

SHORT TITLE

A relict population of Atlantic cod on Baffin Island

The Biology of a relict population of Atlantic cod,

Gadus morhua L., in Ogac Lake, Baffin Island, N.W.T.

by

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INTRODUCTION

Ogac Lake is a salt, meromictic lake located at the head of an inlet on the southern coast of Frobisher Bay at 62°52' N, and 67°21' W. This area is presumably rising as a result of the retreat of the ice cap, and the lake is semi-isolated, inflows of salt water being restricted to the highest summer tides.

Interest in the lake was stimulated by reports of Baffin Island Eskimos fishing 'giant' cod in the lake. Scientific studies were begun in 1951 when the M.V. 'Calanus' of the Fisheries Research Board of Canada was working in the Frobisher Bay area under the leadership of M.J. Dunbar. A one-day survey revealed a unique ecological situation, and subsequent investigations were made during the summer of 1952 when a two man party was landed there from the M.V. 'Calanus' for 36 days, and during the summers of 1957, 1962, and 1965 when more extensive studies were carried out by I.A. McLaren. The material for this thesis was collected during these expeditions.

These cod represent the northernmost population of the Atlantic cod, Gadus morhua, on the western side of Davis Strait. A few cod have been taken at 150 to 200 fathoms off the mouth of Frobisher Bay (Canada, 1960), and a small population has been observed at Resolution Island (Canada, 1952). No cod are taken in Frobisher Bay. On the West Greenland coast, cod are taken as far north as Upernavik (Hansen, 1949).

Temperature is the principal limiting factor in the northern limits of distribution. Atlantic cod avoid temperatures

less than 1°C (Hachey et al, 1954). Spawning has not been recorded in the literature at temperatures less than 2 to 3°C . A temperature of 1.8°C is critical for larvae (Taning, 1953). As a result, the northern limits of distribution, the location of spawning areas, and the abundance of cod in northerly areas vary quite considerably with periodic fluctuations in hydrography. Changes in the abundance of cod in West Greenland waters are well known. In the 1820's and 1840's of the last century cod were numerous in the West Greenland area, but were not again found in large numbers until 1917. From then until the present a large fishery has existed (Hansen, 1949). Dunbar (1955) discusses fluctuations in the marine climate in this area. Water temperatures in the Davis Strait are moderated by the relative and absolute contributions of Atlantic and Polar waters. The West Greenland Current is made up of water contributed from the (cold) East Greenland Current, the (warm) Irminger Current, and Atlantic water from the Labrador Sea. As this flows north, part of it branches westward joining the Canadian Current (Polar) flowing south along the Baffin Island coast to form the Labrador Current at the latitude of Hudson Strait. Increased temperatures of the West Greenland Current in recent years are a result of a greater contribution by the Irminger Current, associated with an overall intensification of meridional circulations. At the same time, Dunbar (1955) points out, an equivalent increase in water temperatures in the Eastern Canadian Arctic is buffered by increased

flow of the Canadian Current. Stronger resulting geostrophic forces also cause the Canadian Current to be pressed more closely against the western side of Davis Strait, and the West Greenland Current to be pressed more strongly against the eastern side. However, Dunbar suggests, at certain lesser intensities of circulation, the transport and geostrophic forces of the two currents may be in such a balance that the Atlantic influence on the western side is greater than at present, and perhaps greater on the western side of Davis Strait than on the eastern side. Biological evidence suggests that the 1880's was one such period. During this period and similar periods previous to this, Atlantic cod were probably present at higher latitudes and in greater numbers in the Eastern Canadian Arctic than at present. Ogac Lake, because of its isolation from the sea and marked stratification, maintains temperatures favourable for Atlantic cod independent of such marine climatic changes.

GENERAL HYDROGRAPHIC CONDITIONS

A detailed description of the morphometry and hydrographic conditions is given by McLaren (MS, 1961). The following is a summary of factors of immediate importance to this study.

The lake consists of three basins, referred to here as Outer, Middle, and Inner, proceeding from the outlet to the inlet (Fig. 1). Because the bottom is aerobic at 20, 25, and 27 meters in the three basins respectively, aerobic organisms are restricted to a bottom area outside of these contours; the

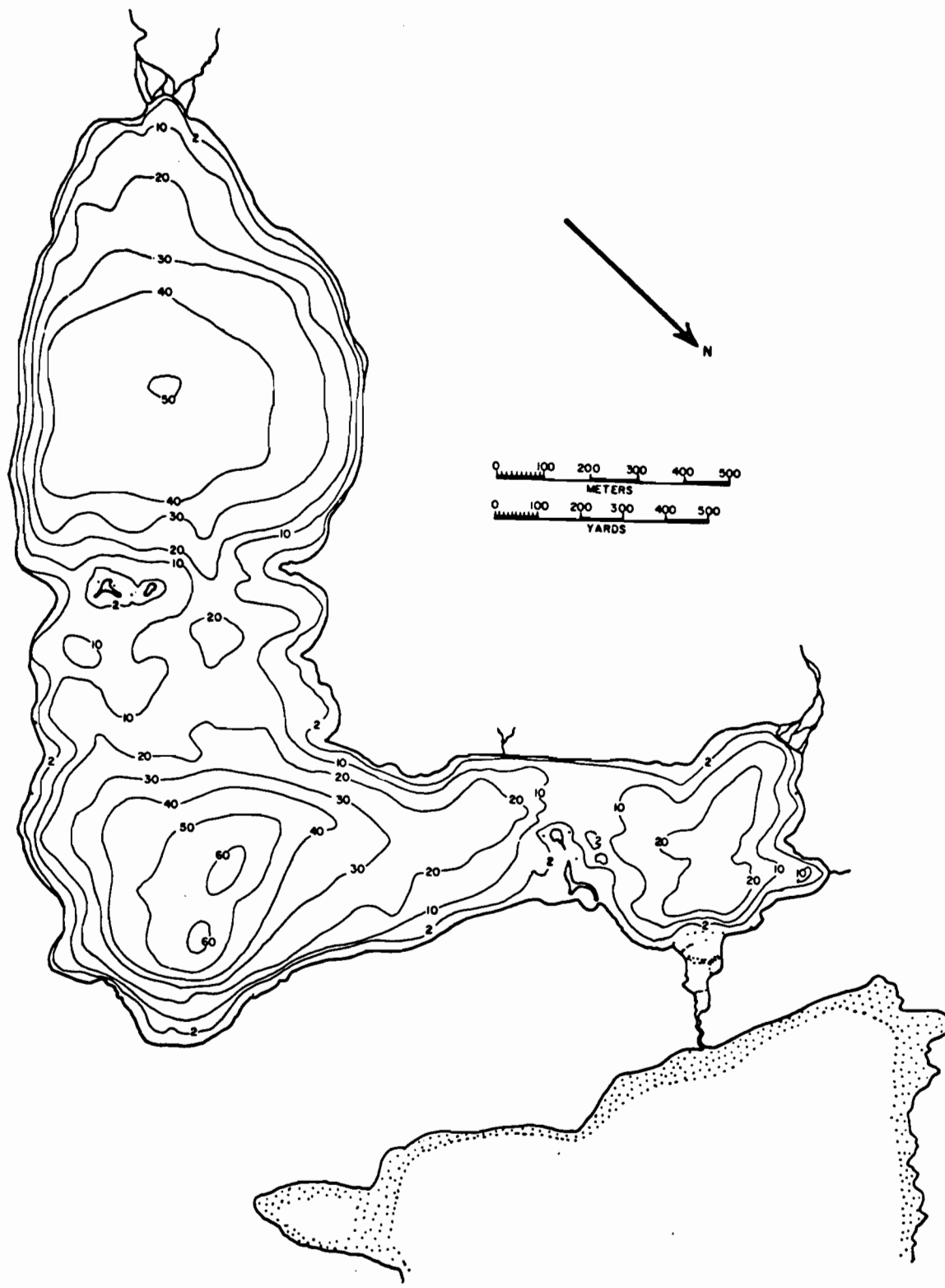


Fig. 1. Ogac Lake, bathymetric chart. Depth in meters.

From McLaren (MS, 1961).

surface area outside of these contours is 0.855 square kilometers. The exact limits will be determined by the physiology of the individual species.

Sundes (1957) found a critical oxygen concentration for cod at 2.8 ml/l in aquarium experiments, and observed asphyxiation at 0.8 ml/l. The depth of an oxygen concentration of 2.0 ml/l in the water column (not over the bottom) was at 18 meters at the beginning of June in the Outer Basin, and at a somewhat greater depth later in the season; in the Middle and Inner Basins this value was found between 25 and 30 meters throughout the 1957 season. Oxygen depletion occurs at approximately the same depths from year to year. Activity of cod is restricted to depths less than these. No fish were caught at depths over 20 meters.

From 5 to 25 meters the salinity in 1957 was maintained within a range of 18 to 28 ‰, 17 to 26 ‰, and 14 to 26 ‰ in the Outer, Middle, and Inner Basins respectively. Salinities in the deeper part of this depth range are stable from year to year. At depths less than 5 meters the water is subject to varying degrees of freshening through runoff, precipitation, and melting.

The Outer Basin maintains the lowest temperatures of the three basins, and the Middle Basin, the highest temperatures. The ranges of temperatures observed in the 1957 season between 2 and 20 meters are given in Table I. The heat budget in 1962 was essentially similar to that of 1957.

Table I. Ranges of temperature ($^{\circ}\text{C}$) between 2 and 20 meters in the three basins through the 1957 season.

Basin	Early June	Mid July	Mid August	Mid September
Outer	-0.02 - 3.04	3.1 - 8.1	3.9 - 8.4	4.1 - 9.6
Middle	0.3 - 6.7	3.8 - 8.4	6.3 - 8.8	7.0 - 9.8
Inner	2.1 - 7.1	6.5 - 7.8	5.9 - 9.2	7.4 - 9.6

Cod can detect a temperature change of less than 0.1°C (Bull, 1936). Large cod are known to prefer lower temperatures than small cod (Wise, 1961). Temperatures selected appear to be more specific in winter than summer. Jean (1964) reports cod on the Nova Scotia Banks in summer at depths of 0 to 65 meters in temperatures from 0 to 10°C , while in winter they are found between 90 and 130 meters at a temperature of 2°C . Lee (1952) reports Bear Island cod residing in temperatures of 1.75 to 3°C in winter, and of 3 to 5°C during the summer. Hachey et al (1954) suggest that cod avoid temperatures less than 1°C , but that at higher temperatures the concentration of cod is probably more closely related to the concentration of food than to temperature. Specific temperatures may be selected for spawning, but these vary between areas. A temperature of 1.8°C is critical for larvae; below this muscular activity is impeded (Taning, 1953). The cod in Ogac Lake are living in both vertical and horizontal gradients of temperature. These differences in temperature may be particularly important during the winter. The level of feeding is probably very low for a long period during the winter darkness; it is then preferable to reside in a temperature region in which metabolism is minimal. Saunders (1963) shows the oxygen consumption of starved cod increases significantly when they are thermally acclimated at higher temperatures. Between 3 and 10°C the oxygen consumption

of a 0.5 kilogram fish increases from 25 to 37 mg/hr, and in a 6.0 kilogram fish increases from 178 to 334 mg/hr.

POPULATION ESTIMATES

METHODS

Because of observations that small fish returned to the water were often captured by large fish, and because of the limited number of large fish and a general desire not to overexploit this unique population, a rather overelaborate program was devised.

Fish were tagged from July 3 to August 12 of 1962, and observations taken from August 13 to August 28. Tagging was restricted to fish of lengths 60 cms. and greater in the Outer Basin and to lengths of 50 cms. and greater in the Middle and Inner Basins. Fish were observed on calm days by dropping a jig into the water and counting the number of fish approaching it, and by counting the number seen from the bow of the canoe while passing over demarcated regions. A total of 233 observations were taken around the perimeter of the lake in this manner. Observations were recorded as follows: total number observed, number greater than 60 cms., number greater than 50 cms., number less than 10 cms., number of tagged individuals. This method of estimating the lengths obviously introduces several possible errors into the estimates made, the most serious of which is that it is difficult to determine the smallest sizes included in the estimate. The number of fish under 10 cms. was negligible with respect to the total

number observed. The estimates of the total population number are considered to apply to fish of lengths greater than 20 to 25 cms. The Outer Basin population is treated separately from the Middle and Inner Basins' population. This will not introduce too serious an error since over short periods there does not appear to be much interchange between the two areas, indicated by the recovery of tagged fish (Table II).

The number of fish over 60 cms. in the Outer Basin, or over 50 cms. in the Middle and Inner Basins, is estimated by application of formula 3.7 of Ricker (1958), and then the total population is estimated from this by use of the proportion no. of fish of taggable size : total no. observed , given in the observations. The data and estimates are given in Table III. Fiducial limits (95%) are calculated from the binomial distribution charts of Clopper and Pearson (1934), and are applied first to the estimate of the number of fish of taggable size (over 50 or over 60 cms. as the case may be) and secondly to the proportion used in estimating the total population. Combination of these estimates gives the limits for the total population estimates.

RESULTS

The fiducial limits of the total population estimates are large. If the sources of error discussed above, which are not included in calculation of these fiducial limits, are also considered, then the estimate of the total population

Table II. Movements of fish between basins from recapture data.

Interval	No. recaptured	No. recaptured in basin
		other than that of origin
2 - 26 days	5	0
36 - 51 days	4	1
3 years	10	5

Table III. Population estimates

Outer Basin

Total observed	413
50 - 60 cms.	22
>60 cms.	33
marked 'recaptures'	15
marked	48

$$\begin{aligned} \text{Estimate of no. of fish } >60 \text{ cms. : } N &= \frac{M(C+1)}{R} \\ &= \frac{48 \cdot 49}{16} = 147 \end{aligned}$$

fiducial limits : 102 - 245

N = population estimate

M = no. marked

C = no. 'captured'

R = no. marked fish 'recaptured'

$$\text{Estimate of no. of fish } >20 - 25 \text{ cms. } ^1 : 147 \cdot \frac{413}{48} = 1264$$

fiducial limits : 630 - 3100

¹ See text for explanation of this calculation.

Table III. continued

Middle and Inner Basins

Total observed	1195
50 - 60 cms.	81
>60 cms.	45
marked 'recaptures'	8
marked	64

Estimate of no. of fish > 50 cms. : $\frac{135 \cdot 64}{9} = 960$

fiducial limits : 490 - 2000

Estimate of no. of fish > 20 - 25 cms. : $960 \cdot \frac{1195}{134} = 8561$

fiducial limits : 3500 - 22,000

Ratios

$$1. \frac{>60 \text{ cms. OB}}{\text{total OB}} = .116 \quad (147 \text{ cod})$$

$$\frac{>60 \text{ cms. MB \& IB}}{\text{total MB \& IB}} = .04 \quad (360 \text{ cod})$$

$$2. \frac{>50 \text{ cms. OB}}{\text{total OB}} = .169 \quad (214 \text{ cod})$$

$$\frac{50 \text{ cms. MB \& IB}}{\text{total MB \& IB}} = .112 \quad (960 \text{ cod})$$

$$3. \frac{>60 \text{ cms. OB}}{>60 \text{ cms. lake}} = .29$$

OB Outer Basin

MB Middle Basin

$$4. \frac{\text{total OB}}{\text{total lake}} = .129$$

IB Inner Basin

of the lake can only be regarded as giving the order of magnitude, i.e. of the order of 10,000 fish of lengths greater than 20 to 25 cms. The estimates of the number of large fish are subject to fewer sources of error and are somewhat more reliable.

Relative population estimates in the Outer, and Middle and Inner Basins may be compared with less error than any application of the total population estimate itself. It is interesting to note, for example, that the proportion of the total population which is found in the Outer Basin is estimated as 12.9%, while the proportion of large fish (greater than 60 cms.) residing in the Outer Basin is estimated as 29%. The proportion of the fish living in the Outer Basin could perhaps be expected to correspond to the proportion of inhabitable bottom area of the lake found in the Outer Basin, Gadus morhua being a demersal fish. The proportion of inhabitable bottom area in each basin may be considered approximately proportional to the surface area lying outside of the 20 meter contours; the Outer Basin includes 24% of this area. There appears, therefore, to be a congregation of large fish in the Outer Basin. This is supported by qualitative observations of schools of large fish there, especially around the entrance from the sea. The Outer Basin is probably preferred by the larger fish because of more nearly optimal conditions (lower temperatures and higher salinities).

GROWTH AND AGE

METHODS

Otoliths were collected from a total of 222 fish in the years 1951, 1952, 1957, and 1965. The (sacculus) otoliths were fractured at the interruption in the sulcus acusticus on the convex side. These were mounted in modelling clay, the fractured surface wetted with a 50% solution of alcohol, and read using a stereoscopic dissection microscope and transmitted blue light.

Interpretation of the ages was complicated by the presence of secondary hyaline zones and indistinct winter zones. This type of otolith structure (Fig. 2) is similar to that described by Hansen (1949) and Otterbach (1954) in Gadus morhua from inner Gothaab Fjord in West Greenland, and inner Oslofjord in Norway, and appears to be characteristic of non-migratory populations. However the ages determined are considered reliable, and those that were very doubtful (8 in number) have been excluded from the data. Seventy-one otoliths were read at the Biological Station of the Fisheries Research Board of Canada at St. Andrews, New Brunswick, and by A.W. May at the Marine Sciences Centre. My own readings agree with 75% of the readings by the above, and differences were at most one or two years.

Sixty-two otoliths were measured to back-calculate growth of individual fish. These otoliths were selected for

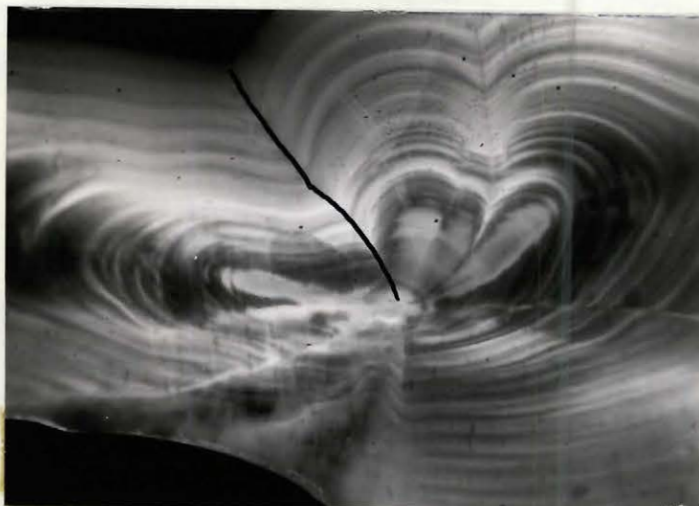


Fig. 2. Sectioned otolith of 13 year old fish. Axis used in measurement is indicated. Photographed under 25 X magnification, transmitted light.

clarity of the winter zones. The surfaces were ground flat by use of a powered graphite disc. The axis used in measurement is indicated in Fig. 2. This axis is defined on nearly all otoliths of the Ogac Lake cod by an indentation in the middle of the hyaline zones on the concave side of the otolith. The axis is not always straight, but was selected because it represents the most consistent aspect in the growth of the various otoliths. Use of the axis is justified by the high degree of log-log correlation ($r = .942$) with body length. Increments were measured from the origin in the initial opaque growth to the outer edge of the hyaline zones. All measurements were read under 50 power magnification using a micrometer mounted in a 10X eyepiece. Measurements were recorded in eyepiece units; 1 unit = 0.007 mm. The estimating equation of the regression (Fig. 3) is :

$$\log_{10} \text{Length} = -1.2707 + 1.2636 \log_{10} \text{Otolith radius}$$

(cms.)
(eyepiece units)

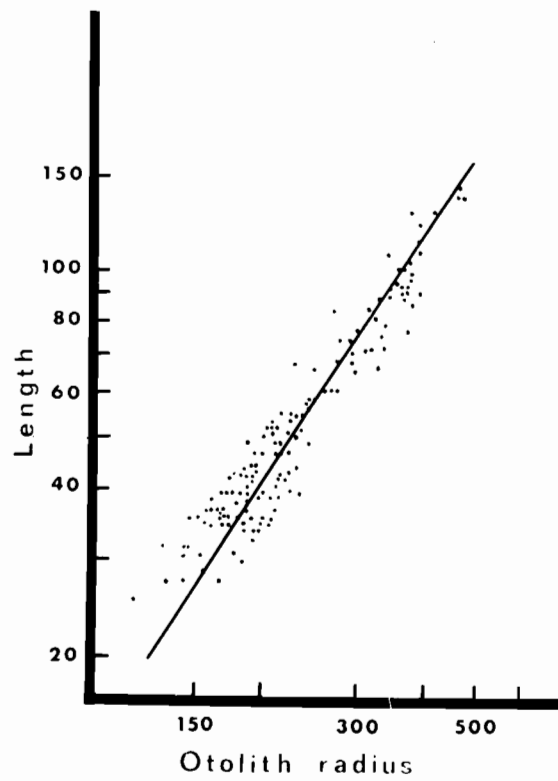


Fig. 3. Log-log regression of length (cms.) on otolith radius (eyepiece units).

Comparison of back-calculated lengths to observed lengths of tagged fish subsequently recaptured in later years provides a check on the adequacy of the above formula. The calculated and observed lengths agree within a few centimeters (Table IV); considering also that these otoliths do not necessarily represent those of greatest clarity, the back-calculations used are considered reliable. This check also suggests the age readings are accurate within ± 1 year.

GROWTH

The dispersion in growth rates of the Ogac Lake cod is greater than that of any population recorded in the literature, and is probably greater than that of any oceanic population.

In Table V the extremes of length at each age for the Ogac Lake population are tabulated together with those of populations of Gadus morhua from Port Burwell, ICNAF AREA 2G, and ICNAF AREA 2J on the Labrador coast. The extremes in length of the Ogac Lake cod are taken from observed or back-calculated values. Most extremes, it will be noted however, are observed values. The back-calculated values are used to smooth out the data somewhat, and to give the lower limits of length where that is less than lengths taken in the samples; sampling was restricted largely to fish over 30 cms. in length. All data include several years' sampling with the exception of the Port Burwell population.

Several factors are of interest in the comparison of

Table IV. Comparison of observed and back-calculated lengths of recaptured tagged fish.

RECAPTURE		FIRST CAPTURE		
Age	Length	Age	Length (observed)	Length (calculated)
9	83	6	66	57+ ¹
11	72	8	61	59+
12	75	9	63	62+
12	66	9	59	59+
12	98	9	95.5	- ²
13	87	10	72	74+
15	98	7	59	61+

¹ (+) signs are used because back-calculated values apply to the end of the winter period. Fish were tagged during the subsequent growing season.

² The last few years were observed only at one portion of the otolith and were very close together. An abrupt decline in growth rate is indicated, probably as a result of wounds from tagging.

Table V. Extremes of length at given ages for various cod populations. Port Burwell figures are taken from data of the Arctic Biological Station of the Fisheries Research Board of Canada on 664 specimens. ICNAF 2G and ICNAF 2J figures are from data contributed by A.W. May of the Marine Sciences Centre. This data was taken from several thousand cod caught by inshore otter trawl in an unexploited area, ICNAF 2G, and an exploited area, ICNAF 2J. Figures marked ' are from back-calculations, and brackets indicate only one specimen was available in that age group.

AGE	LOWER LIMIT				UPPER LIMIT				RANGE			
	Ogac Lake	Burwell	ICNAF 2G	ICNAF 2J	Ogac Lake	Burwell	ICNAF 2G	ICNAF 2J	Ogac Lake	Burwell	ICNAF 2G	ICNAF 2J
1	6'				17'				12			
2	13'				34'				22			
3	21'				45'				25			
4	23'			35	56'			49	34			15
5	27'	38	40	37	65'	55	57	58	39	14	18	22
6	29'	43	41	38	74'	54	60	74	46	12	20	37
7	31'	44	46	40	90'	58	60	80	60	15	15	41
8	33'	46	47	41	91	62	65	81	59	17	19	41
9	33	47	47	48	92	65	66	88	60	19	20	41
10	40	51	49	50	101	67	70	91	62	17	22	41
11	40	53	50	51	109	63	70	85	70	11	21	35
12	58'	53	53	49	112	65	68	99	55	13	16	51
13	60	53	50	50	118	73	67	90	59	21	18	41
14	62'	55	56	51	126	71	70	85	65	17	15	35
15	64'	48	57	53	128	74	73	90	65	27	17	38
16	66	58	57	63	128	71	72	111	63	14	16	49
17	135	64	58	55	141	69	70	103		6	13	49
18		61	58	60		75	67	80		15	10	21
19		62	(60)	70		71	(60)	96		10		27
20			(65)	60			(65)	85				26
21			-	76			-	87				12
22			(78)				(78)					

these figures: (1) The Ogac Lake cod have the greatest range of lengths at all ages. That this is not just a result of yearly variation in feeding conditions is shown by the existence of both extremes in single year classes (Figs. 4 a,b,c,d).

(2) The upper limit of length tends to decrease in the higher age classes of the Burwell and ICNAF cod, but continues to increase in the Ogac Lake cod. A higher relative survival of the faster growing fish in the Ogac Lake population is suggested.

The Ogac Lake population is subject to a certain amount of native fishing; the other areas include many populations in both fished and unfished areas. (3) The lower limit of length of the Ogac Lake cod is less than that of the other populations to the age of eleven (length 40 cms.). At higher ages it is greater than that of the other populations.

In Table VI the growth rates of populations from various areas have been represented by the average length attained at ages 5, 10, and 15. The lower limits of length at ages 5 and 10 in the Ogac Lake population are considerably smaller than the averages of any of the other populations. Of the populations in the North West Atlantic, the growth rate of the Greenland cod approaches that of the faster growing Ogac Lake cod.

Examination of the growth curves of back-calculated individuals reveals three 'types' of growth curves (Figs. 5 a,b,c):

- (1) linear increase of length with age
- (2) decreasing increments of length with age
- (3) alternating periods of increasing and decreasing increments of length with age.

Figs. 4 a,b,c,d. Age samples from the years 1951, 1952, 1957, and 1965. Vertical lines give extremes of lengths encountered. The frequency of lengths at each age are given in histograms.

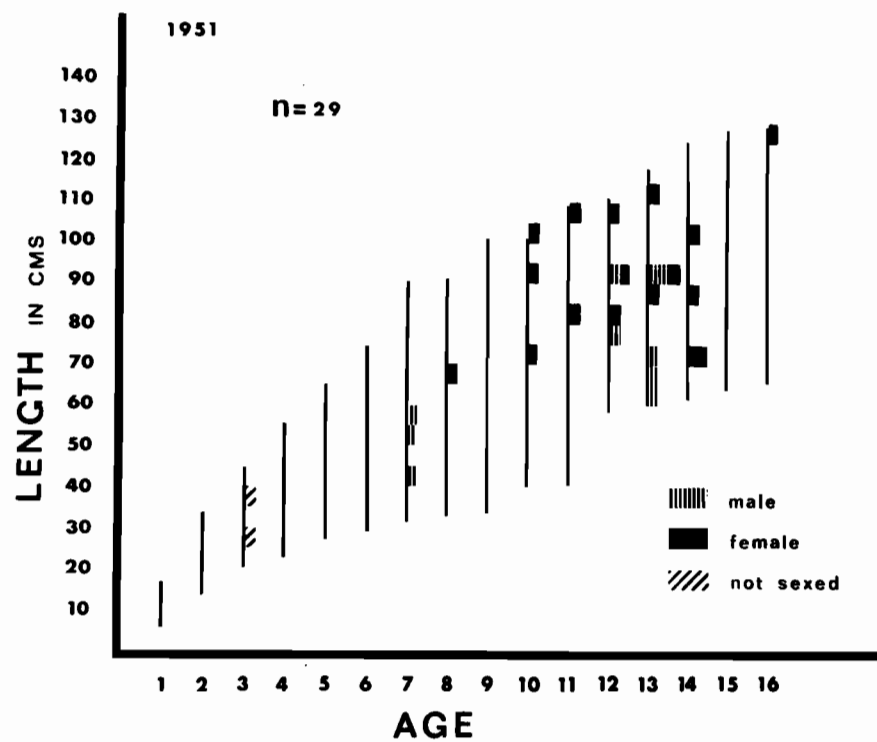


Fig. 4 a.

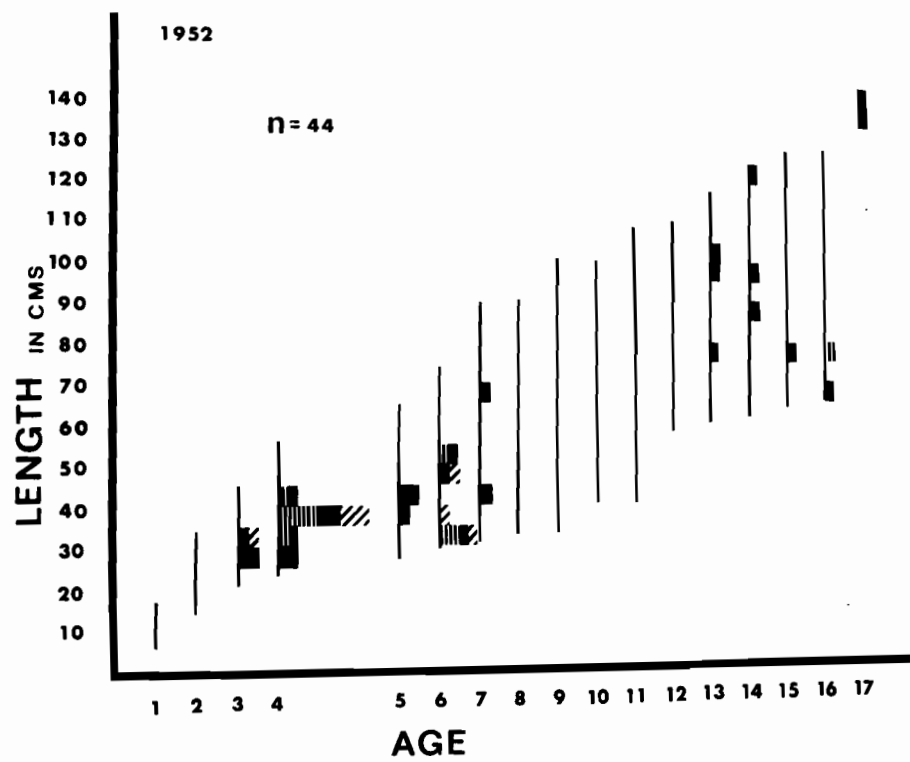


Fig. 4b.

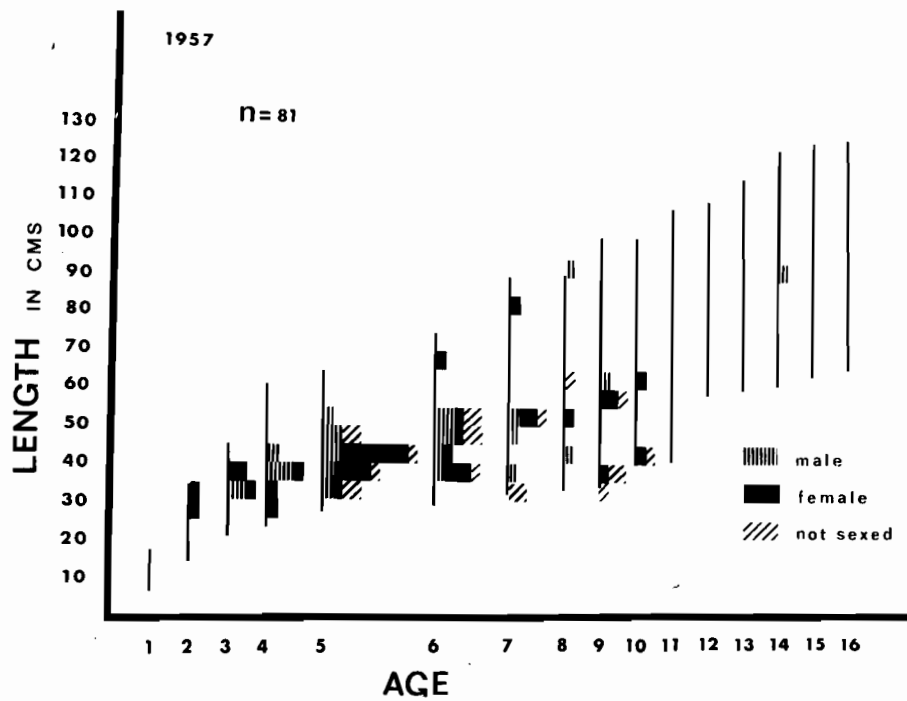


Fig. 4 c.

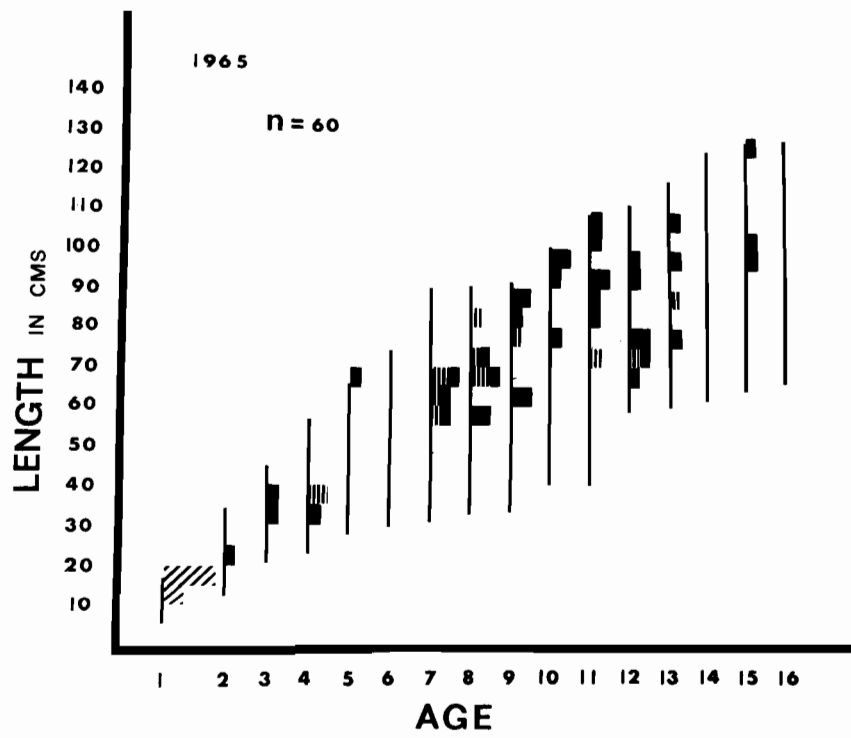


Fig. 4 d.

Table VI. Growth rates of various North Atlantic populations of Gadus morhua represented by average lengths at ages 5, 10, and 15.

	Age	5	10	15	
Location		Length (cms.)			Reference
Faroe Banks		105	-	-	Thompson (1943)
Faroe Islands		87	-	-	" "
North Sea		78	-	-	Graham (1948)
Iceland		68	87	-	Buckmann et al (1958)
N.W. Greenland, 1945		59	77	-	Hansen (1949)
N.W. Greenland, 1929		68	90	-	" "
S.W. Grand Banks		54	88	-	Fleming (1960)
N.E. Grand Banks		52	71	78	" "
ICNAF AREA 2J, 1963		42	65	71	May (MS, 1966)
ICNAF AREA 2J, 1959		42	60	62	" "
ICNAF AREA 2G		40	58	-	" "
Port Burwell		45	56	62	Arctic Biol. Stn.
Resolution Island		-	63	67	" " "
Ogac Lake (extremes)		27 - 65	40 - 101	64 - 128	

Figs. 5 a,b,c. Types of growth curves.

- (a) Linear increase of length with age
- (b) Decreasing increments of length with age
- (c) Alternating periods of increasing and
decreasing increments of length with
age

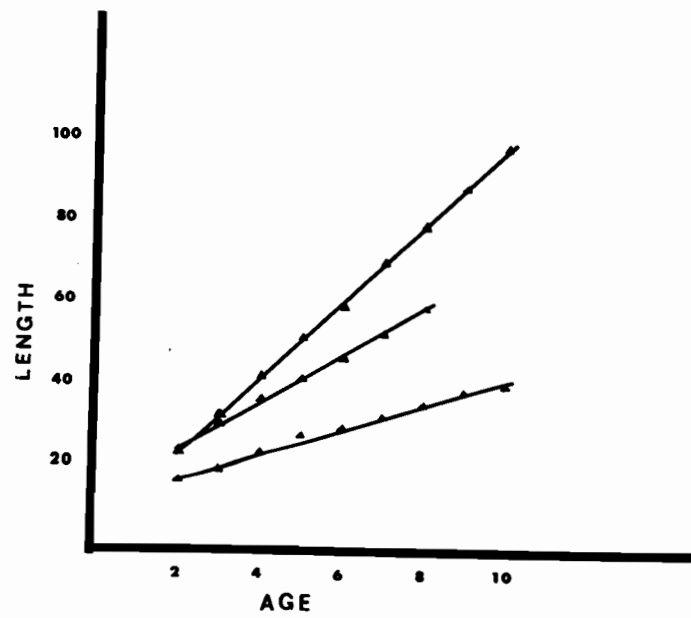


Fig. 5 a.

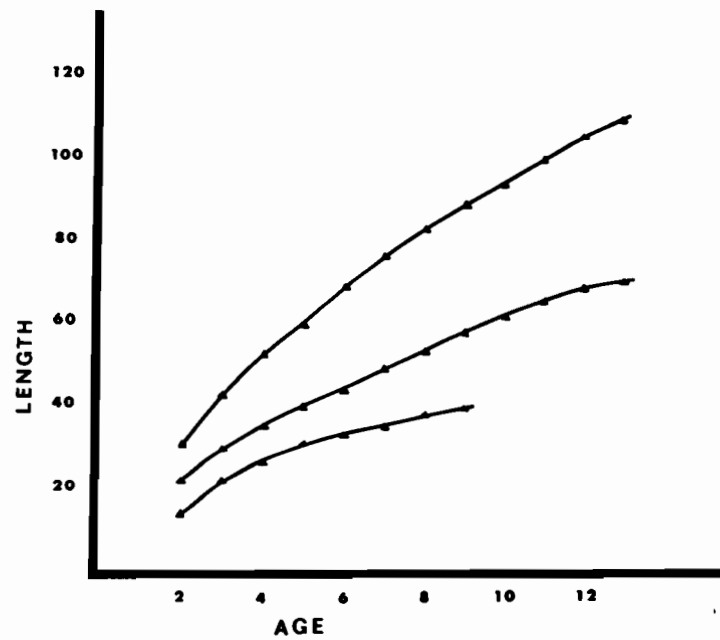


Fig. 5 b.

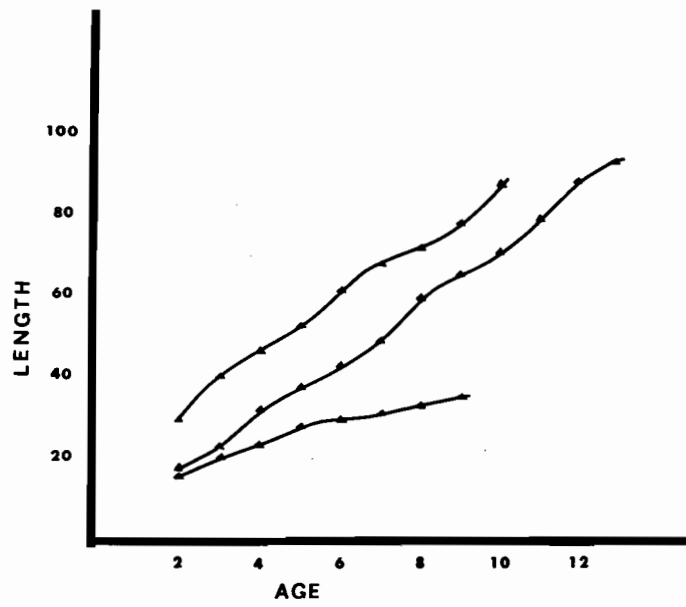


Fig. 5 c.

All three types are found in slow, moderate, and fast growing fish, although type (1) tends to be more common in fast growing fish, and type (2), in slow growing fish. The relative rate of growth (fast, moderate, slow) is established by age 3 or 4. A growth 'advantage' or 'disadvantage' is maintained from an early age on. Even in type (3) fluctuations are not intense. It is difficult to determine if these growth patterns are established at an earlier age because the regression of length and otolith radius is less reliable where it is extrapolated to lower lengths (relative growth patterns may be different) and because the back-calculated first year of growth may involve individual differences of up to two months during the growing season due to variation in the time of spawning and in development rate.

No general correspondence of growth increments between individuals of the same year-class is noted.

In view of the variation in individual growth curves, it is evident that parameters of growth equations based on average values would have no significance. Because of incomplete sampling over the length ranges at various ages, an average growth curve cannot be calculated. In any case the variability is of much greater interest than the average.

LENGTH - WEIGHT RELATIONSHIP

The log-log regression of length on weight is shown in fig. 6. Above 40 cms. this is described by the equation:

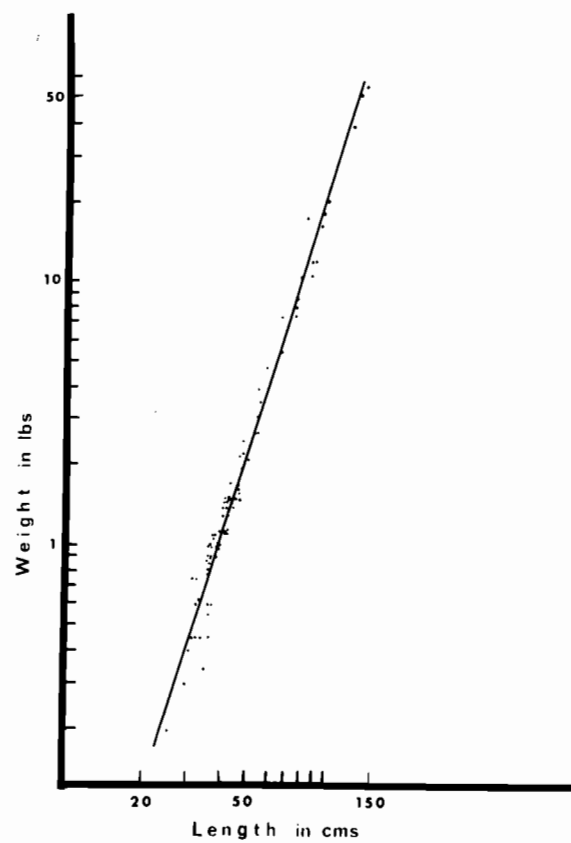


Fig. 6. Log-log regression of length on weight

$$W = 1369 \times 10^{-8} \times L^{3.08}$$

where W is the weight in pounds and L the length in centimeters. At lengths less than 40 cms. the exponent appears to be somewhat greater, but it is difficult to determine the validity of this without smaller lengths and weights. The exponent, 3.08, does not differ significantly from the theoretical exponent of 3.00 for isometric growth.

The weights at given lengths of the Ogac Lake cod are compared with those of other populations in Table VII. The Ogac Lake cod are not particularly 'fat' or 'thin' compared to these other populations.

AGE DISTRIBUTION

Mortality estimates are not possible because of the large sample size required to sample the ages representatively. In Figs. 4 a,b,c,d the frequency distributions of sizes taken at each age are shown. It is evident that there are no strong year-class fluctuations, the slight preponderance of some ages being mainly a result of the length range sampled.

Several factors favor a high survival in the egg and larval stages. Lack of complicating currents prevent massive losses through drift away from coastal areas such as occur in some oceanic situations. The thermal regime of the lake maintains temperatures above the critical 1.8°C for larvae. At the northern limits of cod distribution the temperature during the larval stage is thought to be the main factor controlling year-class abundance. Hachey et al (1954) show

Table VII. Weights at given lengths for various cod populations.
 Labrador from May (MS, 1966), W. Greenland from
 Ruivo (1956) and Banquereau from Ancellin (1955) .

LENGTH (cms.)	WEIGHT (pounds)			
	Ogac Lake	Labrador	W. Greenland	Banquereau (Nfld.)
40	1.2	1.3	-	1.1
50	2.3	2.5	2.4	2.2
60	3.9	4.0	4.4	3.8
70	6.6	7.1	6.7	6.9
80	9.9	10.5	9.6	9.5
90	14.5	15.5	14.5	15.5
100	20	21.5	-	-
110	26.5	29	-	-
120	34.5	37	-	-
130	44.5	47	-	-
140	55.5	61.5	-	-

an excellent correlation between the yield of year-classes in West Greenland and the temperature over the Fylla Bank in June. The time of spawning in Ogac Lake coincides with the plankton bloom (to be discussed below).

The high degree of cannibalism in the Ogac Lake population may be important in moderating year class fluctuations. Ricker (1954) estimates that even in the presence of 95% density independent mortality, cannibalism may be the sole factor regulating the population abundance.

FEEDING

A general qualitative description of the stomach contents was carried out in the field. This general classification is included in Table VIII according to length groups.

Fish of lengths 14 to 28 cms. feed principally on crustaceans. Between 22 and 30 cms. the diet becomes more varied and the sea urchin Strongylocentrotus droebachiensis, molluscs, and the polychaete Pectinaria become important constituents of the diet. At lengths of 50 cms. and greater, smaller cod (less than 40 cms.) are a major constituent of the diet for these large, cannibalistic cod. The lack of small fish in the stomachs of cod of lengths 25 to 40 cms. suggests behavioural differences prevent intense predation on these small cod. These were observed lurking among boulders on steep slopes.

It may be assumed that prior to a length of 14 cms. the food consists mainly of small Crustacea. Marak's (1960) observations of the food habits of larval cod may be summarized

Table VIII. Stomach contents. Food items are given as % of
cod with food in stomachs in which item was found.

FOOD ITEM	COD LENGTH GROUP (cms.)		
	14 - 22	30 - 49	> 50
Seaweeds	-	9.6	19
Polychaetes	20	25	5.7
Amphipods	100	15	13
Molluscs	-	15	15
Sea urchins	-	67	60
Brittle stars	-	7.7	5.8
Small fish	-	3.8	-
Cod	-	-	21
No. examined	6	59	62
Empty (% of total)	17	12	16

as follows: prior to yolk sac absorption copepod nauplii are the principal source of food; from a length of 0.4 to 1.3 cms. small copepods may be the chief source of food. Above this size, any size copepods may be taken, and young amphipods and euphausiids begin to be eaten. The timing of spawning in the lake will be shown to coincide with the reproductive cycle of the most abundant copepod in the lake, Pseudocalanus minutus.

Of particular significance is the cannibalism of the larger cod on the smaller. No cod greater than 41 cms. were found in the stomachs of the larger cod; the lower limit of length of cod taken by these cannibals was about 18 to 20 cms. From the estimate of the number of cod greater than 50 cms., an estimate of the number of cod eaten is possible. This is given by:

$$\frac{\text{no. of large cod} \times \text{av. no. of cod per stomach}}{\text{time required to digest a cod}}$$

$$= \frac{974 \times 0.177}{5 \text{ days}} = 34.4 \text{ cod per day}$$

Powles (1963) applies limits to his estimates of plaice mortality from large cod by using digestion times of 4 and 6 days. If active feeding continues for a period of 100 days, then approximately 3440 cod between the lengths of 20 and 40 cms. are eaten. An estimate of the mortality imposed on this length group is not possible because of the uncertainty of the total population estimate and the lack of data concerning age and length distribution. However, the number of fish eaten is probably sufficient to account for the sharply increased lower limit of size between ages eleven and twelve. At this time the lower limit

of length of fish caught increases from 40 to 58 cms. Higher mortality in the slower growing fish results in high relative survival of faster growing fish.

Of importance in the food supply are the tidal inflows during which fish congregate at the outlet feeding voraciously on young sculpins and mysids which enter in large numbers.

Any population which depends to such a large extent on sea urchins is obviously feeding in very poor conditions. In spite of this the population appears to do well, and the 'average' growth rate is not low. It is, for example, better than that of the Port Burwell population which feeds largely on fishes, decapods, and amphipods (Canada, 1952). Cannibalism must increase the efficiency of utilization of food resources.

MATURATION, SPAWNING, AND EARLY DEVELOPMENT

MATURATION

Methods In August of 1965 observations were made in the field on the state of gonads. The gonads were classified according to the scheme of Sorokin (1958, 1960). The stages in Sorokin's classification may be summarized as follows:

Juvenile; female 1, sex distinguishable; female 2, development of the gonads proceeds untill the year of maturation; female 3 and 4, ripening process; female 5, spawning; female 6, spent. For previously spawned cod the stages are referred to as 6-2, 6-3, and so on. Stages in the development of the male are similarly defined except that stage 2 includes males in the year of spawning only.

There was somewhat more difficulty in classifying males with certainty than females. Determination of the age of first spawning from spawning zones on otoliths was considered unreliable since these 'zones' were found in only a small proportion of the otoliths, and the results completely contradicted field observations on the state of the gonads.

Results The distribution of mature cod taken within the length range sampled is shown in Fig. 7. Fish were in either stage 6 or 2 of Sorokin's scheme with the exception of a few which were classified as 6-2; these were probably recovering from early spawning and have been included with the mature cod. Females begin spawning when they have reached a length of 85 to 90 cms.; males begin when they have reached a length of 60 to 70 cms. The lowest age of spawning females was age 9, and non spawning females included individuals to age thirteen. The lowest age of spawning males was 7 years, and non spawners included individuals to age nine. Initiation of spawning in females is thus primarily a function of length; this is probably true for the males also.

The lower length and age of maturity of males is in agreement with this observation on many cod populations (see, for example, Thompson, 1943), and probably reflects a generally lower growth rate in the males. This is suggested in Figs. 4 a,b,c,d. The male-female sex ratio is 0.43 for the ages 2 to 8; at ages greater than 8 it is 0.19. If on the

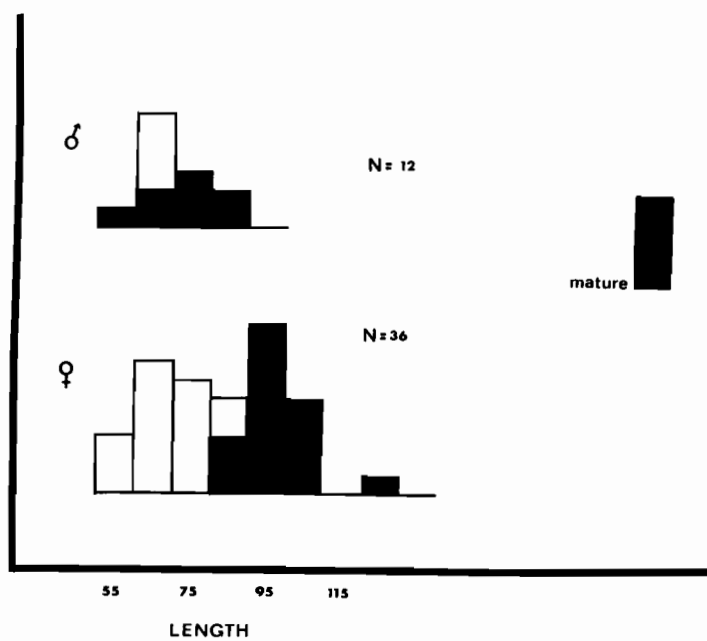


Fig. 7. Length frequency of males and females from 1965 sample showing the proportions of immature and mature fish.

average males grow more slowly than females they will be subject to greater mortality through cannibalism.

The length at which spawning is initiated in the Ogac Lake cod, particularly in the females, is unusually high. It also appears to be initiated over a relatively narrow length range in females; the sample is small, however. Alm (1959) reviews the relationships of age, growth, and maturity, but the significance or causes of differences between populations in age and length at maturity are still largely unanswered.

In Table IX are listed some average lengths and ages of first spawning of cod from various areas. The populations studied by Fleming (1960) from Labrador and Newfoundland agree with the observations of Alm that between populations faster growing populations have a higher length and age of maturity than the slower growing populations. May (MS, 1966) found that the length of maturity of the Northern Labrador cod is slightly less than is found in populations from Southern Labrador. Hansen (1949) observed that the age of maturation of West Greenland cod declined from the 1920's to the 1930's; he attributes this to an increase in the water temperature. However the growth rate also declined during this period. The Sondeledfjord population described by Dannevig (1954) and the Oslofjord population described by Otterbach (1954) mature at exceptionally low ages and lengths. Mortality in these populations is very high, few cod living past the age of five. The low age and length of maturity are adapted to

Table IX. Average length and age at first spawning of Gadus morhua from various areas.

AREA	AV. LENGTH	AV. AGE	REFERENCE
Labrador			May (MS, 1966)
males	43.9	5.8	
females	49.8	6.5	
W. Greenland, Northern districts			Hansen (1949)
Year 1917 ¹	-	8.6	
1924	84	8.4	
1934	74	7.8	
1936	73	6.9	
S.W. Grand Banks	73	7.5	Fleming (1960)
Flemish Cap	57	6.0	" "
Oslofjord (females)	39	2.5	Otterbach (1954)
Ogac Lake			
males	(55 - 70)	-	
females	(85 - 90)	-	

¹ Except where stated, males and females are combined

this situation (or the cause of it). The high length of maturity of the Ogac Lake cod is presumably related to the high survival of large (and fast growing) fish, given a genetic potential of the first inhabitants for a high length of maturity.

SPAWNING AND EARLY DEVELOPMENT

Methods In June and early July of 1962 vertical plankton net hauls were made from the ice through natural fissures and holes. Cod eggs were removed from these samples and examined under a dissection microscope. The individual eggs were classified into one of 12 stages of development following the description of Meek (1924) for the 12 day development of cod eggs at 5.5°C . Egg diameters were measured under 25 power magnification by use of a micrometer mounted in an eyepiece. One eyepiece unit (e.p.u.) = 1.53 mm.

Spawning Development time of eggs is dependent on temperature. Apstein (1909) reared a number of eggs of marine fish including cod to determine the effects of temperature on development time for various stages. Thus some idea of the time an egg was spawned can be determined from a knowledge of its stage of development and temperature of incubation.

In Fig. 8 the frequency distributions of developmental stages are shown for each basin. Only the newly hatched larvae were taken in the plankton net, later stages probably escaping. The highest stage of development in the Outer Basin on June 13 was stage nine. If this developed at the average temperature between 2 and 20 meters, approximately 1.5°C in 1957, then this

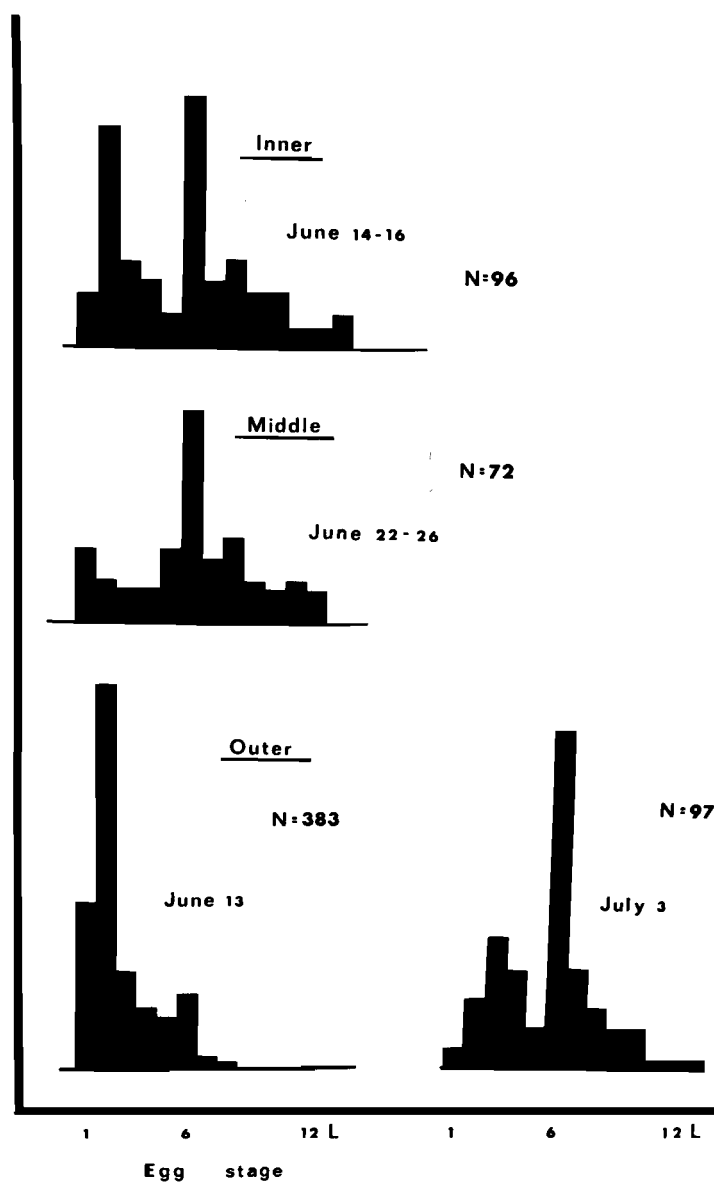


Fig. 8. Frequency distributions of developmental stages.

"L" refers to larvae.

egg would have been spawned 22 to 25 days previously or about 20 days previously if it had developed at a somewhat higher temperature (2.5°C). The highest stage of development taken in the Inner Basin at this time was the newly hatched larva. This requires about the same time for development, that is 22 to 26 days at the average temperature, 3.5°C , or 20 days at 5°C . This suggests spawning began about May 20 to 25. If as is probable, more advanced stages were present but not captured in the Inner Basin, then spawning began somewhat earlier in the Inner Basin.

Both light and temperature are known to influence gonad development. Alm (1959) has reviewed the subject in detail. It seems likely that in Ogac Lake light would be the most influential factor, since the temperature varies so considerably that if it were the principal controlling factor then spawning would be very sporadic and not apt to coincide with the zooplankton cycle. The zooplankton cycle is dependent on the bloom of phytoplankton, which is in turn a function of light. Most eggs were hatched by the beginning of July; Pseudocalanus minutus, the most abundant copepod in the lake, reaches maximum numbers at this time (McLaren, 1961). The bloom of phytoplankton and zooplankton is slightly retarded in the Outer Basin as a result of a later loss of ice cover there; if, as suggested, spawning is also retarded in the Outer Basin then it is appropriately timed, and is presumably

a response to the same factor.

No stage 1 eggs were found after the second week in July. The spawning period in 1962 was thus from the latter half of May to the first half of July. Spawning periods of oceanic populations generally extend from 3 to 6 months (Wise, 1961).

Egg diameters and vertical distribution of eggs In Fig 9 the frequency distributions of egg diameters from a series of vertical tows of increasing depths at one location in the Outer Basin are shown. Above 12 meters no eggs of less than 100 e.p.u. were taken. The modes in the frequency distribution shift with increasing depth, and a second mode of smaller sized eggs appears in the deepest tows. It is concluded that eggs are found throughout the water column to 20 meters, and that smaller eggs are found with increasing depth.

A relation between egg size and depth is also suggested by the observation that the vitelline membrane of the smallest eggs was heavily pigmented. This pigmentation was observed when the eggs were first examined in February of 1965, but when they were re-examined in March of 1966, the pigmentation appeared to have bleached out. I am told by Dr. B. D'Anglejan of the Marine Sciences Centre that such pigmentation may result from the presence of H_2S , forming iron sulfide compounds in the membrane, and that oxidation occurs rapidly in the presence of air and coloration is lost. These eggs were taken from the deepest tows in regions of low oxygen concentration. Within a few meters of these depths oxygen depletion occurs and oxidative processes by sulfate reduction take place. H_2S could diffuse

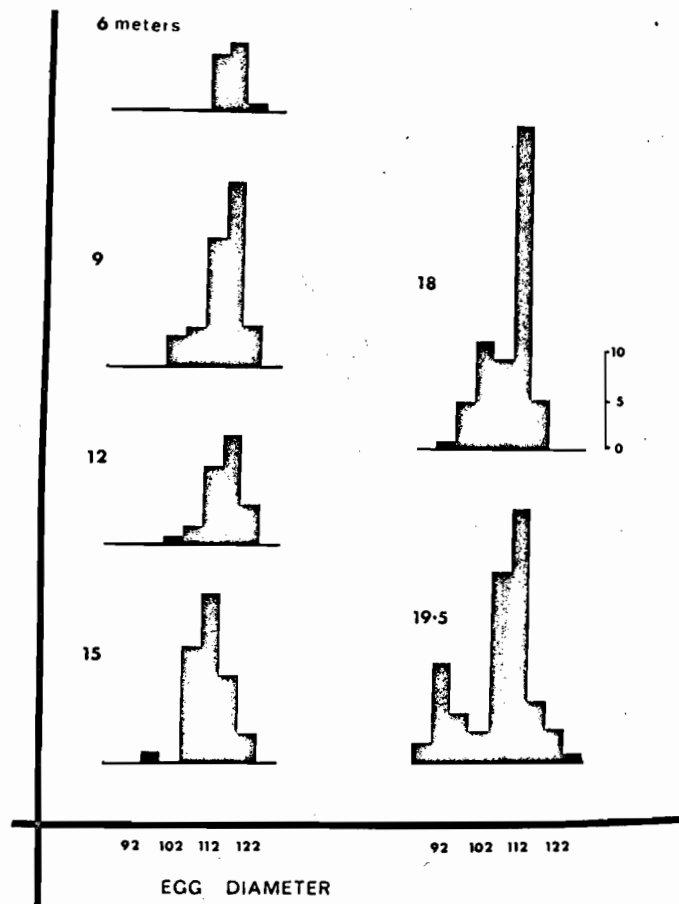


Fig. 9. Frequency distribution of egg diameters in hauls from various depths in the Outer Basin.

upwards into the sampled layers. Nikolski (1963) states that such coloration is inversely proportional to oxygen concentration, but it may in fact be related to H_2S . The low oxygen concentration at these depths may be critical to development, however. Distorted development of the blastodisc prior to epiboly was observed in 73% of the eggs under 100 e.p.u. in the 18 and 19.5 meter tows, and few (17%) were found beyond stage two. Oxygen concentration must therefore become critical in the region of 2 ml/l (see Table X for sigma-t and oxygen values in the Outer Basin).

The range in egg sizes found in the Ogac Lake samples is greater than that found elsewhere (Table XI). Variations in egg diameter produced by differences in water temperatures have been observed by several investigators (e.g. Wheatland 1956, Rass 1936, Fish 1928). This variable effects changes in egg diameter just prior to or at the time of fertilization (Fish, 1928). However the order of the differences produced by temperature are not sufficient to account for the variation found in the Ogac Lake samples. Salinity differences do not account for the differences in egg diameter since in both small and large eggs the egg is closely pressed against the vitelline membrane. The bimodal nature of the egg diameter distribution is curious. Bimodalism would not be caused by a continuous environmental variable. It is suggested, therefore, that the differences in egg diameter are established prior to laying of the eggs. In freshwater fishes the feeding conditions, size, and growth rate of the adult appear to influence egg

Table X. Hydrographic data for the Outer Basin, June 20, 1957.

Oxygen decline with depth was essentially the same
in 1962.

DEPTH (meters)	TEMP. (°C)	SALINITY (‰)	OXYGEN (ml/l)	SIGMA-t
2.5	2.83	22.4	8.92	17.94
5	2.05	22.3	8.57	(17.88)
8	0.68	24.1	7.36	19.37
12	2.02	26.7	5.67	21.44
16	2.96	27.8	2.65	22.30
19.5	3.05	28.2	1.71	22.69

Table XI. Range in diameters of developing eggs of Gadus morhua from various areas.

LOCATION	EGG DIAMETERS (mm)	REFERENCE
Barents Sea	1.13 - 1.63	Rass (1936)
West Greenland	1.37 - 1.65	M.S.C. collections
Halifax Hbr.	1.12 - 1.55	McKenzie (1940)
Gulf St. Lawrence	1.15 - 1.50	Dannevig (1919)
Grand Banks	1.15 - 1.40	Fish (1928)
Labrador Current	1.35 - 1.55	" "
Ogac Lake	1.23 - 1.80	

diameter (Brown, 1957), but this has not been noted in marine fishes.

Meristic characters Taning (1946) has shown that the influence of environmental factors on several meristic characters including vertebral number and the number of rays in the second dorsal fin occurs during the egg development period. He considers only certain stages to be influenced. Vertebral number may be influenced by the environment during the first two-thirds of the incubation period in cod; the number of dorsal fin rays may be subject to environmental factors for a somewhat longer period. The use of these meristic characters as a key to races of cod is well known. Vertebral numbers reflect the temperature at which development takes place, and this together with some genetic differences produces characteristic vertebral numbers for various races and populations. The range in developmental temperatures to which the Ogac Lake eggs are subject is somewhat greater than 7°C . This range is probably greater than that encountered by most oceanic populations. Other factors which may influence vertebral number such as salinity, carbon dioxide, light intensity and duration, and oxygen (Lindsey, 1962) are also more variable in Ogac Lake. The vertebral number of the Ogac Lake cod varies over a range of 3 figures (52 - 54). Most of Schmidt's (1931) figures include ranges of 4 to 5 figures. The low variability of the Ogac Lake figures probably reflects the lack of mixing with other populations and a well

inbred population. At any rate, the data suggest that genetic variability rather than the environment is more important in determining meristic characters of cod. Possibly the meristic counts of the Ogac Lake cod reflect those of the first inhabitants of the lake. The vertebral number and second dorsal rays number of the Ogac Lake cod are closer to those of the Greenland and Iceland populations than to those of Labrador and Newfoundland (Table XII).

DISCUSSION

The population of Gadus morhua in Ogac Lake is unique in several aspects. Most striking is the great variability of growth rates, and particularly the maintenance of a very high growth rate by some individuals in this very poor environment. Maturity is attained at an unusually large size in females, and apparently a large proportion of the population never matures. The wide variation in diameters of developing eggs, and the bimodal distribution of egg diameters are also curious phenomena.

Brown (1957) discusses the 'size hierarchy effect', a kind of 'peck order' in fishes. In any brood of trout raised under the same environmental conditions, and with an excess of food available, certain individuals establish a dominance over others with respect to feeding and growth. The actual size of the largest fish from a brood depends on the time that dominance is established and how effectively this is done; once dominance is established by certain fish, growth or feeding is inhibited in the smaller fish, possibly through stress-produced

Table XII. Vertebral and Second Dorsal Ray numbers of various populations of Atlantic cod. Port Burwell numbers are from Vladykov (1933) and Arctic Biological Station data; all other numbers from Schmidt (1931).

LOCATION	VERTEBRAE	D ₂
Port Burwell	54.90	21.00
N. Newfoundland	55.31	20.52
Belle Isle	55.46	20.86
S. E. Newfoundland	54.91	20.48
Gaspé	53.58	19.96
W. Greenland	53.60	20.32 ¹
S. Greenland	53.42	20.01
E. Greenland	53.14	20.04
W. Iceland	52.29	19.51
E. Iceland	53.26	19.94
Ogac Lake	53.14	19.40

¹ West Greenland D₂ counts of Hansen (1949) include several areas with averages less than 20.

ACTH. When dominant individuals are removed other previously slower growing fish take their place. The normal variability of growth rates within cod populations is not surprising; Brown's hierarchial effect may be responsible for this degree of variability. Nikolski (1963) discusses the work of Poliakov (1959) who showed in pond experiments with carp that when feeding conditions are impoverished, there occurs a reduction in growth rate, and also an increase in the variability of growth. Increased variability of growth under poor feeding conditions has not been noted in natural populations. Certainly nothing of the order of variability found in the Ogac Lake population has been observed. Perhaps some degree of increased variability does occur as Poliakov's experiments suggest, but one would expect this to occur through the lowering of the lower limits of growth. The extremely low growth rates of some of the cod in Ogac Lake are understandable; what has to be explained in this situation is not the very low growth rates of some individuals, but the fact that the maximum rate of growth is not only maintained but appears to have been greatly increased. For this to occur, the first inhabitants of the lake must have had the potential for the high growth rates observed, and some factor must encourage high growth rates.

Cannibalism must exert a very strong selective pressure for high growth rates. It was suggested above that this factor is responsible for the rapid shift upwards in the observed

lower limits of growth between ages eleven and twelve. Slow growing cod that are subject to cannibalism for 9 to 12 years suffer virtually 100% mortality by the end of this time. Faster growing individuals, on the other hand, are subject to the high mortality due to cannibalism for only 3 to 5 years, and will have a much lower mortality rate.

Spawning is initiated at a very high length, and at this time in the history of the population is restricted to the faster growing fish. The population structure (Fig. 10) as it is now favors maintenance of a very high growth rate at least by some individuals despite the very poor feeding conditions.

Even in the presence of the selective pressure exerted by cannibalism, however, the high growth rates and high length of first spawning could occur only if the first inhabitants possessed the potential for these factors. A landlocked population of Gadus morhua on Kilden Island in the Barents Sea, for example, is described as "small" (Zhadin and Gerd, 1963). Populations of lake trout in the Northwest Territories which are confined to small lakes, and in which cannibalism occurs, do not have increased growth rates or notably greater variation in growth (L. Johnson, personal communication). It seems improbable that the Ogac Lake cod could be derived from the Northern Labrador stocks which have a maximum length of 70 cms. at age 10 (101 cms. for the Ogac Lake cod) and which spawn at an average length of less than 50 cms. (May, MS 1966). The West Greenland populations, however, have an average length

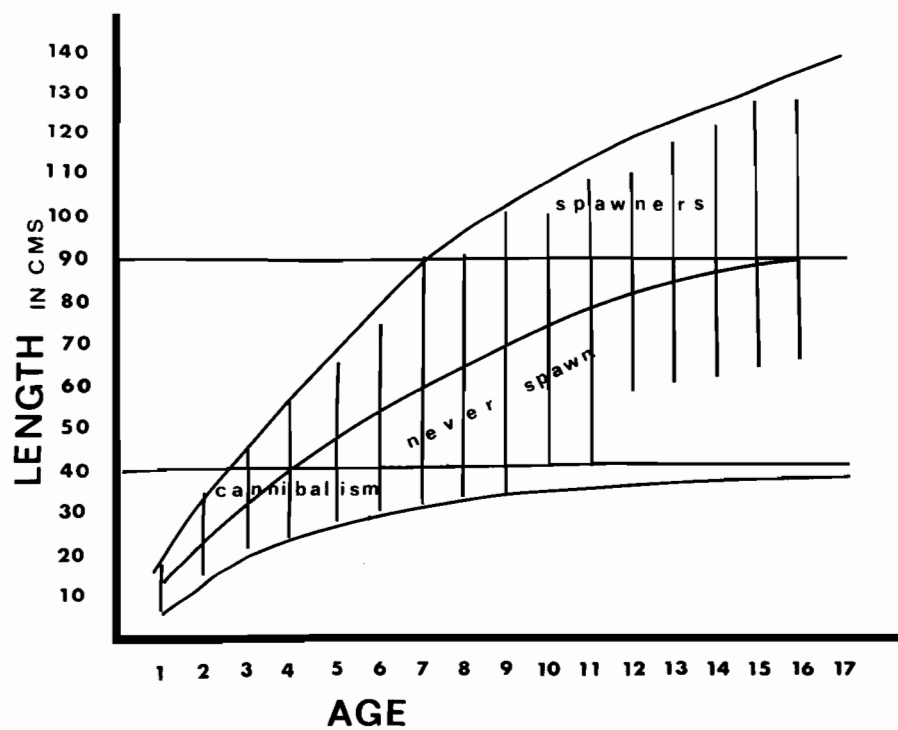


Fig. 10. Population structure showing lengths cannibalized, lengths of spawners (females), and the portion of the population never spawning. Upper and lower limits of growth are smoothed out; vertical lines show observed lengths of fish.

as high as 90 cms. at 10 years of age, and spawn at average lengths within 70 to 85 cms. (Hansen, 1949). If the first inhabitants of Ogac Lake had a very high growth rate and high length of first spawning, then the selective pressure of cannibalism would be sufficient to maintain these, and perhaps increase them somewhat. Environmental conditions and the size hierarchy effect would prevent attainment of high growth rates by the whole population.

The meristic characters of the Ogac Lake population suggest affinity with the West Greenland populations rather than with the Labrador cod. Larval drift is virtually impossible from the coast of Labrador since the Labrador Current will take eggs and larvae south. Stations by Hansen (1955, 1956) in July and August show increasing numbers of larvae from the coast of Greenland to 60° W (63° N), the most westerly stations taken. Poulsen (1960, 1961) and Hansen (1962) raise the question of the fate of these larvae; are they lost, or do they get a chance to settle on the Greenland Banks or coast of Labrador? Conceivably these might drift into Frobisher Bay. Surface temperatures in the latter part of the summer in the Canadian Current in this area are above the critical 1.8°C (Dunbar, 1951). Tidal inflows could carry the larvae into Ogac Lake where temperatures are favorable for further development and the attainment of demersal habit which occurs at about three months of age (Hansen, 1949). Spawning in West Greenland occurs in May and June. From this argument, the population might not in fact be relict. On the other hand, temperatures and circulation would be even more

favorable in those periods when Atlantic water influence was stronger on the western side of Davis Strait and weaker on the eastern side than at present. Adults might have migrated westward into the Frobisher Bay area during such a period, and entered the lake.

Whether the differences in egg diameters have any relationship to the growth rates can only be surmised. The relationship of egg diameter to final size of fishes is not clear. Larger egg size has been found by some investigators to produce a larger larva, and this size advantage may be maintained (Brown, 1957). It was suggested above that the variation in egg diameters is established before spawning. A curious bimodal distribution in egg diameters was observed. The whole situation may be more complicated than has been proposed.

SUMMARY

1. Cod in Ogac Lake are limited to depths less than 20 meters because of oxygen depletion at greater depths, and occupy a bottom area of approximately one square kilometer.

2. The population is estimated at about 10,000 fish of lengths greater than 20 to 25 cms., and 500 fish greater than 60 cms. in length.

3. Ages were determined from the examination of otoliths, and the growth of some individuals was back-calculated. The variability in growth rates is greater than that of any oceanic

population, the slowest growing individuals reaching a length of only 40 cms. at age 11, and the fastest growing individuals reaching a length of 109 cms. at this age. Growth curves of individual fish range from asymptotic to linear, and sometimes show alternately increasing and decreasing growth rates. .

4. No year-class dominance is observed. This is attributed to favorable hydrographic conditions in the egg and larval stages, and to control exercised through cannibalism.

5. Feeding conditions are poor, the main constituent of the diet being sea urchins. Above 50 cms. in length, smaller cod are important in the diet. This cannibalism imposes a high mortality on slow growing fish. Of the order of 3500 cod between the lengths 20 and 40 cms. are eaten each year.

6. Maturation occurs at unusually high lengths, 85 to 90 cms., in females, and at a length of 60 to 70 cms. in males. Apparently a large proportion of the population never spawns.

7. The spawning period in 1962 was from the latter half of May to the first half of July. Spawning is believed to be initiated in response to light. Hatching of larvae coincides with the reproductive cycle of the dominant copepod in the lake.

8. The range in diameters of developing eggs is greater than that of oceanic populations. A curious bimodalism in the frequency distribution of egg diameters is noted.

9. Variation in meristic characters (vertebral number and number of second dorsal fin rays) is principally genetic,

the wide range of the environmental variables having little influence.

10. The causes of the variation in growth rate and the maintenance of a very high growth rate by some individuals in a very poor environment are discussed. It is proposed that the first inhabitants came from the Greenland stock in which growth rates are similar to those of the faster growing Ogac Lake cod, and in which maturity is attained at a fairly high length, and not from the Labrador stock of cod in which growth rates are low and maturity is attained at low lengths. Meristic characters also suggest an affinity with the Greenland stock. It is supposed that cannibalism exerts a pressure for high growth rates, but that the very poor feeding conditions prevent general attainment of high growth rates.

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