RESTRICTED

INTERNATIONAL COMMISSION FOR THE NORTHWEST ATLANTIC FISHERIES

Serial No. 2004
(D. c. 2)

ICNAF Res. Doc. 68/29

ANNUAL MEETING - JUNE 1968

Age determination and growth rate of redfish (*Sebastes* sp.) from selected areas around Newfoundland[1]

By E. J. Sandeman

Fisheries Research Board of Canada

Biological Station, St. John's, Newfoundland

Abstract

Ages have been determined from the otoliths of *mentella* redfish from Hermitage Bay, the southwest slope of the Grand Bank, the Gulf of St. Lawrence, Flemish Cap and Hamilton Inlet Bank and of *marinus* redfish from the latter two areas. Empirically, growth of both *marinus* and *mentella* redfish from these areas was found to be well represented by the von Bertalanffy equation and the parameters of this equation were obtained by least squares fit to the mean length at age values for males and females from each of the areas examined.

A comparison of ages obtained by two independent readers revealed that although considerable differences were apparent in the estimates for individual fish, when the results were expressed as growth curves these were virtually identical.

Differences in growth rate between sexes, between the different areas and, for samples from Hamilton Inlet Bank, between depths were examined using plots of instantaneous growth rate against time. In the latter study the redfish (*mentella*) from the deeper waters were found to grow faster after an age of about 10 years than those of the same age which had been obtained in the shallower waters.

The order of the growth rates found in this study resembles that obtained by recent authors from the USA and USSR, however, it was noted that the resemblance to the work of those authors who used otoliths was closer than to those who used the scale method for estimating ages.

---

[1]This paper is based on material submitted as a thesis in partial fulfillment of the requirements for the degree of M.Sc. at the Memorial University of Newfoundland.

Contents

Introduction

Redfish of the genus Sebastes are widely distributed in the North Atlantic. In Northeastern Atlantic waters they range from the Barents Sea and Norway to the waters off Iceland and Eastern Greenland, while in the Northwest Atlantic commercial quantities are to be found south from Davis Strait to the Gulf of Maine, as well as along the coast of West Greenland (Templeman, 1959). (The area referred to here as the Northwest Atlantic may be defined as the convention area of the International Commission for the Northwest Atlantic Fisheries (Fig. 1). The eastern boundary line of the convention area which, except near Cape Farewell, Greenland, extends along the 42°W longitude line, divides this defined Northwest Atlantic area from the Northeast Atlantic.)

Taxonomic position

The taxonomic position of the various members of the genus Sebastes in the North Atlantic is rather confused. At present the following different forms of redfish can be considered to exist in the area:

Northeastern Atlantic	Sebastes viviparus
	Sebastes marinus
	Sebastes mentella
Northwestern Atlantic	Sebastes mentella
	Sebastes marinus
Bathypelagic stock	Sebastes mentella

Some of these different forms are no doubt similar enough to be considered the same species (S. marinus of the Northwest and Northeast Atlantic); others however show differences which suggest that they may not be as similar as would appear from a superficial external examination. Thus until the taxonomic position is clarified it is probably better to consider the forms from the Northeastern Atlantic separately from those from the Northwestern Atlantic.

The species which are considered in this paper are S. mentella and S. marinus from the Northwestern Atlantic.

Age and growth studies on redfish

From the first information on the likely growth rate of redfish by Jensen (1922) many persons have attempted to age various members of the genus Sebastes. A review of many of the papers pertaining to age and growth studies can be found in a paper by Kelly and Wolf (1959). Suffice it to say here that validation studies by Bratberg (1955, 1956a, 1956b) for redfish from the coast of Norway, by Perlmutter and Clark (1940), Kelly and Wolf (1959), and Sandeman (1961) have shown that redfish grow very slowly and that during their first 10 years of life, one and only one annulus (hyaline layer on the otolith) is laid down. After the age of about 10 years, redfish otoliths and scales become more and more difficult to read, but inspite of this, it is possible to obtain age estimates as has been done by many authors amongst whom were Kelly and Wolf (1959), Surkova (1961, 1962), Zakharov (1962), Savvatimsky and Sidorenko (MS, 1965). These authors all supported the slow growth hypothesis rather than the fast growth hypothesis as put forward by Kotthaus (1949, 1952, 1958).

Methods

The general areas where the samples of fish used in this study were obtained, are shown in Fig. 1. At some of these localities the samples were taken at a single position and depth whereas at others fish from several depths and positions have been combined to provide an adequate sample. At each locality redfish were obtained by otter trawling, the required samples separated from the catch by a sampling procedure and the individual fish examined at sea or at the Biological Station. In most cases the length, sex and maturity were recorded, and the otoliths were removed for subsequent examination.

All fish lengths reported here are "fork lengths", the measurements being taken from the anterior tip of the lower jaw, with the mouth closed, to the end of the median caudal rays.

This study is based on the examination of otoliths, with the exception of data from Hermitage Bay where scales were also used for ageing redfish up to about age 5. It is considered that following the work of Kelly and Wolf (1959) and Sandeman (1961) that the validity of the otolith method as applied to the ageing of Northwest Atlantic redfish (mentella) is established. Kelly and Wolf (1959) refer to the Gulf of Maine redfish as Sebastes marinus marinus. However, it seems clear that these fish are in fact what are being called in this paper North American mentella redfish.

The techniques used for "reading" the otoliths and the estimation of age on a calendar year basis were the same as was previously reported by Sandeman (1961).

With the exception of otoliths from the Gulf of St. Lawrence and Hamilton Inlet Bank, which were read by E. Squires, age determinations were by the author.

Empirically, growth of both marinus and mentella redfish may be quite well represented by the inverse exponential equation, and the parameters of the von Bertalanffy form of this equation (Bertalanffy, 1938) were obtained by a least squares fit to the mean length at age values for males and females from each of the areas examined.

The form of the Bertalanffy growth in length curve which is used in this paper is -

$$l_t = L_\infty \left[1 - e^{-K(t-t_0)} \right]$$

where l_t = The length of the fish (cm), at age t (years)

L_∞ = Theoretical maximum length (asymptotic length).

K = Constant expressing the relative rate of approach to L

t_0 = The theoretical age at which l_t = 0.

The general method described by Tomlinson and Abramson (1961) has been used for fitting the Bertalanffy growth curves to the length at age data. This method has the advantage that it is more objective than the methods which are usually used (Beverton and Holt, 1957; Ricker, 1958) and at the same time it provides estimates of the variance of the parameters. The method as described requires equal sized random samples to be selected from each age group containing a sufficient number of observations. As this would occasion very small samples at each age and the discarding of data (a most undesirable requirement in the light of the tremendous variation in the age estimates), it was apparent that much better use of the material available would result from a least squares fit to data consisting of single points at each age and that these points should be mean length values.

Thus for most of the data here, Bertalanffy growth curves were fitted to smoothed mean length values at even ages (2, 4, 6, etc.) between stated upper and lower limits. These limits were determined by the range of data available for the fit, bearing in mind that the method as described by Tomlinson and Abramson (1961) requires that there be no gaps in the consecutive ages used, and that the tables only allow a total of 18 age groups to be used in this fit. Smoothing was accomplished by the use of the formula

$$\bar{l}_t = \tfrac{1}{2}\,(l_{t-1}/2 + l_t + l_{t+1}/2)$$

where $\bar{l}_t$ is the smoothed mean length at the even age t and l_t is the observed mean length at the same age. Occasionally, where there were gaps in the unsmoothed data, the formula was suitably modified to provide the requisite interpolation.

Where growth curves are presented in figures, the thicker line shows the range of ages to which the curve was fitted, while the thinner line indicates the extrapolated curve.

The growth rate, which in a plot of age against size is represented by the slope of the curve at each instant of its generation is, in Bertalanffy type growth, continually changing and is directly proportional to the length of the organism.

$$\frac{dl}{dt} = KL_{\infty} - Kl_t$$

To obtain the growth rate in terms of time rather than length, the original Bertalanffy equation may be differentiated to yield

$$\frac{dl}{dt} = KL_{\infty} e^{-K(t-t_0)}$$

In both these equations $\frac{dl}{dt}$ represents the instantaneous growth rate. The above equations provide a convenient means of comparing the growth rates of two or more populations having different parameters K, L_{∞} and t_0. Using the former equation, a plot of $\frac{dl}{dt}$ against l_t, results in a straight line having the intercept on the y axis of KL_{∞} and on the x axis of L_{∞}. Similarly a semilogarithmic plot of $\frac{dl}{dt}$ against t for the latter equation can be used for comparing growth rates and how they change with age, viz.

$$\log \frac{dl}{dt} = \log K + \log L_{\infty} + Kt_0 - Kt$$

Although the former plot is very much simpler, it is deceptive in that it is more customary to think of growth rate in terms of age rather than length. Consequently in the comparisons of growth rates presented here it will be most often the latter equation that will be used.

Materials

Hermitage Bay

This area has been of particular interest because in 1953 an isolated year-class of fish in their first year of life was found, and with a relative failure of adjacent year-classes it has been possible to follow this dominant 1953 year-class during several succeeding years (Sandeman, 1957, 1958, 1961). This has allowed a useful check on the validity of the otolith and scale methods of age determination as applied to North American mentella redfish and it has been established in Hermitage Bay that, at least to age 10, in each successive year a further pair of zones, a hyaline and an opaque, are laid down on the surface of the otolith.

The otoliths used in this study and the derived age at length data are the same that were reported previously (Sandeman, 1961). The fish, which were likely all mentella, were obtained at the one position (Fig. 1) and from a rather limited depth range [120-180 fath. (220-330m.)].

Southwest slope of the Grand Bank

The fish on which this study is based were obtained in 1947 during several sets in the general area indicated in Fig. 1. Although the data from this rather wide area have been combined to provide an adequate sample for ageing, the depth variation in these sets was not very great and all the fish were obtained in the rather shallow (for redfish) depth range of 45-115 fath. (82-210m).

The samples were not examined for the presence of marinus, but it is most unlikely, from our subsequent knowledge of the numbers of these fish in the area, that more than the occasional marinus fish was caught and the growth curves presented here can thus be considered as those of North American mentella redfish.

Gulf. of St. Lawrence

The majority of otoliths used in this study were obtained in 1947, 1948 and 1949 from redfish in the area of the Esquiman Channel (Fig. 1). Occasional samples of otoliths obtained during the same period, but from other areas in the nothern part of the Gulf of St. Lawrence, have also been included and, because of the complete dearth of small redfish in the samples obtained during this period, a more recent sample containing some small fish has also been added.

Recent surveys for marinus and mentella redfish in the Gulf of St. Lawrence have revealed only the very occasional marinus specimen and the otoliths considered here can be regarded as from mentella redfish.

Flemish Cap

The fish were all caught on the northern slope of Flemish Cap. Otoliths for growth study were obtained from rather small samples of fish used for detailed studies and because of small number, data from all depths [150-300 fath (274-548)] are combined.

In addition the samples were selected to provide fish only at each length group of 5 cm or multiple thereof. Although this will, of course, affect the calculation of mean length at age, it is considered the the data are adequate for providing at least a preliminary examination of growth rate.

Enough specimens of marinus redfish were obtained in the Flemish Cap area to allow a consideration of the growth rate of these fish, as well as that of the more common and deeper living mentella.

Hamilton Inlet Bank

The otoliths examined from the area of Hamilton Inlet Bank were all taken from fish caught in August 1960. Fishing was carried out on a line across the slope at the northern part of Hamilton Inlet Bank (Fig. 1), and otoliths were obtained as follows :-

Depth		mentella		marinus	
(fath)	(m)	males	females	males	females
140	256	...	...	47	19
150	274	7	9	34	48
175	320	61	47	...	...
200	366	76	37	...	...
250	457	54	54	...	...
300	549	61	41	...	...
400	732	4	11	...	...
Total		263	199	81	67

Results

The growth curves of mentella redfish from the Hermitage Bay area are shown in Fig. 2b. These curves and the Bertalanffy parameters describing them (Table I) are based on the same length at age data that were reported in a previous paper (Sandeman, 1961) when freehand curves were drawn to the data from 366 males and 332 females. As the dominant 1953 year-class appears to have shown unusually fast growth during the first four years, and its numbers are so great (205 fish) relative to the other fish, these fish have been considered separately (Fig. 2a) and are not included in the mean growth curves for the area shown in Fig. 2b.

The very high standard errors in L_∞ and K that were obtained for the 1953 year-class data result from the absence of data for the older ages where the average lengths approach the asymptotic values.

The data from the southwest slope of the Grand Bank have been used to compare the growth curves obtained by two different age readers using the same basic age reading methods on mentella otoliths (Table I, Fig. 3).

Growth curves for mentella redfish from the Gulf of St. Lawrence, Flemish Cap and Hamilton Inlet Bank are shown in Fig. 4 and the parameters of the fitted Bertalanffy equations, years fitted, and number of otoliths read are to be found in Table I.

Growth curves for marinus redfish from Hamilton Inlet Bank and Flemish Cap are presented (Fig. 5) as are also the parameters of their least squares fits (Table I).

Discussion

Comparisons of ages and growth rates as determined by two different persons

The otoliths from the southwest slope of the Grand Bank were examined and ages estimated by two different persons, the author (A) and technician E. Squires (B). This provides an opportunity to examine the variation occurring between the results obtained by the two age readers who are attempting to determine the ages, using the same basic method. Agreement in age assignation is seldom obtained from otoliths of fish above age 10 (agreement was obtained in only 43 of 444 such readings in the present study).

Table II shows the number of times in which agreement or disagreement occurred between the two age readers. It is evident from this table that there is a wide variation between the ages as determined by these two readers. Furthermore, the spread of the data on the upper side of the diagonal of complete agreement indicates that the ages estimated by B are on the average, higher than those estimated by A. This may perhaps be better seen by examining the frequency of agreement or disagreement without reference to the actual ages at which the agreement and disagreements occurred (Fig. 6). The shape of the histogram approximates to a normal curve and indicates a rather large random error but also because the curve is skewed to the right, it indicates that B on the average obtains age estimates that are higher than those of A.

Comparison of the age frequencies obtained by the two readers using χ^2 tests indicates that both for males and females no significant difference exists between the age frequencies obtained by the two readers. (The difference between the two frequencies for the males could be expected to occur with a probability > 0.99 and thus, the frequencies are striking in their similarity, whereas that for the females showed a probability of occurrence of between 0.10 and 0.20). However, in dealing with growth curves it is really the differences between the respective mean lengths at each age that should be considered, and a paired comparisons test between these mean lengths at each age would perhaps be more appropriate. Paired comparison tests indicated that for the males the mean difference between the mean length at age values was not significantly different from zero ($0.90 > P > 0.80$) whereas the mean difference for the females was different from zero. ($0.02 > P > 0.01$).

The values for mean length at each age, as calculated from the age estimations of A and B for males and females separately, are shown in Fig. 3. Also shown are the least squares Bertalanffy curves fitted to the smoothed mean length at age data for ages 8-34 (because of the lack of data at age 33, 34 and 35 for females in A's data, this curve was fitted to the smoothed data for ages 8-32). The curves derived from the age estimations of these two different persons appear so similar in this figure that it is difficult to see any difference at all.

Although the difference between the age estimation of the two readers was found to be significantly different at the 5% probability level when the mean lengths at each age of females are compared, it is apparent (Fig. 3) that many of the mean length at age data occur at ages greater than about 15 when the asymptotic part of the curve is being approached and when the total average change in length represents only about 5 centimeters over a period of 20-25 years. When the variability of the smoothed mean length of age values from the results of both age readers are examined in the light of this, and when Bertalanffy curves are fitted to the data, it is not surprising that the differences between the parameters are small. It is evident from the considerable overlap in the confidence limits of all the parameters (Table I) that, for both males and females, the growth curves derived from the age estimates of A and B can be considered similar.

Differences in growth rate with depth

When the growth curves for male and female mentella redfish from the Hamilton Inlet Bank area (Fig. 4) are compared with the data points from which they are derived, they do not seem to fit the data very well. This is particularly so for the males, where ages 7 - 10 lie well below the fitted line and ages 16 - 21 lie above it, all of which would seem to indicate a steeper slope at this section of the curve. As data from widely different depths have been combined it is proper that the data should be examined for differences in growth rate with depth.

Very few age data are available from 150 and 400 fath and when these are included with the data from 175 and 300 fath respectively, we have the equivalent of four different depth levels: 175 and shallower, 200, 250, and 300 fath and deeper.

Bertalanffy curves have been fitted to the unsmoothed mean length at age data for each of these depth zones. In each case the curves were fitted to the range of data in which there were data for consecutive ages. These were:

	Males	Females
175 fath (320 m)	6 to 22 years	7 to 20 years
200 fath (366 m)	10 to 27 years	10 to 20 years
250 fath (457 m)	9 to 20 years	11 to 21 years
300 fath (549 m)	13 to 25 years	14 to 26 years

These curves are shown in Fig. 7. Apparently the growth patterns of the fish from 175 and 200 fath are rather similar, and that these fish from the shallower depth ranges differ somewhat from those obtained from the deeper zones.

A perusal of the length-frequency distribution of the catches at the different depths shows a general trend of increase in size with increase in depth (Fig. 8). This trend, which is apparent at several localities in the Newfoundland area, and the lack of smaller fish from the greater depths, lead quite naturally to the hypothesis that the fish gradually move deeper as they grow larger and older.

However, when the age frequency distribution of the catches at the different depths is examined (Fig. 9), it is apparent that, although there is a decline in the number of the youngest ages present from the shallow to the deep water, for both the males and females, there is also a scarcity of the oldest males in the deeper levels. This scarcity of older males at the 250 and 300 fath levels is not reflected in the age distribution of the females, but in these frequencies an even more dramatic phenomenon may be noticed, namely that at the deepest levels almost all the females are immature. These characteristics of the male and female redfish from the deeper levels suggest that separate populations may exist at these different depth levels and that such a division might occur between the 200 and 250 fath depth levels.

With this hypothesis in mind, the data from 175 and 200 fath have been combined as have also those from 250 and 300 fath. The growth curves for the combined data, the parameters of which are listed in Table I, were fitted to the unsmoothed data for all available consecutive ages at each depth zone (Fig. 10).

It is evident from this figure that the fitted curve for the male redfish from the deeper depth strata does not fit the data points very well in the region of extrapolation beyond the maximum age used in the fitting process (age 22). This results not only in a high value for L_∞ but also a rather extraordinary value for t_0. Extending the range of the fitting process to higher ages would not alter the parameters to any great degree as the 11 age groups above age 22 include only 12 fish. The results suggest that there are separate populations of redfish which, although they originate from the same shallow water population of young fish, have become separated from each other at an age of about 10-12 years to form a shallow-water stock of slow-growing fish and a deep-water stock of fast-growing fish. With male redfish attaining maturity at an age several years younger than the females, it seems likely that most fish in the deep-water population become separated at an age between that at which the males and that at which the females attain sexual maturity.

Although the hypothesis above suggests the existence of two stocks of redfish having different growth and maturity characteristics, these stocks need not remain separate at all stages of their annual cycle. The hypothesis, based as it is on growth and differences in growth rate, requires a separate identity to the stocks only during the period of active growth, and does not preclude a mixing of stocks or change in depth level of either stock at any time of the year when growth, and presumably also active feeding, are not taking place.

From the growth curves shown in Fig. 10 some idea can be obtained of the growth rates prevailing in the catches at the two depth zones and their respective rates of decrease. However, the direct comparison of the different growth rates can most easily be accomplished graphically by the plot of instantaneous growth rate ($\frac{dl}{dt}$) against either fish length (l_t) or time (age). This has been done to compare the growth rates at the two depth zones for males and females separately in Fig. 11. It is clear from these plots that, both for males and females, the growth rate is higher for the younger ages at the shallower depths, whereas the older fish show faster growth in the greater depths. It is also evident that, if the theoretical curves provide reasonable expectations of growth, and provided other things remain equal, maximum growth rates will be obtained if the males migrate from shallow to deep water at about their eleventh year and females at about their ninth year.

In general a difference in growth rate between the deep and shallow depth zones might be due to either or both of two basic types of causes, the one consisting of factors of the fish themselves, and the other of factors stemming from the environment.

It has already been noted that one of the main features indicating the differences in growth pattern between the depth zones was that of maturity. In particular the age at first maturity was considerably delayed in the deeper zone so much so in the females that no mature fish were found in depths of 300 fath or deeper.

Thus, it is possible that the change in growth rate between the two zones is not so much an increase in growth rate as the fish change from one form of Bertalanffy growth to another, but rather a decrease in growth rate in the shallow zone. This might be caused by the larger and older fish attaining maturity, and devoting much of their growth energy to the exigencies of reproduction, while their relations, who emigrated to the deeper zone, continue to live and grow as adolescents.

However, it is evident from the maturity pattern of the males (Fig. 9) that, in spite of maturity being attained in the deeper water, growth continued at the fast rate that prevailed before maturity. It should be noted here that although in Fig. 9 most of the males in depths of 250 and 300 fath have been recorded here as mature, some doubt exists as to whether or not these were actually so. At depths of 200 fath and shallower, the testes of all the fish with lengths greater than about 25 cm were obviously mature. These fish had large, creamy white testes and milt could easily be seen in the vas deferens. At the 250 fath level and even more so at the 300 fath level, greater numbers of the fish had rather small testes which, although they were large enough to be producing viable sperm, were not creamy white in colour and no milt was visible in the vas deferens. These testes were grey in colour and appeared as if they had produced milt previously but had recovered. The above description is taken from notes made by Dr Templeman who examined the fish in the field and indeed there was enough doubt about them that he made rather complete notes about their peculiarities and only called them mature in a very tentative manner.

The environmental temperature has a very close relationship with metabolism and growth. The prevailing temperatures however, in these waters of 175 fath or deeper, remain very stable from depth to depth, and indeed also from year to year, and thus could not really be expected to affect the growth rate. However, the closer proximity of the cold water layers to the shallower depth zone could limit the foraging area, and the pelagic feeding habits of these fish have not the scope and range that is available to the fish from the deeper zone.

The most likely cause of the faster growth rate in deep water is probably to be found in the interplay of environment and fish physiology that occurs in the process of feeding. Here, unfortunately, we have very little data, although it seems clear that with increase in depth redfish tend to eat more and more fish as opposed to the smaller invertebrates which make up the greatest part of their diet in shallow water (Yanulov, 1962; Rees, MS, 1962, 1966).

Comparison of redfish growth rates in the Newfoundland area

Differences between males and females

Mentella redfish. The data presented indicate a striking difference in growth pattern between the sexes. The total growth of the females is nearly always greater than that of the males, and at any of the older ages the females are on the average very much larger than the males. The parameters of the fitted Bertalanffy curves (Table I) in conjunction with the confidence limits indicate that the main difference between the growth of the sexes lies not so much with the parameter K, but with L_{∞}. At Hermitage Bay, Flemish Cap and Hamilton Inlet Bank the confidence limits of L_{∞} for the males and females do not overlap, and this indicates that the differences are likely to be real. In the areas of the Gulf of St. Lawrence and Southwest Grand Bank, the difference between the L_{∞} values for the males and females is not so clear, but in both these areas the growth curves of the males are rather aberrant, as in each we have a rather large negative t_0 value. This results in a very much lower than usual K value and a slightly higher value for L_{∞}.

The difference in growth rate between males and females is probably not so much the result of the environment, as of the genetics which determine the behaviour and physiology of the fish. The males mature at considerably smaller sizes and ages than do the females (in Hermitage Bay on the average, males mature at about 20 cm at which time they are about 6 years old, whereas females mature at about 30 cm or 10-12 years of age). This suggests that the males will start earlier the processes associated with maturity, namely the pre-spawning reduction in feeding (Yanulov, 1962) and the diversion of energy to the formation of sexual products, with the probable result that less total energy is available for growth. With the reproductive season of the males as well as the pre-spawning season of fast coinciding with the latter part of the season of greatest potential growth, the actual growth season of mature males could be effectively shortened in comparison to that of the immature portion of the stock. Yanulov (1962) has presented evidence to show that the intensity of feeding of mature individuals changes with season and for both males and females it decreases abruptly in April and May. Females begin to feed again in June-July and by August are feeding heavily whereas the males appear to delay active feeding till later and it was not till about October-November that 60% of the fish taken were found to be actively feeding. Rees (MS, 1962) presents some further data on the feeding of redfish, and while he found a different pattern of feeding throughout the year in Hermitage Bay to that found by Yanulov (1962) in the areas he examined, both these authors and Kashinksev (1962) agree that there is a period of pre-spawning fast.

Marinus redfish. The difference in growth pattern between the sexes of *marinus* redfish resembles that observed for the *mentella* of the Southwest Grand Bank and the Gulf of St. Lawrence. The males in these two areas and the *marinus* males from both Flemish Cap and Hamilton Inlet Bank show Bertalanffy growth patterns involving fairly high t_o values and low values for K (Table I). In both these areas the females show higher growth rates than the males during the younger years but, after about age 21 at Flemish Cap and age 33 at Hamilton Inlet Bank, the males exhibit faster growth (Fig. 15).

Differences between areas

The Bertalanffy equation has been found to describe adequately the growth pattern of many species of fish, and several authors have examined the relations of the parameters of this equation to each other and to various environmental factors (in particular Beverton and Holt, 1959; Taylor, 1958, 1959 and 1960). Of the relations between the parameters themselves, K and L_∞ have been found and, indeed, may a priori be expected to show an inverse correlation with each other (Knight, MS, 1962). When t_o has values which depart from zero, it will likely also be inversely correlated with K.

Because studies in which the Bertalanffy parameters have been correlated with various environmental factors have often yielded rather contradictory results, it seems preferable to avoid, for the time being at any rate, any possible physiological connotation which might be placed on these parameters, and to treat this equation in a purely empirical manner. The equation provides a good fit to the age at length data for redfish, as well as a convenient mathematical summary from which age and length values and growth rates can be extracted with ease by simple calculation.

In examining the differences in growth patterns between areas, discussions are here limited to a consideration of how the growth rates vary from area to area.

Growth rates of male mentella redfish. The Bertalanffy growth curves of male redfish from five areas around Newfoundland are plotted on the same coordinate system in Fig. 12. The parameters of these curves are shown in Table I. The growth curves shown for Flemish Cap and Hamilton Inlet Bank represent the data from several widely separated depths, whereas the curves for the Southwest Grand Bank are derived from fish obtained in depths of less than 110 fath and those from Hermitage Bay and the Gulf of St. Lawrence from 140 and 129-142 fath respectively.

The male mentella of Hamilton Inlet Bank seem to have a much faster growth rate, and those of the southwest slope of the Grand Bank a slower growth rate than those of the other areas. This is confirmed when the growth rates are compared by length (Fig. 13). Until about a length of 32 cm, the growth rates at any length are in the order of highest to lowest: Hamilton Inlet Bank, Flemish Cap, Hermitage Bay, Gulf of St. Lawrence and Southwest Grand Bank. In terms of age (Fig. 14), the Hamilton Inlet Bank fish have fastest growth to about the age of 10, but at greater ages the fish from Hermitage Bay grow faster and, after the age of about 15 the fish of the Gulf of St. Lawrence show the fastest growth. Apart from the Southwest Grand Bank fish, after about age 12 those from Flemish Cap show the slowest growth.

An examination of the Bertalanffy parameters and their confidence limits indicates a complete overlap by K and t_o for all areas, and L_∞ for Southwest Grand Bank and Gulf of St. Lawrence with the other areas. Hamilton Inlet Bank can be considered different from Hermitage Bay and Flemish Cap in the maximum length to which fish from these areas may attain.

Growth rates of female mentella redfish. The area differences in growth pattern for female mentella parallel rather closely those of the males (Fig. 12). Over the range of lengths corresponding to the ages for which we have fitted the Bertalanffy curves, there are, relative to length (Fig. 13), 3 main groups of growth rate: the fish from Hamilton Inlet Bank, which show a fast growth rate, and those from Hermitage Bay and the Gulf of St. Lawrence which show a medium growth rate, and those from the southwest slope of the Grand Bank which show a slow growth rate.

When the growth rate is considered with respect to age (Fig. 14), the Gulf of St. Lawrence fish grow fastest till about the age of 28, and apart from these fish, Hamilton Inlet Bank fish grow fastest followed closely by those from Hermitage Bay.

An examination of the Bertalanffy parameters and their confidence limits shows that the K and t_o may overlap from all areas, but that L_∞ provides a likely separation of three differing growth patterns: Hamilton Inlet Bank having a high L_∞; Flemish Cap, Hermitage Bay and the Gulf of St. Lawrence having a medium L_∞; and the southwest slope of the Grand Bank having a low value for L_∞.

Growth rates of marinus redfish. As marinus were available from only two areas, area and sex differences are considered together. The fish from Hamilton Inlet Bank are larger than those from Flemish Cap (Fig. 5). Although the Flemish Cap males show a faster growth rate to about age 13 than the Flemish Cap females or Hamilton Inlet Bank males, after this age both the males and females from Hamilton Inlet Bank display a faster growth rate than the fish from Flemish Cap (Fig. 15).

Comparison of redfish growth curves as derived by different authors

North American mentella redfish

Very little age-length data have been published for redfish of the ICNAF Area. Some data are available from the ICNAF Sampling Yearbooks but only from Russian sources. Data to 1960 are summarized in a paper by Surkova (1962). More recently Savvatimsky and Sidorenko (MS, 1965) have presented growth data for mentella redfish from Hamilton Inlet Bank and the Northeast Newfoundland Shelf.

Perlmutter and Clarke (1949) were concerned primarily with immature redfish and, because much of their market sampling was aimed at these smaller fish, the values for mean length at age for the older fish in their samples are likely to be biased, with lower mean lengths and a flatter growth curve resulting.

Kelly and Wolf (1959) show growth curves of redfish from the Gulf of Maine for the years 1951, 1952 and 1953. While Kelly and Wolf recognize the rather uncertain taxonomic position of the North American form of redfish, they class the Gulf of Maine redfish, in their final table, as Sebastes marinus marinus. As has been already stated, it is the author's opinion and that of Templeman (1959) that the Gulf of Maine redfish belong to the common North American mentella-type.

Canadian and United States length measurements are made to the nearest centimetre, from the anterior tip of the lower jaw, with the mouth closed, to the end of the mid-fork of the caudal fin. The Russian measurements, however, were of total length (to the tip of the caudal fin - Surkova, 1962) and presumably also made to the nearest centimetre. Because of this difference in the basic dimension measured, the Russian measurements will be larger than those of the United States and Canada. The difference will increase with size of fish and, according to Templeman (1959), should be about 1-1½ cm for redfish in the 30-40 cm length range.

The method of age estimation also differs between the United States and Canada on the one hand, whose biologists use otoliths, and Russian biologists who rely almost entirely on scales. In many species of fish, although scales and otoliths agree and provide good age estimates for the younger fish, for the older fish which are forming very little new scale tissue annually, it becomes very difficult to distinguish between the winter and summer growth zones. This often results in an underestimation of the age of old fish by the scale method, as compared with the otolith method.

Gulf of Maine. Bertalanffy growth curves have been fitted for male and female redfish from the data of Kelly and Wolf (1959) for all samples collected in the Gulf of Maine in 1951, 1952 and 1953. The curves were fitted to the unsmoothed length at age data for ages 1-18, for both males and females. These curves, together with the mean length at age values to which they were fitted, are shown in Fig. 16. It is unfortunate that we have no age estimations for this area, but included in the figure are our Bertalanffy curves for Hermitage Bay. It is evident, both from the parameters of the fitted curves (below) and the curves themselves, that differences are not very great.

	Gulf of Maine		Hermitage Bay	
	Males	Females	Males	Females
L_∞	33.4	44.3	35.2	39.7
K	0.13	0.09	0.12	0.11
t_0	-0.5	-0.6	-0.3	0.3

The curves for the males are practically coincident to an age of about 14 years, after which the slightly higher value of L_∞ for the Hermitage Bay curve exerts its influence, and causes the curves to gradually diverge. The curves for the females do not appear quite so similar as those for the males, but the difference in mean length at each age is still less than 1.5 cm up to the age of 18, the largest age to which the curve was fitted. The Bertalanffy curve for the females of Hamilton Inlet Bank is also shown, to indicate how the curve for the data of Kelly and Wolf lies relative to the curves we have derived for various areas around Newfoundland.

ICNAF Subareas 2 and 3. Surkova (1962) has presented age at length data for ICNAF divisions 2J, 3M, 3O, and 3P which may be compared with the growth data in this paper from Hamilton Inlet Bank, Flemish Cap, Southwest Grand Bank and Hermitage Bay respectively. The curves for the area of best agreement - Labrador, and worst agreement - Flemish Cap are shown in Fig. 17.

Surkova's data for ICNAF division 2J were obtained in 1957 and 1958. In the former year the data were based on one rather small sample of fish taken in the same area as was our own, whereas in the latter they were from several samples most of which were obtained in the southern part of ICNAF Division 2J.

When these data points are compared with our fitted curves for the Hamilton Inlet Bank line (Fig. 17) and allowance is made for the mean lengths of Surkova's data being about 1 - 1 1/2 cm higher, except for the few very large males, the agreement between the growth curves is quite close. Why the large males in Surkova's data should diverge so greatly from the general trend is not known. Possibly scales have been used to obtain the age estimates, or, alternatively some fish from the deeper fast-growing population could have been mixed with samples obtained mainly from shallower water. It is to be noted that these large fish occurred only in the 1958 samples.

Surkova's data for the Flemish Cap area are for the years 1956-1960, but only her mean age at length data for 1956 and 1959, the years from which our samples were obtained from the area of Flemish Cap, have been plotted (Fig. 17). Also shown are the Bertalanffy curves fitted to our own data, and fitted to Surkova's data combined and averaged over the five years (unweighted).

The 2 sets of curves are quite different, with Surkova's data showing by far the faster growth rate.

Although differences are apparent between the age estimations of Surkova and the author, they are not of the order found between those who favour the slow growth and those who subscribe to the fast growth hypotheses for redfish. However, a lack of agreement is apparent and it seems unlikely that this could have been caused by between sample differences such as might exist due to the samples being obtained in diverse depths or localities. It is, in fact, difficult to evade the conclusion that the differences found between the results of these authors are due mainly to a difference in the basic method of age estimation. Thus, with otoliths being used by the one worker and scales by the other, the difference reduces to the much-discussed controversy of scales versus otoliths in age determination.

Just as the lack of agreement between the growth curves of Surkova and the author emerges so clearly from the comparisons, so also does the presence of agreement between the curves of Kelly and Wolf (1959) for the Gulf of Maine and those of the author for Hermitage Bay. Although the curves are for redfish from two different areas, it seems highly probable that the close agreement between the growth curves reflects a real agreement with regard to the basic method of age determination. The most striking difference between the data presented by Kelly and Wolf (1959) and our data is the lack in the Gulf of Maine of the large, very old fish which seem so common in the samples from the Newfoundland area in 1947-1953. It is probable that the high sustained fishing pressure to which the Gulf of Maine has been subjected has resulted in the relative absence of the large very old fish. A similar scarcity of these large old fish has been noted from the Gulf of St. Lawrence in recent years.

North American marinus redfish

Unfortunately very little data have been published for marinus redfish in the ICNAF Area. Some age frequencies are shown in the ICNAF Sampling Yearbooks, and Zakharov (1962) shows a table of age and mean length for marinus redfish from Subarea 1 of ICNAF. Zakharov's ages were determined from scales and although he is evidently extremely proficient at reading scales (he is able to read age to as many as 39 years), the growth curve he derives is typical of those obtained from scales. Travin's (1962) age frequency data also show ages to 35 years, with 5 fish being classed as older than 35. In view of the basic discrepancy between growth curves as derived from scales and otoliths of mentella redfish from the same area, little is to be gained by comparing between different areas, marinus growth curves which have been derived from otoliths and from scale age determinations. As the available detailed data on age and growth from both mentella and marinus of the Northeast Atlantic (with the exception of Bratberg, 1955, 1956a and 1956b and Trout, 1961 who worked only with rather young fish; and Kotthaus, 1949, 1952 and 1958) were all from scale readings, it is unlikely that comparisons will be of any real value.

Acknowledgments

It is a pleasure to acknowledge the direct and indirect help of many of the biologists and technicians of the Biological Station in St. John's. Particular mention should be made of E. Squires who read many of the otoliths.

References

Bertalanffy, L. von. 1938. A quantitative theory of organic growth. (Inquiries on growth laws II). Human Biology, 10(2): 181-213.

Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. II, xix, 1-533.

1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. Ciba Foundation Symposium on the Lifespan of Animals, 1959, p. 142-177.

Bratberg, Erling. 1955. Vokser veren langsomt og er det mulig å bestemme dens alder. Fiskets Gang, Nr. 42, p. 552-555.

1956a. Om veksten og tydningen ev de opake og hyaline soner i otolithene hos ikke Kjønnsmoden uer (Sebastes marinus L.). Fiskeridir. Småskr., Nr. 10, 1955.

1956b. On the interpretation of the opaque and hyaline zones in the otoliths of immature redfish (Sebastes marinus L.). J. Cons. Expl. Mer, 22(1): 66-74.

Jensen, Ad. S. 1922. Sebastes marinus. Researches on the distribution, biology, and systematics of the Greenland fishes. Vidons. Medd. Naturh. Foren. Kjobenhavn, 74: 89-109.

Kashintsev, M.L. 1962. [Some notes on the food of redfish in the Newfoundland area.] Soviet Investigations in the North-western Atlantic VNIRO/PINRO, p. 263-271.

Kelly, George F. and Robert S. Wolf. 1959. Age and growth of redfish, Sebastes marinus (Linnaeus) in the Gulf of Maine. U.S. Fish and Wildl. Serv., Fish. Bull., 60(156): 1-31.

Knight, William. MS, 1962. Groundfish sampling studies. Fish. Res. Bd. Canada, Biological Station, St. Andrews, original manuscript No. 940. (Unpublished).

Kotthaus, Adolf. 1949. Alter und Wachstum beim Rotbarsch. Fischereiwelt, 1(5): 68-69.

1952. Ökologische und fischereiwissenschaftliche Untersuchungen über den Rotbarsch (Sebastes marinus L.) II. Zur Altersbestimmung beim Rotbarsch. Ber. Deutschen wiss. Komm. Meeresforsch., N.F., 12(4): 503-511.

1958. Age and growth of redfish, Sebastes marinus (L). Int. Comm. Northwest Atlantic Fish., Spec. Publ., No. 1, p. 217-222.

Perlmutter, Alfred and George M. Clarke. 1949. Age and growth of immature rosefish (Sebastes marinus) in the Gulf of Maine and off western Nova Scotia. U.S. Fish and Wildl. Serv., Fish. Bull., 51(45): 207-228.

Rees, E.I.S. MS, 1962. Food and feeding of redfish in Hermitage Bay. Fish. Res. Bd. Canada, Ann. Rept. Biol. Sta., St. John's, Nfld., for 1961-62, p. 67-72.

1966. Aspects of redfish feeding habits. Rep. Challenger Soc. 3 No. 18.

Ricker, W.E. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Bd. Canada, No. 119, p. 1-300.

Sandeman, E.J. 1957. Redfish grow slowly. Fish. Res. Bd. Canada, Atl. Prog. Rept., No. 67, p. 26-28.

1958. Growth of young redfish. Int. Comm. Northwest Atlantic Fish., Spec. Publ., No. 1, p. 227.

1961. A contribution to the problem of the age determination and growth rate in Sebastes. Ibid., Spec. Publ., No. 3, p. 276-283.

Savvatimsky, P.I. and I.N. Sidorenko. MS, 1965. Results of investigations on deep-sea redfish. Ibid., Ann. Meet., 1965, Doc. No. 46, Ser. No. 1510, p. 1-4. (Mimeographed).

Surkova, R.I. 1961. Redfish, growth and age. Int. Comm. Northwest Atlantic Fish., Spec. Publ., No. 3, p. 285-290.

1962. [Size and age composition of redfish (Sebastes mentella Travin) from the North-west Atlantic.] Soviet Investigations in the North-western Atlantic VNIRO/PINRO, p. 297-311.

Taylor, C.C. 1958. Cod growth and temperature. J. Cons. Expl. Mer, 23(3): 366-370.

1959. Temperature and growth - the Pacific razor clam. Ibid., 25(1): 93-101.

1960. Temperature, growth and mortality - the Pacific cockle. Ibid., 26(1): 117-124.

Templeman, Wilfred. 1959. Redfish distribution in the North Atlantic. Fish. Res. Bd. Canada, Bull. No. 120, p. 1-173.

Tomlinson, P.K. and N.J. Abramson. 1961. Fitting a von Bertalanffy growth curve by least squares. State of Calif. Dept. Fish and Game, Fish. Bull., No. 116, p.1-69.

Trout, G.C. 1961. The otolith of group-O Sebastes mentella Travin. Ibid., Spec. Publ., No. 3, 297-299.

Yanulov, K.P. 1962. Feeding habits of "beaked" redfish (Sebastes mentella Travin) in the Newfoundland-Labrador area. Int. Comm. Northwest Atlantic Fish., Ann. Meet., 1962, Redbook, Pt. 3, p. 132-140.

Zakharov, G.P. 1962. [On the biology of redfish (Sebastes marinus L.) in West Greenland. Soviet Investigations in the North-western Atlantic.] VNIRO/PINRO, p. 319-330.

Table I. Summary table showing the Bertalanffy parameters and their standard errors.

	K	L_∞	t_0	Fitted years	No. of fish
		Mentella redfish			
Hermitage Bay (excluding 1953 year-class)					
*Males	0.119 ± 0.028	35.2 ± 1.0	- 0.3 ± 1.6	6 - 40	....
*Females	0.113 ± 0.019	39.7 ± 0.9	0.2 ± 1.0	6 - 40	....
Hermitage Bay (1953 year-class)					
*Males	0.17 ± 0.35	31 ± 28	- 0.4 ± 1.6	2 - 7	....
*Females	0.10 ± 0.37	43 ± 95	- 0.7 ± 1.7	2 - 7	....
Southwest Grand Bank					
Sandeman					
*Males	0.05 ± 0.05	33 ± 6	-20 ± 6	8 - 34	....
*Females	0.13 ± 0.05	34.2 ± 1.4	- 0.7 ± 3.0	8 - 32	....
Squires					
*Males	0.06 ± 0.04	30.6 ± 2.3	-17 ± 5	8 - 34	....
*Females	0.13 ± 0.07	33.3 ± 2.0	- 1 ± 5	8 - 34	....
Gulf of St. Lawrence					
*Males	0.06 ± 0.04	36 ± 13	- 5 ± 18	12 - 46	....
*Females	0.13 ± 0.04	38.4 ± 1.2	4.4 ± 2.0	12 - 46	....
Flemish Cap					
*Males	0.17 ± 0.05	34.4 ± 1.2	0.1 ± 1.2	4 - 30	53
*Females	0.15 ± 0.06	38.5 ± 1.4	0.6 ± 2.5	6 - 40	62
Hamilton Inlet Bank					
All depths					
*Males	0.16 ± 0.05	38.5 ± 1.0	- 0.1 ± 1.6	6 - 38	...
*Females	0.11 ± 0.04	44.8 ± 2.1	0.0 ± 3.1	8 - 40	....
175-200 fath					
Males	0.21	36.5	2	10 - 22	....
Females	0.16	41.5	2	7 - 20	....
250-300 fath					
Males	0.02	93	-14	10 - 22	....
Females	0.08	52	1	11 - 22	....
		Marinus redfish			
Flemish Cap					
*Males	0.07 ± 0.10	45 ± 14	- 5 ± 8	6 - 34	33
*Females	0.13 ± 0.03	47.8 ± 1.4	1.9 ± 1.3	6 - 40	57
Hamilton Inlet Bank					
*Males	0.05 ± 0.06	55 ± 9	- 9 ± 14	18 - 42	....
*Females	0.10 ± 0.12	60 ± 6	4 ± 18	18 - 42	....

* denotes when fit was made to smoothed data for even years.

AGE READINGS BY (B)

	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	>30	
4		1																											1
5																													
6									1																				1
7					1																								1
8							2		2		4			1															9
9					1			1	2	2	2	3				1													12
10							2			1	3	1	3		1	1		1	2				1						16
11						1	2	2	5	1	6	3		1	4	3	1	1											30
12					1		2		3	3	5	1		1	1	3	1	1	1										23
13							1		3	5	2	4	3	1	1	1	1		1		2		1						26
14							1	1		3	5	5	2	2	1	5	4	4	2	3	1		1						40
15								2	1	1		1	3	3	3		3		2	2	1		1						23
16									2	2		3	6	2	4	2	3	2	2	3	1								32
17									1	1	1	2	7	4			3	2	3	2			1				1		28
18								1		2		3	4	5	2			3	1	1	4					1	1	1	29
19										1	3	2		3	2	2	5	2	1	2	1	2	2		2				30
20									1		1		2	2	2	1	2	5	1	1	2	1	1		1			1	24
21												2	2	2		8	3	1	1	3		2		1			1		26
22														1	5	2	3	2		1	2		1	1			1		19
23														2	1	2	1		2	3	2		1				1		15
24								1	1						1		1	3	1	1			2					1	12
25														1					1		2								4
26																2	2				2	1	2		1				10
27																					1		2			1		1	5
28															1			1		1	1					1			5
29																1				1	1		1		2			4	10
30																											1	1	2
>30																		1	1		2	1	1					6	12
		1			3	1	10	8	22	22	32	30	32	31	29	34	33	29	22	24	25	7	18	2	6	3	6	15	445

Table II. Table showing the frequency of agreement and disagreement between two persons in estimating ages from the same otoliths of male and female fish from the southwest slope of the Grand Bank. The boxed diagonal denotes the frequency of perfect agreement at each age.

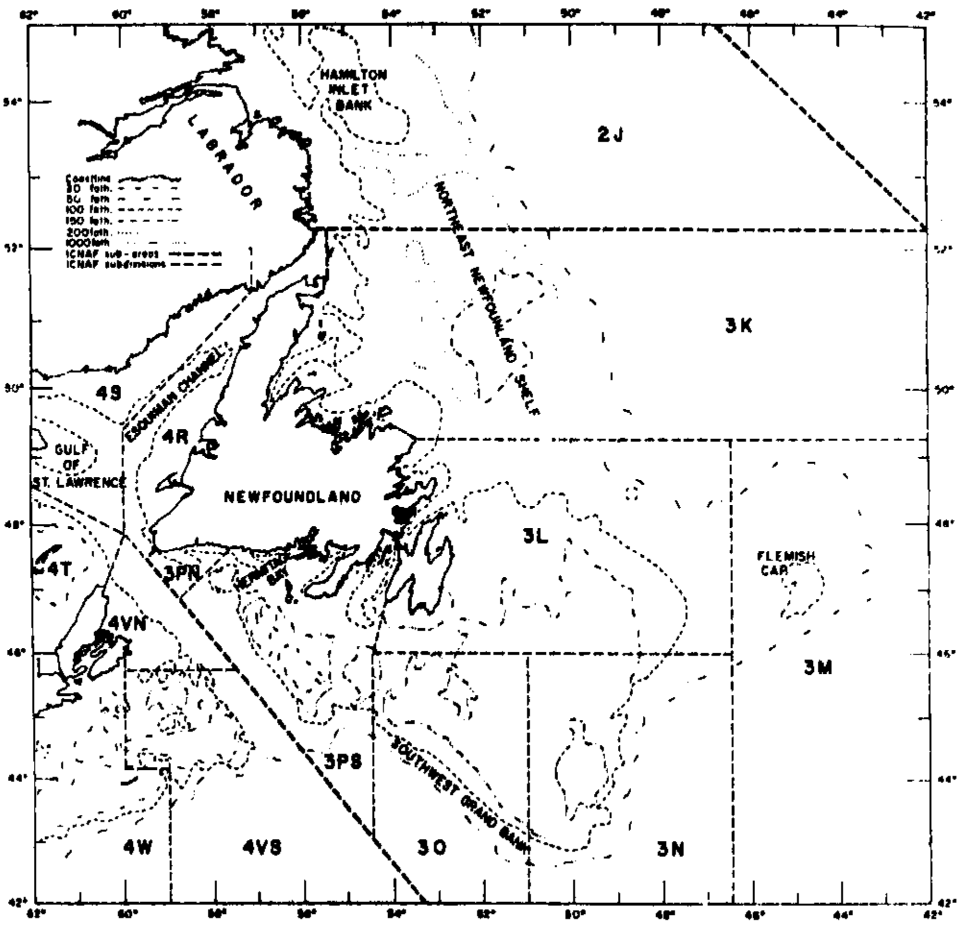
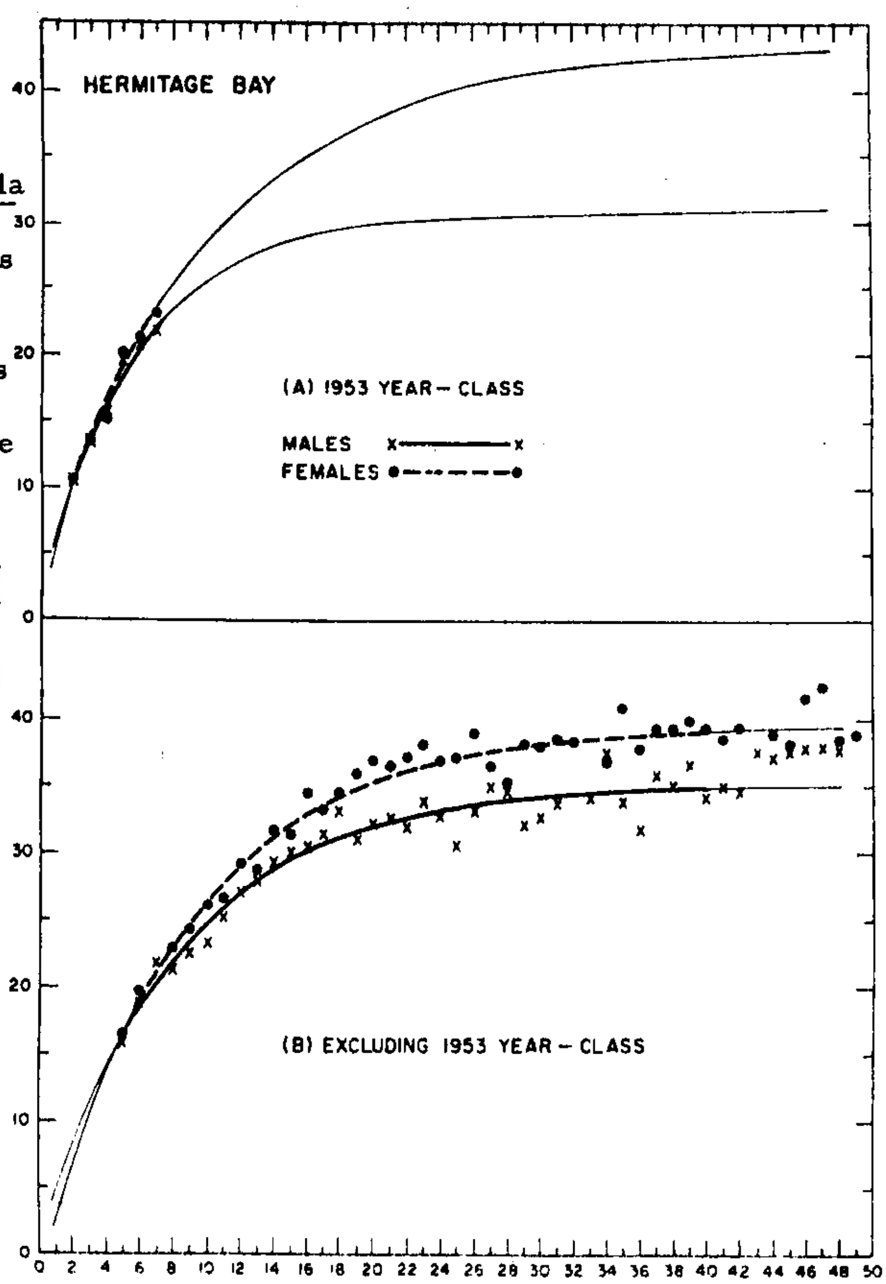


Fig. 1. Map of general Newfoundland area.

Fig. 2. Growth curves of mentella redfish from Hermitage Bay: (A) 1953 year-class (B) All data, 1953 year-class excluded. In this and in subsequent figures showing growth curves and their derivatives, the thicker line shows the range of ages to which the curve was actually fitted while the thinner line indicates the extrapolated curve.



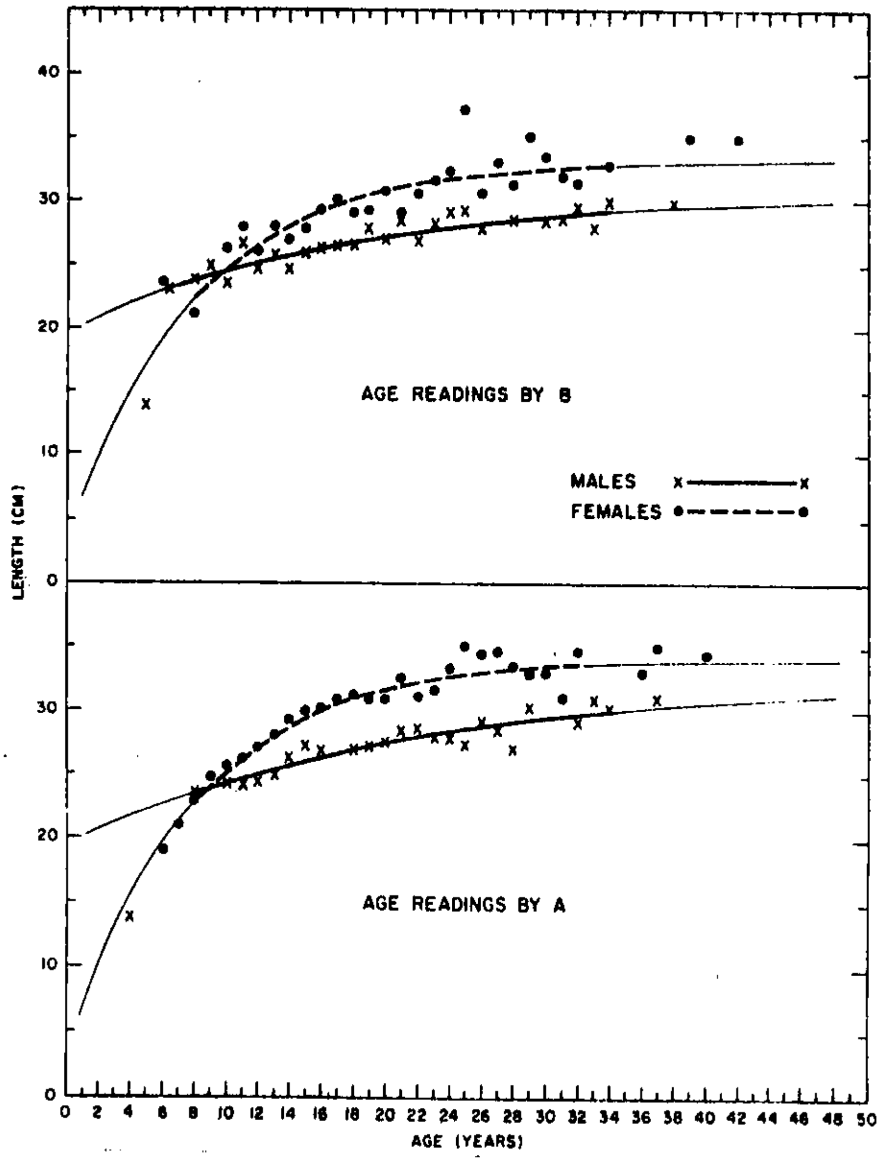


Fig. 3. Growth curves of mentella redfish from Southwest Grand Bank as derived from the otolith age estimates of two different persons.

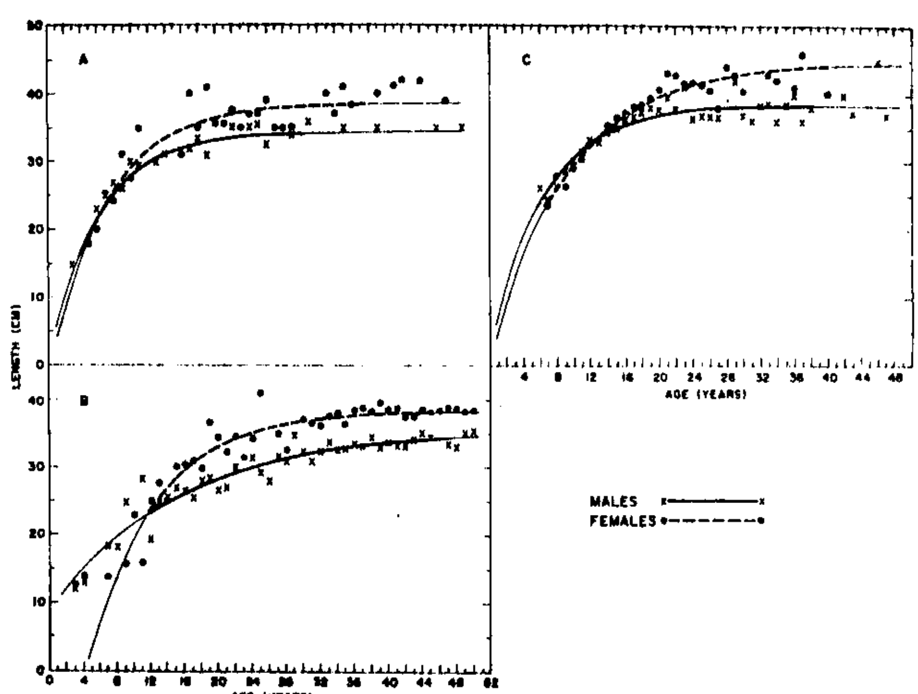


Fig. 4. Growth curves of mentella redfish: A, Flemish Cap; B, Gulf of St. Lawrence; C, Hamilton Inlet Bank.

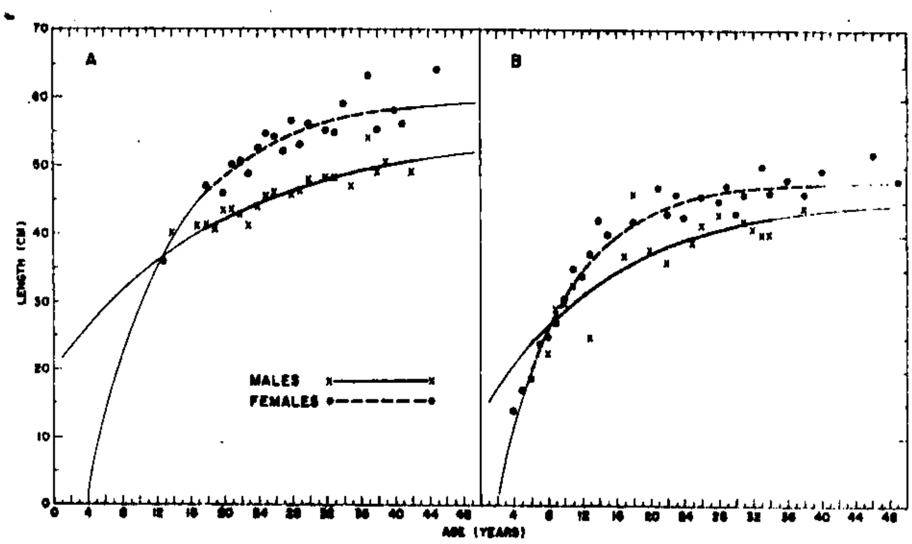


Fig. 5. Growth curves of marinus redfish: A, Hamilton Inlet Bank; B, Flemish Cap.

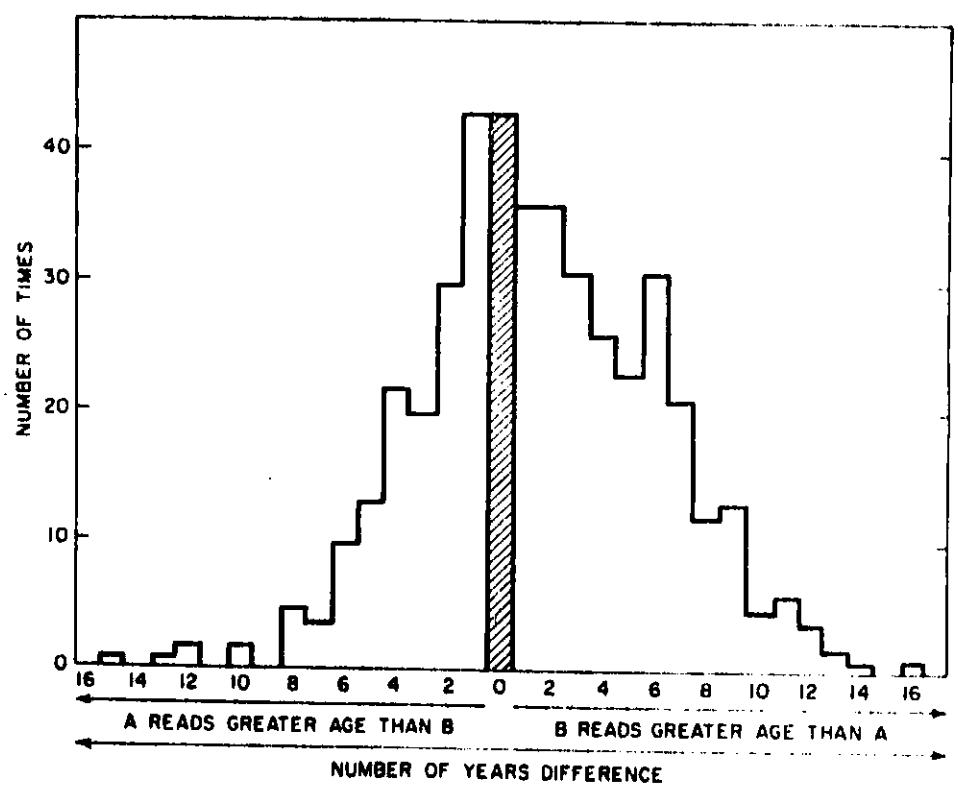


Fig. 6. Agreement-disagreement frequency histogram. Comparison of otolith age estimates by two different persons.

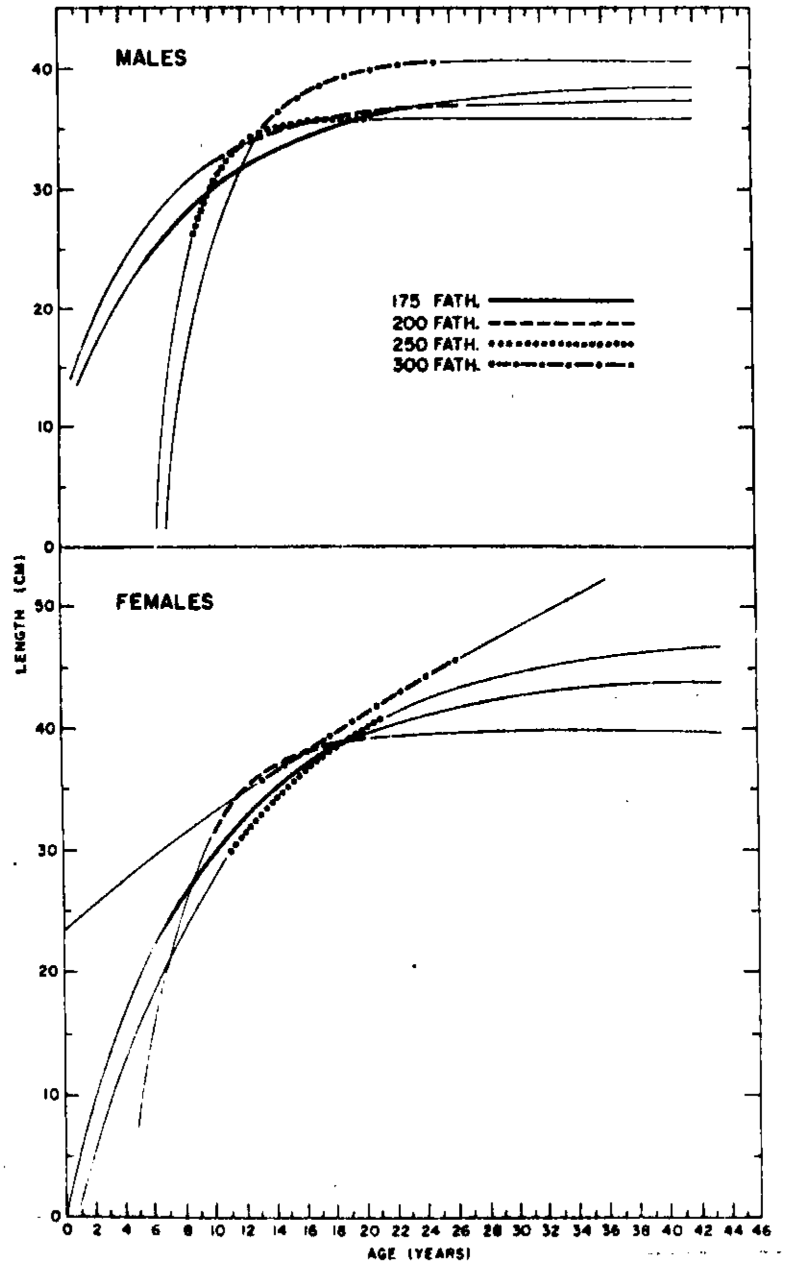


Fig. 7. Growth curves of mentella redfish from different depths, Hamilton Inlet Bank.

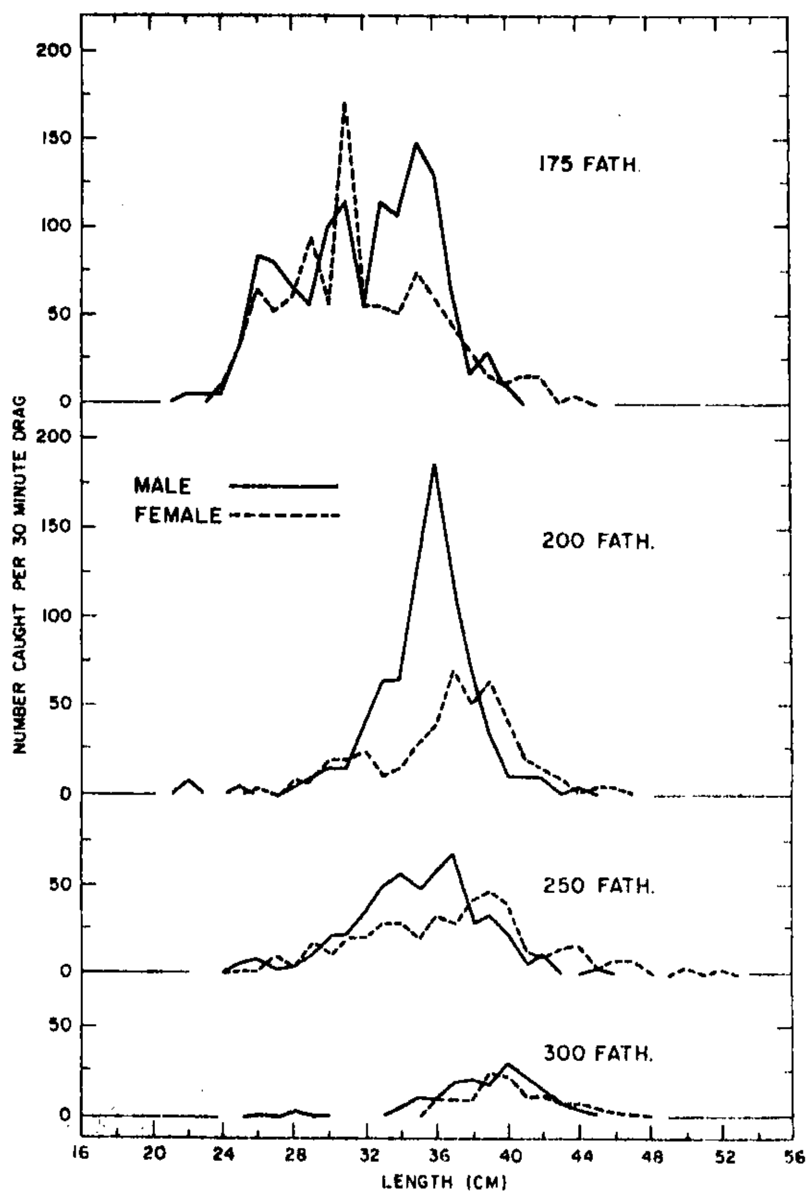


Fig. 8. Length frequencies of mentella redfish from different depths, Hamilton Inlet Bank.

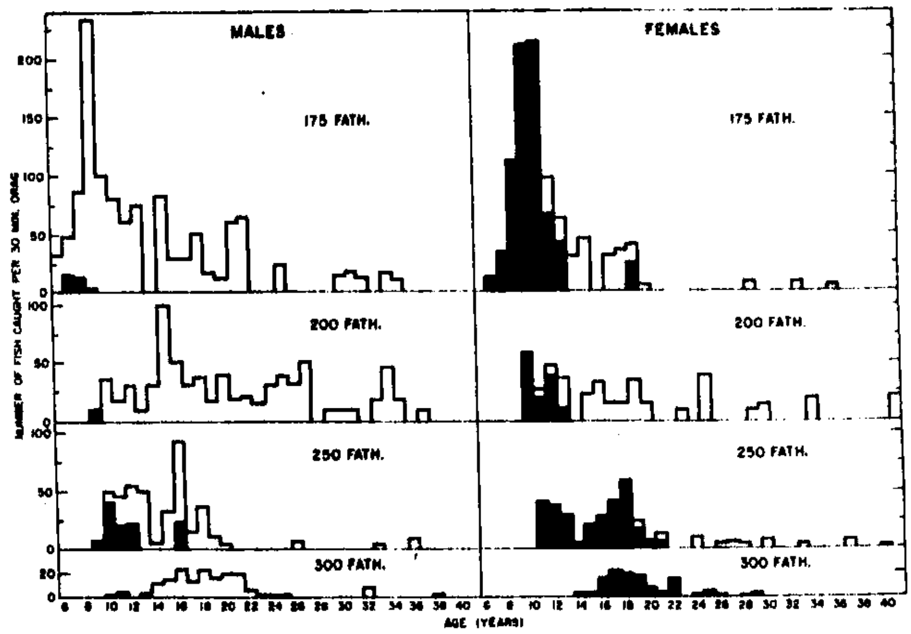


Fig. 9. Age frequencies of mentella redfish from Hamilton Inlet Bank. (Shaded portion shows immature fish, unshaded mature).

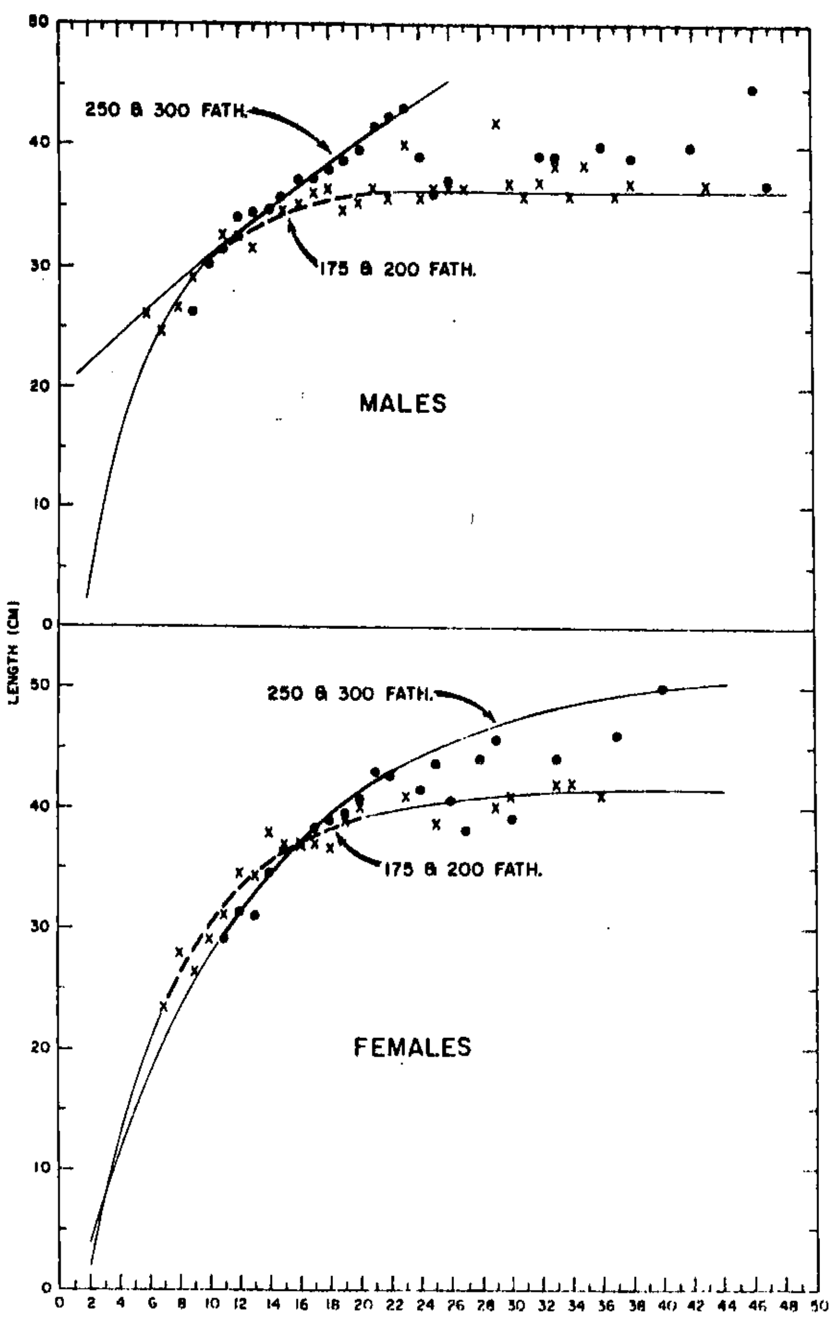


Fig. 10. Growth curves of mentella redfish from Hamilton Inlet Bank. The data from 175 and 200 fath have been combined as have the data from 250 and 300 fath.

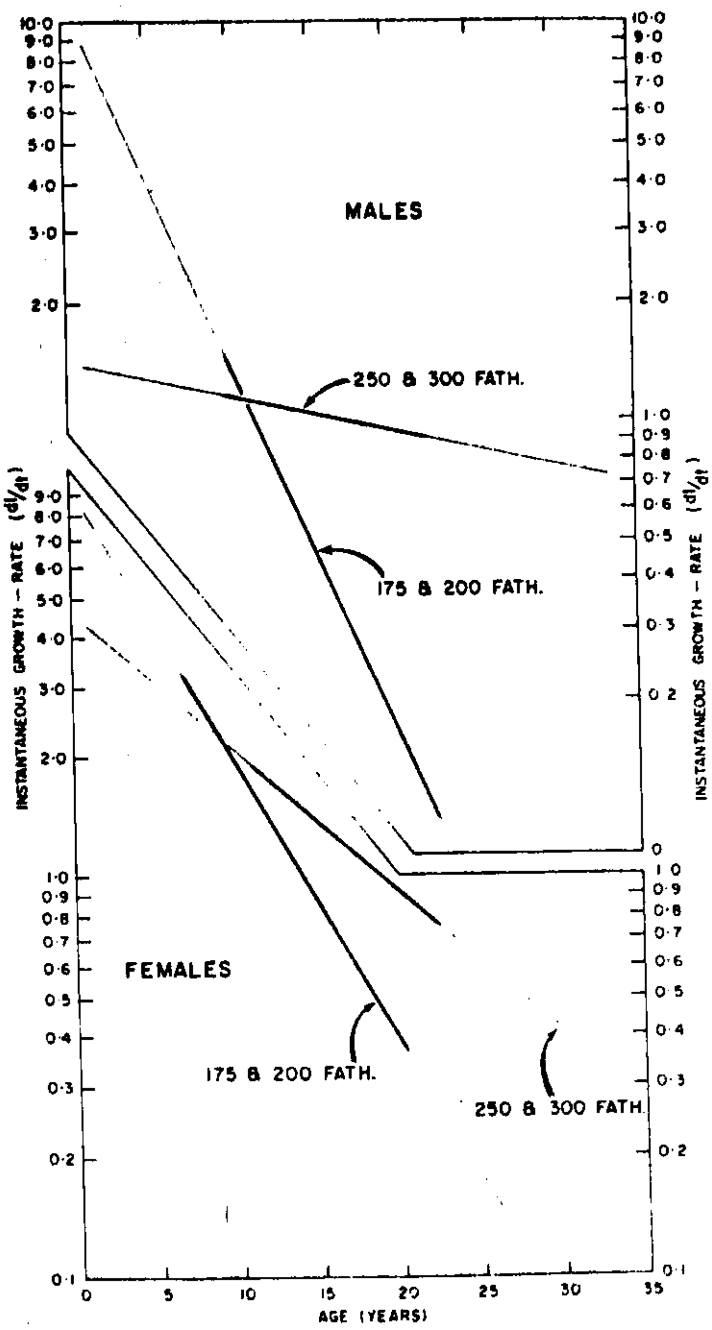


Fig. 11. Plots of growth rate against age for male and female mentella redfish from the shallower (175 and 200 fath) and deeper (250 and 300 fath) depth zones of Hamilton Inlet Bank.

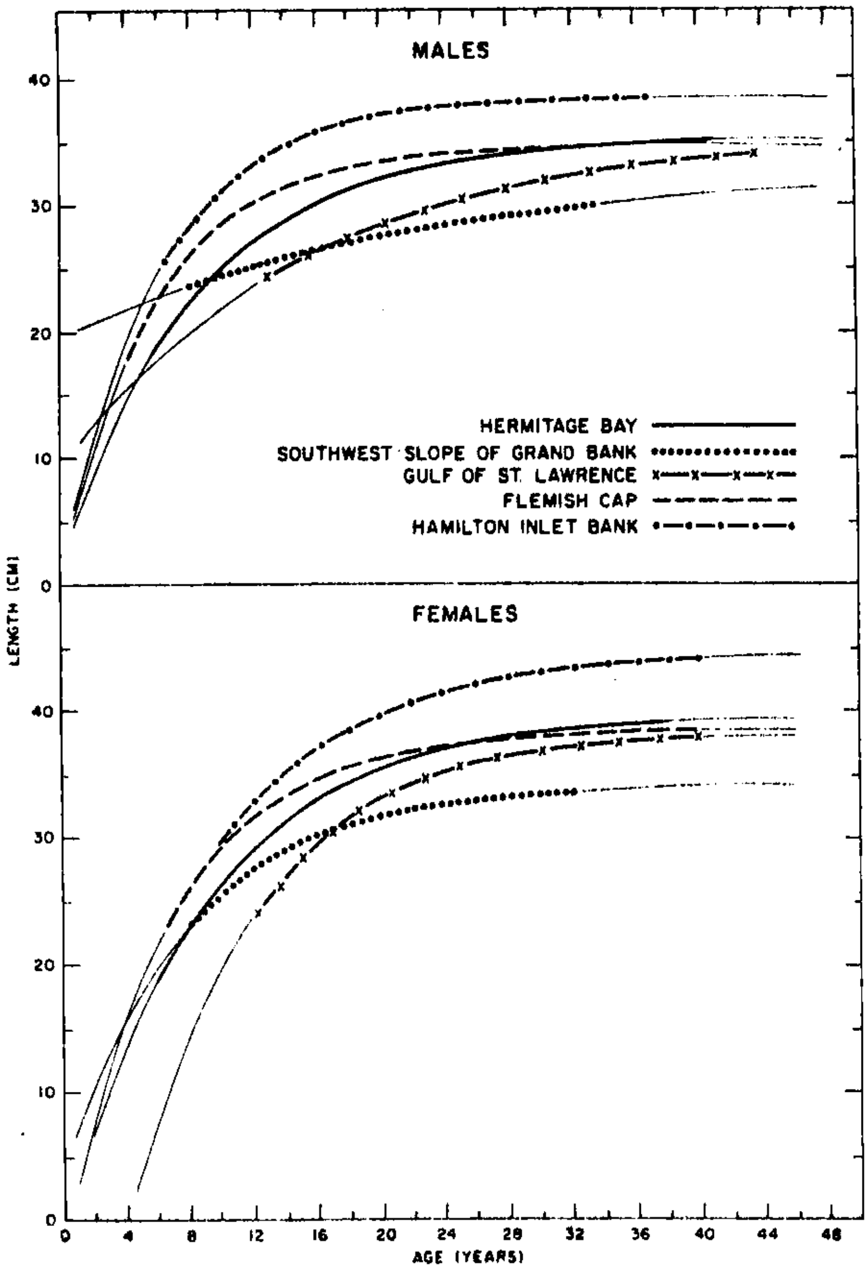


Fig. 12. Growth curves of mentella redfish from five different areas around Newfoundland plotted on the same coordinate system.

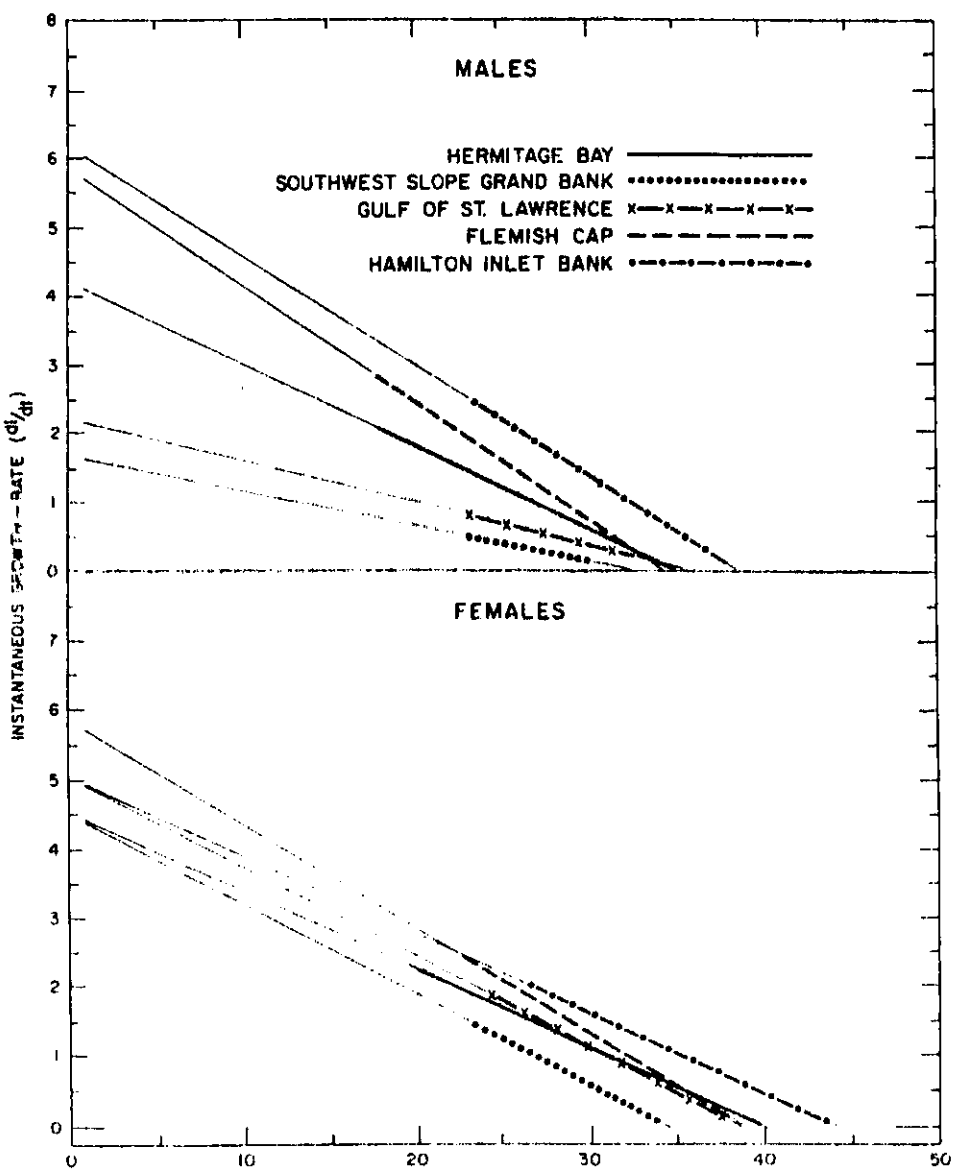


Fig. 13. Growth rate plotted against length for male and female mentella redfish from five areas around Newfoundlar

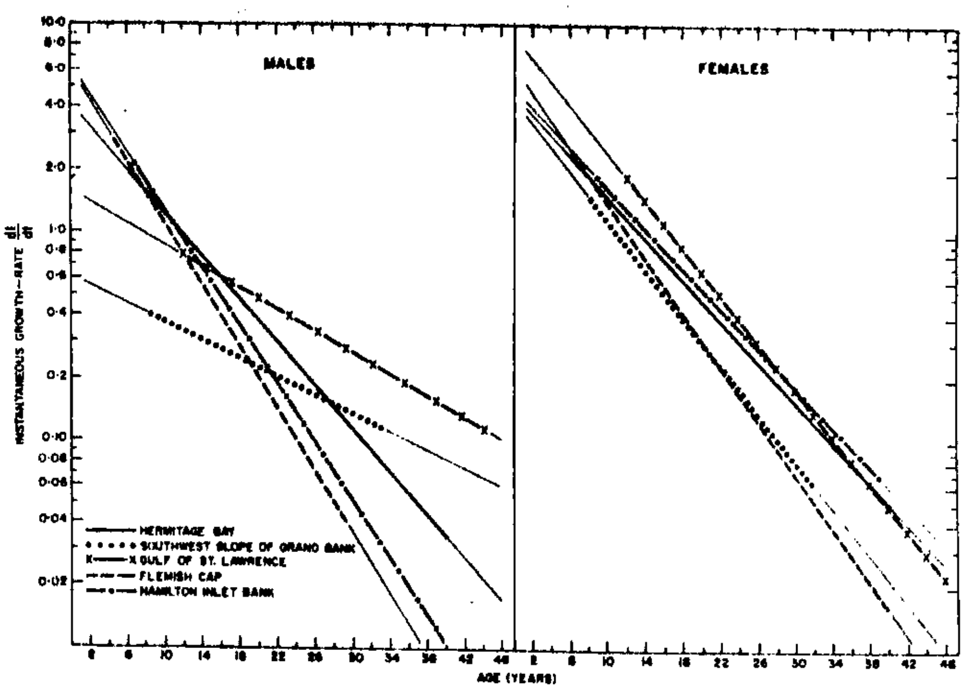


Fig. 14. Growth rate plotted against age for male and female mentella redfish from five areas around Newfoundland.

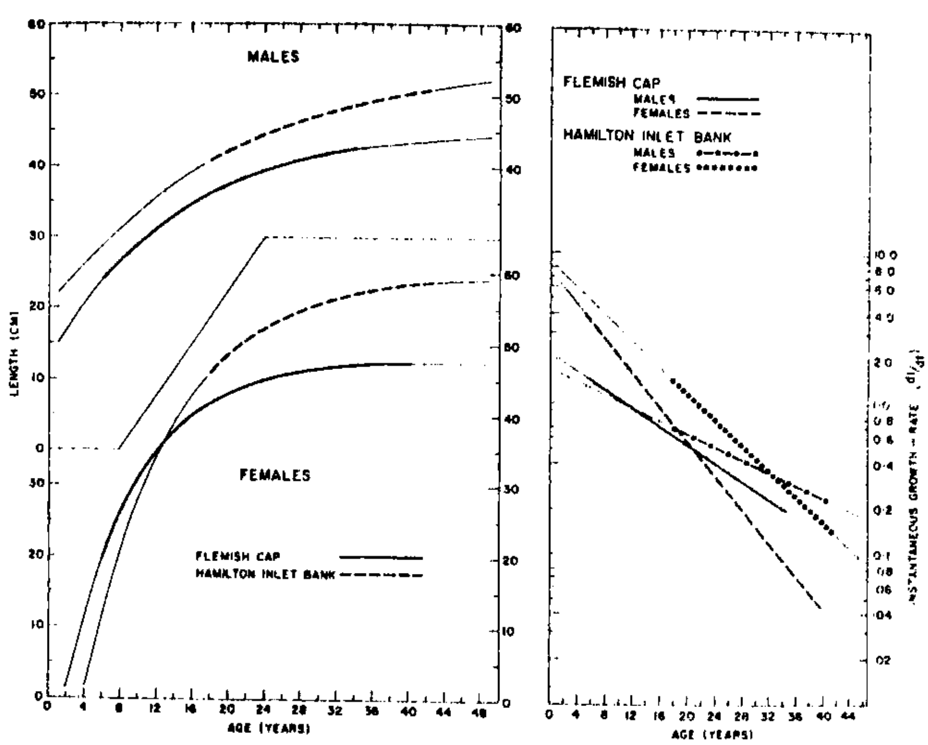


Fig. 15. Growth curves and plots of growth rate against age for male and female marinus redfish from Flemish Cap and Hamilton Inlet Bank.

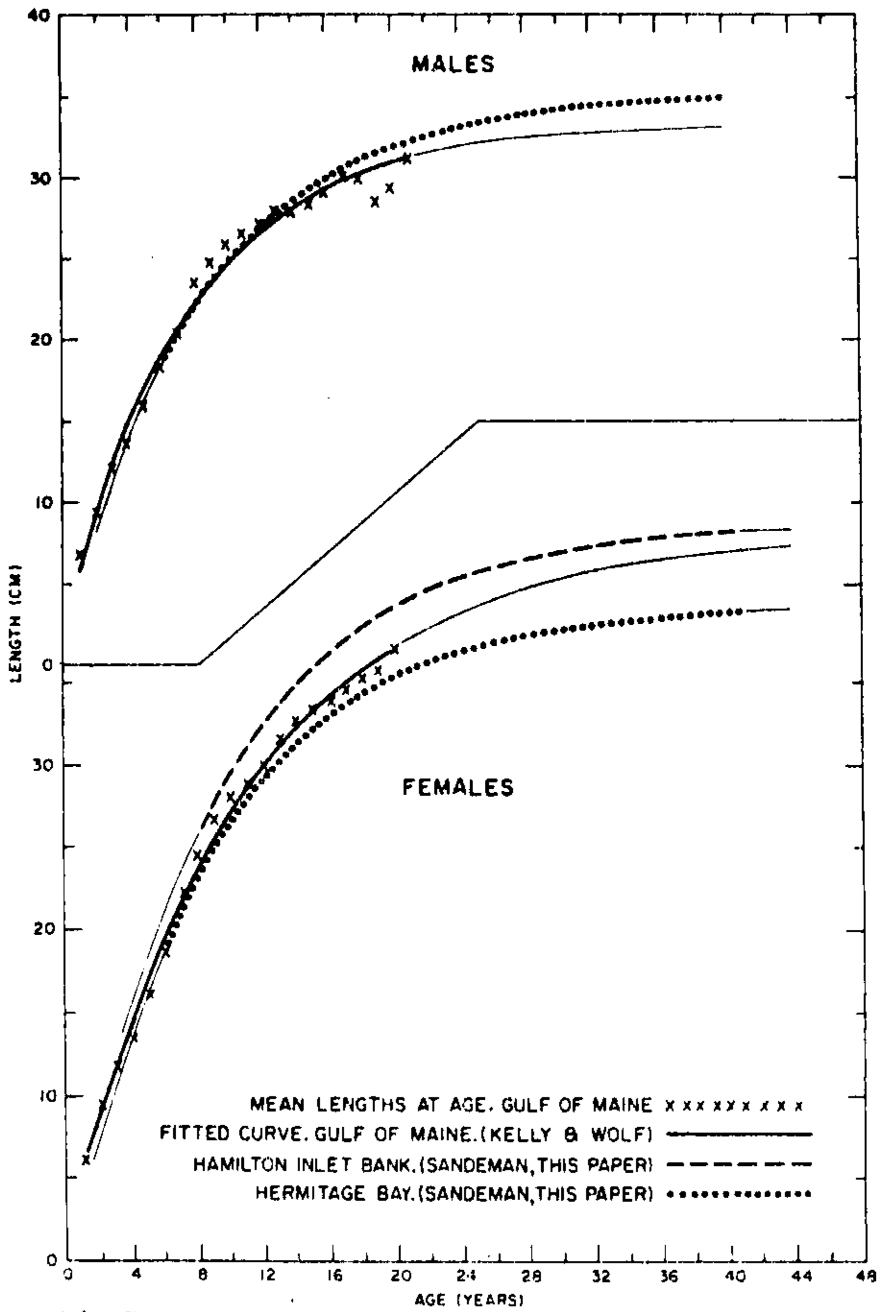


Fig. 16. Growth curves of mentella redfish from the Gulf of Maine (Kelly and Wolf, 1959) compared with mentella from Hermitage Bay and also for the females from Hamilton Inlet Bank.

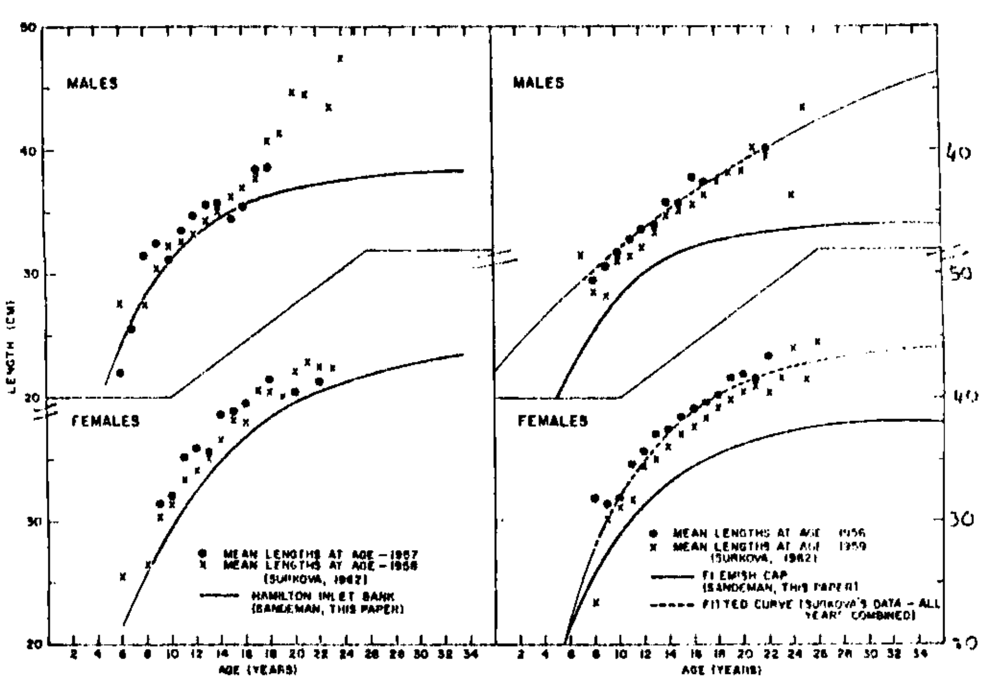


Fig. 17. Growth curves of mentella redfish from Hamilton Inlet Bank (left) and Flemish Cap (right). In each the mean lengths at age by Surkova (1962) are compared with the fitted curve obtained by the present author for the area in question.