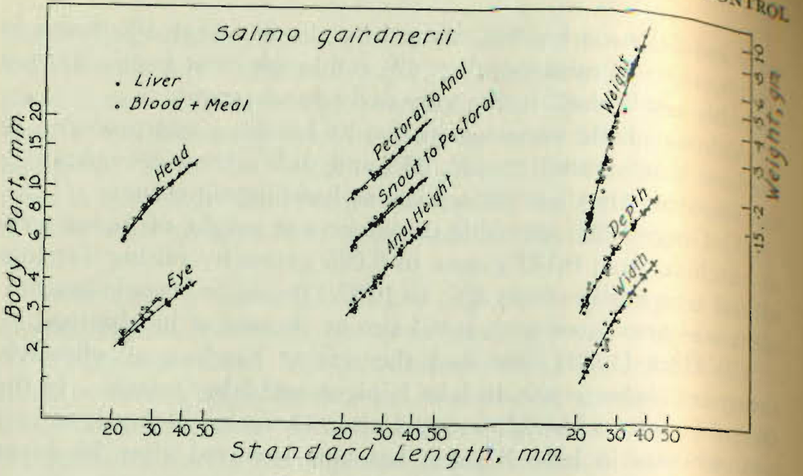


FIGURE 17.—Effect of diet in the control of body form in rainbow trout. Data in tables 11 and 13.

of growth nor were differences in body form apparent. The blood-and-meal diet, however, did appreciably reduce growth rate and effected certain changes in body form. It is apparent from figure 17 that eye size became relatively greater in the slow-growing lot. The relative sizes of head length and snout to pectoral distance were also greater in the lot subjected to a blood-and-meal diet. From larger sizes of head parts it may be inferred that downward inflection had not occurred. Depth and width measurements showed a tendency to fall away from those descriptive of the liver-fed fish. This is reflected in the length-weight measurements as well. It should be noted, however, that at 30 mm. differences in these measurements are not apparent. It seems possible that with a deficient diet there is a tendency for width and depth measurements to decrease, but that growth in length can not continue without conformity to a certain relative-growth pattern. The higher mortality found among fish reared on blood and meal may indicate a lethal effect among fish which cannot conform with the normal relative-growth pattern.

Pectoral to anal and anal height measurements did not differ appreciably over the length range sampled.

Coincident with reduced growth rate, resulting perhaps from a deficient rather than a limited diet, the relative size of eye, head, and snout to pectoral were increased. It should be recalled that such differences were brought about with increased growth rate in the temperature experiments. Thus, relative size of head and eye were increased either by poor diet (slow-growth rate) or higher temperatures (fast-growth rate). The divergence of relative-growth lines within a growth stanza produced by a deficient diet is reminiscent of divergence from parallelism in salmon eyes under slow-growing conditions.

Discussion

The mechanics of environmental control of body form is presented diagrammatically, for summary purposes, in figure 18.

1. By sampling a population at successive time intervals it has been found that "within-times" slopes (S.1, S.2, S.3) are less than the "between-times" slope (L.1). Within an age group the shorter, slower-growing fish have certain parts such as the head which are relatively large. Comparisons of age groups likewise show the older, slower-growing fish to have the larger body parts such as head. These were the findings in the temperature experiments, the comparisons of three sorts of brook trout, and Hile's comparison of individuals within a single stock of ciscoes. In the experimental lots of rainbow trout it was shown that successive "within-times" slopes were comparable, thus indicating a constant variance for both fast and slow-growing individuals.

2. By comparing "between-lots" slopes it has been found that differences in fish size at inflection and differences in body form can be effected by environmental control. These form differences are of the same order throughout the ensuing growth stanza. The importance of body size at inflection has been clearly demonstrated for rainbow trout reared at different temperatures. In these experiments it was shown that by increasing temperature prior to an early inflection, fish size at inflection was increased and the resultant body form was altered in such a way that head size was larger. The effect of the increased size at inflection was sufficiently great to offset the normal tendency toward small heads in fast-growing fish. Only those body parts showing growth inflection appear to be subject to such control of body form.

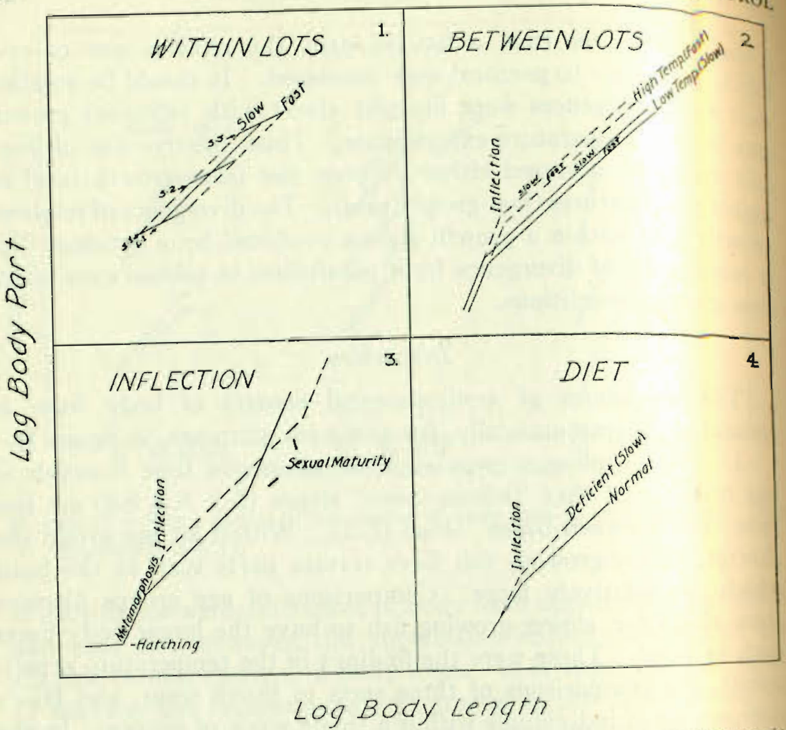


FIGURE 18.—Diagrammatic illustration of the mechanics of environmental control of body form in fishes.

1. "Within-lot" sample slopes (S.1, S.2, S.3) are less than the "between-lots" slope. Fast-growing individuals have smaller heads than slow-growing fish.

2. By raising developmental temperature, size of fish at inflection is increased and the relative size of certain body parts is increased.

3. The direction of inflection is important in determining body form.

4. The slope, *k*, may be changed by diet deficiency.

3. Since the direction of inflection may be either towards a greater or lesser slope depending on the stanza, inflection may result in either relatively larger or relatively smaller body parts, such as head. At the 30 mm. inflection described above for rainbow trout the transition is from tachyauxesis towards bradyauxesis. Thus, with a larger body size at inflection the resultant relative body part size is large. Conversely at sexual maturity the inflection for head and fins is generally towards tachyauxesis. Under such conditions a larger body size at inflection results in relatively small body parts after inflection. It is thus apparent that the

direction of growth inflection and the sharpness of the angle of inflection (*degree* of inflection) are as important as fish *size* at growth inflection in determining body form.

In the brook trout described on page 29 it is apparent that at a length of 15 cm. the maxillaries of sea run fish are larger than those of river stock whereas at 20 cm. the situation is reversed with "sea run" stock having relatively smaller maxillaries; such is the importance of inflection in the control of body form.

4. Changes in body form may be produced through changes in slope of relative-growth lines as well as through changes at inflection. The degree of heterauxesis has been altered under conditions of diet deficiency. Under such conditions the relative size of body parts such as head and fins is increased.

LENGTH-WEIGHT RELATIONSHIP

In spite of the well-recognized differences in the length-weight relationship attributable to feeding, state of maturity, fat storage, and other factors there is a certain trend toward uniformity among populations of the same species in their rate of change of weight during growth.

Since the early work of Crozier and Hecht (1914) and Hecht (1916) describing constant body form throughout the greater part of life in species observed by them, a considerable wealth of knowledge has been accumulated relating weight to length in fishes. With body form constant throughout growth, as was described in early investigations, weight would be expected to increase as the cube of the length. However, many investigations of this relationship for many species, have demonstrated that deviations from the cube relationship are the rule. Among the first of these, Clark (1928) found an equilibrium constant of 3.15 for the California sardine, *Sardinops caerulea*, when weight was related to length on a logarithmic scale and in the same year Keys (1928) recognized the fact that weight increased faster than the cube of the length in certain fishes. Marked deviations from the cube relationship are sometimes observed. Such was found to be the case in the blue marlin, *Makaira nigricans*, for which a growth ratio of 3.93 throughout adult growth was described by Shapiro (1938). However, in most species values more closely approximating 3.0 have been found. As in the study of relative growth of body parts, we find that constant rate of change of form rather than constant form is the rule. Considerable variation has been found in the length-weight growth constant, but deviations from a cube relationship are generally slight during the major part of growth.

An extension of length-weight investigations such that small fish are included reveals that more than one stanza of relative growth in weight may occur. Desbrosse (1936) has described changes in growth ratio from 3.8 to 3.0, from 3.0 to 3.2, and from 3.2 to 3.5 coincident with changes in body proportions. Marshall, Nicholls, and Orr (1937) found weight increasing as the fourth power of length in small Clyde herring, 10 to 40 mm. long. At larger sizes herring weight increases approximately as the cube of the length. Thus growth inflections are found in length-weight growth just as they are in relative growth of body parts. The possible importance of such inflections in the control of body form is assessed here.

The present investigation is concerned with the literature dealing with condition factors since these investigations have provided a large amount of data on lengths and weights which can be used in relative-growth analyses of body form.

Ontogenetic length-weight growth can best be described by the equation $y = b x^k$ or in length-weight terminology $W = C L^n$. Although such a description is applicable for each of the stanzas of relative growth in weight, most data available in the literature apply to the major growth stanza. The length-weight growth of a population can perhaps best be followed by sampling year classes over a number of successive years. The average length and weight followed from one year to the next describes ontogenetic growth whereas differences between year classes, followed in such a manner, describe intra-population variation. In view of the difficulties involved in such sampling, good approximations to the length-weight relationship are generally made by obtaining a large sample of as many age groups as possible and as complete a size range as possible during one season. The line best fitting such a series, although closely approximating length-weight growth, may not adequately describe the extreme sizes sampled. As pointed out in the analysis of body parts, differences between "within-times" and "between-times" slopes may be expected. Such deviations at large and small sizes, together with deviation as a result of year class variation, might affect the length-weight relationship calculated from such a sampling scheme. The closest approximation to ontogenetic growth description by this method is made by fitting a line to average lengths and weights of each age group, thus minimizing the error which might result from differences between "within-age-group" and "between-age-group" slopes. This method of assessing the length-weight relationship offers difficulties where the sample size is short in length range because of reduced growth rate or other reasons.

Differences among Populations

Data from a number of length-weight investigations have been plotted logarithmically as a means of providing further evidence concerning diversity of body form within species and in order to investigate further the relative-growth mechanics involved in such differences.

In figure 19 differences are shown among populations of rock bass, *Ambloplites rupestris*, yellow perch, *Perca flavescens*, cisco, *Leucichthys artedi*, and Pacific herring, *Clupea pallasii*.

The relative increase in weight of rock bass populations has been described by Hile (1941, 1942). Relatively heavy fish were found in Allequash, Silver and Trout lakes, and fast-growing, light fish in Nebish lake. The populations differ in the same direction and to the same degree over the complete size range sampled.

Similarly in the yellow perch populations described by Hile and Jobes (1941, 1942) there is found another example of parallelism. The Green bay and Saginaw bay fish weigh relatively less throughout growth than the lake Michigan perch.

Cisco populations described by Hile (1936) have been shown to differ markedly in relative heaviness. In drawing the length-weight line for Hile's cisco data, the Clear and Silver lake populations are considered to conform with the norm for the species with a slope, *k*, of 3.6. The length-weight lines for Trout and Muskellunge lakes fall away from this norm with slopes considerably less than 3.0. Nearly all of the Muskellunge lake ciscoes were less than four years old, thus indicating that the emaciation which

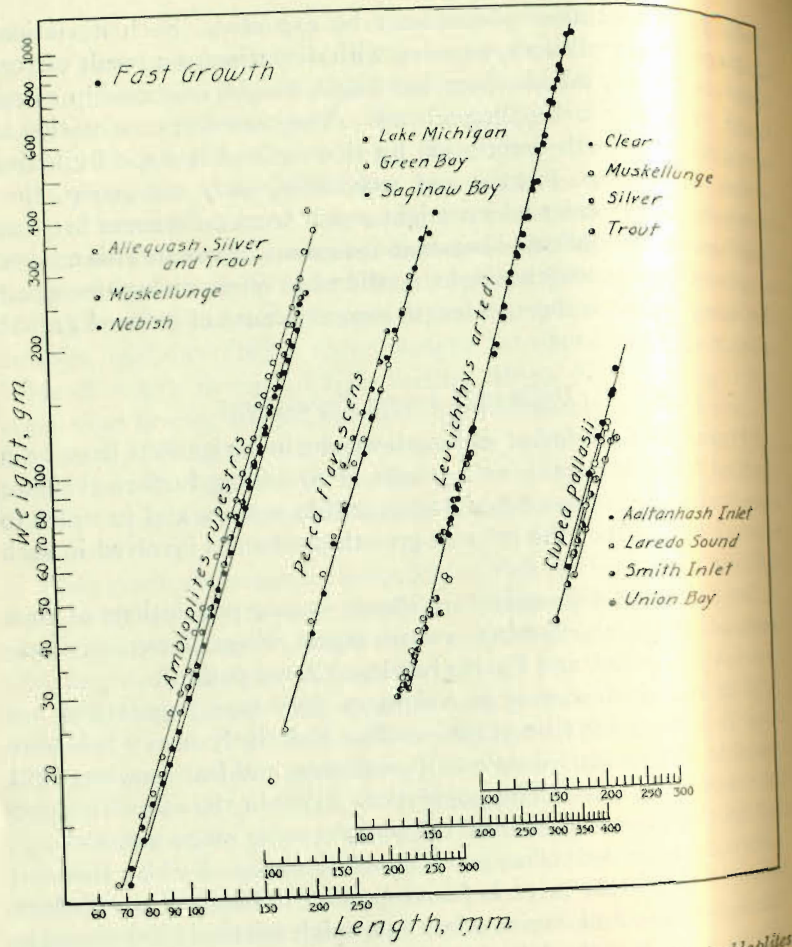


FIGURE 19.—Length-weight relationship in different populations of *Ambloplites rupestris*, *Perca flavescens*, *Leucichthys artedi*, and *Clupea pallasii*. Data from Hile (1941, 1942), Hile and Jobes (1941, 1942), Hile (1936) and Boughton (1941).

developed during growth may have precluded survival to any considerable size and age. The Trout lake ciscoes were also young fish for the most part. Lengths and weights listed for the five longest Trout lake ciscoes taken in 1931 fall on the line which is considered to be the species norm. It may be that Trout lake

individuals, if they are to survive to any considerable size and age must conform to the length-weight relationship characteristic of the species.

In herring we again find the same relative-growth constant for populations differing markedly in growth rate. The data have been taken from Boughton (1941). The herring do not conform with the rock bass and perch relationship between growth rate and relative heaviness since Aaltanhash inlet herring, although showing the fastest growth, are relatively heavy and consistently heavier than the other populations over the length range investigated.

Certain generalizations seem justified from the relative growth analysis of length-weight differences among the populations.

(1) Differences among populations are often such that length-weight lines are parallel with differences resulting from differences in the initial growth index, *b*.

(2) Differences in relative weight among populations of the same species do not appear to be related to rate of growth. Some fast-growing populations have relatively small body weight whereas others are relatively heavy.

(3) The approximate parallelism of length-weight lines describing populations of a given species, together with approximate constancy of variance found throughout growth, within a population, points to the determination of the length-weight relationship at an early stage of development. Such predetermined relative growth may be altered by starvation.

Experimental Control of the Length-Weight Relationship

The importance of growth inflection in the control of relative body weight has been investigated by analysing differences among the rainbow trout reared under different environmental conditions. The data concerned with length-weight growth under different temperature conditions are shown in figure 20 and table 12. Each circle represents ten to twelve fish and each cross one fish. The latter were one to two years old and were reared to more than 30 mm. standard length at 45°F. All fish were weighed and measured before preservation. The first point worthy of note is the growth inflection apparent at about 30 mm. standard length.

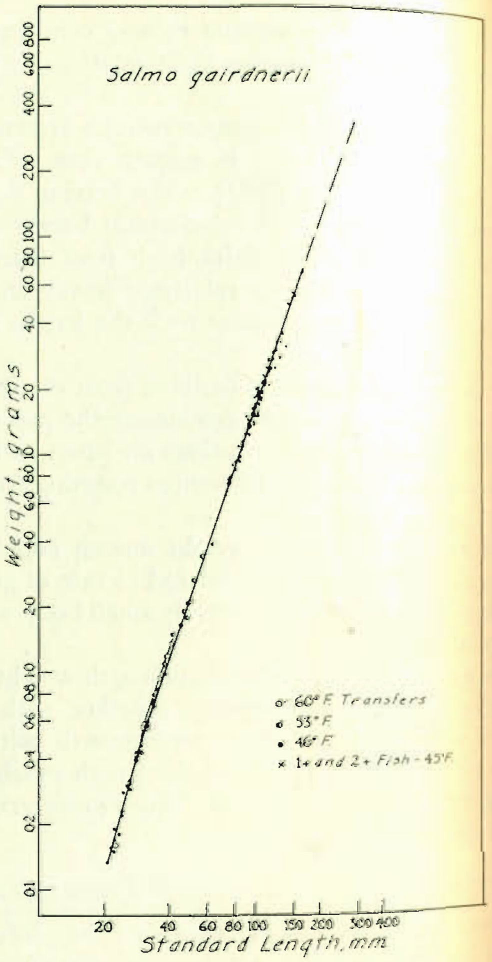


FIGURE 20.—Length-weight relationship found in rainbow trout reared under different developmental temperatures.

The reality of this inflection is borne out by the fact that measurements made on one and two-year-old fish do not fall in line with those made on 20 to 30 mm. fish but do fall in line with small fish greater than 30 mm. long. It should be pointed out that weight measurements can be taken precisely with less margin for personal error than can body measurements. The precision with which weights may be determined adds credence to the reality of growth inflection at about 30 mm.

The point of major interest is the fact that fish reared from the egg at 46°F. and 53°F. appear to follow the same relative-growth line whereas fish transferred from 46°F. to 60°F. at about 20 mm. standard length appear to follow the same relative-growth line until growth inflection but a different line thereafter. The data have been analysed statistically in accordance with the method presented in appendix I. Comparisons of samples have been made on fish greater than 30 mm. standard length and beyond inflection.

A comparison of 46° and 53° lines indicates no difference in slopes and no difference in adjusted sums of squares. The slopes, k, and intercepts, b, describing the two lines are not significantly different ($p > 5\%$ in each case).

A comparison of 46° and 60° transfer lines indicates no difference in slopes but a significant difference in adjusted sums of squares. The lines have similar slopes, k ($p > 5\%$) but different intercepts, b ($p < 1\%$).

By shifting rainbow trout from 46°F. to 60°F. at about 20 mm. standard length the growth rate was increased (figure 14). This apparently resulted in an increase in size at growth inflection which in turn altered relative growth in weight.

Fish reared from the egg at 46°F. and 53°F. did not differ in body form. Several explanations might be suggested for such identity.

(1) The difference in temperature may have been too small to effect an appreciable difference in body form.

(2) Differences produced at an early inflection may have been cancelled out at a later inflection.

(3) A change in temperature during development may have a greater effect on body form than that found under uniform but different temperature conditions during development.

The experimental evidence supports the thesis that differences in body form may be effected by differences in body size at growth inflection.

Stability of Slope

A striking example of the stability of the equilibrium constant k, in spite of differences in growth rate as a result of differences in diet, has been found in data presented by Karzinkin (1939) concerning lengths and weights of pike, *Esox lucius*. Karzinkin discussed differences in length and weight growth resulting from differences in diet. Pike reared on *Daphnia* and *Cyclops* were believed by Karzinkin to show continuous growth in length but a decrease in weight growth as compared with continuous growth in both length and weight when reared on a fish diet. The data have been plotted logarithmically in figure 21. It is apparent that whether the diet was *Cyclops*, small or large *Daphnia* or *Rutilus* fry one relative-growth line was followed. For fish reared at different growth rates, all points fall on one relative-growth line characterized by a relative-growth constant of 3.26.

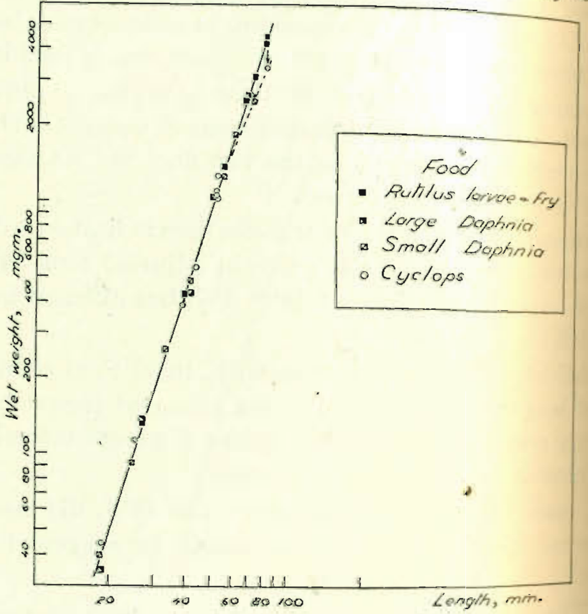


FIGURE 21.—Length-weight relationship is *Esox lucius*. Data from Karzinkin (1935). The slope k is constant independent of diet. The points diverging are cases of starvation.

Large fish when transferred from a diet of large to small *Daphnia* and from *Rutilus* fry to *Cyclops*, lost weight and fell away from the length-weight line. This is probably the result of sudden diet deficiency since fish reared from very small sizes on a zooplankton diet did not fall away from the relative-growth line. Data were not available for analysis of continued relative growth after the sudden changes to ration feeding or on the effect of returning these ration-fed fish to a well-fed condition. The data demonstrate stability of the length-weight equilibrium constant, k, in spite of forced differences in growth rate, as long as the animals were not starved following a period of good diet. Within a growth stanza, differences in growth rate did not effect differences in body form.

Shifts in Slope

Deviations from a straight line length-weight relationship similar to that described above for pike can result from either environmental or genetic control.

The length-weight relationship of lake trout, *Cristivomer namaycush*, for lake Opeongo, Ontario, as described by Fry (1940) demonstrates the effect of starvation in shifting the relative weight of fish. Between 17 and 21 inches there was a change from the length-weight relationship which was followed at smaller sizes. The shift has been attributed to food deficiency since, coincident with the change in relative weight, the amount of food per stomach was small, percentage of infertile fish was high, and egg counts were fewer than normally expected. At 21 inches, food per stomach rapidly increased and the length-weight relationship resumed a slope somewhat greater than that found prior to the starvation period such that at a length of 34 inches they were as heavy as they would have been had they followed the original slope.

A shift in the length-weight relationship is apparent in Atlantic salmon, *Salmo salar*, at the transition from parr to smolt. Such a shift appears to be a genetic characteristic of the species (figure 22).

Inadequacy of Coefficient of Condition

The data plotted in figure 22 were presented by Hoar (1939) and plotted by Fry (unpublished). Hoar was concerned with variation in the coefficient of condition, $\frac{100\,W}{L^3}$, with size, age, sex,

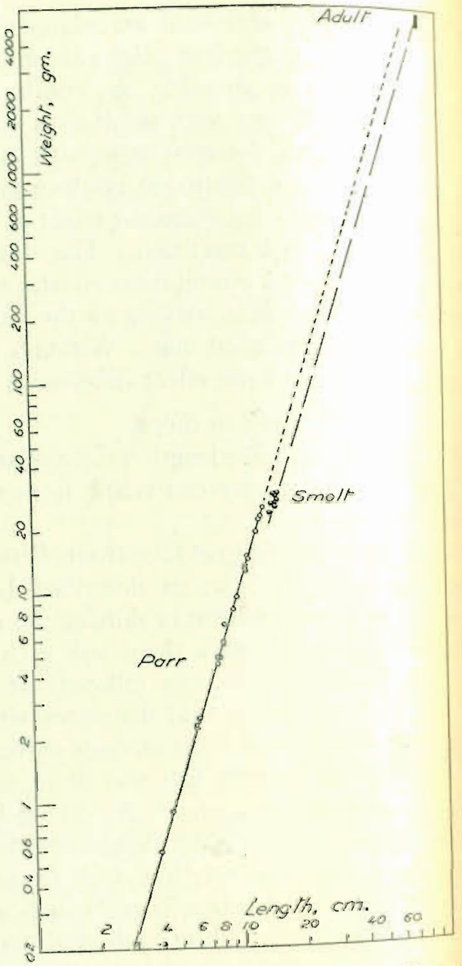


FIGURE 22.—Length-weight relationship of *Salmo salar*. Data from Hoar (1939). The stability of slope, k, (3.15) is apparent.

season, and environment. He found that the coefficient of condition deviated from 1.0 at the beginning of river life and again at the beginning of sea life. Values varying from 0.8 to 1.2 were correlated with different factors. The data when plotted on a logarithmic scale show clearly the remarkable consistency with

which salmon adhere to one relative growth constant. During life as parr the equilibrium constant, k, was 3.15. After a sudden downward shift in relative weight at the transition to smolt the equilibrium constant again resumed a value of 3.15. Wilder (1940) has extended this analysis with further salmon data and confirmed the validity of the constancy of slope and the reality of a shift in intercept, b. The calculation of coefficients of condition thoroughly confused the picture of simple length-weight growth in salmon.

The value of the constants K and C for the assessment of degree of wellbeing has been questioned by Tester (1940). He found no correlation between oil content or fatness of herring, *Clupea pallasii*, and K or C, and suggested the use of specific gravity for determination of the fat factor, as being more informative of fish condition.

The inadequacy of "condition factors" as they have been calculated to date has been discussed further by Kesteven (1947). He suggested the use of volume and weight measurements in the investigation of differences in fish condition.

"Within-times" and "Between-times" Slopes

Foerster (1944) has described the variation in the length-weight relationship found among seaward migrating salmon, *Oncorhynchus nerka*, during different years. Growth constants, as calculated by the method of least squares, varied from 2.5 (1930) to 3.5 (1927). This may be considered to represent the "within-age-group" variation. Foerster's data are such that an opportunity for a comparison of "within-season" and "between-season" equilibrium constants is afforded. The relative growth in weight of 1928, 1929, and 1933 year classes is presented in figure 23, where average lengths and weights for one and two-year-old fish have been plotted. It is clear that all points follow one relative growth line with a slope of about 3.0. Although considerable variation was found within age-groups the "between-years" slope appears to be constant. The scatter within an age-group is generally such that the line best fitting the points is not descriptive of the ontogenetic growth of the species considered. However, group averages when followed from one year to the next are considered to be descriptive of the length-weight relationship for the species concerned. Such a distinction between "within-age-group" and "between-age-group" slopes is but an extension of the distinction between "within-times" and "between-times" slopes described for body proportions on page 40.

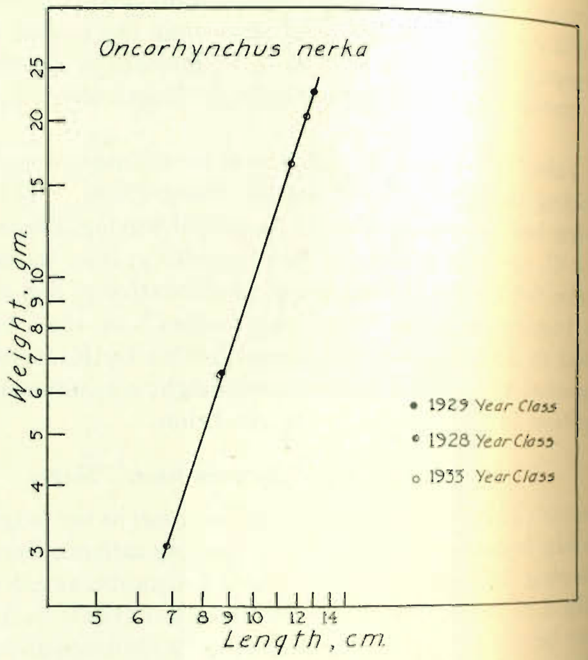


FIGURE 23.—Length-weight relationship in *Oncorhynchus nerka*. Data from Foerster (1944). The "between-age-groups" slope is constant ($k = 3.0$).

Discussion

The relative-growth analysis of variation in the length-weight relationship gives both indirect and direct evidence that body size at inflection is a major factor in the control of relative heaviness. Indirect evidence is the approximate parallelism of relative-growth lines describing infraspecific length-weight differences in various species. Direct evidence is the increase in growth rate, in body size at inflection, and in body weight beyond inflection brought about when rainbow trout which had been reared to 20 mm. standard length at 46°F. were thereafter subjected to a temperature

of 60°F. The conclusions conform with those established for part-length relationships.

Changes in slope of length-weight lines may be effected by such factors as malnutrition.

The inadequacy of analyses of a single age group or a small size group in describing ontogenetic length-weight growth is pointed out.

General Applicability of Hypothesis

The importance of size at growth inflection in the control of body form is by no means restricted to fishes. Numerous investigations have established the fact that relative growth is best expressed as a series of stanzas of heterauxesis separated by critical inflection points. The slopes of the relative-growth lines describing any particular stanza of growth of a body part are characterized by stability in the examples cited. Many cases of variation in the initial growth index, *b*, have appeared as indirect evidence of the influence of growth inflections in the determination of body form. Finally, evidence has been found to illustrate the direct effect of variation in size at inflection in bringing about divergence in body form in spite of constancy of growth ratios.

Relative-growth lines have been used by many authors to describe the growth of different body parts. Heterauxesis has been described, for example, in crabs (Huxley, 1924, Huxley and Richards, 1931, Mackay, 1942, 1943), centipedes (Lichen, 1943), prawns (Huxley, 1932), insects (Hersh, 1928, Teissier, 1931, Huxley, 1932, Clark and Hersh, 1939), molluscs (Hamai, 1937), amphibians (March, 1937), mice (Green, 1933), and ungulates (Huxley, 1932) and therefore appears to be a general phenomenon.

Inflections from one relative-growth stanza to another appear also to be of general occurrence. They have been described, for example, in crabs (Weymouth and Mackay, 1936, Williams and Needham, 1938), isopods (Miller and Hoy, 1939), *Daphnia* (Anderson, 1932, Anderson, Lumer and Zupancic, 1937) molluscs (Hamai, 1937), amphibians (March, 1937), mice (Green and Fekete, 1933), rabbits (Robb, 1929), ant-eaters (Reeve, 1940), sheep (Hamond, 1921), macaques (Lumer and Schultz, 1941), and the house wren (Huggins, 1940; Huggins, Huggins and Hellwig, 1943). Thus, when relative growth is studied over a large size range, stanzas of heterauxesis separated by critical points of inflection are the general rule. In most examples the inflections described are related to birth or to the attainment of sexual maturity. Except for fishes, no studies have been found dealing with stanzas of heterauxesis during earlier development.

The stability of the equilibrium constant, *k*, has been demonstrated in phylogenetic groups of titanotheres (Hersh, 1934), horses (Robb, 1935), anthropoid apes (Lumer, 1939) and dogs (Lumer, 1940). Feeding differences changed rate of growth of white rats but did not change either *b* or *k* in the length-weight relationship (Moment, 1933). Distinct strains of fowl (Lerner, 1943) and mice (MacArthur and Chiasson, 1945) exhibit identical relative-growth constants, even beyond growth inflection, adding evidence to the hypothesis of stability of *k*.

Constancy of slope in closely related groups does not necessitate identical intercepts (initial growth indices) as may be seen in the parallelism which regularly appears in a survey of relative-growth investigations. Related species of crab (Teissier, 1937), molluscs (Nomura, 1926), horses (Robb, 1935) and anthropoid apes (Lumer, 1939) exhibit similar growth constants, *k*, but differences in intercept, *b*. Similarly different year groups of *Carcinus* (Needham, 1935b) demonstrate parallel relative growth. Parallel relative-growth lines describe differences in the body form of amphibians (Atlas, 1935; Hutchinson, 1939) and chicks (Needham, 1934). In all these investigations the slopes, *k*, of the relative-growth lines are constant. The observed variation among groups results from differences in intercept, *b*. As with fishes, such parallelism invites speculation concerning the importance of relative-growth inflections in the fixation of body form.

Some published evidence demonstrates late inflections that influence body form directly. In amphipods, Chevais (1937) has shown that the growth of the second antennae in related forms is such that prior to inflection relative-growth lines are identical but that after inflection the slopes are the same while the intercepts are different. When curves describing differences in male chela size and female abdominal width in lobsters, *Homarus americanus* (Templeman 1935, 1944), are plotted logarithmically, as in figure 24, it becomes apparent that rate of change of form remains constant but that differences in body size at sexual-maturity inflection result

in marked differences in the body form of mature lobsters taken from different localities. The precocious female crab, *Carcinus maenas*, described by Williams and Needham (1937), was characterized by reaching sexual maturity and with this a relative-growth inflection at a small size. This resulted in an abnormally wide abdomen despite the fact that the growth pattern was normal in respect to slope and to inflection at a critical point in development.

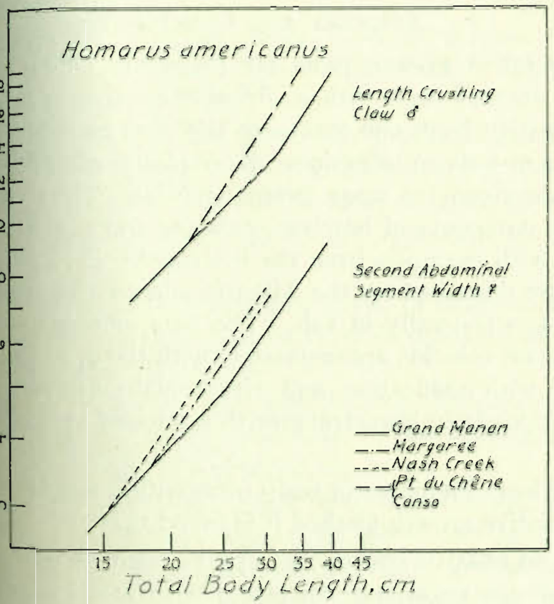


FIGURE 24.—Growth inflection as it changes body form in the lobster, *Homarus americanus*. Data from Templeman (1935, 1944).

Body form thus differed as a result of change in the size at sexual maturity.

According to Allen's Rule, races of mammals found in cold climates may have relatively short ears, feet, and tails. Certain birds have been found to have short tails and tarsi when reared in cold temperatures (Allee and Lutherman, 1940). It would be of interest to investigate the relative-growth involved in these differences to determine the possible influence of size at inflection on body form. A hint of the potential influence of inflection size is apparent in figure 2, page 308, of MacArthur and Chiasson (1945). Beyond growth inflection the relative foot size of a small race of mice appears to be smaller than that of the larger race. Relative growth of ear and tail were identical in the two races, however. Relative-growth inflections for foot, ear, and tail are so marked that differences in size at inflection might readily produce differences in body form.

SUMMARY AND CONCLUSIONS

1. Relative growth plots for fishes are characterized by a series of stanzas each with a different relative growth constant. The transition from one stanza to the next generally takes place by means of a sharp inflection. Examples of such relative-growth curves are given for some twenty species. These were derived from measurements of hatchery samples and museum collections together with examples from the literature. Five relative-growth stanzas are described for the Atlantic salmon and appear to occur more or less generally in fish. The four inflections that delimit these stanzas coincide approximately with the eyed egg stage, with hatching, with ossification, and with sexual maturity. The greatest deviations from isometric growth are found in the early growth stanzas.

2. When differences in body form within species are analysed by the relative growth method it is found that:

(*a*) The relative size of body parts, such as head and fins, is not always negatively correlated with rate of growth. Relatively small heads have been found in both fast-growing and slow-growing groups.

(*b*) Differences in the relative-growth lines, describing body form variation within species, are usually due to differences in the intercepts of these lines rather than to differences in their slopes.

(*c*) There appears to be but little variation in the growth constant even among individuals as well as between infraspecific groups.

(*d*) The relative size of body parts is correlated with the number of meristic parts in the examples cited.

All these lines of evidence indicate that early development is more important than subsequent growth rate in the determination of the relative size of body parts. They further indicate that differences in body size at growth inflection are of more frequent occurrence than differences in the slope of relative-growth lines.

3. The importance of body size at growth inflection in the control of body proportions is demonstrated by several lines of direct evidence:

(*a*) Differences in the body form of certain mature trout populations are largely due to differences in the size at which the fish attain maturity.

(*b*) Differences in body form were produced experimentally by controlling temperature during early development.

(*c*) Early inflections as well as those at about 30 mm. standard length and at sexual maturity are important in the control of body form.

4. The results of a detailed analysis of temperature-controlled lots of rainbow trout offer a rational explanation of observations made on natural populations:

(*a*) Within a group the fast-growing individuals have small body parts such as head and fins. These differences are apparent at both large and small sizes.

(*b*) A fast-growing group of individuals may, on the other hand, have relatively large body parts such as head and fins. By raising developmental temperature, growth rate was increased, body size at the 30 mm. inflection was increased, and fish with relatively large heads and fins resulted.

(*c*) Only those body parts showing growth inflection were found to be subject to such control of body form.

(*d*) The direction of growth inflection and the degree of inflection, as well as body size at inflection, are important factors in the determination of the relative size of body parts.

5. Rate of early development and subsequent rate of growth may both influence body form through their effect on body size at inflections. The direction of inflection determines whether the relative sizes of body parts, following at a relatively large body size, are large or small.

6. By controlling diet during early growth in rainbow trout, differences in body form were produced. Relatively large eyes and heads resulted from malnutrition. The relative-growth analysis showed that these differences were due to slope differences rather than to differences in intercept.

7. The slopes of relative-growth lines describing body form of fish of the same age group differ from those describing body form for fish of successive age groups and thus cannot be considered to be descriptive of ontogenetic relative growth.

8. Differences in the length-weight relationship, found within a species, are in part attributable to factors comparable with those that effect differences in the relative size of body parts. Difference in fish size, at growth inflection, is shown to be one of the factors important in the control of relative heaviness. This early control of the length-weight relationship may be modified later by such factors as diet deficiency.

9. Differences in body form result directly from differences in body size at growth inflection in other animals as well as fishes.

10. It is concluded therefore that in general there is no causal connection between body form in fishes and either rate of development or subsequent growth rate, although either of these processes may indirectly affect control of body form through their influence on size at inflection.

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APPENDIX I

STATISTICAL PROCEDURE USED IN THE COMPARISON OF LOG-LOG REGRESSION LINES

x = log standard length
y = log body part measurement
n = number of individuals in a sample
N = number of individuals in lot 1
${}^1N$ = number of individuals in lot 2
p = number of samples in lot 1
q = number of samples in lot 2

Time	1		2		3		. . .	p		Totals	
	x	y	x	y	x	y		x	y		
Lot 1	x_1	y_1									
	x_2	y_2									
	.	.									
	.	.									
	.	.									
	.	.									
	x_n	y_n									
N	$Tx1$	$Ty1$	$Tx2$	$Ty2$	$Tx3$	$Ty3$	. . .	Txp	Typ	Tx	Ty
Lot 2											
${}^1N$	${}^1Tx1$	${}^1Ty1$	${}^1Tx2$	${}^1Ty2$	${}^1Tx3$	${}^1Ty3$	. . .	${}^1Txp$	${}^1Typ$	${}^1Tx$	${}^1Ty$

"*Within-times*" sums of squares and products

$$A = \Sigma x^2 - \frac{(Txt)^2}{n} \qquad B = \Sigma xy - \frac{Txt\ Tyt}{n} \qquad C = \Sigma y^2 - \frac{(Tyt)^2}{n}$$

Source	Degrees of freedom	X^2	XY	Y^2	k	Reduced sum of squares	Degrees of freedom
"Within times" 1	$n-1$	A_1	B_1	C_1	$\frac{B_1}{A_1}$	$C_1 - \frac{B_1^2}{A_1}$	$n-2$
2	$n-1$	A_2	B_2	C_2	$\frac{B_2}{A_2}$	$C_2 - \frac{B_2^2}{A_2}$	$n-2$
.							
.							
.							
p	$n-1$	A_p	B_p	C_p	$\frac{B_p}{A_p}$	$C_p - \frac{B_p^2}{A_p}$	$n-2$
Total "within times"	$p(n-1)$	A	B	C	$\frac{B}{A}$	$C - \frac{B^2}{A}$	$p(n-1)-1$

Deg. of freedom

Sum of reduced sum of squares (experimental error) $\Sigma\left(C_i - \frac{B_i^2}{A_i}\right) = E$ $p(n-2)$

Sum of squares due to differences among k's $C - \frac{B^2}{A} - E = H$ $p-1$

$$F = \frac{\frac{H}{p-1}}{\frac{E}{p(n-2)}}$$

tests differences among "within-times" slopes

"*Between-times*" sums of squares and products

$$P = \frac{\Sigma\,(Txt)^2}{n} - \frac{(Tx)^2}{np} \qquad Q = \frac{\Sigma\,Txt\;Tyt}{n} - \frac{Tx\;Ty}{np} \qquad R = \frac{\Sigma\,(Tyt)^2}{n} - \frac{(Ty)^2}{np}$$

Source	Degrees of freedom	X^2	XY	Y^2	k^1	Reduced sum of squares	Degrees of freedom
"Between times" Lot 1	$p-1$	P_1	Q_1	R_1	$\frac{Q_1}{P_1}$	$R_1 - \frac{Q_1^2}{P_1}$	$p-2$
"Between times" Lot 2	$q-1$	P_2	Q_2	R_2	$\frac{Q_2}{P_2}$	$R_2 - \frac{Q_2^2}{P_2}$	$q-2$
"Between times" total	$p+q-2$	P	Q	R	$\frac{Q}{P}$	$R - \frac{Q^2}{P}$	$p+q-3$
Sum of reduced sum of squares (aggregate deviation about the "Between-times" regression line)						$\Sigma\left(R_i - \frac{Q_i^2}{P_i}\right) = S$	$p+q-4$
Sum of squares due to difference between k's						$R - \frac{Q^2}{P} - S = T$	1

$$F = \frac{\frac{T}{1}}{\frac{S}{p+q-4}}$$

tests difference between the "between-times" slopes

If the lines are parallel "intercepts" are compared.

"*Between-lots*" sums of squares and products

$$X = \frac{Tx^2}{N} + \frac{{}^1Tx^2}{{}^1N} - \frac{(Tx + {}^1Tx)^2}{N + {}^1N} \qquad Y = \frac{Tx\;Ty}{N} + \frac{{}^1Tx\;{}^1Ty}{{}^1N} - \frac{(Tx + {}^1Tx)\;(Ty + {}^1Ty)}{N + {}^1N}$$

$$Z = \frac{Ty^2}{N} + \frac{{}^1Ty^2}{{}^1N} - \frac{(Ty + {}^1Ty)^2}{N + {}^1N}$$

Source	Degrees of freedom	X^2	XY	Y^2	Adjusted sum of squares	Degrees of freedom
"Between lots"	1	X	Y	Z	$Z - \frac{(Y+Q)^2}{X+P} + \frac{Q^2}{P}$	1
"Between times"	$p+q-2$	P	Q	R	$R - \frac{Q^2}{P}$	$p+q-3$
Sum	$p+q-1$	$X+P$	$Y+Q$	$Z+R$	$Z + R - \frac{(Y+Q)^2}{X+P}$	$p+q-2$

$$F = \frac{\dfrac{Z - \frac{(Y+Q)^2}{X+P} + \frac{Q^2}{P}}{1}}{\dfrac{R - \frac{Q^2}{P}}{p+q-3}}$$

tests difference in intercept between the two samples

"*Within-times*" *vs.* "*Between-times*" slopes

Source	Degrees of freedom	X^2	XY	Y^2	k	Reduced sum of squares	Degrees of freedom
"Within times"	$p(n-1)$	A	B	C	$\frac{B}{A}$	$C - \frac{B^2}{A}$	$p(n-1)-1$
"Between times"	$p-1$	P_1	Q_1	R_1	$\frac{Q_1}{P_1}$	$R_1 - \frac{Q_1^2}{P_1}$	$p-2$
Sum	$pn-1$	L	M	N	$\frac{M}{L}$	$N - \frac{M^2}{L}$	$pn-2$
Sum of reduced sum of squares						$C - \frac{B^2}{A} + R_1 - \frac{Q_1^2}{P_1} = D$	$pn-3$
Sum of squares due to difference between k's						$N - \frac{M^2}{L} - D = G$	1

$$F = \frac{\frac{G}{1}}{\frac{D}{pn-3}}$$

tests difference between the "within-times" and "between-times" slopes.

APPENDIX II

TABLE I

Lake Trout—average measurements of body parts in mm. for samples taken at Oden hatchery in 1941.

	Number	Standard length	Head	Eye	Pectoral	Dorsal to caudal	Depth	Width	Anal height	Snout to dorsal	Ventral length
Feb. 22	10	20.6	4.8	1.8	2.3	10.7			2 6	10.0	1.3
Mar. 22	10	23.6	5.9	2.1	3.0	12.3	3.6	2.3	3.1	11.9	1.9
Apr. 8	6	26.3	6.6	2.3	3.7	13.7	3.9	2.3	3.9	12.9	2.5
Apr. 19	10	26.2	6.7	2.4	3.8	13.6	3.7	2.2	3.9	13.4	2.9
May 17	10	31.2	8.7	2.7	4.9	16.2	5.2	3.0	4.8	16.0	3.7
May 31	10	34.8	9.7	2.9	5.4	18.0	5.9	3.3	5.2	18.3	4.3
July 12	10	44.8	12.4	3.5	6.9	23.2	7.9	4.9	6.6	23.2	5.0
Aug. 1	9	50.8	13.9	4.0	7.7	26.0	8.5	5.3	7.4	26.7	6.0
Sept. 6	10	58.1	16.0	4.3	8.9	29.3	10.2	6.4	8.8	30.0	7.1
Sept. 20	10	59.4	16.3	4.6	8.7	30.4	10.1	6.5	8.4	30.7	7.0

TABLE 2

Brook Trout—average measurements of body parts in mm. for samples taken at Oden hatchery in 1941.

	Number	Standard length	Head	Pectoral	Snout to dorsal	Dorsal to caudal	Eye	Depth	Width	Anal height	Ventral length
Small sort											
June 28	12	27.1	7.9	5.6	13.3	15.1	2.8	5.6	3.8	5.5	4.7
July 12	11	28.0	8.1	6.0	13.1	15.5	2.9	6.0	3.9	5.8	5.0
Aug. 23	11	38.4	10.7	7.8	18.4	21.5	3.6	8.4	5.2	7.7	5.9
Sept. 6	10	30.1	8.6	6.4	14.8	16.4	3.2	6.2	3.7	6.2	5.0
Medium sort											
May 31	10	33.9	9.3	6.8	16.0	19.5	3.0	8.0	5.0	6.2	5.4
June 28	12	40.2	11.0	8.0	19.1	23.0	3.5	9.9	6.1	7.8	6.4
July 12	10	43.8	12.0	8.9	20.5	24.7	3.6	10.7	6.9	8.2	6.1
Aug. 23	10	48.2	13.1	10.0	22.9	27.4	4.1	11.4	7.2	9.3	7.8
Sept. 6	10	47.6	13.0	8.9	22.5	27.0	4.0	11.6	7.0	9.0	7.1
Sept. 20	10	57.4	15.2	11.0	27.0	32.9	4.6	13.1	8.4	10.8	8.6
Large sort											
June 28	9	48.0	11.6	9.0	23.4	26.8	3.9	12.1	6.9	9.1	7.4
Aug. 23	10	62.9	16.3	10.4	30.3	34.9	4.8	14.8	9.1	11.1	9.0
Sept. 6	9	83.6	20.7	14.1	39.0	47.6	5.7	20.8	11.1	14.1	11.7

TABLE 3

Leucichthys artedi—average standard lengths and head lengths for lake Nipissing, Ontario from Fry unpublished data.

Mean standard length mm.	Mean head length mm.	Number measured	Year class	Age	Sex
55.7	14.9	70	1934	0	♂ + ♀
140	35.2	98	1933	1	♂
141	35.4	108	1933	1	♀
147	35.0	24	1932	1	♂
149	36.3	17	1932	1	♀
154	37.4	27	1934	1	♂ + ♀
187	45.5	76	1933	2	♂
188	45.4	64	1933	2	♀
192	46.3	58	1932	2	♀
196	47.1	31	1932	2	♂
200	47.8	61	1931	2	♂
203	48.4	26	1931	2	♀
218	52.4	46	1932	3	♂
219	52.5	69	1931	3	♂
220	52.3	44	1932	3	♀
220	53.4	101	1931	3	♀
226	53.5	260	1930	3	♂
228	53.5	258	1930	3	♀
238	56.8	205	1930	4	♀
238	57.1	289	1930	4	♂
239	57.7	82	1931	4	♂
241	57.3	68	1931	4	♀
246	59.1	103	1929	4	♂
247	58.7	93	1929	4	♀
251	60.8	33	1930	5	♀
253	62.0	54	1929	5	♀
255	60.9	72	1928	5	♀
255	61.7	66	1928	5	♂
255	62.0	51	1930	5	♂
257	62.0	43	1929	5	♂
260	62.6	92	1927	6	♀
261	64.2	22	1926	7	♂
263	63.8	20	1928	6	♂
264	64.4	89	1927	6	♂
267	64.7	38	1928	6	♀

TABLE 3—Continued

Mean standard length mm.	Mean head length mm.	Number measured	Length-range	Sex
			Length Range	
264	64.3	56	260-269	♂
265	64.2	72	260-269	♀
274	66.0	72	270-279	♀
274	66.2	58	270-279	♂
282	68.0	36	280-289	♂
283	68.9	31	280-289	♀
292	70.4	14	290-299	♀
294	70.8	8	290-299	♂
303	73.1	7	300-309	♂
305	75.6	3	300-309	♀
312	78.2	2	310-319	♀
324	77.7	2	320-329	♀
334	80.0	2	330-339	♂
338	86.5	1		♀
344	81.0	1		♀
349	81.8	1		♂
352	85.0	1		♂
356	85.0	2		♀
365	88.9	2		♂
367	87.7	1		♀
370	90.0	1		♀
385	94.0	1		♂
392	93.4	9		♂
396	96 8	2		♂
404	94.0	1		♀
405	99.0	1		♂

TABLE 4

Numbers of fish dying by two-week periods in well-fed (H) and ration-fed (L) lots of rainbow trout reared at different temperatures at Oden hatchery in 1941.

	46°F.		53°F.		60°F.
	H	L	H	L	Transfers
March 8—March 17	4	4	11	4	12
March 18—March 31	14	12	6	2	62
April 1—April 18	14	24	4	5	3
April 19—May 2	8	8	5	3	4
May 3—May 16	3	0	0	1	0
May 17—May 30	20	5	0	2	17
May 31—June 13	4	2	3	2	9
June 14—June 28	2	4	0	4	0
June 29—July 12	2	0	4	2	2
July 13—July 26	2	0	0	0	16
July 27—Aug. 9	0	0	3	15	4
Aug. 10—Aug. 23	0	0	0	0	0
Aug. 24—Sept. 6	1	0	6	1	1
Sept. 7—Sept. 20	0	1	1	2	4
Total	54	60	43	43	134

TABLE 5

Feeding experiment growth by months for rainbow trout reared at Oden hatchery in 1941 on diets of liver (I and VIII), liver and kelp (II and VII), liver and blood (III and VI) and blood and meal (IV and V).

	I	II	III	IV	V	VI	VII	VIII
May 27	403	318	297	59	46	483	623	400
June 24	41	90	84	110	110	76	77	81
July 22	276	533	478	540	502	485	542	357
Aug. 19	89	26	21	475	332	26	24	14
Sept. 16	21	20	29	279	144	25	28	34
Total	830	987	909	1463	1134	1095	1294	886

TABLE 6

Feeding experiment growth—weight per fish in gms., at monthly intervals, as calculated from number of fish per 1,000 gms. Diets numbered as in table 5.

	I	II	III	IV	V	VI	VII	VIII
May 5	.25	.24	.23	.23	.20	.24	.22	.22
May 27	.39	.40	.39	.28	.30	.40	.39	.42
June 24	.73	.73	.69	.39	.39	.70	.68	.69
July 22	.84	.86	.79	.40	.36	.83	.79	.86
Aug. 19	.95	1.06	.96	.44	.45	.96	1.05	.98
Sept. 16	1.26	1.47	1.32	.64	.66	1.35	1.42	1.33

TABLE 7

Rainbow trout—average measurements of body parts in mm. for 46° and 53° (well-fed) and 60° transfer samples taken at Oden hatchery in 1941.

	Number measured	Standard length	Head	Eye	Snout to pectoral	Pectoral	Pectoral to anal	Anal to caudal	Depth	Width	Anal height
46°											
Apr. 5	10	22.6	6.4	2.2	5.8	3.8	10.3	6.8	4.4	3.1	3.3
Apr. 19	10	24.5	7.5	2.5	6.4	4.2	11.3	7.5	5.5	3.8	3.8
May 17	10	28.7	8.9	2.8	7.6	4.7	13.6	8.8	6.5	4.1	4.8
May 31	11	29.3	9.0	2.9	7.5	4.9	13.4	8.9	7.0	4.4	4.7
June 13	10	31.4	9.6	3.0	8.1	5.3	14.5	9.5	7.4	4.6	5.2
June 28	11	35.6	10.5	3.2	8.8	5.7	16.3	11.0	8.5	5.1	5.7
July 12	12	34.1	10.2	3.2	8.6	5.6	15.4	10.7	8.0	4.6	5.6
July 26	10	38.4	11.4	3.4	9.2	6.3	18.0	12.0	9.0	5.2	6.3
Aug. 9	10	44.4	13.0	3.8	10.4	7.2	21.5	13.8	10.9	6.1	7.1
Aug. 23	9	43.8	12.9	3.9	10.5	7.2	20.7	13.5	10.3	6.0	7.0
Sept. 6	10	45.7	13.3	4.0	10.6	7.6	22.3	14.1	11.2	6.2	7.4
Sept. 20	10	50.0	14.2	4.3	11.8	7.9	24.9	15.2	12.3	6.8	7.9
53°											
Feb. 22	6	22.3	6.5	2.2	5.8	3.9	10.4	7.0	4.6	3.1	3.4
Mar. 8	10	25.6	7.8	2.5	6.9	4.4	11.8	8.0	5.9	3.7	4.4
Mar. 22	10	29.0	8.8	2.8	7.6	5.0	13.5	9.0	6.8	4.3	4.8
Apr. 5	10	32.2	9.9	3.3	8.4	5.6	15.3	9.7	7.8	5.1	5.6
Apr. 19	10	33.6	10.5	3.5	8.7	6.0	15.8	10.5	8.5	5.3	6.1

TABLE 7—Continued

	Number measured	Standard length	Head	Eye	Snout to pectoral	Pectoral	Pectoral to anal	Anal to caudal	Depth	Width	Anal height
May 3	10	37.0	11.5	3.4	9.2	6.7	17.5	11.4	9.1	5.5	6.5
May 17	10	38.7	11.9	3.8	9.7	7.2	18.3	11.9	9.7	5.9	7.0
May 31	10	41.9	12.7	3.9	10.2	7.7	20.3	12.4	10.7	6.1	7.4
June 13	10	46.0	13.8	4.3	11.0	8.2	22.6	13.6	11.9	6.6	8.1
June 28	10	48.5	14.4	4.7	11.5	9.1	24.5	14.4	12.3	6.9	8.7
July 12	10	48.9	14.8	4.8	11.8	9.3	24.6	14.4	12.2	7.2	8.9
July 26	9	55.7	16.4	5.2	12.9	10.3	28.5	16.2	13.9	8.1	10.0
Aug. 9	10	53.0	15.8	5.1	12.9	9.1	25.5	15.8	13.2	7.6	9.4
Aug. 23	10	57.6	17.1	5.4	13.9	10.3	27.9	17.2	14.0	8.4	10.0
Sept. 6	10	61.6	18.0	5.6	14.8	10.8	30.9	18.0	14.7	8.8	10.5
60°											
May 3	10	30.7	9.6	3.1	8.0	5.0	14.0	9.3	7.4	4.3	5.1
May 17	10	30.2	9.5	3.1	8.0	4.9	13.5	9.1	7.5	4.4	5.0
May 31	10	36.5	11.3	3.5	9.1	6.2	16.9	11.2	9.1	5.2	6.0
June 13	10	36.9	11.6	3.6	9.1	6.4	16.8	11.3	9.3	5.5	6.2
June 28	12	40.0	12.3	3.7	9.7	7.3	18.8	12.5	9.9	5.6	6.8
July 12	11	41.2	13.1	4.0	10.0	8.0	19.2	12.8	10.4	6.0	7.2
July 26	10	38.8	12.7	3.9	9.7	7.4	18.2	12.0	10.0	5.5	6.8
Aug. 9	10	46.0	14.1	4.3	11.2	8.5	22.1	14.3	11.7	6.6	7.9
Aug. 23	10	49.5	15.5	4.8	12.0	9.1	23.3	15.5	12.6	7.2	8.5
Sept. 6	9	47.2	15.0	4.6	11.6	8.8	22.4	14.3	11.8	7.2	8.0
Sept. 20	9	53.5	16.7	4.9	13.2	10.0	25.9	16.6	14.3	8.3	9.1

TABLE 8

Rainbow trout—average measurements of body parts in mm. for 46° and 53° ration-fed samples taken at Oden hatchery in 1941.

	46°					53°				
	Number measured	Standard length	Head	Eye	Anal height	Number measured	Standard length	Head	Eye	Anal height
Feb. 8						6	18.0	4.6	1.8	2.4
Feb. 22						10	21.8	6.0	2.1	3.0
Mar. 8	10	18.7	4.9	1.7	2.3	10	25.9	7.6	2.5	4.0
Mar. 22	10	20.3	5.5	2.0	2.9					
Apr. 5	10	23.4	6.4	2.2	3.3	10	29.4	8.8	2.8	4.7
May 3	10	25.6	7.5	2.5	3.8	10	33.6	10.3	3.2	5.6
May 17	10	29.0	8.7	2.7	4.4	10	33.7	10.3	3.1	5.5
May 31	10	31.1	9.3	2.8	4.7	10	37.7	11.6	3.4	6.3
June 13	9	31.7	9.6	2.9	4.9	10	39.4	11.9	3.5	6.4
June 28	10	35.0	10.8	3.2	5.6	10	44.9	13.1	4.0	7.7
July 12	10	37.1	11.1	3.3	6.0	10	44.8	13.1	4.0	7.7
July 26	10	36.0	10.8	3.3	6.0	10	50.5	15.0	4.4	8.6
Aug. 9	10	41.4	12.4	3.7	6.7	10	51.1	15.0	4.5	8.7
Aug. 23	10	43.5	13.1	3.8	7.0	10	57.5	17.1	5.0	9.6
Sept. 6	10	42.3	12.3	3.7	7.0	10	56.9	16.5	4.9	9.3
Sept. 20	10	45.2	13.2	3.8	7.2	10	59.4	17.1	5.1	9.8

TABLE 9

Head comparisons of 46° and 60° transfer well-fed samples of rainbow trout.

	Source	d. f.	X^2	XY	Y^2	k	red. s. s.	d. f.
46°								
	1	9	.009578	.006568	.005657	.686	.001154	8
	2	10	.012653	.010421	.011682	.824	.003100	9
	3	11	.034260	.029155	.027742	.851	.002932	10
	4	9	.019136	.018190	.017786	.951	.000496	8
	5	9	.011732	.007907	.006668	.674	.001339	8
	6	8	.013400	.010817	.010789	.807	.002058	7
	7	9	.006258	.004680	.004132	.748	.000633	8
	8	9	.004501	.005190	.008449	1.153	.002465	8
		74	.111518	.092928	.092905	.833	.015469	73
Sum of red. s. s.							.014177	66
s. s. due to diff. among *k*'s							.001292	7
			$F = 0.86$	$p > 5\%$				
60° T								
	1	9	.015953	.012704	.012032	.796	.001916	8
	2	11	.024452	.020644	.020388	.844	.002959	10
	3	10	.025093	.023098	.022905	.920	.001644	9
	4	9	.018287	.016975	.017742	.928	.001985	8
	5	9	.030897	.027428	.025757	.888	.001409	8
	6	9	.030173	.025063	.022254	.831	.001436	8
	7	8	.027332	.021908	.019353	.802	.001793	7
	8	8	.098431	.083392	.071847	.847	.001197	7
		73	.270618	.231212	.212278	.854	.014734	72

TABLE 9—Continued

Source	d. f.	X^2	XY	Y^2	k	red. s. s.	d. f.
Sum of red. s. s.						.014339	65
s. s. due to diff. among *k*'s						.000395	7
		F = 0.26	$p > 5\%$				
Between times 46°	7	.351030	.312850	.290152	.891	.011330	6
Between times 60° T	7	.201328	.193237	.190965	.960	.005494	6
Between times total	14	.552358	.506087	.481117	.916	.017425	13
Sum of red. s. s.						.016824	12
s. s. due to diff. between *k*'s						.000601	1
		F = 0.43	$p > 5\%$			*adj. s. s.*	
Between lots	1	.055529	.098725	.175517		.037457	1
Between times total	14	.552358	.506087	.481117		.017425	13
Total	15	.607887	.604812	.656634		.054882	14
		F = 27.94	$p < 1\%$				
Within times 46°	74	.111518	.092908	.092905	.833	.015469	73
Between times 46°	7	.351030	.312850	.290152	.891	.011330	6
Total	81	.462548	.405778	.383057		.027082	80
Sum of red. s. s.						.026799	79
s. s. due to diff. in *k*'s						.000293	1
		F = .086	$p > 5\%$				
Within times 60° T	73	.270618	.231212	.212278	.854	.014734	72
Between times 60° T	7	.201328	.193237	.190965	.960	.005494	6
Total	80	.471946	.424449	.403243		.021511	79
Sum of red. s. s.						.020228	78
s. s. due to diff. in *k*'s						.001283	1
		F = 4.95	$p = 4\%$				

TABLE 10

Summary of comparisons of 46° and 60° samples of rainbow trout listed in tables 9 to 17.

	Head	Eye	Snout to pectoral	Pectoral	Pectoral to anal	Anal to caudal	Depth	Width	Anal height
46° well-fed									
Total "within-times" *k*	0.833	0.601	0.762	0.724	1.150	0.982	1.080	1.181	0.723
"Between-times" *k*	0.891	0.774	0.810	0.963	1.221	1.001	1.137	0.920	0.940
"Within-lot" *k*	0.877	0.732	0.798	0.905	1.206	0.996	1.123	0.983	0.888
"Within-times" difference in *k*'s	> 5%	> 5%	> 5%	> 5%	> 5%	> 5%	> 5%	> 5%	> 5%
"Within" *vs.* "between" difference in *k*'s	> 5%	< 1%	> 5%	3%	> 5%	> 5%	> 5%	< 1%	< 1%
60° transfer									
Total "within-times" *k*	0.854	0.697	0.847	0.870	1.099	1.056	1.003	1.074	0.888
"Between-times" *k*	0.960	0.924	0.993	1.085	1.118	1.007	1.102	1.132	0.985
"Within-lot" *k*	0.899	0.794	0.909	0.962	1.107	1.035	1.046	1.120	0.930
"Within-times" difference in *k*'s	> 5%	> 5%	> 5%	> 5%	> 5%	> 5%	> 5%	> 5%	>5%
"Within" *vs.* "between" difference in *k*'s	4%	< 1%	< 1%	< 1%	> 5%	> 5%	> 5%	> 5%	> 5%
Comparison of 46° and 60° transfer									
"Between-times" difference									
in *k*'s	> 5%	> 5%	< 1%	> 5%	3%	> 5%	> 5%	> 5%	> 5%
b's	< 1%	< 1%	3%	< 1%	3%	> 5%	< 1%	< 1%	< 1%

Differences recorded are p values from Snedecor (1946) for significance of difference.
< 1% is considered to be significant and >5% not significant.

TABLE 11

Rainbow Trout—average body measurements in mm. for samples reared on liver (I and VIII), liver and kelp (VII), liver and blood (VI) and blood and meal (IV and V) diets at Oden Hatchery in 1941.

	Number measured	Standard length	Head	Eye	Snout to pectoral	Pectoral	Pectoral to anal	Anal to caudal	Depth	Width	Anal height
I											
Apr. 5	10	21.5	5.9	2.1	5.5	3.0	9.2	6.8	3.3	1.6	3.2
Apr. 19	10	22.2	6.5	2.3	5.8	3.2	9.6	7.0	3.5	1.7	3.4
May 17	10	27.2	8.2	2.6	7.2	3.7	11.6	8.3	5.2	2.5	4.1
May 31	10	28.8	8.6	2.7	7.3	3.9	12.5	8.6	5.7	2.8	4.3
June 26	10	34.4	10.2	3.1	8.7	4.7	14.8	10.5	7.2	3.6	5.3
July 26	10	35.3	10.6	3.2	9.0	4.9	15.0	10.7	7.3	3.6	5.8
Aug. 23	12	38.9	11.5	3.5	9.9	5.2	16.9	11.5	8.3	3.8	6.1
Sept. 20	11	43.8	12.5	3.8	11.1	5.7	19.3	13.3	9.5	4.6	6.9
IV											
April 5	10	22.2	6.0	2.1	5.7	2.8	9.7	6.8	3.3	1.7	3.0
April 19	10	22.3	6.6	2.2	6.1	3.2	9.7	6.7	3.8	1.8	3.3
May 31	10	27.3	8.2	2.7	7.2	3.8	11.9	8.3	4.8	2.3	4.0
June 26	10	27.2	8.1	2.7	7.3	3.6	11.9	8.2	4.8	2.1	4.0
July 26	10	26.9	7.9	2.8	7.2	3.3	11.6	8.0	4.4	1.8	4.0
Aug. 23	10	30.2	9.3	3.2	8.0	3.9	13.2	9.0	5.8	2.8	4.6
Sept. 20	10	31.9	9.7	3.3	8.7	4.2	13.9	9.5	6.6	3.2	4.7
V											
April 5	10	21.9	5.8	2.2	5.8	2.4	9.8	6.7	3.2	1.8	3.0
April 19	10	22.6	6.4	2.4	6.2	3.2	9.8	6.9	4.0	1.9	3.2
May 17	10	24.4	7.2	2.6	6.6	3.2	10.2	7.6	4.2	2.2	3.5
June 13	10	26.4	8.1	2.8	7.2	3.5	11.1	8.1	5.2	2.7	3.8
July 12	10	28.5	8.7	2.9	7.8	3.6	12.6	8.9	5.4	2.5	4.2
Aug. 9	10	26.8	8.3	3.0	7.6	3.8	11.4	8.0	5.2	2.3	4.2
Aug. 23	10	26.8	8.3	3.0	7.6	3.5	11.7	8.0	4.6	2.2	3.9
Sept. 6	10	28.1	8.8	3.1	7.4	3.6	11.8	8.6	5.8	2.7	4.3
Sept. 20	10	30.8	9.7	3.3	8.5	4.0	13.3	9.2	6.6	3.1	4.8
VI											
April 5	10	22.1	6.1	2.2	6.0	2.7	9.8	6.8	3.2	1.9	3.0
May 3	10	25.9	7.3	2.4	7.2	3.5	11.6	7.7	4.5	2.1	3.6
May 31	10	29.3	8.8	2.9	7.7	3.9	12.7	9.1	5.7	3.0	4.4
June 28	10	34.1	10.2	3.1	8.8	4.8	14.5	10.5	6.9	3.4	5.3
July 26	10	34.6	10.4	3.2	9.2	5.1	14.7	10.5	7.1	3.7	5.6
Aug. 23	10	38.8	11.6	3.6	10.1	5.2	16.7	11.9	8.1	4.4	6.1
Sept. 6	10	42.6	12.4	3.9	11.0	6.0	19.0	12.7	9.2	4.9	6.7
Sept. 20	10	40.4	12.0	3.7	10.3	5.4	17.8	12.5	8.5	4.6	6.3
VII											
April 5	10	22.1	6.0	2.2	5.8	2.8	9.8	6.7	3.4	1.7	3.0
April 19	10	22.3	6.5	2.4	6.2	3.1	9.7	7.0	3.6	1.9	3.1
May 3	10	25.4	7.3	2.4	7.1	3.4	11.8	7.6	4.3	2.2	3.7
May 17	10	27.3	8.1	2.6	7.2	3.3	11.8	8.3	5.1	2.6	3.8
May 31	10	28.7	8.5	2.7	7.5	3.8	12.5	9.0	5.6	2.8	4.0
June 28	10	34.9	10.3	3.2	9.0	4.9	15.2	10.8	7.2	3.7	5.5
July 26	10	34.0	10.3	3.3	8.9	5.1	14.8	10.5	7.2	3.6	5.4
Aug. 23	10	37.8	11.4	3.5	10.0	5.7	16.3	11.6	8.0	4.2	6.0
Sept. 6	10	41.6	12.4	3.7	10.7	6.3	18.4	12.8	9.3	5.0	6.5
VIII											
April 5	10	21.5	5.9	2.1	5.7	2.6	9.6	6.6	3.4	1.7	3.0
May 3	10	23.6	6.8	2.4	6.4	3.4	10.0	7.2	3.9	2.0	3.6
May 17	10	27.0	8.0	2.5	7.0	3.7	11.6	7.6	5.2	2.5	3.9
May 31	10	28.2	8.6	2.7	7.4	4.0	12.1	8.7	5.4	3.0	4.2
June 28	10	35.2	10.4	3.1	9.1	4.6	15.2	10.9	7.5	3.9	5.3
July 26	10	37.3	11.1	3.4	9.6	5.4	16.0	11.8	8.2	4.4	6.0
Sept. 6	10	39.2	11.6	3.5	10.1	5.3	17.1	12.1	8.4	4.3	6.4
Sept. 20	10	41.4	12.3	3.8	10.7	5.6	18.1	12.6	9.2	4.7	6.8

TABLE 12

Rainbow Trout—average lengths (L) and weights (W) of 46°, 53°, and 60° transfer well-fed samples taken at Oden hatchery in 1941. The eggs were taken on Dec. 23.

Date	46°			53°			60°T.		
Jan. 22	—			Hatch			—		
Feb. 9-11	Hatch			First Fed			—		
Mar. 11	First Fed			—			—		
	L.	W.	Number	L.	W.	Number	L.	W.	Number
Mar. 22	21.8	.16	11	28.8	.43	11	22.8	.16	11
April 5	22.6	.17	10	32.0	.55	10	26.6	.31	10
April 19	25.0	.28	10	34.2	.73	10	28.5	.42	11
May 3	26.0	.30	10	37.5	.93	10	31.0	.58	10
May 17	29.4	.43	10	39.0	1.08	10	30.6	.56	10
May 31	29.6	.45	11	42.3	1.5	11	36.6	.94	10
June 13	31.8	.57	10	47.5	1.92	10	37.1	.98	10
June 28	35.9	.84	11	49.8	2.09	10	40.1	1.19	12
July 12	34.6	.70	12	50.6	2.11	10	41.7	1.36	11
July 26	38.8	.98	10	58.0	3.44	10	39.8	1.19	10
Aug. 9	44.9	1.53	10	53.8	2.56	10	39.7	1.20	10
Aug. 23	—	—	—	—	—	—	50.2	2.29	10

TABLE 13

Rainbow Trout—average lengths (L) in mm. and weights (W) in gms. for samples taken from lots reared on diets of liver (I and VIII), liver and kelp (II and VII), liver and blood (III and VI) and blood and meal (IV and V) at Oden hatchery, in 1941.

Date	I			II			III			IV		
	L	W	No.	L	W	No.	L	W	No.	L	W	No.
April 5	22.0	.14	11	22.4	.15	12	22.1	.14	11	22.7	.16	10
April 19	22.7	.19	14	22.6	.19	10	23.0	.17	12	22.8	.18	10
May 3	25.6	.26	11	26.1	.26	11	25.7	.23	13	25.1	.22	13
May 17	27.5	.36	13	27.6	.36	11	26.4	.28	11	25.6	.25	11
May 31	29.3	.43	10	27.4	.32	11	27.8	.34	10	27.6	.31	10
June 13	31.4	.53	10	32.7	.64	10	33.3	.66	11	27.6	.34	10
June 28	34.9	.72	12	33.5	.64	11	33.6	.70	11	27.6	.32	10
July 12	33.5	.63	12	34.2	.68	11	35.2	.71	13	27.1	.25	12
July 26	36.8	.84	15	37.8	.85	11	34.9	.73	11	27.4	.27	12

Date	V			VI			VII			VIII		
	L	W	No.	L	W	No.	L	W	No.	L	W	No.
April 5	22.4	.14	11	22.9	.15	12	22.8	.15	11	22.1	.15	12
April 19	22.8	.18	11	21.9	.16	12	22.5	.16	12	23.0	.16	12
May 3	26.4	.27	12	24.4	.22	11	24.2	.22	14	24.2	.22	12
May 17	24.8	.24	11	27.1	.35	10	27.7	.36	10	28.2	.38	11
May 31	25.6	.20	12	29.7	.44	11	31.6	.45	11	28.8	.43	12
June 13	26.8	.34	10	32.4	.61	10	33.6	.66	10	32.4	.61	10
June 28	28.2	.34	11	34.9	.71	11	35.6	.76	11	36.4	.81	9
July 12	28.9	.38	12	35.3	.74	12	35.1	.70	12	34.5	.70	12
July 26	29.1	.40	12	34.8	.73	11	34.6	.70	12	38.3	.94	10