DETERMINATION OF FISH GROWTH BY BACK-CALCULATION FROM SCALES WITH APPLICATION TO HADDOCK (MELANOGRAMMUS AEGLEFINUS (L.)) OF THE NEWFOUNDLAND AREA

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DETERMINATION OF FISH GROWTH BY BACK-CALCULATION FROM SCALES, WITH APPLICATION TO HADDOCK (Melanogrammus aeglefinus (L.)) OF THE NEWFOUNDLAND AREA

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A thesis presented to the Memorial University of Newfoundland in partial fulfilment of the requirements for the Degree of Master of Science in Fisheries Biology

March 16, 1964

ABSTRACT

Methods of determining age and growth of fish are reviewed. In particular, the scale method of ageing and procedures for back-calculation of growth from scales are reviewed in some detail, and are applied to haddock of the Newfoundland area.

Plots of fork length on scale diameter are used to determine the body-scale relationship, and are found to be linear. Differences between the fitted regressions for the sexes, year-classes and areas are examined by analysis of covariance. It is concluded that a general body-scale relationship, having a regression coefficient of 4.62 and L-intercept value of 6.57 cm, provides an adequate description of the relative growth of body and scales in the area as a whole.

The L-intercept value was used to correct the simple proportionality (Dahl-Lea) formula for back-calculation of growth. Values of back-calculated average lengths at age were slightly higher (of the order of 1 cm) than empirical averages. Lee's phenomenon, the apparent decline in average length at age when calculations are made from successively older fish, does not appear in its usual form in the data, but occurs in reverse form in growth calculations from the most recent year-classes. Differences in growth are found between immature and mature fish, males and females, year-classes and areas and possible reasons for these differences are discussed. Average lengths at age of Newfoundland area haddock are shown to be less than those for other areas of the northwest Atlantic over the range of ages compared.

CONTENTS

I. INTRODUCTION

A. IMPORTANCE OF GROWTH STUDIES

A study of growth is basic to any fisheries biology programme. Carlander (1956) pointed out that fish growth rates are readily modified and very responsive to environmental factors, making growth data valuable as indicative of the general welfare of fish populations. In studies of fish population dynamics and mathematical formulations of optimum yield, or greatest sustained yield under existing conditions of exploitation, it is essential to be able to describe growth as precisely as possible as a mathematical function in terms of age and weight. Thus a knowledge of growth variations and their causes within a species is of paramount importance to the ultimate aim of determining ways and means of making the most effective use of a fishery resource.

B. DEFINITION OF GROWTH

Growth is the result of the various forces by which material is introduced into an organism, transferred throughout its system and assimilated to produce new living material. The end result of these processes is an increase in size and the simplest definition of growth would be increase in size with time. The time factor is basic in describing growth, either in terms of rates, attained sizes or increments, and in most growth studies automatically introduces the problem of age determination. A discussion of age determination methods, especially the scale method on which this growth study is based, is found in Section ID.

C. EXPRESSION OF GROWTH

The end-product of growth is increase in size, and this increase is most appropriately expressed in units of weight or volume. Growth must invariably be expressed in terms of weight if the growth data are to be used in mathematical formulations for estimation of yield such as those of Baranov (1918), Thompson and Bell (1934), Ricker (1945) and Beverton and Holt (1957). However, since most data for growth studies are collected at sea or elsewhere in the field, it is both difficult and time consuming to obtain accurate weight or volume measurements. The length measurement, therefore, is the one most often used in growth studies since fairly rapid and accurate measurements of this variable can be obtained under field conditions.

A good deal of confusion has occurred concerning the most appropriate measure of a fish's length. While it is generally agreed that measurement should begin from the anterior tip of the snout (or lower jaw if this protrudes) with the mouth closed, a variety of terminal positions have been used. This has resulted in the evolution of three basic types of length measurement, which may be broadly defined as follows:

(1) Standard length - snout to region of caudal peduncle. A great deal of ambiguity exists with regard to this measurement. Ricker and Merriman (1945) present definitions for 8 "standard" lengths.

(2) Fork length - snout to mid-fork of caudal fin. This has also been described as the mid-caudal or median length and is sometimes classified with total length.

(3) Total length - snout to end of caudal fin. The caudal rays may be spread to the "natural" position (natural tip length) or pressed together to obtain the position of maximum extension (extreme tip length). In either case the measurement is made to the tip of the longest lobe of the caudal fin.

Standard length was used to a large extent in the United States in freshwater studies during the early part of the present century, but was largely replaced during the 1940's by fork or total lengths. Many authors of age and growth studies of American freshwater fishes have measured the same fish by several methods and present conversion factors for transforming one type of length measurement to others. Such factors are apt to vary with fish size as pointed out by Carlander and Smith (1945) and Beckman (1948), and with measurer (Carlander, 1950b), as well as with a number of other variables, including sex and the area of capture. In any case repetitious measurement of length is recognized as a wasteful and time-consuming procedure and a number of proposals for uniformity have been made.

Royce (1942) concluded that extreme total length produced best results (less scatter) for weight-length plots of four freshwater species. Carlander and Smith (1945) obtained equally accurate weight estimates from two different standard lengths, fork length and extreme total length, but favoured the latter since it could be obtained with greatest accuracy. Extreme total length is also favoured by Hile (1948). On the other hand Merriman (1941), Ricker (1942) and Ricker and Merriman (1945) present a number of reasons for the adoption of fork length. Ricker and Merriman (1945) point out, however, that any clearly defined length measurement is sufficiently accurate for ordinary purposes, since errors in estimates of any variable due to inconsistency of measurement are negligible in comparison with natural variation. Thus the choice of length measurement becomes essentially a matter of convenience and uniformity.

Fork length is the most commonly used measurement for marine species, at least in North America. It is used by the St. John's Biological Station for all routine fish measurements and is the length measurement made on all haddock in the present study.

Having obtained the growth history of a species in terms of length it is generally a fairly simple matter to obtain the relation of weight to length, and thus express growth in terms of weight should this be desired. Thompson (1917) drew attention to the elementary mathematical principle that "in similar solid figures the surface increases as the square, and the volume as the cube, of the linear dimensions," or:

$$S = kL^2 \qquad (1)$$

and

$$V = k'L^3 \qquad (2)$$

where S = surface area, L = length, V = volume, and k and k' are constants.

If it is assumed that:

(1) the weight of a fish is proportional to its volume, and

(2) that the form and specific gravity do not change throughout the fish's life, then the formula

$$w = kL^3 \qquad (3)$$

can be used to described the relation between fish weight and length. Crozier and Hecht (1914) and Hecht (1916) found, for a number of marine species, that the body proportions were constant throughout life, and were able to apply this relation directly to length and weight data. It has also been used in describing length-weight relationships of the Pacific edible crab, Cancer magister (Dana), and the Pismo clam, Tivela stultorum (Mawe), by Weymouth (1918 and 1923), of Atlantic salmon, Salmo salar L., by Corbett (1922), and for lake herring, Coregonus artedii LeSueur, of Lake Huron by Van Oosten (1929).

If the length-weight relation follows exactly the form as described in (3) the fish is said to grow isometrically. This means that the weight of the fish increases at the same rate or in the same proportion as the cube of the length. Such a relation in fish is the exception rather than the rule, though it is approached in many species. Variations in the simple cube law relationship are brought about by the fact that the body proportions of a fish (or any other animal) are prone to change throughout life. As early as 1904, Fulton found in investigating the length-weight relations of 19 marine species, that the cube law relation underestimated fish weight at any given length, and he concluded that "if the specific gravity of the fishes remains constant they must increase somewhat more in other dimensions than in length." Hart (1931) demonstrates that in whitefish, _Coregonus clupeaformis_ (Mitchell), various body proportions change as the fish increases in size; in particular the body depth increases proportionately although size of the head and its parts decreases, and he concludes that this increased proportionate depth is related with an excess over the cube law relationship between length and weight. Martin (1949) has demonstrated changes in relative growth of body parts for more than 20 fish species. In view of the foregoing, departures from the simple cube law relation are to be expected and are well-documented in the literature.

Most authors have described the length-weight relation in terms of the general formula

$$y = bx^{a} \qquad (4)$$

or the logarithmic transformation

$$\log y = \log b + a \log x \qquad (5)$$

which Reeve and Huxley (1945) refer to as the simple allometry formula, and which Huxley (1924) recognized as possibly expressing a general law of differential growth. Values of $\underline{a}$ in excess of 3 have been reported for a variety of marine and freshwater species by many authors, including Clark (1928), Hart (1931), Carlander (1943), Deason and Hile (1947), Van Oosten and Hile (1949), Tate (1949), Lewis and English (1949), Cleary (1949), Carlander (1950a), Carlander et al. (1953), Parsons (1951), Kennedy (1953), Hennemuth (1955), Sprugel (1955), and Forney (1955). Values of $\underline{a}$ smaller than 3, suggesting that the cube of the length increases proportionately faster than weight as the fish gets older, are rarer in the literature, but are reported at least by Forney (1955), Hennemuth (1955) and Kohler (1960). Deason and Hile have found sex differences in $\underline{a}$ values; Hennemuth (1955) and Forney (1955) give examples of differences in the length-weight relationship for 2 different years and Forney (1955) lists area differences for the same lake in the same year. Neturally the value of $\underline{b}$ will also vary in such circumstances.

Reeve and Huxley (1945) and Richards and Kavanagh (1945) discuss the theoretical basis and evolution of the simple allometry formula and point out the need for an adequate statistical approach to the fitting of it. Its unrestricted use has been criticized by Beverton and Holt (1957) on the basis that "the values of $\underline{b}$ and $\underline{a}$ found may vary within wide limits for very similar data, and are sensitive to what may be quite unimportant variations in the latter," and also since "the exponent $\underline{a}$ bears no simple relation to the dimensions of the animal unless it is exactly 3 ..... correspondingly, the constant $\underline{b}$ no longer has the simple interpretation of the constant $\underline{k}$" (equation 3). They conclude that the growth of North Sea plaice can be regarded as isometric, and use a simple cubic equation in their population model. For most fish species it would appear that radical departures from isometric growth are rare and that in many cases use of the simple cube law relation may solve more problems than it introduces. Further discussion of the problem may be found in Hile (1936), Reeve and Huxley (1945), LeCren (1951) and Beverton and Holt (1957).

D. DETERMINATION OF AGE

Age determination is fundamental to growth studies since we wish to determine exactly when a fish reaches a certain size as well as the rate at which change in size takes place. Three general methods of age determination have been adopted.

1. Petersen's Method

This is based on the polymodal nature of length frequency distributions of samples containing fish of more than one age group, and was originally developed by C.G.J. Petersen to determine growth of plaice from the Danish fisheries of the 1890's. The basic principles on which the method relies are as follows:

(1) If a fish population has a single restricted spawning season, then the length frequency of each age group tends to form a normal distribution.

(2) The modes of the length frequencies of successive age groups are separated along the length axis so as to be readily recognized.

(3) The separate modes represent the approximate mean sizes of the age groups present.

The usefulness of the method has been extended in recent years, notably through the development by Buchanan-Wollaston and Hodgson (1929) and Harding (1949) of procedures for dissection of the polymodal curve into its normal constituents.

The following limitations to Petersen's method have caused it to be replaced as a rule by more direct and reliable methods of age determination:

(1) Length frequency distributions of individual age groups do not always approach normality, usually because of a prolonged spawning season or non-random selection by the sampling gear.

(2) If spawning occurs more than once in a year or if young individuals of the same year-class but from different areas intermix, two or more modes may occur in the length distribution of one age group.

(3) The growth increments from year to year, particularly in older fish, may be insufficient to allow separate modes to be recognized, i.e. the length distributions of each age group overlap.

(4) The age at first capture by the sampling gear must be known.

(5) Various year-classes may be poorly represented either in the sample or in the population as a whole.

(6) The method cannot, as a rule, be applied to determine ages of individual fish.

Petersen's method has often been used in conjunction with skeletal structures (e.g. Hickling, 1933; Graham, 1934; Sandeman, 1957, 1961), particularly when the skeletal structures do not readily lend themselves to interpretation of age.

2. Skeletal Structures.

Determination of ages from skeletal structures is dependent on changes in growth rate or metabolism during certain periods of the year, these changes resulting in periodic markings on the hard parts of the organism. The structures most often employed have been scales and otoliths, though a number of other structures have been used, among them fin rays and spines, vertebrae and various bones of the skull and pectoral girdle. As the haddock growth study here presented is based on measurements of growth zones in scales, further discussion will be limited to the scale method of age determination.

Fish scales are classified into 5 types: cosmoid, ganoid or rhomboid, placoid, cycloid and ctenoid.

Cosmoid scales, consisting of an inner layer of compact lamellar bone, a second layer of spongy vascular bone, a third layer of dentine-like cosmine and a fourth thin outer layer of enamel-like vitrodentine, are found only in fossil crossopterygians and lungfishes. True ganoid scales consist of an inner layer of lamellar bone, a middle dentinal layer and an outer covering of many layers of ganoine. In living fishes they occur in modified form in the Acipenseridae (sturgeons) and Polyodontidae (paddlefishes) among other groups. Placoid scales, consisting of a flattened basal plate and a protruding spine of dentine covered by vitrodentine, are found mainly in the Chondrichthys (sharks, rays and chimaeras). Cycloid and ctenoid scales, found in teleostean fishes, contain a basal layer known as the lamellar layer or fibrillary plate, and a surface layer referred to as the bony or hyalodentine layer. Both types are generally thin, flexible and transparent. They are differentiated mainly by the fact that ctenoid scales, found in spiny-rayed teleosts, have a number of spines or "ctenii" at the posterior edge of the scale, whereas in cycloid scales, found in soft-rayed teleosts, there are no such structures.

The internal structure of both cycloid and ctenoid scales is basically the same. At the center of the scale is found a clear area known as the "focus" or nucleus" which probably represents growth in the larval stages. Around the nucleus are found rows of more or less concentric striations known as "ridges", "circuli" or "striae", containing individual raised portions known as "sclerites", separated by radial grooves (radii or sulci) directed toward the focus. The exact form of the periodic markings on scales may vary from one species to another, but are very similar for related species. For example, cod and haddock scales are similar in that the periodic markings are evidenced by variations in size and spacing of sclerites, whereas in the herring they are characterized by distinct breaks in the rows of closely spaced sclerites. When reading, the periodic markings are differentiated into zones of "fast" and "slow" growth; thus age is interpreted by assigning one "fast" zone plus one "slow" zone to each year of life. The situation may be complicated by the presence of "secondary" or "check" zones, slow growth zones formed at some time other than the time of "annual" zone formation, and usually attributed to adverse environmental conditions or major physiological phenomena such as spawning.

Scales are of various sizes and shapes depending on species and on the area of the fish from which the scales are taken. Irregularities are frequently observed, one of the most common being "regeneration", when the clear nucleus and a varying part of the area surrounding it are replaced by an expanded central area containing no sclerites and having a granular appearance and irregular outline. Detailed descriptions of the embryology and histology of fish scales may be found in Thomson (1904), Taylor (1916), Paget (1920), Neave (1940) and Van Oosten (1957).

The age determination of fish through use of scales, though brought to fruition mainly during the present century, is by no means a recent development in natural history. Thompson (1942) refers to the fact that Aristotle was shown by Greek fishermen that the age of the purple Murex could be estimated by counting the whorls and ridges of the shell, and that the age of scaly fishes could be estimated by the size and hardness of the scales. The invention of the microscope made detailed scale studies possible. Thomson (1904) refers to a description of the microscopic appearance of a fish scale by Borello (1566). Van Oosten (1929) notes that further descriptions were written by Fabricius (1618, 1621, 1625) and Hooke (1677). He also refers to the first record concerning growth of scales as contained in a letter by Leeuwenhoek dated July 25, 1684, and describing the microscopic appearance of eel scales as follows: "although all the scales (of an individual) are not of the same shape, I have yet observed, in many of them as I judged, the same number of Circular lines. From whence I conclude that every year the scale encreased one Circular line; and by consequence, the number of these Circular lines, being seven; the Fish must have been seven years old." Correlations between the appearance of the scale and fish age and growth were also made by Réamur (1718), Agassiz (1834), Mandl (1839), Vogt (1842), Steenstrup (1861), Hintze (1888) and others. Detailed reviews of the early scale literature may be found in Thomson (1904), Turrell (1911), Taylor (1916), Creaser (1926), Van Oosten (1929) and Graham (1929b).

The foundation for modern scale studies was laid by Hoffbauer (1898, 1900), who made a critical examination of the scale method, and tested its validity by reading ages and observing the appearance of the edge of the scales of pond carp at different seasons of the year. After 1898 the scale method became firmly established and was widely applied in growth studies of many marine and freshwater species. Recently, it has been replaced for many species by age determination from otoliths, as it has been found that annuli may be missing from the scales of old fish (Saetersdal, 1953) as well as being difficult to interpret at the older ages (Rollefsen, 1933).

A good deal of work has been devoted to testing the validity of age determination from scales. Most of the procedures are included under one of the following categories.

(1) Marking experiments

Fish are tagged, released, and recaptured with the scales being examined at release and again at recapture.

(2) Aquarium experiments

Scales are taken and examined at intervals during a prolonged period of captivity in order to determine exactly when the periodic zones are laid down. Experiments to determine the causes of zone formation are conveniently carried out at the same time.

(3) Agreement with Petersen's method of age determination

Observations may be made on scales of a predominant size group in the commercial catches. These are repeated from year to year, and it is seen that the number of well defined rings in these structures increases by one each year.

(4) Use of marked scales

Abnormal scale characteristics may occur early in the life of a particular year-class of fish. This year-class may then be identified throughout later life, and the addition of rings followed from year to year. Scales may also be artificially marked. Hiyama and Ichikawa (1952) have used lead acetate, and Fry *et al.* (1960) lead versenate to accomplish this.

(5) Other skeletal structures

This is not strictly applicable as evidence of the validity of the scale method, but is useful in evaluating its possibilities in comparison with another structure whose reliability has already been tested by other means. Thus if otoliths have been proved reliable, they may be used in testing the validity of scales.

(6) Seasonal changes in the edge of the scale

By examination of scales taken at different times of the year, it can be determined approximately when the various periodic markings are laid down; thus the time to complete one ring can be ascertained.

Many of the above procedures are of course applicable also to validity tests of other skeletal structures.

3. Marking and Recapture

This is the most direct and positive way of determining age and consists of tagging or marking in some other way a fish of known age. The fish is then released, and when and if recaptured, there can be no doubt as to its age, providing the original age determination is correct. The method is obviously not applicable to everyday work because of the time and expense involved and because of the low percentage of returns normally expected. Its chief value thus lies in checking ages determined by other means. An example is the work of Sund (1922) on the saithe or coalfish (*Gadus virens*) of northern Norway.

E. THE AGE-LENGTH RELATIONSHIP

The length or weight data for a growth study may be obtained by making repeated measurements on the same individuals over long periods of time, or by making measurements on samples taken at intervals from the population. The former method is applicable only to aquarium studies and sometimes to tagged fish. In any case it can only be applied in determining the growth history of individuals, though aquarium studies are useful in observing growth under varying conditions.

Most growth studies of marine species have been made through use of measurements made on samples taken at successive intervals by some type of sampling gear, thus permitting evaluation of the average growth history of the population. Such data normally cannot be used to determine the growth history of individuals.

Errors may occur in the growth curve for a fish population if the sampling gear is selective for certain sizes of fish, or if their behaviour at some stage of their life history is such that they avoid or otherwise escape capture by the sampling gear. Gill nets take only fish in a certain size range; otter trawls and hook and line gears do not generally take very small fish; the most active members of a population may be able to avoid trawl gear; depth stratification by size groups may allow some size groups to escape capture, or the fish may be inaccessible to the gear for various reasons at certain periods in their life history. Choice of the most suitable sampling gear will depend on the behaviour of the species and the nature and extent of the data required.

In comparing average growth rates from year to year and one area to another, the time of collection of samples must be taken into account. Samples may be taken at various points in the seasonal growth cycle, thus at various stages in annulus formation, making it necessary to equate average lengths to a common time base within any year in order to make realistic comparisons. This problem may be eliminated by making collections for age and growth purposes at the same time each year.

Fish exhibit "indeterminate" growth in that they continue to grow even in extreme old age. For this reason, growth curves in length or weight draw toward the "ultimate" or "limiting" size very slowly. The type of curve used to represent growth is a time diagram. The typical curve of growth in weight is an assymmetrical S-shaped or sigmoid curve. Thus growth in weight is at first slow, then becomes faster and faster until an inflection point is reached. Beyond this point the growth rate slows more and more as time goes on. Curves of growth in length usually take the form of a decaying exponential, i.e. without an inflection. Such curves describe the velocity of change in length or weight, or rate of growth. They do not necessarily describe the precise mode of growth of a species, but are the simplest mathematical curves which fit mean lengths or weights at the end of each successive year of life or some other point in the yearly cycle of growth. They are adequate for determination of average growth rates.

It is useful to be able to describe the growth of fish in mathematical terms in order that the data may be readily incorporated in mathematical formulations of yield from a given fishery. One may choose from a number of mathematical expressions, some of which are purely empirical, while others claim to have a physiological basis.

Beverton and Holt (1957) point out that weight as a function of age may be expressed on a purely empirical basis by means of the general polynomial

$$w_t = a_o + a_1 t + a_2 t^2 + \; \dots \; a_x t^x \; \dots \; a_r t^r = \sum_{x=o}^{r} a_x t^x \qquad (6)$$

where w_t = weight at age t
and a_o, a_1, etc. are constants.

Such an expression may be made to fit any number of points by using a sufficiently large value of r. However the constants are subject to change, depending on which points are used, and will change if additional points are added and the equation fitted again.

It may sometimes be possible over a limited range of ages to represent growth linearly. A yield equation based on linear growth in weight has been developed by Hulme, Beverton and Holt (1947), and applied to the Japanese "Buri" (Seriola quinqueradiata)fishery by Doi (1951) who uses the relation

$$w_{(x)} = m(b + x) \qquad (7)$$

where $w_{(x)}$ = average weight at age x,
and m and b are constant.

Thompson and Bell (1934), using age and weight data over a limited range of ages, have described growth in weight of Pacific halibut as increasing by a constant percentage of the preceding year's growth in each year of life. Beverton and Holt (1957), regard this as an approximation of exponential growth, as described by Ricker (1944) and Doi (1951). The latter describes the general exponential growth equation as

$$w_{(x)} = me^{a(x-a)} \qquad (8)$$

where m and a are constant,
and e is the natural logarithmic base.

Again, such an expression is purely empirical and should not be extrapolated beyond the range of the data used to obtain it.

Ottestad (1933) suggested that growth in weight could be represented by the symmetrical sigmoid (ogive of the normal curve). Ottestad regarded growth as a complex process due to a "whole chain of causes," and considered that mathematical formulations should aim at providing a means of adequately describing growth without necessarily attempting to explain the causes underlying it. The method is criticized by Beverton and Holt (1957) because of its empirical basis and since symmetrical growth curves are seldom found in fish populations.

Another symmetrical formulation of growth, the autocatalytic or logistic equation, was developed by Robertson (1923), and has found limited use (e.g.Yoshihara, 1951). It is based on the differential equation

$$\frac{dw}{dt} = kw(A-w) \qquad (9)$$

which may be written as

$$\frac{dw}{dt} = Akw - kw^2 \qquad (10)$$

where w = weight, t = time, and k and A are constants. Equation (10) implies that the processes tending to increase weight are a function of the weight itself, while those tending to decrease weight proceed at a rate proportional to its square. Solution of the differential equation gives

$$w_t = \frac{A}{1 + e^{-Akt}} \tag{11}$$

In order to render the equation asymmetrical so that it may more closely describe actual curves of growth, a polynomial in _t_ may be introduced in the exponent (Pearl and Reed, 1923) to obtain

$$w_t = \frac{A}{1 + be^{-(k_o + k_1 t + k_2 t^2 + \ldots k_n t^n)}}$$

Such a step has no biological significance; neither does there seem to be any physiological evidence to support the implications of equation (10).

Weymouth and McMillin (1930) and Weymouth, McMillin and Rich (1931), with reference to the work of Minot (1891, 1908), give physiological significance to a curve originally developed by Gompertz (1825) for use in analysis of human mortality. They regard growth as an additive process which is constantly decreasing, and found the following relation to apply to relative growth in length of the Pacific razor clam (Siliqua patula):

$$P_L = \frac{d \log L}{dt} = \text{relative growth rate} \tag{12}$$

$$\log P_L = a - kt$$

where a = initial growth rate, k = rate of decline and t = time.

Thus $$\frac{d \log L}{dt} = e^{a-kt} \tag{13}$$

When integrated, this becomes:

$$L = Be^{-ce^{-kt}} \tag{14}$$

where B, c and k are constants.

The equation has been criticized (Beverton and Holt, 1957) on the basis that no physiological significance has been attached to the three constants, that available evidence points to the fact that growth is not merely additive so that breakdown of body material must be taken into account, and that the curve has an inflection point. The latter is not often seen in length curves and Beverton and Holt (1957) suggest that the inflection in the data of Weymouth and McMillin (1931) is so near the origin that it could be due to a qualitative change in the growth pattern in early life. Thus although the Gompertz curve may provide an adequate asymmetrical formulation for description of growth, it again is largely empirical.

Brody (1927, 1945) developed two separate equations for description of growth, one to be used below the inflection point, and the other above it. His equations, and the following one by von Bertalanffy (1934, 1938, 1949, 1957) utilize the concept that growth is the result of processes tending to increase the weight of an organism minus processes tending to decrease it. Brody regards the lower portion of the weight growth curve (origin to the inflection point) as the "self - accelerating" phase, and the upper portion (inflection point to the asymptote) as the "self - inhibiting" phase. For the first portion of the curve he writes

$$\frac{dw}{dt} = kw \qquad (15)$$

which on solution gives

$$w_t = Ae^{-kt} \qquad (16)$$

where w = weight, t = time, and A and k are constants. This represents simple exponential growth.

For the upper portion of the growth curve the equation is

$$\frac{dw}{dt} = k(A - w) \tag{17}$$

which on solution gives

$$w_t = A - Be^{-kt} \tag{18}$$

Brody's equations, in effect, allow the logistic curve to be fitted in two sections, with a good deal of freedom in positioning the inflection point. However, the implication that there is a qualitative change in the manner of growth at the inflection point is not borne out physiologically.

Following its application to North Sea haddock and plaice by Beverton (1954) and Beverton and Holt (1957) the equation developed by von Bertalanffy (1934, 1938, 1949, 1957) has received widespread attention. The equation has a physiological basis in that von Bertalanffy has regarded growth as the result of the processes tending to increase mass (anabolism) and those tending to decrease it (catabolism), all factors operating continuously. His work has been thoroughly reviewed by Beverton and Holt (1957), from which the following brief summation is taken.

The rate of change in weight of an organism, dw/dt, is expressed in terms of the body weight, w, by some powers n and m as follows:

$$\frac{dw}{dt} = Hw^n - kw^m \qquad (19)$$

where H is the coefficient of anabolism and k is the coefficient of catabolism. From general physiological concepts, von Bertalanffy assumes that the rate of anabolism will be proportional to the resorption rate of nutritive material, thus proportional to the magnitude of the resorbing surfaces, while the rate of catabolism may be taken as proportional to the total mass being broken down per unit time, giving

$$\frac{dw}{dt} = Hs - kw \qquad (20)$$

where s is the effective physiological surface of the organism, H becomes the rate of synthesis of mass per unit of physiological surface and k the rate of destruction of mass per unit mass.

If it is further assumed that fish grow isometrically and have a constant specific gravity, then

$$s = pl^2 \qquad (21)$$

and $$w = ql^3 \qquad (22)$$

where p and q are constants.
By expressing (20) in terms of l, substituting (21) and (22) for s and w, transforming, and integrating, we obtain

$$l_t = \frac{E}{K} - \left(\frac{E}{K} - L_o\right)e^{-Kt} \qquad (23)$$

where L_o is the length when t (age) = 0

As t approaches ∞, l_t approaches $\frac{E}{K}$ (the asymptotic length). This theoretical maximum length is denoted by L_∞; thus (23) becomes

$$l_t = L_\infty - (L_\infty - L_o)e^{-kt} \qquad (24)$$

Substituting w in terms of l in (24) gives the equation for growth in weight

$$w_t = \left\{W_\infty^{1/3} - (W_\infty^{1/3} - W_o^{1/3})e^{-kt}\right\}^3 \qquad (25)$$

where W_∞ and W_o are the weights at lengths L_∞ and L_o.

By putting $l_t = w_t = 0$, at $t = t_o$, (24) and (25) may be written in a more useful form, viz.

$$l_t = L_\infty\left\{1 - e^{-k(t - t_o)}\right\} \qquad (26)$$

and $$w_t = W_\infty\left\{1 - e^{-k(t - t_o)}\right\}^3 \qquad (27)$$

A geometrical interpretation of growth in length similar to that of von Bertalanffy's equation was developed independently by Ford (1933) and Walford (1946).

Recently, Parker and Larkin (1959) have suggested use of the parabolic function

$$\frac{dw}{dt} = kw^x \ (x<1) \tag{28}$$

to describe growth, on the basis that many physiological rates have been shown to be related to weight in such a manner. It is seen that if x is unity the equation becomes a simple exponential.

The approach to mathematical description of growth and the choice of a suitable growth equation must depend on the purpose for which such mathematical formulation is required and on the nature of the observed data. Medewar (1945) regards the growth equation's chief function as facilitation of the analysis of growth curves and doubts whether "any one concretely specified function can be a characteristic expression for biological growth in general." He further considers that no biological significance can be attached to the particular form such a function happens to take. On the other hand it does seem desirable, particularly in fisheries biology, to choose an equation which is based on biological principles, since such an equation can logically be extended beyond the range of the data used to obtain it.

F. GROWTH VARIATIONS, THEIR CAUSES, AND EFFECTS

The exact manner in which fishes grow is more complex than shown by yearly means of size at each age. Growth is the result of metabolic activities which may be accelerated or retarded by various physical and biotic environmental factors. Seasonal, yearly and regional variations in growth are common and there may, within the same species, be wide variations in length or weight of individuals of the same age.

Since growth is ultimately dependent on the amount of food consumed and utilized by the fish, any factors which affect the rate or frequency of feeding and the amount of food consumed will affect growth. Temperature has been shown to affect both rate of food intake (Hathaway, 1927; Baldwin, 1956;) and rate of digestion (Markus, 1932). The general result, at least within the range of temperature tolerance, is that low temperatures decrease both rate of feeding, rate of digestion, and ultimately, growth (Kohler, 1964). Decline in growth from south to north (or at least from warmer to cooler waters) in the northern hemisphere has been demonstrated for some species (Jónsson, MS, 1964; May et al, MS, 1964). On the other hand, Baldwin (1956) found that the ratio of weight gain to food consumed decreased with rising temperature, indicating that at high temperatures a lesser proportion of food was utilized in the synthesis of new tissue.

Although temperature is the only physical factor which has received general attention, feeding and growth are undoubtedly affected as well by other features of the physical environment. Darnell and Meierotto (1962) suggest that light, through its influence on activity, may affect the rate of digestion, and further that "the rate of movement and digestive breakdown of food materials may be influenced by a host of unknown factors including various psychological phenomena." Of course the distribution, and thus the availability, of the particular food organism or organisms will also be affected by a number of physical factors including temperature, salinity, light and water movements.

Apart from any inherent variation within the species, (sex variations are very common), various biotic factors are also of importance in regulating growth. Primarily these are density of the species and density of prey. Abundance of prey has been found to affect rate of food intake (Ivlev, 1961), and amount of food consumed to affect rate of digestion (Pierce, 1936; Tanaka, 1955). The rate of food intake may also affect rate of food passage as food may tend to be passed more quickly through the digestive tract, whether or not fully digested, as the fish feeds more frequently (Dawes, 1930).

The availability of food organisms will be dependent on the density of the predator species. As the predator species increases, increased competition for food will result in a decreased rate of growth, and vice versa. This has been clearly demonstrated for North Sea Plaice as reviewed by Graham (1956) and is also indicated for haddock of the same area (Raitt, 1939).

Growth may often be influenced by man due to fishing activity. If a dense stock is underfished growth may be slow, and catches may be mainly of small fish. On the other hand, overfishing may cause the growth rate to increase, but so few fish will attain old age that catches may still consist mainly of small fish. Thus both "overpopulation" and "overfishing" may be undesirable in commercially exploited species. Further, assuming a size-selective gear, varying rates of growth may affect mortality by causing fish to enter the exploited phase of their life history at different ages.

Growth variations affecting the fish population as a whole are a reflection of changing conditions in the population, and must be taken into account in any fisheries management program. On the other hand individual growth variations, causing fish of the same age to be of different sizes, do not seriously impair the results of dynamical studies based on average growth formulae, providing the mean lengths or weights of the age groups are unbiased estimates for the whole population.

It is of interest to note that individual variations in size, particularly at the end of the first year of life, may tend to be minimized in later years due to a tendency for the smaller young fish to grow more rapidly than the larger young fish during later years of life. This is termed "growth compensation". Such an effect has been observed by many authors, including Gilbert (1914), Van Oosten (1929), Ford (1933), and

Hile (1941). A similar process is described by von Bertalanffy (1949) who defines the "equifinality of growth" as the process whereby the same final state results from different initial sizes or after temporary suppression of growth. Ricker (1958) describes the effect as a negative correlation between the increments in size in successive years of life among the fish of a given year-class. Positive correlation or the reverse of growth compensation, also occurs. Taylor (1958) and Jones (1960) have shown that for haddock, fish which begin life as fast growers tend to retain this advantage. Ricker (1958) suggests that such an effect be termed "growth depensation."

Apparent changes in growth, in that older individuals of a given year-class appear to have grown less at a certain age than younger individuals of the same year-class, have been found in many studies employing skeletal structures to determine growth by back-calculation of sizes at annuli. This has come to be known as "Lee's Phenomenon", and is discussed in detail in a later section.

II. THE LITERATURE OF BACK-CALCULATION OF GROWTH FROM SCALES

A. UTILITY OF THE METHOD

If some detectable relation exists between growth of the fish as a whole and growth of its scales, if this relation can be described in mathematical terms, and if annular periods of growth are recognizable in the scale then the relation between body growth and scale growth may be used to determine growth of the fish during each year of life. The fundamental assumptions on which the procedure is based are dealt with more thoroughly in succeeding sections.

If back-calculations of growth from scales (or for that matter from any other structure) can be made, a number of advantages exist over the conventional method of describing growth by the relation of ages and lengths at capture. These may be enumerated as follows:

(1) The growth history of individual fish may be traced from the first year of life to capture. Thus a great deal of information may be obtained from a relatively small sampling.

(2) If samples are collected from a commercial fishing gear it is likely that the youngest age-groups of

the population will not appear at all in the sample, and the youngest age groups that do occur will not be sampled randomly because of the selective action of the gear. In such cases the early growth history can only be determined by back-calculation.

(3) Since fish in temperate regions are normally growing fastest during the period (late spring to autumn) in which field collections are most likely to be made, scales and length data must be taken at the same time of year in order for data from different areas and years to be strictly comparable. However, in back-calculation, the end of each year of growth can be delimited, and comparable calculations made.

(4) In the back-calculation method, since growth in each year of life for each fish can be determined, there will be no "weak" points on the growth curve due to absence or scarcity of some year-classes in the population.

(5) Through back-calculation, it is possible at the beginning of an investigation, to determine size at age in previous years during which collections might not have been made.

B. ASSUMPTIONS OF THE METHOD

In essence the scale method of determining growth rests on the premise that growth of the fish and growth of the scales are related in some way. Various aspects of relative growth in general and changes of form (correlated with differential relative growth), are dealt with by a number of authors, and comprehensive reviews may be found in Huxley (1932), Thompson (1942) and Clark and Medawar (ed., 1945).

For many species it has been noted that certain organs increase in relative size with the absolute size of the body which bears them, and further that for long periods of the life history this differential growth proceeds at a constant rate, and may be described by a formula previously mentioned (4), i.e.

$$y = bx^a$$

$$\text{or } \log y = \log b + a \log x$$

where y is the size of the body part or organ, x is the absolute body size and b and a are constants.

This type of growth has come to be known as allometry (positive or negative depending on the value of a) after Huxley and Teissier (1936). Huxley (1932) claims to have been the first to point out (in 1924) the general applicability of the above formula in describing differential growth. He gives the name "constant differential growth ratio" to the constant a. In the special case of $a = 1$, when the allometric formula becomes

$$y = bx \qquad (29)$$

growth is said to be isometric. Both the allometric and isometric formulae have been used in describing the relation between fish growth and scale growth.

The basic assumptions of the scale method, how these were developed, and evidence from many early workers bearing on their validity are reviewed by Van Oosten (1929). He lists the fundamental assumptions as follows:

(1) that the scales remain constant in number and (retain their) identity throughout life,

(2) that the annual increment in the length (or some other dimension) of the scale maintains, throughout the life of the fish, a constant ratio with the annual increment in body length, and

(3) that the annuli are formed yearly, and at the same time each year.

These assumptions have been validated for many species in the voluminous scale literature of the past 50 years. The use of lateral line and other scale counts to distinguish species shows that scales remain constant in number throughout life. The structural identity of the central area of scales from young and old fish proves that scales retain their identity. Agreement among the growth histories of different age groups of the same year-class, and among different year-classes, for the relative amount of growth in certain years has proved the correlation between fish and scale growth. Both direct and experimental evidence has attested to the suitability of the annulus for determining age. One or more of the assumptions are reviewed in more detail by Thomson (1904), Lea (1911), Winge (1915), Lee (1920), Van Oosten (1923, 1929), Graham (1929), Hile (1941) and Rounsefell and Everhart (1953), among many others.

C. HISTORY AND APPLICATIONS

The literature of back-calculation of growth from scales is diverse and very extensive. The following review is not intended as a complete literature survey, but is rather an attempt to trace the evolution of the method and to emphasize various points bearing on its applicability and accuracy. More comprehensive reviews are given by Taylor (1916), Lee (1920), Creaser (1926), Van Oosten (1929), Graham (1929), Mohr (1927, 1930, 1934), Saetersdal (1953) and Whitney and Carlander (1956), among others. The method has been extensively applied to freshwater fishes, and most of the pertinent papers in this field are listed by Carlander (1953).

1. Direct Proportion or Dahl-Lea Method

Many of the early workers on scales, as indicated in a previous section, recognized that the scales increased in size as the fish grew larger. Hoffbauer (1899) and Walter (1901), both working on pond carp, showed that scale growth bore some relation to growth of the fish as a whole. Thomson (1904) made various measurements of the growth zones in some Gadidae, but was more concerned in showing the annual nature of the zones, and did not use these measurements to compute length. Creaser (1926) refers to Johnston (1905) as the first to "calculate length of a fish for each year of its life by a comparison of the proportional width of the yearly areas on the scale". Dahl (1907) showed that the growth history of individual herring was recorded on their scales, and further that the growth pattern, as indicated by the scale, could be used to distinguish different types or "tribes" of herring (e.g. spring and autumn spawners).

In investigating the possibility of using scales to demonstrate the early growth history of individual fish, Lea (1910) found that in herring a constant ratio existed, over a wide range of fish lengths, between length of a particular scale and length of the scale covered part of the body. He further determined that the scales between myomeres 25-29 bore a constant ratio to total fish length, and postulated a linear relation between scale length and fish length for scales selected from a particular body region. On the basis of Lea's work, the simple proportionality formula for back-calculation of fish lengths was developed. It was applied by Dahl (1910) to scales of salmon and trout from Norway, and by Lea (1910, 1911) to Norwegian herring scales, and has come to be known as the Dahl-Lea formula. Its form is as follows:

$$\frac{V}{L} = \frac{v_n}{l_n} \qquad (30)$$

or

$$\frac{v_n}{V} = \frac{l_n}{L} \qquad (31)$$

which when solved for l_n gives:

$$l_n = \frac{v_n L}{V} \qquad (32)$$

$$\text{or} \quad l_n = \frac{L}{V} v_n \tag{33}$$

where l_n = length of fish at annulus n,
v_n = length of scale at annulus n,
L = length of fish at capture,
and V = length of scale at capture.

Equation (32) implies that the ratio between the size of a particular annulus and the size of the scale should be the same for any scale on the same fish. From (33) we see that for a particular scale at any time the ratio of attained sizes of fish and scale is the same. Since the formula describes a proportional relationship between attained sizes, these assumptions hold even though all scales on the fish are not of the same size. The relationship between growth of body and scales is described by a straight line passing through the origin in a cartesian coordinate system, i.e. of the form:

$$L = bV \tag{34}$$

where L = body length,
V = scale length,
and b = a constant (slope of the regression line).

It may be pointed out that (34) represents isometric growth between scales and body, being a special case of the general allometric formula

$$y = bx^a$$

where the exponent $a = 1$.

Some authors have determined the body-scale relationships of various species, and shown them to be related in direct proportion, or nearly so. Hjort (1914) gives measurements of fish length and length of scales from the lateral line region below the third dorsal fin of 16 coalfish and 8 cod, and shows the relationship in each case to be close to direct proportion. Rich (1920) described a proportional relationship between fish length and anterior scale radius for chinook (spring) salmon. Thompson (1923, 1924) showed that haddock scales taken below the third dorsal fin grew in close proportion to the body as a whole. Creaser (1926) kept bluegills (*Helioperca incisor*) in aquaria until a growth increment of 10 mm was attained, and showed that for a corresponding scale increment of about 0.2 mm there was little deviation from direct proportion between fish and scale growth for scales from different areas of the body. Hile and Jobes (1941) showed that standard length and anterior scale radius of yellow perch, Perca flavescens (Mitchill), in Saginaw Bay, Michigan, were related in direct proportion for fish lengths above 101 mm. Jobes (1952) described the same type of relation for the same species in Lake Erie. Smith (1955) showed that the relation between scale diameter and body length was in direct proportion for Kamloops trout, Salmo gairdneri Richardson, over 4.5 cm in fork length.

On the other hand, many authors have assumed scale length and body length to be related in direct proportion without actually determining the body-scale relationship (e.g. Parsons, 1951), often because of insufficent material to construct the relationship. It has frequently been found that assuming a simple proportional relationship leads to errors in back-calculated lengths (as compared with observed or "empirical" lengths) because of disproportionate growth of body and scale. Some authors have considered such errors to be negligible in relation to others and thus have used direct proportion (Van Oosten, 1929; Deason and Hile, 1947).

2. Straight Line Regression with Intercept

Recent reviews of the back-calculation methods (Schuck, 1949; Whitney and Carlander, 1956) have stressed that the body-scale regression rarely passes through the origin, though it may often be described by a straight line having an intercept on either the fish length or scale length axis. Assumption of direct proportion in such cases would lead to errors in calculations of length.

Body-scale regressions which do not pass through the origin imply that the body length-scale length ratio (L/V) is not constant throughout the life of the fish. If a positive intercept on the fish length axis is obtained, the ratios of L/V are decreasing with increase in size, i.e. large fish tend to have relatively larger scales than small fish. A negative intercept on the fish length axis denotes increasing values of L/V as the fish and scale become larger, i.e. the scales tend to be relatively smaller in large fish than in small fish. Relationships of the former type are more common, and if growth is calculated by direct proportion without taking the actual body-scale relationship into account, calculated lengths at annuli decrease regularly when calculated from older and older fish. This is an error of the Lee's Phenomenon type, as discussed in a following section.

Ottestad (1938) refers to a positive correlation between L and L/V as indicating that large fish have relatively smaller scales than smaller fish, i.e. that the L-intercept is negative. However, a positive correlation between L and L/V also occurs at zero L-intercept and could occur even if the L-intercept were positive (Ricker, pers.comm.), and therefore cannot be used to define the L-intercept's sign. As further evidence of a positive correlation between L and L/V Ottestad refers to the finding of Lee (1920) that younger fish at any size tend to have smaller scales than older fish at the same size. Ottestad's reasoning on this point is repeated by Saetersdal (1953). Lee's observation, also made by Molander (1918) and Huntsman (1918), leads to the conclusion that in fast growing fish the scales are not developed to the same degree as in slow growing fish. However, there seems to be no reason to connect this fact with the correlation between L and L/V, much less to accept it as evidence that such a correlation is positive.

A straight line relation between fish and scale sizes which does not pass through the origin will be described by an equation of the form

$$L = bV + C \tag{35}$$

where the constant C represents the intercept (positive or negative) on the fish length axis. If this intercept is positive, C is subtracted from each value of L, and the simple proportionality formula (31) is modified from

$$\frac{v_n}{V} = \frac{l_n}{L}$$

$$\text{to} \quad \frac{v_n}{V} = \frac{l_n - C}{L - C} \tag{36}$$

$$\text{or } l_n - C = \frac{v_n}{V} \; (L - C) \tag{37}$$

which when solved for l_n becomes:

$$l_n = C + \frac{v_n}{V} \; (L - C) \tag{38}$$

Thus it is seen that attained sizes of fish and scale are no longer proportional, though increments of the two are so.

3. Lee's Phenomenon

Lea (1910) recognized that the growth of fish and scales could not always be represented by simple proportion, and in fact pointed out that the ratio of L/V decreased with age. However, he considered that simple proportion was so closely approximated that errors in growth calculations using this relation were negligible. On the other hand, Sund (1911), on applying the simple proportionality formula to sprat (Clupea sprattus), found that lengths at age back-calculated from scales did not agree with those determined by actual observation. Lea (1913) refers to Sund as the first to describe such disagreement between calculated and empirical lengths, later referred to as "the phenomenon of apparent change in growth rate" by Lee (1912). In essence this refers to the fact that there is a progressive decrease in back-calculated lengths at age when calculations are made from successively older fish. Thus there is an apparent progressive increase in growth rate from the older to the younger year-classes. Lee (1912) reviewing the trout and herring data respectively of Dahl (1910) and Lea (1910, 1911) showed that the phenomenon occurred when the data were arranged by ages in a single calendar year, and demonstrated it also for haddock. It has since been described for a large number of species and has come to be known as "Lee's Phenomenon".

Many explanations for the phenomenon have been proposed, and these are summarized below.

(1) The simplest explanation of the phenomenon is that there actually was an increase in growth rate prior to the collection of each sample. In most cases this is extremely unlikely. Also the phenomenon has been demonstrated for the same year-class during successive years of life by Menzies and Macfarlane (1926a and b) for salmon and by Jones (1958) for haddock.

(2) Use of the simple proportionality formula when the body-scale relationship is not actually in direct proportion will cause errors of the Lee's phenomenon type. This may be seen by transforming equation (38) as follows:

$$
\begin{aligned}
l_n &= C + \frac{v_n}{V}(L - C) && (38) \\
&= C + \frac{Lv_n - Cv_n}{V} \\
&= \frac{VC}{V} + \frac{Lv_n - Cv_n}{V} \\
&= \frac{Lv_n}{V} + \frac{C(V - v_n)}{V} \\
&= \frac{Lv_n}{V} + C\left(1 - \frac{v_n}{V}\right) && (39)
\end{aligned}
$$

The second term in equation (39) which was developed by Lea (1938), is seen to become progressively greater as V (scale length) increases, thus compensating for the progressive decrease in the values of l_n as calculated from the simple proportionality formula. The magnitude of the bias introduced by the latter formula will depend on the magnitude of C.

The constant C has often been regarded as the length of the fish at time of scale formation. Graham (1929b) refers to Meek (1916), Fraser (1916, 1917), Molander (1918) and Lee (1920) as having all "independently realized the necessity of correcting for the time at which the scale was first formed." Fraser (1916, 1917) found that if lengths calculated by direct proportion were corrected by a value representing the average fish length at time of scale formation, then Lee's phenomenon did not appear. Lee (1920) expressed the correction in the form of equation (38), again regarding it as the body length at time of scale formation. In later years the same biological interpretation of the correction factor has been given by Merriman (1941), Carlander and Smith (1944), Rounsefell and Everhart (1953) and many others. However, Van Oosten (1929) considered that late scale formation was not responsible for Lee's phenomenon in lake herring, reasoning in part that growth calculations assume a fixed relationship between growth of body and scale after the first year of life irrespective of the relation during the first year, and that a "rapid proportional increase in the length of the scale during the first year of life counteracts late scale formation in its effect on the computations of length." Thus Lea (1938) pointed out that the intercept in equation (35) should not be invested with any biological significance. Schuck (1949) emphasized that fish size at time of scale formation and the relation of fish size and scale size during the first year were of no importance in back-calculating lengths at various annuli.

It is obvious of course that a fish has attained some length at the time the scales form, and that early in life the scales must grow proportionately faster than the body in order to overlap. When the scales are fully formed the degree of overlapping may be expected to remain approximately constant; thus the growth of the scale relative to the growth of the fish must decrease greatly. In any case an intercept determined by extrapolation of the body-scale relationship must be regarded as purely empirical. Indeed, attempting to attach biological significance to a negative intercept on the fish length axis (as is sometimes found) would lead to the meaningless conclusion that the scales had attained some length at zero fish length.

As noted at the beginning of this section, wrong use of the simple proportionality formula to back-calculate lengths when this formula does not actually hold will lead to errors of the Lee's phenomenon type. However, due to other sources of error, it does not necessarily follow that calculations based on an actual body-scale relation for the particular data will eliminate Lee's phenomenon. Van Oosten (1929) and Hile (1936) showed that use of an equation with an intercept failed to eliminate such discrepancies in calculated growth.

(3) Errors in age reading due to the presence of "check zones" or "accessory annuli" will of course lead to errors in growth calculations. Lee (1912) regards such errors as especially likely in older fish. However Lea (1913) points out that the presence of such zones cannot affect growth calculations for the early years in the scale since they do not affect the relation between the size of an early annulus and the total size of the scale. Taking the first annulus as an example he notes that the decrease in calculated length "during several years can only be effected.....when the

number of these (check zones) inside the first real ring increases with age," and points out the absurdity of such a supposition. However it is conceivable that the phenomenon might be partly explained in this way for old fish, and Buchanan-Wollaston (1924) holds that in old fish it may be explained by the presence, in the scales commonly used, of false rings not found in all scales on the same fish.

(4) If for some reason the inner part of the scale contracts or shrinks to some extent as the fish becomes older, errors in growth calculations will certainly appear. The hypothesis of scale shrinkage was put forward by Lee (1912) as one possible explanation of the phenomenon of apparent change in growth rate. An effect of this sort is known to occur in salmon, where part of the scale edge is absorbed during the maturation process, producing a definite mark on the scale. However no evidence for scale shrinkage occurs for marine fishes, either continuously throughout life or during maturation. In fact Lea (1913) points out that even if some such process did operate at maturation, the effect would be to increase the ratio of v_n/V in the early years thus causing the reverse of Lee's phenomenon. He also presents evidence to show that there is no tendency for herring

scales to shrink with age.

Even though scale shrinkage is ruled out as a possible cause of the phenomenon, it has been shown by Lee (1912), Thompson (1923) and Jones (1958) that mean scale sizes at annuli are smaller in older age groups. This could occur because of the reasons outlined in (5) to (7) below.

(5) Lea (1913) suggested that the presence of Lee's phenomenon in his herring data was due to a segregation by maturity of fast and slow growing fish, i.e. the mature and immature fish did not school together. Thus if slow growing fish matured later than fast growers, and part of the slow growing group each year, as they matured, intermingled with the fast growers, the effect would be to reduce calculated lengths at age, the reduction being greater as more and more slow growers were added. The explanation is not entirely satisfactory as it does not explain the phenomenon for the older ages, at which all the fish are mature.

(6) A hypothesis on similar lines was tested by Jones (1958), for haddock and shown by him to be unsatisfactory. Assuming a segregation of immature and mature haddock at the spawning season, fishing activity at that time is concentrated on the fast growing mature fish. As a result,

in any year-class, the slow growing fish have the greatest likelihood of survival, and each year's survivors, over the age range of maturity, will tend more and more to be those fish which started life as slow growers.

(7) A differential mortality rate, favouring slow growing fish could also account for Lee's phenomenon. Differential mortality of fast and slow growers undoubtedly operates in fish populations fished by commercial gears, which almost invariably select fish by size, tending to capture the largest sizes at the early ages. Robertson (1936) attributes his phenomenon in the sprat to this cause. However this can account for the phenomenon only over the selection range of the gear.

For older fish a selective mortality rate might be caused by a behaviour difference between fast and slow growers on approach of the trawl (Thompson, 1923), or might occur naturally due to a differential metabolic rate between the two groups (Jones, 1958). A similar hypothesis of "physiological mortality" is suggested by Taylor (1958) to account partially for the phenomenon in Georges Bank haddock. Hile (1936) also suggested that differential mortality of fast and slow growers might account for Lee's phenomenon in the cisco, and reviewed experimental evidence from fish, insects and mammals to support this hypothesis. Jones (1958) shows that for haddock and plaice, in order to explain the phenomenon by a greater mortality rate for fast growers than for slow growers, "the range of mortality rate would have to be improbably large." A combination of two explanations, i.e. failure to allow for a curvilinear body-scale relationship along with differential mortality rates, could account for the phenomenon in one set of haddock data but failed to do so in another. Taylor (1958) pointed out that if Lee's phenomenon is caused by selective removal from the population of the faster growing fish, it should be eliminated if the data were arranged so that fish of different ages of capture had common growth rates. This was done for Georges Bank haddock, using the calculated length at age one to separate fast and slow growing fish. This treatment did not eliminate the phenomenon but rather showed that it was greatest in the smallest sizes, becoming progressively less with increase in l_1, and occurring in reverse form at the largest l_1's. Taylor further showed that the growth parameters of the von Bertalanffy growth equation "change systematically with l_1 and age at capture," and that the estimated life span "declines with (increasing)l_1

at all ages at capture, the rate of decline being much more marked at the older ages." However the change in apparent growth rate with age at capture, calculated by the application of differential mortality rates to a normal distribution of sizes at age one, is not as great as that actually observed in the haddock data, and selective fishing is suggested as a possible cause of Lee's phenomenon.

Although Lee's phenomenon has been widely observed, its absence in back-calculation data has also been reported. Graham (1929b) refers to Hodgson (1925) as obtaining agreement between calculated and empiric lengths of herring using the simple proportionality formula. Similarly Van Oosten (1929) reports the same observation by Nall (1926a,1926b) for sea trout, and the same is repeated by Nall (1930). Taylor (1958) shows that in Georges Bank haddock, plots of l_2 on l_1, l_3 on l_1, etc. for each age of capture are linear, tending to intersect at a common point. He suggests that the absence of Lee's phenomenon in some species might be due to the range of sizes at age one being near such a point of intersection.

From the foregoing, it is seen that although a number of causes have been shown to contribute to the phenomenon, it cannot yet be said to be entirely satisfactorily explained.

4. Curvilinear Regressions

A number of non-linear regressions have been used to describe the body-scale relationships of various species. Sherriff (1922) proposed that the parabola

$$L = A + BV + CV^2 \qquad (40)$$

where A, B and C are constants, gives the best description between growth of body and scales, and suggested its general application.

Monastyrsky (1930), having tried the equations of Lee (1920) and Sherriff (1922), found that best results could be obtained by describing the body-scale relationship by the allometric formula

$$L = cV^n \qquad (41)$$

in its logarithmic form

$$\log L = \log c + n \log V \qquad (42)$$

He thus proposed that logarithms of fish size and scale size exhibited a straight line relationship.

Fry (1943) modified the allometric formula by adding a constant a to correct for body length at time of scale formation (a concept open to criticism as noted previously), the equation becoming

$$\log (L-a) = \log c + n \log V \qquad (43)$$

where c and n are constants.

Carlander (1945a, 1945b, 1950a) has adopted a purely empirical approach, fitting the curve that best describes the relationship. Thus Carlander (1945a) uses the third degree polynomial

$$L = A + BV + CV^2 + DV^3 \qquad (44)$$

to describe the body-scale relationship of yellow pike-perch, Stizostedion vitreum vitreum (Mitchill). Carlander (1945b) describes the body-scale relationship of the tullibee, Leucichthys artedi tullibee (Richardson), by a fourth degree polynomial, i.e. of the type

$$L = A + BV + CV^2 + DV^3 + EV^4 \qquad (45)$$

For yellow perch, Perca flavescens (Mitchill), Carlander (1950a) describes the body-scale relationship by two third degree polynomials, one to fit the data at both ends of the distribution and the other to fit the data in the centre.

The variety of mathematical descriptions applied to body-scale relationships serves to indicate that the nature of the relation between growth of body and scales cannot be generalized. Rather the relationship is apt to be different for different species, and even for different populations of the same species. The various types of curvilinear relationships described above have received variable application, the equations of Sherriff and Monastyrsky probably being the ones most widely applied.

Segerstråle (1933) determined the average scale lengths at various body lengths by a large series of measurements of "normal" or key scales. The body-scale relationship, in tabular form, then served as a basis for individual growth calculations. A correction was made for fish at any length whose scales were not of the "normal" size for that length. By this method the ratio between actual and "normal" scale size at a particular length is used to adjust scale sizes at earlier annuli, and growth calculations are based on those adjusted or "normalized" measurements. Hile (1941) describes the procedure in detail, using "key" scales to determine the body-scale relationship, and "normalizing" unselected scales taken from the same general region of the fish. However the procedure has also been applied (e.g. Carlander, 1945a) using a general body-scale relationship rather than one constructed from "key" scales only. It is criticized by Whitney and Carlander (1956) on the basis that the regression of body length on scale length is used to estimate the "normal" scale measurement. They consider that a more correct procedure would be to use the regression of body length on scale length to determine a "normal" body length at a particular scale length, and to use the ratio between observed and normal body lengths at a certain scale size to correct calculations of body length at earlier annuli. They state that computed lengths will be the same with either procedure if the body-scale relationship is linear but will differ if the relationship is curvilinear. However, they further point out that for a curvilinear regression the latter procedure does not take advantage of the assumption that estimates of body growth are related to proportionate growth of the scale (i.e. the ratio between the size to any annulus and the total size of the scale is the same for all scales on the same fish) rather than absolute scale size. Thus large and small scales of fish of the same length and age, with annuli in the same relative position on each, would give different growth histories.

In many cases where curvilinear regressions seem to best describe the body-scale relationship, deviations from a straight line may actually be so slight that a straight line regression is sufficiently accurate for most purposes. In such cases the straight line regression would appear to be more suitable on theoretical grounds.

D. COLLECTING AND ANALYZING THE DATA

1. Selecting the Scales

The same criteria used to select scales for age reading apply to selection of scales for growth calculations. The scales should be taken from an area where they occur in regular order, with little variation in size and a minimum of regeneration. For ctenoid scales this generally seems to be an area underneath or just posterior to the tip of the pectoral fin, (Perlmutter and Clarke, 1949; Mansueti, 1960) and for cycloid scales (of which the scales of haddock are typical) from an area about three-quarters of the way back on the body in the region of the lateral line. Thompson (1923) showed that for haddock the largest scales were found in the region of the lateral line below the third dorsal fin and considered this to be the best area from which to collect scales. Anterior to this position calculated lengths at age were found to decrease, this being most pronounced in scales from the area under the pectoral fin. Dannevig and Høst (1931) showed for a number of species (haddock included) that, except for the last scales on the tail, computed values of l_1, l_2 and l_3 decreased anteriorly. A similar tendency is also reported for haddock by Saetersdal (1953). He found smallest variations in calculated lengths for scales taken under the posterior part of the second dorsal fin, either above or below the lateral line.

Some authors have taken the trouble to locate exactly corresponding scales from different fish, using one or several of these "key" scales to construct the body-scale relationship (Creaser, 1926; Hile, 1941). This is a rather laborious practice and Everhart (1950) has shown that it is not justified by increased accuracy in back-calculation of lengths. Carlander (1945a, 1945b) used a larger sample size to counteract variations in scale size when key scales were not used. Rounsefell and Everhart (1953) suggest that collection of scales from the same general area on each fish is sufficient.

2. Mounting, Reading and Measuring

Scales are generally removed from the fish by means of a knife or pair of forceps, and temporarily stored in envelopes or between small pieces of paper. Cleaning is sometimes required preparatory to mounting, and this may be accomplished using dilute sodium hydroxide and, if necessary, a small brush. Temporary mounts may be made either wet (in water or glycerin) or dry.

Permanent mounts may be made on glass slides with cover slips or by plastic impressions. Rounsefell and Everhart (1953) emphasize the importance, for glass mounts, of using a mounting medium of different refractive index from that of the scale, and suggest euparol, glycerin-gelatin, or gum arabic.

Lea (1918) and Lea and Went (1936) describe a process for the production of "negative" impressions of fish scales in celluloid, and the production of "positive" copies from these by filling the impressions with a gelatine solution. The negative impressions alone are quite sufficient for age reading and scale measurement, and the method of producing them has become very much modified and simplified in recent years. Essentially, the method consists of pressing the sculptured surface of the scale on to slides of cellulose acetate or some other transparent plastic which is pre-heated or treated with acetone or alcohol to soften it. Presses of various sorts are described by Nesbitt (1934), Greenbank and O'Donnell (1950), Arnold (1951), Butler and Smith (1953) and Smith (1954).

Plastic impressions are often more satisfactory for examination than the original scales. This is particularly so for scales of old fish where the detail at the centre may be obscured because of the scale's thickness and opacity. Such mounts also have the advantages of being rapidly prepared, permanent, unbreakable and easy to store. Further, Butler and Smith (1953) show that any differences in size between the original scales and the plastic impressions are reflected proportionately at each annulus, and that growth calculations from impressions are just as valid as those made from the original scales. They also report that the impressions do not alter in size in storage for several years at temperatures within the range 5°C. to 30°C.

Ages may be read and measurements of annuli made by means of a binocular microscope fitted with an eyepiece micrometer, but the tedium is considerably alleviated by means of a projecting device. Van Oosten (1923) describes an early model. Van Oosten, Deason and Jobes (1934) describe a projector at which the operator can sit, and which presents the image on a screen at right angles to the line of sight. This model with some modifications (e.g. Johnson, 1953; Phillips and Webster 1960), has achieved widespread use and acclaim. Another projector, assembled from a microscope, mirror, prism and "beehive" lamp is described by Mosher (1950). Hagen (1956) describes a lens attachment for an ordinary 35 mm slide projector to accomplish projection of scales.

A semi-automatic scale reading device, which presents variations in light intensity, caused by variation in size and spacing of circuli, as pips on a strip-chart recorder, is described by van Haagen and Dale (1959). Hartley (1958) describes a projector incorporating an electrical potentiometer system by means of which back-calculated lengths based on the simple proportionality formula may be read directly from the machine.

Having selected scales suitable for measurement and provided a means of reading and measuring, there remains a choice of which scale dimension or dimensions to measure. Everhart (1950) measured the anterior radius, antero-lateral radius and width of scales of smallmouth bass and found the anterior radius to be most efficient for back-calculation. This species has ctenoid scales, and for ctenoid scales in general the anterior radius is the measurement most often employed . Van Oosten (1929), working with the cycloid scales of the lake herring, found that the scale diameter gave more accurate calculated lengths than did the anterior radius. Saetersdal (1953), for haddock, found no essential difference in the distribution of the points of regressions of scale diameter and posterior radius on body length, and preferred the posterior radius as being most convenient.

3. Choice of Regression

In order to describe the body-scale relationship it is necessary to correlate the two variables of body measurement and scale measurement. Two regressions may be derived: that of scale measurement on body length, of the type

$$S = a + bl \tag{46}$$

and that of body length on scale measurement, of the type

$$L = a' + b'S \tag{47}$$

(assuming a linear relationship). These two lines will coincide only if the correlation is perfect, i.e. if the coefficient of correlation is unity. The value of the L-intercept for use in the proportionality formula (38) will depend on the regression chosen.

The computation of a regression implies that one of the variables is fixed or independent, and the usual procedure is to plot the regression of the dependent variable (denoted as $\underline{Y}$) on the independent variable (denoted as $\underline{X}$), and to use the regression to estimate $\underline{Y}$, given $\underline{X}$. Assuming fish length as the independent variable in body-scale relationships, a regression of type (46) would normally be used. However, since we wish to use the regression to estimate fish length, a regression of this type is unsatisfactory (Whitney and Carlander, 1956). The proper regression to use is that of the independent variable on the dependent variable, or fish length on scale measurement (Winsor, 1946).

With a straight line relationship, back-calculated body lengths may be obtained by substituting absolute scale size in the body-scale regression, or by using the value of the L-intercept to "correct" the simple proportionality formula. If the body-scale relationship has been adequately described and if scales are collected from a corresponding area on each fish, substitution of actual scale measurements in the body-scale regression may be satisfactory for back-calculation of lengths. However, Whitney and Carlander (1956) in computing lengths by both methods, conclude that "although the assumption that the body growth is strictly proportional to scale growth is not met, ... this assumption gives a better approximation than can be secured by relying upon absolute scale size and the regression method."

Whitney and Carlander (1956), referring to Anderson and Bancroft (1952), state that the computation of a body-scale regression assumes that variance of body lengths is the same for each scale length. They point out however, that more likely the variances of the body lengths increase with scale size. Transforming the data to logarithms would eliminate this correlation, but would add greatly to the labour involved in back-calculation. Whitney and Carlander (1956) conclude that in general the assumption may be ignored, the transformation to logarithms being not justified by any increase in accuracy.

In fitting the regression line it has often been the practice to group fish by length and fit the regression to the average scale measurement for each length group. Whitney and Carlander (1956) point out that if it is desired to group data, it is preferable to group by scale measurement, fitting a regression of type (47).

In most growth studies back-calculated lengths have been computed for individual fish, and the average growth rate for any group obtained from these data. Van Oosten (1929, 1953) suggests that a good deal of labour would be saved by first averaging the scale measurements for each age and length of fish and computing average lengths from these data. He shows that the method gives similar results.

4. The Use of Nomographs

Nomographic devices of various sorts, designed to speed up back-calculation of lengths, have been described by a number of authors. The form of nomograph used depends on the nature of the body-scale relationship and the method of recording scale measurements. Some are constructed so as to render recording of scale measurements unnecessary, being fitted on the projection machine used to measure the scales.

Huntsman (1918) used a movable cardboard curve on a nomograph, the curve representing the true body-scale relationship of the species, provided this relationship was of the same type for all scales of the fish. Lea (1919) proposed that the position of annuli and of the edge of the scale be marked on cardboard strips placed on the scale image. A simple nomograph based on a body-scale relationship in direct proportion was used to compute lengths at annuli from the cardboard strips. Cardboard strips are also utilized in a modification described by Carlander and Smith (1944) of a nomograph designed by Hile (1941), and may be used with a "body-scale ruler" described by Hile (1950). Such nomographs may be adapted to any type of body-scale relationship provided the relationship for the particular species is known. Fry (1943) describes a nomograph to be used when the body-scale relationship can be described by a logarithmic straight line.

Nomographs used directly with scale projectors, eliminating the need to record scale measurements, are described by Joeris (1950), Schuck (1949) and Lowry (1951), the latter based on that of Carlander and Smith (1944).

If the body-scale relationship is linear and particularly if growth calculations are made from average scale measurements, a modern, high-speed calculator is adequate for the purpose. However if individual growth calculations are required or the body-scale relationship is curvilinear, the use of a nomograph simplifies and speeds up the operation. In such cases the most efficient nomograph would be of the type that attaches directly to the scale projector, permitting back-calculations of growth to be made from the scale image, and thus combining the measuring and calculating procedures into one operation.

III. APPLICATION TO HADDOCK OF THE NEWFOUNDLAND AREA

A. INTRODUCTION

1. The Newfoundland haddock stocks

Haddock of the northwest Atlantic can be separated into three major stocks, one inhabiting Georges Bank, another the Nova Scotian banks and the third the Newfoundland banks (Needler, 1930; Vladykov, 1935; Templeman, 1955; Clark and Vladykov, 1960). The latter two of these, at least, contain relatively independent sub-groups. In the Newfoundland area two major sub-groups are present: one on the Grand Bank and the other on St. Pierre Bank (Fig. 1). These haddock, while occupying the southernmost fishing grounds of the Newfoundland area, are actually at the northern extremity of their range in the northwest Atlantic.

Intermingling of adult haddock from the Grand Bank and St. Pierre Bank is apparently limited by hydrographic barriers. A moderately deep channel is present between Green Bank and the Grand Bank, and water temperatures in this channel and on Green Bank itself are generally lower than those preferred by haddock. In fact, the St. Pierre Bank haddock population in recent years consisted almost entirely of fish born in 1949, although other year-classes, as well as that of 1949, were well represented

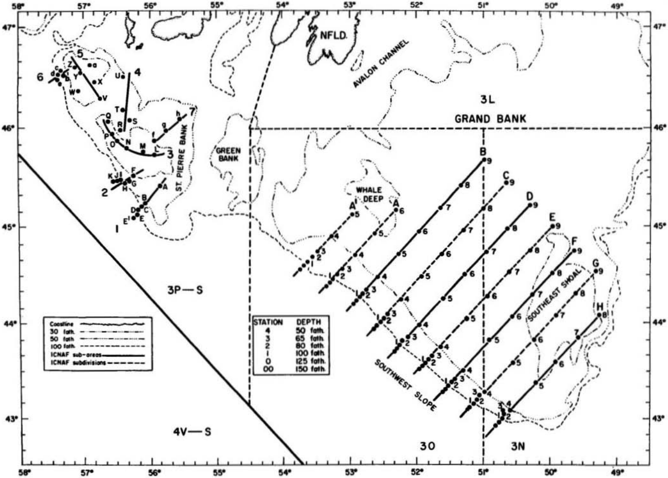


Figure 1. Map of the Grand Bank and St. Pierre Bank showing lines of stations fished by research vessels of the St. John's Biological Station.

on the Grand Bank.

The Grand Bank stock usually spends the winter and early spring in deep water along the southwest slope (Fig. 1) in depths of 65 - 150 fathoms and at temperatures between 2.5 and 9°C (Templeman and Hodder, MS, 1964a). This concentration begins to disperse in late spring, and by May and June many of the haddock are found at shallow depths on the bank plateau at temperatures between 2 and 4°C (Fig. 2). Movement toward the shallow water begins before spawning, which occurs in May and June. By July, great concentrations of haddock are found on the Southeast Shoal (Fig. 1), the shallowest part of the southern Grand Bank. At this time they have been noted to be feeding on capelin eggs and capelin (Pitt, 1958; Templeman, MS, 1964). With the advent of lower temperatures in autumn, the haddock return to the deep water of the southwest slope of the bank. Variations in timing of these seasonal movements do, of course, occur, but can generally be related to variations in temperature conditions from year to year.

Information from catches of both research and commercial vessels fishing on St. Pierre Bank indicates that haddock are most abundant in depths of 20 to 40 fathoms from June to January, and 80 to 120 fathoms

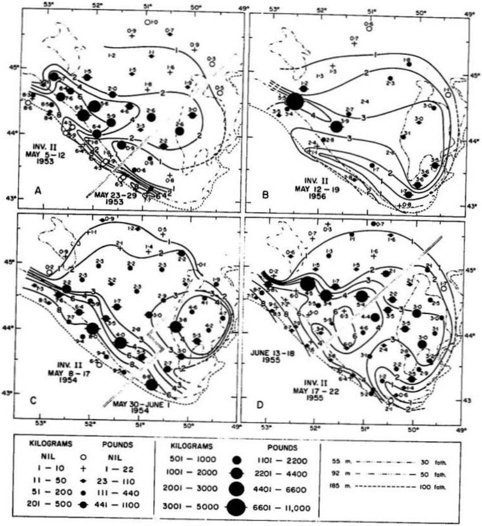


Figure 2. Distribution of haddock on the southern Grand Bank in relation to bottom temperature, as indicated by research vessel catches per half-hour fishing. (Templeman and Hodder, MS, 1964a, Fig. 4).

from February to April (Templeman and Hodder, MS, 1964b). The largest shallow water catches obtained by research vessels from late May to early July were taken at temperatures between 2.5 and 7.0°C. The movement to deep water in January - February and the return to shallow water in May - June are probably related to low temperatures on top of the bank during the former period, and subsequent warming of the shallow water during the latter. Spawning, as on the Grand Bank, occurs in May and June.

Small quantities of haddock are found inshore in summer along the Newfoundland south coast, and haddock are often found, and occasionally taken in large quantities, along the east coast in mid-summer (Templeman and Hodder, MS, 1964a). The movements along the east coast generally occur when surface water temperatures are highest, and it is possible that the fish are following and feeding on schools of capelin which spawn in July and August in deep water beyond the beaches (Templeman, 1948). It is known that haddock feed on capelin, as well as various pelagic and demersal invertebrates (Thompson, 1939; Rojo, 1959).

The haddock populations of the northwest Atlantic have a unique character in common, i.e. that annual production of young fish is subject to great fluctuation. This reaches such an extreme in the Newfoundland area that survival of one year-class may be several hundred times greater than that of another. During the period from the end of World War II to the present the only year-classes experiencing significant survival beyond the early stages were those of 1946, 1949, 1952, 1953, 1955 and 1956. Of these, the 1953 and 1956 year-classes experienced only moderate survival, while survival in all years other than the 6 listed was almost non-existent. This is well illustrated in Fig. 3, which shows the proportions of each year-class in the Grand Bank population during the years 1953 to 1958. Since, for the period represented, good survival occurred only once in every three or four years, the various year-classes can be recognized also as distinct modes in the yearly length compositions of the population.

On St. Pierre Bank the 1946 year-class experienced moderate survival, while the 1949 year-class was present in large numbers. There has not been significant survival of new year-classes on St. Pierre Bank since 1949. Thus research vessel surveys during the period 1953 to 1955 indicated that 80 to 95% of the St. Pierre Bank haddock population in those years consisted of fish of the 1949

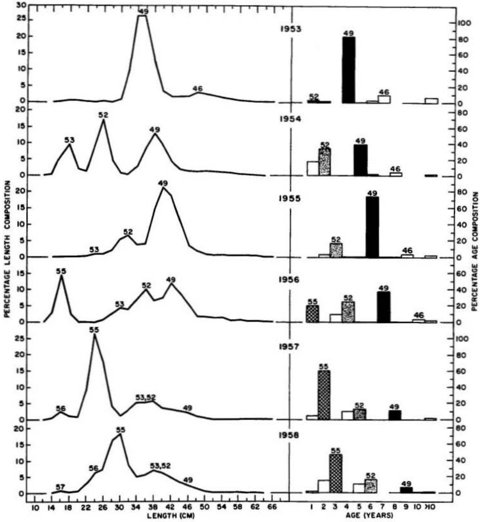


Figure 3. Percentage length and age composition of the Grand Bank haddock population during the years 1953 - 1958, as determined by research vessel surveys.

year-class. Since 1956 the population in this area has been very small.

Much of the foregoing review has been taken from mimeographed Annual Reports of the St. John's Biological Station (FRB, 1950-1963). A more complete account of the biology of haddock from the Newfoundland area is given by Rojo (1959).

2. The haddock fishery

Haddock were abundant on the southern Grand Bank in the 1930's (Thompson, 1939), but a significant fishery did not develop until the end of World War II. The fishery is carried on almost entirely by otter trawlers fishing offshore. From 1945 to 1959, 90% or more of the catch was taken by Canada and Spain, with Spain alone taking about three-quarters of the catch up to 1953. The Spanish fishery has declined very rapidly since 1955, and by 1959-1960 the Canadian catch was more than double that of Spain. An intensive fishery was carried on by the USSR in 1960 and 1961, but by 1962 the fishery was largely abandoned by European fleets, leaving Canada to harvest 80% of the relatively small catch of that year (Fig. 4 and Table 1).

The fishery is intimately related to the seasonal distribution and year-class survival of the fish. The

Canadian fishery on the Grank Bank takes place mainly during the winter and early spring when the haddock are concentrated on the southwest slope. In mid-summer, when the fish are heavily concentrated on the Southeast Shoal, they are fished mainly by Spanish and Russian (1960 and 1961) trawlers. Canadian trawlers generally do not participate in the latter fishery because of the distance from port and problems of spoilage caused by the warm summer temperatures. Spanish trawlers overcome this by salting the catch and Russian trawlers by salting, or by freezing on board large factory vessels. On St. Pierre Bank fishing takes place in shallow water (20 to 40 fathoms) from June to January and in deeper water (80 to 120 fathoms) from February to April (Templeman and Hodder, MS, 1964b). Landings from the whole area increased rapidly from 1945 to a peak of almost 80 thousand tons in 1949. During this period the fishery harvested many of the old and large fish of the virgin population, and a good deal of wastage of the resource occurred. In 1949 and 1950 Newfoundland trawlers landed very few fish under 45 to 50 cm in length, though many fish of smaller sizes were caught, mainly from the 1946 year-class. Thus in these two years more than 50% of the fish caught were discarded as too small to fillet (Templeman and Handrigan, MS, 1950). During the period 1950 to 1953 total landings

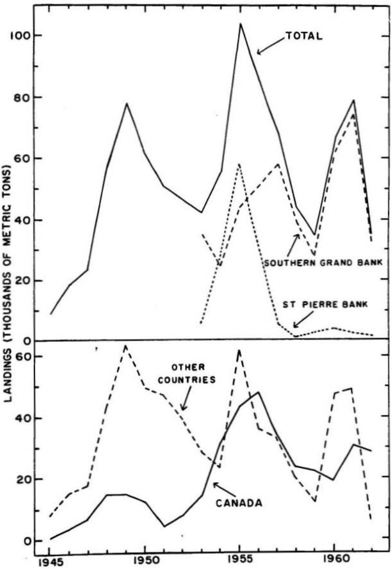


Figure 4. Newfoundland area haddock landings, 1945 - 1962.

declined (Fig. 4) due to a decline in numbers of large fish and a reduction of fishing effort. However as the 1949 year-class reached commercial size (at ages 5, 6 and 7 in 1954, 1955 and 1956) a great increase in fishing occurred both on the Grand Bank and St. Pierre Bank, and landings in 1955 reached 105 thousand tons. Part of the reason for this increase was the acceptance of smaller haddock (33 to 43 cm) by Newfoundland fish plants. In 1953 the 1949 year-class had entered the commercial fishery, but was largely discarded, discards from trawler catches in that year amounting to 55% of the weight of the catch. With the acceptance of smaller fish late in 1953 (Templeman and Fleming, 1958), discards were substantially reduced and landings increased. As the 1949 year-class passed through the fishery landings again declined both on the Grand Bank and St. Pierre Bank (Fig. 4) reaching a low of 35 thousand tons in 1959. Since the 1949 year-class was the last to experience significant survival on St. Pierre Bank the fishery in that area has remained at a very low level since 1957. On the Grand Bank the 1949 year-class, along with those of 1952, 1953 and 1955, continued to support a reduced fishery in 1957, 1958 and 1959. The increase in landings from the Grand Bank in 1960 and 1961 (Fig. 4) was due largely to the Russian fishery in those years. In 1960 this was mainly on the Southeast Shoal during the period July - November, but in 1961 also included fishing on the southwest slope in winter (Noskov, MS, 1962). Research vessel surveys indicate that the 1955 year-class accounted for a good deal of the catch in 1960 and almost all the catch in (1961 (Hodder, MS, 1962b). Catches in 1962 again declined to a low level and will probably continue to decline because of the poor survival of young fish since 1956.

3. Previous use of scales in haddock age and growth studies

Thomson (1904) showed that the periodic markings found in the scales of haddock and other Gadidae were formed annually, and could be used to determine age. Lee (1912) used the simple proportionality formula to back-calculate lengths of haddock and found that "the phenomenon of apparent change in growth rate" was exhibited. Evidence bearing on the validity of the scale method of ageing, through agreement with Petersen's method, was presented by Thompson (1923), who also made back-calculations of growth from the simple proportionality formula and found that Lee's phenomenon was present. Aquarium experiments to determine the validity of the scale method were also carried out by Thompson (1926).

Graham (1929b) reviewed evidence to that time bearing on the validity of the scale method in haddock and various other species.

From the 1920's onward the scale method of ageing haddock was widely applied. Saemundsson (1925) used scales to determine age and growth of haddock from Iceland. Dannevig and Høst (1931), for Norwegian haddock, investigated the sources of error involved in back-calculation when scales were taken from different areas on the same fish. Raitt (1939) analysed mortality of North Sea haddock using scale ages. Scales were used by Thompson (1939) to age haddock from the Newfoundland area, and by Schuck and Arnold (1951) to compare age distribution and growth of haddock from Georges Bank and Browns Bank. Saetersdal (1953) established the validity of scale ageing and calculated growth of Norwegian haddock from scales using the corrected proportionality formula. Wise (1957) used a curvilinear body-scale relationship and nomograph to calculate growth from scales of Browns Bank haddock. Kohler and Clark (1958) compared ages from scales and otoliths, showing that differences in age interpretation increased with age of the fish, producing differences in relative strengths of year-classes, but not in growth rates. Jones (1958) and Taylor (1958) investigated possible causes of Lee's phenomenon in European and Georges Bank haddock respectively when growth was back-calculated from scales. McCann and Dreyer (1963) present age data based on scale reading for haddock from Georges Bank and the Gulf of Maine. Because of difficulties in interpretation at the oldest ages, some authors (e.g. Kohler, 1958, 1960) have in recent years turned to otoliths to determine age.

Although no formal presentation of the validity of scale ageing of Newfoundland area haddock is included here, various unpublished data of the St. John's Biological Station relating to seasonal changes in the margin of the scale and the following of dominant year-classes (Fig. 3) indicate that the method is accurate, at least to ages 8-10.

B. MATERIALS AND METHODS

1. Collections

The material was obtained from random samples of the catches of the research vessel Investigator II during the period 1953 to 1958. The Investigator II is an 82-foot, 250-H.P. otter trawler and fished for haddock at a towing speed of about 3 knots. The gear consisted of a No. 36 manila net, having a 60-foot headline and 80-foot footrope. The codend was of double knit manila with an external mesh size (between knot centres) of 3½ inches when dry. In all cases the codend was either lined or covered with small meshed netting to prevent the escape of small fish, and thus sample the population as randomly as possible. In 1953 a manila liner, having an external dry mesh size of 1 and 3/4 inches, was used, while the same material was used as a cover from 1954 to 1957. A nylon liner having 1 and 1/8 inch meshes was used in 1958.

Fishing in each year was carried out along standard lines of stations on the Grand Bank and St. Pierre Bank (Fig. 1). On the Grand Bank, these were generally Lines B, D, F and H of Fig. 1. Depths fished ranged from the shallowest available (about 20 fathoms on St. Pierre Bank and 25 fathoms on the Southeast Shoal of the Grand Bank) to 150 fathoms. The surveys were carried out mainly in Spring. The 1953-1958 scale collections from the Grand Bank were obtained between April 30 and June 18, but mainly in May of each year. The St. Pierre Bank collections were obtained between May 18 and June 30, but the collection from this period in 1956 was so small that a sample taken in early October was included in the data for that year.

Scale samples were removed by forceps from both sides of the fish, between the second and third dorsal fins, and below the lateral line (Fig. 5). The scales were stored dry between a folded piece of absorbent paper in a coin envelope. The length, sex, maturity and other biological data were recorded on the front of the envelope along with the basic sample details. Lengths were measured from snout to mid-fork of the caudal fin to the nearest whole centimetre (Fig. 5).

The numbers of scales examined for purposes of the present study are listed by year-class for each year and area in Table 2.

2. Mounting, reading and measuring the scales

Scales were prepared for reading and measuring by a process very similar to that described by Arnold (1951) for haddock scales, involving the impression of the sculptured surface of the scale on to a plastic slide. The slides used were of transparent cellulose acetate, 3/4 x 2 and 3/4 inches and .03 inch thick, cut from 20 x 50 inch sheets. The scale press was similar to

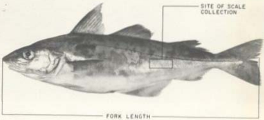


Figure 5. Haddock showing site of collection of scales, and length measurement used.

Figure 6. Scale of 4-year-old haddock showing method of measuring annuli.

that described by Arnold (1951), having a heating platform to soften the slide and so aid impression, and a pair of polished steel rollers to effect the impression. The procedure was to place 4 scales, sculptured side down, on the plastic slide, place the slide and scales on the heating platform for 5 to 10 seconds (depending on size of scales) and then run the slide and scales through the press. Having made the impression, the scales were discarded. A sample of 25 scales, selected at random, were mounted dry between glass slides and measurements of overall diameter were made. These measurements were subsequently repeated for scale impressions made from the same scales. The diameters from impressions were on the average 1.3% shorter than from the dry scales. Butler and Smith (1953) have shown that such differences are reflected proportionally at each annulus, and thus do not affect growth calculations.

Measurements were made from the centre of the scale to the end of each annulus and to the scale edge, both anteriorly and posteriorly, along the longest scale radius (Fig. 6). These measurements were later added to obtain the scale diameter at each annulus. The outer edge of the narrowest sclerite in each annulus was taken as the end of the year's growth.

The growing season for haddock of the Grand Bank and St. Pierre Bank, as evidenced by the presence of wide sclerites at the edge of the scale, begins in May-June, or at the time most of the data were collected. This being so, the last annulus on the scale was considered as a full year's growth if narrow sclerites were present at the scale edge. If one or more wide sclerites were present, these would be considered to represent the beginning of the next year's growth. Thus if a scale had four annuli, plus some wide sclerites, the end of the fourth year of growth would be taken as the outer edge of the narrowest sclerite in the fourth annulus.

Only those scales taken from the area below the lateral line and between the second and third dorsal fins were used in the present study. Sometimes, especially for small fish and large catches, the scales from this area of the fish are lost in the process of bringing the catch to the surface and on board the vessel. In such cases scales were collected for age reading from under the pectoral fin or some other area of the body. The position from which such scales were taken was recorded on the scale envelope, and these scales were rejected for purposes of the present study. Also rejected were regenerated scales, scales obviously eroded at the edges and scales exhibiting breaks in structure or of irregular shape because of damage or injury. Of the four impressions on each slide, the second was chosen for measurement in order to avoid any possible bias. If this proved unsuitable for any of the reasons outlined above, the first, third or fourth scales were chosen, in that order. Since pectoral region scales only were available for many of the smallest fish at ages one and two, an unavoidable bias was introduced toward measurement of scales of the larger fish at these ages. Since scales from the pectoral region were generally of irregular size and shape, no attempt was made to construct a separate body-scale relationship for these scales.

Measurements of annuli in old fish were made only to the end of the seventh year because of difficulties in interpretation at older ages and possible erosion of the edge of the scale. Ages from the 1953 to 1957 scale collections had previously been read by Dr. W. Templeman, Director of the St. John's Biological Station.

Otolith ages, by Mr. V.M. Hodder, were available for all fish from the 1956 to 1958 collections, and for all above age 7 from the 1953 to 1955 collections. In doubtful cases an agreed age was assigned on the basis of scale-otolith comparisons.

The scale measurements were made by means of a microprojection machine of the type described by Van Oosten, Deason and Jobes (1934), which presents the scale image at right-angles to the line of sight of the seated operator. Basically, this consists of a Bausch and Lomb VH microprojector, equipped with a 48 mm Macro-Tessar lens and eyepiece micrometer. A front-surface mirror is used to reflect the image on to the viewing screen. Originally, front-surface silvered mirrors of ¼-inch plate glass were prepared at the St. John's Biological Station using Brashear's process (Anon., 1935), but these were found to tarnish fairly quickly and had to be replaced every 3 to 4 months. This type of mirror was later replaced by an aluminized mirror of ½-inch polished plate glass, supplied by the Garnett Optical Co., Halifax, N.S. The screen consisted of a piece of Imperial blue-tinted tracing cloth placed between two pieces of glass.

Scale measurements were made (at a magnification of approximately 67.5 diameters) to the nearest hundredth of an eyepiece unit (EPU) by means of an eyepiece micrometer graduated in millimetres and tenths. The conversion factor from EPU to millimetres, as calculated by calibration against a stage micrometer, is 0.68, i.e.

Actual measurement of scale (mm) = EPU x 0.68.

Since no practical purpose is served by converting the scale measurements to millimetres, this has not been done. The quality of the optical system was such that distortion of the scale image within the field of measurement was negligible.

C. RESULTS

1. The body-scale relationship

The body-scale relationship has been examined by analysis of regressions of body length on scale diameter as suggested by Whitney and Carlander (1956). The scale diameter measurements were grouped into intervals of 0.25 EPU, i.e. 1.88-2.12, 2.13-2.37, 2.38-2.62, 2.63-2.87, etc., with midpoints 2.00, 2.25, 2.50, 2.75, etc., and average body lengths were plotted at the midpoint of each scale diameter interval. The material for each area, sex and year-class was examined separately to determine whether the body-scale relationship was consistent. The regressions invariably took a linear form and straight lines were fitted to the data by the method of least squares, the equation (47) being

$$L = bS + a$$

where L is the fish length at capture, S is the scale diameter at capture, b is the slope of the regression line and a is the L-intercept.

Fitted regressions of body length on scale diameter for males and females separately are shown for the Grand Bank in Fig. 7 and for St. Pierre Bank in Fig. 8. The average body lengths at each scale diameter interval, as well as the numbers of fish on which these averages are based, are listed in Table 3. In both cases the slopes of the regression lines for females are greater than the slopes for males, while the female L-intercepts are smaller than those for males. The regression equations for each sex between the two areas are very similar.

Analysis of covariance by the method of Snedecor (1961) was used to test the differences in slope and intercept within each area (Table 4). The F-value derived from the ratio of mean square for regression coefficients to mean square within samples measures the significance of differences in slope of the regression lines. The significance of differences in intercept is measured by the F-value derived from the ratio of mean square for adjusted means to mean square for common regression. Snedecor (1961) points out that if the slopes (regression coefficients) are found to differ significantly, in which case the lines are not statistically parallel, the question of differences in elevation (intercept) has little meaning. The analysis of covariance for the sexes, as summarized in Table 4, shows that the slopes for the Grand Bank are significantly different at the 1% level. No difference is indicated between the slopes for St. Pierre Bank, but the intercepts are significantly different at the 1% level.

Since the regression lines for the sexes within each area appeared so similar to the eye, these statistical differences were rather unexpected. In order to resolve the differences, the analysis was carried a stage further. Regressions of body length on scale diameter were fitted to the data for the sexes within each year-class and area, and are listed in Table 5. Analysis of covariance

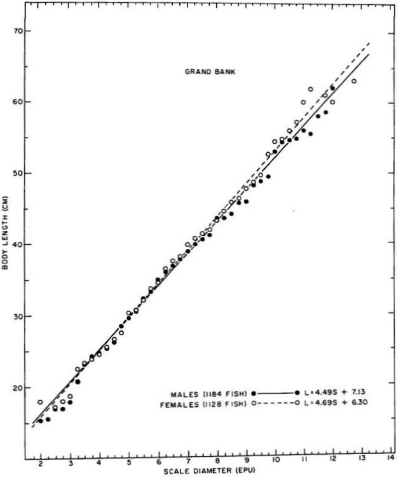


Figure 7. Regressions of body length on scale diameter for males and females separately, Grand Bank, 1953 - 1958.

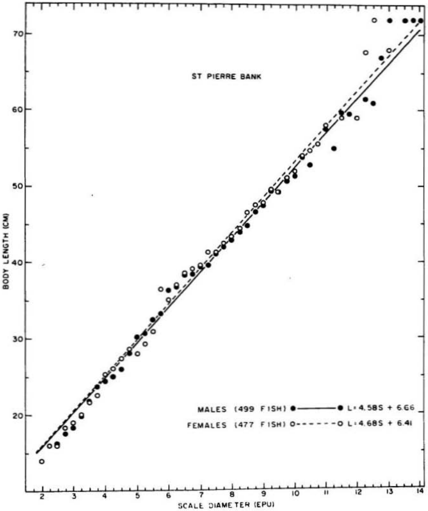


Figure 8. Regressions of body length on scale diameter for males and females separately, St. Pierre Bank, 1953 - 1958.

was carried out for each pair of regressions, and the results are summarized in Table 6. Data for the 1956 year-class, available only for the period 1957-1958, is included with the material for the minor year-classes. Table 6 indicates only one significant difference in slopes between the sexes, and this only at the 5% level for the 1953 year-class from the Grand Bank. High F-values, and significant differences in intercept at the 1% level are shown for the 1949 year-class both from the Grand Bank and St. Pierre Bank. These significant differences result from differences in L-intercepts for this year-class of 0.86 cm on the Grand Bank and 0.51 cm on St. Pierre Bank. Differences in male and female L-intercepts for other year-classes are as great as 11.68 cm, yet the differences are not statistically significant.

The material for the 1949 year-class differs from that of all other year-classes in one essential feature, i.e. the bulk of data available. In such cases, small differences are likely to be found significant in statistical tests. Southward (1962) quotes from a discussion of the testing of statistical hypotheses by Hodges and Lehmann (1954) as follows:

"...whenever the available data are extensive, the tests may become embarrassingly powerful ...". Southward (1962) found statistical differences between regressions of body length on otolith radii for Pacific halibut, but concluded that large sample sizes caused analyses of covariance to be "...too sensitive for the biological purposes intended". While this is a potentially dangerous supposition on its own, the fact that differences in intercepts between the sexes are found in the present data only for the largest year-class adds weight to the argument that the differences detected are not of practical importance. Again the difference in slopes at the 5% level for the Grand Bank 1953 year-class is translated to a difference at the 1% level when all the Grand Bank data are combined (Table 4). Thus sex differences in the body-scale regression are not considered to be of importance, and the sexes have been combined for purposes of further analysis.

It is obvious from the regression equations of Table 5 that rather large differences in slopes and intercepts exist between the oldest and most recent year-classes. The fitted body-scale regressions, plotted for the range of data on which they are based, are shown for the Grand

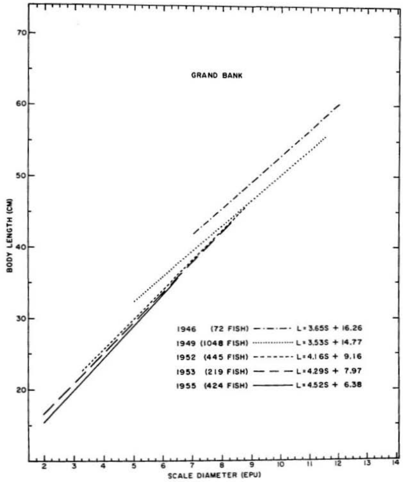


Figure 9. Regressions of body length on scale diameter for each year-class, plotted for the range of data available in each case, Grand Bank.

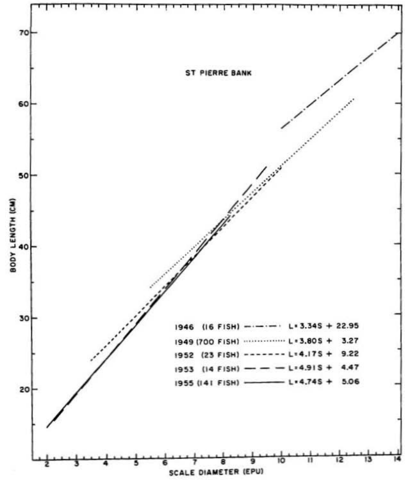


Figure 10. Regressions of body length on scale diameter for each year-class, plotted for the range of data available in each case, St. Pierre Bank.

Bank and St. Pierre Bank in Fig. 9 and 10 respectively. The data on which these figures are based, together with the combined data for each area, are given in Tables 7 and 8. In general there is in both areas a progressive increase in slope and decrease in L-intercept proceeding from the oldest to the most recent year-classes. The fact that this trend appears so clearly in each area is rather remarkable considering the very small numbers of fish represented by some of the St. Pierre Bank regressions. As might be expected, analysis of covariance (Table 9) indicates significant differences at the 1% level between the slopes and intercepts of each group of regressions.

The fact that these differences between year-classes proceed in such a regular fashion in each area causes one to wonder whether they do indeed represent real changes in the pattern of relative growth between scales and body from one year-class to another. While this is theoretically possible, there is no reason to suppose that it should be so for the present data. More likely, these differences are related to the fact that the body-scale regressions of Fig. 9 and 10 are based on different age ranges. Since the data were collected during the period 1953-1958, the regressions for the 1946 year-class are based on ages 7-12, the 1949 year-class on ages 4-9, the 1952, 1953 and 1955 year-classes on ages 1-6, 1-5 and 1-3 respectively. Thus the regressions in each area tend to fall into two groups: those based on older fish of the two oldest year-classes, with slope and intercept values less than 4 and greater than 10 respectively, and those based on younger fish of the three most recent year-classes, with slope and intercept values greater than 4 and less than 10 respectively.

The combined regressions for each area (Fig. 12) tend to have a greater slope and lesser intercept than the individual year-class regressions. The same is true when the regression for a year-class is broken down by ages, and straight lines fitted for each age (Fig. 11 and Table 10). Thus differences of the type noted in Fig. 9 and 10 are inherent in the data, and are to be expected when the data are arranged in this way. Further evidence to support the argument that these differences between year-classes are not real results from the fact that trial growth calculations, using the high intercepts found for the oldest year-classes, resulted in artificially high values of length at age, particularly for the early years. The calculated average values

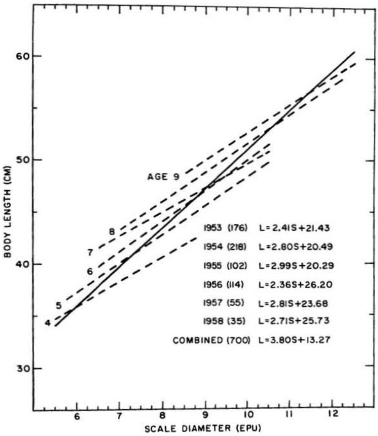


Figure 11. Regressions of body length on scale diameter for each age, 1949 year-class, St. Pierre Bank, 1953 - 1958. The solid line represents the combined regression. Numbers in brackets are numbers of fish.

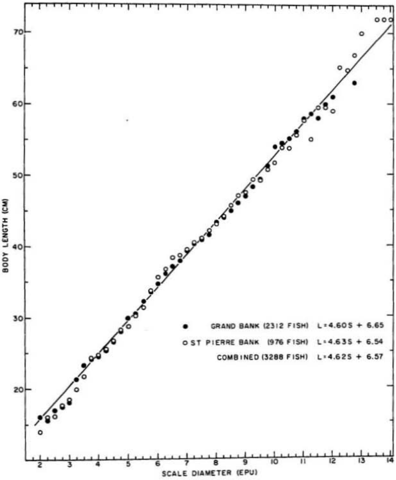


Figure 12. Plots of average body length versus scale diameter for the Grand Bank and St. Pierre Bank. The fitted line represents the combined data.

for age 1 of fish of the 1949 year-class from the Grand Bank were as much as 6 cm above the empirical average for that area.

The overall average values for body length versus scale diameter are listed for the Grand Bank and St. Pierre Bank in Tables 7 and 8 respectively, and are compared graphically in Fig. 12. The fitted regression lines are seen to be quite similar, and analysis of covariance (Table 11) indicates that the slight differences in slope and intercept of the regressions from the two areas are not statistically significant. Thus the combined regression for all the data, i.e.

$$L = 4.62\ S + 6.57 \qquad (48)$$

provides an adequate description of the relation of body length and scale diameter for Newfoundland area haddock.

2. Back-calculated growth

Back-calculations of length at each annulus were made by means of the corrected proportionality formula (38), using the L-intercept value from the general body-scale relationship (48) as the correction factor, i.e.

$$l_n = 6.57 + \frac{s_n}{S}(L-6.57) \qquad (49)$$

where l_n = fish length at annulus n,

s_n = scale diameter at annulus n,

L = fish length at capture, and

S = scale diameter at capture.

The calculations were not made for individual fish. Instead, the scale and length data were first averaged for each year-class, year of capture, sex and maturity, and growth calculations made from the averaged data. Each method gives the same result, as seen in Table 12.

Comparisons of calculated average length at age for immature and mature fish of each sex are shown in Fig. 13 and 14, based on the data of Tables 13 and 14. The comparisons were necessarily restricted to those year-classes containing reasonably large numbers of immature and mature fish. It is obvious from the numbers of fish available in each category (bottom section of

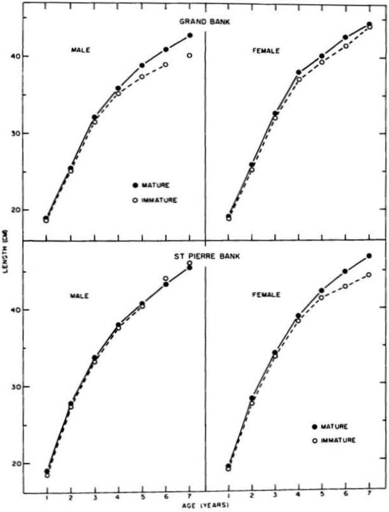


Figure 13. Average length at age of the 1949 year-class by sex and maturity, Grand Bank and St. Pierre Bank. Unconnected points are based on less than 5 fish.

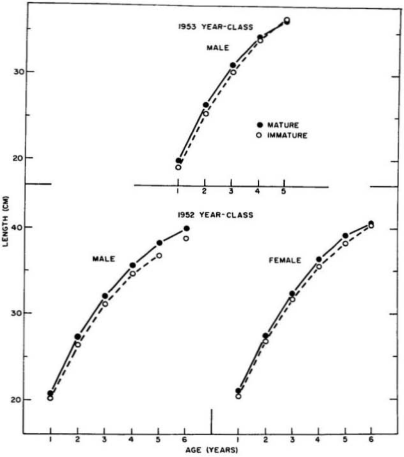


Figure 14. Average length at age of immature and mature males and females of the 1952 year-class, and immature and mature males of the 1953 year-class from the Grand Bank. The unconnected point is based on less than 5 fish.

Tables 13 and 14) that first maturity in males occurs mainly within the age range 4-6, and in females mainly within the range 5-7. This being so, and since the data were collected during the period 1953-1958, very few immature fish were present in the 1946 year-class material (ages 7-12), and few or no mature fish for females of the 1953 year-class (ages 1-5) and both sexes of the 1955 and 1956 year-classes (ages 1-3 and 1-2 respectively). Comparing the back-calculated average lengths at age shown in Fig. 13 and 14, it is seen that the averages for mature fish are almost always greater than those for immatures, though the differences tend to be minimized at the oldest ages. The latter is particularly noticeable in Fig. 14.

Calculated average lengths at age for each of the major year-classes, by sex and year of capture, are listed in Tables 15-19. Summaries by year-class and sex are given for the Grand Bank and St. Pierre Bank respectively in Tables 20 and 21. The data are presented in this detailed form in order to determine whether Lee's phenomenon occurs. This, as described in Section II.C.3, refers to a progressive decrease in back-calculated lengths at age when the calculations are made from successively older fish. Examination of

Tables 15 and 16 reveals no consistent trends in back-calculated lengths at age for the 1946 and 1949 year-classes from each area. However, the Grand Bank data of Tables 17 and 18 (1952 and 1953 year-classes respectively), and both the Grand Bank and St. Pierre Bank data of Table 19 (1955 year-class), show a trend toward increase in calculated average lengths at age, or the reverse of Lee's phenomenon, from the youngest to the oldest fish. This is particularly marked for the 1955 year-class (Table 19). A possible reason for this is proposed in the next section.

With reference to growth of the sexes, it is seen from Tables 15-19, and the summaries of Tables 20 and 21, that calculated average lengths of females tend to be greater than those of males at each age. The summary data for each sex of Tables 20 and 21 are shown graphically for the Grand Bank and St. Pierre Bank respectively in Fig. 15 and 16.

Growth of the major year-classes may also be compared by examination of the summary data of Tables 20 and 21, and plots of this data are presented for the Grand Bank and St. Pierre Bank respectively in Fig. 17 and 18. For the Grand Bank there is a general trend, at least beyond age 1, toward lower average lengths proceeding from the oldest to the most recent year-classes. The same trend is present in the St. Pierre Bank data for the 1946, 1949 and 1952 year-classes, but does not hold for the more recent ones. In each area the differences in average length at age between year-classes are very marked for the 1946 year-class at age 3 and above in comparison with all others. It may also be noted from Tables 20 and 21 that average lengths at age of "other" year-classes, these being largely fish born in the 1940's, are also very high.

Average lengths at age based on combined data from the Grand Bank and St. Pierre Bank (Tables 20 and 21 respectively) are plotted in Fig. 19. The St. Pierre Bank averages are seen to be greater than those of the Grand Bank from age 2 onwards. Von Bertalanffy growth curves have been fitted to the data (Tables 22 and 23) and are plotted in Fig. 19. The higher k, and lower L_∞ values for St. Pierre Bank indicate that the curves would cross over when extrapolated beyond age 7.

The ultimate test of the adequacy of the back-calculation method is a comparison of back-calculated

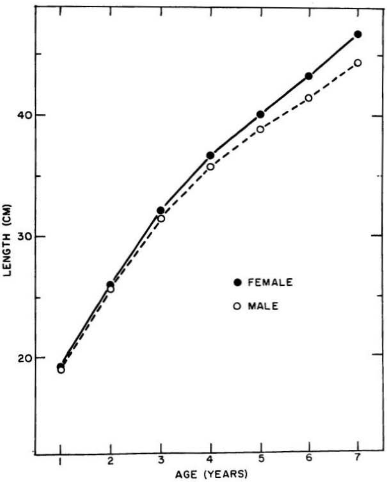


Figure 15. Average length at age of male and female haddock from the Grand Bank.

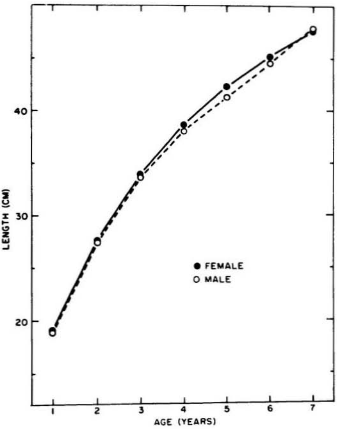


Figure 16. Average length at age of male and female haddock from St. Pierre Bank.

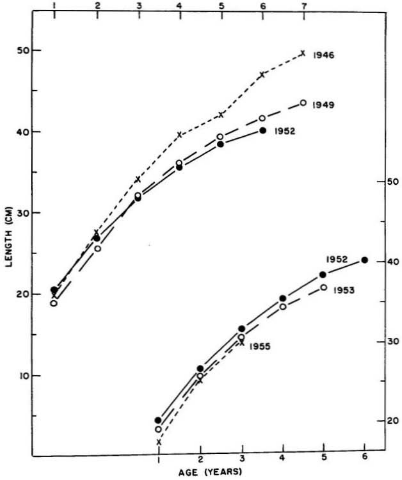


Figure 17. Average length at age for each year-class, Grand Bank.

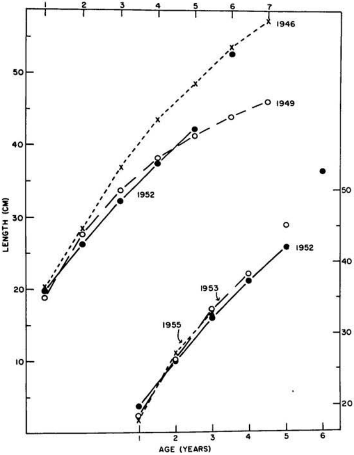


Figure 18. Average length at age for each year-class, St. Pierre Bank. Unconnected points are based on less than 5 fish.

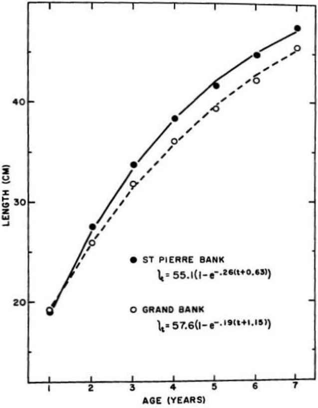


Figure 19. Average length at age and fitted growth curves for the Grand Bank and St. Pierre Bank.

and empirical data, i.e. lengths and ages at capture. Tables 20 and 21 give a comparison of the back-calculated and empirical averages for each area. The empirical averages are generally lower, though seldom by more than 1 centimetre.

In order to determine whether growth compensation occurs in haddock of the Newfoundland area, growth calculations were made from individual fish of the Grand Bank 1949 and 1952 year-classes at age 5. These data were then arranged in ascending order of calculated length at age 1, and are shown in summary form in Table 24. If growth compensation occurred, it would be expected that fish which began life as slow growers would later tend to grow relatively faster than those which began life as fast growers, and vice versa. The result would be a tendency toward attainment of the same final size from different initial sizes. Ignoring those calculations based on only 1 or 2 fish, there is little indication of this in Table 24. Although a good deal of variability exists, it is obvious that fish which have a larger size at age 1 tend to retain this size advantage throughout life. In fact, plots of selected data for each year-class (Fig. 20 and 21) show that the growth curves tend to be parallel, and that

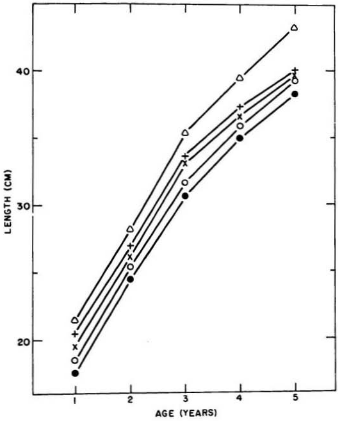


Figure 20. Comparison of calculated average lengths at ages 2 - 5 for fish having calculated average lengths at age 1 of 17.5, 18.5, 19.5, 20.5 and 21.5 cm, 1949 year-class, Grand Bank.

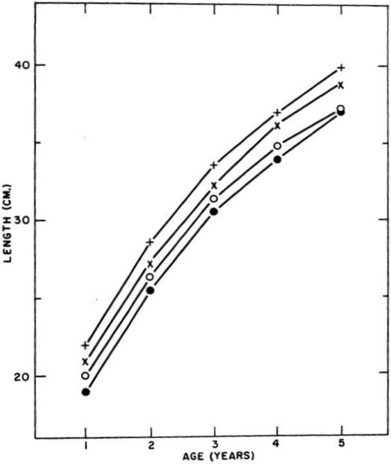


Figure 21. Comparison of calculated average lengths at ages 2 - 5 for fish having calculated average lengths at age 1 of 19.0, 20.0, 21.0 and 22.0 cm, 1952 year-class, Grand Bank.

the order of difference in calculated lengths at the older ages is similar to the difference at age 1. This would indicate a tendency for fish to attain the same rate of growth in later life, but this tendency is not sufficient to cancel out differences in attained sizes due to differential growth in early life.

An effect similar to that of growth compensation might be supposed to be present in growth curves of the Grand Bank 1946 and 1949 year-classes shown in Fig. 17. The growth curves for other year-classes and for St. Pierre Bank (Fig. 18) show the typical pattern of continuous bending over with time. However, the abnormally low average at age 2 for the 1949 year-class, and age 5 for the 1946 year-class, causes the curve to straighten out between ages 1 and 3 in the former case, and gives it a convex shape between ages 4 and 6 in the latter. The straightness between ages 1 and 3 is also evident in the 1949 year-class data of Fig. 20. The low average at age 2 for the 1949 year-class (Fig. 17) causes the growth curve to pass below that of the 1952 year-class, in contrast to the St. Pierre Bank pattern for the 2 year-classes (Fig. 18). However, the fact that the curve approaches a straight line in the one case, and even becomes convex in the other, shows that there is a tendency to recover in the following year and so "compensate" for the previous slow growth. It is not likely, however, that this is due to any inherent compensatory mechanism. It may be noted that the low averages at ages 2 and 5 for the 1949 and 1946 year-classes respectively both occurred in the same growing year, i.e. 1950-51, resulting from abnormally small scale growth in that year. In fact, growth of the scales was so slight that the retarded growth in this year served as a mark to aid age interpretation. On the other hand, scale growth in 1951-52 was abnormally great. This is well-illustrated in Fig. 22 for scales of each year-class. It is known that water temperatures over the Grand Bank were much colder than normal in 1950 and warmer than normal in 1951. Temperatures from surface to bottom along the 150-fathom contour of the southwest slope of the Grand Bank are shown for March, 1950 and 1951 in Fig. 23. The shaded area of each section, representing water of temperature less than 0°C, affords a good comparison of the thermal environment in each of these years. Since at this time of year the haddock usually occupy depths of 65-150 fathoms and temperatures between 2.5 and 9°C (Templeman and Hodder, MS, 1964a) it is obvious that they must have been

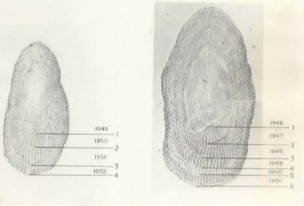
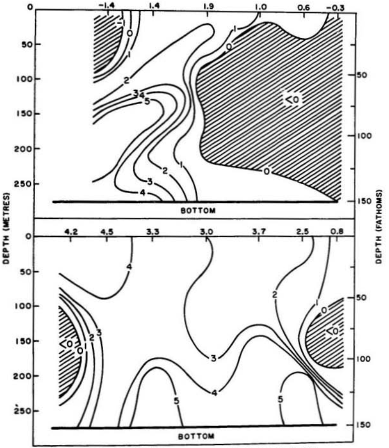


Figure 22. Scales of haddock of age 4 from the 1949 year-class, and age 6 from the 1946 year-class, both from the Grand Bank, to show poor growth in 1950 and good growth in 1951. (X20).



Above: Mar. 10–14, 1950 Below: Mar. 10–16, 1951

Figure 23. Vertical temperature profiles at 150 fathoms along the southwest slope of the Grand Bank in March, 1950 and 1951. Temperatures are in degrees C.

excluded from large areas of the bank in 1950, while in 1951 the conditions were ideal, allowing maximum dispersal. Thus the poor growth in 1950 and good growth in 1951 was in each case very likely related to temperature conditions, acting either directly on metabolic rate or indirectly through varying competition for food as a result of varying density of fish.

D. DISCUSSION AND CONCLUSIONS

Many authors (e.g. Lee, 1920; Carlander and Smith, 1944; Rounsefell and Everhart, 1953) have attempted to invest the L-intercept of body-scale regressions with a biological meaning, regarding it as the fish length at time of scale formation. Some have taken the trouble to determine this length by direct observation. Thus Lee (1920) gives values of 3-5 cm for length at scale formation in herring, and Thompson (1922) gives 3 cm for haddock. The fallacy of this approach has been discussed in Section II.C.3. A fish must attain some length before the scales are formed, and in early life the scales must grow proportionately faster than the body in order to overlap. Martin (1949) states that "the relative growth of any body part ..... is characterized by a series of relative-growth stanzas that differ in slope and in the size range over which each is applicable," and that the size of the animal at the inflections which delimit these stanzas is important in determination of form. For haddock it is apparent that such an inflection in the body-scale regression must occur before the end of the first year. Certainly the L-intercepts of Fig. 7-12 cannot bear any relation to time of scale formation.

Molander (1918, Lee (1920) and Ottestad (1938) have observed that in fish of the same length, but different ages, the older fish have larger scales than the younger. Thus the scales are not developed to the same degree in fast-growing fish. Martin (1949) has shown that the fast-growing individuals of a group have relatively small body parts, but that a fast growing group of individuals may have relatively small or relatively large body parts. The regressions of Fig. 11 indicate that the latter applies to relative growth of scales and body in Newfoundland area haddock. Thus at a particular length the younger fish tend to have larger scales than the older, i.e. fast-growing fish have larger scales than slow growers of the same length. In the regressions of Fig. 11 the slopes for each age are less than the overall slope. If the within age slopes were greater than the overall slope the condition observed by Molander (1918), Lee (1920) and Ottestad

(1938) would apply.

It was noted in Fig. 13 and 14 that lengths back-calculated from mature fish were on the average greater than those for immature fish from age 1 onwards, with a tendency for the differences to be minimized at the oldest ages. It would thus appear that mature fish were faster growing in the early years, supporting the generally accepted contention (e.g. Jones, 1958) that fast-growing fish mature at an earlier age than slow growers. The fact that the curves tend to come together at the oldest ages (Fig. 13 and 14) indicates that onset of maturity and development of the gonads has slowed growth in the maturing fish and allowed the remaining immatures at these ages to catch up. These relations could be better examined if it were possible to tell the age at first maturity from the scale, i.e. to determine, for example, whether a 6-year-old mature fish has matured for the first time at age 6 or at some earlier age. Presumably those fish maturing at the earliest ages would be the fastest growing of all. Rollefsen (1933) has determined age at first maturity from cod otoliths, but neither otoliths nor scales of Newfoundland area haddock lend themselves to this sort of interpretation.

Fig. 15 and 16 show that females are of greater average length than males from age 1 onwards, and that the differences tend to increase with age. The exception for fish of age 7 in Fig. 16 was caused by a reversal of this trend in a few old fish (Table 21). Saemundsson (1925) shows average lengths of females to be greater than those of males for Icelandic haddock from age 2 onwards. Greater growth of females is the general finding in fisheries biology, and is usually explained by the fact that females tend to mature at a later age than males. Thus growth of males is slowed at an earlier age due to development of the gonads. This does not explain why the females should have an advantage in size, however slight, at the earliest ages.

The differences in year-class growth evident in Fig. 17 and 18 are probably best explained by a combination of factors. The reduction in growth of the 1949 year-class as compared to that of 1946 may have been due to the great abundance of the former, resulting in increased competition for food. Although fish of both year-classes would be present after 1949, those of 1946 would be 3 years older and probably would compete more effectively for food, thus would not suffer reduced growth. The great abundance of the 1949 year-class on the Grand Bank might also, through competition, have influenced growth of the succeeding year-classes (Fig. 17). Though competition between the 1949 year-class and the later year-classes would not be important at the smallest sizes of the latter, it would have an increasing effect with time. Further evidence to support this argument comes from the fact that recent (unpublished) data collected by the St. John's Biological Station indicate an increase in growth on the Grand Bank as the population has decreased. Templeman (MS, 1964a) has shown that during the years 1950-1962, mean annual water temperatures at a hydrographic station near St. John's have shown a slight downward trend, If such was the case on the Grand Bank as well it could have had a detrimental effect on growth. Again, on St. Pierre Bank the great abundance of the 1949 year-class probably caused the decline in growth as compared to the 1946 year-class. The 1952 and 1953 year-classes were very small, and show no further decline (Fig. 18). The 1955 year-class, which experienced moderate survival, would not suffer from competition since by 1956-1958 the St. Pierre Bank population had become relatively small.

Tables 20 and 21 show slight differences between calculated and empirical average lengths at age, with the empirical averages tending to be lower. This is to be expected in the present material since not all of the fish had completed their "annual" growth at the time of collection of the data. Although a fish of age 5, for example, shows narrow sclerites at the edge of the scale, it is possible that more narrow sclerites would have formed, and more growth occurred, had the fish escaped capture. Thus the empirical averages tend to be less than the calculated ones, the latter being heavily weighted by calculations for years inside the scale edge, where the end of "annual" growth can be delimited with certainty.

Although Lee's phenomenon was not present in any of the data, the reverse trend was shown for fish of the 1952, 1953 and 1955 year-classes from the Grand Bank and the 1955 year-class from St. Pierre Bank (Tables 17-19). Taylor (1958) gives regressions of length at age 2 on length at age 1, length at age 3 on length at age 1, etc. for each age of capture of Georges Bank haddock and shows that the regressions of each group tend to intersect at a common point. He states that Lee's phenomenon would not occur if the range of sizes at age 1 were near such a point of intersection, and would occur in reverse form above such a point. In the present data this might explain the absence of Lee's phenomenon in the 1946 and 1949 year-class material, but since average lengths at age 1, and presumably the range of sizes at age 1, are lower for the more recent year-classes, it would be expected that Lee's phenomenon would occur in these in its usual form. It need not, however, if Taylor's points of intersection were different for the different year-classes.

Values of average length at age for Grand Bank and St. Pierre Bank haddock are compared with earlier Newfoundland area data, and data from other areas of the Northwest Atlantic in Table 25. Thompson's (1939) values were back-calculated from scales, and like those of the present material, were slightly higher than empirical values. Thompson's material covers both the Grand Bank and St. Pierre Bank, but was largely from the southwest Grand Bank. Wise's (1957) data were also back-calculated from scales, while those of Schuck and Arnold (1951) are based on scale readings. Kohler(s (1960) material is based on otolith ages. Wise (1957) and Kohler (1960) give fitted von Bertalanffy growth curves for their data. The author has fitted such curves for ages 1-7 of Thompson's (1939) material and ages 1-5 of that of Schuck and Arnold (1951). The point at age 6 in Schuck and Arnold's material was based on only 6 fish. The parameters of the various curves are compared in Table 25, and curves for the offshore banks of Newfoundland, Nova Scotia and New England are shown in Fig. 24. It may be noted from Table 25 that average length at age in the Newfoundland area has declined greatly since the 1930's, and present values are generally lower than for recent data of other areas. Figure 24 shows that average length at age increases from north to south, at least for ages 1-6. However, the low L_∞ and high K values for Georges Bank, indicate that although growth in this area is very rapid in the early years, it quickly tapers off to a relatively low ultimate size. On the other hand, extrapolation of these fitted curves must be regarded with some caution. Jones (1962) and May _et al_ (MS, 1964) have noted that the estimated values of L_∞ and K are very susceptible to small changes in the observed data, and Taylor (1962) shows that unrealistic values of L_∞ may be obtained by the usual method of estimation. Thus while the curves of Fig. 24 provide an adequate description of growth for the ages on which they are based, the age range is not sufficient to allow meaningful comparison of extrapolated values.

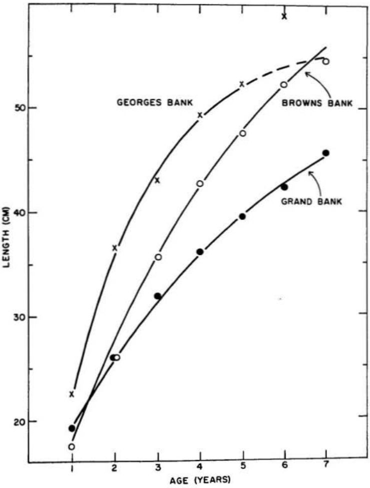


Figure 24. Comparison of haddock growth from the Newfoundland, Nova Scotian and New England regions. The parameters of the fitted curves and sources of data are given in Table 25.

E. ACKNOWLEDGEMENTS

The author wishes to acknowledge with sincere gratitude the assistance of many persons in the collection, analysis and ultimate presentation of the foregoing material. The study was suggested and directed by Dr. W. Templeman, who also provided scale ages for the greater part of the material. The author's training in the reading and measuring of scales was accomplished under the direction of Mr. V.M. Hodder, who was also responsible for construction of the scale projector. Mr. Hodder also provided the material for Fig. 3.

The original manuscript was read by Dr. Templeman and Mr. Hodder, and their many useful suggestions for improvement are gratefully acknowledged.

Many technicians of the St. John's Biological Station have assisted in collection of material, mounting of scales and preparation of the material for analysis. Particular thanks are due to Mr. N. Batten, who was associated with the study from the beginning and who prepared most of the figures, and to Mr. E. Rowe, who was responsible for the photographic reproductions.

Finally, the timely presentation of the material has been due in no small part to the encouragement of an understanding wife, and the typing ability of a willing sister.

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APPENDIX I - LIST OF FIGURES

APPENDIX II - TABLES

Table 1. Newfoundland area haddock landings in metric tons, 1945 to 1962.

Year	Southern Grand Bk.	St. Pierre Bank	Other[(2)]	Canada	Other Countries	Total
1945				701	7770	8471
1946				3258	14990	18248
1947				6263	17447	23710
1948				14593	42442	57035
1949				14855	63656	78511
1950				12184	49557	61741
1951				4153	47143	51286
1952				7644	38883	46527
1953	35248	5849	1738	14126	28709	42835
1954	24528	27587	3220	32269	23066	55335
1955	44072	58032	2367	43153	61318	104471
1956	50246	29940	4096	48396	35886	84282
1957	57988	6079	4019	34603	33483	68086
1958	39278	956	4150	23405	20979	44384
1959	27328	2777	4935	22330	12710	35040
1960	61800	4159	525	18970	47514	66484
1961	74703	2858	2093	30414	49240	79654
1962	32759	1557	829	28421	6724	35145

Notes

(1) Statistics for 1945 - 1957 from Hodder (MS, 1962a), for 1958 - 1962 from ICNAF Statistical Bulletins, Vol. 8 - 12.

(2) Includes amounts not allocated to a specific area, and small amounts from the northern Grand Bank and Flemish Cap.

(3) 1 metric ton = 2204.6 pounds.

Table 2. Numbers of scales examined by year-class for each year and area.

Year	Year-classes - Grand Bank							
	1946	1949	1952	1953	1955	1956	Other	Total
1953	32	221	2	-	-	-	17	272
1954	16	219	64	19	-	-	22	340
1955	17	399	117	34	-	-	27	594
1956	6	137	131	70	23	-	10	377
1957	1	48	68	36	209	3	1	366
1958	0	24	63	60	192	20	4	363
Total	72	1048	445	219	424	23	81	2312

Year	Year-classes - St. Pierre Bank							
	1946	1949	1952	1953	1955	1956	Other	Total
1953	5	176	0	-	-	-	4	185
1954	2	218	2	8	-	-	5	235
1955	2	102	0	0	-	-	6	110
1956	1	114	2	1	37	-	4	159
1957	4	55	18	3	49	0	4	133
1958	2	35	1	2	55	30	29	154
Total	16	700	23	14	141	30	52	976

Table 3. Average fish lengths at scale diameter intervals of 0.25 EPU by sexes, Grand Bank and St. Pierre Bank, 1953 - 1958. Numbers in brackets are numbers of fish.

Midpoint of scale diameter interval	Grand Bank		St. Pierre Bank	
	Males	Females	Males	Females
2.00	15.3(3)	18.0(1)		14.0(1)
2.25	15.5(2)	-		16.0(2)
2.50	16.9(7)	17.2(5)	16.3(4)	16.0(1)
2.75	17.0(6)	18.0(5)	17.5(10)	18.3(4)
3.00	17.9(7)	18.7(3)	18.3(7)	19.0(3)
3.25	20.8(8)	22.5(4)	19.9(8)	20.0(2)
3.50	23.2(13)	23.4(13)	21.8(5)	21.7(7)
3.75	24.4(26)	23.9(13)	23.7(9)	22.6(5)
4.00	24.8(33)	24.6(32)	24.4(8)	25.3(6)
4.25	25.4(36)	25.6(39)	25.0(4)	26.0(6)
4.50	26.2(35)	26.7(46)	26.0(8)	27.4(10)
4.75	28.5(56)	27.6(40)	28.0(7)	28.6(7)
5.00	29.6(45)	30.3(35)	30.2(6)	28.0(10)
5.25	30.6(50)	30.7(45)	30.6(8)	29.3(3)
5.50	32.4(64)	32.2(37)	32.5(4)	30.9(9)
5.75	33.3(62)	33.7(56)	33.2(11)	36.5(2)
6.00	35.0(53)	34.6(52)	36.3(15)	35.1(14)
6.25	36.0(67)	36.5(53)	36.7(27)	37.0(15)
6.50	36.9(78)	37.6(59)	38.3(28)	38.5(25)
6.75	37.8(85)	38.2(74)	38.4(32)	39.2(37)
7.00	38.9(90)	39.9(78)	39.4(37)	39.5(32)
7.25	39.9(70)	40.7(76)	39.6(29)	41.3(34)
7.50	40.6(69)	41.4(73)	41.1(40)	41.2(24)
7.75	41.2(55)	41.9(68)	41.9(27)	42.5(47)
8.00	43.5(40)	43.3(51)	42.9(27)	43.4(24)
8.25	43.6(29)	44.6(35)	43.9(18)	44.4(23)
8.50	44.2(26)	45.8(25)	44.8(20)	46.6(26)
8.75	45.7(14)	46.3(28)	46.6(11)	47.5(15)
9.00	45.9(11)	47.7(15)	47.4(19)	47.8(10)
9.25	48.2(6)	48.6(12)	49.3(8)	49.5(12)
9.50	48.8(4)	49.6(12)	49.3(11)	49.3(11)
9.75	49.4(5)	52.6(9)	50.6(12)	51.1(12)
10.00	53.0(3)	54.4(7)	51.3(6)	52.0(6)
10.25	54.3(7)	54.7(7)	53.8(4)	54.0(5)
10.50	54.6(5)	56.0(3)	52.9(7)	54.7(7)
10.75	54.8(4)	57.2(6)	-	55.6(9)
11.00	56.0(1)	60.0(1)	57.5(2)	58.0(4)
11.25	55.5(4)	61.8(4)	55.0(5)	-
11.50	58.0(2)	-	59.7(3)	59.0(1)
11.75	58.5(2)	61.0(3)	59.5(2)	-
12.00	62.0(1)	60.0(1)	-	59.0(1)
12.25		-	61.5(2)	67.7(3)
12.50		-	61.0(2)	72.0(1)
12.75		63.0(2)	67.0(1)	-
13.00			72.0(1)	68.0(1)
13.25			-	
13.50			72.0(1)	
13.75			72.0(2)	
14.00			72.0(1)	
Total fish	1184	1128	499	477

Table 4. Comparisons of the regressions of body length on scale diameter by analysis of covariance for the sexes, Grand Bank and St. Pierre Bank. (The double asterisk indicates significance at the 1% level).

		Errors of Estimate			
Test	Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Between sexes, Grand Bank	Within Samples	2308	12613.52	5.465	10.61 **
	Reg. Coefficients	1	57.99	57.985	
	Common Regression	2309	12671.50	5.488	19.61 **
	Adjusted Means	1	107.62	107.617	
	Total	2310	12779.12		

At df 1 and ∞: F(.05) = 3.84, F(.01) = 6.64.

Between sexes, St. Pierre Bank	Within Samples	972	6373.31	6.557	1.56
	Reg. Coefficients	1	10.25	10.247	
	Common Regression	973	6383.56	6.561	10.88 **
	Adjusted Means	1	71.36	71.360	
	Total	974	6454.92		

At df 1 and 1000: F(.05) = 3.85, F(.01) = 6.66.

Table 5. Equations for regressions of body length on scale diameter for the sexes within each year-class, Grand Bank and St. Pierre Bank.

Area	Year-classes	Sex	No. Fish	Fitted Regressions
Grand Bank	1946	M	26	L = 3.66S + 15.55
		F	46	L = 3.70S + 16.22
	1949	M	535	L = 3.44S + 14.96
		F	513	L = 3.69S + 14.10
	1952	M	219	L = 4.14S + 9.28
		F	226	L = 4.18S + 9.01
	1953	M	121	L = 4.50S + 6.87
		F	98	L = 4.05S + 9.23
	1955	M	227	L = 4.51S + 6.40
		F	197	L = 4.55S + 6.33
	Other	M	56	L = 4.63S + 6.09
		F	48	L = 4.80S + 5.83
St. Pierre Bank	1946	M	9	L = 3.62S + 18.91
		F	7	L = 2.75S + 30.59
	1949	M	354	L = 3.71S + 13.61
		F	346	L = 3.86S + 13.10
	1952	M	14	L = 3.86S + 11.57
		F	9	L = 4.62S + 5.92
	1953	M	10	L = 4.95S + 4.12
		F	4	L = 4.60S + 6.64
	1955	M	67	L = 4.78S + 4.84
		F	74	L = 4.71S + 5.31
	Other	M	45	L = 4.93S + 4.38
		F	37	L = 5.04S + 4.27

Table 6. Summary of covariance analyses for regressions of body length on scale diameter for the sexes within each year-class, Grand Bank and St. Pierre Bank. (A single asterisk indicates significance at the 5% level, a double asterisk significance at the 1% level).

Area	Year-class	Mean Squares		F	Mean Squares		F
		Within Samples	Reg. Coeff.		Common Regression	Adjusted Means	
Grand Bank	1946	7.146	.023	.003	7.043	17.744	2.52
	1949	5.350	11.936	2.23	5.356	799.927	149.35 **
	1952	4.510	.139	.03	4.500	1.081	.24
	1953	3.027	18.047	5.96 *	3.097	.701	.23
	1955	3.296	.086	..03	3.288	.457	.14
	Other	10.439	4.842	.46	10.384	28.343	2.73
St. Pierre Bank	1946	8.639	3.270	.38	8.226	10.622	1.29
	1949	5.766	5.916	1.03	5.766	85.082	14.76 **
	1952	6.956	7.158	1.03	6.966	.172	.02
	1953	5.816	1.529	..26	5.426	1.045	.19
	1955	3.644	.275	.08	3.620	1.070	.30
	Other	5.378	2.784	.52	5.345	6.028	1.13

Table 7. Average fish lengths at scale diameter intervals of 0.25 EPU by year-classes, Grand Bank, 1953 - 1958. Numbers in brackets are numbers of fish.

MP of sc. diam. int.	Year - classes 1946	1949	1952	1953	1955	Other	Overall Average
2.00				17.5(2)	14.5(2)		16.0(4)
2.25				-	15.5(2)		15.5(2)
2.50				19.5(2)	16.4(9)	17.0(1)	17.0(12)
2.75				18.7(3)	16.7(6)	18.0(2)	17.5(11)
3.00				18.1(7)	18.0(3)	-	18.1(10)
3.25			24.0(1)	20.0(5)	22.0(6)	-	21.3(12)
3.50			23.6(5)	22.8(5)	23.4(16)	-	23.3(26)
3.75			24.3(3)	25.0(7)	24.0(27)	24.0(2)	24.2(39)
4.00			25.1(13)	25.8(5)	24.5(44)	25.3(3)	24.7(65)
4.25			26.0(9)	25.9(10)	25.4(50)	24.7(6)	25.5(75)
4.50			26.8(12)	27.0(7)	26.4(58)	26.0(4)	26.5(81)
4.75			28.3(25)	28.2(19)	28.1(47)	26.8(5)	28.1(96)
5.00		32.5(2)	29.7(18)	29.9(13)	30.0(45)	26.5(2)	29.9(80)
5.25		36.0(1)	31.1(29)	31.1(15)	30.1(50)	-	30.6(95)
5.50		34.8(6)	32.5(40)	32.6(22)	31.0(28)	34.8(5)	32.3(101)
5.75		34.9(37)	33.4(44)	32.8(16)	31.7(20)	34.0(1)	33.5(118)
6.00		35.7(47)	34.0(31)	34.5(21)	32.7(6)	-	34.8(105)
6.25		36.8(68)	35.9(38)	35.1(10)	32.5(4)	-	36.2(120)
6.50		37.6(86)	36.6(40)	36.4(9)	34.0(1)	34.0(1)	37.2(137)
6.75		38.3(103)	37.6(39)	36.6(16)		44.0(1)	38.0(159)
7.00	41.0(1)	40.0(119)	38.4(35)	36.2(13)		-	39.4(168)
7.25	-	40.5(120)	38.8(18)	39.3(4)		41.0(4)	40.3(146)
7.50	-	41.2(120)	39.9(16)	39.3(4)		43.5(2)	41.0(142)
7.75	-	41.8(103)	39.9(13)	40.5(2)		42.4(5)	41.6(123)
8.00	49.0(2)	43.4(75)	41.3(7)	39.0(1)		45.2(6)	43.4(91)
8.25	46.3(4)	44.1(52)	43.2(6)	39.0(1)		45.0(1)	44.1(64)
8.50	48.5(4)	44.8(43)	42.0(2)			45.5(2)	45.0(51)
8.75	47.9(9)	45.4(26)	44.0(1)			47.0(6)	46.1(42)
9.00	48.4(5)	46.8(19)				44.5(2)	47.0(26)
9.25	49.7(9)	47.2(9)				-	48.4(18)
9.50	49.8(8)	47.3(3)				50.0(5)	49.4(16)
9.75	49.0(3)	49.2(5)				54.5(6)	51.4(14)
10.00	55.5(4)	50.0(1)				53.6(5)	54.0(10)
10.25	54.7(10)	-				54.0(4)	54.5(14)
10.50	54.0(1)	60.0(1)				54.5(6)	55.1(8)
10.75	55.5(4)	58.0(1)				56.4(5)	56.2(10)
11.00	58.0(2)	-				-	58.0(2)
11.25	56.0(5)	-				63.0(3)	58.6(8)
11.50	-	57.0(1)				59.0(1)	58.0(2)
11.75	-					60.0(5)	60.0(5)
12.00	62.0(1)					60.0(1)	61.0(2)
12.25						-	-
12.50						-	-
12.75						63.0(2)	63.0(2)
Total fish	72	1048	445	219	424	104	2312

Table 8. Average fish lengths at scale diameter intervals of 0.25 EPU by year-classes, St. Pierre Bank, 1953 - 1958. Numbers in brackets are numbers of fish.

MP of sc. diam. int.	Year - classes 1946	1949	1952	1953	1955	Other	Overall Average
2.00					14.0(1)		14.0(1)
2.25				17.0(1)	15.0(1)		16.0(2)
2.50				16.0(1)	16.3(4)		16.2(5)
2.75				17.8(5)	16.0(3)	18.5(6)	17.7(14)
3.00				-	18.5(4)	18.5(6)	18.5(10)
3.25				18.0(1)	-	20.1(9)	19.9(10)
3.50			22.0(1)	-	22.6(7)	20.3(4)	21.8(12)
3.75			25.0(1)	-	23.4(10)	22.3(3)	23.3(14)
4.00			-	-	24.6(10)	25.3(4)	24.8(14)
4.25			-	-	25.6(7)	25.7(3)	25.6(10)
4.50			-	-	26.1(13)	28.6(5)	26.8(18)
4.75			-	-	27.4(7)	29.1(7)	28.3(14)
5.00			-	-	28.8(10)	28.8(6)	28.8(16)
5.25			-	-	30.1(10)	32.0(1)	30.3(11)
5.50		36.0(1)	-	-	31.1(10)	30.5(2)	31.4(13)
5.75		36.5(6)	-	-	31.3(7)	-	33.7(13)
6.00		37.3(19)	-	-	32.8(10)	-	35.7(29)
6.25		37.0(36)	-	-	35.8(6)	-	36.8(42)
6.50		38.5(43)	-	-	37.7(10)	-	38.4(53)
6.75		39.0(62)	39.0(2)	37.7(3)	35.5(2)	-	38.8(69)
7.00		39.5(62)	38.0(2)	44.0(1)	38.0(4)	-	39.5(69)
7.25		40.7(59)	41.0(2)	-	36.5(2)	-	40.5(63)
7.50		41.1(61)	40.0(1)	-	42.0(1)	42.0(1)	41.1(64)
7.75		42.3(71)	41.5(2)	-	40.0(1)	-	42.2(74)
8.00		43.0(49)	-	45.0(1)	-	46.0(1)	43.1(51)
8.25		44.3(37)	44.0(2)	-	41.0(1)	44.0(1)	44.2(41)
8.50		45.9(40)	44.4(5)	-		49.0(1)	45.8(46)
8.75		47.4(24)	43.0(1)	-		45.0(1)	47.1(26)
9.00		47.4(25)	44.5(2)	-		51.5(2)	47.5(29)
9.25		49.2(19)	53.0(1)	-		-	49.4(20)
9.50		49.3(20)	-	47.0(1)		51.0(1)	49.3(22)
9.75		50.8(22)	-			51.0(2)	50.8(24)
10.00	57.5(2)	50.6(9)	50.0(1)			-	51.7(12)
10.25	57.0(1)	53.5(8)				-	53.9(9)
10.50	60.0(2)	53.0(11)				50.0(1)	53.8(14)
10.75	-	54.5(6)				57.7(3)	55.6(9)
11.00	60.0(1)	58.7(3)				55.5(2)	57.8(16)
11.25	59.0(2)	52.3(3)				-	55.0(5)
11.50	59.7(3)	59.0(1)				-	59.5(4)
11.75	-	56.0(1)				63.0(1)	59.5(2)
12.00	59.0(1)	-				-	59.0(1)
12.25	68.0(1)	58.0(1)				66.7(3)	65.2(5)
12.50	62.0(1)	60.0(1)				72.0(1)	64.7(3)
12.75	-					67.0(1)	67.0(1)
13.00	68.0(1)					72.0(1)	70.0(2)
13.25	-					-	-
13.50	-					72.0(1)	72.0(1)
13.75	-					72.0(2)	72.0(2)
14.00	72.0(1)						72.0(1)
Total fish	16	700	23	14	141	82	976

Table 9. Comparisons of the regressions of body length on scale diameter by analysis of covariance for the various year-classes from the Grand Bank and St. Pierre Bank. (The double asterisk indicates significance at the 1% level).

		Errors of Estimate			
Test	Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Between year-classes, Grand Bank	Within Samples	2198	10944.18	4.979	14.60 **
	Reg. Coefficients	4	290.69	72.672	
	Common Regression	2202	11234.87	5.102	21.11 **
	Adjusted Means	4	430.83	107.707	
	Total	2206	11665.70		

At df 4 and ∞ : F(.05) = 2.37, F(.01) = 3.32.

Between year-classes, St. Pierre Bank	Within Samples	884	4922.27	5.568	11.02 **
	Reg. Coefficients	4	245.48	61.370	
	Common Regression	888	5167.75	5.820	29.21 **
	Adjusted Means	4	679.97	169.992	
	Total	892	5847.71		

At df 4 and 1000: F(.05) = 2.38, F(.01) = 3.34.

Table 10. Average fish lengths at scale diameter intervals of 0.25 EPU by ages for the 1949 year-class, St. Pierre Bank, 1953 - 1958. Numbers in brackets are numbers of fish.

MP of sc. diam. int.	Year					
	1953	1954	1955	1956	1957	1958
5.50	36.0(1)					
5.75	34.0(3)	39.0(3)				
6.00	36.5(10)	38.1(9)				
6.25	36.1(18)	37.9(18)				
6.50	37.7(19)	38.6(20)	42.0(1)	42.0(3)		
6.75	37.8(33)	39.7(24)	42.0(4)	46.0(1)		
7.00	37.8(24)	39.6(25)	41.4(9)	45.3(3)	45.0(1)	
7.25	39.4(22)	40.5(19)	41.5(13)	44.6(5)	-	
7.50	39.3(20)	41.3(27)	43.4(7)	43.3(7)	-	
7.75	39.4(13)	42.0(25)	43.3(17)	43.5(13)	46.7(3)	
8.00	41.0(9)	42.9(14)	43.5(13)	44.2(12)	44.0(1)	
8.25	41.0(2)	42.6(9)	44.9(13)	45.4(12)	45.0(1)	
8.50	43.0(1)	45.0(9)	44.2(6)	46.9(16)	45.7(6)	49.5(2)
8.75	47.0(1)	45.7(7)	47.0(4)	47.0(7)	51.3(3)	49.5(2)
9.00		46.8(4)	47.3(4)	47.4(10)	47.4(5)	49.5(2)
9.25		46.5(2)	48.4(5)	48.6(7)	52.3(4)	51.0(1)
9.50		48.0(1)	49.0(1)	46.7(6)	50.0(6)	51.5(6)
9.75		-	49.0(2)	50.7(7)	51.3(8)	51.0(5)
10.00		47.0(1)	52.0(1)	49.3(3)	49.0(1)	53.5(2)
10.25		-	53.0(1)	51.0(1)	54.3(3)	53.7(3)
10.50		52.0(1)		54.0(1)	52.5(6)	54.0(3)
10.75					53.0(4)	57.5(2)
11.00					-	58.7(3)
11.25					-	52.3(3)
11.50					59.0(1)	-
11.75					56.0(1)	-
12.00					-	-
12.25					58.0(1)	-
12.50						60.0(1)
Total fish	176	218	102	114	55	35

Table 11. Comparisons of the regressions of body length on scale diameter by analysis of covariance for the Grand Bank and St. Pierre Bank.

Test	Source of variation	Errors of Estimate Degrees of freedom	Sum of squares	Mean square	F
Between areas	Within Samples	3284	19234.04	5.856	0.30
	Reg. Coefficients	1	1.79	1.786	
	Common Regression	3285	19235.83	5.856	2.12
	Adjusted Means	1	12.43	12.432	
	Total	3286	19248.26		

At df 1 and ∞: F(.05) = 3.84, F(.01) = 6.64.

Table 12. Comparison of average lengths at age based on growth calculations for individual fish and calculations for averaged scale and length data. Age 5 fish of the 1949 and 1952 year-classes from the Grand Bank are used to effect the comparisons.

Year-class	No. of fish		Back-calculated average lengths at age 1	2	3	4	5
1949	219	Individuals	19.00	25.76	32.26	36.21	39.32
		Averages	19.00	25.76	32.29	36.25	39.33
1952	68	Individuals	20.82	27.16	32.00	35.60	38.37
		Averages	20.80	27.15	32.01	35.61	38.37

Table 13. Back-calculated average lengths at age of the 1949 year-class by sex and maturity, Grand Bank and St. Pierre Bank, 1953 - 1958. Numbers in brackets are numbers of fish. Also shown are the numbers of fish of each category and age on which the calculations are based.

Age	Grand Bank				St. Pierre Bank			
	Males		Females		Males		Females	
	Immature	Mature	Immature	Mature	Immature	Mature	Immature	Mature
1	18.8(125)	18.9(410)	18.9(239)	19.1(274)	18.5(58)	18.9(274)	18.9(193)	19.3(130)
2	25.1(125)	25.4(410)	25.3(239)	26.0(274)	27.4(58)	27.7(274)	27.5(193)	28.1(130)
3	31.5(125)	32.1(410)	32.1(239)	32.8(274)	33.2(58)	33.7(274)	33.7(193)	34.1(130)
4	35.2(125)	35.9(410)	36.2(239)	37.1(274)	37.6(58)	38.0(274)	38.3(193)	38.9(130)
5	37.4(35)	38.9(382)	39.5(136)	40.3(274)	40.4(12)	40.7(235)	41.4(102)	42.8(130)
6	39.0(23)	41.0(272)	41.6(73)	42.8(240)	44.1(1)	43.3(124)	42.8(28)	44.8(108)
7	40.2(1)	42.8(105)	44.2(4)	44.5(99)	46.0(1)	45.6(69)	44.3(11)	46.8(78)

	Numbers in Collections				Numbers in Collections			
4	90	28	103	-	46	39	91	-
5	12	110	63	34	11	111	74	22
6	22	167	69	141	-	55	17	30
7	-	70	3	64	1	27	11	30
8	1	27	-	20	-	24	-	31
9	-	8	1	15	-	18	-	17
Totals	125	410	239	274	58	274	193	130

Table 14. Back-calculated average lengths at age of immature and mature males and females of the 1952 year-class, and immature and mature males of the 1953 year-class from the Grand Bank. Numbers in brackets are numbers of fish. Also shown are the numbers of fish of each category and age on which the calculations are based.

	1952 Year-class				1953 Year-class	
Age	Males		Females		Males	
	Immature	Mature	Immature	Mature	Immature	Mature
1	20.2(136)	20.7(83)	20.5(192)	21.1(34)	19.1(86)	20.0(35)
2	26.4(134)	27.4(83)	26.9(192)	27.5(34)	25.4(75)	26.5(35)
3	31.2(101)	32.2(83)	31.8(161)	32.5(34)	30.3(56)	31.2(35)
4	34.7(45)	35.7(82)	35.7(101)	36.5(34)	34.1(20)	34.5(33)
5	36.9(9)	38.4(55)	38.4(36)	39.3(31)	36.6(11)	36.4(26)
6	39.0(4)	40.0(32)	40.5(12)	40.7(15)		

		Numbers in Collections			Numbers in Collections	
1	2	-	-	-	11	-
2	33	-	31	-	19	-
3	56	1	60	-	36	2
4	36	27	65	3	9	7
5	5	23	24	16	11	26
6	4	32	12	15		
Totals	136	83	192	34	86	35

Table 15. Growth by back-calculation for the 1946 year-class from the Grand Bank (above) and St. Pierre Bank (below), sexes separate and combined.

Year	Age	Sex	No. Fish	Back-calculated average lengths at age 1	2	3	4	5	6	7
1953	7	M	9	19.6	27.3	33.3	38.3	40.6	45.0	47.4
		F	23	19.8	27.4	33.8	38.7	41.1	46.2	49.1
		T	32	19.8	27.3	33.6	38.6	41.0	45.9	48.6
1954	8	M	6	20.1	28.0	35.1	41.1	44.9	50.1	52.2
		F	10	19.7	27.8	34.5	40.4	43.4	48.2	50.3
		T	16	19.9	27.9	34.7	40.6	44.0	48.9	51.0
1955	9	M	8	19.6	26.8	33.8	38.8	41.1	46.0	48.8
		F	9	20.2	27.9	34.8	40.3	43.2	48.5	51.5
		T	17	19.9	27.4	34.3	39.6	42.2	47.3	50.3
1956	10	M	2	20.7	27.0	34.1	39.6	42.1	47.3	49.6
		F	4	20.4	29.0	36.8	41.9	44.5	50.4	52.7
		T	6	20.5	28.3	35.9	41.1	43.7	49.4	51.6
1957	11	M	1	24.3	29.9	33.9	37.0	40.2	44.1	45.8
		F	0	-	-	-	-	-	-	-
			1	24.3	29.9	33.9	37.0	40.2	44.1	45.8
1953	7	M	1	19.7	27.6	37.1	45.0	52.1	57.1	62.0
		F	4	20.5	28.2	36.9	44.6	49.0	55.5	60.0
		T	5	20.4	28.1	37.0	44.7	49.6	55.8	60.4
1954	8	M	2	20.5	28.5	36.3	43.5	49.0	54.1	56.4
		F	0	-	-	-	-	-	-	-
		T	2	20.5	28.5	36.3	43.5	49.0	54.1	56.4
1955	9	M	2	20.2	27.9	36.0	43.2	46.5	52.1	56.0
		F	0	-	-	-	-	-	-	-
		T	2	20.2	27.9	36.0	43.2	46.5	52.1	56.0
1956	10	M	1	21.7	31.0	40.2	46.3	50.8	55.5	56.8
		F	0	-	-	-	-	-	-	-
		T	1	21.7	31.0	40.2	46.3	50.8	55.5	56.8
1957	11	M	1	19.9	27.4	35.6	40.4	45.5	48.7	52.5
		F	3	19.2	29.2	36.9	42.7	47.3	51.3	54.7
		T	4	19.4	28.7	36.6	42.1	46.9	50.7	54.1
1958	12	M	2	20.0	28.8	36.9	43.0	49.5	53.6	58.1
		F	0	-	-	-	-	-	-	-
		T	2	20.0	28.8	36.9	43.0	49.5	53.6	58.1

Table 16. Growth by back-calculation for the 1949 year-class from the Grand Bank (above) and St. Pierre Bank (below), sexes separate and combined.

			No.	Back-calculated average lengths at age						
Year	Age	Sex	Fish	1	2	3	4	5	6	7
1953	4	M	118	18.7	25.1	31.5	35.4			
		F	103	18.8	25.1	32.0	36.0			
		T	221	18.8	25.1	31.7	35.7			
1954	5	M	122	19.0	25.7	32.2	35.8	38.8		
		F	97	19.0	25.9	32.5	36.8	40.0		
		T	219	19.0	25.8	32.3	36.3	39.3		
1955	6	M	189	18.9	25.4	32.0	35.8	38.7	40.7	
		F	210	19.0	25.9	32.6	36.8	40.0	42.4	
		T	399	19.0	25.7	32.4	36.3	39.3	41.6	
1956	7	M	70	18.5	25.1	32.1	36.1	39.0	41.0	42.7
		F	67	19.2	25.9	32.7	37.1	40.2	42.7	44.3
		T	137	18.9	25.5	32.4	36.6	39.6	41.8	43.5
1957	8	M	28	19.1	25.5	31.8	35.9	39.0	41.3	43.0
		F	20	19.1	26.0	32.6	37.0	40.1	42.8	44.4
		T	48	19.1	25.7	32.2	36.4	39.4	41.9	43.6
1958	9	M	8	18.6	24.6	31.2	35.3	37.8	40.0	41.7
		F	16	19.1	25.2	32.6	36.7	40.0	43.0	45.2
		T	24	19.0	25.0	32.1	36.2	39.3	42.0	44.0
1953	4	M	85	18.7	27.7	33.6	37.8			
		F	91	18.8	27.6	33.8	38.4			
		T	176	18.8	27.6	33.7	38.1			
1954	5	M	122	18.8	27.5	33.6	37.8	40.3		
		F	96	19.1	27.7	33.8	38.5	41.8		
		T	218	18.9	27.6	33.7	38.1	41.0		
1955	6	M	55	18.9	28.1	34.2	38.7	41.6	43.6	
		F	47	19.3	28.1	34.3	39.2	42.5	44.6	
		T	102	19.1	28.1	34.2	38.9	42.0	44.1	
1956	7	M	28	18.9	27.4	32.8	37.2	39.8	41.7	44.2
		F	41	19.1	27.3	33.5	38.0	41.5	43.7	45.8
		T	69	19.0	27.4	33.2	37.7	40.8	42.8	45.2
1957	8	M	24	18.9	27.8	33.6	38.2	41.9	44.6	47.2
		F	31	19.4	28.1	34.1	38.9	42.4	44.9	46.9
		T	55	19.2	28.0	33.8	38.6	42.2	44.8	47.1
1958	9	M	18	19.0	27.3	33.1	37.7	40.7	43.2	45.7
		F	17	19.0	27.9	33.7	38.4	41.8	44.8	47.3
		T	35	19.0	27.6	33.4	38.0	41.2	44.0	46.5

Table 17. Growth by back-calculation for the 1952 year-class from the Grand Bank (above) and St. Pierre Bank (below), sexes separate and combined.

				Back-calculated average lengths at age					
Year	Age	Sex	No. Fish	1	2	3	4	5	6
1953	1	M	2	20.4					
		F	0	-					
		T	2	20.4					
1954	2	M	33	20.0	25.9				
		F	31	19.8	26.3				
		T	64	19.1	26.1				
1955	3	M	57	20.4	26.7	31.5			
		F	60	20.5	26.8	31.6			
		T	117	20.4	26.8	31.5			
1956	4	M	63	20.4	26.9	31.4	35.1		
		F	68	20.7	27.1	32.1	35.9		
		T	131	20.6	27.0	31.7	35.5		
1957	5	M	28	20.6	27.0	31.9	35.3	37.9	
		F	40	20.9	27.3	32.1	35.8	38.7	
		T	68	20.8	27.2	32.0	35.6	38.4	
1958	6	M	36	20.6	27.3	32.1	35.8	38.4	39.8
		F	27	20.6	27.2	32.1	35.8	38.9	40.6
		T	63	20.6	27.3	32.1	35.8	38.6	40.2
1954	2	M	1	19.3	23.9				
		F	1	17.7	21.6				
		T	2	18.5	22.7				
1956	4	M	2	20.0	27.9	35.6	40.5		
		F	0	-	-	-	-		
		T	2	20.0	27.9	35.6	40.5		
1957	5	M	10	19.6	26.9	32.4	37.6	42.1	
		F	8	20.3	26.0	31.2	36.1	41.9	
		T	18	19.9	26.5	31.9	36.9	42.0	
1958	6	M	0	-	-	-	-	-	-
		F	1	22.0	27.7	34.6	41.3	46.8	52.7
		T	1	22.0	27.7	34.6	41.3	46.8	52.7

Table 18. Growth by back-calculation for the 1953 year-class from the Grand Bank (above) and St. Pierre Bank (below), sexes separate and combined.

Year	Age	Sex	No. Fish	Back-calculated average lengths at age				
				1	2	3	4	5
1954	1	M	11	18.0				
		F	8	18.6				
		T	19	18.2				
1955	2	M	19	18.8	24.7			
		F	15	19.3	25.3			
		T	34	19.0	25.0			
1956	3	M	38	19.4	25.5	30.3		
		F	32	19.9	26.1	30.6		
		T	70	19.6	25.8	30.4		
1957	4	M	16	19.6	26.2	30.9	34.3	
		F	20	19.5	25.8	30.5	34.5	
		T	36	19.5	26.0	30.7	34.4	
1958	5	M	37	20.0	26.3	30.8	34.3	36.4
		F	23	19.5	26.3	31.2	35.0	37.2
		T	60	19.8	26.3	31.0	34.6	36.7
1954	1	M	7	17.6				
		F	1	17.0				
		T	8	17.5				
1957	4	M	1	20.3	28.3	37.1	42.5	
		F	2	20.5	26.3	31.4	36.0	
		T	3	20.4	27.0	33.3	38.1	
1958	5	M	2	20.1	25.8	33.2	38.7	45.2
		F	0	-	-	-	-	-
		T	2	20.1	25.8	33.2	38.7	45.2

Table 19. Growth by back-calculation for the 1955 and 1956 year-classes from the Grand Bank (above) and St. Pierre Bank (below), sexes separated and combined.

Year-class	Year	Age	Sex	No. Fish	Back-calc. av. lengths at age		
					1	2	3
1955	1956	1	M	16	16.1		
			F	7	17.1		
			T	23	16.4		
	1957	2	M	101	17.8	25.0	
			F	108	17.7	24.9	
			T	209	17.7	24.9	
	1958	3	M	110	18.5	26.2	30.1
			F	82	18.5	26.4	30.6
			T	192	18.5	26.3	30.3
1956	1957	1	M	2	17.0		
			F	1	19.0		
			T	3	17.7		
	1958	2	M	12	18.3	25.0	
			F	8	18.6	25.3	
			T	20	18.5	25.1	
1955	1956	1	M	8	16.5		
			F	6	16.9		
			T	14	16.7		
	1957	2	M	22	18.1	26.5	
			F	27	17.9	26.6	
			T	49	18.0	26.5	
	1958	3	M	24	18.9	27.5	33.0
			F	31	18.6	28.6	33.4
			T	55	18.7	28.2	33.2
1956	1958	2	M	16	20.0	25.7	
			F	14	20.1	26.7	
			T	30	20.0	26.2	

Table 20. Summary of back-calculated lengths at age for the Grand Bank. Numbers in brackets are numbers of fish. Empirical averages are included for comparison.

Year-class	Sex	Back-calculated average lengths at age						
		1	2	3	4	5	6	7
1946	M	20.0 (26)	27.4 (26)	33.9 (26)	39.2 (26)	41.8 (26)	46.6 (26)	49.1 (26)
	F	19.9 (46)	27.7 (46)	34.4 (46)	39.6 (46)	42.3 (46)	47.5 (46)	50.2 (46)
	T	19.9 (72)	27.6 (72)	34.2 (72)	39.5 (72)	42.1 (72)	47.2 (72)	49.8 (72)
1949	M	18.9 (535)	25.4 (535)	31.9 (535)	35.8 (535)	38.8 (417)	40.8(295)	42.7(106)
	F	19.0 (513)	25.7 (513)	32.5 (513)	36.7 (513)	40.0 (410)	42.5(313)	44.5(103)
	T	18.9(1048)	25.5(1048)	32.2(1048)	36.2(1048)	39.4 (827)	41.7(608)	43.6(209)
1952	M	20.4 (219)	26.8 (217)	31.6 (184)	35.3 (127)	38.2 (64)	39.9 (36)	
	F	20.5 (226)	27.0 (226)	31.9 (195)	35.9 (135)	38.8 (67)	40.6 (27)	
	T	20.5 (445)	26.9 (443)	31.8 (379)	35.6 (262)	38.5 (131)	40.2 (63)	
1953	M	19.4 (121)	25.7 (110)	30.6 (91)	34.3 (53)	36.4 (37)		
	F	19.5 (98)	26.0 (90)	30.8 (75)	34.8 (43)	37.2 (23)		
	T	19.4 (219)	25.9 (200)	30.7 (166)	34.5 (96)	36.7 (60)		
1955	M	18.0 (227)	25.6 (211)	30.1 (110)				
	F	18.0 (197)	25.5 (190)	30.6 (82)				
	T	18.0 (424)	25.6 (401)	30.3 (192)				
1956	M	18.1 (14)	25.0 (12)					
	F	18.7 (9)	25.3 (8)					
	T	18.4 (23)	25.1 (20)					
Other	M	20.0 (42)	27.3 (42)	32.8 (41)	37.1 (40)	41.4 (36)	44.6 (34)	47.2 (26)
	F	20.3 (39)	28.2 (39)	33.6 (39)	38.4 (38)	43.2 (36)	46.8 (34)	50.3 (26)
	T	20.2 (81)	27.7 (81)	33.2 (80)	37.7 (78)	42.3 (72)	45.7 (68)	48.7 (52)
MALES		19.1(1184)	25.8(1153)	31.6 (987)	35.8 (781)	38.9 (580)	41.5(391)	44.5(158)
FEMALES		19.3(1128)	26.1(1112)	32.2 (950)	36.7 (775)	40.1 (582)	43.3(420)	46.8(175)
ALL DATA		19.2(2312)	26.0(2265)	31.9(1937)	36.2(1556)	39.5(1162)	42.4(811)	45.7(333)
EMPIRICAL		17.7 (47)	25.3 (328)	30.8 (381)	35.7 (394)	38.7 (351)	41.5(478)	44.7(177)

Table 21. Summary of back-calculated lengths at age for St. Pierre Bank. Numbers in brackets are numbers of fish. Empirical averages are included for comparison.

Year-class	Sex	Back-calculated average lengths at age 1	2	3	4	5	6	7
1946	M	20.3 (9)	28.5 (9)	36.8 (9)	43.5 (9)	48.7 (9)	53.4 (9)	56.9 (9)
	F	20.0 (7)	28.6 (7)	36.9 (7)	43.8 (7)	48.3 (7)	53.7 (7)	57.7 (7)
	T	20.2 (16)	28.5 (16)	36.9 (16)	43.6 (16)	48.5 (16)	53.6 (16)	57.3 (16)
1949	M	18.8(332)	27.7(332)	33.6(332)	37.9(332)	40.7(247)	43.3(125)	45.6 (70)
	F	19.1(323)	27.7(323)	33.9(323)	38.5(323)	42.0(232)	44.4(136)	46.5 (89)
	T	18.9(655)	27.7(655)	33.7(655)	38.2(655)	41.3(479)	43.9(261)	46.1(159)
1952	M	19.7 (13)	26.8 (13)	32.9 (12)	38.1 (12)	42.1 (10)	-	
	F	20.2 (10)	25.7 (10)	31.6 (9)	36.6 (9)	42.4 (9)	52.7 (1)	
	T	19.9 (23)	26.3 (23)	32.3 (21)	37.4 (21)	42.3 (19)	52.7 (1)	
1953	M	18.4 (10)	26.6 (3)	34.5 (3)	40.0 (3)	45.2 (2)		
	F	19.3 (3)	26.3 (2)	31.4 (2)	36.0 (2)	-		
	T	18.6 (13)	26.5 (5)	33.3 (5)	38.4 (5)	45.2 (2)		
1955	M	18.2 (54)	27.0 (46)	33.0 (24)				
	F	18.1 (64)	27.7 (58)	33.4 (31)				
	T	18.2(118)	27.4(104)	33.2 (55)				
1956	M	20.0 (16)	25.7 (16)					
	F	20.1 (14)	26.7 (14)					
	T	20.0 (30)	26.2 (30)					
Other	M	19.6 (29)	28.8 (14)	36.0 (13)	41.5 (13)	47.0 (12)	52.0 (11)	55.4 (10)
	F	19.5 (23)	28.4 (14)	35.2 (13)	40.9 (13)	45.2 (12)	49.0 (10)	52.4 (7)
	T	19.5 (52)	28.6 (28)	35.6 (26)	41.2 (26)	46.1 (24)	50.6 (21)	54.1 (17)
MALES		18.9(463)	27.5(433)	33.7(393)	38.2(369)	41.3(280)	44.6(145)	47.8 (89)
FEMALES		19.0(444)	27.7(428)	33.9(385)	38.7(354)	42.3(260)	45.2(154)	47.7(103)
ALL DATA		19.0(907)	27.6(861)	33.8(778)	38.4(723)	41.8(540)	44.9(299)	47.7(192)
EMPIRICAL		18.2 (46)	27.2 (82)	34.4 (56)	38.4(183)	41.2(240)	44.4(107)	46.5 (78)

Table 22. Worksheet for fit of the von Bertalanffy growth curve to Grand Bank length at age data.

A	B	C	D	E	F	G	H
t	l_t	$L_\infty - l_t$	log $(L_\infty - l_t)$	$t-t_o$	$k(t-t_o)$	$1-e^{-k(t-t_o)}$	Calc. l_t = L_∞ x(col G)
0				1.15	.2193	.1968	11.33
1	19.17	38.42	3.6486	2.15	.4100	.3363	19.37
2	25.96	31.63	3.4542	3.15	.6007	.4516	26.01
3	31.92	25.67	3.2453	4.15	.7914	.5468	31.49
4	36.23	21.36	3.0615	5.15	.9821	.6255	36.02
5	39.50	18.09	2.8953	6.15	1.1728	.6905	39.77
6	42.40	15.19	2.7205	7.15	1.3635	.7442	42.86
7	45.72	11.87	2.4742	8.15	1.5542	.7887	45.42

$$l_t = L_\infty 1-e^{-k(t-t_o)}$$

$L_\infty = 57.59$ $k = .191$ $t_o = -1.15$

L_∞ derived from regression of l_{t+1} against l_t , i.e.

$$l_{t+1} = L_\infty(1-e^{-k}) + l_t e^{-k}$$
$$= .82\ l_t + 10.17.$$

k and t_o derived from regression of $\log(L_\infty - l_t)$ against t, i.e.

$$\log(L_\infty - l_t) = \log L_\infty + kt_o - kt$$
$$= -.19\ t + 3.83.$$

Table 23. Worksheet for fit of the von Bertalanffy growth curve to St. Pierre Bank length at age data.

A	B	C	D	E	F	G	H
t	l_t	$L_\infty - l_t$	log $(L_\infty - l_t)$	$t - t_o$	$k(t-t_o)$	$1-e^{-k(t-t_o)}$	Calc. l_t = L_∞ x(col G)
0				.63	.1632	.1507	8.30
1	18.95	36.10	3.5863	1.63	.4223	.3445	18.96
2	27.60	27.45	3.3124	2.63	.6814	.4941	27.20
3	33.77	21.28	3.0577	3.63	.9405	.6096	33.56
4	38.43	16.62	2.8106	4.63	1.1996	.6987	38.46
5	41.78	13.27	2.5854	5.63	1.4587	.7674	42.25
6	44.90	10.15	2.3173	6.63	1.7178	.8205	45.17
7	47.74	7.31	1.9892	7.63	1.9769	.8615	47.43

$$l_t = L_\infty 1-e^{-k(t-t_o)}$$

$L_\infty = 55.05$ $\qquad$ $k = .259$ $\qquad$ $t_o = -.63$

L_∞ derived from regression of l_{t+1} against l_t , i.e.

$$l_{t+1} = L_\infty (1-e^{-k}) + l_t e^{-k}$$

$$= .77\ l_t + 12.69.$$

k and t_o derived from regression of $\log(L_\infty - l_t)$ against t, i.e.

$$\log(L_\infty - l_t) = \log L_\infty + kt_o - kt$$

$$= -.26\ t + 3.84.$$

Table 24. Comparison of calculated average lengths of age 5 fish at ages 2 - 5 for the 1949 and 1952 year-classes from the Grand Bank, when the data are arranged in ascending order of calculated length at the end of the first year.

		Back-calculated average lengths at age				
Year-class	No. fish	1	2	3	4	5
1949	1	15.5	24.5	31.9	36.5	39.0
	4	16.0	22.5	27.6	30.9	34.8
	7	16.5	23.9	29.5	33.7	37.2
	17	17.0	24.5	30.6	34.7	37.5
	18	17.5	24.5	30.7	35.0	38.3
	24	18.0	24.9	31.1	34.9	38.0
	20	18.5	25.4	31.8	35.9	39.3
	25	19.0	25.9	32.7	36.6	39.5
	37	19.5	26.2	33.1	36.7	39.7
	19	20.0	26.3	32.6	36.9	40.1
	24	20.5	27.0	33.7	37.3	40.1
	10	21.0	26.7	33.0	37.5	40.7
	11	21.5	28.2	35.4	39.5	43.3
	1	22.0	28.4	35.2	39.7	42.0
	1	22.5	29.0	36.8	41.4	44.0
1952	1	18.0	26.3	31.8	34.8	38.0
	1	18.5	25.2	31.1	35.0	38.0
	9	19.0	25.5	30.6	34.0	37.0
	5	19.5	25.7	30.2	33.9	36.6
	9	20.0	26.4	31.4	34.8	37.2
	11	20.5	27.2	32.0	35.4	38.4
	9	21.0	27.4	32.3	36.3	38.9
	4	21.5	26.8	31.2	35.7	38.9
	8	22.0	28.6	33.6	37.0	39.9
	5	22.5	28.4	32.6	36.3	39.0
	2	23.0	29.0	33.6	37.2	39.5
	2	23.5	30.1	35.2	38.7	41.0
	2	24.0	29.1	33.3	37.0	40.0

Table 25. Comparison of haddock growth from various areas of the northwest Atlantic. Also shown are parameters of the von Bertalanffy growth equation for each area.

	Average length at age						
Area and Source	1	2	3	4	5	6	7
Nfld. area (Thompson, 1939)	17.0	27.9	36.9	43.5	48.6	53.0	56.6
Grand Bank (1953 - 1958)	19.2	26.0	31.9	36.2	39.5	42.4	45.7
St. Pierre Bank (1953 - 1958)	18.2	27.2	34.4	38.4	41.2	44.4	46.5
Browns Bank (Wise, 1957)	17.5	27.2	35.6	42.7	47.6	52.3	54.6
Lockeport, N.S. (Kohler, 1960)	-	-	43.0	45.0	49.7	54.2	57.9
Georges Bank (Schuck & Arnold, 1951)	22.7	36.6	43.2	49.4	52.4	59.1	-

	L_∞	k	t_0
Nfld. area (Thompson, 1939)	68.9	0.24	-0.17
Grand Bank (1953 - 1958)	57.6	0.19	-1.15
St. Pierre Bank (1953 - 1958)	55.1	0.26	-0.63
Browns Bank (Wise, 1957)	72.1	0.20	-0.45
Lockeport, N.S. (Kohler, 1960)	68.2	0.28	0.91
Georges Bank (Schuck & Arnold, 1951)	56.8	0.51	0.03

NOTE: Thompson's averages are taken from the table on p. 18 of his paper. The values for ages 1 - 3 are the same as those given in his Table 3, p. 16. The values for ages 4 - 7 are 0.3 to 1.4 cm less than those of Table 3. Thompson offers no clue as to the reason for these differences.