VARIATIONS IN THE GROWTH OF ATLANTIC COD

(GADUS MORHUA L.)

by

A. Carl Kohler, M.Sc.

A thesis submitted to the Faculty of
Graduate Studies and Research in partial
fulfilment of the requirements for the
degree of Doctor of Philosophy.

Department of Zoology,
McGill University,
Montreal.

March 1961.

TABLE OF CONTENTS

	<u>Page</u>
INTRODUCTION	1
ACKNOWLEDGMENTS	3
COD GROWTH RATES	3
Methods of Estimation	3
Validity of Age Determinations	9
Growth from Age and Length Data	17
Growth Changes in Division 4T	19
COMPARATIVE FISHING -- LINE VERSUS OTTER TRAWL	25
Methods	25
Results	27
OTOLITH MEASUREMENTS AS GROWTH INDICATORS	31
Methods	32
Results	33
RECENT LITERATURE ON FACTORS AFFECTING FISH GROWTH	45
GROWTH EXPERIMENTS	50
Collection and Transportation of Cod	50
Physical Set-up for Experiment	53
Feeding and Growth	59
Maintenance-Fed Fish	59
Fish fed at Intermediate and Maximum Rates	61
Length and Weight Increment for Year	65
Relative Merits of Length and Weight	
Measurements as Growth Indicators	66
Food Consumption and Conversion to Cod Weight	69
Spawning Activity in the Tanks	72
Temperature, Feeding, and Growth Relations	74

	<u>Page</u>
EFFECTS OF WATER TEMPERATURE, POPULATION DENSITY AND FOOD AVAILABILITY ON GROWTH OF GULF OF ST. LAWRENCE COD	78
Water Temperature	78
Population Density	82
Availability of Food	86
CONCLUSIONS	91
SUMMARY	93
BIBLIOGRAPHY	97

INTRODUCTION

Rates of growth and the multiple factors affecting them are of primary concern to those involved with the production of food, both plant and animal, for human populations. Knowledge of critical factors influencing growth is of use in farming animals and plants because some of these factors can be directly controlled. This knowledge is also useful in dealing with crops growing in situations where most of the factors in the environment are at present outside the influence of man, including many commercial forms of marine fish. The value of studying such factors lies in the possibility of predicting the production to be expected from populations, given a certain set of environmental conditions.

This dissertation is concerned with the growth of an important commercial marine fish, the Atlantic cod (Gadus morhua L.). The species is widely distributed. A general summary of its distribution is given by Graham (1956), page 269 "... extending from the Arctic southwards on both sides of the Atlantic to the Bay of Biscay on the east and Cape Hatteras on the west. Within these limits it is the basis of the great trawl and line fisheries of northern Europe and off the east coast of the North American continent. In the northeast Atlantic, large concentrations are found in the Barents and White Seas, on the Faroe plateau, and at Iceland, along the west coast of Norway, on the North Sea

plateau, and off the west coasts of the British Isles. It is also widely distributed throughout the Baltic and its outlet to the North Sea. In the northwest Atlantic it abounds along the coasts of Greenland, along the eastern seaboard of North America and on the banks off Newfoundland where it forms one of the world's richest fish supplies. Species other than Gadus callarias^{1,2} but commonly called "cod" are found in the north Pacific, around the coasts of Japan and off the western seaboard of North America". The populations dealt with specifically here are mainly those resident near Canada's east coast.

The circumstance that brought about this investigation was an observed change in the growth pattern of a population of cod which has supported an otter-trawl fishery by Canadians in the Gulf of St. Lawrence since about 1947. In order to elucidate the factors involved in this change, sampling data from the area were analysed and laboratory experiments were devised in an attempt to separate out the factors involved. In the following pages differences in cod growth patterns in certain North Atlantic areas at various times are demonstrated. A discussion of the changes is followed by a recounting of experimental work designed to sort out the relative importance of certain environmental factors.

¹"These include the Japanese sukedo-dara (Theragra chalcogramma), the Alaska cod (Gadus macrocephalus), and the cods of Arctic Asia (Eleginus navaga and G. gracilis)."

²The proper scientific name of the common cod now appears to be Gadus morhua L. See Cohen (1959).

ACKNOWLEDGMENTS

I wish to express my appreciation for guidance given by Dr. M. J. Dunbar during the course of my studies and for his critical reading of the text of the thesis. The problem was selected in consultation with Dr. W. R. Martin and he has been most helpful in discussions of the investigation.

Several people were kind enough to permit use of data for which they were responsible and which were, at the time of writing, unpublished. These benefactors were P. Brunel, L. M. Dickie, Y. M. L. Jean, L. M. Lauzier and P. M. Powles.

Various members of the male technical staff of the St. Andrews Biological Station's groundfish investigation were responsible for routine observations on the tank experiments and for sampling landings of commercial vessels. They are to be complimented on the efficient manner in which these duties were performed.

The work carried out at sea was facilitated by the fine co-operation of the crews of the M.V. "Harengus" and the M.B. "Lameque No. 2".

COD GROWTH RATES

Methods of Estimation

As is usual in fishery investigations, the information on the growth of cod populations dealt with here is established by estimation of parameters from samples

of the populations. Age and length data collected from commercial vessel landings of cod are used to estimate growth. Since the accuracy of estimation of the growth parameter in this case is dependent mainly on the validity of ages assigned to the fish, the development and use of ageing methods for Atlantic cod is dealt with here in detail.

The measurement of the fork lengths of individual cod in samples of commercial landings, together with the removal of some part from which the age of the fish can be determined, such as a scale or otolith, has become a routine in the seaports of many countries interested in biological research on cod. Canadian mainland landings of this species have been sampled intensively and routinely in this way since 1946. Thus, a backlog of data has been built up on the age and length composition of the landed part of the population. More recently, with the acquisition by the St. Andrews Biological Station of additional scientific and technical personnel and research vessels for them to use, age and length sampling has increased at sea. Here a better picture of the population on the grounds in the area can be obtained. However, these latter types of data are only now being built up, so for the bulk of our comparisons to data we have had to rely on the commercial sampling.

One of the main drawbacks of commercial sampling of cod, when the investigator is concerned with what is happening to the whole population, is that the smaller members (in Canadian landings, those under about 40 cm. fork

length) are virtually eliminated from the samples because of cull by fishermen at sea. The picture is usually further complicated by the landing of cod sorted into a number of size categories that bring different prices on the market. This complication is eliminated by the port sampler who uses a system of weighting factors in order to randomize the sample of the catch obtained. The method used has been explained by Kohler (1958) for haddock landings and operated in the following way for cod.

As commercial catches of cod were landed, they were divided roughly into three size categories, scrod (ca. 40-49 cm. in length), market (ca. 49-73 cm. in length), and large (ca. 73 cm. and over in length). These groups were sampled separately and randomly for length and age. As a rule otoliths were taken from one-fifth of the fish measured. In order to weight the sample groups to correspond to the amounts of the three size categories landed, total weights of each category landed by the vessel from the area for the trip were used. Average weights of individuals in the three categories were obtained by counting the number of cod in a sample of boxes in which they were landed and dividing this figure into the total weight of fish in the box.

The equation used to obtain the weighting factor for each of the groups was as follows:

$$W_x = \frac{t_x}{T} \times \frac{n}{n_x}$$

where T = total number of fish in catch
 t_x = total number of one size category in catch
 n = total number of fish sampled
 n_x = total number of the size category in the sample

t_x was estimated by taking the average weight for individuals of the size category in question and dividing the total landed weight of that category by this average. T was found as the total $t_x + t_x + t_x$ from each size category. This procedure for weighting samples of commercial groundfish landings was initiated by Dr. W. R. Martin in 1946. The use of these weighting factors adjusted the data so that a good picture of age and length composition and growth of the stock caught at intermediate and older ages could be obtained.

The most useful tool for determining the age of Atlantic cod has been found to be the sacculus otolith. Thompson (1943) used scales for ageing cod from the Newfoundland area and indicated that he had confidence in his readings up to about eight years of age. Scales have also been used by biologists working on cod in northeastern Atlantic areas (see Graham, 1929a; Dannevig, 1933). However, more recent reports from laboratories working on cod biology in the north Atlantic indicate that they have turned rather to the otolith, as affording the best means of age determination of the fish (e.g., Trout, 1958; May, 1959; Dannevig, 1956). All ages used here have been determined from otoliths.

Methods of storing and reading cod otoliths vary among the workers concerned with this task. Accordingly, the techniques used in this investigation are outlined here.

Earlier samples (1946-1954) of cod otoliths taken by personnel of the Biological Station's groundfish investigation were removed from the fish and stored in vials in a 50% glycerin solution containing enough thymol to prevent fungus growth. A comparison of storage methods in 1954 showed that the readability of the otoliths was not adversely affected by dry storage in coin envelopes. Since this method was much more convenient for both samplers and readers it was adopted.

The actual determination of ages was carried out as follows: The otoliths were fractured across the longitudinal axis at a point near the interruption in the sulcus acusticus, the longitudinal groove on the convex side. The pieces were then imbedded in a cube of modelling clay, the fracture surfaces being set flush with the horizontal upper surface of the cube. They were covered with 50% glycerin solution and then examined with the aid of a stereoscopic microscope (usually 9X) using reflected blue light. Hyaline and opaque zones in the otolith cross-section were counted to give the age of the fish. The interpretation of the zone at the edge of the otolith varies according to the season of capture of the fish, and makes a difference to age-group assignation (see Table I). Interpretation of a hyaline edge in the third (Aug.-Oct.) and fourth (Nov.-Jan.) quarters of

Table I. Examples of observed ring counts and edge types on cod otoliths, and the resulting assignation to age groups.

Time of capture		Number of hyaline zones	Type and width of edge zone	Age group assignation
Quarter of year	Months			
I	Feb.	5	narrow hyaline	5
	Mar.	5	wide hyaline	5
	Apr.	5	narrow opaque	5
	May	5	wide opaque	5
II	June	5	narrow hyaline	5
	July	5	wide hyaline	5
	Aug.	5	narrow opaque	5
	Sept.	5	wide opaque	5
III	Oct.	5	narrow hyaline	4a
	Nov.	5	wide hyaline	5 (4a in Oct.)
	Dec.	5	narrow opaque	5
	Jan.	5	wide opaque	5
IV	Feb.	5	narrow hyaline	4a
	Mar.	5	wide hyaline	4a
	Apr.	5	narrow opaque	5
	May	5	wide opaque	5

^a In these cases it is assumed that a new hyaline zone has formed at the edge of the otolith before the assumed birthday of the fish in the following February. Therefore, it is not counted as a year-zone for age-group assignation.

the sampling year may also vary slightly, depending on the particular population from which the cod came, but is normally handled as shown in the Table.

Validity of Age Determinations

The importance of verifying methods of fish age determination when these are involved in the estimation of population parameters has recently been re-emphasized (see Saetarsdal, 1953; Graham, 1956). Several methods of verification of otolith age determinations are now commonly used by fishery biologists. Among them are the establishing of an annual change in the type of edge material found in the cross-section of the otolith, the consistency of age data showing strong and weak year-classes in a population, and the consistency of yearly production of annuli in the otoliths of fish in definable length groups found by the Petersen method. These three methods have been used to establish the validity of our otolith age determinations for cod populations considered in the following pages, and some examples of the data coming out of these validity studies will be shown here. The areas from which the examples are taken are those for which the best data are available.

Variations in edge types of otoliths of cod from inshore Lockeport, N.S. landings are shown in Figure 1. The data include samples for 11 years, from 1948 to 1958, inclusive. They are broken down into months and the percentages of fish having otoliths with hyaline or opaque edges are indicated. The yearly cycle shows hyaline edges

Figure 1. Type of edge deposition on cod otoliths from the inshore Lockeport area. Numbers of fish in each sample are shown. Shaded parts of the blocks indicate opaque edges. Light parts indicate hyaline edges.

predominating from December to April while the majority of the material examined exhibited opaque edges in the months of June to September. In the intervening months the dominant edge type varied from year to year. This indication of annual formation of one hyaline and one opaque zone on the periphery of the otolith is accepted by fisheries biologists as justification for the use of a combination of the two as representing one year in the life of the fish. The same type of evidence has been used by Saetarsdal (1953) for haddock and by Hickling (1933) for hake.

For the population of cod in the Gulf of St. Lawrence we are unable to get as good information on otolith edge turnover since weather conditions and sea ice often preclude sampling the same elements of the stock in both summer and winter. However, there is evidence of consistency of readings because of the way certain year-classes maintain their relative strengths over a series of sampling years. The data used here are taken from August-October commercial otter-trawl landings from the southwestern Gulf of St. Lawrence for the years 1949 to 1952 and 1955 to 1959. They are plotted in the form of percentage age frequencies in Figure 2. It will be noted that the changing age structure of the population has made the identification of strong and weak year-classes easier in the 1955-59 period than in the earlier period. In the early period which coincided with the postwar buildup of the otter-trawl fishery in the area, a relatively large proportion of the cod landed were over

Figure 2. Age composition of otter trawl caught cod landed in northern New Brunswick from Division 4T (Aug.-Oct.).

10 years of age. In this situation where as many as 12 age-groups were contributing substantially to the fishery, only the 1941 year-class showed dominance in more than one sampling year. However, in the later period when the effects of the intensive fishery were reflected in the virtual disappearance from the landings of cod 10 years old and over, the relative strengths of the younger year-classes became more apparent. In the sampling years 1955 to 1958 the 1950 year-class passed through a period of dominance followed by a weak 1951 year-class. During the first three of these years the 1948 year-class was also consistently of medium strength followed by a rather mediocre 1949 year-class. Hile (1936), Dannevig (1933) and Graham (1929b) have all used such evidence of continued abundance and scarcity of year-classes to validate the majority of age determinations.

It will be noted that the sampling for 1958 and 1959 shows a tendency toward even greater percentages of young fish in the catch. It is possible that the increased intensity of the fishery will eliminate the future possibility of following dominance of year-classes in the landings by greatly diminishing their numbers at the recruitment stage.

Some trouble was experienced in making a positive identification of the first two or three annuli in the otoliths of the Gulf of St. Lawrence cod population. This was noted when some disagreeing age readings were found upon back-checking readings, a job carried out intermittently during routine age analysis. In this phase of our age-determination

studies samples of cod otoliths are reread by the same reader after a year or more has elapsed since the first reading. A check of the first readings against the second set shows whether the reader has been using a constant set of criteria for differentiating between true and false annuli. In a like manner checks of consistency of interpretation between readers are carried out.

In this particular case, there was some difficulty in identifying the first annulus. Subsequently this was found to be because of the relatively small central portion of the otolith that it encompassed and because of the narrowness of the hyaline ring itself. In order to establish objective criteria for identifying these annuli formed in pre-commercial sizes of fish, special collections of baby cod from the population in question were started in 1959.

These young cod were located and caught using otter-trawling gear aboard the M.V. "Harengus", an 84-foot research vessel used in groundfish surveys by the Biological Station. Specifically, the trawls were a 40-foot shrimp trawl with a $3/4$ -inch codend liner, and the usual No. 36 trawl used by the "Harengus" with the codend cover lined with $1/2$ -inch mesh netting. Data were also collected in the area in January 1960 by the Fisheries Research Board's research vessel "A. T. Cameron", using a No. 41-5 trawl with a $1\ 1/8$ -inch codend liner.

The most useful collections of data taken so far were in June and October 1959 and January 1960. The length distributions for these fish are shown in Figure 3.

Figure 3. Length distributions of special collections of small cod from ICNAF Division 4T taken to check age determination methods.

To interpret the meaning of the peaks in the frequencies of the smaller fish in the Figure, the Petersen method of assigning ages to length-frequency modes was followed (see Graham, 1956, p. 285). With the aid of knowledge of spawning times and growth of this cod population, age I was assigned to the peak at 13 cm. and age II to the peak at 19-20 cm. in the June sample. Similarly, the October sample has a peak of young-of-the-year (age-group 0) at 6 cm. and the age I mode had moved to 17 cm. due to growth of the group. Again in the following January the age-group 0 fish were approaching their first birthday, which is arbitrarily set at February 1, and had a mode at 10 cm., while the one-year-olds approaching their second birthday had a peak at 19 cm.

The ages of these small fish having been indicated by the length-distribution modes, the otoliths were then examined. Study of their structure indicated the way in which the hyaline and opaque zones should be interpreted in order to arrive at the age of the fish. In particular, a small check appearing in the centre of some of the otoliths, which had previously been thought to indicate only a change from the pelagic to the bottom environment, was found to be an annulus. Apparently the reason for the reduced size of this year-zone was the relatively late spawning of many of these cod, which resulted in subnormal growth of the otolith in the young fish of this population before the first birthday. Examination of these small otoliths also showed

that further ageing troubles might arise because of the prevalence of "false checks" in some of the material. Most of this type of error has now been eliminated by use of a "ring-spacing" criterion. This criterion has been established by observations indicating that the opaque zones between each hyaline annulus normally become progressively smaller from the centre to the edge of the cross-section of the otolith. Thus when the reader is doubtful about the validity of an annulus, careful observation of the spacing of annuli in the otolith is often of great aid in making a decision as to whether it should be counted.

Growth from Age and Length Data

Average size at any particular age is one of the parameters of a cod population that is relatively easy to sample. The observations also provide an easy means of calculating growth rates, either by comparing the differences in length or weight between a number of age-groups sampled at one particular time, or by following separate year-classes over a series of years. As is the case for many other fish species, size-at-age and growth rates vary greatly from one population to another and even from year to year within the same population.

As an example of variation from population to population, data for mean lengths of various age-groups of cod taken by otter trawlers in the northwest Atlantic are

Figure 4. Cod growth from ICNAF Sampling Yearbook Vol. 3 and unpublished data of the Fisheries Research Board. Data from Division 1F are for Jan.-Feb. 1958, Division 1D for April 1958, Division 3P south for Feb. 1958, and Division 4W, Western Bank, for Feb.-Apr. 1956-58.

plotted in Figure 4. The information concerns cod populations from four widely separated statistical Divisions laid out by the International Commission for the Northwest Atlantic Fisheries (see Appendix Map # 1 for location of these statistical areas which will be referred to elsewhere in the text). Averages for Divisions 1D, 1F, and 3P south are taken from the ICNAF Sampling Yearbook, Vol. 3, for the year 1958, while the data for 4W are from files of unpublished material at the Biological Station, St. Andrews. Variances of means for the Division 1D, 1F, and 3P data were not available, however the means for fastest and slowest growth seemed sufficiently well spread to indicate that there are differences in rates for different populations. The data for five- and six-year-olds are no doubt affected by fishermen's cull and gear selection for large fish, which would tend to bias the means upwards. Size-at-age in the data changes from area to area being greatest in Division 4W, the most southerly of the group. The growth rate as represented by the increment in centimetres from one age-group to the next is also consistently greater.

Growth Changes in Division 4T

In order to elucidate these growth variations further, a more detailed study of the cod population exploited in parts of Division 4T was made, using commercial age and length data gathered by the groundfish staff during 1949-1958. The data are taken from landings of a fleet of 60-foot

draggers, all of similar design and power, using similar types of trawl gear. The fleet is based in the area of Caraquet, N. B., where a postwar expansion in the number of otter trawlers made it possible to study the effects of increasingly concentrated effort on the population. The definition of the cod population has been made clear by McCracken (1959) through a series of tagging experiments. There seems to be a definite shift of concentrations of cod found in the offshore northern New Brunswick area (Unit Areas 4Tk, 4Tl, 4Tn; see Appendix Map # 2) in the "summer" (June-November) to the Cape Breton area (Unit Areas 4Tf, 4Va) in the "winter" season. This shift, combined with adverse weather conditions in the winter in the northern New Brunswick area, results in a fishery in the area by the Caraquet draggers limited to the months of May to October-November. The fish have returned to the northern New Brunswick area each summer during the years they have been under observation.

Sampling of the catch over the years 1949-1958 has been carried out in the months of May to October by groundfish technical staff. Data for 1954 have not been used because of inadequacies in information used to calculate weighting factors. As these age and length data were worked up year by year a remarkable fluctuation in average growth in length of the various age-groups was noted. This is illustrated in two Figures.

Figure 5. Mean lengths of age-groups of cod sampled from ICNAF Division 4T otter trawl catches landed in the area of Caraquet, N. B., during the months of May to October.

The first of these, Figure 5, shows variation in average size of age-groups 6 to 10 over the years sampled from 1949 to 1959. Younger age-groups are taken in the samples but gear selection and fisherman cull bias their mean lengths upwards. For age-groups over 10 years of age there are not usually enough fish in any one sampling year to give a good estimate of the mean length. The exact data used are shown in Table II.

The main change in size-at-age evident in Figure 5 is the rise of all age-groups from a low mean length in sampling year 1950 to a high in 1955-57 and an evident returning to lower levels in 1958 and 1959. The change in growth rate in these years can be demonstrated by comparing differences in mean length of age-groups. During 1952 the difference in average length between 6- and 10-year-olds was 12.0 cm., while in 1956 it was 22.0 cm., indicating a greatly increasing increment per year in the intervening period.

In Figure 6 the same basic data were used but they were combined and averaged to show the general shape of the curves during the fast- and slow-growth periods. Again, the differences in size at age are obvious, the 1955-57 averages for these cod being about 3 to 13 cm. higher than those for 1950-52 for ages 6 to 10, where the various types of selection are thought to bias estimates the least. The slopes of the two lines are different, indicating a change in actual rate of growth between the two periods.

Table II. Mean lengths (cm.) and their standard errors for some age groups of cod sampled from Division 4T otter-trawl landings in the May-October period 1949-1953 and 1955-1959.

Age Group		Year of Sampling									
		1949	1950	1951	1952	1953	1955	1956	1957	1958	1959
6	$\bar{x}$	57.80	56.16	58.37	58.87	58.32	60.06	60.84	62.58	58.97	55.82
	$S_{\bar{x}}$	0.75	0.74	1.09	0.99	0.75	1.35	0.62	1.84	0.87	0.56
7	$\bar{x}$	63.07	58.49	61.31	63.28	65.74	66.71	65.51	64.85	64.07	60.96
	$S_{\bar{x}}$	0.87	0.66	1.74	1.47	1.54	1.49	1.34	0.69	2.24	1.09
8	$\bar{x}$	66.57	60.57	64.41	64.61	69.03	73.90	74.00	71.36	68.08	66.33
	$S_{\bar{x}}$	0.84	1.34	0.96	1.33	2.62	1.84	1.37	2.13	1.23	2.32
9	$\bar{x}$	70.14	65.62	67.65	65.88	70.15	79.67	79.84	78.92	72.69	70.52
	$S_{\bar{x}}$	1.56	0.79	2.12	1.51	2.41	3.35	1.31	1.52	3.57	2.26
10	$\bar{x}$	76.06	67.55	72.75	70.95	73.47	77.19	82.79	82.15	78.47	74.16
	$S_{\bar{x}}$	3.02	1.66	1.94	2.08	3.48	11.10	3.77	1.79	3.90	5.38

Figure 6. Cod growth in Division 4T, May-Oct., averaged for two periods. Curves were fitted by eye to points for age-length means from commercial landings data.

The question that arose at this point in the investigation was whether our data represented a true change in growth or whether the differences were due to some artifact in sampling the population, such as a varying availability of the longer fish in the age-groups to the otter-trawl fishery. This possibility has been suggested by Dickie (1960) who was investigating the validity of the use of growth curves derived by various sampling methods for mesh regulation assessment purposes. His data indicate disparities between sizes of cod in various age-groups caught by line and by otter trawl. There was a possibility that longer fish of an age-group might be available in an area to line fishing but not to otter trawling. If individuals such as these did suddenly become available to the otter-trawl fishery, an apparent rise in the growth rate would be indicated. This possibility demanded field investigation and the first experiment along these lines was carried out by the author in June 1960.

COMPARATIVE FISHING -- LINE VERSUS OTTER TRAWL

Methods

The Fisheries Research Board's M. V. "Harengus" was used as an otter trawler fishing alongside the "Lameque No. 2", a 55-foot commercial longliner from Lameque, N. B. Cod populations were fished for three days on the grounds in Unit Areas 4Tn and 4Tl (see Appendix Map # 2) near the New Brunswick coast using regular commercial gear on each boat. All cod taken by both boats were sampled for lengths

Figure 7. Length composition of line and otter trawl catches of cod taken in June 1960 on the same fishing grounds.

and otoliths in order to have a substantial amount of data for comparison of the sizes and ages of fish caught by the two methods.

Results

Examination of the percentage length composition of the cod catches of the two boats (Fig. 7) indicated a marked difference in the length selection by the two fishing gears operating on the same population of fish. The otter trawl tended to take intermediate sizes of cod (40-70 cm.) as the greatest proportion by numbers of its catch. Most of the smaller ones escaped through the fairly large ($4 \frac{3}{8}$ inches, stretched) meshes of the regular commercial codend used on the trawl. On the other hand, the line-trawl catch contained a much greater proportion of cod over 70 cm. in length, with a resultant smaller proportion in the 40-70 cm. range. Smaller cod were probably eliminated from the catch of this gear by large hooks and bait of the wrong type to attract them. The skipper of the longliner was of the opinion that the larger percentage of fish over 70 cm. taken by his gear were caught as the baited gear settled through the water to the bottom. He felt that the bulk of the larger cod were up off the bottom in such a position that they would not be as vulnerable to the otter trawl. This theory was supported by casual observations by the technician aboard who stated that more large fish seemed to be caught near the buoyed ends of the gear which were presumably up off bottom.

Figure 8. Growth curves for longline and otter-trawl catches of cod taken in June 1960 on the same fishing grounds.

It remained to check on the ages of these fish, especially the ones over 70 cm. to see if they were faster-growing individuals or merely older ones. This was done by taking a stratified sample of otoliths from those which had been collected (the theory of this type of sampling as applied to fish age determination is reviewed by Gulland (1955)). When the otoliths were read the resulting age and length data were summarized in the form of growth curves for the two types of fishing gear. These are seen in Figure 8. It seems obvious that there were no consistent differences in growth of cod caught by the two methods. The otter trawl line follows the smoothest curve while the longline curve seems to vary around it. These variations were most likely due to sampling error since the same readers made age determinations for both samples. When the age compositions of the catches were examined (Fig. 9) they showed a much greater abundance of fish eight years old and over in the longline than in the otter-trawl catch. Thus, the abundance of long (over 70 cm.) cod seen in the longline catch in Figure 7 was due to older fish rather than fish growing faster than those caught by otter trawl.

It is of interest to note here the similarity in relative year-class strength in the younger age-groups of the two samples. The indication is that detection of a strong year-class, in this case the 1954 year-class, in an area could be made by examining commercial landings from either fishing gear. Also of interest is the fact that the

Figure 9. Age composition of longline and otter-trawl catches of cod taken in June 1960 on the same fishing grounds.

strong 1950 year-class already mentioned in connection with Figure 2 is still noticeable in the catches of large cod of the longliner.

Thus, the differences in growth noted by Dickie (1960) did not seem to be explained by selectivity of fishing gears within age-groups. To date, the differences have not been satisfactorily explained but are suspected to be a result of inadequate sampling of line-caught cod and difficulties in age-determination methods for these cod of the type mentioned in an earlier section.

OTOLITH MEASUREMENTS AS GROWTH INDICATORS

Further corroboration of the growth change in Gulf cod was sought by measuring annual increments on otoliths. Trout (1953) has reviewed some of the more important contributions concerning factors related to otolith growth, particularly by Buckmann (1931), Rollefson (1933 and 1935), Hickling (1933), Jensen (1938), Menon (1950) and Einarsson (1951). He goes on in his 1953 paper to demonstrate variations in yearly otolith increments in different parts of the Barents Sea stock of cod and uses this as part of a basis for his thesis on the migrations and movements of Bear Island cod (1957). The methods he used served as a guide for those used in the present study and are set out below.

Methods

The objective here was to investigate whether or not an increase in growth of the otolith coincided with the apparent increase in growth in length shown in Figure 5. For this purpose a number of otoliths were selected which were taken from fish sampled in the years 1957 and 1959. These otoliths were broken across the interruption in the longitudinal groove (the sulcus acusticus) found on the convex side. The surface was then ground down until the fracture surface was smooth and in the same relative position on each one. The posterior piece of the left-hand otolith was used for measuring. It was placed in plasticene and the fracture surface was covered with glycerin solution in the normal way.

The instrument used for measuring distances between rings was a stereoscopic microscope, manufactured by Watson of England, and fitted with one of their screw micrometer eyepieces made especially for this job. The otolith was viewed using 6X oculars, 1.25X objectives and reflected blue light. The drum on the screw micrometer was divided into 100 divisions for one complete rotation and one of these divisions was found to measure .0048 mm. of the field of view when using the forementioned lens combination. Experimentation showed a maximum of two to three divisions variation when measuring the same sequence of rings a number of times. Thus, as long as the points

between which measurements were made, in this case the inner edges of hyaline rings, were clearly defined, the instrument gave quite accurate measurements. All measurements were recorded in terms of one unit on the rotating drum, called one eyepiece unit (e.p.u.).

Measurements were made from the inner edge of one hyaline ring to the inner edge of the next ring except in the case of the first measurement which was from the centre or origin in the initial opaque growth to the inner edge of the first hyaline year ring. This grouping was adopted so that each measured increment would correspond most closely to a calendar year, where hyaline growth is found in the winter and spring and opaque growth in the late summer and autumn. The axis of measurement was from the origin to the edge at the middle of the concave side of the cross-section, the side opposite that one having the sulcus acusticus.

Results

Because of irregularity in increments on cod otoliths during their first two or three years of life, selections had to be made to eliminate use of these increments and to give an indication of variation caused only by differences in growth conditions during the years in question. Trout's (1953) Figure 2 shows a definite decrease in otolith increment with age. This also appeared in the data dealt with here. Thus, to demonstrate increments

differing in two different years, say 1954 and 1952, it was necessary to compare growth at the same age. For instance, the distance from age ring 5 to age ring 6 was compared on fish of the same age, sampled in different years. For this sort of comparison the most suitable data available at the time of writing were measurements on 10-year-old fish sampled in 1957 and 1959. This allowed comparison of the fast-growth period 1953-1955 against slower-growth periods in 1950-1952 and 1956 to 1958. The summary of data used is shown in Tables III and IV.

The average increments for the two sampling years were plotted in Figure 10. The first point to be dealt with in this Figure was the rise in increment in the second year. This was the result of a small increment in the first year, caused by late spawning of these fish and resultant lack of opaque growth included in the measurement. Thus, this first increment measured represents only about five to seven months of growth as compared to full year growth measured in the following cases. It will be noted that the trend toward smaller increments, the older the fish becomes, is apparent in samples for both years.

Differences in otolith growth were reflected in the 1957 and 1959 samples. For the 1957 sample the Figure shows a bump in the curve for otolith growth in 1953 and 1954. The increments for 1954 and 1955 averaged considerably higher than for the slower growth years 1956 and 1957 as indicated in the age-length data in Figure 5. In the same

Table III. Measurements of yearly increments on 10-year-old Subdivision 4T cod otolith cross-sections, sampled in 3rd quarter, 1957; measurements in e.p.u.'s.

Code No.	Centre to ring 1	R1-R2	R2-R3	R3-R4	R4-R5	R5-R6	R6-R7	R7-R8	R8-R9	R9-R10
X4186	39	68	96	55	45	36	38	29	26	18
X4188	44	78	64	47	39	27	26	25	32	22
X4194	76	70	60	41	41	33	21	23	19	14
X4288	63	106	57	51	34	25	22	28	19	23
X4324	24	65	46	46	39	34	32	45	40	33
X4316	54	66	51	58	52	33	33	38	34	33
X4315	46	53	96	42	42	39	48	41	26	30
X4313	62	67	78	58	45	35	34	36	33	23
X4311	23	68	55	51	47	44	35	48	49	37
X4864	67	42	86	36	41	30	41	27	28	26
X4853	81	68	33	35	39	48	43	45	37	28
Mean ($\bar{x}$)	52.6	68.3	65.6	47.3	42.2	34.9	33.9	35.0	31.2	26.1
S $\bar{x}$	5.8	4.7	6.2	2.5	1.5	2.0	2.6	2.7	2.7	2.1

Table IV. Measurements of yearly increments on 10-year-old Subdivision 4T cod otolith cross-sections, sampled in 3rd quarter, 1959; measurements in e.p.u.'s.

Code No.	Centre to ring 1	R1-R2	R2-R3	R3-R4	R4-R5	R5-R6	R6-R7	R7-R8	R8-R9	R9-R10
T2462	42	55	44	62	39	41	33	35	23	21
T2453	43	45	51	74	51	43	38	31	22	17
T2926	70	66	48	58	50	35	24	20	20	21
T2752	37	38	60	49	50	50	35	31	28	24
T2930	41	65	45	51	42	49	48	39	44	34
T2732	34	50	64	43	61	50	37	22	23	21
T2654	45	50	43	51	48	34	30	25	21	21
T2473	51	65	77	42	42	27	28	19	17	17
T2206	76	51	45	28	31	34	28	26	20	21
T2344	43	80	92	67	44	43	41	34	31	20
T2555	26	78	52	30	40	25	23	25	19	19
T2553	43	57	37	52	46	47	44	30	15	26
T2566	38	56	61	32	38	33	31	26	23	23
T2576	41	54	48	41	50	41	28	29	23	23
T2582	61	76	62	50	69	65	56	45	33	30
Mean ($\bar{x}$)	46.1	59.7	55.3	48.7	46.7	41.1	34.9	29.1	24.1	22.5
S $\bar{x}$	3.5	3.2	3.8	3.4	2.4	2.7	2.5	1.8	1.9	1.2

Figure 10. Yearly increment on the periphery of otolith cross-sections from 10-year-old cod sampled from ICNAF Division 4T.

way the 1959 sample gave higher increments for 1953 and 1954 growth than that for corresponding ages in years 1951 and 1952 which also were slow growth years. Thus, the trends in these measurements of otoliths indicate verification of the theory of changing growth in the fish if the premise is accepted that growth of this structure is relative to growth of the fish. This sort of relationship has been indicated by Trout (1953) but must be used with care (see Saetarsdal, 1953, p. 38). To have an absolutely sound basis for following growth changes in this way a great many measurements should be available in order that the data can be subjected to rigorous statistical analysis.

Because of lack of shore sampling in Division 4T in 1954, it has been difficult to pin down the exact years when growth rate increased. Assuming that the otolith growth reflects the growth of the fish in any one year, some use can be made of these measurements to show more specifically which years were the more important in changing the size-at-age of Gulf cod. To carry this out a method for showing "goodness of growth" in various years by comparing growth rings on scallops (Pecten grandis Solander) given by Dickie (1951, pp. 11-13) was followed.

An upper asymptote for average data on measurements (Table V) was found by plotting W_r , W_{r+1} points for otolith rings 3 to 10 as shown in Figure 11. Following the method of Walford (1946) the asymptote is read off the graph where the straight line fitted to the data passes through the

Figure 11. Graph used to estimate asymptote (K) of accumulated average annual increments on 10-year-old Division 4T cod otoliths.

Figure 12. The relation between measurements on otoliths and age at that otolith size. K is the estimated maximum average measurement of the otolith and Y is the average size of the otolith attained at each age. K-Y is the size still to be attained at any given age.

point where W_r equals W_{r+1} . In this case the value so found is 648 e.p.u.'s (K).

Average data on increments to successive rings (Y) were then calculated as $K-Y$ (Table V) and $\log (K-Y)$. Values of $\log (K-Y)$ were plotted against age and an excellent straight-line fit to these points could be made by eye (Fig. 12). The data on increments for successive years given in Table V were then recalculated as $K-Y$ and $\log (K-Y)$ (Table VI) so that a comparison could be made between them and the average growth data shown in Figure 12.

An example of the way this was done is to take data for the increment on a 2+ year otolith in 1949 ($\log (K-Y) = 2.664$) and plot this on the average line in Figure 12. Then take the $\log (K-Y)$ value for the same (average) otolith at 3+. The value from Table VI is 2.617. When this is plotted, growth taking place mostly in 1950 is represented between the two points. The percentage of an average full year's growth achieved for this particular measurement is indicated (by reading off the abscissa). This has been done for averages for sampling years 1957 and 1959 in the bottom of Table VI. The values are arranged so that a grand average for growth deviations in years 1949 to 1958 can be calculated and this is included and plotted in Figure 13.

The indication from Figure 13 is that the 1954 sampling year, which is missing from the age-length sampling (Fig. 5), showed a positive deviation from average growth. The Figure also shows that of the three good years 1953,

Figure 13. Percentage deviation from average annual increment on Division 4T cod otoliths.

Table V. Increment (in e.p.u.'s) on 10-year-old 4T cod otoliths and their relation to asymptotic length.

Sampling year	Centre to R1	R2	R3	R4	R5	R6	R7	R8	R9	R10
1959	46.1	105.2	160.5	209.2	255.9	297.0	331.9	361.0	385.1	407.6
1957	52.6	120.9	186.5	233.8	276.0	310.9	344.8	379.8	411.0	437.1
Av. (Y)	49.4	113.1	173.5	221.5	266.0	304.0	338.3	370.4	398.1	422.3
Av. K-Y			474.5	426.5	382.0	344.0	309.7	277.6	249.9	225.7
log (K-Y)			2.676236	2.629919	2.582063	2.536558	2.490941	2.443419	2.397766	2.353532
			Age 2+WO	3+WO	4+WO	5+WO	6+WO	7+WO	8+WO	9+WO

K = asymptote 648.0 e.p.u.'s

Table VI. Average growth to be achieved and its logarithm on measured otoliths from 47 cod; theoretical maximum size of otolith 648 e.p.u.'s (K); actual size is Y.

Measurement	Growth Year															
	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958						
	K-Y	log(K-Y)	K-Y	log(K-Y)	K-Y	log(K-Y)	K-Y	log(K-Y)	K-Y	log(K-Y)	K-Y	log(K-Y)	K-Y	log(K-Y)	K-Y	log(K-Y)
Centre 9+ to R10													210.9	2.324		240.4 2.381
8+ R 9													237.0	2.375		262.9 2.420
7+ R 8											268.2	2.428			287.0	2.458
6+ R 7									303.2	2.482			316.1	2.500		
5+ P 6						337.1	2.528				351.0	2.545				
4+ P 5					372.0	2.570			392.1	2.593						
3+ R 4			414.2	2.617			438.8	2.642								
2+ R 3	461.5	2.664			487.5	2.688										

Per cent of average annual growth achieved by year-classes and age-groups measured.

	<u>1949</u>	<u>1950</u>	<u>1951</u>	<u>1952</u>	<u>1953</u>	<u>1954</u>	<u>1955</u>	<u>1956</u>	<u>1957</u>	<u>1958</u>
9+								110		85
8+							105		80	
7+						125		70		
6+					99		120			
5+				100		102				
4+			100		105					
3+		102		100						
2+										
Average		102	100	100	102	113	113	90	80	85

1
7
1

1954 and 1955, the latter two were the best, and that there seems to have been a recession in growth in 1956, 1957 and 1958. Thus, the analysis of otolith measurements may be used to corroborate the cod growth changes that occurred in Division 4T and, more important, to fill in data for years that have not been covered by age-length sampling. This step will also be of use in a later section dealing with factors responsible for the change. The next step was to review what these factors might be.

RECENT LITERATURE ON FACTORS AFFECTING FISH GROWTH

The majority of investigations on growth of fish populations in specific areas have brought to light changes in the growth pattern of one type or another. Almost always the papers on the subject contain speculations supported by varying amounts of evidence on factors responsible for the change. A review of some of the most recent works along these lines shows that factors of the type shown diagrammatically in Figure 14 are at present thought to be of more or less importance in limiting the rate at which the individual can grow. Thus, in the primary analysis it was found that the majority of effort has been concentrated on investigating environmental rather than genetic influences. A review of the problem by Brown (1957) indicates that the genetic factors influencing the growth of fish have not yet been clearly demonstrated. She concluded that they were "difficult to assess, but since they may control the age at which fish mature, they may affect

Figure 14. Schematic representation of some factors affecting fish growth.

considerably the maximum size likely to be attained by different races as well as affecting the growth patterns of immature fishes to some extent".

Environmental influences on growth have, of course, been widely discussed in the literature and these effects may be roughly broken down into physical factors presumably having some effect on the metabolism of the individual, and factors related to the density of the particular population of fish in an area and its influence on growth. Of the physical factors in the environment, the one most popular in correlations is water temperature, probably because of its recognized influence on metabolism, the ease with which it can be measured, and the vast amounts of temperature data that have been accumulated in most aquatic biological investigations. The influence of water temperature on growth of fresh and salt water forms is greatly varied both among species and among the areas in which they are found. For instance, LeCren (1958) found that year-to-year variations in growth of perch in Windermere Lake were correlated with the number of days that the temperature was over 14°C. Hempel (1958), investigating growth of plaice in the German Bight, indicated that increased growth was coincident with higher water temperatures in the feeding season. Molander and Molander-Swedmark (1957), keeping populations of the same species under controlled conditions in the aquarium, also found that growth was more rapid in high and slower in low temperatures. Brown's (1946a) tank

experiments on trout showed a more complicated temperature relationship with growth maxima in two separated temperature ranges, 7 to 9° C. and 16 to 19° C. This she found was caused by the varying values for appetite, maintenance and growth at different temperatures.

On the other hand, examples can be found of growth changes in aquatic species where no temperature correlations were found. To note a few recent references one might refer to el-Zarka's (1959) study of growth changes in yellow perch in Saginaw Bay where no temperature correlation was evident. In shellfish species Barnes (1959) found that temperature was not a controlling factor in the growth of Balanus balanoides. Here the best correlation seemed to be between food abundance (e.g., diatoms) and growth. Dehnelt (1956) found no difference in intrinsic growth rate of mussels from Alaska and California despite the temperature difference. He states (p. 52) "...even though relative rates in a population of Mytilus californianus from southern California are greater, mussels from Alaska, if chosen from a level with the same periods of submergence, would grow at approximately the same rate in spite of the lower temperature". In the same area, however, Taylor (1959) has shown what appears to be a good correlation between an index of environmental temperature, namely mean annual air temperature and growth of the Pacific razor clam. This author (1958) has also indicated that a similar generality exists for cod from widely separated areas in

the North Atlantic. Holt (1959, 1960) agrees with the general thesis of growth-temperature relations although at odds with Taylor on certain other mathematical relationships involving natural mortality.

The other factor affecting growth of fish that has been discussed most widely in the literature is the density of the population in the area of investigation. This factor has been shown to affect growth in two ways, namely, in terms of relative availability of food for individuals, and the more difficult to analyse, space or crowding factor. Recent reviews of the literature by Watt (1956) and Beverton and Holt (1957) indicate that it is the rule for fish to respond to changing density by altering their growth and that the former of the two types of density effects just mentioned is the one usually operative. In fact, LeCren's (1949) perch data are quoted as a notable exception to this rule. The space or crowding factor has been speculated upon in many works but the actual evidence for it has come only from a few isolated experiments on fish in captivity. Willer (1929) is quoted as having noted a crowding factor in tank experiments which reduced the growth of fish even though a good food supply was available. More recently, Yoshihara (1952) has written of the space factor involved in the growth of carp in ponds. Brown (1946b) is more specific in her observations on the effects of crowding on trout in tanks. She found that very crowded and very uncrowded trout in tanks grew less well than those

in densities of an intermediate range. Regarding the uncrowded individuals, she wrote that a certain amount of "social stimulation" seemed to be conducive to rapid growth. Thus, density effects on growth of fish seem to be well established, although as with temperature, the effect seems to vary with the species and the environment.

In order to provide information on the way in which some of these factors affect the growth of cod, a controlled growth experiment was carried on for a year at St. Andrews.

GROWTH EXPERIMENTS

Collection and Transportation of Cod

For experimental work the fish used had to be in good physical condition. In order to get cod that had no injuries due to capture, it was decided to obtain them from the commercial shore traps near Lockeport, N. S. Figure 15 is a picture of the particular seining of the trap from which the experimental fish were obtained on July 8, 1957. The cod were mixed with many pollock which were taken in the same haul. The cod were dipped out with scoop nets and handed aboard the Biological Station's M. B. "Mallotus" where they were placed in the enclosed tank shown in Figure 16. A pump shown in the upper left corner of the photo circulated fresh sea water through the tank during the trip back to St. Andrews.

Figure 15. Live cod along with many pollock were taken from this trap operated by John Swim, Jr. at West Head near Lockeport, N. S.

Figure 16. The cod were transported to St. Andrews, N. B., in this special tank aboard M.B. Mallotus.

Physical Set-up for Experiment

On arrival the fish were placed in the puncheon-type tanks shown in Figure 17. These tanks were each supplied with running sea water, pumped in from Passamaquoddy Bay and aerated through air-stones attached by rubber hose to a large compressor. The screens seen in the picture were placed on top of the tanks to foil attempts by the fish to jump out.

Six of these tanks were used for the experiment. As a preliminary step the captured cod were divided into two size-groups, one of 33-40 cm. and the other 40-46 cm. Then each of these two groups was divided into three equal parts and the resulting six groups were placed in separate tanks. Numbers of fish in each of the tanks at the beginning and end of the experiment are shown in Table VII. The reduction in numbers in each tank as the experiment progressed is due in part to mortalities and in part to removals of fish in poor shape. Any cod that was observed to be behaving abnormally or whose physical condition deteriorated badly in a three-week period was removed from the tank at the end of that period.

From July 10 until August 22, trial and error experiments were carried out to discover the best methods of feeding in order to achieve a maximum, intermediate and maintenance feeding rate in one of each of the tanks containing large and small cod. The maximum rate of feeding for large and small fish was that rate at which the fish would consume

Figure 17. The cod were held for a year in puncheon-type tanks in an experimental room at the Biological Station, St. Andrews.

Table VII. Numbers of cod in tanks at beginning and end of the experimental period.

Tank no.	Initial size fish	Rate of Feeding	Number of Cod	
			Beginning	End
5	large	maximum	7	2
6	small	maximum	17	8
7	large	intermediate	8	3
4	small	intermediate	17	4
9	large	maintenance	6	3
8	small	maintenance	17	7

the most food over a period of a year. The maintenance rate of feeding for both sizes was that rate at which the average weight of fish in the tank could be kept constant over the experimental period. The intermediate rate was between these two for both large and small fish. For large fish it was 82% and for small fish 72% of the maximum rate (see Table IX). Herring was selected as a natural food which was easily available, kept well frozen, and most important of all, seemed to be the food involved in the previously mentioned growth change in Division 4T. The trials showed that if the cod were fed a limited amount of food each day, the amount dictated by the feeding rate desired, the more aggressive fish in the tank got most of the food while some got virtually none at all. It was found that to

Figure 18. Measurement of live cod from the growth experiment.

Figure 19. Weighing of live cod from the growth experiment.

establish the three rates, the six tanks of fish had to be given all they would take at one feeding, the differences in rates being established by the number of times they were fed in any one three-week period. Thus the best schedule was found. Cod on maximum rations were usually fed five times in a three-week period; those on intermediate rations three times; those on maintenance rations twice, after the trial period was concluded. The excess herring were removed 24 hours after the feedings and their weight, corrected by a factor for water absorption, was subtracted from weight of herring introduced the previous day.

The experiment proper was started on August 22, 1957, and lasted until September 4, 1958, giving 54 weeks of continuous records. Just prior to the start some fish in each tank were tagged in order that we might have records of growth of individuals as well as averages for the six groups. Measurements of growth in length and weight were taken for each individual every three weeks. Figures 18 and 19 demonstrate the techniques used. Length was measured to the nearest millimetre on a standard fish-measuring board with headpiece. Weights were recorded to the nearest half ounce using the Toledo scale shown in Figure 19, placing the fish in a butter tub full of water during the operation. At this time notations as to the condition of the fish were made, including spawning state, wounds, infections, condition of tag scar and so on.

Temperature of the water in the tanks was recorded each day. Since the water was pumped direct from Passamaquoddy Bay to a small reservoir and thence to the tanks, the water temperature fluctuated in the same fashion as the Bay water, with a summer high and a winter low.

In order to ensure that the fish were in approximately the same condition, not varying greatly in relative plumpness, their initial lengths and weights were plotted in Figure 20. The double log plot of data for initially small fish indicates a straight-line relationship with no bias in any one tank toward a majority of thin or fat fish. In the tanks containing initially large fish there is no bias for those on maintenance and intermediate rations. For those on maximum rations, the inclusion of one individual of 43 cm. length and 1.1 lb. weight reduces the average weight for the tank by one ounce. This may have made the average growth for large fish on maximum rations abnormal for the early periods because such individuals are often unusually hungry with resultant greater than normal feeding and growth.

Feeding and Growth

Maintenance-Fed Fish. In order to separate amounts of food required to maintain the fish at a constant weight from that used for growth, one tank of the large and one tank of the smaller fish were kept on maintenance rations. The amount fed to these fish to keep them at a constant size

Figure 20. Length-weight relationship for cod at the beginning of the growth experiment.

had to be established on a trial and error basis, weighing them every three weeks to see whether a gain or loss had been registered. Over the year the approximate feeding schedule was defined and at the end a 45-week period was selected, at the beginning and end of which the average weight of cod in the tank was the same. For use in calculations with other growth data which have been summarized on a yearly basis, the maintenance requirements were extrapolated to cover a 52-week period. The data showed that for the initially large cod 48.5 oz. of frozen herring per cod were required to maintain constant average weight for a year. The tank of initially smaller cod required 41.5 oz. per fish per year for maintenance.

Fish fed at Intermediate and Maximum Rates. One tank of large cod and one of small cod were each fed at the previously defined intermediate rate. The two remaining tanks, one of large and one of small fish were kept on maximum rations. Average food consumption per fish in grams and growth in ounces are shown for each of these four tanks in Figure 21. Growth data for males and females are not separated because information from cod surveys (Jean, 1960) in ICNAF Area 4 has shown no difference in average rates between sexes. Differences in weight units used came about because of limited capacities of weighing devices used. Amounts of food were small enough to be weighed on a balance to a decigram accuracy. However the weight of the cod plus

Figure 21. Growth of cod in four separate tanks from August 22, 1957 to September 4, 1958. Growth (●—●) and food consumption (○- - -○) were summarized for three-week intervals (two exceptions). The curves are from the data smoothed by three's.

the water in which they were held (Fig. 19) forced the use of an instrument of greater capacity. The only such instrument available was a Toledo scale which could be read to an accuracy of one-half ounce.

The data in Figure 21 are given by three-week periods for a total of 54 weeks, the duration of the experiment. Since the basic data on food consumption and growth of individuals are so voluminous they are not included in tabular form here, but are available on file at the Biological Station, St. Andrews.

The simple plot of food consumption and growth in Figure 21 shows some trends which are worthy of mention. Food consumption for both large and small cod on maximum rations shows a summer high and winter low, reaching the low point in the January-February period. This is coincident with the rise and fall of water temperature in the tanks (Fig. 22), and will be further dealt with in a later section. Food consumption of fish on intermediate rations shows an initial high followed by a levelling off at a lower rate due to limitation of the amount of herring made available in any three-week period.

Growth of cod on maximum rations generally reached a low coincident with the low in winter feeding but some positive growth was registered at all times of the year. Fish on intermediate rations grew more irregularly from period to period and the trend throughout the year is not

Figure 22. Average water temperatures in the experimental tanks for each three-week period.

well defined. The initially large ones exhibited an irregular decline in increment. The smaller cod indicated a tendency to follow the pattern of those on maximum rations with faster growth in the summer and variable fluctuations in the winter.

Length and Weight Increment for Year

Totals of growth in length and weight for the three-week periods indicated in Figure 21 gave average growth of fish of different initial sizes and on different feeding rates for $\frac{52}{54}$ weeks. These totals were reduced by $\frac{52}{54}$ to give averages for one year. Table VIII gives the results.

Table VIII. Average growth in length and weight of cod during 52 weeks in captivity.

Rate of feeding	Initial Size	Initial		Growth in		Increase in weight
		Length	Weight	Length	Weight	
		cm.	oz.	cm.	oz.	%
Maximum	Large	42.5	26.7	10.9	26.2	98
Maximum	Small	34.4	15.7	14.9	24.6	157
Intermediate	Large	41.2	26.4	10.2	16.0	61
Intermediate	Small	35.6	15.8	8.9	13.3	84

First of all, the Table shows that both large and small fish on maximum rations grew more in length and weight than their counterparts on intermediate rations. The differences

in length increment for the two rates of feeding were much more noticeable for initially small cod than for the larger ones. Differences in weight increments are not quite so obvious until expressed on a percentage increase basis. Here the Table shows that initially large fish almost doubled their weight on maximum rations while increasing by little more than half on intermediate rations. Initially smaller fish increased more than one and one-half times in weight on maximum rations while those on intermediate rations gained close to seven eighths of their initial weight.

Relative Merits of Length and Weight Measurements as Growth Indicators

When average amounts of food ingested were compared to growth in length and weight of the cod, certain anomalies indicated that weight of the fish was a more sensitive indicator of growth than fork length. Figure 21 shows that average weight increments varied quite markedly by three-week periods while length increments, although not plotted, showed much less variation. Figure 23 is a simple plot of yearly increments in length and weight for fish on maximum and intermediate rations. The left-hand side of the Figure shows average increment in weight over the year, with fish of two initial sizes on maximum rations showing relatively greater growth than those on intermediate rations. This is the sort of relationship that would be expected after noting food consumption figures shown in Table IX (next sub-section).

Figure 23. Average lengths and weights of cod on maximum rations and on intermediate rations at the beginning and end of the experimental period. Solid lines indicate cod on maximum rations. Dashed lines indicate those on intermediate rations.

However, moving to the right-hand side of Figure 23 where length increment is plotted, it is obvious that the initially smaller fish showed the expected difference in growth in length while those initially larger gained almost the same amount in length while on different rations. Further data of this type were found on examination of length changes in the cod kept on maintenance rations for 45 weeks. Here, although weight was the same at the beginning and the end of the period, there was an average increase in length of 6.5 cm. for initially small cod and 6.0 cm. for initially larger ones. Obviously, fork length is only a reflection of growth of the skeletal structure, and in experiments of this type is not the best indicator of total growth of the fish.

In connection with variations in weight as indicators of growth, the question arose as to whether there are differences in the composition of the flesh, particularly the water content, in cod fed at such varying rates. Considerable work has been done along these lines by Love (1960). He has found that the greatest variation in water content of flesh throughout a year in freshly-caught cod is from about 83.5% in March to 79.5% in October, a difference of 4%. In cod artificially starved to the point of death water content can increase to as much as 88% as compared to 80.5% in normal fish. These are extremes however, and the average change is not nearly so great. Thus any change in water content of flesh would not be great enough to affect seriously

calculations on conversion of food to cod weight at the feeding rates used in this experiment.

The next point of interest to be investigated was the variation in relative amounts of food required to produce these differences in growth.

Food Consumption and Conversion to Cod Weight

Figures on food consumption for 52 weeks were interpolated in the same way as for growth in order to examine consumption and conversion of frozen herring to weight of live cod. The data used are given in Table IX for the same four tanks as shown in Table VIII. Because averages of measurements of fish growth in weight were accurate only to a tenth of an ounce, amounts of food consumed, measured in decigrams, were converted to the units used for the cod. The Table shows that average yearly food consumption per fish in the tanks was greater at the maximum rate of feeding for both large and small fish than it was at the intermediate rate. In order to calculate amounts of food used for growth by the cod in each tank the amount of food used for maintenance, found as described above, was subtracted from the total food consumption for one year. Then, in order to find the efficiency of conversion of herring to cod weight, the total average growth for the year was divided into the amounts of food used for growth to get the conversion factor.

The final figures for these conversion rates for a year of feeding were quite similar. Maximum-fed fish of

either initial size converted at an average rate of 2.2 ounces of herring for growth producing one ounce of cod weight. Those on intermediate rations showed slight variations, the initially large ones converting at a rate of 2.4 and the smaller ones at 2.1. Comparisons of this rate of conversion with those published for other fish are complicated by the fact that the majority of publications do not have data on maintenance requirements separated from food used for growth (see Brown, 1957, p. 386). However, some examples for marine fish are available. Dawes (1930, 1931) shows that in his experiments in controlled feeding of Mytilus to plaice, fish on maximum rations converted at a rate of 4-5 grams of food for growth to one gram in increase in weight of fish. The efficiency of conversion here is not as great as our cod showed. Buckmann's (1952) experiments on the plaice gave what seem to be better conversions although only overall figures including maintenance rations are mentioned. He indicated that his "food quotient" of 5.8 g. food to 1 g. herring showed considerably greater efficiency than data he refers to from Dawes (1930, 1931), giving a 10.8/1 ratio.

There has been a much greater amount of work done on freshwater than on marine fish in regard to efficiency of conversion of food, particularly for those species which have been hatchery reared on a large scale. Variation is considerable between various foods fed to a single species.

Table IX. Average yearly food consumption of cod, and conversion of food (frozen whole herring) to cod weight.

Rate of feeding	Initial size	Food consumed	Food for maintenance	Food for growth	Average growth	Conversion factor	
	oz.	oz.	oz.	oz.	oz.		
Maximum	Large	26.7	106.7	48.5	58.2	26.2	2.2
Maximum	Small	15.7	96.5	41.5	55.0	24.6	2.2
Intermediate	Large	26.4	87.3	48.5	38.8	16.0	2.4
Intermediate	Small	15.8	69.0	41.5	27.5	13.3	2.1

Brown (1957) shows that on live food alone conversion factors from 2.3/1 to 7.1/1 have been found for brown trout, (as just mentioned, these factors do not take into account maintenance requirements), quoting such sources as Annual Reports of the Cortland Hatchery, New York State, and authors Shaeperclaus (1933), Surber (1935) and Pentelow (1939). Indications here are that some of the factors responsible for variation aside from intrinsic calorie value of the food itself are size of the fish, appetite, water temperature, spawning and cycles in growth related to yearly seasons. Some of these factors were investigated in our cod experiment.

Spawning Activity in the Tanks

When measuring and weighing the experimental fish on March 20, 1958, it was first noticed that some of them were in a ripe state of maturity. Eggs or milt from certain individuals were expelled when they were being handled. Records of numbers of fish in the tanks in this condition were kept from this time until the end of the experiment. The ratio of fish in spawning condition during each measuring period is shown in Table X.

The expulsion of spawning products in the tanks undoubtedly affected the average weight of cod from period to period but there was no way of correcting for this. Since not all individuals spawned and not all spawners reached the running stage at the same time, the changes due to this phenomenon were not evident at the periodic measuring times.

Table X. Ratio of fish recorded in a ripe state of maturity in tanks during growth experiments, 1958.

Tank No.	March 20	April 10	May 1	May 22	June 12	July 3	July 24	Aug. 14	Sept. 4
4	$\frac{3}{10}$	$\frac{2}{8}$	$\frac{1}{7}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{7}$	$\frac{2}{4}$	$\frac{2}{4}$	$\frac{1}{4}$
5	$\frac{0}{3}$	$\frac{0}{3}$	$\frac{0}{3}$	$\frac{0}{3}$	$\frac{0}{3}$	$\frac{0}{3}$	$\frac{0}{3}$	$\frac{0}{2}$	$\frac{0}{2}$
6	$\frac{2}{9}$	$\frac{3}{9}$	$\frac{2}{9}$	$\frac{2}{8}$	$\frac{2}{8}$	$\frac{2}{8}$	$\frac{2}{8}$	$\frac{0}{8}$	$\frac{0}{8}$
7	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{0}{3}$	$\frac{0}{3}$	$\frac{1}{3}$	$\frac{0}{3}$	$\frac{0}{3}$	$\frac{0}{3}$
8	$\frac{0}{9}$	$\frac{1}{9}$	$\frac{0}{9}$	$\frac{0}{9}$	$\frac{1}{9}$	$\frac{0}{9}$	$\frac{0}{9}$	$\frac{0}{8}$	$\frac{0}{7}$
9	$\frac{0}{3}$	$\frac{0}{3}$	$\frac{0}{3}$	$\frac{1}{3}$	$\frac{0}{3}$	$\frac{0}{3}$	$\frac{0}{3}$	$\frac{0}{3}$	$\frac{0}{3}$

In tanks # 8 and 9 where the cod were on maintenance rations, very little spawning activity took place, there being only two observations of one spawner each on April 10 and June 12, 1958. This may be an indication that when food supplies are low cod may fail to complete the maturing process, especially at sizes where they may be maturing for the first time. The probability that most of these fish were going through this stage for the first time is indicated by comparing average initial lengths (TableVIII) with length at first maturity of cod in Figure 2 of Powles (1958). Tank # 5 where three fish were on maximum rations produced no spawners. Subsequently, although sex and maturity data are missing for one individual,

the others were found to be immature females. Powles (1958) has shown that females reach first maturity at a greater length than males, and this may have been the reason for the lack of spawners in this tank.

It will also be noted that in tanks # 4 and 6 where most of the ripe fish were found, the condition persisted over most of the summer. This was during a water temperature rise of from about 4° to 13°C. (Fig. 22) which indicates that a change in temperature of this magnitude did not produce any critical point at which there was a marked change in gonad condition. The other point to be noticed was that while there were changes in appetite during this period, as will be seen in a later section on water temperature - food consumption relations, the rather irregular changes in stage of maturity did not seem to bear any constant relationship to appetite.

Thus, while it was realized that there were some small variations in weight due to spawning, the indication was that spawning activity did not seriously interfere with data on other relationships that came out of these experiments. With regard to its effect on conversion factors for food to fish flesh, it was recognized that the same sort of loss of weight occurs in nature, so that the use of these figures in population dynamics models should not be any the less valid because of the inclusion of data on fish that spawned.

Temperature, Feeding, and Growth Relations

Fluctuations in food consumption and growth over the year are shown in Figure 21. There was some indication of a

downward trend in both factors as the winter season approached with an upswing in the spring. The only obvious environmental factor that changed in a like manner in the tanks was temperature (Fig. 22). The amount of food that was offered to fish on maximum rations remained at a level higher than they would consume, so the variation in food consumption was due to changes in appetite rather than lack of food to eat.

In order to examine the relationships involved between temperature and food consumption, and food consumption and growth, correlation coefficients were calculated using the data shown in Figures 21 and 22 for 3-week periods. The groups of data for which positive correlations were found are plotted in Figure 24 together with the correlation coefficients and the probability of the correlation occurring by chance. The method of calculation followed was that given by Snedocor (1946, pp. 138-141).

Examination of the three graphs showing the relationship between food consumption of the cod and water temperature in the tanks (Fig. 24) indicated a good positive correlation for initially small cod on both maximum and intermediate rations, a rise in food consumption being associated with a rise in temperature. Data for initially large fish on maximum rations did not give such a high value for "r", probably because of a drop in food consumption during high temperature periods at the beginning and end of the experiment. R. A. McKenzie (1935) has noted that small cod will continue to feed in higher water temperatures than large ones will. It is likely that

Figure 24. The relationship of food consumption to water temperature and cod growth during the 54-week experimental period. Data points are averages for three-week periods. Open circles indicate data for summer of 1957 to winter of 1958. Solid circles indicate data for winter of 1958 to summer of 1958.

the temperature in the tanks (13°-14°C.) was reaching the upper critical limit for feeding for the large fish. Since the fish were always offered more than they would take at any one feeding, it should be noted that variations in the intermediate ranges of temperature, at least, can be considered to be direct reflections of appetite. Brown (1957) has reviewed the problem of varying appetite and points out that studies of this phenomenon seem to be correlated with environment, temperature and crowding being two of the most pertinent factors. The crowding factor did not vary greatly within either size-group of fish held in any one 3-week period as the experiment progressed.

A trial plot of data on the temperature-food consumption relation for large cod on intermediate rations indicated poor correlation ($r = .331$, $P > 5\%$). This effect was the result of experimentally limiting one variable, food consumption, to the extent that it was not allowed to fluctuate normally with changing temperatures as in the other tanks.

The other three graphs in Figure 24 show the relationship between growth and food consumption for the same tanks of cod. The "r" and "P" values for these data indicate a highly significant positive correlation in each tank. It would have been better to have been able to relate food used for growth to growth of the cod, eliminating food used for maintenance. However, figures indicating how maintenance requirements might vary with the different water temperatures in each 3-week period were not available from this experimental work. Only averages for the year were obtained. This point will be one of the objects of future study.

The relationship between changing water temperature and growth was examined for the two tanks which showed best "r" values in Figure 24, namely those containing small cod on maximum and intermediate rations. Calculations showed relatively poor correlation. Small cod fed at a maximum rate gave values of $r = .357$ and $P > 5\%$ while those on intermediate rations had values $r = .598$ and $5\% > P > 1\%$. The experimental work indicated that any correlation found between temperature and growth would likely be an indirect one working through food consumption and its resultant effect on growth. Thus the variation in food consumption at any given temperature plus the variation in growth at a given rate of food consumption could combine to produce even greater variation in growth at any particular temperature. This effect would result in relatively poor correlation coefficients such as those just mentioned.

EFFECTS OF WATER TEMPERATURE, POPULATION DENSITY AND FOOD AVAILABILITY ON GROWTH OF GULF OF ST. LAWRENCE COD

Water Temperature

Water temperatures in the Gulf of St. Lawrence have been discussed by Lauzier (1957a, 1957b). The variations do not follow any regular pattern and in his words (1957a, p. 267) "Below the surface erratic variations seem to mask year-to-year variations". In his 1957b (p. 285) publication, he notes that "The smallest seasonal variations are found over bottom exposed only to the cold layer and the largest seasonal variations are found over bottom exposed to the surface-layer

waters in the summer time". Lauzier (1960) has shown that fluctuations in water deeper than 30 fathoms are of the order of 3°C. from about -1°C. to 2°C., while in shallower waters fluctuations are greater. Charts of these variations in the Gulf of St. Lawrence (Lauzier, 1957a, 1957b) indicate that very precise information on cod distribution by depth and area would be necessary in order to correlate the 1949-1959 growth changes (Fig. 5 and 6) with water temperature fluctuations. This type of information is not available. In any event the experimental work dealt with in an earlier section indicated that good correlations between growth of cod and water temperature are not evident. Water temperature apparently has some control over amount of food consumed and this in turn limits growth. The data on the food consumption-water temperature relation show that a low of about 2°C. does not prevent cod from feeding, and feeding increases with temperature until there is some fall off in food consumption at 13°-14°C. for the larger specimens.

Year-to-year trends in surface temperature in the region were investigated for the possibility that their fluctuations over a long series of years might account for changes in food consumption, and ultimately, growth. Figure 25 shows a series of these temperatures for the months of May to August in the years 1937 to 1959 (from Lauzier and Marcotte, 1960). Trend lines have been drawn in by these authors for the Grand River and Entry Island data. Here, although there is a tendency toward an upswing in the early

Figure 25. Average surface water temperature in the Gulf of St. Lawrence (May-August). Curved lines show the trend. From Lauzier and Marcotte (1960).

1950's at both places, the magnitude of the change (ca. 1°C.) is not of the order that produced major changes in food consumption and resultant growth in the experimental work. It seems reasonable to assume that much greater fluctuations in water temperature in the area would be required to result in growth variations of the magnitude shown in Figures 5 and 6.

In fact, although a growth and temperature relation for cod has been postulated by Taylor (1958), closer examination of specific data shows that his statement does not always hold. His thesis is based on correlating surface water temperature for several different North Atlantic areas and analysis of some previously published cod growth data. The suggestion from his analysis is that at relatively low water temperatures cod grow more slowly but live to an older age and reach a greater ultimate size (Walford's ℓ_{∞} (1946)) than those living at higher temperatures.

However, if one specific part of the growth data already demonstrated in Figure 4 is taken as an example, it is obvious that Taylor's generalities must be used with care. In this Figure cod growth data for ICNAF Divisions 1F and 4W were plotted. Bailey, Templeman and Hunt (1954) in their Figures 2 and 3 show temperatures at 50 and 100 metres on these two widely separated fishing grounds in August of 1950. Here, the temperatures shown for the 1F area are very similar, or if any different, slightly higher than those in 4W, probably because of the effect of the Irminger current (see Hachey, Herman and Bailey (1954) p. 72). The contrast

between surface temperatures for these two areas given in their Figure 1 would be quite misleading if given as an indicator of environmental temperature for pelagic and bottom-living cod in this season of the year.

Referring back to our Figure 4, data for Division 4W indicate a high growth rate and ultimate size in a relatively low water temperature. The Division 1F data show much slower growth and lower ultimate size in water of the same or higher temperature. Thus, the growth patterns of these two cod populations do not follow the relationship that Taylor suggests for cod growth rates and water temperature.

This example has been included to show that no matter what broad generalities may be apparent from temperature-growth relations taken from greatly separated areas, unless the data are from the specific environment of the cod they can be misleading. Other important environmental factors may enter the picture and the manner in which two of these, population density and availability of food, affected growth of Gulf cod is dealt with in the following sections.

Population Density

Literature on the effects of population density on the growth of individual fish was discussed in an earlier section. The consensus was that it had been shown to be effective, especially in regard to its relation to the availability of food. In general, where density changes were demonstrated, relatively large changes in the abundance of the organism were registered.

Figure 26. Statistics of the fishery on the southern Gulf of St. Lawrence cod population. Relative density data are based on catch per unit effort in numbers by otter trawls and longlines.

An examination of landings and catch per unit effort of cod for the years 1947 to 1959 from the Gulf of St. Lawrence population was carried out since these statistics were relevant to cod population density in the area. In Figure 26 available landings and catch-per-unit-effort data are plotted. These data have been summarized by L. M. Dickie (1960) in connection with an assessment of the effect that various sizes of codend meshes might have on the fishery.

The upper graph in Figure 26 shows landings by various fishing units from the cod population for the years 1947 to 1959. Total yearly landings in round fresh weight have almost tripled during the period, rising from about 39,000 metric tons in 1947 to over 115,000 metric tons in 1959. The breakdown by groups of fishing vessels indicated that much of the increase was due to rapidly mounting landings of the European trawling fleet from Spain, Portugal and France. Their landings have increased from nil in 1951 to 59,000 metric tons in 1959. Landings of the Canadian otter trawlers have also increased greatly during the period from about 1,000 metric tons in 1947 to 24,000 metric tons in 1959. This increase has almost all been due to the great expansion of the small dragger fleets of northern New Brunswick and the Gaspé coast of Quebec. Canadian landings from hook and line and trap fisheries have fluctuated in a different manner, being relatively high in the 1947 to 1950 period, dropping from 1951 to 1955 and increasing again from 1956 to 1959.

Usually, greatly increased landings of this type would be expected to have some effect in markedly reducing the abundance of the population. The large catches of the European trawlers are made while the population is assumed to be concentrated by hydrographic conditions near Cape Breton in the winter. The increased landings of the Canadian otter trawlers reflect the build-up of a fleet which prosecutes a summer fishery when the fish are spread out over the Magdalen Shallows. However, the best estimates do not indicate a dominant trend toward a decrease in density in numbers as yet.

The bottom graph in Figure 26 shows relative density based on statistics of the catch per unit effort of draggers and longliners engaged in the summer fishery on the Magdalen Shallows which takes the bulk of the Canadian landings. For the years 1947 to 1956 the relative density index fluctuates between 4 and 6. For 1957 and 1958 the index rises to about 7 and actually is a continuance of a steady rise from a low in 1954. Although this may reflect increasing skill on the part of the fishermen in using otter trawling gear and electronic aids to fishing with which they were relatively unfamiliar in the late forties and early fifties, there is no doubt that a rise in density and resultant availability of about 75% was realized from 1954 to 1958. Reference to Figures 5, 13 and 26 again shows that in this later period, 1954 and 1955 were low density and good growth years while 1957 and 1958 were relatively

high density and poor growth years. Thus, it seems that a change in density of the cod population great enough to affect the growth of individuals has occurred. However, it must be realized that if a similar change in density and availability of food for cod had occurred the growth of the species would not have been greatly affected. If, on the other hand, the availability of food stayed the same or increased as the density of the cod population dropped an opportunity for increased food intake and resultant growth would have been afforded.

Availability of Food

A study of the feeding of Gulf of St. Lawrence cod has been published by Powles (1958). One paragraph of his abstract sums up the facts pertinent to this study and is therefore quoted here: "Small cod of 11 to 30 cm. in length selected a diet of pelagic crustaceans, namely mysids, euphausiids and amphipods. With increase in size cod adopted a more varied diet, in which fish and benthic invertebrates became increasingly important. At lengths over 70 cm., pelagic and bottom forms were taken in approximately equal volumes. Herring was the most important fish in the diet of large cod over 50 cm. in length." Thus it was evident that one of the chief components of the diet of the cod of sizes shown in our Figure 5 was likely to be herring.

It happened that in the period of growth change described in previous sections, the herring population in

Figure 27. Locations of observed or reported mortalities of sea herring in the Gulf of St. Lawrence. From Sindermann (1958). Localities of observations are shown by dots.

the Gulf of St. Lawrence underwent an epizootic of a systemic fungus disease caused by the organism Ichthyosporidium hoferi. The course of the disease through the population is described by Sindermann (1958). Figure 27 is taken from this paper and shows locations of observed or reported mortalities of herring in the Gulf of St. Lawrence during the years 1954, 1955 and 1956. The effect of the disease on the Gulf herring population is most aptly described by Sindermann....."dead fish (herring) were observed floating in shoals at the surface, were washed up on the shores of the Gulf, and were taken in the nets of otter trawlers"....."abnormal, lethargic, moribund herring could be seen inshore, particularly near the breakwaters, throughout the period. Deaths occurred sporadically in such inshore aggregations, the dying fish sinking to the bottom to become part of an extensive litter of herring carcasses". In his paper Sindermann estimated that at least one quarter of the mature herring in the Gulf were affected in 1955, and that some Gulf areas in 1954 had at least as severe mortalities. Observations for 1953 were not given, but for 1956 and 1957 the incidence was much lower.

With a large part of the herring population in this condition, the predator-prey relationship between cod and herring was altered markedly. Herring became much more easily available as food for cod, both on the bottom as dead fish and pelagically as slow-moving, moribund individuals. Casual observations by two Fisheries Research Board biologists, F. D. McCracken and P. M. Powles, in the summers of 1954 and

Figure 28. Percentage of feeding cod from the southern Gulf of St. Lawrence whose stomachs contained herring. Exact length groupings for 1958 data are 20-29, 30-49, 50-69 and >69 cm. Number of stomachs per sample are shown. Shaded areas indicate stomachs containing herring.

1955, indicated that cod stomachs were unusually full of herring.

By use of data from Corbeil and Brunel (1960) for 1951-54, from Powles (1960) for 1955-56, and Jean (1960) for 1957-58, Figure 28 was constructed to give an estimate of incidence of herring in cod stomachs over the years of growth change. First of all, it will be noticed that percentage incidence of herring in each sampling year increases with the size of the fish as was noted by Powles (1958). Turning to variation in percentage of stomachs containing herring by years, it is evident that the peak year for both the 51-70 cm. fish and the group over 70 cm. was 1954. A general rise to this peak may be seen for years 1951 to 1953 and a more rapid drop in years 1955 to 1958. Referring back again to Figure 5, it will be noted that these were the sizes of fish with which the growth change was associated and the rise in size-at-age certainly occurred during these years when herring were most easily available as food. Figure 13 gives years 1954 and 1955 as those when growth was furthest above average and these years are coincident with those in which Sindermann (1958) observed peaks in herring mortalities.

The rapid drop in cod size-at-age in 1958 and 1959 (Fig. 5) could also be associated with the drop in incidence of herring as cod food (Fig. 28) and the reduction of Gulf herring stocks indicated by Sindermann.

Quantitative data on the varying availability of food for fish stocks is usually very difficult to obtain. Methods of assessing such factors require a great amount of time spent on examination of stomach contents and investigation of the environment for abundance of organisms prevalent in the stomachs. Methods for deriving such abundance data are as yet poorly developed, and our only reasonable estimates come from abundance estimates as catch-per-unit-of-effort indices for species which are fished commercially to a certain extent. It is possible that for this reason few data have been collected on this factor and its relation to growth changes. However, for this particular change in growth of Gulf of St. Lawrence cod we have ample evidence of a change in availability of food both from observations on the effect of widespread disease on the prey species itself and the incidence of the prey in the stomach contents of the predatory organism. The data indicate that food availability was a prime factor contributing to the growth change.

CONCLUSIONS

From an analysis of field collections of cod data it was established that cod growth can vary both between populations and in time in the same population. Laboratory experiments were devised in an attempt to elucidate factors responsible for such changes, particularly changes of the latter type. From an analysis of the controlled experiments

a number of facts were established. Food consumption increased up to a point with increasing availability of food. With an unlimited food supply, maximum food consumption was related to and increased with water temperature over a wide range of water temperatures (at least 2°-12°C.). Growth of cod increased with increasing food consumption. Examination of temperature-growth correlations indicated that growth of cod in tanks was only indirectly related to temperature through food consumption.

Possible reasons for the changes in growth of southwestern Gulf of St. Lawrence cod were investigated. Rises in growth were coincident with increased availability of herring, an important food of cod, high percentages of cod stomachs containing herring and a relatively low density of cod in the area. A subsequent reduction in cod growth was coincident with a subsidence in the herring disease which greatly diminished the availability of moribund individuals, a reduction of herring stocks due to the disease and a rise in density of cod stocks. Available water temperature data did not indicate variations that could be associated with large fluctuations in food consumption and resultant growth. It is concluded that changes in abundance and availability of the herring as a food organism plus changes in availability of food as a result of density changes in the cod population were the prime factors responsible for the growth change.

SUMMARY

1. Methods of estimation of growth of cod resident in the waters over the continental shelf on Canada's east coast were examined. The main method used in this investigation was that of sampling commercial otter-trawl landings for age and length data. In order to investigate the validity of growth data from this source, the otolith method of age determination used was tested. The validity of age determinations was confirmed by establishing that the regular formation of one hyaline and one opaque zone in the cross-section of the otolith is a yearly occurrence, by showing the consistency of relative strength of year-classes in the age data from year to year, and by demonstrating the yearly production of one annulus in the otoliths of fish in definable length groups found by the Petersen method.
2. Changes in growth of cod in the area were demonstrated both for widely-separated populations such as those in ICNAF Divisions 1F and 4W during the same years and in a single population such as that resident in ICNAF Division 4T over a series of years. The latter growth change was selected for detailed study because of a better backlog of data on environmental variations during the growth change. The change itself was indicated by age and length parameters taken from commercial sampling, which showed a rise in mean length of age-groups from a low in 1951 to a high in 1955-57 and a return to lower levels in 1958 and 1959.

3. It was suggested that the change in size-at-age might have been due to varying availability of cod normally caught only by the longline fishery over rough bottom. This fishery had been shown to take fish of larger average size than the otter-trawl fishery and suspicion had been voiced that the longlines might select faster-growing, more voracious fish than the otter trawls. A comparative fishing experiment showed that on the same fishing grounds longlines took longer cod than the otter trawl but age determinations showed them to be older also. There were no consistent differences in average size-at-age of cod between the two catches.
4. Annual increments on otolith cross-sections were measured to see if their relative sizes corresponded with good and poor growth years found by commercial landings sampling. The data from the two methods agreed as to good, poor and average growth years with years 1954 and 1955 showing up as the best years for growth.
5. Recent literature on factors affecting fish growth was reviewed. Pertinent factors could be divided into genetic and environmental groups. Little work has been done on genetic factors affecting growth of wild fish populations. Of the environmental factors, most emphasis to date has been placed on water temperature, density of the population and availability of food.

6. Laboratory experiments were devised in order to assess some of the factors that might have an important influence on cod growth rates. Cod were kept under controlled conditions at the St. Andrews Biological Station for over a year. Groups of small and large fish (initially 33-40 cm. and 40-46 cm.) were fed at maximum, intermediate and maintenance rates, while the water temperature in the tanks was allowed to fluctuate with normal seasonal variations found in the sea water from the area. Results showed that amounts of frozen whole herring needed to maintain cod at a constant weight for a year under these conditions were 48.5 ounces for initially large cod and 41.5 ounces for initially small ones. Conversion factors for food used for growth to cod weight were constant at 2.2/1 for maximum-fed fish and 2.4/1 and 2.1/1 for initially large and small fish, respectively, on intermediate rations.
7. Some of the captive cod were in spawning condition over the latter half of the experimental period. Individuals were in the ripe stage in various months from March to September, and the attainment of this stage did not appear to be correlated with any one environmental factor. Loss of weight due to expulsion of spawning products was not taken into account in calculating food conversion factors, both because the loss was difficult to estimate and because it would be a normal occurrence in the wild population.

8. Calculation of correlation coefficients showed that when the food supply was unlimited, food consumption increased with increasing temperature. Also, growth increased with increasing food consumption. Increasing temperature was not well correlated statistically with increasing growth.
9. Data on water temperature, cod density and availability of food were investigated for the Division 4T cod environment during the years of growth change. It was concluded that changes in abundance and availability of herring as a food organism plus changes in availability of food to individuals as a result of density changes in the cod population were the prime factors responsible for the growth change.

BIBLIOGRAPHY

- Bailey, W. B., W. Templeman, and R. P. Hunt. 1954. The horizontal distribution of temperatures and salinities off the Canadian Atlantic coast. Fish. Res. Bd. Canada, MS Rept. Biol. Sta. No. 584, 39 pp.
- Barnes, H. and M. 1959. A comparison of the annual growth patterns of Balanus balanoides (L.) with particular reference to the effects of food and temperature. Oikos, 10(1): 1-18.
- Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. U. K. Min. Agr., Fish. and Food, Fish. Investig., Ser. 2, 19, 533 pp.
- Brown, M. E. 1946a. The growth of brown trout (Salmo trutta Linn.). III. The effect of temperature on the growth of two-year-old trout. J. Exp. Biol., 22: 145-155.
- 1946b. The growth of brown trout (Salmo trutta Linn.). II. The growth of two-year-old trout at a constant temperature of 11.5°C. Ibid.
1957. Experimental studies on growth. in the Physiology of Fishes, Vol. 1. Metabolism, pp. 361-400. Academic Press Inc., New York.
- Buckmann, A. 1931. Breittenmessungen an den Jahresringen und ihre Anwendbarkeit bei der Untersuchung der Nordseeschulen. VIIe Congr. Internat. d'Aquicult. Pêche, Paris 1931, Sr. I, Sect. 2, Orleans.

Buckmann, A. 1952. Vorläufige Mitteilung über Futterungs- und Wachstumsversuche mit Schollen im Aquarium. Mitteilungen aus der fischereibiologischen Abteilung. Max Planck Inst. Meeresbiol., Wilhelmshaven, Nr. 1, pp. 8-20.

Cohen, Daniel M. 1959. The scientific name of the common cod. J. Cons. Expl. Mer., 25(1): 50-52

Corbeil, H. E. and P. Brunel. 1960. Unpublished data.

Dannevig, A. 1933. On the age and growth of the cod (Gadus callarias L.) from the Norwegian Skagerrak coast. Rept. Norwegian Fish. and Mar. Invest., 4(1): 145 pp.

Dannevig, E. H. 1956. Chemical composition of zones in cod otoliths. J. Cons. Expl. Mer., 21(2): 156-159.

Dawes, Ben. 1930. Growth and maintenance in the plaice (Pleuronectes platessa L.), Part I. J. Mar. Biol. Assoc. U. K., 17(1): 103-174.

1931. Growth and maintenance in the plaice (Pleuronectes platessa L.), Part II. J. Mar. Biol. Assoc. U. K., 17(3): 877-948.

Dehnel, P. A. 1956. Growth rates in latitudinally and vertically separated populations of Mytilus californianus. Biol. Bull., 110(1): 43-53.

Dickie, L. M. 1951. Boughton Island, P.E.I. scallop investigations, 1946. Fish. Res. Bd. Canada, MS Rept. Biol. Sta., No. 415, 33 pp.

1960. Determining cod growth curves. Fish. Res. Bd. Canada, Annual Report and Investigators' Summaries 1959-60, St. Andrews, N. B.

1960. Unpublished data.

Einarsson, H. 1951. Racial analyses of Icelandic herrings by means of the otoliths. Rapp. Cons. Expl. Mer., 128: 55-74.

Graham, M. 1929a. Studies of age determination in fish. Part II. A survey of the literature. U. K. Min. Agr. and Fish., Fish. Investig., Ser. 2, 11(3): 50 pp.

1929b. Studies of age determination in fish. Part I. A study of the growth rate of codling on the inner herring trawling ground. U. K. Min. Agr. and Fish., Fish. Investig., Ser. 2, 11(2): 88 pp.

1956. Sea fisheries, their investigation in the United Kingdom. Edward Arnold Ltd., London.

Hachey, H. B., F. Hermann, and W. B. Bailey. 1954. The waters of the ICNAF Convention Area. Int. Comm. NW Atlantic Fish., Ann. Proc., 4: 67-102.

- Hempel, C. G. 1958. Zur beziehung zwischen bestandichte und wachstum in der schollenbevölkerung der Deutschen bucht. Ber. Dtsch. Wiss. Komm. Meeresforsch., 15(2): 132-144.
- Hickling, C. F. 1933. The natural history of the hake. Part IV. Age determination and the growth rate. U. K. Min. Agr. and Fish., Fish. Investig., Ser. 2, 13(2): 120 pp.
- Hile, Ralph. 1936. Age and growth of the cisco (Leucichthys artedi (LeSueur)) in the lakes of the northeastern highlands, Wisconsin. Bull. U. S. Bur. Fish., 48(19): 211-317.
- Holt, S. J. 1959. Water temperature and cod growth rate. J. Cons. Expl. Mer., 24(2): 374-376.
1960. Water temperature and cod growth rate. J. Cons. Expl. Mer., 30(2): 225-227.
- Jean, Y. M. L. 1960. Unpublished data.
- Jensen, A. J. C. 1938. Factors determining the apparent and the real growth. Rapp. Cons. Expl. Mer., 108: 109-114.
- Kohler, A. C. 1958. The validity of otolith age determinations for haddock (Melanogrammus aeglefinus L.) from the Lockeport, N. S. area. J. Fish. Res. Bd. Canada, 15(6): 1229-1238.
- Lauzier, L. 1957a. Variations of temperature and salinity in shallow waters of the southwestern Gulf of St. Lawrence. Bull. Fish. Res. Bd. Canada, No. 111: 251-268.

- Lauzier, L. 1957b. Bottom temperatures on the Magdalen shallows. Bull. Fish. Res. Bd. Canada, No. 111: 269-285.
- Lauzier, L. 1960. Unpublished data.
- Lauzier, L. M., and A. Marcotte. 1960. Unpublished data.
- LeCren, E. D. 1949. The interrelationships between population, production and growth rate in fresh-water fish. Proc. Limn. Soc. London, 161(2): 131-136.
1958. Observations on the growth of perch (Perca fluviatilis L.) over twenty-two years with special reference to the effect of temperature and changes in population density. J. Animal Ecol., 27(2): 287-333.
- Love, R. M. 1960. Water content of cod (Gadus callarias L.) muscle. Nature, London, 185(4714), p. 692.
- May, A. W. 1959. Cod from Labrador. Fish. Res. Bd. Canada, Rept. Biol. Sta., St. John's, Newfoundland, for 1958-59, App. 10: 23-26.
- McCracken, F. D. 1959. Cod tagging off northern New Brunswick in 1955 and 1956. Fish. Res. Bd. Canada, Atlantic Prog. Rept., No. 72, pp. 8-19.
- McKenzie, R. A. 1935. Codfish in captivity. Canadian Biol. Bd., Prog. Rept. Atlantic Biol. Sta. and Fish. Exptl. Sta. (Atlantic), 16, pp. 7-10.

Menon, M. D. 1950. Bionomics of the poor-cod (Gadus minutus L.) in the Plymouth area. J. Mar. Biol. Assoc. U. K., 29: 185-229.

Molander, A. R. and Märtha Molander-Swedmark. 1957. Experimental investigations on variation in plaice. Inst. Marine Res. Lysekil, Series Biology Report No. 7, 45 pp.

Pentelow, F. T. K. 1939. The relation between growth and food consumption in brown trout (Salmo trutta L.). J. Exp. Biol., 16, p. 445-473.

Powles, P. M. 1958. Studies of reproduction and feeding of Atlantic cod (Gadus callarias L.) in the southwestern Gulf of St. Lawrence. J. Fish. Res. Bd. Canada, 15(6): 1383-1402.

1960. Unpublished data.

Rollefsen, G. 1933. The otoliths of the cod. Fiskeridirekt. Skr., Ser. Havunders., 4(3), Bergen.

1935. The spawning zone in cod otoliths and prognosis of stock. Fiskeridirekt. Skr., Ser. Havunders., 4(11), Bergen.

Saetarsdal, G. S. 1953. The haddock in Norwegian waters. Norwegian Fish. and Marine Investig., 10(9), 46 pp.

Schaeperclaus, W. 1933. Textbook of pond culture. Translated by E. Hund as U. S. Fish and Wildlife Serv. Fish. Leaflet 311, 260 pp.

Sindermann, Carl J. 1958. An epizootic in Gulf of St.

Lawrence fishes. Trans. 23rd North American Wildlife Conference, pp. 349-360.

Snedecor, George W. 1946. Statistical methods. Iowa State College Press, 485 pp.

Surber, E. W. 1935. Trout feeding experiments with natural food. Trans. Am. Fish. Soc., 65th Ann. Meeting, pp. 300-304.

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

1959. Temperature and growth. The Pacific razor clam. J. Cons. Expl. Mer., 25(1): 93-101.

Thompson, H. 1943. A biological and economic study of cod (Gadus callarias L.) in the Newfoundland area. Newfoundland Dept. Nat. Res., Fish. Res. Bull., No. 14, 160 pp.

Trout, G. C. 1953. Otolith growth of Barents Sea cod. Rapp. Cons. Expl. Mer., 136: 89-102.

1957. The Bear Island cod: Migrations and movements. U. K. Min. Agr., Fish. and Food, Fish. Investig., Ser. 2, 21(6): 51.

1958. Otoliths in age determination. Int. Comm. NW Atlantic Fish., Special Publication No. 1, pp. 207-214.

- Walford, L. A. 1946. A new graphic method of describing the growth of animals. Biol. Bull., 90(2): 141-147.
- Watt, K. E. F. 1956. The choice and solution of mathematical models for predicting and maximizing the yield of a fishery. J. Fish. Res. Bd. Canada, 13(5): 613-645.
- Willer, A. 1929. Untersuchungen über das Wachstum von Fischen. Verh. Intern. Vereinigung. f. Limnologie, 4: 668-684.
- Yoshihara, T. 1952. Effect of population density and pond area on the growth of fish. J. Tokyo Univ. Fish., 39(1): 47-61.
- el-Zarka, Salah el-Din. 1959. Fluctuations in the population of yellow perch, Perca flavescens (Mitchill) in Saginaw Bay, Lake Huron. U. S. Fish and Wildlife Serv., Fish. Bull., 151: 365-415. (Fish. Bull. No. 59).