## SHORT TITLE

BIOLOGY AND FISHERY OF LABRADOR COD

# BIOLOGY AND FISHERY OF ATLANTIC COD (*Gadus morhua morhua* L.) FROM LABRADOR

by

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## PREFACE

The basic life history of northwest Atlantic cod is relatively well known over most of its range. The Labrador area, where the species approaches its North American northern limit, is an exception. Occasional collections were made from the area during 1948 to 1958 by the St. John's Biological Station of the Fisheries Research Board of Canada. Larger and more widespread collections were made from 1959 to 1964. These provided the basis for descriptions of some aspects of life history and population characteristics for the first time, and descriptions of others in more detail than formerly. These are examined in relation to knowledge of the species in other areas.

Profound changes have occurred in the Labrador commercial fishery in recent years, in particular the development of an offshore fishery to huge proportions by 1960-64. Responses of the species to this upset in its equilibrium are described.

The findings in each major aspect of the study are discussed under each subject heading. Biology of Atlantic cod in general and previous knowledge for the Labrador area in particular are reviewed in a general introduction. Present findings are integrated into an overall description for the area in a summary and conclusions section at the end. Data are presented in figures, rather than tables, wherever possible.

# 1. INTRODUCTION

The presence of great quantities of cod along much of the North American eastern seaboard was a significant factor in the early settlement and economy of the area. European fishing fleets first appeared before 1510 (Innis, 1954). Cod has always been the single most important species in the northwest Atlantic fisheries. From 1960-64 it accounted for about 50% of the landings of all species (including shellfish), averaging about 1.3 million metric tons (almost 3 billion pounds) annually. Cod accounts for more than 90% of the landings from Labrador.

Because of its great commercial importance, in the northeast Atlantic as well as the northwest, the species has received a good deal of scientific attention. Wise (1963) gives a bibliography of 1020 titles to 1959, and disclaims complete coverage of the literature, particularly that of Russia and Scandinavia. Research was given particular impetus in the northeast Atlantic by the formation of the International Council for the Exploration of the Sea in 1899, and in the northwest Atlantic by formation of the International Commission for the Northwest Atlantic Fisheries in 1949. The area covered by the latter, with statistical Subareas and Divisions, is shown in Fig. 1. The present study is primarily concerned with the coastal and offshore areas of Labrador (Subarea 2, Divisions 2G, 2H and 2J).

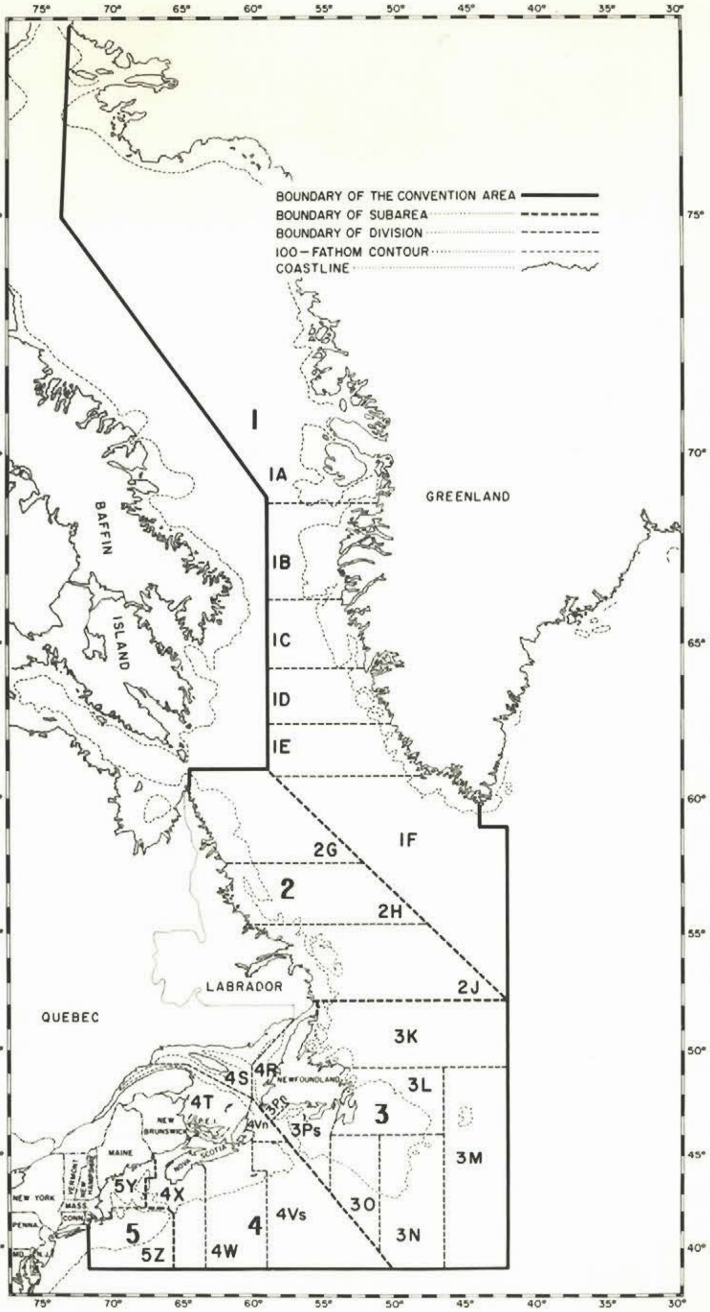

Figure 1. Map of the ICNAF area showing statistical Subareas and Divisions.

While the general life history of the species is known throughout most of its range, some areas have received scant attention. In particular, quantitative descriptions of the population characteristics necessary to scientific management of the fisheries (i.e. recruitment, growth and mortality - and their interrelations) are often lacking. In a recent ICNAF assessment of some northwest Atlantic fisheries, based on information to 1958, no long term predictions for the Labrador codfishery were possible because of lack of essential data (Beverton and Hodder, editors, 1962). Thus the objectives of the present study were:

(1) a general survey of life history and ecology of Labrador cod, on a quantitative basis where possible, and with particular reference to those aspects related to fisheries management, and

(2) an examination of population characteristics for changes due to fishing.

The following brief outline of cod distribution and life history, with emphasis on present knowledge for Labrador, serves as general background for the study. Aspects of particular relevance are treated in more detail in the appropriate sections.

The synonymy of the species is reviewed by Svetovidov (1948), Cohen (1959) and Wise (1961). Confusion as to the proper scientific name has resulted from Linnaeus' description of the species under two names on the same page

(p. 252) of the *Systema Natura* (10th edition, 1758), i.e. *Gadus callarias* from the European Seas and Baltic, and *Gadus morhua* from European Seas only. Though *callarias* takes precedence on the page, *morhua* was assigned in 1956 as the official specific name by the International Commission on Zoological Nomenclature (Official List of Species Names in Zoology, Species Number 1079). Svetovidov (1948) regards the Atlantic and Baltic cod as subspecies, naming the former *Gadus morhua morhua* and the latter *Gadus morhua callarias*. Much of the early literature on Atlantic cod uses the specific name *callarias* or the erroneous variant *morrhua*.

In the northeast Atlantic the range of Atlantic cod includes southern East Greenland and Iceland, extending northward to Novaya Zemlya and Spitzbergen (at least to 77°N) and southward to the northern Bay of Biscay (Svetovidov, 1948, Bigelow and Schroeder, 1953). In the northwest Atlantic it reaches latitude 73°N in West Greenland (Hansen, 1949, 1954), latitude 63°N in deep water north of Frobisher Bay (Templeman, 1960), occurs in Ungava Bay, exists as a relict stock in Ogac Lake, Frobisher Bay (McLaren, MS, 1961) and extends southward to Cape Hatteras (Bigelow and Schroeder, 1953). Trans-Labrador Sea and trans-Atlantic movements of cod are rare, though a few are recorded (Templeman, 1962; Gulland and Williamson, 1962). They are distributed in greatest quantity between the surface and about 200 fathoms, depending on area and season, but occasionally occur at least to 300 fathoms (May and Williamson, MS, 1962). The adults are usually demersal, but may move into surface waters at certain periods of the year (Templeman and Fleming, 1956).

Within the broader areas of their range cod are subdivided into a number of more or less well-defined stocks. The word is used in the sense ascribed by Templeman (1962) who regards a stock as a "recognizable unit in which most of the fish have a similar area-occupying and migratory pattern" along with unity of certain characters within itself. The word has often been used synonymously with "population", but Templeman (1962) refers to the latter as a group "occupying any defined area at a particular time". The terms are used in this sense throughout this study.

Fish stocks are usually recognized on the basis of differences in meristic characters (generally vertebral counts), physiology (growth rate, size at maturity) and from studies of migratory patterns based on returns of tagged individuals. Parasites are sometimes useful as "biological tags" (Templeman and Fleming, 1963). More recent methods include recognition of different patterns of otolith structure (Trout, 1957), paper chromatographic analysis of muscle proteins (Dannevig, 1956b) and serological analyses (Moller, 1963; Vrooman, 1964).

Present knowledge of stock division and general distribution in the ICNAF area is summarized by Templeman (1962), who lists eight separate stocks from the Labrador and Newfoundland areas alone, though some of these are ill-defined. On the basis of information available to that time the whole area from northern Labrador to the northern Grand Bank (ICNAF Subarea 2 plus Divisions 3K and 3L) was described as being inhabited by a single stock, termed the Labrador-Newfoundland stock, though the author pointed out that further subdivision would probably be indicated with increasing knowledge of the area.

Each of the many separate cod stocks on both sides of the Atlantic has its own peculiar characteristics. The following generalities are taken from Svetovidov (1948), Bigelow and Schroeder (1953) and Wise (1961), except as otherwise noted.

Adult cod may be found in temperatures from -1.6 (Thompson, 1943) to 16°C, though usually in the range 0 to 7 or 8°C. Spawning occurs once per year and is possible at temperatures from -1.1 to 12°C, though probably 2 to 6°C is more usual. Fecundity increases with size to 9 million eggs or more. The eggs are buoyant but may be distributed in intermediate depths. Hatching takes 15 days at 6°C to 43 days at 0°C. The upper lethal limit for developing eggs is 12°C (Bonnett, 1939) and in hatcheries only 25-50% hatch at 0°C (optimum hatching temperatures are 5 to 8°C). Newly hatched larvae float with the yolk sac upward for 2 days after hatching at 6°C (Bonnett, 1939); the yolk sac is absorbed within 6-12 days, depending on temperature.

First feeding is on small copepods and various crustacean larvae. The fry feed mainly on larger crustacea and small worms. Fish and benthic invertebrates assume increasing importance as food with increase in size. Bathypelagic fishes are often eaten, and smaller cod also occur in the diet. Adult cod are voracious feeders; among the more unusual items found in their stomachs are seabirds, pieces of old clothing, wood, rope and jewellery. Feeding is curtailed during the spawning season.

Size and age structure of various cod groups depends on the extent to which they are fished. Growth is extremely variable. The heaviest weight recorded appears to be 211¼ pounds (Bigelow and Schroeder, 1953) for a cod over 6 feet (6 ft. = 183 cm) in length. Storer (1858) reports a cod 251 cm. in length. The maximum age is given by Wise (1961) as 22, by Svetovidov (1948) as 24. Two specimens of age 26 were recorded in the present study. Size and age at maturity are variable. The youngest mature fish are age 2; the oldest immature fish age 15, depending on the area.

Some Atlantic cod stocks may undertake extensive seasonal migrations (Hansen, 1954; Jonsson, 1954; Rollefsen, 1954; Trout, 1957; Templeman, 1962; Jean, 1964). Others remain in relatively restricted areas (Hansen, 1949; Templeman, 1962). Seasonal migration is related to spawning, feeding and hydrographic influences.

The Labrador-Newfoundland cod stock (Templeman, 1962) occupies the area along the coasts of Labrador and northeast Newfoundland, extending southward to the northern Grand Bank. Within this very large area gradations in growth (Fleming, 1960; May et al, 1965) and size and age at maturity (Fleming, 1960) are known to occur. Specifically, size at maturity, age at maturity and average length and weight at age all decline from south to north. A similar south to north decline in average counts of circuli in the first year of cod scales was noted by Thompson (1943). On the other hand, vertebral counts are similar throughout the area (Thompson, 1943; Templeman, 1962). Tagging experiments (Thompson, 1943; Templeman and Fleming, 1962) have resulted in relatively few returns outside the area and period of tagging, but from Labrador taggings indicated a general summer dispersion southward in succeeding years along the Labrador coast and to the northeast Newfoundland coast, while northeast Newfoundland taggings indicated dispersion both south and north along the Newfoundland coast, though seldom north to Labrador. Combined with other experiments, a high degree of independence from neighbouring areas (Gulf of St. Lawrence in the west, and the southern Grand Bank) was displayed. The lack of more detailed data generally, and absence of well-defined hydrographic and physiographic barriers, have prevented further stock division in the area though such divisions almost certainly occur. Thus local depletion of fish through intensive fishing (Fleming, 1965) indicates some "localized" distribution within the Labrador-Newfoundland stock.

Seasonal distribution of the stock is discussed in general terms by Templeman (1962), and in detail for a portion of the northeast Newfoundland Shelf by Templeman and Fleming (1956) and for the Hamilton Inlet Bank area (ICNAF Division 2J) by Templeman and May (1965). In April-May, when most of the area is ice-covered, there is a large spawning and post-spawning concentration of cod on the southeast part of Hamilton Inlet Bank, largely in depths of 125 to 180 fathoms at temperatures of 2.5 to 3.1°C. The larger mature fish are in the greater depths. Early spring concentrations are also known to occur on the northeast Newfoundland Shelf (May and Wells, MS, 1964). Onshore movement begins in late May or early June, apparently a migration in the surface layers following the onshore spawning migration of capelin (Mallotus villosus). Time of appearance inshore is progressively later from south to north, extending from mid-June to early August. On arrival the cod are distributed in the surface layers and may often be seen in pursuit of capelin at the very surface. Movement is progressively deeper over the summer period of the inshore fishery, culminating in eventual return to the deep offshore spawning grounds in winter. On the northeast Newfoundland Shelf the oldest and largest fish may not fully complete the inshore movement, remaining in deep water 18-20 miles from shore (Templeman and Fleming, 1956).

Descriptions of food and feeding in the area are given by Popova (1962) and Templeman (1965a). The summer inshore diet consists mainly of capelin in early summer and squid (Illex illecebrosus) in late summer. In general the food spectrum is extremely wide. Popova (1962) lists twenty-two species of fish and more than seventy species of pelagic and bottom invertebrates (including Ctenophores, Coelenterates, Annelids, Molluscs, Crustacea, Chaetognaths and Echinoderms) from offshore collections during June-August. An important food item in areas of concentrated fishing by trawlers is the cod offal dumped overboard during processing (Templeman, 1965a).

Throughout its range the Labrador-Newfoundland cod stock inhabits the southward flowing waters of the Labrador current. Origins of the current and physical oceanography of the area are described by Iselin (1930), Smith, Soule and Mosby (1937), Dunbar (1951), Bailey and Hachey (1951), Hachey, Hermann and Bailey (1954) and in continuing reports of the International Ice Patrol (U.S. Treasury Department, Coast Guard Bulletins - from 1965 U.S. Coast Guard Oceanographic Reports). The Labrador Current as such originates south of the Davis Strait ridge where cold, southward-moving arctic water is joined by a greater volume of warmer water from West Greenland. Water of each type is recognizable as an "inner" and "outer" branch of the Labrador Current throughout the Labrador-northeast Newfoundland area. The inner colder portion covers the continental shelf from shore to about 100 fathoms. The influence of the warmer

West Greenland water is increasingly evident in the "slope water" beyond the 100-fathom contour. In vertical temperature sections in summer from the coast seaward the water of arctic origin is evident as a cold intermediate layer (0 to -1°C), very broad near the coast, becoming thinner and nearer the surface with increasing distance over the shelf (May <u>et al</u>, 1965). The volume of this cold central core decreases from north to south. Temperatures in the inner portion of the current are too low for continued presence of cod and they are distributed inshore in summer in the solar-warmed surface layers, and offshore in winter in the relatively warm slope water. The onshore migration in spring is apparently accomplished by vertical movement offshore where the cold layer is narrowest, and inshore movement in the surface layers (Templeman and Fleming, 1956). By late autumn the cold layer is sufficiently warmed and reduced in size to allow seaward migrating cod to pass downward through it (Templeman and Fleming, 1956).

## 2. THE FISHERY

### Early History

The beginnings of the Labrador codfishery are outlined by Black (1960). French vessels are known to have fished along the coast at least as early as the early 1700's. The French were restricted in the 1760's and a fishery based in the English West Country developed, so that by 1775 about 100 vessels took part. The English fleet declined during the Napoleonic Wars and was gradually replaced by a ship fishery based in Newfoundland. In 1823 the English fleet had declined to 15 vessels, while by 1825 the Newfoundland fleet had increased to about 250. Growth of the Newfoundland-based fishery was given added impetus by the British-French settlement in 1818 which ceded part of the Newfoundland coast to French fishermen. By this time also a shore-based Labrador fishery was established.

The fishery grew rapidly until the early 1900's and three categories of fishermen were recognized:

(1) Livyers - resident fishermen,

(2) Stationers - those who came from Newfoundland each summer and operated from shore bases,

(3) Floaters - Newfoundland fishermen who operated from fishing schooners.

Each group carried on the fishery from small open boats. The schooners were used only for storage of the catch and accomodation. No catch statistics are available for the early period of the fishery, but on the basis of figures given by Black (1960) for numbers of ships in the floater fishery, the catch must have been substantial even by modern standards. In the 1850's over 700 vessels were on the coast each summer, By 1908 the number had reached 1400 and operations had extended along the whole coast. The average catch per ship in the 1940's was of the order of 200 tons (metric, round fresh weight). On this basis the total catch would have approached at least 300 thousand tons annually.

The decline of the floater fishery was even more spectacular than its rise. The number of ships was reduced by one-half from 1910 to 1920. By 1955 the fleet had completely disappeared, due mainly to loss of traditional markets for the heavy salted "Labrador cure". Numbers of stationers also declined. Catch statistics are available from the 1930's (Fig. 2). The decline of the inshore fishery was interrupted only by a brief period of recovery toward the end of World War II, and reached a minimum in 1956. There has been a gradual buildup since then, including a minor revival of the floater fishery (43 vessels in 1963). The catch has doubled since 1956 but remains far below former levels.

## Development of the Offshore Fishery

The post-war development of fishing fleets by many European countries gave rise for the first time to an offshore fishery. These began fishing off Labrador in the early 1950's (Fig. 2). Catches by area, country and month are available from Statistical Bulletins of the International Commission for the Northwest Atlantic Fisheries (Vols. 1-14). Figures for 1952 and 1953 are doubtful as these were the early organizational years of statistical reporting. The fishery quickly reached a phenomenal level, almost $\frac{1}{4}$ million tons annually in 1961 and 1962, or 10 times the amount taken in the inshore fishery in those years. Between 1954 and 1961 the fishery as a whole increased twelvefold. From 1960 to 1964 15-20% of the annual cod catch in the northwest Atlantic came from Labrador (Fig. 2). Most of the Labrador catch is taken by France, Portugal, Spain and the USSR (Fig. 3B).

In the past the inshore fishery was carried on along the entire coast. Recently only the southern one-third of the coast (ICNAF Division 2J) has been fished to any great extent, with minor contributions from Eskimo communities further north. The offshore fishery also is almost entirely based on Hamilton Inlet Bank (Fig. 9), directly east of the southern part of the coast. Thus more than 90% of the annual catch is taken in Division 2J (Fig. 3A). Eskimos from the northern third of the coast have been resettled southward in recent years and in Division 2G the fisheries both inshore and offshore are negligible; in some years nonexistent.

The offshore fishery originally developed (1954-58) as a relatively small autumn fishery. Beginning in 1959, and with the appearance of a large Russian fleet in 1960 (Fig. 3B), fishing was extended throughout the year (Fig. 4). The autumn fishery increased and a new spring fishery quickly reached major proportions in spite of wide ice coverage in the area at this time. The spring fishery appears to be based largely on spawning and post-spawning concentrations on the southeastern edge of Hamilton Inlet Bank. By June the concentrations break up and begin to move inshore where they are fished in July and August, when the offshore fishery is at a minimum (Fig. 4). The autumn offshore fishery builds up as fish move away from shore toward the spawning area, being interrupted in winter because of bad weather and ice.

## Trends in Abundance

In view of the recent large expansion of the offshore fishery, and the fact that it operates on the same stock of fish later fished inshore, it is of interest to examine inshore catches in relation to effort expended to determine whether the large offshore fishery is having any effect. Unfortunately it is difficult to get a good measure of effort in the inshore fishery. At least four gears of varying efficiency are in wide use (codtrap, handline, longline and gillnet) and the fishery is effectively decentralized. The catch of each fishing crew (often by several gears) is salted and disposed of at the end of the season. The greater part of the catch is probably taken by codtraps but actual quantities taken by each gear are unknown. However numbers

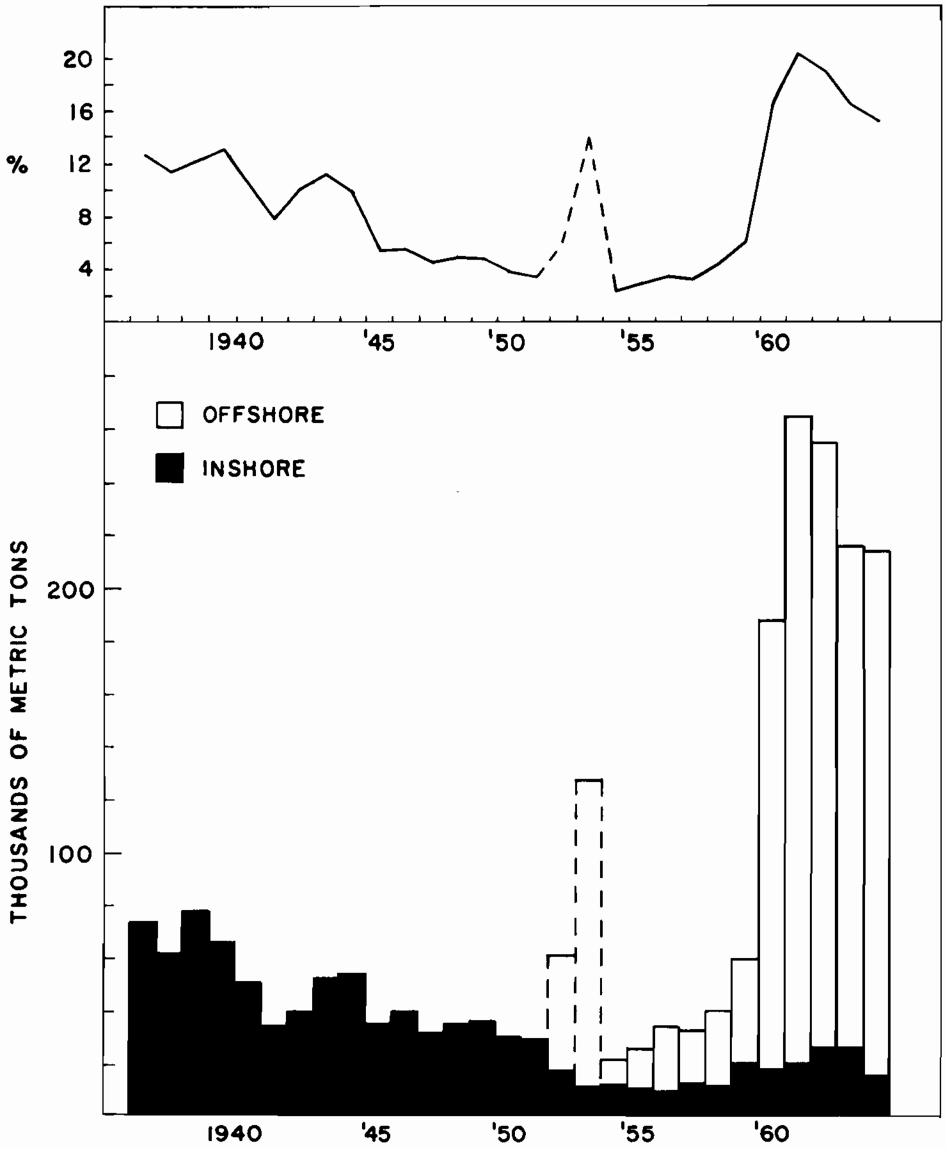

Figure 2. (Top). Relative contribution of cod landings from Labrador to total cod landings for the northwest Atlantic fishery. (Bottom). Inshore and offshore Labrador landings, 1936-64.

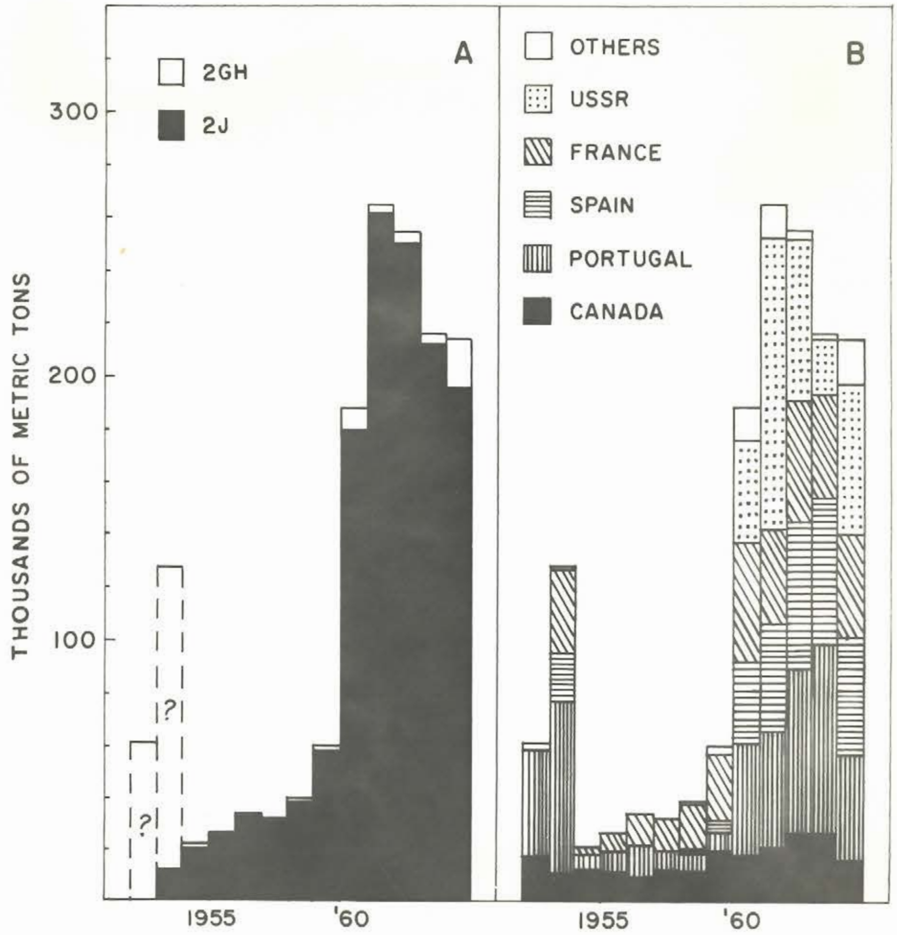

Figure 3. Labrador cod landings by ICNAF Division (A) and country (B), 1952-64.

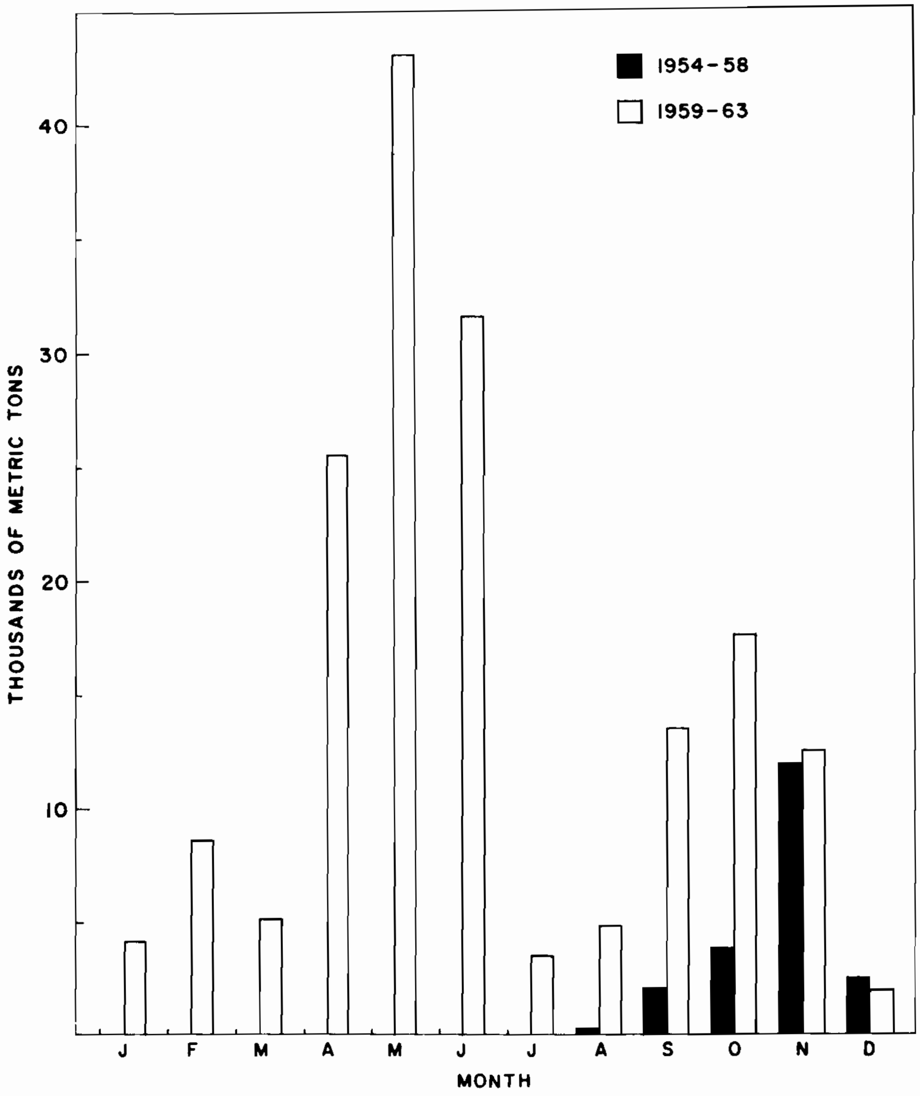

Figure 4. Monthly landings from the offshore fishery averaged for 1954-58 and 1959-63.

of men employed in fishing are known from the 1930's onward. Catch per man is not a good measure of effort since it does not take into account varying fishing practices and changes in fishing efficiency over the years. However if shore-based and ship-based fishermen are treated separately such changes may be regarded as minimal in Labrador over the period considered.

Statistics of the inshore fishery were obtained from the Annual Reports of the Newfoundland Fisheries Board from 1937 to 1948, and from files of the Canada Department of Fisheries (at St. John's, Nfld.) after 1948. Data for shore-based and ship-based fishermen are separable. Shore-based fishermen here include both those resident on the coast and summer migrants from the Island of Newfoundland, and for convenience are labelled together as stationers. Unfortunately the data are not directly comparable over the whole period. The area covered from 1937 to 1953 included the North Shore of the Strait of Belle Isle as well as the coast of Labrador proper. The effect is not serious as recent statistics indicate that landings from the former area account for less than 15% of the total. However the early figures are reported as "equivalents, light salted dry cure" in quintals (1 qtl. = 112 lbs). Most cod production from this area is "heavy salted wet cure". Conversion factors from one to the other have altered over the years and it is not certain which of several was used from 1937 to 1953. For rough comparability with recent data the landings in equivalent light salted dry quintals were converted to metric tons, round fresh weight, by applying the following modern standard conversions:

(1) Quintals to lbs ........................ x 112
(2) light salted dry to round fresh ........ x 4.88
(3) lbs to metric tons ..................... x 1/2204.6

Since cod from the Quebec North Shore and the Strait of Belle Isle belong to a different stock than those fished along the Labrador coast (Templeman, 1962) it is desirable to separate the statistics of the two fisheries. Landings have been reported separately since 1954 (ICNAF Statistical Bulletins, Vols. 3-14), and these were used in analysis of the fishery from that time.

The numbers of fishermen and total landings declined sharply during the early years of the second World War (Fig. 5). There was a brief recovery in 1943 and 1944 as the numbers of stationers increased, with a coincident increase in catch per man of both floaters and stationers. The numbers of floaters remained about the same during the mid-forties while stationers increased, but low catches per man from 1945 to 1947, and decreasing numbers of men after 1946 resulted in an overall downward trend in landings from 1945 to 1953. There is a general correspondence in the trends in catch per man of floaters and stationers. The low periods of 1940-41 and 1945-47 may be indicative of declined stock abundance, or simply lessened availability to the inshore fishery because of anomalies in fish distribution due to hydrographic conditions.

The 1954-64 period must be considered separately for reasons previously outlined. Thus the high levels of catch per man in the mid-fifties are not directly comparable with earlier data because of different area coverage and probable differences in conversion factors to round fresh landings. Landings and numbers of men reached their lowest levels in 1956 (Fig. 5). The floater fishery temporarily disappeared. Numbers of floaters were so low during the period 1954-59 (less than 50 men) that figures for catch per man have no meaning. The number of stationers has doubled since 1959 but their landings exhibit a downward trend from that time. Increased total landings in 1962 and 1963 were due to renewed participation in the fishery by floaters. The very pronounced decline in catch per man of stationers since 1959 and floaters since 1961 coincides exactly with the period of great increase in offshore fishing (Fig. 2).

Variations in catch per unit effort may be due to variations in fishing effort or to natural variations in stock abundance (or at least availability to the fishing gear). It was previously noted that some of the variation in catch per man may be due to decreased availability of cod to the inshore fishing areas. Thus catch per man was abnormally low in 1958, but cod catches and catch per unit effort were low in this year throughout the Newfoundland and Labrador areas (Hodder, 1965). This has been considered to be due to unusually warm temperatures and lack of cold water barriers, allowing cod to be less concentrated and thus less easily fished than normally (Hodder, 1965). A difference in availability, rather than a decline in abundance, is indicated. On the other hand general oceanic warming in the northwest Atlantic since the early 1900's is considered responsible for increased cod fisheries off West Greenland (Jensen, 1939) and increased abundance of several typically warmer-water forms in other areas (Templeman and Fleming, 1953; Taylor, Bigelow and Graham, 1957).

Increased fishing will result in proportional increases in catch only as long as there are reserves of stock to draw from (Ricker, 1958). At higher effort levels catch per unit effort will decline due to a real decline in stock abundance as a result of fishing. Prior to 1954, with the possible exception of 1952 and 1953, the inshore fishery alone was responsible for removals from the available stock (Fig. 2). Using catch per unit effort as a relative measure of abundance the data were examined to determine the relation of effort to catch per effort for this period. It is obvious (Fig. 5) that numbers of men cannot be used directly as a measure of effort since floaters fish more efficiently, probably due to their greater mobility and extensive use of traps rather than less efficient gears. A plot of catch per floater against catch per stationer (Fig. 6A) revealed

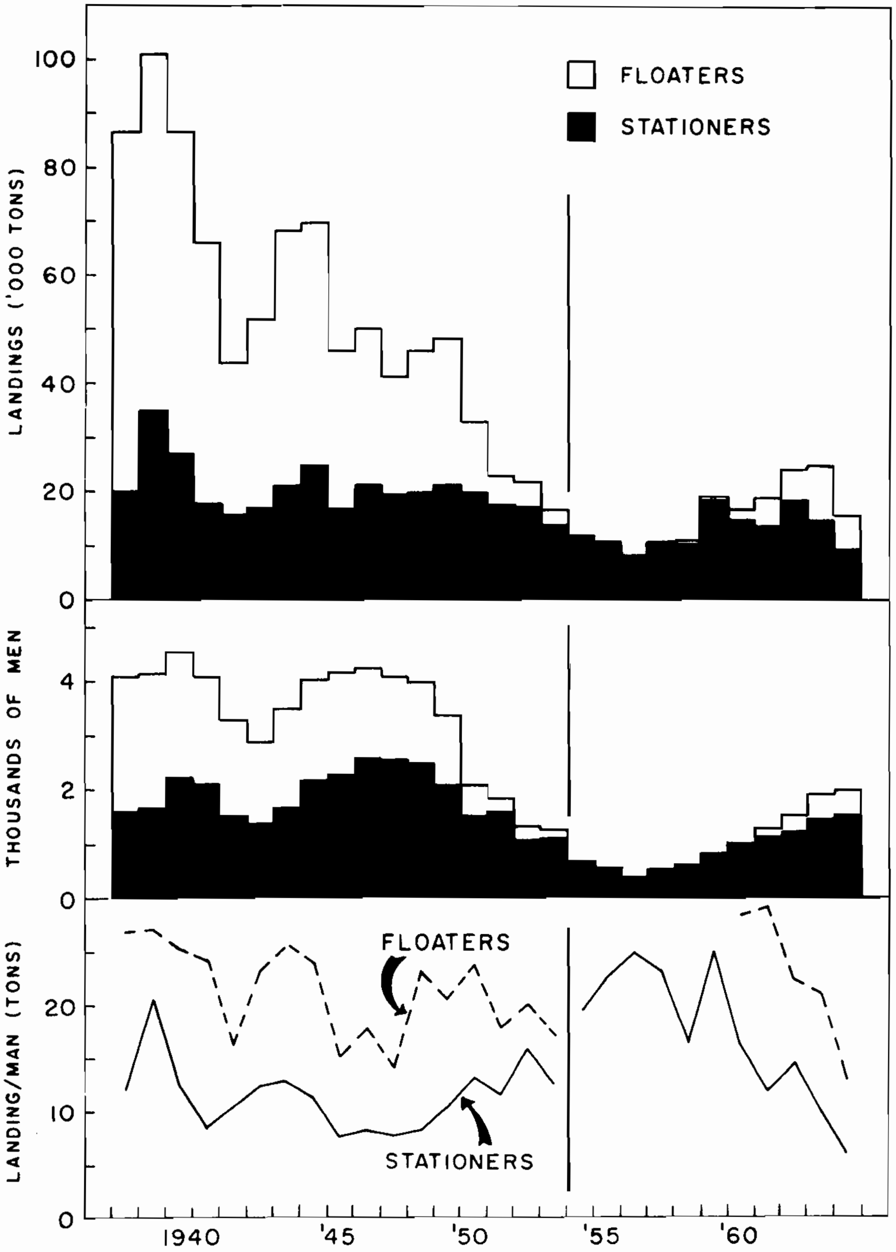

Figure 5. Landings, effort and landing per unit effort in the inshore fishery, 1937-64.

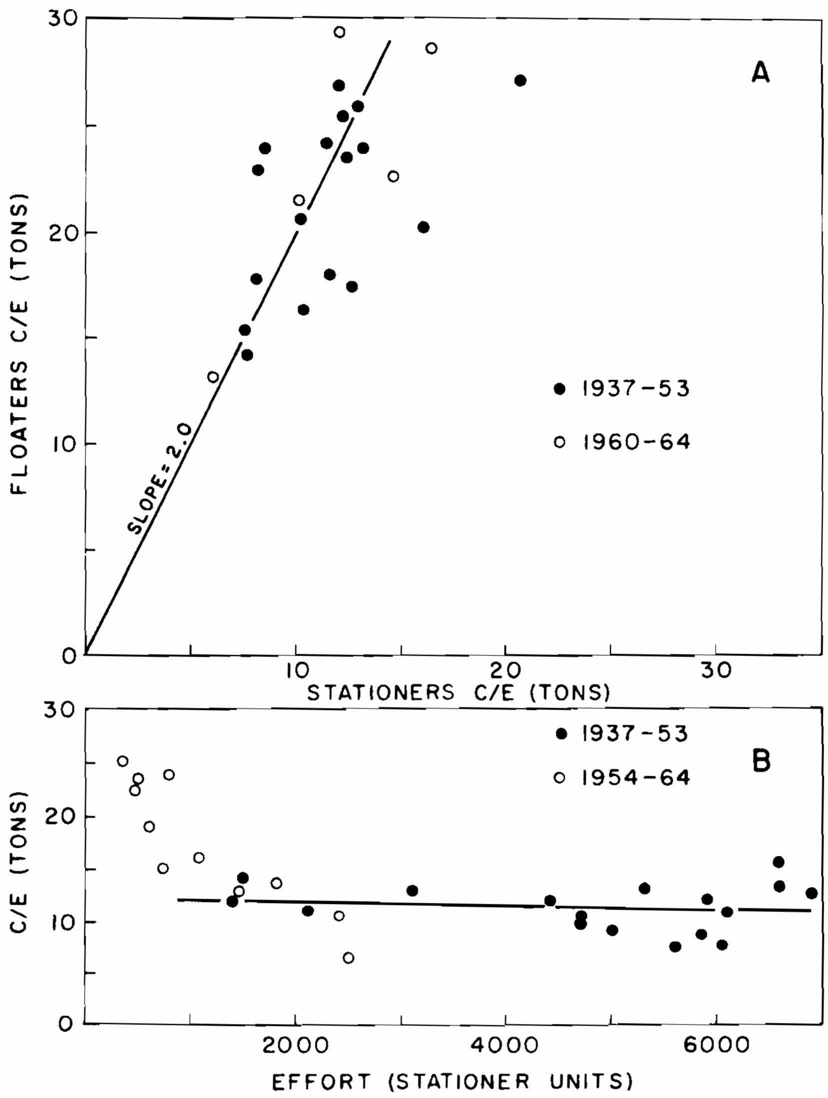

Figure 6. A. Relation between catch per man of floaters and stationers. B. Catch per unit effort versus effort in the inshore Labrador fishery.

that floaters were on the average twice as efficient. Total effort was thus estimated in stationer units by applying this factor, i.e.

Total effort (stationer units) = number of stationers + 2 (number of floaters).

Dividing these values into annual catch gave catch per stationer unit for each year. A plot of catch per stationer unit against number of units (Fig. 6B) showed no significant correlation for the period 1937-53 ( $r = -0.16$, $.50 > P > .40$). It may be concluded that even at the highest levels of effort during this period the inshore fishery had little or no effect on overall stock abundance, and that variations in abundance were due to "natural" causes.

The pattern for 1954-64 is quite different (Fig. 6B), producing a significant negative correlation ( $r = -0.90$, $P < .01$). In view of the foregoing it is most unlikely that this is a real effect of increased inshore effort. In fact three of the cluster of four high values are for the years 1955-57; the four lowest values are for 1961-64. It is most likely that the increase in offshore fishing since 1959 has resulted in decreased stock abundance, reflected as a much lower catch per man inshore. A similar pattern of decline in catch per man inshore on the east and northeast coasts of Newfoundland, coincident with increased participation in the fisheries by trawlers, has been reported by Hodder (1965).

It should be emphasized that decline in stock abundance is not necessarily harmful, except as it affects the economics of the fishery. In fact Beverton (1965) observes that fairly intense fishing would be necessary to attain maximum sustained yield in the Labrador area, but that decline in catch per unit effort as fishing increased would, for economic reasons, restrict exploitation to levels below that required. To date there is no indication of this. Catch per unit effort in the offshore fishery shows a general increase from 1954-63 (Hodder, 1965) as the fishermen have become increasingly familiar with seasonal cod distribution and devoted increasing effort to the spring spawning concentrations. There is however a slight decline in catch per unit effort in autumn.

## 3. COLLECTIONS

Prior to 1959 sporadic collections are available, almost entirely from the offshore fishing grounds. From 1959 to 1964 collections were made on an annual basis (except 1961) both inshore and offshore. These were designed to give the widest possible coverage for each ICNAF Division within the limits of available ship time. Inshore this meant sampling from a number of fishing communities along the coast (Fig. 7). Offshore it involved coverage of the depth range inhabited by cod as well as area coverage. The procedure for examination of samples was essentially the same both inshore and offshore. Usually a large random sample of the catch would be measured (fork length) and a smaller random sample selected from these for more detailed examination. This included collection of otoliths and scales for age reading, recording of sex and stage of maturity, and sometimes weight and girth.

It was soon discovered that random samples were not entirely adequate for correlations involving length as the independent variable since the smallest and largest sizes in the catches naturally occurred in very small numbers in the samples. In order to obtain adequate coverage over the whole length range extra fish were selected for detailed examination from the small and large size categories (in addition to those in these categories which had already been selected in the random sample). These were kept separate and identified as category samples.

Beginning in 1959 inshore collections were made by the MV Parr and MV Marinus during the fishing season (mainly July-August) at a number of villages along the coast (Fig. 7). In northern areas where no commercial fishery existed collections were made using a commercial gear (jigger). An extra effort was made to obtain pre-commercial sizes by fishing with hook and line in shallow water (1-2 fathoms). Because of the wide area to be covered in the short fishing season it was usually possible to sample only from the major gear in use in each area. This was the codtrap in Division 2J and jigger in areas to the north. The collections are summarized for each area and gear in Table 1.

There is no offshore Canadian commercial fishery in the area; all offshore collections were made by research vessels of the St. John's Biological Station. All were from otter trawls except two samples taken by longline in 1953. Most of the material prior to 1959 was collected by the MV Investigator II and from 1959 by the MV A. T. Cameron. In each case the otter trawl codend was either lined or covered with small-meshed netting to prevent the escape of small fish. The vessels always towed along a depth contour, attempting to hold the same depth in any one set. From 1959 onwards the usual procedure was to fish a series of depths on lines of stations across the offshore banks, from the shallowest depths available to that where the cod catch became very small. These were usually about 60 or 80 fathoms, then 100, 125, 150, 175 and occasionally 200 fathoms and deeper. A few spot samples are available from research vessel cruises for other purposes and species. The collections are listed for each month and area in Table 2, and are summarized by area and season in Figs. 8 and 9, with the exception of the small collections from the Baffin Island - Ungava Bay area. In late August, 1959, fishing was carried on in a series of depths off Baffin Island at each latitude line from 62°N to 67°N. The northern limit of cod was at 63°N where two specimens were taken in 125 fathoms and fourteen in 150-160 fathoms (Templeman, 1960). At 62°N, off the mouth of Frobisher Bay, a single specimen was taken in 155 fathoms and four in 200 fathoms. Numbers of cod taken in 7 tows at depths of 28 to 200 fathoms in Ungava Bay varied from 3 to 64.

Because of limitations in available time and working space at inshore fishing premises no special procedures could be followed to ensure random sampling of inshore catches. That adopted was simply to start at one corner of a pile of cod and measure until the desired number was obtained or the whole of a small catch had been measured. Where possible, measurements were obtained from the catches of several fishermen. The consistency of results between fishermen, neighbouring areas and even years was sufficient to give confidence that sampling was effectively random. Offshore the catch on deck was stratified into basket lots according to the order of filling, and baskets of cod for length measurement selected at random from these lots. The procedure is described in detail by May and Hodder (in press). Experience has shown that measurements from 300 to 400 cod give an adequate representation of length distribution at each sampling station, i.e. when this many or more are caught.

From the sample for length measurement the sub-sample for detailed examination was usually drawn at proportions of 1 in 10 up to 1 in 3 by use of series of pre-selected random numbers unknown to the measurer. Otoliths and scales were stored between pieces of blotting paper in a coin envelope for each fish. Common data for the sample (date, gear, etc.) plus the data for each fish (length, maturity stage, etc.) were recorded on the front of the envelope.

Otolith collections and detailed examination were made for more than 20,000 fish in all, equally divided inshore and offshore. Data analysis was greatly facilitated by transfer to IBM cards, machine sorting, and preliminary tabulation by IBM 402 and 403 accounting machines.

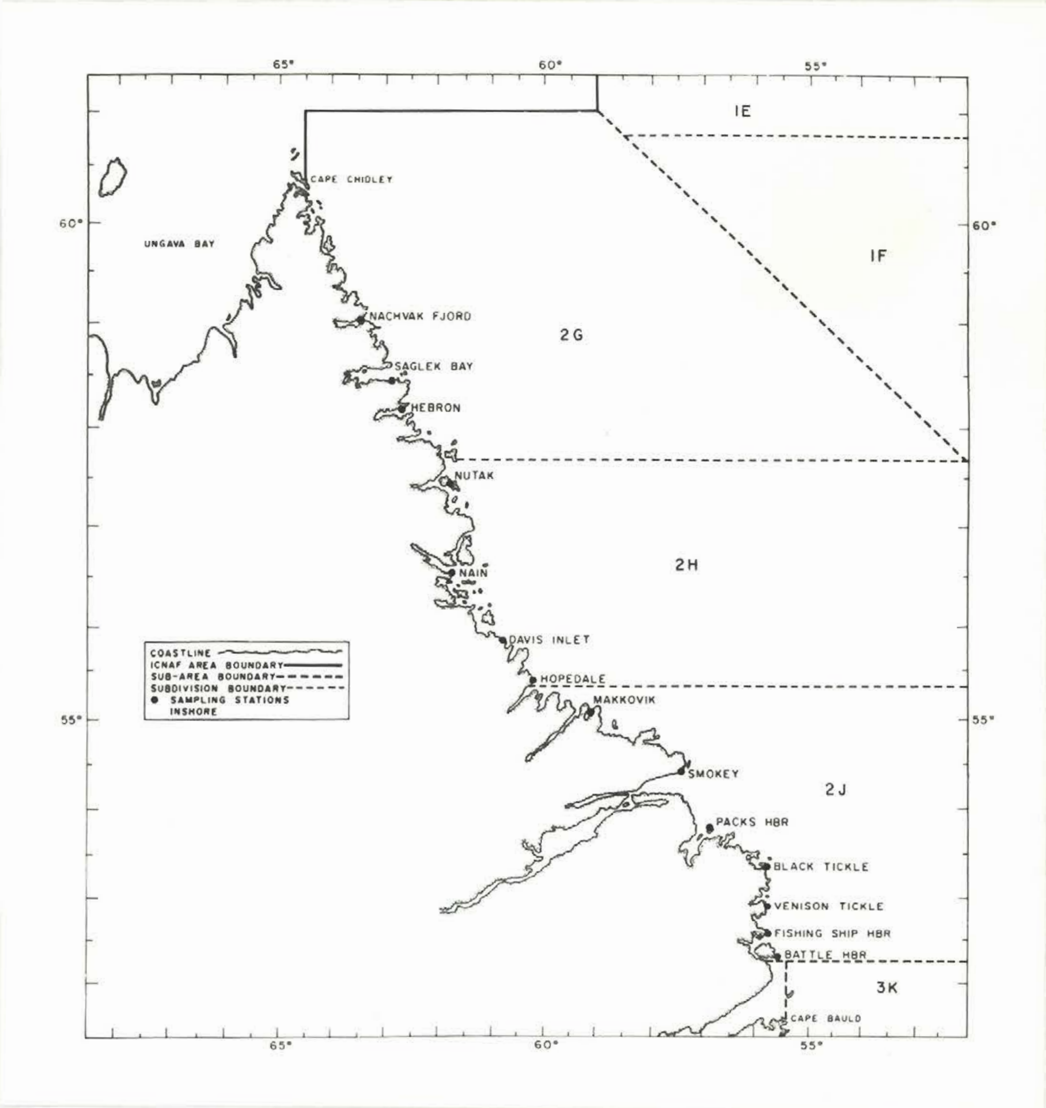

Figure 7. Coast of Labrador showing inshore sampling stations.

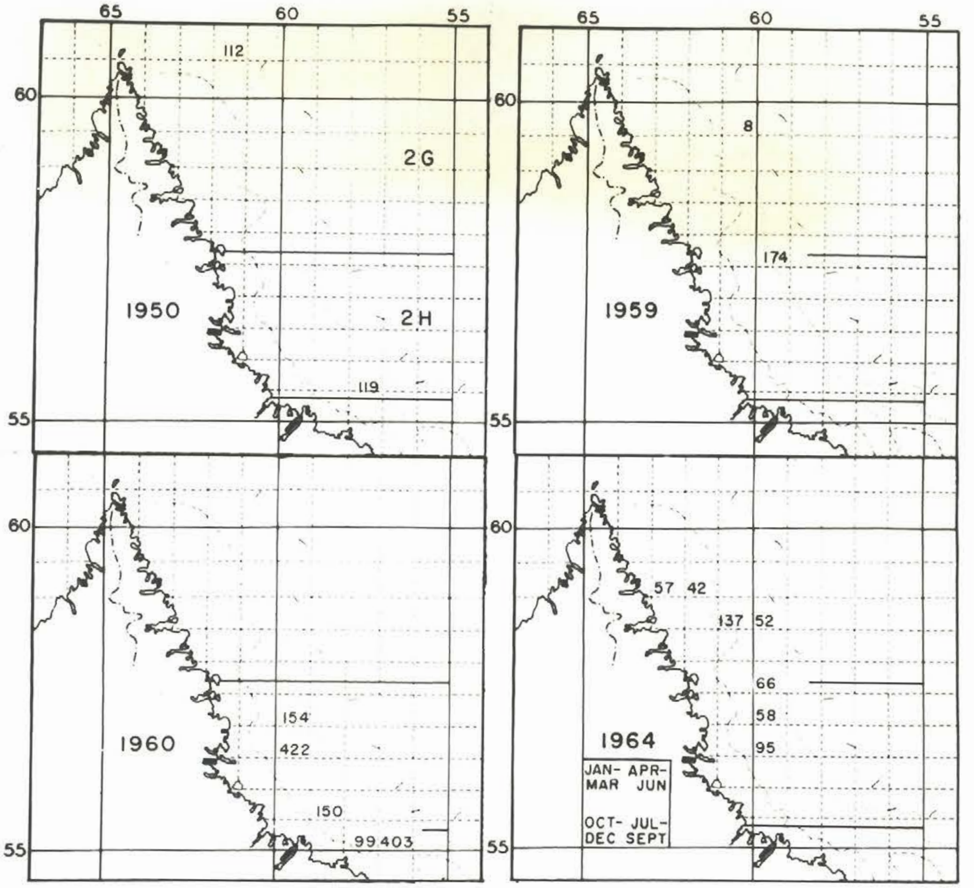

Figure 8. Cod otolith collections offshore from ICNAF Divisions 2G and 2H, 1950-64, shown for each season and combined into areas of ½-degree latitude by 1-degree longtitude.

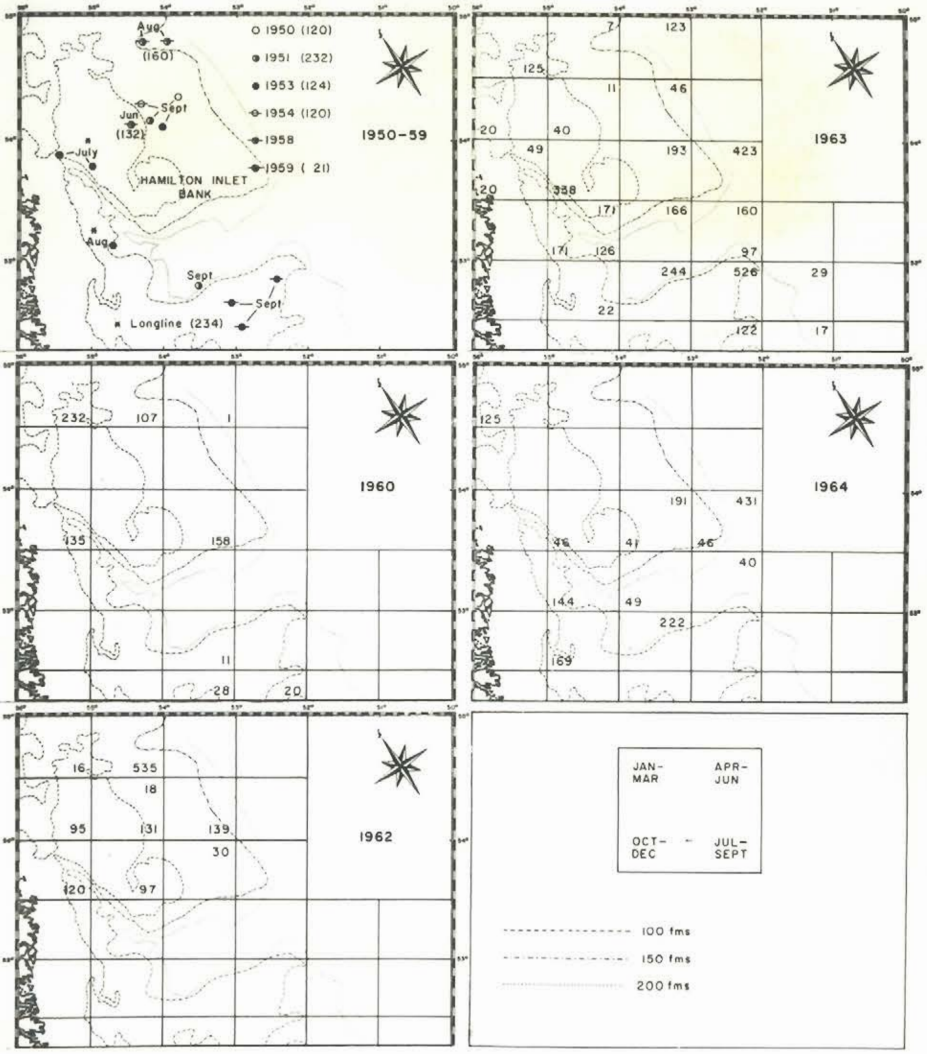

Figure 9. Cod otolith collections offshore from ICNAF Division 2J, 1950-64, shown for each season, and from 1960-64 combined into areas of ½-degree latitude by 1-degree longtitude.

## 4. SIZE AND AGE COMPOSITION

### Ageing Technique

Determination of age from skeletal structures is almost universally applied in fisheries biology. It is dependent on changes in growth rate or metabolism during the year, these changes resulting in periodic markings within the skeletal parts. The structures most often employed have been scales and otoliths, though fin rays and spines, vertebrae and various bones of the skull and pectoral girdle have also been used (Menon, 1950; Gulland, 1958).

It was early assumed that regular alternations in the internal structure of fish scales bore some relation to age. The scale method of ageing received earliest attention and Van Oosten (1929) reviews descriptions by the seventeenth century microscopists. It gained wide acceptance after the critical studies of Hoffbauer (1898, 1900). Graham (1929) reviews the early literature. The method was probably first applied to ageing of cod by Thomson (1904) and was used by Thompson (1943) for cod of the Newfoundland-Labrador area. The scale method has now been replaced for many species, including cod, by age determination from otoliths. Scales become increasingly difficult to interpret at the older ages (Rollefsen, 1933; Fleming, 1960) and annual markings may be missing at the edges of the scales of old fish (Dannevig, 1933; Saetersdal, 1953). Otoliths have been used in all recent cod growth studies (Ancellin, 1953; Rojo, 1955;

Figueras, 1957, 1963a, 1963b; Fleming, 1960; Kohler, 1964).

In the present study cod ages were determined from otoliths. All otoliths were read by the author. Cod contain 2 pairs of otoliths (Parker, 1884); on each side a large sagitta within the sacculus of the inner ear and a much smaller astericus in a posterior saccular diverticulum. The sagitta (sacculotolith) is that used for ageing.

The otoliths were stored dry until read, and prepared for reading by cutting with a sharp scalpel through the depression in a prominent ridge on the medial (convex) surface. Each half was mounted in plasticine with the cut surface well above the plasticine block, and moistened with a 50% ethanol-water solution. The otoliths were read by transmitted light directed toward the concave surface at about 30° to the horizontal, shading the cut surface with the edge of a scalpel, and using a binocular stereoscopic microscope at 15x magnification. The magnification was sometimes increased to 20 or 25 to distinguish narrowly spaced zones in old fish.

In cross-section and under transmitted light the cod otolith exhibits alternating bands of dark and light appearance (Fig. 10). The dark (opaque) zones contain inorganic calcium salts plus the protein conchiolin (Dannevig, 1956a) and are associated with periods of fast growth (Fleming, 1960). The light (translucent or hyaline) zones contain only inorganic calcium and are associated with periods of slow growth. Age determination depends on the formation of one zone of each type in each year. On very rare occasions the otolith pair from the same specimen may indicate different ages (May, 1964). Error may be avoided by examining the pair for obvious size differences or by mounting both otoliths. Examination of scales will assist in determining the true age.

## Validity of Ageing Technique

The validity of any ageing technique may be tested in 5 ways:

(1) the structure is examined, the fish released, and the structure examined again on recapture. This is limited to scales and possibly fin rays and is more suited to the laboratory than the field. A useful adjunct is the marking of scales by injecting fish with various lead salts before they are released (Hiyama and Ichikawa, 1952; Fry *et al*, 1960).

(2) The appearance of the edge of the structure in question is examined throughout the year to determine whether changes occur on an annual basis.

(3) Interpretation of periodic markings in skeletal structures may be checked against age assignation to modes in the length distribution (Petersen's method). The principles underlying this method are reviewed by Parrish (1956).

Figure 10. Cross-section of cod otolith, age 4, photographed under transmitted light. The dorsal edge is at the right.

(4) Year-classes which turn up consistently abundant or scarce in samples over a series of years provide evidence that periodic markings are formed annually.

(5) One structure may be tested against another whose validity has previously been determined by one of the direct methods.

Many authors have accepted past validation of skeletal ageing techniques as sufficient, and have applied those techniques to widely different areas and different species without further validity tests. The importance of a critical approach to methods of age determination, in order to produce comparable results from different authors and areas, has been stressed by Dannevig (1933) and Saetersdal (1953). Determination of age from skeletal structures usually involves interpretation of zone patterns rather than straightforward counting because of the occasional formation of secondary or "check" zones due to temporary slowing or cessation of growth. Validity studies provide the criteria for such interpretation.

Previous validity studies of otolith ageing of northwest Atlantic cod have been reported by Fleming (1960) based on otolith edge appearance for Newfoundland area cod, Kohler (1964) using methods (2) to (4) above in the southwestern Gulf of St. Lawrence, Williamson (MS, 1965) and May (1965) for southern Grand Bank cod using the edge appearance method and Petersen's method respectively. The only previous data in this connection from Labrador were those of Fleming (1960) who reported on samples taken in July and August.

The present material offers several avenues of approach for testing the validity of otolith ages. Considering first the appearance of the otolith edge, material covering 8 consecutive months was obtained by combining collections from Division 2J for 1958-64. This was entirely offshore material except for July, when no offshore data were available. Collections from codtraps inshore in Division 2J were made almost entirely during the latter half of July and these were combined with the offshore data to complete the picture. Type of edge deposit (opaque or hyaline) was recorded as a routine in all age reading. The percentage of otoliths having opaque edge deposits is plotted for each month in Fig. 11A. A few fish show opaque edges as early as April, and they are present in more than 80% of the material from September to November. It is evident that only one opaque (and one hyaline) zone is formed each year. Age was estimated by counting hyaline zones. Beginning in September some fish show a narrow hyaline zone at the otolith edge. This is regarded as the beginning of the next annual hyaline zone, but would not be counted for ageing purposes until January 1 of the next year. A few otoliths, even in November, exhibit no opaque material at the otolith edge. These are invariably from very old fish, which typically have very much reduced opaque zones. These are so narrow in fact that they often appear as seemingly paper-thin separations between broad hyaline zones, and are almost impossible to recognize unless followed by a hyaline zone. This is typical in old mature fish and follows Rollefsen's (1933) description of "spawning zones".

The dorsal edge of cod otoliths is thinner than the ventral (Fig. 10) and it is on this pointed (in cross-section) edge that opaque material first occurs. It is not until several months later that it appears all round the otolith. Opaque edge deposits occur much sooner in the year in young fish. Considering the material from Division 2J in August, when about 50% of the sample shows opaque edges (Fig. 11B), the opaque edge deposits by age range from 100% of the fish at age 1 to zero at age 14. When these values are plotted the result is a double reverse sigmoid. The interruption between ages 5 and 6 is due to the attainment of maturity by many fish at these ages (Section 7). As a result of the spawning process the onset of body growth and formation of the opaque zone are delayed, resulting in wider hyaline zones than in immature fish, again conforming to Rollefsen's (1933) description.

Cod from Labrador grow very slowly (May _et al_, 1965). Thus Petersen's method, which requires recognition of separate modes in length frequency distributions, cannot be applied for much of the data since length distributions

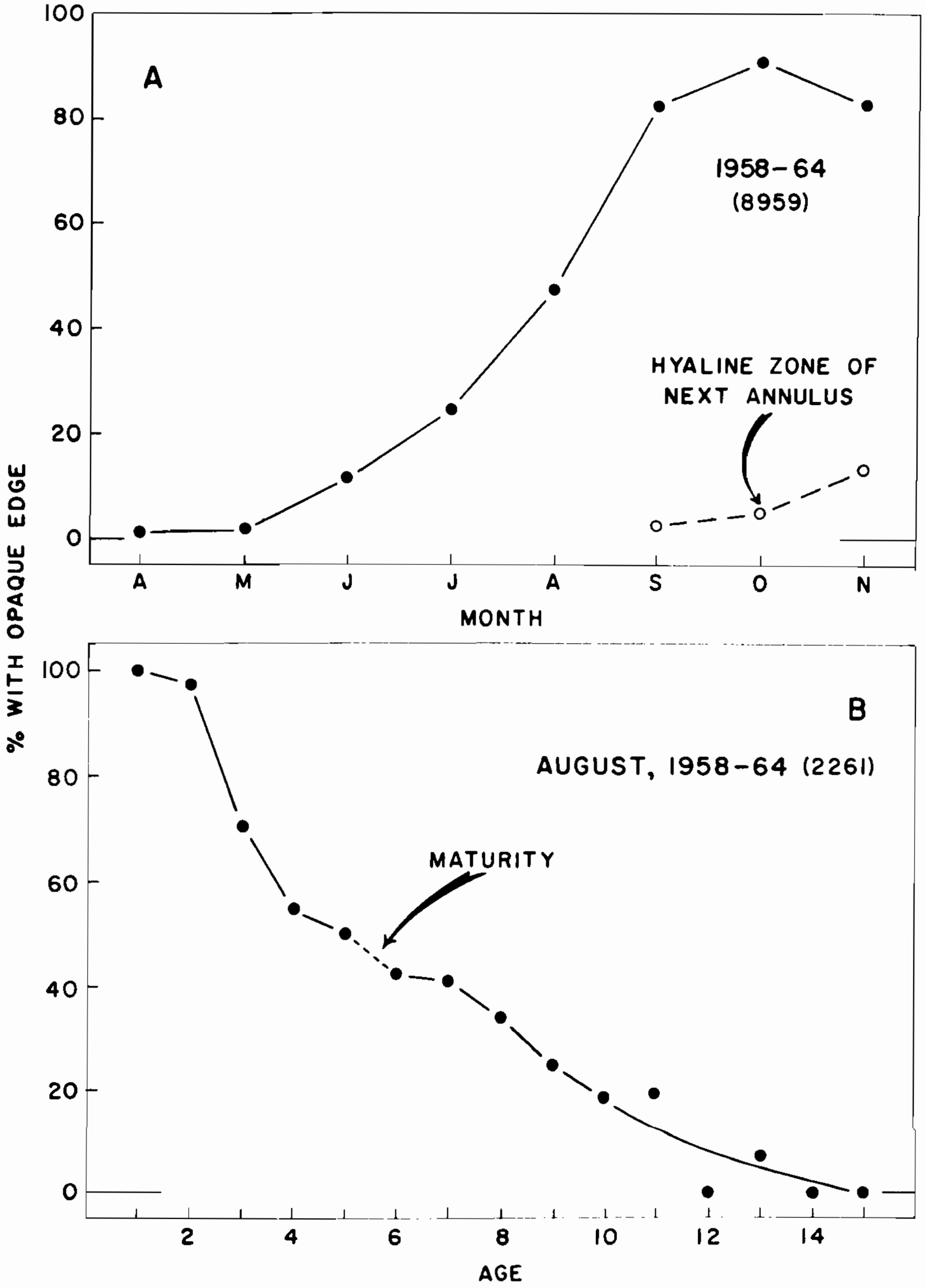

Figure 11. A. Monthly incidence of opaque edge deposits on otoliths from Division 2J. B. Incidence of opaque edge deposits by age for August. Numbers of fish are in brackets.

for each age overlap widely and catch length distributions tend to be unimodal. It can however be applied to the special collections of small fish inshore and to data from certain offshore collections where small fish were plentiful. Examination of length distributions of small cod taken inshore in Division 2J in August of 1959 to 1963 (Fig. 12A) reveals two fairly consistent modes, one at 13-16 cm and the other varying between 19-22 cm. Otoliths of fish in the first mode typically show an opaque central area, one narrow hyaline zone and a substantial amount of opaque material at the otolith edge. These were regarded as having completed one year of growth plus a good deal of the second year's growth. The next mode should thus consist of fish which have completed 2 years of life, and otolith ages agree with this interpretation. Modes in the offshore data of Fig. 12B are ill-defined, but extension of the method would result in age assignations to each mode as shown in the figure. These are in substantial agreement with age interpretation from otoliths, though it will be noted that because of overlap of the length distributions of each age group the method would be of little use beyond age 5. It must be emphasized that Petersen's method is a population rather than an individual technique and would never be used alone unless no other method of age determination were available. When it is the only technique available its usefulness may be greatly extended by statistical treatment of the data so that the

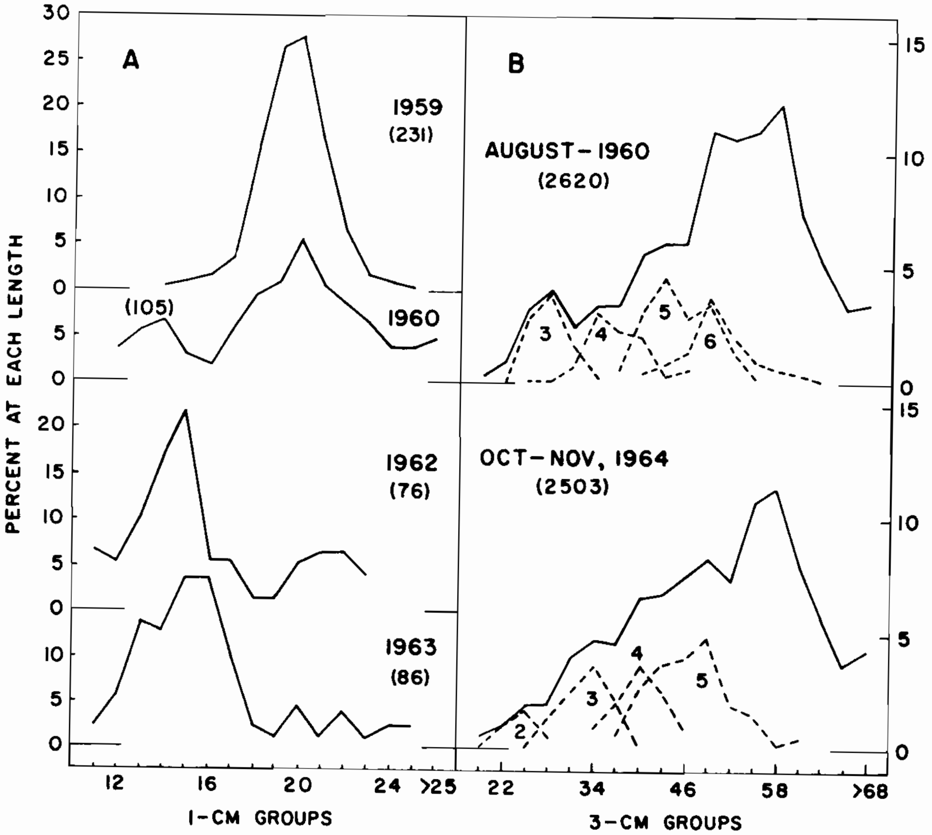

Figure 12. A. Length distributions of small cod taken inshore in Division 2J in August of each of the years indicated. B. Selected length distributions from research vessel catches offshore in Division 2J, showing also length distributions of the youngest age groups. Numbers of fish are in brackets

polymodal curve may be broken down into its unimodal constituents (Buchanan-Wollaston and Hodgson, 1939; Harding; 1949; Cassie, 1950, 1963).

Finally, the consistent trends in abundance or scarcity of certain year-classes in yearly age distributions (Figs. 14-18) give further evidence of the annual nature of zone formation in the otoliths. Occasional formation of an extra (secondary or check) zone does occur. These must be interpreted as such on the basis of their appearance and size, and a knowledge of the typical zone pattern of the area.

## Trends in Size and Age Composition

The inshore sampling was designed with the express purpose of determining size and age compositions of the commercial catches by various gears. This is relatively simple along the Labrador coast since the fish are highly concentrated in a narrow depth range close to shore, and merely requires the presence of observers to sample from the landed catch. Determination of the size and age structure of the population which is being fished is a more difficult proposition. Commercial gears are selective for large sizes and in Labrador scarcely any fish below 40 cm in length and age 5 occur in the catches.

The best means of approaching the size and age structure of the population is by means of research vessels fishing with small meshed otter trawls when the population is distributed offshore. Before this can be done some knowledge of population distribution must be available. Statistics of a national commercial fishery are of inestimable value in this respect, and it is unfortunate that there is no Canadian fishery in the area. Efforts by Canadian research vessels during the 1950's were limited to collections for other purposes, but more recently have concentrated on the necessary first step of working out seasonal distribution by area and depth. The present knowledge for Hamilton Inlet Bank (Division 2J) is recorded by Templeman and May (1965).

If distributional surveys are sufficiently complete, information on the size and age structure of the population emerges as a by-product. Templeman and May (1965) have shown that there is size segregation by depth during the spawning season on Hamilton Inlet Bank. This distributional pattern also extends to other areas and other seasons (Fig. 13). The relative numbers in various size groups may also change quite markedly in corresponding depths over fairly short distances (compare distributions at 125 and 120 fathoms in Fig. 13B and 13C). Templeman and May (1965) have noted that catches at a single position can alter by as much as 15 times (weight) over a period as short as 5 days. It is obvious that determination of the population age and size structure on even a qualitative basis requires systematic collections over a wide range of area and depth. Several offshore surveys have been sufficiently extensive to allow some generalizations to be made.

Age and length distributions off southern Labrador (mainly Hamilton Inlet Bank) are shown in Fig. 14, and selected distributions for areas to the north in Fig. 15. In some instances length distributions for corresponding periods were available from commercial catches of various nations (Table 3) and these are also shown for comparison. Year-to-year consistency within the research vessel data (Fig. 14) and the general close correspondence of length distributions from catches of commercial vessels (excluding small sizes because of the larger mesh sizes - Table 3) justify the assumption that the research vessel length distributions are representative of the population structure, exclusive of ages 1 and 2 which were never taken in appreciable numbers. The only significant discrepancy between the research vessel and commercial data was in the 1962 distributions of Fig. 14, and here the commercial sample was small. Otherwise the agreement is surprisingly good considering that the commercial samples may have been taken at quite different positions within the areas (exact positions are not available) and that ordinary commercial practise is to fish in areas and depths where largest sizes are found.

The research vessel length distributions have been adjusted upward to total catch by the vessel in each period (numbers in brackets in the figures). This was accomplished by the simple expedient of multiplying each sample frequency by the reciprocal of the fraction sampled. This was seldom more than 5 and in most cases the whole catch was measured. The age distributions were similarly adjusted by constructing an "age-length key" using the otolith samples from each of the distributions shown. An analogous procedure is described by Ketchen (1950). A portion of the key for Division 2J, 1963 (Table 4) illustrates the method. Adjustments were unnecessary for the 1959 data shown in Fig. 15 since otoliths were collected from all fish caught. The commercial length distributions are of actual numbers of fish measured (numbers in brackets, Figs. 14 and 15).

From the consistent dominance of certain year-classes in the distributions of Figs. 14 and 15, it is evident that wide variations in survival occur. These are generally considered in many fish species to be due to annual variations in mortality during the first year of life, probably at egg and larval stages. It would appear that survival of new year-classes was particularly good in 1950, 1953, 1957, and 1959.

Length and age distributions from the inshore commercial fishery in Divisions 2G, 2H and 2J are presented in Figs. 16, 17 and 18 respectively. The pattern of year-class dominance is essentially the same as indicated by the offshore distributions, with a time lag which may be partly, though not entirely (see next section) due to inshore gear selection. From 1959 to 1962 the fishery in each area was dependent on relatively old fish. The pattern altered in 1963 as the 1957 year-class entered the fishery in huge numbers in all areas. To this point there was no substantial difference in the catch length distributions by the two major gears in use (Fig. 18). In 1964 the pattern reverted to its previous form in the northern areas (Figs. 16 and 17). In Division 2J the 1964 pattern in the jigger fishery was similar to that of 1963, though the 1957 year-class was much reduced and older year-classes relatively more prominent than in 1963, while in the trap fishery the 1957 year-class remained at its 1963 level and the 1959 year-class entered in force. These changes in 1964 were accompanied by a significant reduction in catches and catch per unit effort (Fig. 5). An examination of possible causes for these changes inshore follows the next section.

## Size Structure of Population and Catch

It was earlier noted that for such comparative data as were available, the size distribution of cod taken in offshore commercial catches was similar to that expected from examination of population length distributions, allowing for the greater mesh sizes in commercial nets and the commercial practise of fishing largest sizes when practicable. It is of interest to examine size distribution of fish taken inshore from the same viewpoint.

Estimates of population size distribution are available from Division 2J from offshore research vessel surveys in 1960, 1962, 1963 and 1964. In 1960 and 1962 the size distributions are of that part of the population left behind after inshore migration had taken place (August surveys). In 1963 and 1964 they represent the population prior to spring migration. The data thus afford means to determine whether the existing inshore and offshore divisions of the population had similar size distributions in summer of 1960 and 1962, and whether the inshore size distributions in 1963 and 1964 were similar to those indicated by surveys of the offshore area prior to spring migration.

Direct comparisons are not possible since no direct measure of population size structure can be obtained from the catches by inshore gears. However it is possible to predict what should have been the size distribution caught by one of the inshore gears. Boulanger (MS, 1962) gives selection data for a codtrap having a 4½-inch nylon back, i.e. percent of fish entering the trap which are retained by this particular mesh size, assuming that most escapement of small sizes occurs through the back. A symmetrical sigmoid, with 50% retention at 48 cm, fitted by eye, described the selection curve extremely well (Fig. 19A). The curve does not strictly apply to codtraps used in the Labrador fishery since these have mesh sizes at the back of 3 to 4 inches and are constructed of tarred cotton. Application

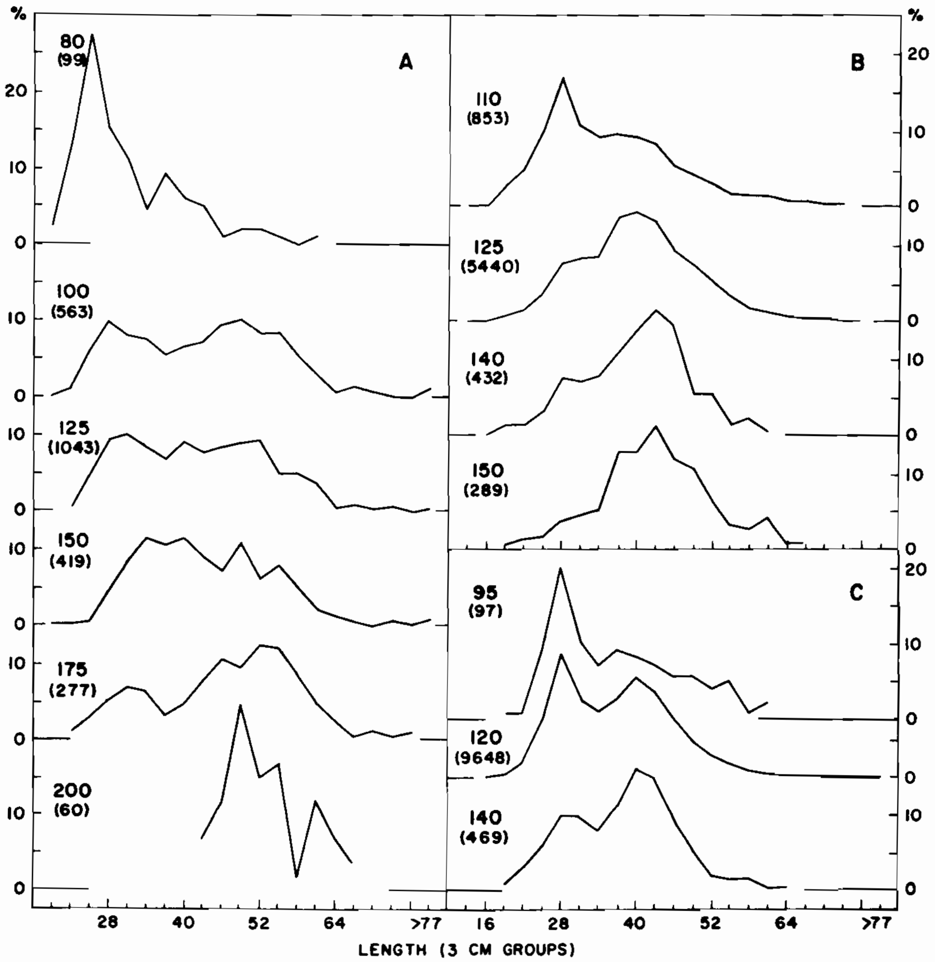

Figure 13. Cod length distributions by depth.
A. Division 2H, August, 1960 - combination of data from series of stations at 55°30'N and 57°N.
B. Division 2J, August, 1962 - 54°50'N.
C. Division 2J, August, 1962 - 54°N.
Numbers of fish are in brackets. Depths are in fathoms.

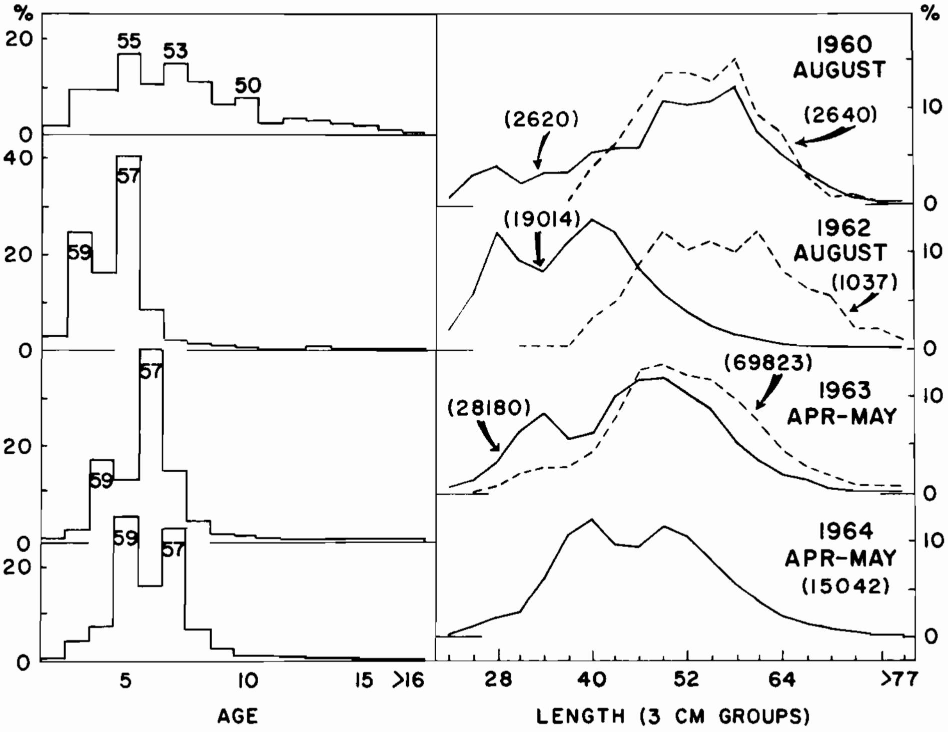

Figure 14. Adjusted age and length distributions of research vessel catches from southern Labrador. Available comparable data from commercial fishing vessels are also shown (broken curves). Numbers of fish are in brackets.

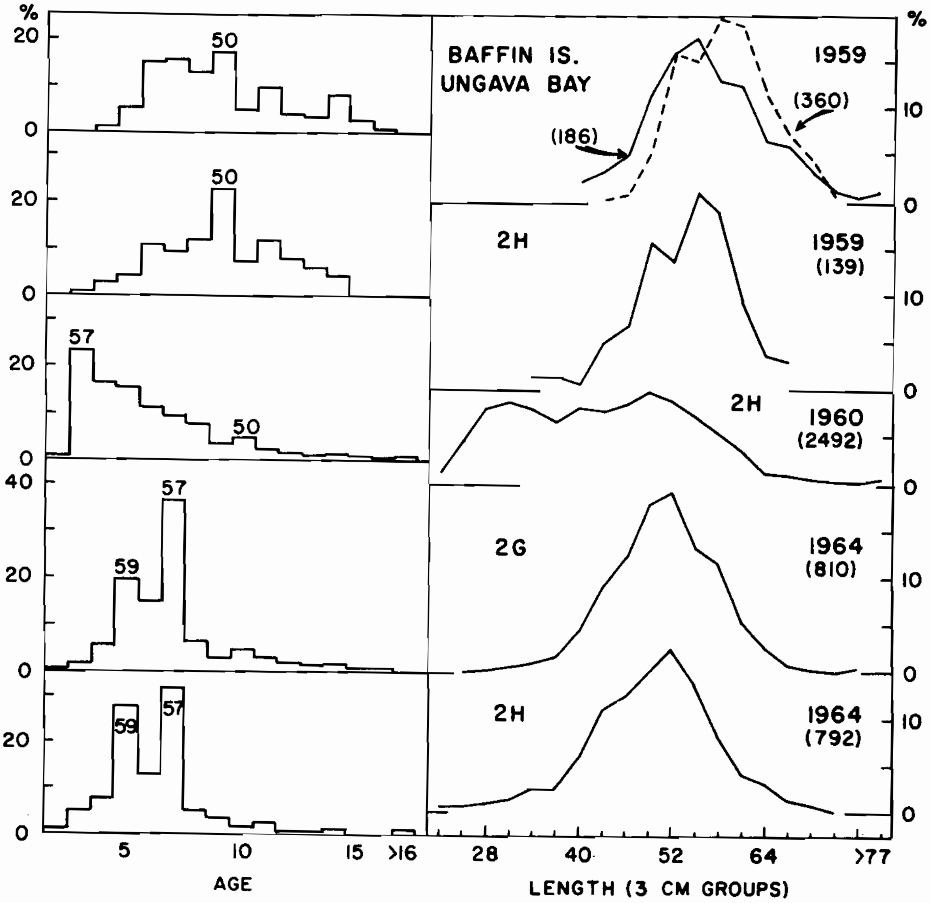

Figure 15. Adjusted age and length distributions of research vessel catches from southern Baffin Island to northern Labrador. Also shown (broken curve) is the length distribution of a sample from a commercial trawler fishing in Ungava Bay.

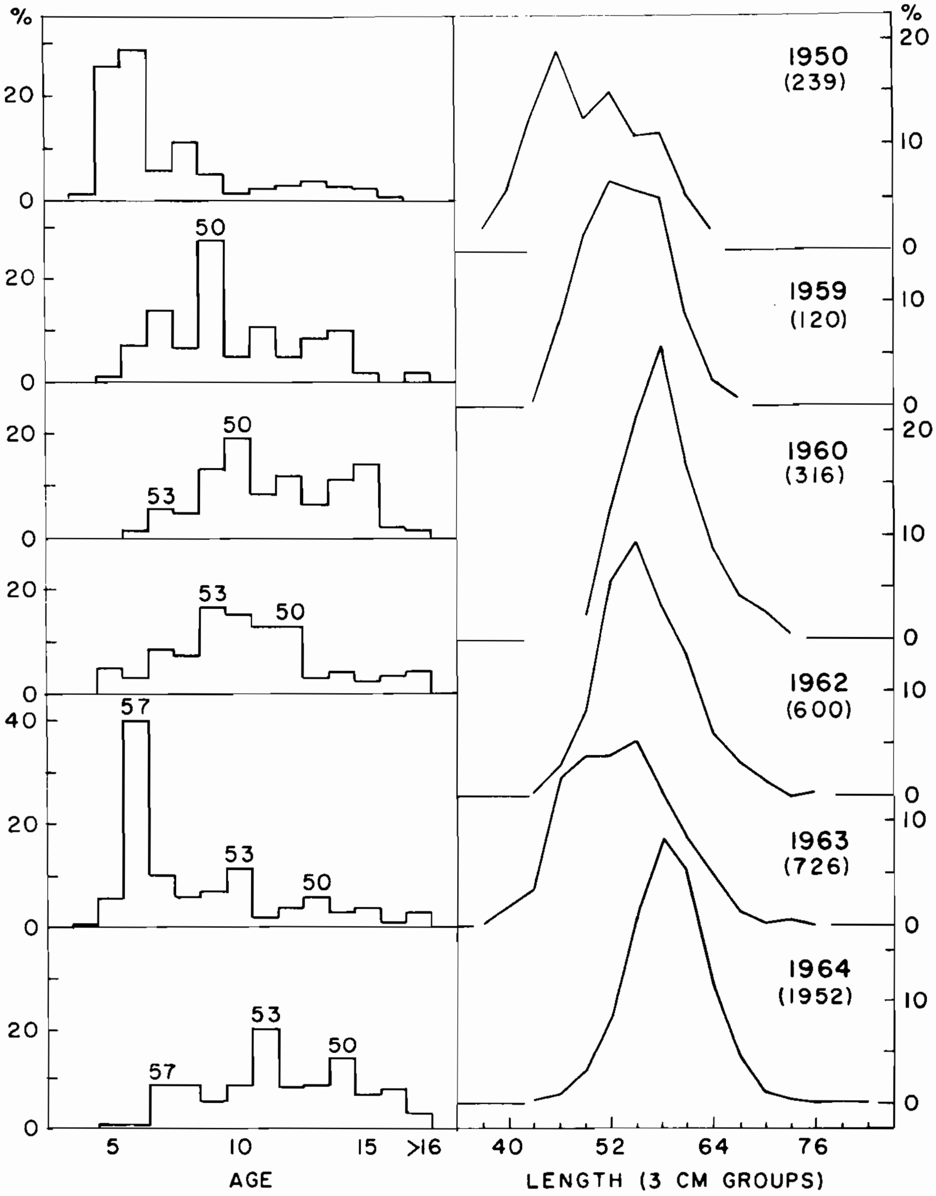

Figure 16. Age and length distributions of cod taken by jigger, Division 2G inshore.

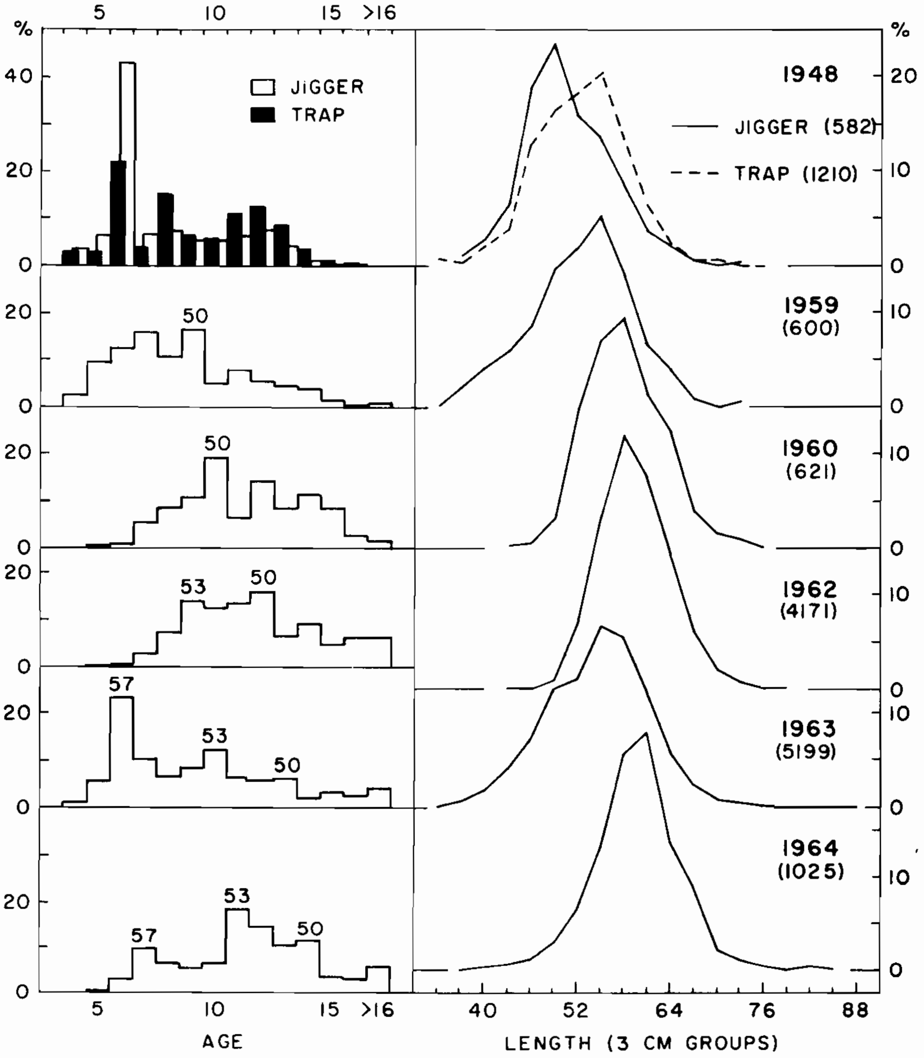

Figure 17. Age and length distributions of cod taken in the inshore commercial fishery, Division 2H.

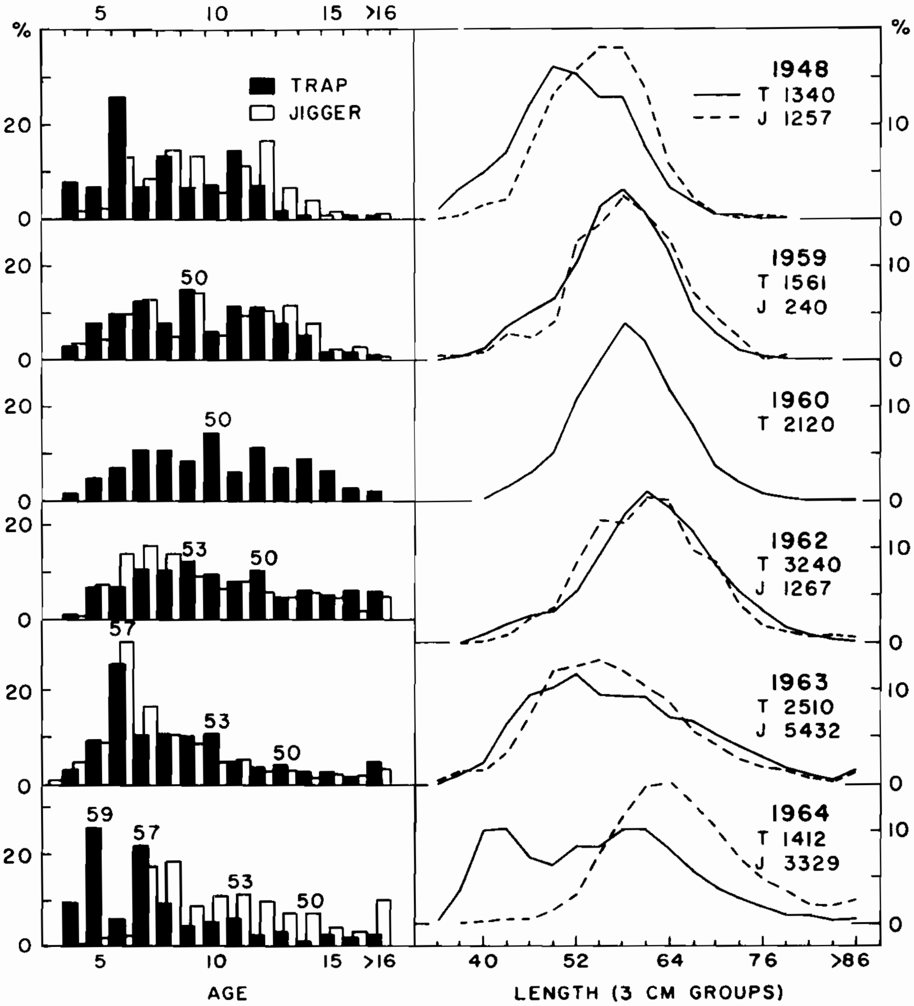

Figure 18. Age and length distributions of cod taken in the inshore commercial fishery, Division 2J.

of the curve to offshore length distributions allows prediction of size distributions that would have occurred had fishing been done with a codtrap having a 4½-inch nylon back. More smaller-sized fish would be taken with the traps in use in Labrador.

Predicted size distributions were obtained by multiplying numbers at each length in the offshore distributions of 1960 and 1962-64 by the percent retention values from the fitted selection curve. The resultant distributions were converted to percentages and are shown in Fig. 19B, with the inshore distributions for traps in Division 2J shown for comparison (the original offshore distributions are shown in Fig. 14). Considering the approximateness of the adjustment of offshore length distributions, the predicted distributions for 1960, 1963 and 1964 are in substantial agreement with those determined from codtrap catches. The peak at 40-43 cm in 1964 was not predicted from the selection curve, but is not unexpected in view of the smaller mesh sizes actually used in Labrador. The 1962 distributions are very dissimilar, the more so when it is considered that the predicted distribution is for a 4½-inch mesh and would have been even further displaced from the actual catch distribution had it been calculated for a smaller mesh size.

It is evident that in 1960 both inshore and offshore segments of the population in summer had similar size dis-

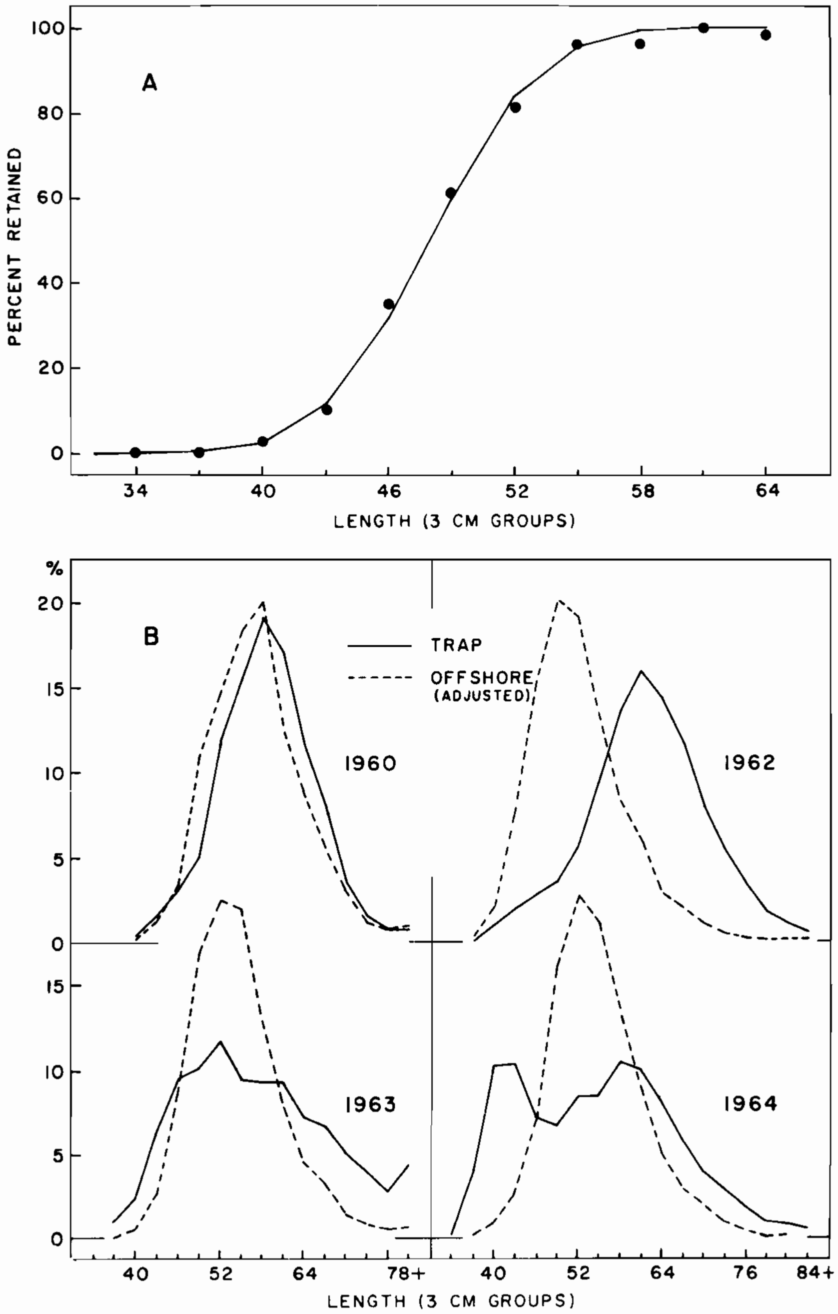

Figure 19. A. Selection curve for codtrap having a 4½-inch nylon back.
B. Length distributions of cod taken by traps in Division 2J and predicted length distributions assuming a similar population size structure inshore and offshore.

tributions. In 1963 and 1964 those sizes available on the offshore fishing grounds in spring were available as well to the inshore fishery in summer. However in 1962 the small fish taken in the offshore survey were not present in similar proportion in the inshore areas.

## Discussion and Conclusions

The various patterns and anomalies in the length and age distributions, in the light of existing theories of stock delimitation and seasonal migration, generate several important questions with regard to whereabouts of certain segments of the population at certain times, in particular:

(1) Why was the large 1959 year-class plentiful as age 3 in the 1962 offshore age distributions for Division 2J (Fig. 14), while the large 1957 year-class at the same age in 1960 was relatively scarce (though it was plentiful in Division 2H)?

(2) Why were the small fish, so relatively abundant offshore in 1962 (Figs. 14 and 19B), not available to the inshore fishery at the same time? More specifically, why did the 1959 year-class occur in quantity as age 5 in the 2J inshore trap age distributions in 1964, while the 1957 year-class at age 5 in 1962 did not (Fig. 18)?

(3) Why did the 1957 year-class, so abundant in Divisions 2G and 2H inshore in 1963 (Figs. 16 and 17), not maintain its prominence in the inshore commercial fishery in these areas in 1964?

(4) Why were so few fish younger than age 3 taken in the offshore surveys (Figs. 14 and 15)?

Considering the first question, fish of age 3 occurred in quantity offshore in Division 2H in 1960, but not in Division 2J, although in 1962 age 3 fish were abundant offshore in Division 2J. It is most likely that this anomaly was due to incomplete coverage of the population in Division 2J in 1960. More than 80% of the fish measured were taken from only 6 stations across the northeast part of Hamilton Inlet Bank, and fish of age 3 were not plentiful at these stations. Only one other series of stations was fished and cod were scarce at these. Fish of age 3 from the 1959 year-class were taken in quantity in the 1962 survey in Division 2J, and age distributions in all areas since 1960 (Figs. 14 and 15) indicate that the 1957 year-class was no less abundant. There is thus no reason to suppose that it was not present in Division 2J in 1960.

With reference to question (2), the 1957 year-class at age 5 did not appear in quantity in trap catches inshore. The 1959 year-class at age 5 was relatively abundant. This again is probably an anomaly due to deficient sampling in 1964. Due to an engine breakdown the inshore vessel did not arrive in the area until July 25, about one month after the start of the trap fishery. Trap fishing was then very much reduced, and ceased altogether by August 4 due to the poor fishing in 1964. During this period measurements and otolith samples were obtained from two traps only, and one of these consistently caught small fish. The 1964 length and age distributions thus cannot be regarded as representative.

From a consideration of the age and size at maturity (Section 7) it is apparent that the inshore migration each spring primarily involves mature fish. The scarcity of age 5 fish inshore in 1962 is probably related to the fact that no more than one-quarter of these were mature. In 1963, when they appeared in quantity at age 6, at least half those from the offshore surveys in spring were mature, but possibly 75% of those taken inshore were mature (Section 7, Fig. 35A). Further consideration is given in Section 7.

The answer to question (3), concerning the relative decline of the 1957 year-class in the 1964 age and length distributions of Divisions 2G and 2H (Figs. 16 and 17), may be related to the general decreased availability inshore in this year. This may have been due to unusual hydrographic conditions affecting fish distribution or to an actual decline in abundance due to offshore fishing. The annual mortality of fish of ages 7-8, estimated from offshore surveys in 1963-64, is of the order of 70% (Section 5). If this year-class (age 7 in 1964) was fished at this rate before coming inshore, its decline in the 1964 catches is not surprising.

In fact it is probably too early to make a satisfactory assessment of the anomalies in the 1964 inshore data generally. The effects of the high levels of fishing in 1960-64, whether or not these levels are maintained, will continue to be evident for a number of years in the future. The patterns in size and age distributions in 1964 will be better assessed with reference to those of later years.

Finally, with regard to question (4), i.e. the scarcity of fish of ages 1 and 2 in offshore surveys, it appears that these fish are simply not available in significant quantities in the offshore areas, at least in the thoroughly surveyed areas of Division 2J. Cod of these ages do occur in appreciable quantities in research vessel catches in more southerly areas (May, 1965), though certainly not in proportion to their abundance. Many may escape through the large meshes in the forward parts of the otter trawl or they may be generally distributed sufficiently far off bottom to be out of range of the trawl. In any case their great comparative scarcity in research vessel surveys off Labrador is indicative of actual scarcity within the area. Russian surveys for young fish support this conclusion. In a survey covering much of the ICNAF area for the period December, 1961 to March, 1962 Nevinsky (1962) shows a length distribution for Division 2J with the smallest mode at 25 cm. These were most likely age 3 fish of the large 1959 year-class (see Fig. 14). Again Bulatova (1962), reporting on young cod taken in 50 research cruises from 1954-61, shows fish below 25 cm in length to be extremely scarce off Labrador, but also scarce in all areas surveyed. Possibly the mesh sizes used, which are not mentioned, were incapable of retaining smaller individuals. A more interesting observation is that a concentration of cod of length 26-35 cm occurs in all years on the southern side of the channel south of Hamilton Inlet Bank (the Bank and channel may be seen in Fig. 9).

This distributional pattern is probably related to the particular hydrographic conditions of the Labrador-northeast Newfoundland area. Spawning of cod off Labrador occurs in March-April (Section 7) and the southeastern edge of Hamilton Inlet Bank is known to be an area where large concentrations of cod occur during the spawning season. The spawning area is covered by water of the West Greenland portion of the Labrador Current (Smith, Soule and Mosby, 1937), though in April and early May temperatures in the upper 50 fathoms are below 0°C and much of the area is covered by ice (Templeman and May, 1965). Detailed hydrographic data during the spring spawning period are scarce, but velocity profiles in July show a southward flow greater than 20 metres/second from surface to 200 metres (110 fathoms) with the current also extending much deeper (Smith, Soule and Mosby, 1937). The summer average surface velocity of this portion of the Labrador Current is given by Smith, Soule and Mosby (1937) as 11.1 miles/day. Postolaky (1965) gives the average surface velocity as 0.5 knots (12 miles/day) in April, 1963. It is therefore most unlikely that fry from the spring spawning on Hamilton

Inlet Bank settle on the Bank.

Recent Russian investigations indicate spawning in northern Labrador as well as on Hamilton Inlet Bank (Postolaky, 1965; Serebryakov, 1965), and development of eggs and larvae in negative temperatures in the surface layers. Considering that hatching takes about 40 days at 0°C (Apstein, (1909), and if the surface velocity were 12 miles/day, the eggs would drift 480 miles (8 degrees of latitude) before hatching. Eggs spawned in the extreme north of Labrador (60°N) would be carried to the extreme south (52°N). Eggs from southeast Hamilton Inlet Bank (53°30'N) would be carried to the central Grand Bank. Further drift must be contemplated before the newly hatched larvae settle, or at least become free-swimming. Postolaky (1962) reports the average vertebral count from a sample of 2-3 year old cod from the east-central Grand Bank to be higher than normal for the area, but similar to Divisions 2J and 3K.

On the other hand the surface current is shown to flow on to the coast in central and southern Labrador and northeast Newfoundland (Smith, Soule and Mosby, 1937, Fig. 47). Off northeast Newfoundland the streamlines are almost perpendicular to the coast. It is therefore likely that many of the developing eggs are carried into coastal waters. Frost (1938) shows large numbers of eggs, which she believes to be mainly those of cod, along the coasts of southern Labrador and northeast Newfoundland from 1933-35. Eggs were numerous in both spring and autumn, suggesting extended spawning. Serebryakov (1965) reports the presence of cod eggs off southern Labrador in July. Frost (1938) also shows cod larvae to be concentrated on various sections of the coast during 1931-35, apparently dependent on variations in the strength of the Labrador Current. In the present investigation young cod were usually plentiful in southern inshore Labrador (Fig. 12A). Spring-hatched cod and cod of ages 1 and 2 are often abundant in shallow water off beaches on the northeast Newfoundland coast in autumn (Fleming, MS, 1960-64).

The possibility of larval drift from West Greenland has been proposed as a source of recruitment to northern Labrador (Poulsen, 1960; Hermann, Hansen and Horsted, 1965). The latter show that larval distribution in summer is concentrated to the north and west of the southwest Greenland spawning area, following the branch of the West Greenland Current across Davis Strait. The question of drift to northern Labrador remains open due to lack of complete surveys from Greenland to Labrador and general lack of knowledge from northern Labrador. Vertebral counts from northern Labrador and West Greenland do not correspond (Templeman, 1962), thus mixing of adult stocks is unlikely. However vertebral counts are subject to environmental influence at the egg or larval stages (Tåning, 1952; Molander and Molander-Swedmark, 1957), so cannot be used as evidence against larval drift to Labrador.

For the southern Labrador-northeast Newfoundland area the following hypothesis may be formulated. The inshore areas of southern Labrador and northeast Newfoundland are important "nursery grounds" for young cod which are spawned in the north and drift south in the Labrador Current. These remain inshore at least until age 2. There is then a general offshore and northward return movement, and many fish are distributed well offshore by age 3. The majority remain offshore, at least in Labrador, until maturity is attained. Larval drift downstream with return migration to spawning areas has been described for cod in other areas (Hansen, 1949; Rollefsen, 1954). The foregoing description appears to be the simplest which is consistent with the observed facts of distribution and environment. It is undoubtedly an over-simplification in some respects. The annual migration of adult cod to the coast is examined in Section 9.

The variation in year-class survival of Labrador cod was noted earlier. It is notoriously difficult to determine causative factors for year-class fluctuations generally. Recent considerations are given by Hermann, Hansen and Horsted (1965), Martin and Kohler (1965) and Templeman (1965b). In West Greenland survival of good year-classes is positively correlated with water temperatures (Hermann, Hansen and Horsted, 1965). A negative correlation is indicated in the southern ICNAF area, i.e. good year-classes are produced in cold years (Martin and Kohler, 1965). A rigorous appraisal for Labrador has not been attempted but two points of probable relevance may be noted. The largest year-classes in Labrador since 1942 appear to have been those of 1942 and 1947 (May, 1959); 1950, 1953, 1957 and 1959 (Figs. 14-18). The largest year-classes in West Greenland over the same period occurred in exactly the same years (Hermann, Hansen and Horsted, 1965; Templeman, 1965) with two exceptions. Survival in 1945 was good in West Greenland; about average in Labrador. Survival in 1959 was poor in West Greenland and good in Labrador. The other point of relevance is that three of the last four large year-classes from Labrador, and these were probably the largest three, occurred in years (1950, 1957 and 1959) described as abnormally cold (Soule and Morse, 1960; Templeman, 1965c). In particular, 1957 and 1959 were years of heavy iceberg penetration to the Grand Bank (Soule and Morse, 1960). It might be postulated that low temperatures (extended hatching time) and high rates of water transport are necessary to ensure larval drift to favourable settlement areas. These appear to be the inshore areas of southern Labrador and northeast Newfoundland and possibly as far south as the northern Grand Bank.

# 5. MORTALITY

## Introduction

Of several methods for estimating mortality in commercial fish populations, that most applicable to the present study is analysis of age composition data. This involves estimation of rate of decline in abundance with increasing age. The principles underlying the method are reviewed by Beverton and Holt (1957) and Ricker (1958). Some special applications are presented by Robson and Chapman (1961).

Application of the method to fisheries followed the discovery by Edser (1908) that when length distributions were plotted as the logarithms of numbers at each length, the result was a curve with a steeply ascending left limb, a rounded upper portion and a long and nearly straight descending right limb. Baranov (1918) gave the name "catch curve" to such graphical presentations. A more suitable procedure is to use distributions of age rather than length.

The ascending left limb of such curves is the result of selective sampling by the collecting gear, i.e. the youngest ages are not sampled in proportion to their actual abundance due to non-availability to the gear or, as is usual with fishing gear, selection of the larger sizes. In order for the descending right limb to be straight, the conditions listed below must be met.

(1) Recruitment of each age-group to the sampling gear is uniform, i.e. when the various age groups are first taken by the gear they appear in similar numbers.

(2) The mortality rate of each age is the same.

(3) There is no change in mortality rate over the period considered.

(4) Sampling of the age groups involved is random.

Fluctuations in recruitment are common in fisheries, but may be minimized for purposes of mortality estimates by combining data over several years, or by considering each year-class individually. Departures of the descending right limb of the catch curve from a straight line indicate increasing mortality rate with age if the resultant is convex, decreasing mortality with age if it is concave. These situations are treated in detail by Ricker (1958).

Absolute numbers at each age are seldom known, but the method holds for indices of abundance based on catch per unit effort or simply actual numbers or percentages present in random samples.

## Material and Method

The following description of the mathematical basis of catch curves is adapted from Beverton and Holt (1957). The symbols are those recommended by Holt *et al* (1959). The abbreviation *ln* is used to denote natural (base e) logarithms.

Beverton and Holt (1957) define mortality due to natural causes and mortality due to fishing in terms of instantaneous rates, i.e.

$$ {}_{M}\frac{dN}{dt} = -MN $$

and

$$ {}_{F}\frac{dN}{dt} = -FN $$

where the left hand side of each equation represents the rates of natural mortality and fishing mortality respectively at any time, M is the instantaneous natural mortality coefficient, F is the instantaneous fishing mortality coefficient and N is the number of fish. The minus signs indicate that the number decreases. The instantaneous coefficients M and F are additive and we may write

$$ {}_{Z}\frac{dN}{dt} = -Zt $$

where Z is the instantaneous total mortality coefficient.

Considering the decline in numbers of a single year-class between any age t and age t+1 one year later, and representing the numbers of fish present as $N_t$ and $N_{t+1}$ respectively, the above differential equation may be solved between these limits to obtain the number remaining at age t+1, i.e.

$$ \begin{aligned} N_{t+1} &= N_t e^{-Z(t+1-t)} \\ &= N_t e^{-Z}. \end{aligned} $$

For a 2-year period the equation would become

$$N_{t+2} = N_t e^{-2Z}$$

and for a general number of r years we can write

$$N_{t+r} = N_t e^{-rZ} .$$

Taking natural logarithims of each side,

$$\ln N_{t+r} = \ln N_t - rZ \qquad (1)$$

$$rZ = \ln N_t - \ln N_{t+r}$$

$$Z = 1/r(\ln N_t - \ln N_{t+r}) \qquad (2)$$

It will be seen that equation (1) above describes a straight line relationship between the variables r and $\ln N_{t+r}$, with slope $-Z$ and intercept $\ln N_t$. This represents the descending right limb of the catch curve. From one year to the next ($r = 1$) the relation becomes

$$Z = \ln N_t - \ln N_{t+1} \qquad (3)$$

Mortality estimates for a series of years may be obtained by fitting a least squares straight line to the natural logarithms of numbers at age. Alternately the values for the first and last years in the series may be taken from the fitted line and substituted in equation (2).

The above description applies to a single year-class, experiencing a constant mortality rate throughout its life.

It would exhibit a perfectly straight catch curve beyond the point of full retention by the sampling gear. The conditions necessary for extension to age compositions of mixed year-classes and the results of mortality changing with age have been noted earlier.

The material used was essentially that presented in the previous Section, i.e. age compositions adjusted to number measured inshore and to catch from research vessel surveys offshore. Combinations to reduce irregularities due to variable year-class survival were made by adding the percentage values for each age and dividing by the number of years combined, giving the average situation for a particular period. The northern offshore data were considered generally insufficient for the purpose, except for the large sample from Division 2H in 1960. The southern offshore data (Division 2J) were combined into three periods to examine the effects of the fishery, i.e. 1950-58, 1960 & 62 and 1963-64. The atypical 1964 inshore data were not used, and the remainder combined into two areas and periods, i.e. northern Labrador (Divisions 2G and 2H) and southern Labrador (Division 2J) for the periods 1959-60 and 1962-63. Due to the long life of cod in the area in relation to length of the period of intensive sampling, fluctuations in relative abundance from year to year, and because of the smallness of the samples prior to 1959, year-classes could not be examined individually. Inshore and offshore data were treated separately because of differences in selectivity of the respective gears and the differences in size and age structure discussed earlier.

## Total Mortality Estimates

Catch curves for the various data combinations are presented in Figs. 20 and 21. The trend lines (drawn by eye) allow the following general observations.

(1) Age at full recruitment to the research vessel gear (Fig. 20) appears variable. In fact recruitment is probably complete at age 3 as indicated by the curve for Division 2H, but does not appear so in the other three curves because of variable year-class strength in the combined data. In particular the peaks of the 1960 & 62 and 1963-64 catch curves are determined by the great relative abundance of the 1957 year-class at age 5 in 1962 and ages 6 and 7 in 1963-64 (Fig. 14). For the inshore gears (Fig. 21) recruitment is not complete until ages 8-10, though appears earlier (age 6) in Division 2J in 1962-63 because of the large contribution of the 1957 year-class in 1963 (Fig. 18).

(2) The descending right limbs are never straight throughout their length. Those for 2H offshore, 1960 and 2J offshore 1950-58 (Fig. 20) are distinctly convex; the recent curves for Division 2J distinctly concave, though in all cases portions of the curves may be described

by straight lines. Due to the great relative scarcity of old fish offshore in 1962 compared to 1960, there is a pronounced decline at the end of the 1960-62 curve. The inshore catch curves (Fig. 21) exhibit a distinct change in slope, as well as a change from concavity to convexity, between the middle and older age-groups.

(3) In spite of data combination for 2 or more years the effects of variable year-class survival (no doubt variable availability and sampling error also) are evident as irregularities in the trends.

The particular attributes of the various curves are extremely useful in drawing conclusions regarding changes in mortality with age and over the period of the study, and these are considered at the end of this Section.

It is obvious that estimates of mortality for the whole descending right limb of each catch curve will not have much meaning. Accordingly average estimates for straight or nearly straight portions of each curve beyond the recruitment age were determined by substitution in equation (2) of values taken from by-eye lines. These values and the estimated total mortality coefficients from them are listed in Table 5. The comparable annual rates in percents (a) from the conversion table given by Ricker (1958) are also shown. Separate estimates between each age are given for the area of greatest curvature of the 1963-64 offshore 2J curve.

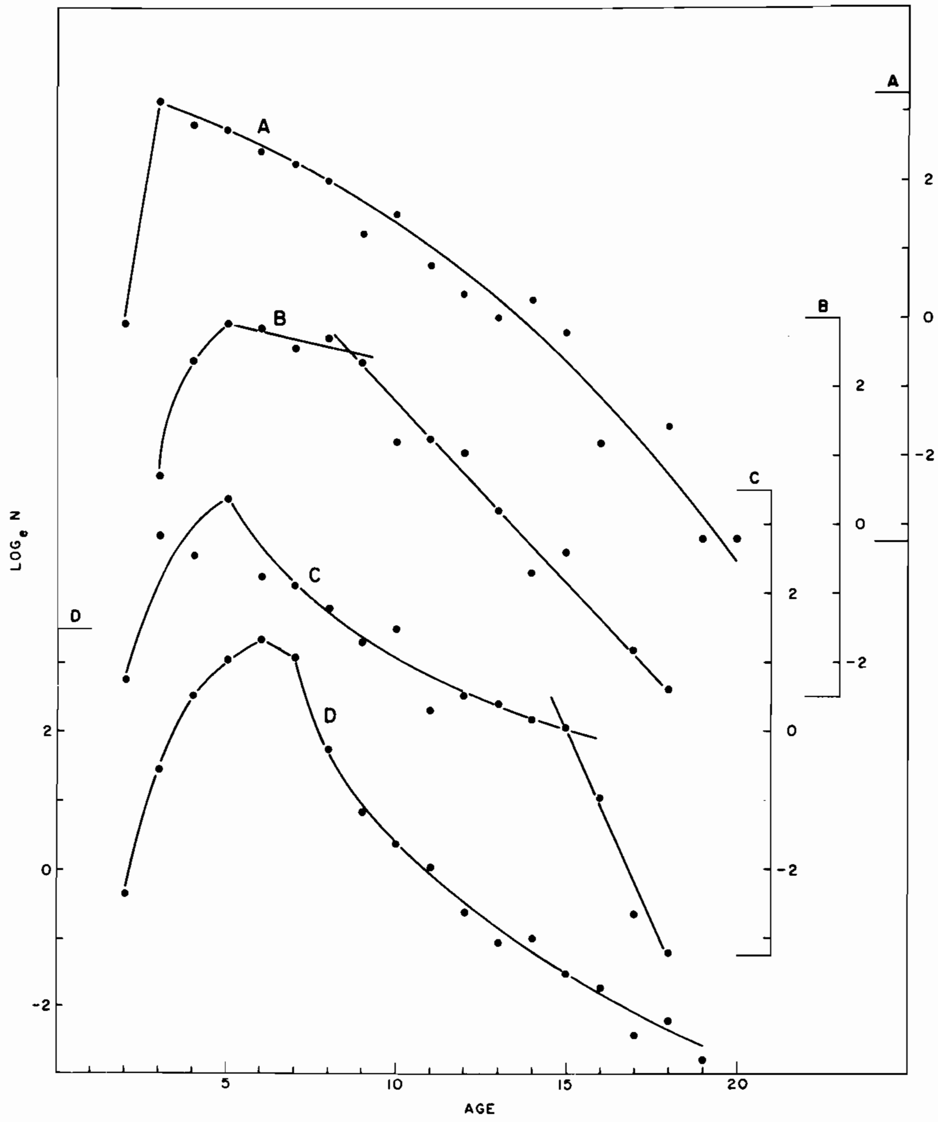

Figure 20. Catch curves from research vessel surveys offshore:
A. Division 2H, August, 1960,
B. Division 2J, 1950-58,
C. Division 2J, 1960 & 62,
D. Division 2J, 1963-64

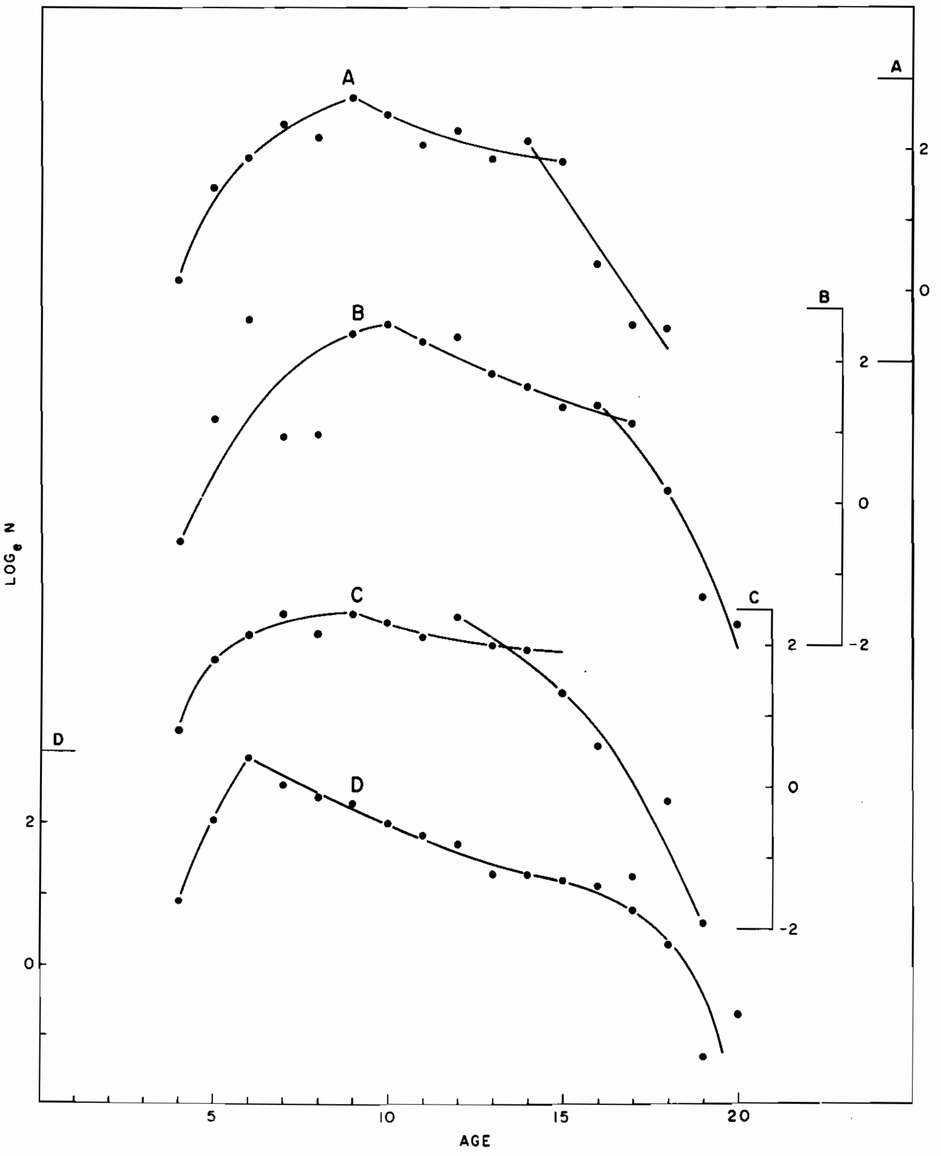

Figure 21. Catch curves from the inshore fishery:
A. Divisions 2GH, 1959-60,
B. Divisions 2GH, 1962-63,
C. Division 2J, 1959-60,
D. Division 2J, 1962-63.

The estimates are highly variable but some general similarities between the curves are evident. For the three offshore curves to 1962 (Fig. 20) estimates of Z for ages up to 8 or 9 are very low. Similarly low estimates are obtained inshore (Fig. 21) for ages up to 13-15, most approaching a value of 0.2. The oldest age-groups (above 14-15) usually exhibit Z-values about 3 to 4 times greater than this.

## Separation of Natural and Fishing Mortality

The great variation in mortality estimates for the offshore 2J curve of 1963-64 is of particular interest. Ricker (1958) shows that curves of this type are typical following an increase in fishing. The newly recruited age-groups are subjected to the full force of the higher fishing mortality from their entry to the fishery. The oldest age-groups reflect the effects of fishing at the earlier, lower levels. Thus a measure of present and previous mortality rates may be obtained from the areas of greatest and least slope respectively on the right limb of such curves. For the above mentioned curve the area of greatest slope, between ages 7 and 8, yields a Z-value of 1.31 (Table 5). A least-squares straight line fitted to the fairly straight portion between ages 12 and 19 gives a negative slope (i.e. Z) of 0.31.

In such a situation, if the fishing effort is known to have increased from a former stable level to a new stable level, and if a measure of this increase is available, it is possible to separate the components of mortality into that due to fishing and that due to natural causes. The procedure is ascribed to Silliman (1943) and is reviewed by Ricker (1958).

The increase in offshore fishing effort in Labrador appears to meet the conditions outlined. Hodder (1965) shows offshore effort in standard trawler hours for Subarea 2 during 1955-57 as about 10 to 15 thousand hours, and increasing rapidly from about 30 thousand hours in 1959 to almost 110 thousand hours in 1961-62. Trawler landings in 1963-64 decreased 18% from the 1961-62 period. If this is indicative of reduced effort the comparable effort figures for 1963-64 would be about 90 thousand hours. Taking 100 thousand hours as the average figure for the recent level, and 12.5 thousand hours as representative of the 1955-57 level, the ratio between the old and new effort levels is 8.

Since F and M are additive, and assuming that M has remained the same while F is proportional to the fishing effort, values of Z may be substituted in the relation

$$Z = F + M$$

for each period as follows:

for the earlier period $.31 = F + M,$

for the present $1.31 = 8F + M.$

Solving the simultaneous equations gives a value for M of 0.17 and values for Z of 0.14 for the earlier period and 1.14 for the present.

## Discussion and Conclusions

Ricker (1958), from theoretical consideration of the effect of increased fishing on a fish stock in which recruitment occurs over a series of years, shows that there is a considerable time lag between application of a new fishing rate and reflection of that rate as a steeper right limb in catch curves. If the right limbs of catch curves under the old and new stable rates are straight, those in the intervening period exhibit increasingly wider concave sections with time until all the year-classes which experienced the old rate have passed out of the fishery. The model assumes constant natural mortality rate with age.

This general pattern appears to hold in the present study, unless the convexities noted in some of the catch curves are indicative of increase in natural mortality rate with age. The convex offshore catch curve for Division 2J during 1950-58 (Fig. 20) implies that mortality increased with age during the period of low fishing. Ricker (1958) makes the point that catch curves correctly represent increase in natural mortality rate with age if rate of fishing is the same for all ages (or even if it decreases with age). Neither situation is necessarily true in Labrador, considering the commercial practice of fishing largest sizes if large-sized fish are sufficiently concentrated, and the fact that cod may be **segregated** by size in different depths (Fig. 13 and Templeman and May, 1965). The points for the older ages in the curve for Division 2H in 1960 (Fig. 20) are irregular though the curve as a whole appears **convex.** The same arguments therefore apply.

Again the sharp increases in slope at the oldest ages inshore (Fig. 21) may be the result of factors other than increase in natural mortality. Thus jiggers might be expected to select the largest fish in a school if these are as active as the smaller ones. On the other hand the largest and oldest fish may become increasingly unavailable to the inshore gears through failure to migrate inshore (Templeman and Fleming, 1956), and the decline in numbers may not be due to an actual increase in mortality. For the moment it is difficult to choose between the alternatives, but it may at least be concluded that natural mortality is not as variable as the catch curves indicate.

Otherwise the curves reflect in a general way the changes in mortality which have occurred over the period of study. Thus the inshore curves show concave sections as a result of recently increased fishing, though the steepness of the concavities is not nearly as great as might be expected considering the slopes of the recent offshore curves. The latter, at least in Division 2J, take the form predicted by Ricker (1958) for such situations. The 1960 curve for Division 2H may not be particularly instructive since it is based on data for a single survey cruise. However if allowance is made for the fact that the point at age 10 is too high (large 1950 year-class) the section from ages 8-15 appears concave.

The average natural mortality estimate from relation of effort data to total mortality estimates prior to and since the increase in fishing is probably too low. In general the curve for Division 2J offshore in 1963-64 is considered to be the best of the lot because of the large numbers represented (more than 28,000 fish in 1963 and 15,000 in 1964). However due to the great relative abundance of the 1957 year-class in each year (Fig. 14), and its inclusion in the curve at age 7 but not at age 8, the estimate of recent total mortality (Z) of 1.31 based on these ages may be too high. If the Z-value for ages 8-9 is taken instead, the calculated value of M becomes 0.22 instead of 0.17. Also Ricker (1958) in discussing Silliman's method, observes that if the unit of gear used becomes more efficient (i.e. F is not actually proportional to fishing effort as the method assumes), the estimated values of M will be too low and values of F too high. The effect is to increase the ratio between the previous and present F-values in the equations, with resultant higher estimates of M. The change in pattern of the fishery over the period has previously been noted (Fig. 4), and Hodder (1965) shows that catch per unit effort is much higher in the spring period which has accounted for most of the increased catch. This is a clear demonstration that the efficiency of the gear has indeed increased.

Beverton and Hodder (editors, 1962) give an estimate of Z of 0.5 in Subarea 2 for ages above 13 during the period 1956-58. This is based on age data from commercial trawler samples and compares well with the estimate of 0.54 for ages 9-18 from the combined 1950-58 research vessel data presented here for Division 2J offshore. No previous estimates of M for Subarea 2 have been made but Beverton and Hodder (editors, 1962) consider M for Divisions 3K and 3L, immediately to the south, to lie within the range 0.15 to 0.35. The value of M in Subarea 2 would appear to be close to the mid-point of this range. The calculated value of 0.17 is certainly a minimum.

In general it may be concluded that due to changes in mortality over the period of study, the shortness of the data series and the evident fluctuations in recruitment, the mortality estimates should be considered as no more than first approximations.

# 6. GROWTH

## Introduction

Growth is the result of the various forces by which material is introduced into an organism, transferred throughout it and assimilated to produce new living material. The end result is increase in size, the amount or rate of increase dependent on the complex interaction of the factors influencing availability of food and its assimilation to form new somatic tissue. Increase in size is probably best expressed in terms of weight or volume, and growth in weight is a necessary parameter in formulations of maximum sustained yield in fisheries. However since most data for growth studies are collected at sea or elsewhere in the field, the more easily obtained length measurement is that most often used. The relationship of length to weight is likely to be stable within a stock (except for seasonal variation related to feeding and the sexual cycle) and may be determined from fairly small samples. Growth data relating age and length can then be transformed in terms of weight as desired. Growth is expressed in terms of length in the present study and a description of the length-weight relationship given.

Rate of growth and final size of poikilothermic species are fairly plastic, depending on environmental conditions, and growth data may be useful as an indicator of "general welfare" in fish populations (Carlander, 1956). Growth of cod appears to be readily modified by external factors and is quite different from one area to another throughout its range. Wise (1961) shows that average size of cod of age 6 ranges from less than 40 cm to more than 90 cm, depending on area. Variations in time within a single area are described by Kohler (1964). Some indication of variation in size at age within the same area and time may be seen from Table 4 of the present study.

Cod growth studies are numerous in the literature. Wise (1963) lists 120 papers containing information on cod growth, and Wise (1961) gives a partial survey. Recent studies, relating variations in cod growth to environmental influences, have been presented by Taylor (1958a), Kohler (1964), Dementyeva and Mankevich (1965), Hermann and Hansen (1965), Jonsson (1965), May et al (1965) and Williamson (MS, 1965). Information on cod growth in Labrador prior to 1959 is contained in studies by Thompson (1943), Ancellin (1953), Ruivo (1957), Figueras (1963b), May (1959) and Fleming (1960). These are usually general descriptions as part of descriptions over a wider area. The present study is a detailed consideration of growth variations in relation to area and time.

It is useful to express curves of growth in quantitative terms for purposes of incorporation into mathematical formulations of yield and for comparisons between areas, species, etc. A number of mathematical growth functions are available, some claiming a physiological basis and others purely empirical. A detailed review is given by Beverton and Holt

(1957). More recent proposals and discussions are presented by Riffenburgh (1960), Pothoff and Roy (1964), Kruger (1965) and Paloheimo and Dickie (1965).

The growth curve developed by von Bertalanffy (1938, 1949, 1957) was chosen by Beverton and Holt (1957) for incorporation in their population models, and shown to describe their data very well. It has since been widely applied in fisheries biology and has been used in this study. The curve has been given a physiological basis and Beverton and Holt (1957) review its derivation from first principles. Further discussions are contained in Ricker (1958), Richards (1959), Taylor (1962) and McLaren (1963). The physiological basis of the von Bertalanffy equation has been disputed, but the curve remains useful as a description of fish growth because of its simplicity, and as long as it fits the data adequately and is used on an empirical basis.

## Material and Method

The collections on which the growth analyses are based are described in Section 3 and listed in Tables 1 and 2. Random samples only were used. Original data for the 1948 inshore Labrador growth curves presented by Fleming (1960) were provided by Mr. A.M. Fleming, allowing an area separation. Ages were determined from otoliths (Section 4) and growth is expressed as average length at age. Inshore and offshore data were considered separately because of differences in gear selectivity. Averages based on 1 or 2 fish only (usually ages beyond 18) were not considered in the analyses.

Since the data were collected at various times throughout the year the collections from one year to the next were not always directly comparable because of seasonal growth differences. However most of the collections were obtained in the July-September period, while none were obtained during January-March. The convention has been adopted, for purposes of visual display and fitting mathematical functions, of adding $\frac{1}{4}$ to the otolith age for each quarter of the year beyond the January-March period. A 5 year old fish would then be regarded as $5\frac{1}{4}$ years old in April-June, $5\frac{1}{2}$ in July-September and 5 3/4 in October-December.

The study is primarily concerned with growth variations in area and time and the von Bertalanffy growth curve has been used to describe the most significant variations as well as to provide a quantitative description for the most recent data from each area. The curves were fitted using the "trial $L_\infty$" approach suggested by Ricker (1958) and are presented in the form

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

where $l_t$ is length at age t, $L_\infty$ is the theoretical maximum or final length, k is a constant determinating the rate of change in length increment and $t_o$ is a scale correction giving the hypothetical age at zero length.

The 3 constants ($L_\infty$, k and $t_o$) are estimated simply by fitting least squares straight lines to 2 expressions derived from the above equation (Ricker, 1958), i.e.

$$l_{t+1} = L_\infty(1 - e^{-k}) + l_t e^{-k} \qquad (2)$$

$$\ln (L_\infty - l_t) = \ln L_\infty + kt_o - kt \qquad (3)$$

where ln is the logarithm to base e.

The first equation describes a straight line between $l_t$ and $l_{t+1}$ (length one year later) with slope $e^{-k}$ and intercept $L_\infty(1-e^{-k})$; values of $L_\infty$ and k are determined from exponential tables. The second describes a straight line between t and $\ln (L_\infty - l_t)$, with slope -k and intercept $(\ln L_\infty + kt_o)$, from which a second estimate of k and the value of $t_o$ can be determined directly.

Following Ricker (1958) a trial value of $L_\infty$ was estimated from (2) and, using this as a first approximation, successively smaller or larger values as necessary substituted in (3) to obtain the straightest line. Values of k and $t_o$ were obtained from a least squares fit to (3) using this "best estimate" of $L_\infty$.

## Variations in Growth

An inshore-offshore growth comparison is of interest in view of differences noted earlier in size and age distributions and mortality. All the inshore data were collected during July-August and in some years offshore collections were made at the same time, affording comparative material. Plots of average length at age are shown in Fig. 22. The inshore averages for at least ages 4-6 are too high (e.g. curve B) due to selection of the fastest-growing fish at these ages by the inshore gears (the inshore averages for ages 1-3 are from hook and line fishing in shallow water). The offshore averages were greater from age 7 onwards in 1960 (curve B) but less for most ages in 1962 (curve C). Except for the area of artificially high inshore values (at least ages 4-6) the averages are seldom more than 2 cm apart in these curves, and are generally even closer in curve A (Division 2H, 1960). It will be shown that the July-September quarter is the period of most rapid seasonal growth (next paragraph); therefore differences of this order are not surprising. Since the relative positions of the curves are reversed in Division 2J for 1960 and 1962 it may be concluded that there are no consistent differences in growth between the inshore and offshore populations in summer.

Seasonal data were not available on a continuing basis, nor throughout the whole of any one year. Such offshore data as were available are shown for individual recent year-classes in Fig. 23, supplemented by inshore averages for the third quarter of 1964. These latter averages are again probably too high for ages 4-6 (1958, 1959 and 1960 year-classes), but even allowing for this it is evident that the period of greatest growth in any year is that from July to

September, at least for the ages represented (up to age 8). This fits in well with the appearance of opaque material on the otolith edge (increasing from 24% of the fish in July to 82% in September - Fig. 11) and the evidence that by November more than 10% have stopped growing or at least slowed enough to exhibit the hyaline or "winter" zone (Fig. 11).

Considering growth on an area basis, the most recent inshore and offshore data are shown in Fig. 24. No old fish were taken in the small sample from Division 2H offshore in 1964 (Fig. 24A), and though 3 of the 4 averages above age 7 are higher than those of Division 2G, all 4 are based on very small numbers of fish (5 to 14). The much better series of inshore data (Fig. 24B) indicate that growth in these northern Divisions is similar. The single curve describing the data from both Divisions (2G and 2H, 1963-64) is a fitted von Bertalanffy curve, with the following form:

$$l_t = 65(1 - e^{-.20(t-.35)}).$$

It is evident that wide differences in growth exist beyond age 6 between Division 2J and the northern Divisions. The averages for Division 2J do not follow a von Bertalanffy or any other curve of constantly decreasing slope, exhibiting a distinct break in the region of ages 7-9. This will be shown to be due to an increase in growth at these ages and beyond.

The small amount of data from southern Baffin Island and Ungava Bay was combined and is shown for comparison (Fig. 24B). The averages are very close to those for Divisions 2G and 2H up to age 10 (the points are displaced to the right to make them visible), but assume an intermediate position between the northern and southern Labrador data at the older ages. This may be due to the small size of the combined sample, but is more likely an expression of the true pattern of growth. A "levelling-off" around ages 9-11, and increased growth beyond these ages, is often observed in growth curves from the Labrador area (e.g. it is detectable on a smaller scale in the inshore data for Divisions 2G and 2H).

Plots of average length at age offshore (Fig. 25) from 1950 to 1964 allow examination of variations with time in the offshore data. The lines are drawn by eye. None of the points are displaced but are plotted according to the convention described. The 1950 samples from Divisions 2G and 2H are small, but the averages are usually high. However there is no consistent trend from the earliest to the latest collections in the data from Division 2H. A trend is apparent in Division 2J. From age 8 onward the curves suggest an increase in average length at age over the period. Below age 7 there is an apparent decline since 1950.

Changes in growth with time are better examined from the inshore data which were all collected at the same time each year (July-August). Plots of average size at age for a number of ages over the years show no consistent trends between 1950 and 1959 in Division 2G (Fig. 26A) and between 1948 and 1959 in Division 2H and 2J (Figs. 27A and 29A). From 1959-64 the averages are variable, but in general show slight upward trends in Divisions 2G and 2H (Figs. 26A and 27A), and very pronounced upward trends from age 8 in Division 2J (Fig. 29A). The upward trend is less pronounced for age 7 and barely perceptible for age 6, while the averages for ages 4-5 exhibit a decline over the period.

Trends in the averages for available offshore data are shown in Fig. 29B. The material was collected in August and September in 1950-54, 1960 and 1962. The 1963 data were from April-May and September; the 1964 data from April-May and October-November (Table 1). For rough comparability with the earlier data unweighted averages were calculated from the two series in each year, and these values plotted in Fig. 29B. These may be expected to be generally lower than true August-September averages in 1963 but about the same in 1964. The general pattern (Fig. 29B) is the same as inshore (Fig. 29A) except that age 6 now shows a definite downward trend.

Inshore growth curves from beginning to end of the period (Figs. 26B, 27B and 28) also indicate slight increases in average size at age in Divisions 2G and 2H, and a much greater increase for ages above 7 in Division 2J. The curves of Fig. 28 are almost 10 cm apart at the point of widest separation as against 3 cm in Fig. 26B. Data for 1963, rather than 1964, were used in Divisions 2H and 2J because of the relatively small collections obtained in 1964 (Table 1). Here again (Fig. 28) it is impossible to fit a von Bertalanffy curve to describe the whole of the 1963 data. The averages for ages 4-7 in 1963 are similar to those for 1959, though consistently below them, while growth is considerably greater beyond age 7. The fitted curves which are shown are as follows:

$$1963 \qquad l_t = 74(1 - e^{-.21(t - .26)})$$

$$1959 \qquad l_t = 63(1 - e^{-.36(t - 1.85)}).$$

It is evident that for ages 7 and above growth has increased slightly in Divisions 2G and 2H and very markedly in Division 2J. Data were insufficient to examine the younger ages in the northern Divisions, but average sizes in Division 2J appear to have declined for ages below 7.

Considering variation with sex, it was found that females are larger than males at most ages, particularly from age 6 onwards, though the differences tend to be constant at the older ages. Selected data for 1963-64 (Fig. 30) illustrate the point.

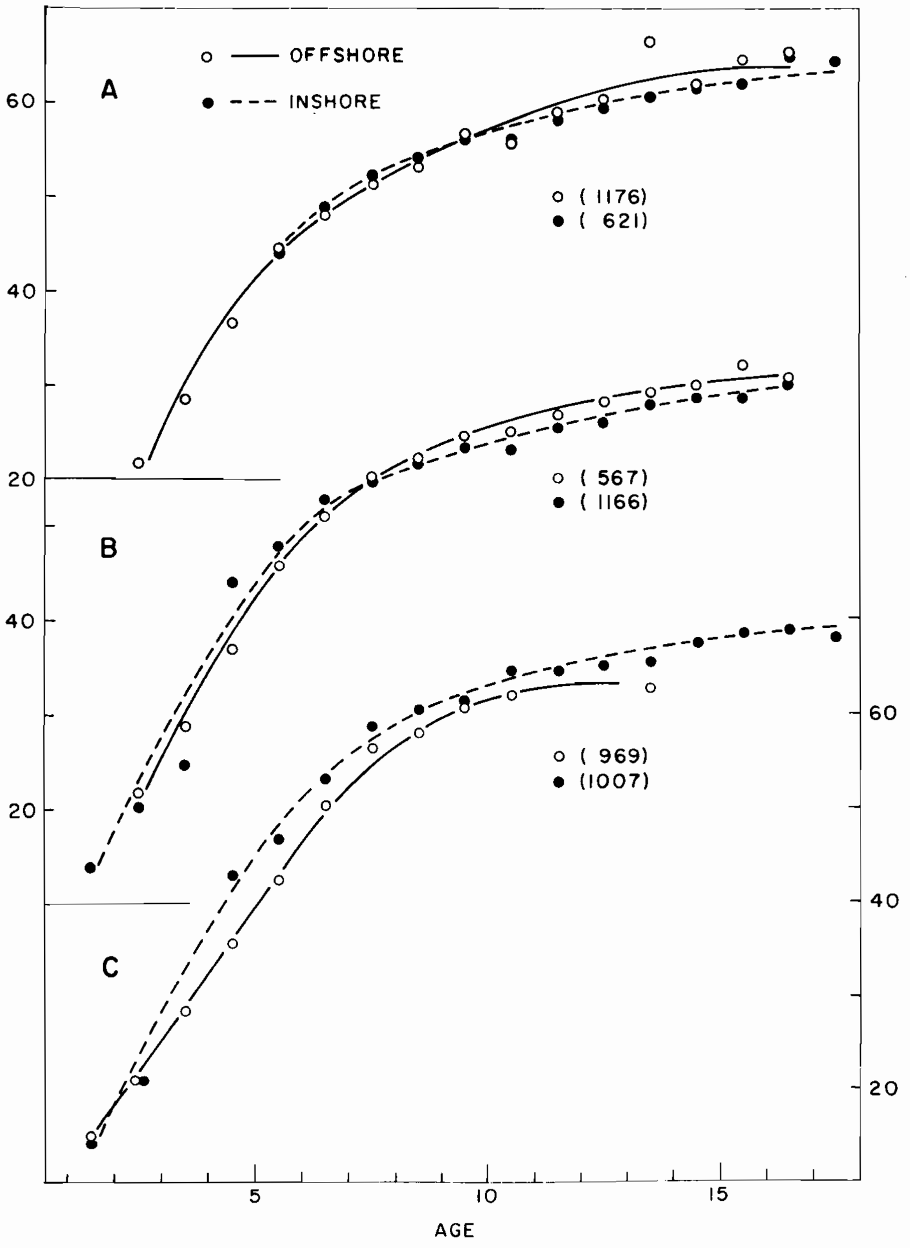

Figure 22. Average length at age, inshore and offshore, July-August. A - 2H, 1960; B - 2J, 1960; C - 2J, 1962. Average lengths are in cm. Numbers of fish are in brackets.

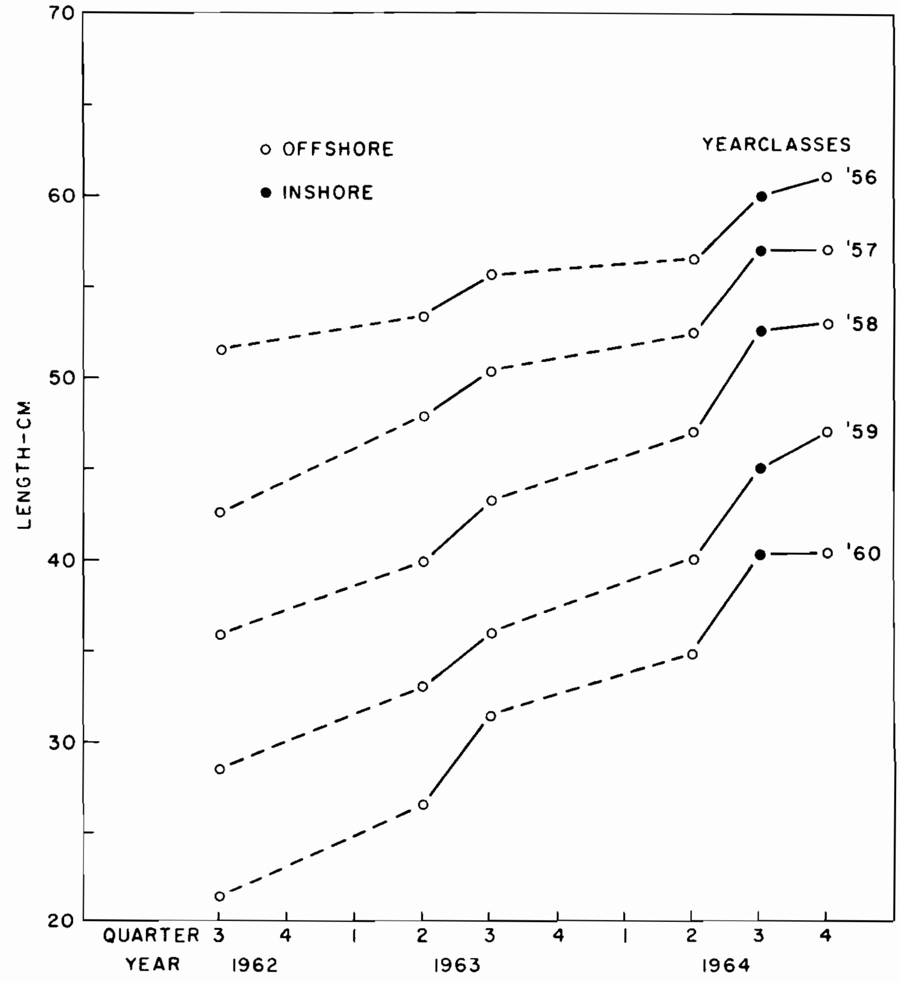

Figure 23. Seasonal growth of recent year-classes, Division 2J.

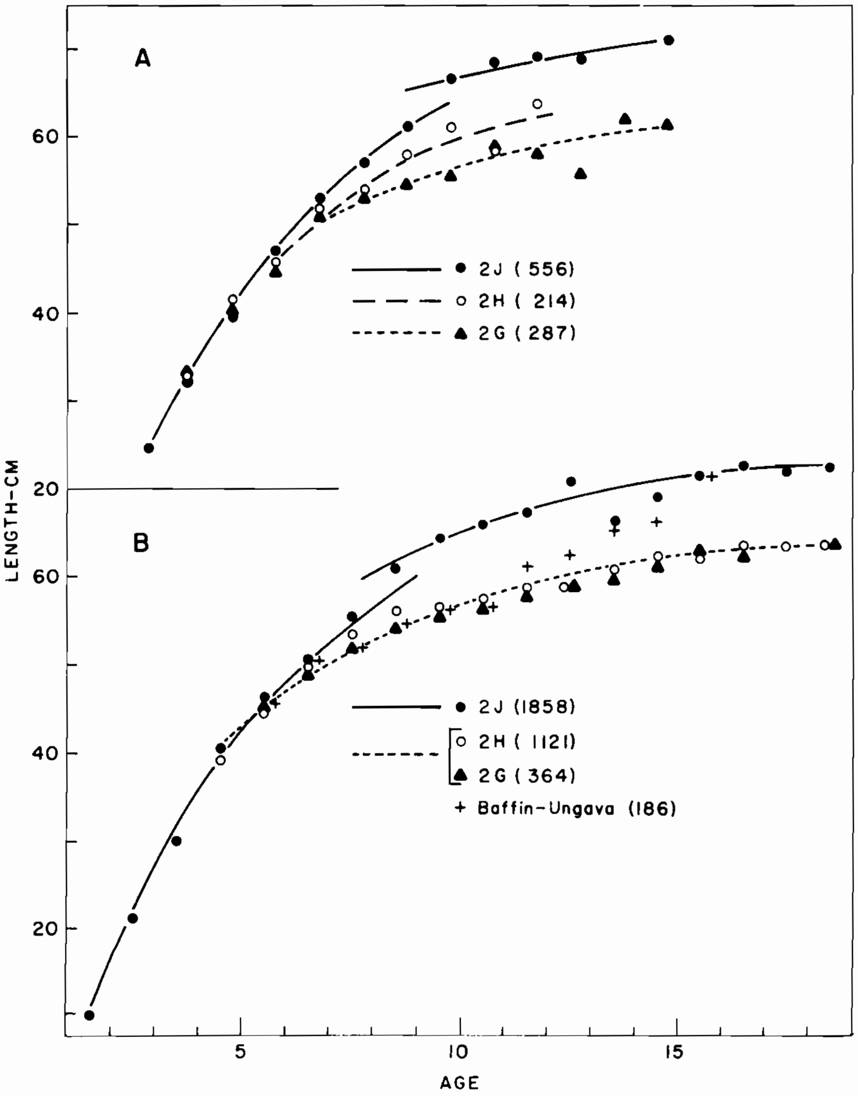

Figure 24. Average length at age from south to north.
A. October-November, 1964 (offshore);
B. July-August, 1963-64 (inshore), and southern Baffin Island to Ungava Bay, September, 1959. Numbers of fish are in brackets.

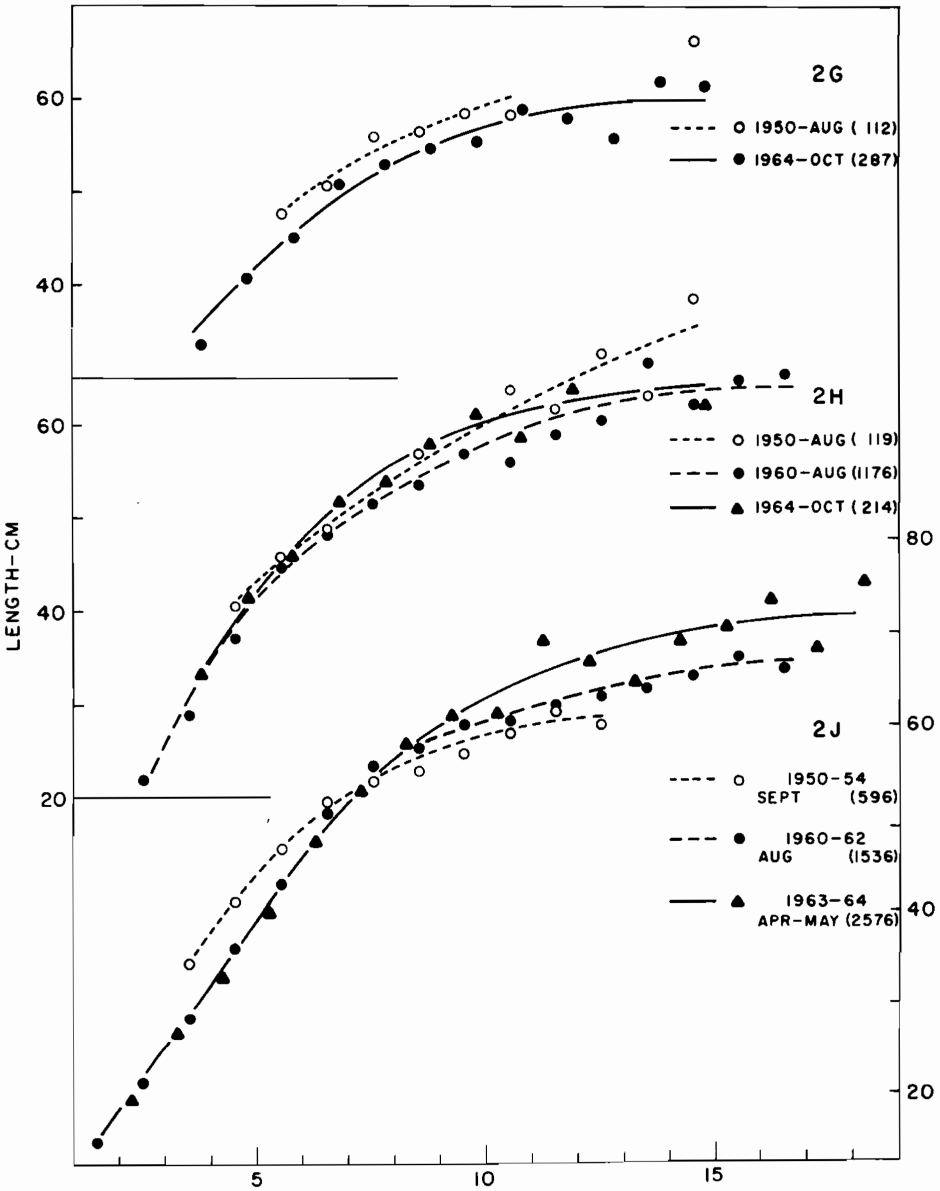

Figure 25. Average length at age from selected offshore data, 1950-64. Numbers of fish are in brackets.

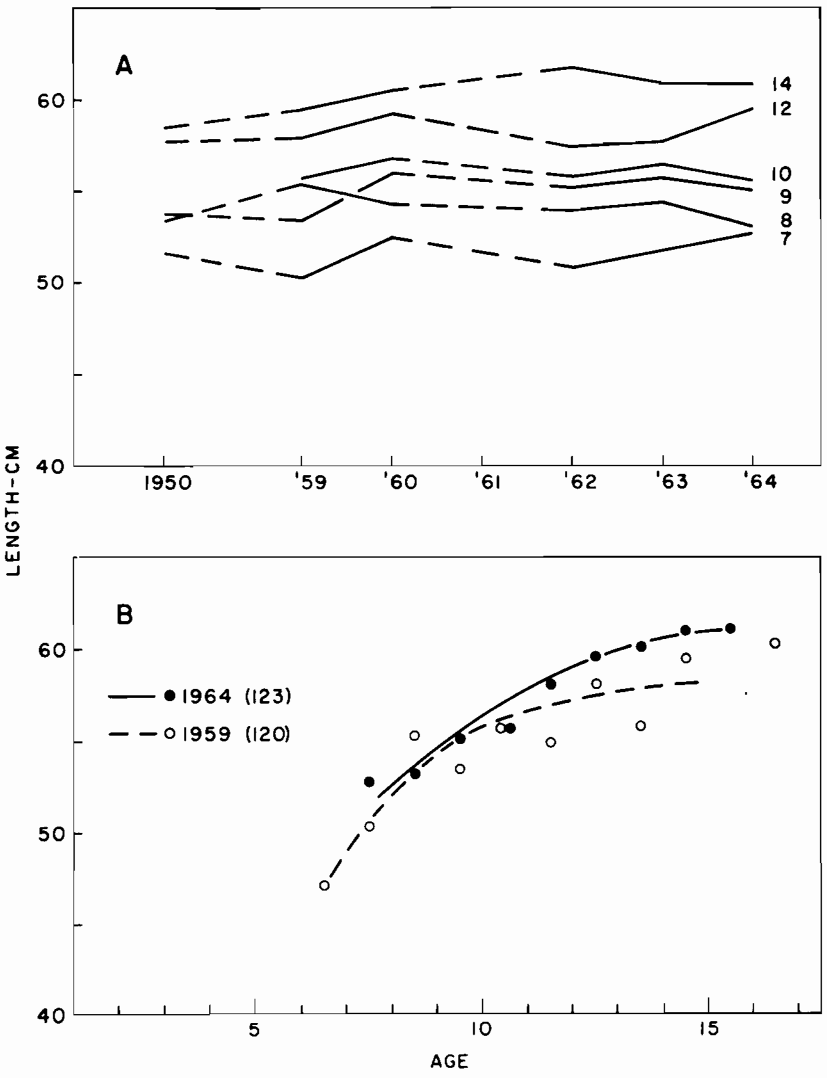

Figure 26. A. Trends in average length at age, Division 2G (inshore data).
B. Growth curves for 1959 and 1964. Numbers of fish are in brackets.

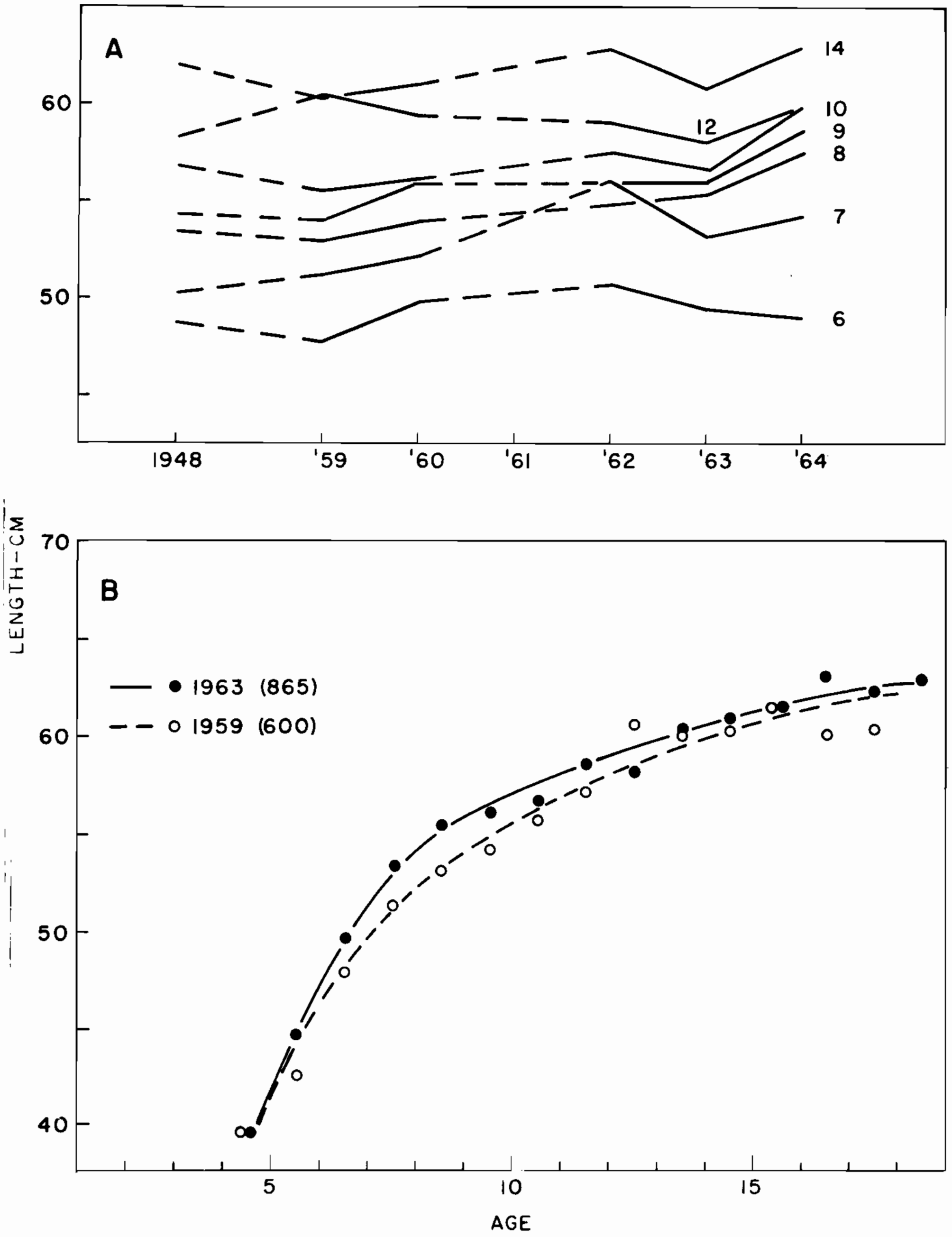

Figure 27. A. Trends in average length at age, Division 2H (inshore data).
B. Growth curves for 1959 and 1963. Numbers of fish are in brackets.

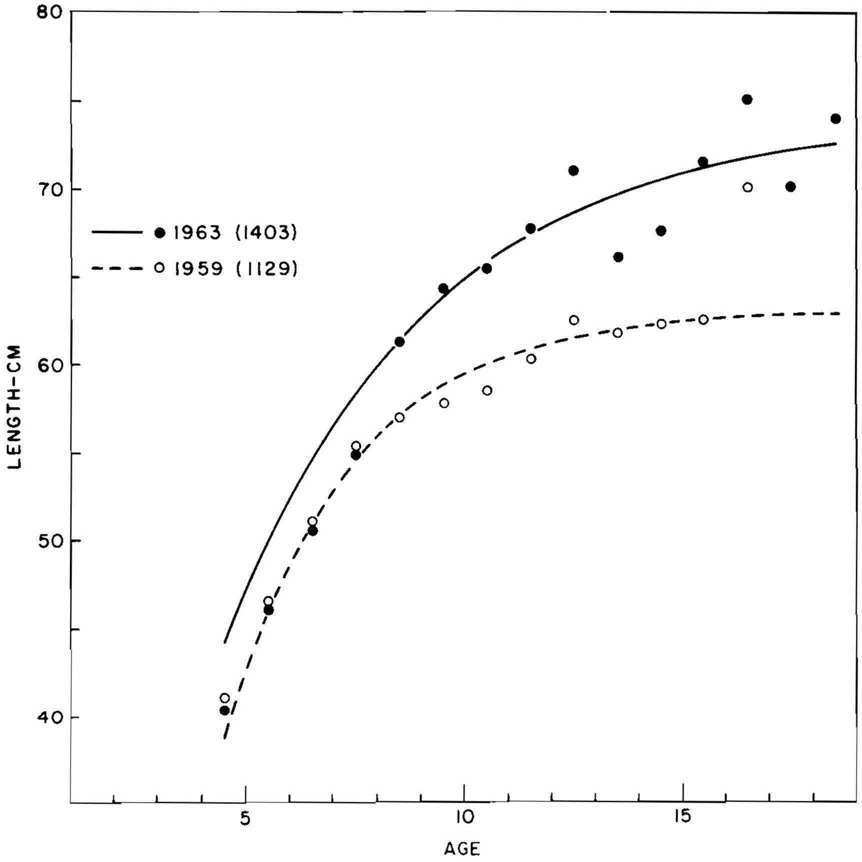

Figure 28. Growth curves for Division 2J, 1959 and 1963 (inshore data). The 1963 curve is fitted only between ages 8 and 18. Numbers of fish are in brackets.

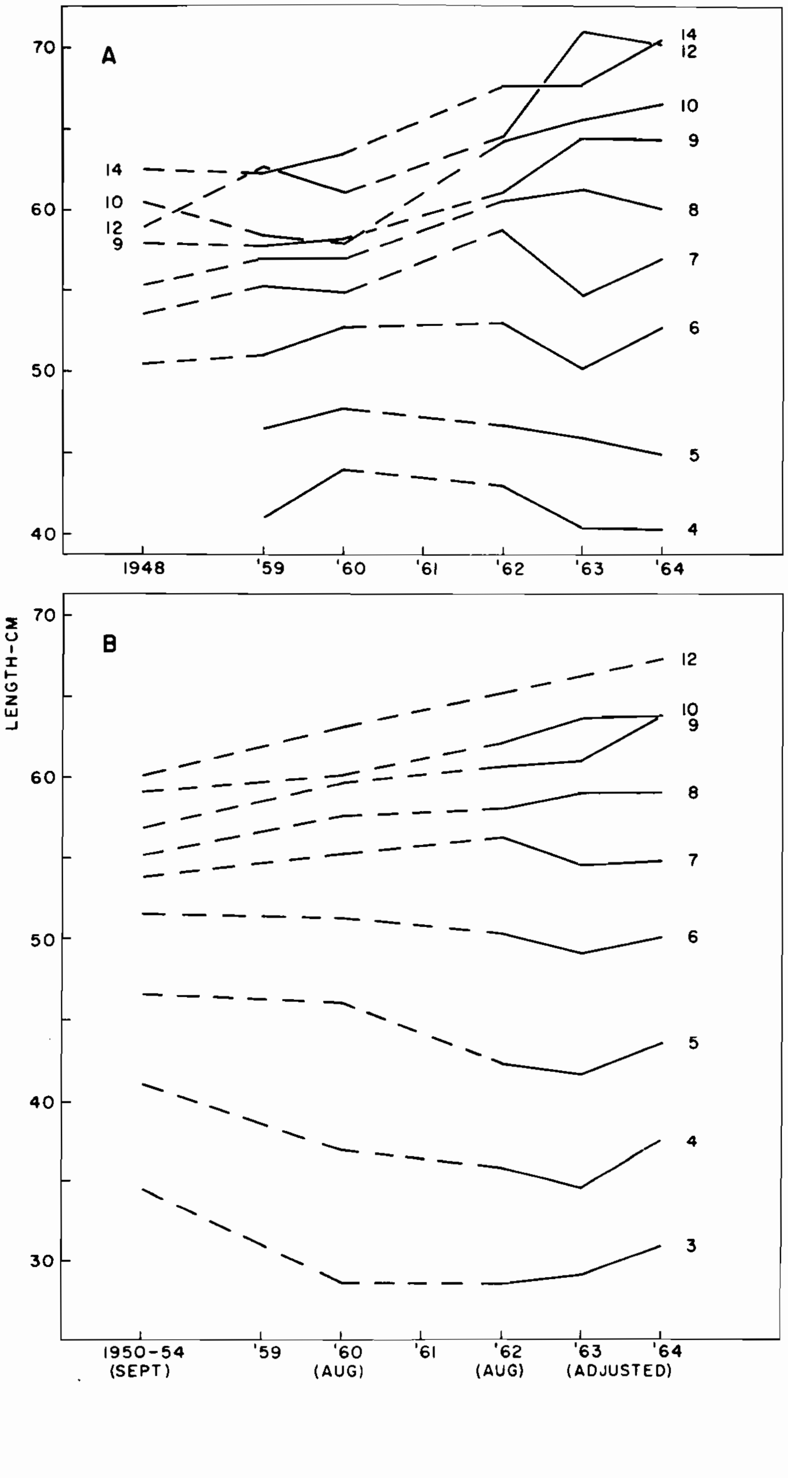

Figure 29. Trends in average length at age, Division 2J. A - inshore; B - offshore.

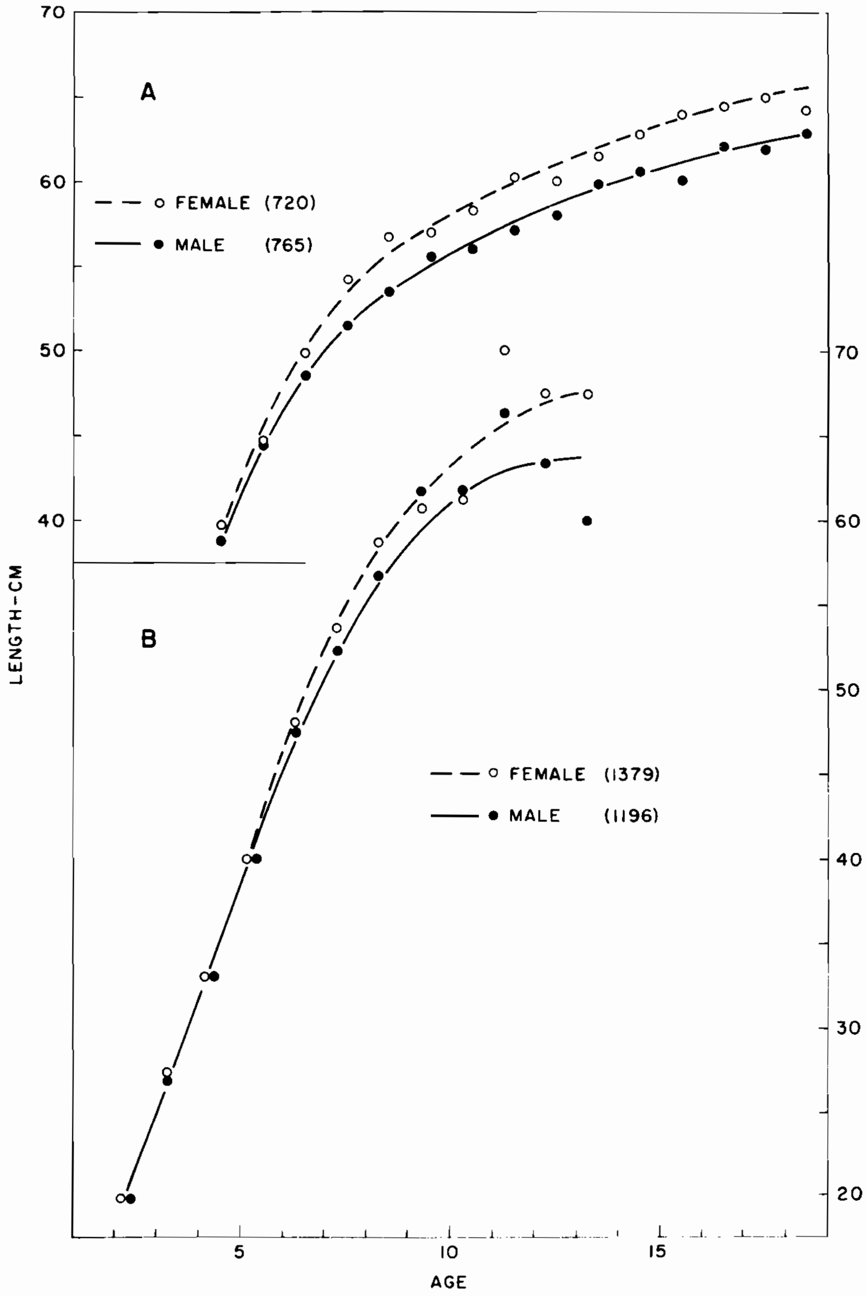

Figure 30. Growth curves for males and females. A. Divisions 2G and 2H (inshore), July-August, 1963-64; B. Division 2J (offshore), April-May, 1963-64. Numbers of fish are in brackets.

## The Length-Weight Relationship

Thompson (1917) drew attention to the principle that "in similar solid figures the surface increases as the square, and the volume as the cube, of the linear dimensions". If it is assumed that the weight of a fish is proportional to its volume, and that form and specific gravity do not change throughout its life, then the formula

$$w = kl^3$$

can be used to describe the length-weight relationship. The fish is said to grow "isometrically". Though most reported length-weight relationships approach this form, authors usually prefer to use the more general formula

$$w = kl^n$$

which is the "simple allometry formula" of Reeve and Huxley (1945), and which Huxley (1924) recognized as possibly expressing a general law of differential growth. Taking logarithms of each side the formula becomes

$$\log w = \log k + n \log l$$

i.e. a straight line relationship between log l and log w with slope n and intercept log k. Thus log-log plots of weight versus length should fall on a straight line if the formula holds throughout life.

Whole fresh weights and weights with viscera and gills removed were obtained for almost 10,000 specimens in the present study. Data for random samples and special "category" samples of the largest sized were combined. Because of the difficulty of obtaining accurate weights at sea, more than 80% of the data were collected inshore from 1959-64. Average weights were calculated for each centimetre length. Preliminary log-log plots revealed that the points for average weight at length were not distributed on a single straight line, but instead along two straight lines with the change occurring at 60 cm (Fig. 31). Accordingly two separate allometric functions were fitted to each series (Fig. 32), giving the following constants:

| | n | k |
|---|---|---|
| Whole weight to 60 cm | 2.83 | .00003864 |
| above 60 cm | 3.12 | .00001225 |
| Gutted-gilled weight to 60 cm | 2.77 | .00003939 |
| above 60 cm | 3.16 | .0007874 |

Only one or two specimens were available for occasional lengths above 100 cm, and these were not included in fitting the curves.

## Discussion and Conclusions

The unrestricted use of the simple allometry formula in fish length-weight descriptions has been criticized by Beverton and Holt (1957), who point out that the values of

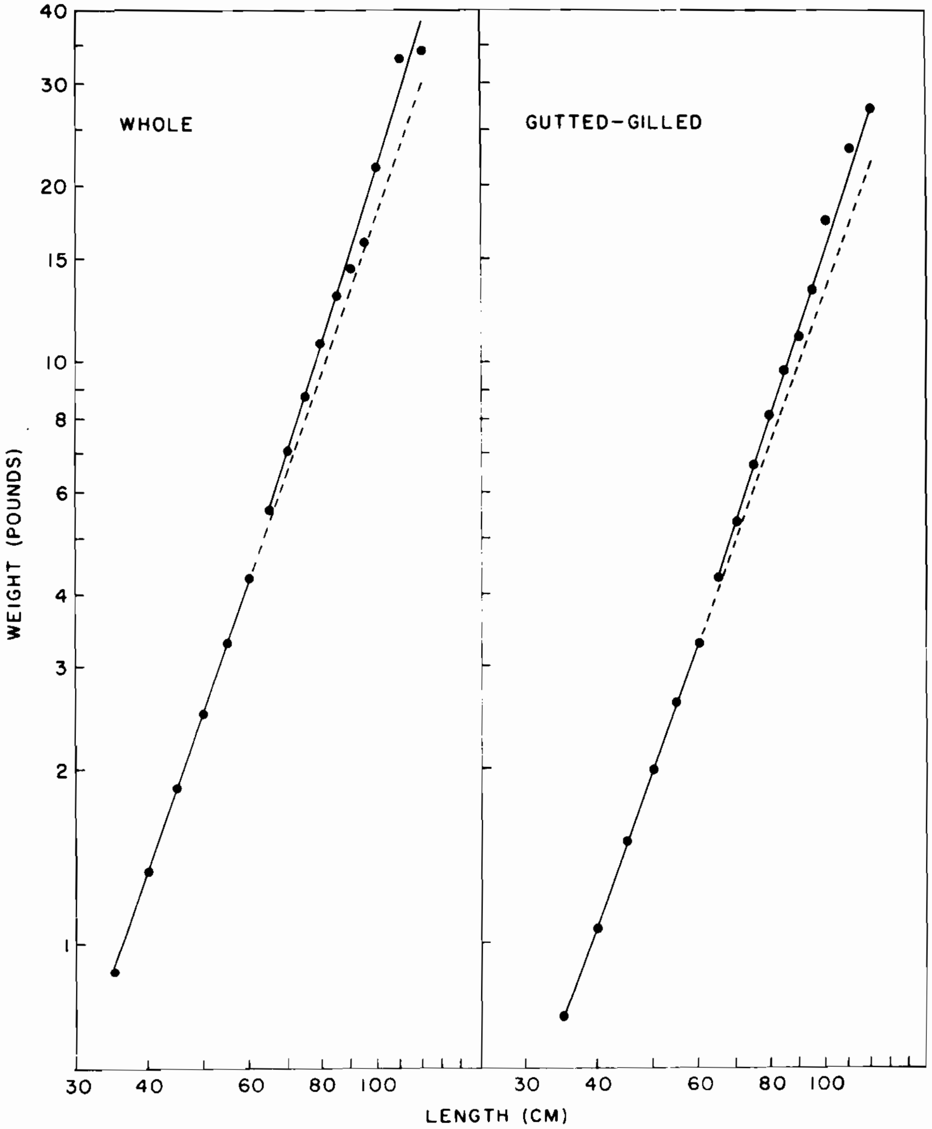

Figure 31. Length versus whole and gutted-gilled weights. Plots of every fifth average value to show distribution in each case along two log-log straight lines.

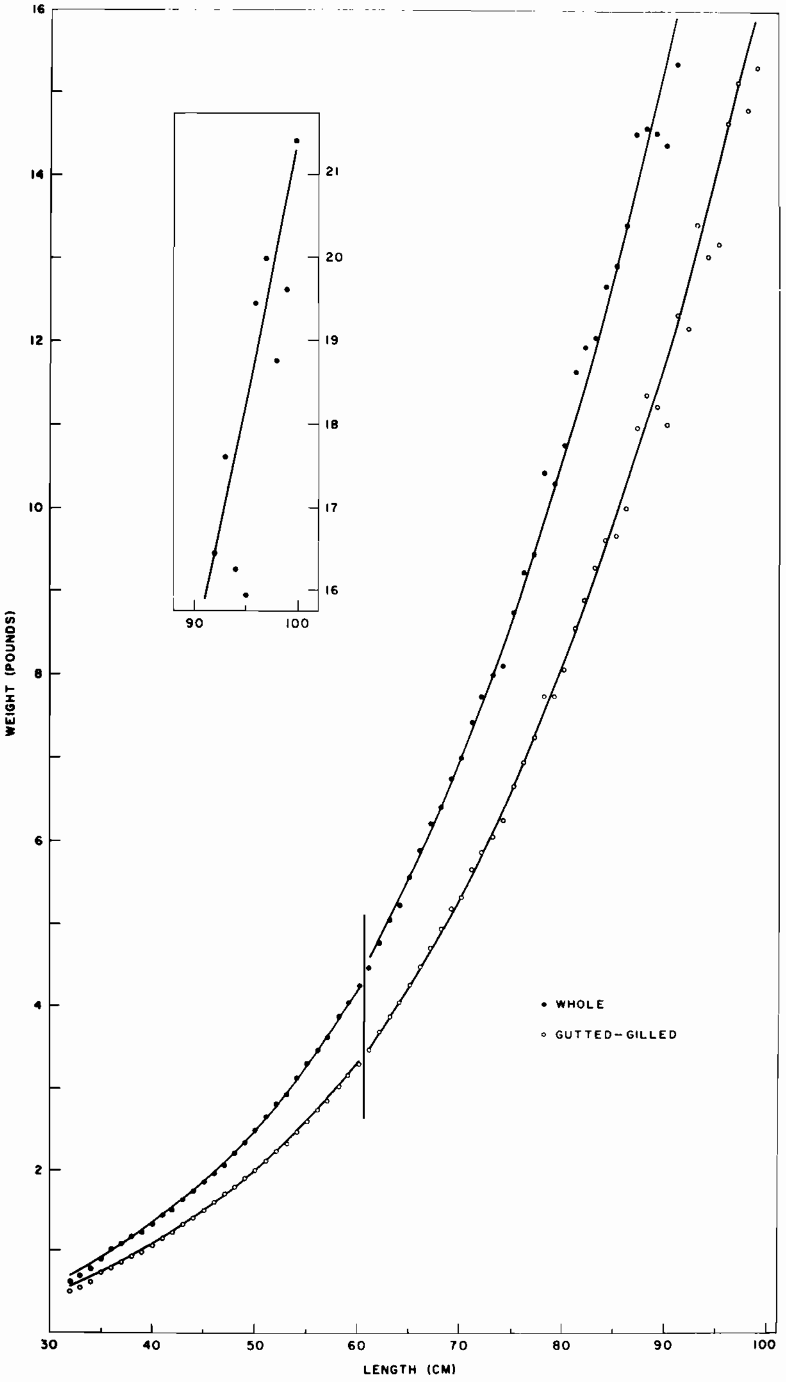

Figure 32. Average whole and gutted-gilled weights at each length, with fitted curves. Inset shows the upper portion of the whole weight curve.

the constants "may vary within wide limits for very similar data, and are sensitive to quite unimportant variations in the latter". They describe their length-weight data by the cubic equation (isometric growth) and incorporate this in their population model. While this is a simpler assumption, allometric functions can be incorporated as well (Paulik and Gales, 1964). A cubic equation could not describe the present data, as it would underestimate the weight values at the higher lengths and overestimate them at the lower.

The change at 60 cm is considered to be a real description of an actual change in the length-weight relationship, since it occurs in both the whole and gutted-gilled weights and since the averages from 40-70 cm are each based on weights of more than 100 specimens. Furthermore such a change has been noted for cod from the Grand Bank-St. Pierre Bank areas (ICNAF Divisions 3L, 3N, 30 and 3P), though here it occurs at about 90 cm (Williamson, MS, 1965). The reason for such a change is not easy to postulate, but it may be related to a metabolic change (possibly more food intake per unit body weight or lesser activity) at a certain age. Cod of average length 60 cm were age 10 in Labrador in 1959, age 8 in 1963. Cod of age 10 on the southern Grand Bank have an average length of almost 90 cm (May _et al_, 1965).

While the change in the length-weight relationship is of biological interest it raises some practical problems for incorporation in yield equations. However since the equations fitted to lengths up to 60 cm do not seriously underestimate average weights for lengths to about 80 cm (<10%), and since fish above 80 cm are extremely scarce in the area (Figs. 14-18), these equations can probably be used as representative of length-weight for practical purposes.

It was noted in Section 1 that the heaviest cod recorded was 211¼ lb (Bigelow and Schroeder, 1953) and the largest 251 cm (Storer, 1858). The whole weight of the latter, predicted from the length-weight relationship given here, would be 380 lb. The largest and heaviest cod taken in the Labrador collections was 144 cm and 71 lb whole weight, though this was not the oldest fish taken (age 20 as against two specimens of age 26). It is of interest to note that this length is almost double that of the calculated $L_\infty$ of 74 cm for recent Division 2J data. However the calculated $L_\infty$ is an average value for the population and cannot be considered as a maximum attainable length for individuals.

Growth data from Labrador prior to 1959 are available from studies by Thompson (1943), Ancellin (1953), Ruivo (1957), May (1959) and Fleming (1960). The data of May (1959) and Fleming (1960) were incorporated here. Thompson's (1943) material is not comparable since scales were used to determine age (Section 4). From the present study no trends were apparent from 1950-59 in Division 2G and from 1948-59 in Divisions 2H and 2J. It is difficult to compare the data with those of other authors because of seasonal differences in the time of collection. However Fleming (1960) has compared his 1948 material with that of Ancellin (1953) and Ruivo (1957). Ancellin's data are for 1952 and his averages are generally 4-5 cm higher than those of Fleming for 1948 material. However Ancellin's collections were made at the end of August and from southern Labrador only, while Fleming's were made from July 8 to August 30 (July 8-16 in southern Labrador) and included northern Labrador as well. Ruivo's data are for 1955 and his averages close to those of Fleming's 1948 averages. Figueras (1963b) gives averages for southern Labrador from collections made in September-December, 1960 which are usually 3-4 cm above those for 1960 offshore data shown here, based on August collections. This order of difference is therefore to be expected. Growth differences can also occur through different interpretation of otolith ages, but in view of the seasonal variation in collection times and annual variation in growth evident from Figs. 26A, 27A and 29, it seems likely that these are the responsible factors for the differences noted. In any case there is no apparent trend in average lengths to 1959, though growth has increased from age 7 onwards since then, particularly in Division 2J and particularly in 1962-64. The value of $L_{\infty}$ in this area has increased from 63 cm in 1959 to 65 cm in 1960-62 (May _et_ _al_, 1965) to 74 cm in 1963.

Two aspects of this increase are of particular interest: first that the increase is very much less in the north than in the south, and second that it is not general for all ages. Ages below 7 in Division 2J seem to have declined in average size if anything. Prior to 1963 growth in Division 2J was only slightly greater than in Division 2H (May et al, 1965) with $L_\infty$ and k in the former area 65 cm and 0.31 and in the latter 64 cm and 0.24. Data for Divisions 2G and 2H in 1963-64 gave an $L_\infty$ of 65 cm and k of 0.20. The fact that a slight cline in growth was previously evident, and that growth has increased so markedly in the south and so little in the north, is indicative of relatively little mixing between the populations in each area.

Variations in cod growth with time in West Greenland have been associated with temperature (higher temperatures give higher mean lengths) by Hermann and Hansen (1965). Differences in growth between areas have also been associated with temperature (Taylor, 1958a; Jonsson, 1965; May et al, 1965). The effect of temperature is usually considered to be indirect, through its influence on feeding, food assimilation and distribution of the predator and prey. Kohler (1964), in aquarium experiments, found correlations between temperature and food consumption and correlations between food consumption and growth, but a direct temperature-growth correlation could not be demonstrated. Taylor (1958a) suggests that if "temperature-dependent changes should occur, they might be mistakenly interpreted as effects of fishing".

It is virtually impossible that the growth changes observed in Division 2J were due to temperature changes. The whole Labrador area is under the influence of the Labrador Current, and any growth changes due to temperature would have to be general throughout the area, and for all ages. The fact that they occurred only in the area heavily fished since 1960 (Fig. 3A), and only for those ages taken in quantity by the fishery, strongly suggests that the thinning out of the older ages through fishing was in fact the responsible factor. Kohler (1964) attributes changes in cod growth in the western Gulf of St. Lawrence to actual changes in food supply plus changes in competition for food as a result of density changes due to fishing. Williamson (MS, 1965) considers that increased growth of cod from the southern Grand Bank is at least partly due to increased fishing.

Reported mesh sizes in use in the offshore fishery are of the order of 110-120 mm (Table 3). Hodder and May (1965) report 50% retention lengths for mesh sizes within this range of about 40 cm, with 25-75% selection spans of about 10 cm, and suggest that higher 50% retention lengths are possible for much used gear in which large catches have been obtained. The 50% retention length for a nominal 120-mm mesh in such a situation was 47.5 cm and the 25-75% selection span 10.5 cm. Full selection does not occur until the fish have attained lengths above 50 cm. No selection data for inshore Labrador gears are available, but Boulanger's (MS, 1962) value for 50% retention length of a codtrap with 4½-inch nylon back is 48 cm. The average lengths of age 7 fish inshore and offshore during the 1959-64 period (summer data) were about 55 cm (e.g. Fig. 28). While there is fairly large variation in length within any age (Table 4) it appears that growth has increased only for those ages in which most of the individuals are beyond the selection range of the various gears.

Area differences in cod growth within the Labrador-Newfoundland area have been associated indirectly with decrease in the volume of cold water ($<0^\circ C$) in the Labrador Current from north to south, i.e. this is used as an indicator of generally warmer conditions in southern areas (May et al, 1965). Values of $L_\infty$ increase from north to south, while values of k decrease . Taylor (1958a) presents data showing that $L_\infty$ decreases with increasing temperature, while k increases. No data for the Labrador-Newfoundland area are included, and the opposite findings are not easily reconciled. However Taylor's results should perhaps be regarded with caution in view of the short-term non-temperature-controlled changes demonstrated here (his data covered a period of 30 years from widely different areas), his use of surface temperatures as an indicator of cod thermal environment, and his calculation of some $L_\infty$ values (up to 200.3 cm) higher than any likely to occur in natural populations.

A further point of interest in the growth data is the "levelling-off" in growth at ages 9-11 and subsequent increase. It is noticeable particularly in the Baffin Island-

Ungava Bay data (Fig. 24B), also in the Division 2H inshore data in the same figure, and generally for those growth curves having substantial data beyond these ages (Figs. 22, 25 - Division 2J, 27B, 28 - 1959 data) and is evident for the sexes separately in Fig. 30A. The phenomenon was noted by Thompson (1943) though no doubt exaggerated in his curves because of the use of scale ages. It has also been reported by Poulsen (MS, 1957) for West Greenland cod, and for other northwest Atlantic areas by Fleming (1960) and May _et_ _al_ (1965), and has been attributed to a possible change to a more substantial diet, as these old and large cod probably consume relatively more fish (including younger and smaller cod) than smaller individuals. Powles (1958) shows that fish are the main food item of cod from 71-100 cm in length in the southwest Gulf of St. Lawrence; of much lesser importance in smaller sizes.

The fact that average size of females is larger than that of males is almost a universal finding in fisheries biology, and was previously noted for the Labrador-Newfoundland area cod by Fleming (1960). It is usually associated with earlier maturation in males (Section 7), resulting in slowed growth due to development of the gonads. This is not entirely satisfactory since immature females are usually larger than immature males, though by a much lesser amount.

## 7. MATURITY AND SPAWNING

### Introduction

Size and age at first maturity in fishes are related to rate of growth. Whether attained size or attained age is the most important factor is often not clear from the fairly large literature on the subject. The question is thoroughly reviewed by Alm (1959), who also presents evidence from several species raised in small lakes, and who concludes that "in different populations of the same species ... the age for maturity depends mainly on size, thus indirectly on the growth rate". In view of the growth changes described in Section 6, it is of interest to examine size and age at maturity over the period.

Size and age at first maturity in cod are known to vary widely between areas (Wise, 1961). Previous information for the northwest Atlantic is given by Hansen (1949) for West Greenland, Fleming (1960) for the Labrador-Newfoundland area and Powles (1958) for the southwest Gulf of St. Lawrence. Within the Labrador-Newfoundland area both size and age at first maturity increase from north to south (Fleming, 1960), even though greater growth is achieved in the southern areas.

The required data for relation of maturity to age and size may be obtained by field observations of the appearance of the gonads. The macroscopic appearance is usually sufficient. An alternate method for age at first maturity is to count the number of "spawning zones" in the otoliths (Rollefsen, 1933). This was found to be impractical in the present investigation since the first such zone often could not be determined with any degree of confidence. The results of exchanges of Labrador-Newfoundland area cod otoliths among biologists in various countries, sponsored by ICNAF, indicate much disagreement in locating the first spawning zone. Accordingly size and age at maturity were determined from field observations of the gonads.

Histological changes in cod gonads throughout the annual sexual cycle are described by Sorokin (1957, 1960). Hermaphroditism occurs rarely (Howes, 1891; Williamson, 1905). Several early descriptions of the spawning act are repeated by Templeman (1958). Reproductive behaviour in aquaria is described by Brawn (1961).

## Material and Method

Observations on stage of maturity were made for all the material described in Section 3, i.e. the complete collection of some 20,000 specimens. Random samples only were used in relating maturity and age. Special samples of size categories were included in determining length at maturity.

The gonads were classified into a number of maturity stages, depending on their appearance, using a system devised by Dr. W. Templeman, Director of the St. John's Biological Station and in use at that Station for a number of years. For present purposes these stages were combined into four general categories for each sex, as described below.

MALES

Immature. Testes narrow and fairly straight. Vas deferens narrow and thin-walled.

Pre-spawning. Testes increased in volume. Lobular appearance. Pink in early stages, becoming white in late stages. No milt in vas deferens.

Spawning. Testes white and distended. Milt running freely.

Post-spawning. Testes shrunken and reddish in early stages. Residual milt sometimes present at inner edges. Vas deferens wide and often filled with residual milt. Recovery first noticeable as pink colouration of outer edges. Residual milt gradually lost or resorbed. Passes gradually into pre-spawning stage as season progresses.

FEMALES

Immature. Ovaries small. Pink to orange. Wall thin and transparent. No eggs visible.

Pre-spawning. Ovaries enlarged. Small opaque eggs visible in early stages, becoming larger and transparent in later stages.

Spawning. More than half of eggs transparent in early stages. Ovaries gradually becoming flaccid with a few thousand clear eggs remaining in later stages.

Post-spawning. Ovaries shrunken and purplish. Wall thick and tough. Residual transparent or white eggs sometimes present. Passes gradually into pre-spawning stage as season progresses.

One difficulty arises in this or any other description (e.g. "recovering" stage of Powles, 1958), and that is the maturity classification of small fish some months after spawning is complete. Small mature fish recover from spawning very quickly and their gonads often revert to an immature appearance between one spawning and the next, i.e. as they pass from the post-spawning to the pre-spawning category. Thus a seemingly immature fish midway through the annual cycle may actually have spawned at least once before. At the same time it is often difficult to determine whether a pre-spawning fish has or has not spawned previously, and this difficulty increases as the cycle progresses. If it has not it is technically immature. For present purposes all such individuals were considered mature. It is evident however that attainment of first maturity can only be determined with confidence from data collected immediately prior to, during and immediately after the spawning period.

Length and age at maturity were determined by tabulating numbers immature and mature for each age, and separately for each 3-cm length group, and calculating percent mature for each.

## Seasonal Cycle in Maturity

Since data were collected only from April to November, examination of the complete seasonal cycle was not possible. However it is apparent from a combination of inshore and offshore material for 1958-64 from Division 2J (Fig. 33A) that spawning in this area probably begins in March. The April data were actually collected from April 2-16 and by this time 82% of the males and 75% of the females had either completed or were in the process of spawning.

The largest sizes are usually the last to spawn. Average lengths of males and females of each maturity category for combined April data (Fig. 33B) show a progressive decline from pre-spawning to post-spawning individuals.

Spawning is virtually complete by the end of May, yet a few individuals are still in the pre-spawning or spawning stages during June-August. The distribution of these by sexes inshore and offshore (1958-64) is given below.

| | Pre-spawning and spawning | | Total Mature | |
|---|---|---|---|---|
| | Inshore | Offshore | Inshore | Offshore |
| Male | 90 | 7 | 2368 | 529 |
| Female | 65 | 1 | 2164 | 447 |

Tests of the significance of the difference in proportions for each sex show that the inshore and offshore proportions are significantly different for each (t for males = 2.87, t for females = 3.41, t at P of .01 = 2.58).

## Size and Age at Maturity

It was previously noted that size and age at maturity are most accurately determined close to or during time of spawning. This requirement was met only in Division 2J in 1963-64. However, in order to effect comparisons summer data from other areas and periods have been used, where material over the maturity range was sufficient, and with the stated limitations taken into account. Material collected offshore during October-November was unsuitable for the purpose. Inshore data were generally unsatisfactory because of the small numbers of immature cod taken (Table 6), with the exception of the collections from Division 2J in 1963-64.

The best series of data (April, 1963) were examined for effect of attained size on maturity. The material was separated by sex, and average lengths of immature and mature individuals determined for each age over the age range from 0% mature to 100% mature. Average lengths of mature fish were higher than those of immature fish at each age for both sexes (Fig. 34). It is obvious that those fish which have grown fastest are the first to mature.

Variation in size and age at maturity was examined in relation to area (inshore-offshore and north-south), time and sex, and percents mature plotted for each length and age over the maturity range (Figs. 35 and 36). Trend lines were drawn by eye.

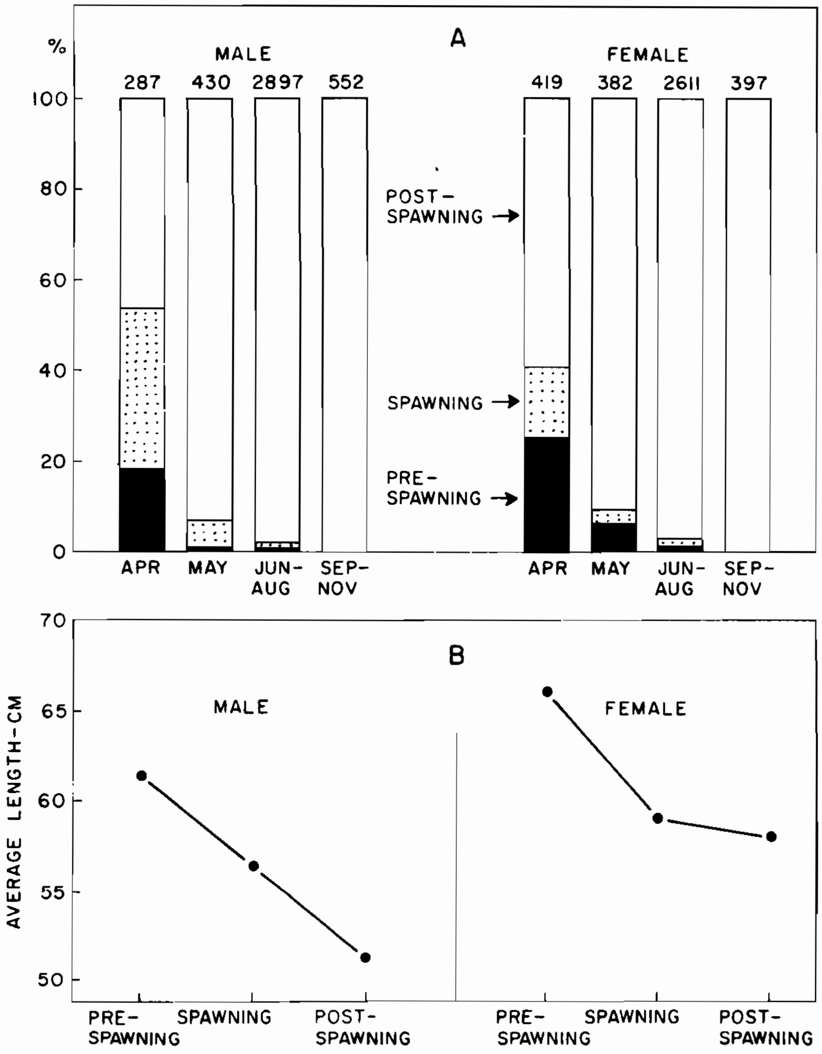

Figure 33. A. Seasonal cycle of maturity in mature males and females from Division 2J based on data from 1958-64. Numbers refer to numbers of fish. B. Average length of male and female cod at each stage of maturation, April, 1963-64.

The inshore-offshore comparisons were made from 1963-64 Division 2J data (Fig. 35A). There is no consistent difference in length at maturity, but age at maturity appears less inshore. From south to north (Fig. 35B) length at maturity appears less in the north (though the curves cross over at the bottom), while age at maturity appears greater. No change in length at maturity is apparent from 1950-62 (Fig. 36A), but has possibly increased in 1963-64. Age at maturity shows a general increase over the period.

Considering the sexes separately for the most reliable data, it is evident (Fig. 36B) that males attain maturity at a smaller size and younger age than females. Maturity occurs over a wide range of lengths and ages. In males it occurs over a length range of 37-61 cm (mid-points of 3-cm groups from first mature individuals to 100% mature); in females over a length range of 40-73 cm. The corresponding age ranges are 4-8 for males and 5-11 for females. The lengths and ages at which 50% of the individuals attain maturity, with the 25-75% ranges, allow more meaningful comparison. These were estimated from straight lines through plots of the data on probability paper and are listed below. Values are also given for the combined spring data (shown in Fig. 36A).

| | Males | Females | Combined |
|---|---|---|---|
| Length at 50% maturity (cm) | 43.9 | 49.8 | 47.2 |
| 25-75% range (cm) | 41.2-46.6 | 46.8-52.8 | 43.4-51.0 |
| Age at 50% maturity | 5.8 | 6.5 | 6.2 |
| 25-75% range | 5.3-6.3 | 6.0-7.0 | 5.7-6.7 |

## Discussion and Conclusions

Earll (1880) noted that spawning cod did not shed all their eggs at once and supposed that the fish must release eggs gradually over the spawning season, or deposit them at intervals. Sorokin (1957), from histological examination of ovaries, concluded that the spawning period of cod was of relatively long duration and that at least three separate periods of release occurred. The possible adaptive significance of this phenomenon for fish in general is considered by Nikolsky (1953) who points out that in some species the interval between deposition of individual batches of eggs is similar to the duration of the first stage of active feeding by the fry. Thus each new group of fry begin active feeding at a time when the food spectrum of the previous group has altered. He also suggests that the size of the individual batches of eggs may be related to the available supply of suitable food for the young stages. This appears to presuppose a self-regulatory mechanism of the type proposed by Wynne-Edwards (1965). Krivobok (1963) explains duration of the spawning season in Baltic herring in terms of individual fecundity differences. He shows that in fish

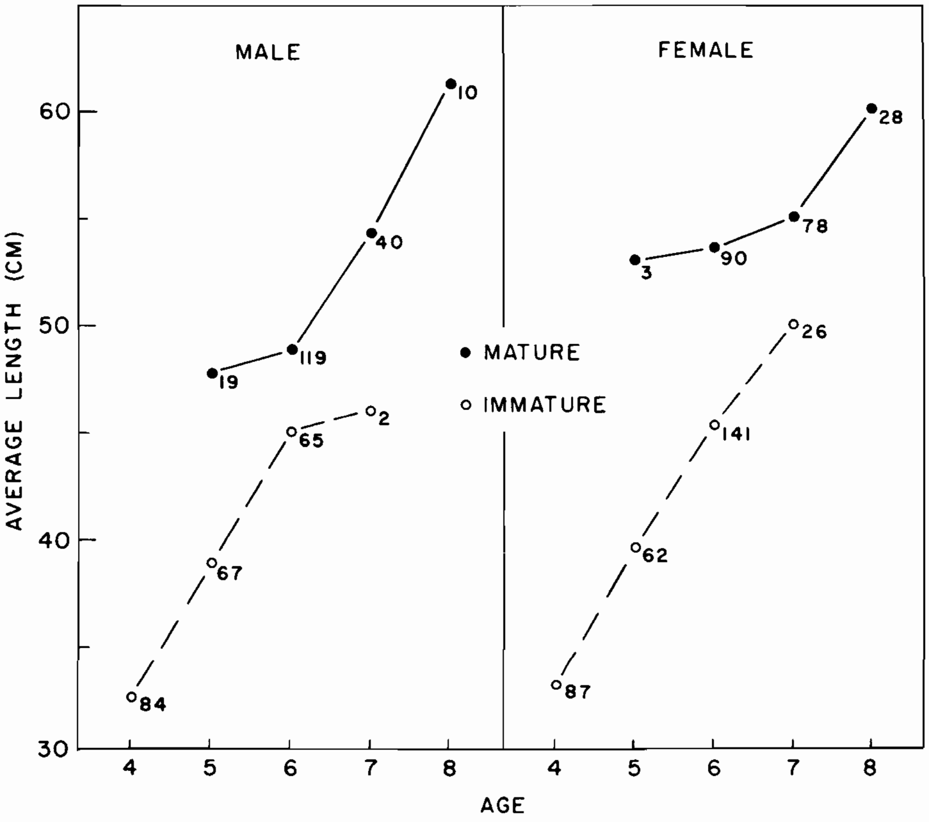

Figure 34. Average length at age, mature versus immature fish, Division 2J offshore, April, 1963. Numbers at each point are numbers of fish.

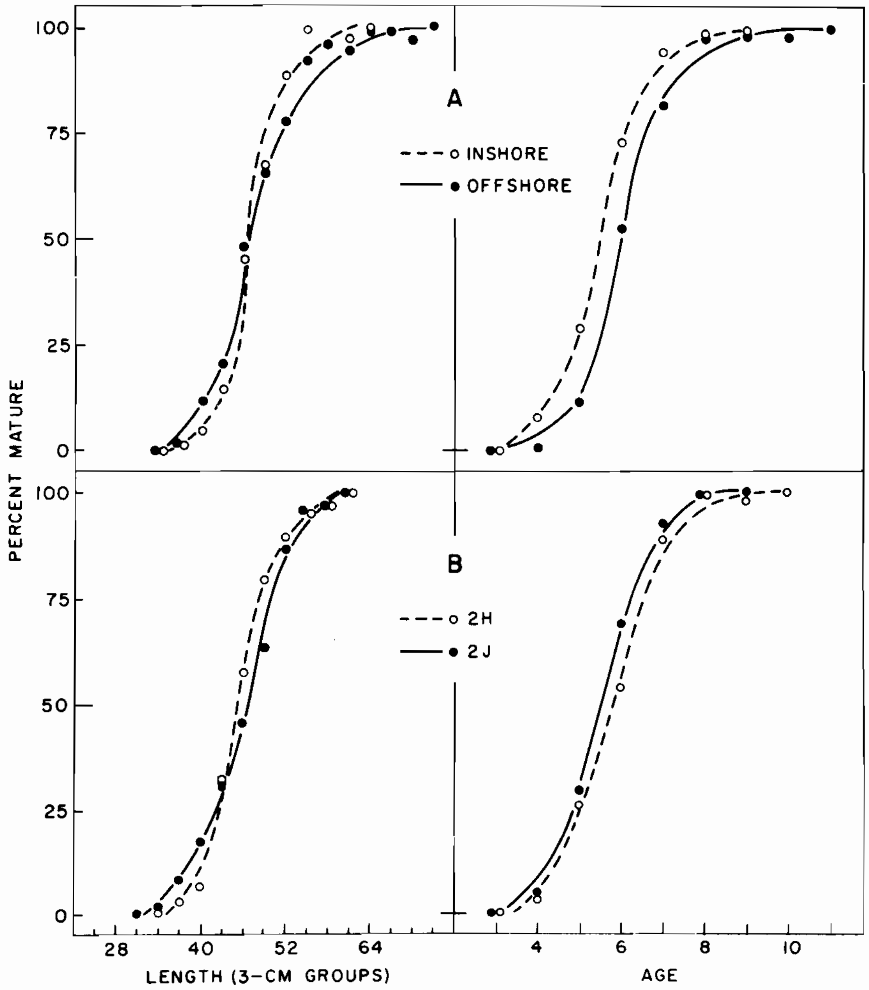

Figure 35. Length and age at maturity. A. Division 2J inshore, July-August, 1963-64; Division 2J offshore, April-May, 1963-64. B. Division 2H offshore, July-Sept., 1959-60; Division 2J offshore, June-Sept., 1958-62.

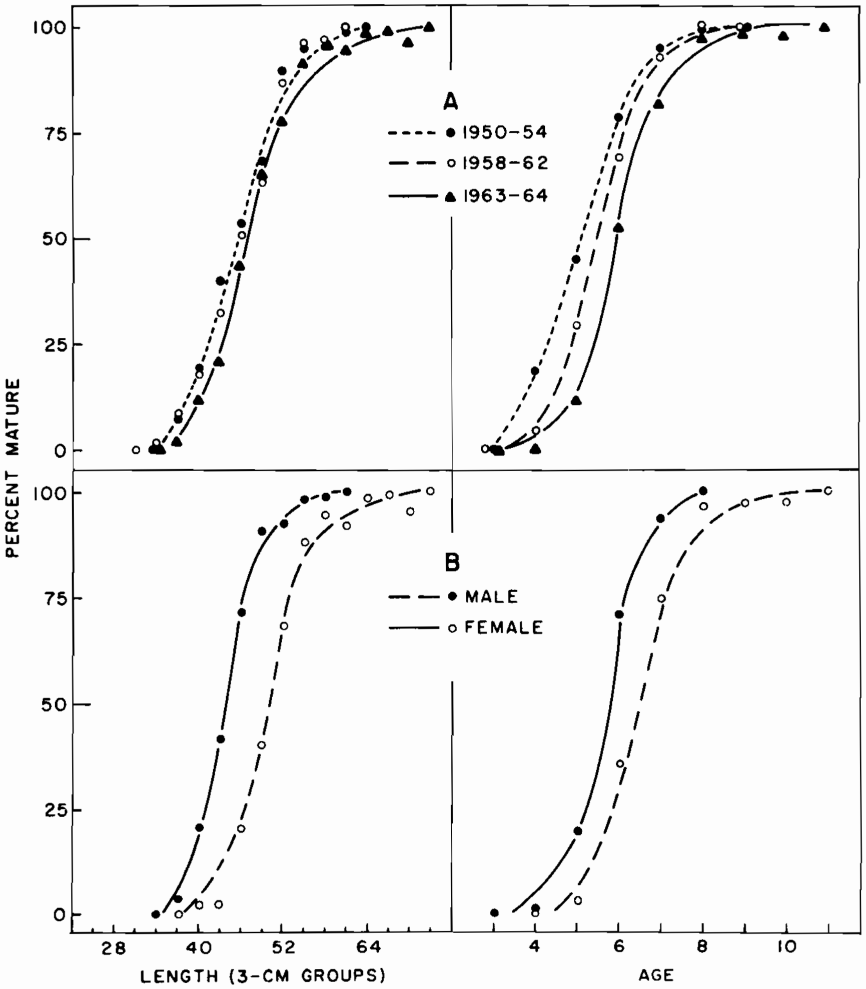

Figure 36. Length and age at maturity. A. July-Sept., 1950-54; June-Sept., 1958-62; April-May, 1963-64. B. Males and females, April-May, 1963-64. All data are from Division 2J offshore.

of the same length those with low fecundity are the first to spawn. It has been shown here that time of spawning is delayed with increase in size. The largest sizes are most fecund (Section 8).

It appears then that fish have at least two general ways of prolonging the spawning season, i.e. successive liberation of batches of eggs and earlier spawning of less fecund individuals. Prolongation of the spawning season is undoubtedly of selective value in northern forms inhabiting an environment in which the short season of high biological production and appearance of suitable food for the young may vary in timing from year to year. The cod spawning season is of about 3-6 months duration in most of its range (Wise, 1961; Powles, 1958; Kazanova and Pertseva-Ostroumova, 1960), though the period of peak spawning is much less.

Thompson (1943) placed the time of maximum spawning on the Grand Bank as early June, and assumed that it must be later in Labrador because of lower temperature conditions. More recent (unpublished) data of the St. John's Biological Station indicates that time of maximum spawning is delayed from north to south, e.g. being mainly in April and May on the northern Grand Bank and mainly during the last half of May on the southern Grand Bank. Powles (1958) reports peak spawning in the southwest Gulf of St. Lawrence in June.

Cod from New England however spawn mainly in December (Bigelow and Schroeder, 1953). West Greenland fjord stocks spawn mainly in May-June (Hansen, 1949). The present study has indicated that time of maximum spawning in southern Labrador is March. Postolaky (1965) reports concentrations of pre-spawning and spawning cod in northern Labrador in mid-March.

Environmental temperature is undoubtedly of importance in relation to spawning. The principle has been referred to as Orton's Rule as he was apparently the first to state it precisely (Orton, 1920). However Wise (1961) gives a wide range of spawning temperatures in nature for cod (0-12°C). It appears that cod in the Labrador area locate the necessary temperature conditions by moving into the relatively deep and warm "slope water". Postolaky (1965) gives depths and temperatures for northern Labrador of 150-190 fathoms and 2.0-3.5°C. The corresponding figures for southern Labrador are 125-180 fathoms and 2.5-3.1°C (Templeman and May, 1965). Both reports are based on observations made in 1963. It seems likely that within the Labrador-Newfoundland area generally spawning may occur at similar temperatures.

The delay in spawning time from north to south is probably an adaptation to life in the Labrador Current. Early spawning is necessary in the north to ensure a long developmental period in the cold surface layers with subsequent drift to areas for favourable settlement in the south (see Section 3). Later spawning in more southerly areas allows a reduced hatching time in the now warmer surface waters, and consequently reduced drift. The fjord stocks of west Greenland spawn at a time when temperatures in the surface layers are higher than those in the spawning depths, thus probably at the most suitable time for rapid development and minimal larval drift away from the coast. The winter spawning of New England cod is probably related to their position at the southern extreme of the species' range.

The spawning season in a number of species in British waters is considered in relation to their range (i.e. Arctic-Boreal versus Mediterranean-Boreal) by Qasim (1956). Here the Mediterranean-Boreal forms show a more extended breeding season than the Arctic-Boreal forms, and breed during warmer periods. Both findings are probably explainable in terms of the position of the species concerned in the northern parts of their ranges. However Qasim (1956) argues further that sufficient food in the breeding seasons of southern forms allows liberation of successive batches of eggs, while northern forms "spawn at a season which is not very favourable for feeding (of adults), so the females put all their reserves into a single batch". He points out that the maturing eggs of northern forms are all of similar size. Cod is included as a northern form but previous descriptions (see first paragraph of this discussion) do not agree with this one. Qasim

(1956) gives the size range of maturing cod eggs as 1.2-1.4 mm, referring to Fulton (1891). However Fulton states quite clearly that these were measurements of "clear eggs", and gave diameters of opaque yolky eggs as 0.5-0.8 mm. Neither does Qasim (1956) mention Fulton's (1891) proposal that species with high fecundity (of which cod is one) probably did not release all their eggs at once. Measurements of maturing eggs in the present study gave a range of 0.4-1.1 mm for yolky eggs during the spawning season (Section 8). Egg measurements for several other of Qasim's (1956) northern species are similarly misinterpreted from Fulton (1891). It is possible that intra-ovarian egg sizes from Qasim's northern forms are distributed in a broad normal distribution, while those from the southern forms (as his measurements for a single species suggest) are distributed over an equally broad range but in a polymodal distribution. Thus his conclusions may be sound, though the descriptions inadequate.

It was noted that while spawning in Labrador is almost complete by the end of May, significant proportions of prespawning and spawning individuals were taken inshore in July-August. This is possibly an indication of some inshore-offshore stock separation. Such local stocks are known to occur in other areas (Hansen, 1949), and Thompson (1943) refers to an account by Munn (1922) of coastal spawning in Newfoundland.

Turning to a consideration of the described variations in length and age at maturity in Labrador, it was noted that age at maturity is apparently lower inshore (Fig. 35A). This may or may not be real, depending on its cause. Three alternatives are possible.

(1) Because of the stated difficulty in determining maturity in small fish several months after spawning, fish which were actually immature may have been called mature. The effect would be an increase in percent mature at each age, and apparent reduction in age at maturity. Such an effect should also show up in the length-maturity relation. However the inshore collections were taken several months later in the year when the fish would be expected to have grown several cm. If the inshore length maturity curve were displaced a 3-cm group to the right it is apparent that the opposite problem in determining maturities, i.e. calling mature fish immature, is more likely to have occurred.

(2) An apparent higher age at maturity inshore could be caused by gear selection since only the larger fish (therefore the mature fish) would be taken at the younger ages, and age at full recruitment is about 8-10 (Section 5), i.e. the selection range and maturity range cover the same ages. However the effect would be expected to diminish with age more than is apparent, since the fastest-growing fish of each age should become relatively less abundant with increasing age

(since they are selectively fished). There should be no noticeable effect on length at maturity since each length group should contain a random distribution of ages, therefore a mixture of fast and slow-growing fish.

(3) If, as was proposed in Section 4, the onshore migration primarily involves mature fish, the inshore-offshore differences noted in age at maturity would be expected, and would even be greater than shown if some mature fish were mistakenly called immature. If it were further supposed that the smaller sizes inshore in the length-maturity curve had grown more than the larger sizes from spring to summer, the higher percentages mature at the larger sizes and lower percentages at the smaller sizes are explainable in the same terms. This seems to be the most satisfactory explanation and provides further evidence for the hypothesis that the inshore migration is mainly of post-spawners.

Length at maturity appears less in the north than in the south (Fig. 35B) though the curves cross below 43 cm. This again may be a result of faulty maturity determinations at the smallest sizes, though all the material was collected during the same seasonal period. In any case a slight decline in length at maturity is expected on the basis that it declines from south to north elsewhere in the Labrador-Newfoundland area (Fleming, 1960). The increase in age at maturity (Fig. 35B) is explainable in terms of the much lesser growth in the north (Fig. 24). The length at maturity is virtually the same in both areas, but the northern fish take a longer time to attain it.

No change in length at maturity is evident over the period 1950-62 (Fig. 36A) but a small increase is evident to 1963-64. Again the 1950-62 data were collected in summer, thus the separation of the curves may be artificial. In any case it may be concluded that there has been no response, in terms of decreased size at maturity, to depletion of the population by fishing. The increase in age at maturity from 50% mature at age 5.1 in 1950-54 to age 6.0 in 1963-64 is probably real, though not as much as the curves indicate, due again to difficulty in recognizing first maturity in summer (1950-62 data). Fleming (1960) gives the age at which 50% are mature as 5.4 years in 1948, but this includes northern data. It may be seen from the graph (Fig. 36A) that the changes have occurred only below age 8, i.e. only for those ages for which growth has decreased over the period (Fig. 25 - Division 2J curves, Fig. 28). Therefore whether size at maturity has actually stayed the same or increased slightly, age at maturity must have increased. Rollefsen (1938) has ascribed a decreased age at maturity in cod to increase in growth rate.

It has been shown that maturity occurs earlier in males than in females (Fig. 36B). The difference in size at age of the sexes beyond the age at maturity is usually ascribed to this. Alm (1959) reviews a number of authors on the subject, but does not himself consider this explanation to be valid. He points out that fast-growing individuals, which mature earliest, continue to show increased growth throughout life. Thus early attainment of maturity has had no effect on the growth rate. The fact that fast-growing individuals in early life maintain this advantage in later years has also been demonstrated by Taylor (1958b) and May (MS, 1964) from back-calculation of growth in haddock. Since the growth differences between males and females tend to exist below the maturity age range as well (Fig. 36B), it is possible that differences in growth between the sexes are genetically determined.

Differences in size and age at maturity within the general Labrador-Newfoundland area are described and discussed by Fleming (1960). It is pointed out by Alm (1959) that age at maturity may be genetically determined in "different forms of the same species. It is then usually higher in large-sized and often fast-growing forms". This is the pattern found within the Labrador-Newfoundland stock, and suggests genetic differences within the area. Otherwise the trends would be expected to be reversed, due to faster growth in the southern areas. Within each area the rule that maturity occurs first in fastest-growing individuals holds true.

## 8. FECUNDITY

### Introduction

The huge egg production of marine fishes attracted the attention of the early naturalists, and fecundity estimates for a few specimens of Atlantic cod are available. Harmer (1768) reported that in a cod "of middling size Lewenhoek... affirmed there were 9,384,000 ..." eggs, and himself gave an estimate of 3-4 million for a specimen of 18-20 pounds. Earll (1880) gave estimates of about 9 million for each of two specimens of 51 and 75 pounds. Fulton (1891) reviewed the literature for a number of species and reported numbers of eggs between 2.964 million and 6.653 million for three specimens of cod ranging in length from 35 to 38 inches. More complete data are given by the recent studies of Powles (1958) and Botros (1962). The present material is treated in some detail because of the general paucity of information and lack of previous data for the Labrador and Newfoundland areas.

### Material and Method

Immediately prior to spawning cod ovaries contain three sizes of eggs: large translucent eggs about 1.5 mm in diameter which are almost ready for release, intermediate-sized yolky eggs which would presumably be released within a few weeks, and very small whitish eggs 0.1 to 0.2 mm in diameter. The smallest eggs are second generation, i.e. to be spawned in the following season, and must not be included in fecundity estimates (Raitt, 1933). It was early recognized (Earll, 1880; Fulton, 1891) that because of the large size of translucent eggs a cod could not possibly contain at one time all such eggs that it would produce in a year, and that the shedding of ova must begin soon after the first clear eggs are produced. To avoid error fecundity determinations therefore must be made late enough in the seasonal maturity cycle so that present-generation and second-generation eggs can be separated, and early enough to avoid losses of clear eggs. Thus collections were made just prior to and during the spawning season with only females showing no clearing of eggs being taken. Areas and dates of collections are shown in Figs. 37 and 38. For comparative purposes, material was obtained from the southerly areas as well as the area under study.

Some of the material was collected at sea, some from samples brought to shore in ice by research and commercial fishing vessels. Otoliths and fork length measurements were obtained from all fish sampled, and body weights except where sea conditions made this impractical. The ovaries were stored in Gilson's fluid, using double the normal amount of acetic acid, as recommended by Simpson (1951). This solution causes breakdown of connective tissue and separation of the eggs from each other and the ovarian wall. The process was aided by slitting the ovaries within the collecting jars and shaking the jars vigorously every few days. The eggs were

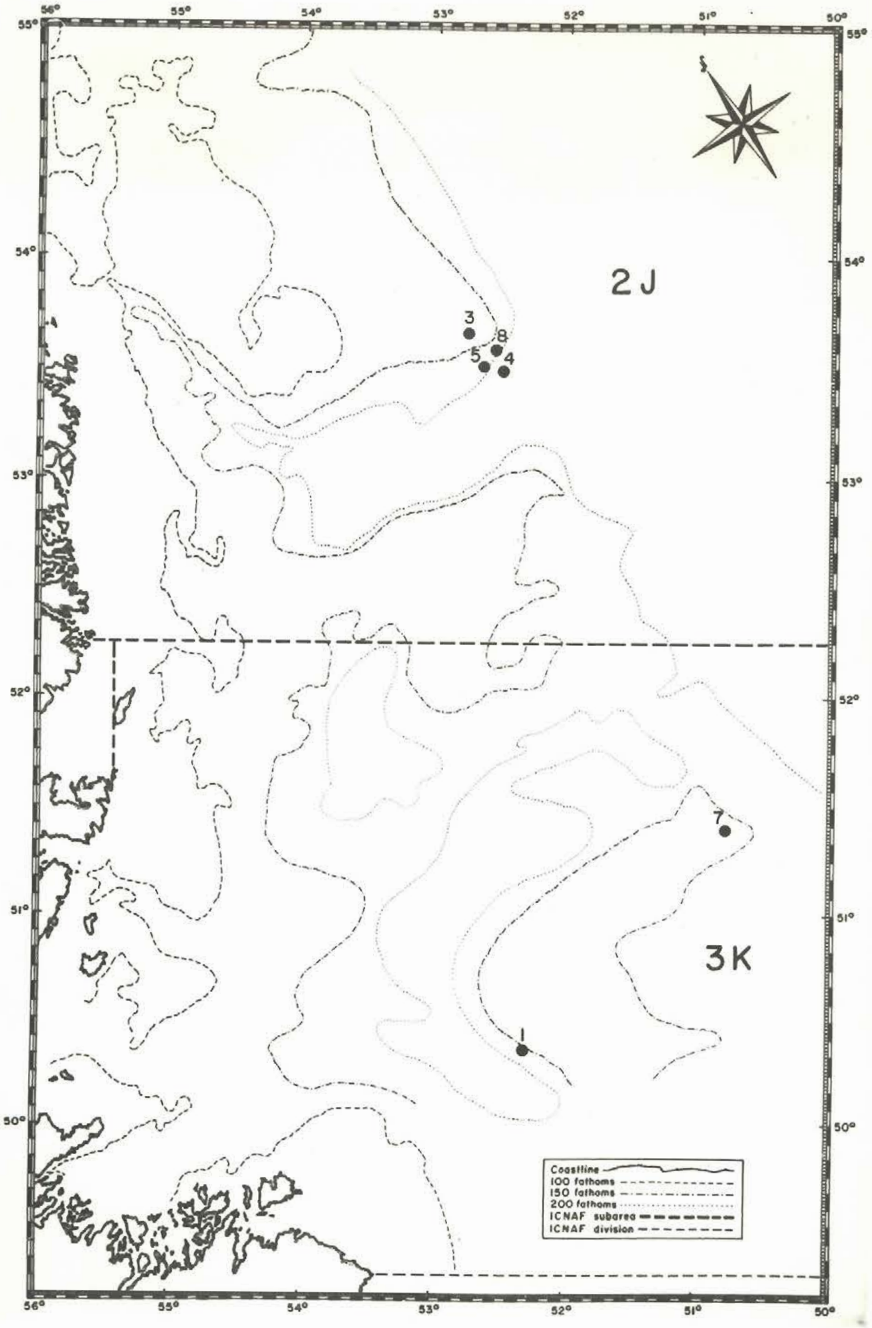

Figure 37. Collections for fecundity studies, Labrador and NE Nfld. Shelf, Mar. 31 - Apr. 6, 1964. The lone specimen between Latitudes 50N and 51N was taken on May 19. Numbers refer to number of specimens.

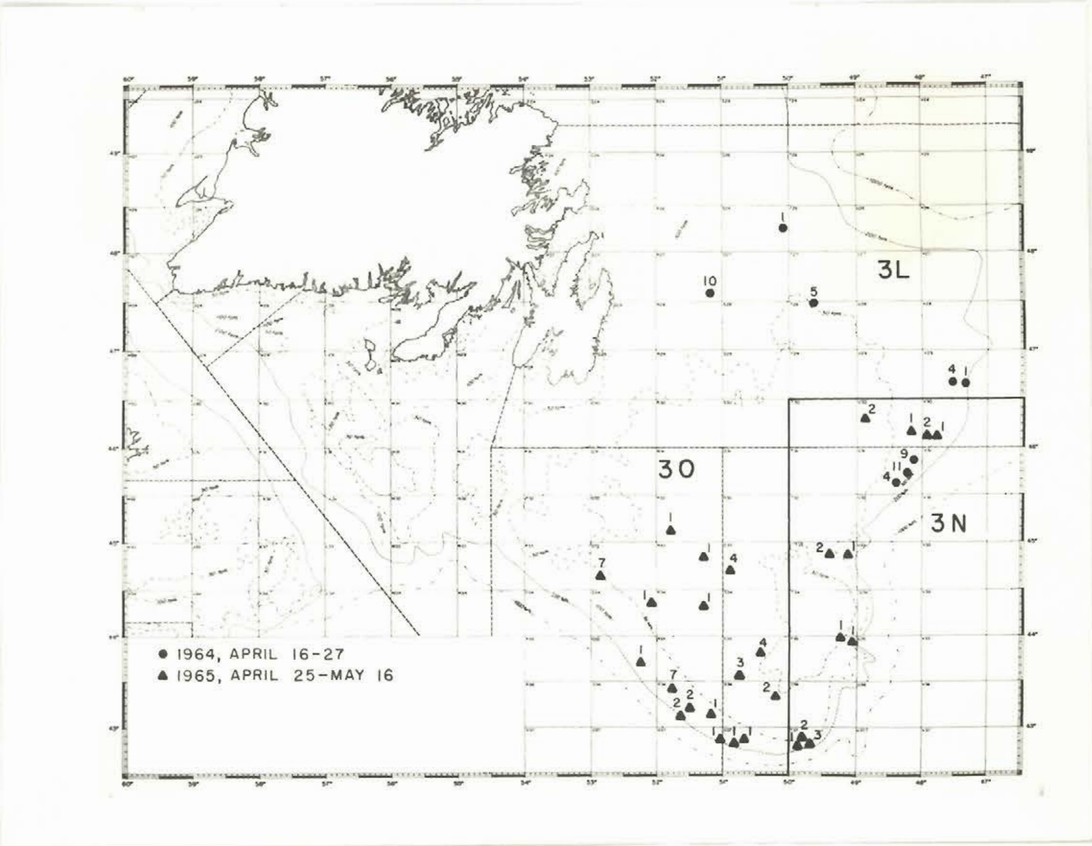

Figure 38. Collections for fecundity studies, Grand Bank, 1964 and 1965. Numbers refer to numbers of specimens.

cleaned by decanting on to a large funnel covered by nylon bolting cloth of the type used in plankton nets and having 26 meshes to the cm. Second-generation eggs and disintegrated tissue were washed through using a fine jet of tap water. Eggs were gently scraped from larger pieces of the ovarian wall and the latter removed with forceps. The procedure is relatively simple for ovaries stored from 3-8 weeks in the fluid. Shorter periods are insufficient for separation of egg clusters and separation of eggs from the ovarian wall. Longer periods allow disintegration of the ovarian wall to such an extent that the pieces are difficult to remove. After cleaning, the eggs were stored in 5% formalin until counted.

A variety of procedures for egg counting have been described. Parrish _et_ _al_ (1960) describe an automatic herring egg counter, consisting basically of a fine tube through which the eggs pass in single file, interrupting a beam from a photoelectric cell attached to a recording device. No attempt was made to construct such an apparatus in the present investigation because of the large variation in size (0.4 to 1.1 mm) of the yolky present-generation eggs (Fig. 39).

Most fecundity estimates have been based on counts from small egg samples, adjusted to count for the fish by the ratio of weight or volume of total eggs to weight or volume of the sample. This involves counting the eggs in a known weight or volume or determining the weight or volume of a certain number. Both wet (Schaner and Sherman, 1960) and dry (Nagasaki, 1958; Thomson, 1962) weights have been used. Graduated cylinders are used to determine volumes of egg samples (Raitt, 1933; Thompson, 1959); pipettes to obtain standard volumes (Simpson, 1951; Bagenal, 1957a). A variation of the volumetric method is described by Vladykov and Legendre (1940), who calculated the volume of one egg from the average diameter of a series, and related this to total volume of eggs. A more recent variation is based on the use of the "whirling vessel" originally designed for sampling from collections of plankton (Wiborg, 1951). Eggs are agitated and allowed to settle into ten compartments in the bottom of the vessel. They are then drawn off and further fractionation of one or more of them to 1/100 or 1/1000 carried out. One or more of these small fractions may be counted and the total eggs determined by multiplication by the appropriate ratio. This method has been used by Hodder (1963) and Pitt (1964), and a modification of the instrument described by Pitt (1965).

All sampling methods are subject to error. Ordinary volumetric methods appear particularly inappropriate for cod eggs because of the small size of the smallest yolky eggs encountered (diameter .04 cm, volume = $1/6\pi d^3$ = .000033 cc). Careful dry weights would seem to offer the best possibility of minimizing error due to sampling techniques, but Wiborg (1951) and Pitt (1964) obtained consistent results in trials

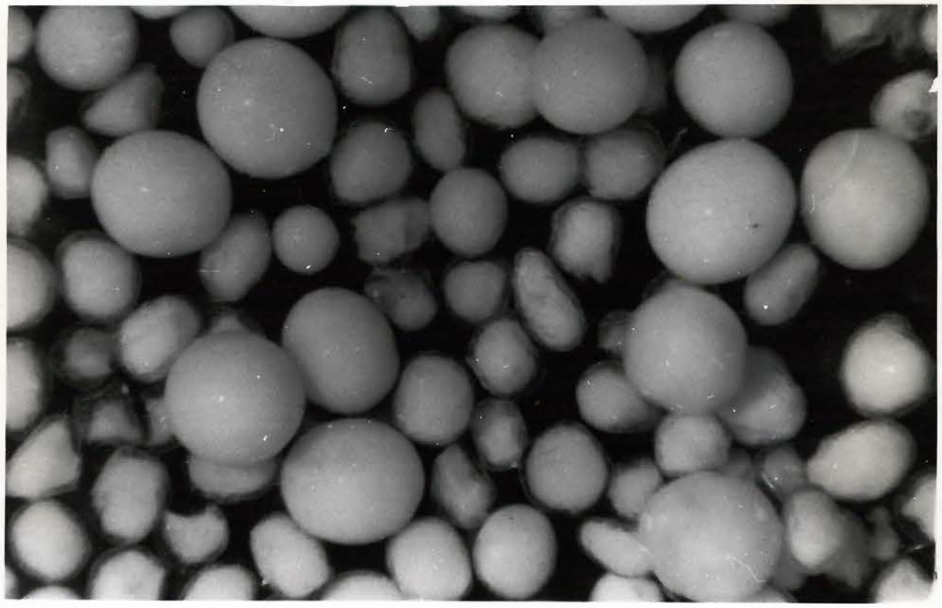

Figure 39. Ova of Atlantic cod to show size variation prior to clearing. No second-generation eggs are present. The largest eggs shown are 1 mm in diameter.

using the whirling vessel. Accordingly it was decided to test the efficacy of both the dry weight and whirling vessel methods for cod eggs.

Eggs from a single fish were placed into the whirling vessel as modified by Pitt (1965), the vessel agitated, and a 1/10 sample taken at random from one of the compartments after the eggs had settled. This was successively fractionated to 1/100 and 1/1000 of the original number. The ten resulting samples of 1/1000 were counted. Each of these was then dried to constant weight (accomplished in 24 hours in an oven at 55°C) and weighed to the nearest .0001 gm. The remaining eggs were similarly dried and weighed. Fecundity estimates from the whirling vessel method were obtained by multiplying each of the counts by 1000. Estimates from the dry weight method were obtained by substitution in the formula:

$$\text{Total eggs} = \frac{\text{Weight of Total}}{\text{Weight of Sample}} \times \text{Number in Sample.}$$

The results for each method are compared in Table 7, which includes a paired comparisons test for the two series. The mean estimates by each method were significantly different ($t = 4.88$; at df 9 $P < .01$). The fact that nine of the ten estimates by weight were higher than the whirling vessel estimates may mean that one of the samples (1/10 or 1/100) selected in the fractionation procedure was something less than 1/10 or 1/100, or alternatively that the total weight of eggs was too high in relation to the sample weights.

Considering the variability in counts of the 10 1/1000 samples the former is most likely. Estimates from the whirling vessel were much more variable than those from weights. The coefficient of variation (S.D./mean) was 6.0% for the whirling vessel, only 3.1% for the weight method. In two tests of the whirling vessel using a small known number of eggs and a large unknown number Pitt (1964) obtained coefficients of variation of 9.5% and 10.9% respectively. Individual estimates from the whirling vessel in the present experiment differed from the mean estimate by -6.4% to 13.1%, whereas weight estimates differed from their mean by -5.2% to 3.7%.

The possibility of significant variation in sampling by the whirling vessel to levels of 1/100 or less has been recognized, and insurance taken against it by parallel fractionation from the 1/10 level and subsequent combination of two or more lower-level samples (Pitt, 1964), or simply by combination of two or more samples from the original 1/10 (Hodder, 1963). Even so, Hodder (1963) shows that for 180 specimens of haddock where two subsamples were taken, percentage deviations from the mean fecundity derived from the two subsamples exceeded 10% in 43 cases, and 20% in 5 of these.

A further test was made on the present material to determine the effect of combining parallel whirling vessel samples against estimates by weight for the same samples. Eight fish of length 76 to 80 cm, and collected from the eastern Grand Bank, were chosen for the test. The eggs from each specimen were fractionated to 1/10 in the whirling vessel. Two of these samples were chosen at random and each fractionated to 1/100. Two of the samples of 1/100 were chosen for fractionation to 1/1000. Fecundity estimates were made from one sample of 1/1000 from each series. Estimates by the weight method were also made for each of these. Some difficulty was experienced in obtaining constant weights but this was overcome by drying for at least 48 hours at 110°C.

There was wide variation in fecundity estimates within each series (Table 8). Standard deviations in each case were about 27% of the mean. A paired comparisons test revealed that differences between the means were probably not significant ($t = 2.46$, at df 7 $.05 > P > .02$). Nevertheless individual fecundity estimates from each of the two fractions for each fish were still more variable with the whirling vessel, percent deviations from the mean estimate for each fish ranging from 0.9% to 8.8% (average 3.8%), while percent deviations by the weight method were 0.3% to 3.2% (average 1.1%).

Thus with procedures as outlined in the second test similar results are achieved with each method. However there is still more inherent variation in the whirling vessel method. Since this method also involves more handling time, particularly with parallel fractionations and with the large numbers of eggs found in cod, it was decided to apply the weight method in the present study. The procedure adopted was as follows:

(1) The eggs were stirred vigorously and a sample removed by pipette.

(2) From 1,000 to 10,000 or more eggs were counted, depending on the volume from each fish. Successive sampling by pipette was thus carried out as necessary.

(3) The counted sample was transferred to an aluminum crucible and dried at 110°C for at least 24 hours.

(4) The remaining eggs from each fish were partially dried by vacuum filtration using a coarse filter paper, then transferred to large Petri dishes and dried at 110°C for at least 24 hours. The eggs were then transferred to beakers (to facilitate weighing) and dried for a further 24 hours.

(5) After removal from the oven eggs were transferred to a dessicator containing phosphorus pentoxide and let stand several hours to cool, following which weights were obtained to the nearest .0001 gm.

(6) Fecundity estimates were made by substitution in the formula given previously.

## Results

Since the data were obtained over a wide area in two different years (Figs. 37 and 38), the collections were grouped as follows to facilitate analysis:

(1) ICNAF Divisions 2J and 3K, 1964

(2) Division 3L, 1964

(3) Division 3N, south of 46°30'N and east of 50°W, 1964 and 1965

(4) Division 3O, west of 50°W, 1965.

The latter two areas overlap ICNAF boundary lines but are more natural for present purposes because of the distribution of the collections in area and time.

Fecundity versus length showed a linear trend on a log-log plot, indicating that the simple allometry formula would hold. Data were accordingly transformed to logarithms and a least squares straight line fitted, giving for all the data:

$$\log F = 3.42 \log L - 0.30$$

or in the arithmetic transformation:

$$F = 0.50 \, L^{3.42}$$

This line gives a good fit to the data except for points beyond 110-115 cm (Fig. 40) where fecundity appears to be underestimated. As there are only five points beyond 115 cm this is not considered serious. Straight lines fitted to the unweighted geometric mean fecundities at 1-cm and 3-cm length groups were similar to that describing the individual points.

Log-log straight lines were also fitted to each area separately (Fig. 42A). The regression constants, correlation coefficients (r) and tests of significance of r are listed in Table 9. All correlation coefficients were significantly different from zero. Analyses of covariance (Snedecor, 1956)

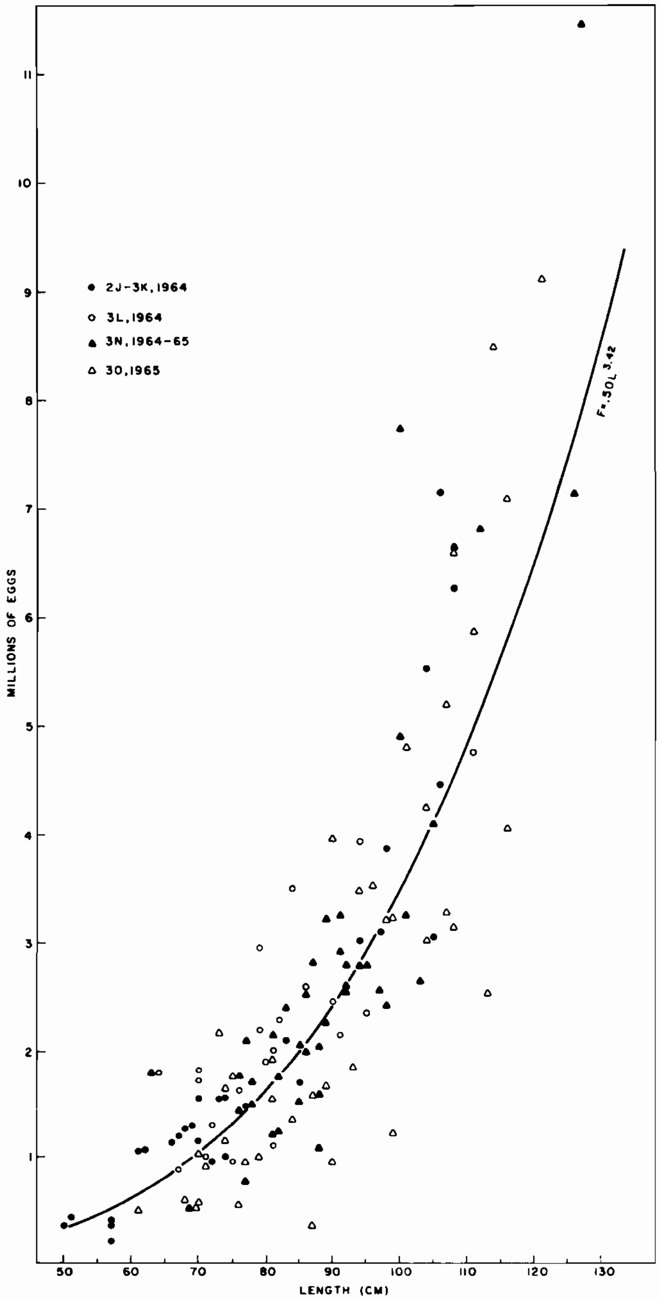

Figure 40. Scatter diagram of cod fecundity against length with fitted regression for all data.

were carried out to examine differences between the resulting regressions (Table 10). In these analyses the F-value derived from the ratio of mean square for regression coefficients to mean square within samples gives a measure of the variation in regression coefficients (m) , i.e. whether the regression are parallel. The F-value derived from the ratio of mean square for adjusted means to mean square for common regression measures the variation in intercepts, or vertical separation of the regression lines. If the first F-value indicates that the regressions are not statistically parallel there is no point in comparing elevation of the regressions.

In one case only were collections obtained from the same area (3N) in the two years of sampling. Analysis of covariance (Table 10, test 1) showed no significant differences in the data, thus justifying combination for further analysis. Analysis of covariance for all four areas (test 2) revealed no differences in slope, but a difference in elevation at the 1% level. Further analyses, eliminating one area at a time (tests 3-6) showed the significant difference in elevation to be due to inclusion of data from Division 3O. There is a progressive elevation of fecundity-length regressions from south to north, with the exception of the 3L regression, which intersects the others. Thus there is a tendency for northern fish to produce more eggs than southern fish at similar lengths.

Since data from Division 3O were available for one year only it was impossible to determine directly whether the observed differences were real area differences or due rather to variation between the years of collection. However since a comparison of 1965 data from the nearest area (Table 10, test 7) showed no differences, while inclusion of 1964 data (test 8) indicated a possible difference (5% level) in elevation, it is possible that the observed differences were due to slightly higher than usual fecundity in 3O in 1965. Additional evidence for this is offered by the fact that cod from these two areas are considered to belong to the same population (Templeman, 1962).

Plots of log fecundity versus log age (from otoliths) also resulted in linear trends with slopes approaching 2 (Table 9). Variation was much greater than for plots of fecundity against length (Fig. 41), and correlation coefficients lower for each area, but still significantly different from zero (Table 9). Analyses of covariance (Table 10, tests 9 and 10) revealed a possible difference (5% level) between the areas which disappeared when 3L data were excluded. The differences in elevation however were highly significant. This is not surprising in view of the separation of regression lines evident from Fig. 42B. In contrast to the fecundity-length regressions the data from 3N and 3O were similar (Table 10, test 11) and the relative positions of northern and southern regressions were reversed, i.e. at

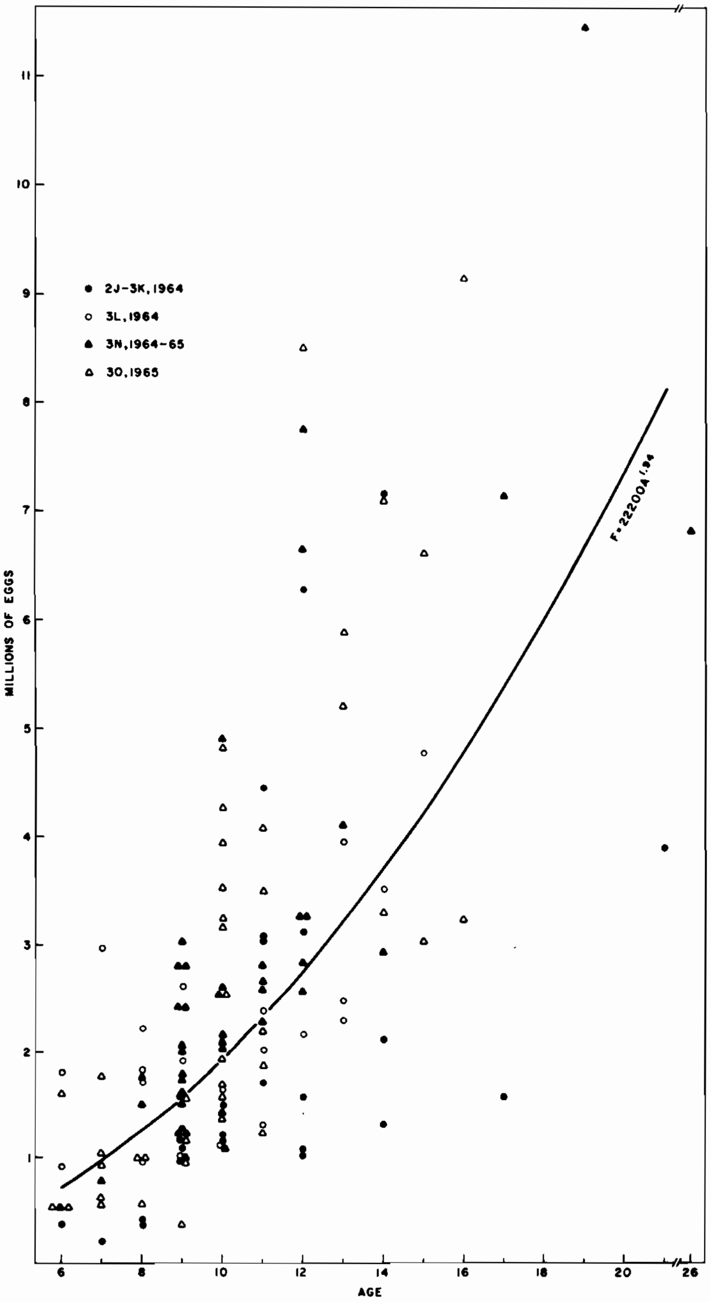

Figure 41. Scatter diagram of cod fecundity against age with fitted regression for all data.

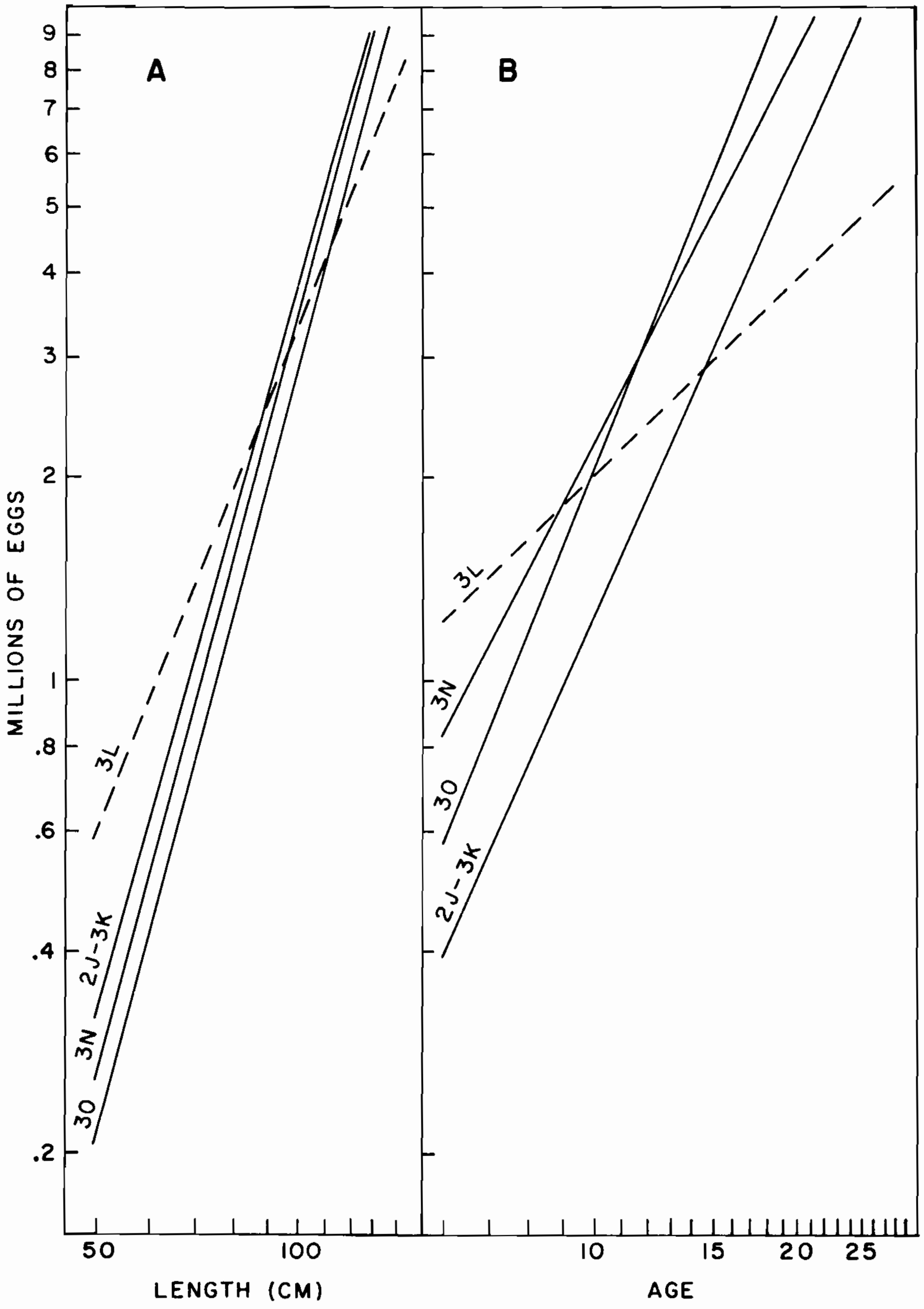

Figure 42. A. Regressions of log fecundity on log length for each area. B. Regressions of log fecundity on log age for each area.

similar ages (and ignoring 3L momentarily) fish from the southern areas produced more eggs than those from the north. The overall fecundity-age relationship was as follows:

$$\log F = 1.94 \log A + 4.35$$

or

$$F = 22200\ A^{1.94}$$

It appears that fecundity is related both to length and age, though in light of the lesser variation in scatter diagrams (Figs. 40 and 41) and higher correlation coefficients (Table 9) more to length than age. However, length and age are also related. Elucidation of these mutual relationships, particularly the relative contributions of length and age to variations in fecundity, may be effected by multiple correlation. The data were analysed on this basis following Croxton (1953). The northern (2J,3KL) and southern (3NO) areas were considered separately. Fitted regression equations for each area were as follows:

Northern area (2J,3KL)

$$X_1 = -.21 + 3.36X_2 + .08X_3$$

Southern area (3NO)

$$X_1 = .14 + 2.72X_2 + .88X_3$$

where $X_1$ = log fecundity, $X_2$ = log length and $X_3$ = log age. Further statistics related to the analysis, with explanation of symbols, are listed in Table 11.

Considering first the separate regressions of length and age on fecundity in the southern area it is seen that an estimating equation employing only length explains 70.5%

of the variation in fecundity ($r^2_{12}$ = .705), while one involving only age explains 61.0% of the variation ($r^2_{13}$ = .610). When both variables are employed in the same estimating equation, they together account for 74.0% ($R^2_{1.23}$) of the variation in fecundity. For the northern area $R^2_{1.23}$ = .797 as opposed to values of .796 for $r^2_{12}$ and .325 for $r^2_{13}$ in the separate regressions.

To determine whether inclusion of age in the regressions accounts for a significant added amount of explained variation, the values of $r^2_{13.2}$ may be tested for significance of the difference of each from zero. Values of $\underline{t}$ and $\underline{P}$ are given in Table 11 and indicate no significance in each case. It may thus be concluded that age has no significant effect on fecundity and that variation in fecundity is adequately explained in terms of length alone. Bagenal (1957a) and Nagasaki (1958) have applied multiple regressions to data from European long rough dab and Pacific herring respectively and found the same to apply.

The coefficients of multiple determination ($R^2_{1.23}$) may also be tested for significance from zero. The values of $\underline{F}$ in Table 11 indicate that each $R^2_{1.23}$ is highly significant (for the north $\underline{F} = 9.29$, $F_{.05} = 3.20$, $F_{.01} = 5.10$; for the south $\underline{F} = 10.54$, $F_{.05} = 3.11$, $F_{.01} = 4.88$). The fact that these values are significant while those for $r^2_{13.2}$ are not indicates that the significance of length is so marked as to offset the lack of significance of $r^2_{13.2}$. This may be confirmed by testing the significance of $r^2_{12.3}$ (the coefficients of partial determination for fecundity and length, independent of age). Calculated t values for each area were high (Table 11) and both P values less than .01, indicating high significance. The relatively low value of $r^2_{12.3}$ in the southern area is due to the high correlation between age and length in this area ($r_{23} = .794$). Thus age gives a correlation with fecundity ($r_{13} = .781$) almost as good as the fecundity-length correlation ($r_{12} = .840$). In the northern area the age-length correlation is not as good ($r_{23} = .618$) because of wide differences in growth within this much larger area.

Two ages (9 and 10) were well represented in data from Divisions 3N and 30. Plots of fecundity against length for each age separately (Fig. 43) are illustrative of the fact that variations of fecundity within age are explainable in terms of length variation within age. Hence the wide scatter in the fecundity-age plot (Fig. 41). The multiple regression equations for each area predict that at a given age fecundity will increase with length; also that at a given length fecundity will increase, but insignificantly, with age.

Enough weight data were available (weights whole and with viscera and gills removed) to determine the form of the fecundity-weight relationship. The gutted-gilled weight was chosen as that least susceptible to variation due to feeding. Log-log plots for 83 specimens spread over the four areas gave slopes of 0.8 to 1.2 with a slope for all data of 1.04, indicating close adherence to linearity on an arithmetic plot. The arithmetic correlation coefficient was slightly higher (.862) than that derived from a log-log transformation (.827). Arithmetic least squares straight lines were fitted to all the data and to each area separately (Table 9, Fig. 44). All correlation coefficients were high and significantly greater than zero.. Analysis of covariance (Table 10) revealed no differences in slope or elevation between the areas, though the individual plots (Fig. 44 inset) followed the same trend as in the length-fecundity plots, i.e. at similar weights northern fish produced more eggs than those from the south. Again the 3L line intersected the others. Taking all the data into account fecundity (F) was related to gutted-gilled weight (W) by the equation

$$F = .48W + .12$$

## Discussion and Conclusions

Beverton and Holt (1957) observe that if the ovary were growing isometrically and size of eggs did not vary with fish size, egg number would be proportional to the area of the germinal epithelium and thus to the 2/3 power of weight. They point out however that the germinal epithelium is so convoluted that it completely fills the ovary; thus fecundity should be proportional to body weight itself. The present

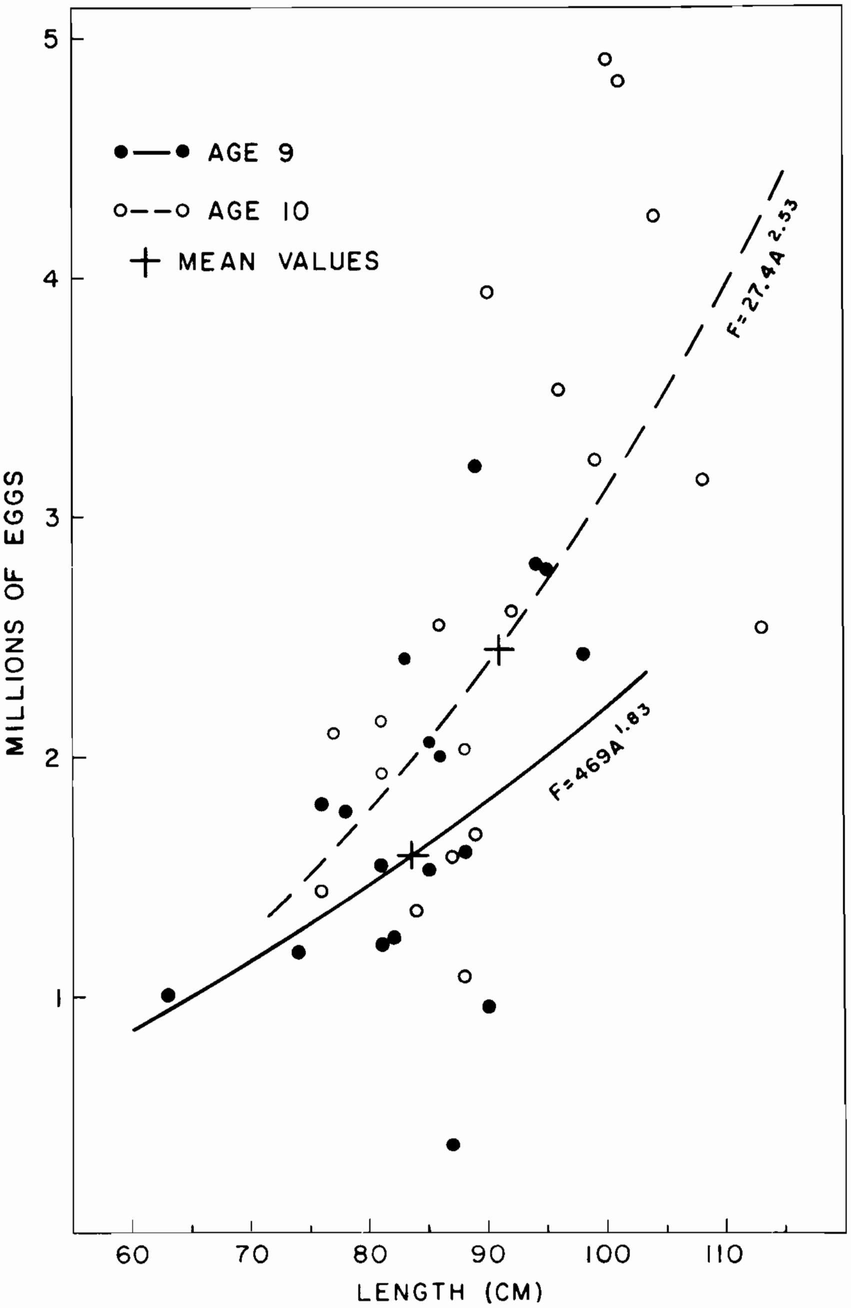

Figure 43. Regressions of fecundity on length for fish of ages 9 and 10 from ICNAF Divisions 3N and 3O.

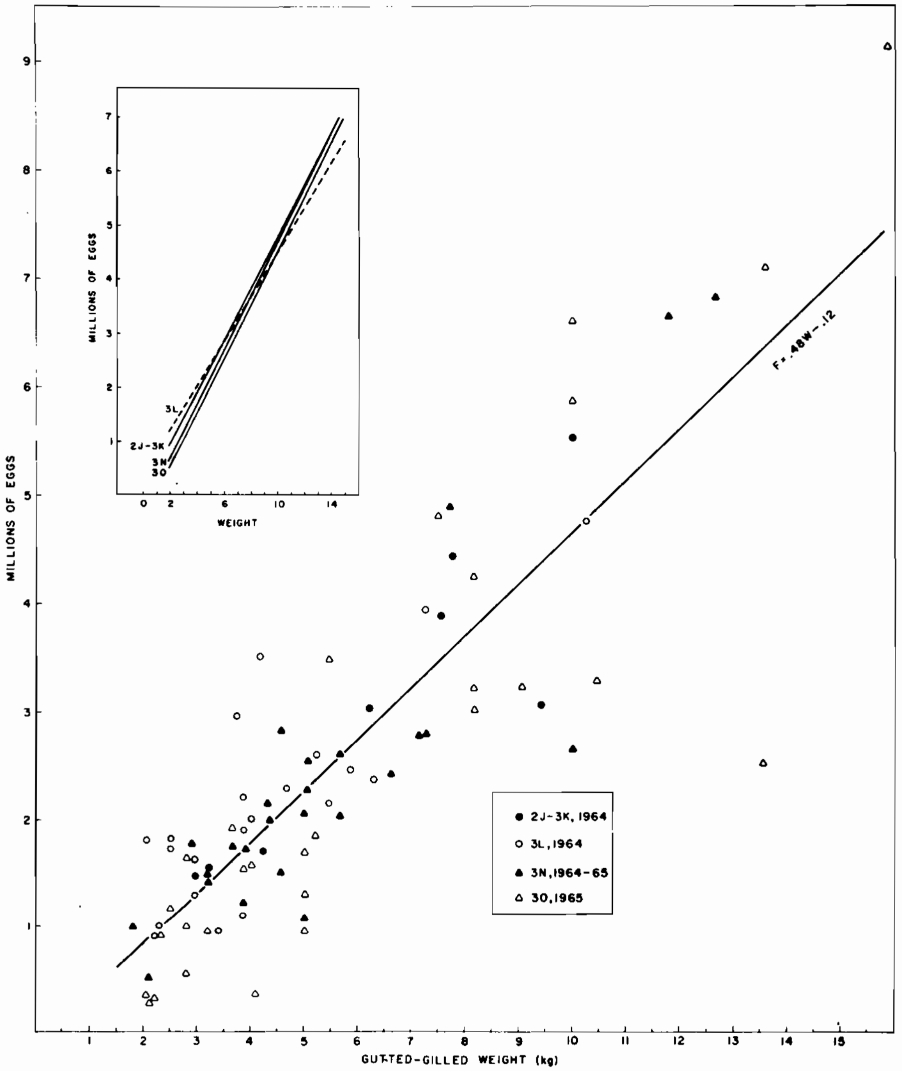

Figure 44. Scatter diagram of cod fecundity against gutted-gilled weight with fitted regression for all data. Inset shows regressions for each area.

data conform to this conclusion.

In the comparisons of fecundity with length, age and weight the data from 3L invariably followed an atypical trend, with lesser slope and greater intercept than those from the other areas. No obvious biological explanation for this anomaly presents itself. It is most likely that the atypical trends observed were due to sampling error. The sample from this area was the smallest and least representative of the lot. Nineteen of the 21 specimens were taken in only three positions, ten of these from one position (Fig. 38).

Hodder (1964) proposed that fecundity of individual fish may be related to the number of times the fish has spawned (greater fecundity in fish which have spawned more often) as well as to its length and age, and presented some indirect evidence for Grand Bank haddock to support this hypothesis. For the present material an attempt was made to determine the number of spawnings through recognition of "spawning zones" in the otoliths, following the descriptions of Rollefsen (1933). While spawning zones could be easily distinguished in most otoliths the first such zone was difficult to assign. An examination of the best series of age data (ages 9 and 10, 3NO - Fig. 43) from this viewpoint produced inconclusive results (Table 12). However, in view of the small amount of data coupled with the uncertainty of positioning the first spawning zone, the possibility noted by Hodder (1964) is not invalidated.

Comparison of the correlation coefficients for relationship of fecundity to length, age and weight separately (Table 9) indicates that variations in fecundity are explained as well or better in terms of weight as in terms of length, Botros (1962) concluded that the fecundity-weight relationship gave the best description of egg production of northeast Atlantic cod. However it is well known that weight at length of fish varies seasonally. This would not be important in the present investigation where all fish were taken during the same season and at the same stage of maturity. Nevertheless length measurements are more easily obtained, do not of course vary with stage of maturity and describe fecundity variations adequately.

The north-south trends in individual regressions are explainable in terms of differences in growth and size at maturity in the various areas. The individual fecundity-length regressions (Fig. 42A) indicate that at similar lengths egg production is greater in the north. While the differences in trends are not statistically significant they might be expected since northern fish grow more slowly and mature at a smaller size than those from the south. Thus at similar sizes they will be older and have spawned more often, and the combination of these two factors might account for greater fecundity at length. The individual fecundity-weight regressions show the same pattern for the same reasons (Fig. 44).

Since northern fish grow much more slowly than those from the south the trends in fecundity at age (Fig. 42B) are reversed. At a given age the larger southern fish produce more eggs. In fish of the same length and age the multiple regressions indicate that fecundity is higher in the north. This has also been noted for Pacific herring (Nagasaki, 1958). Bagenal (1962) reports that at the same length fecundity of European plaice increases from the North Sea to southern Norway, and from south to north on the Norwegian coast.

No significant differences in fecundity-length were evident between areas 2J-3K, 3L and 3N (Table 10). Inclusion of 3O data resulted in differences which were likely due to sampling in different years. The results suggest that the areas concerned are inhabited by a series of intergrading populations. Nagasaki (1958) has made similar conclusions in north-south comparisons of fecundity, length and age of Pacific herring. Annual variations in fecundity do occur, presumably due to varying environmental conditions (Bagenal, 1957b; Hodder, 1963). Account must be taken of these in area comparisons.

Comparable data on the fecundity of northwest Atlantic cod are available from the study by Powles (1958). Individual fecundity estimates are not given but inspection of a log-log plot of fecundity versus length of 39 specimens from the southwestern Gulf of St. Lawrence indicates a relationship as follows:

$$\log F = 4.64 \log L - 2.58$$

Comparable data for the northeast Atlantic are given by Botros (1962), who describes fecundity of cod from the western Baltic by the relation

$$F = .6082\ L^{3.587}$$

$$\text{i.e.} \quad \log F = 3.59 \log L - 0.22$$

and from southern Norway by the relation

$$F = 1.3015\ L^{3.401}$$

$$\text{i.e.} \quad \log F = 3.40 \log L + 0.11.$$

Sorokin (1957) gives fecundity estimates for a few specimens taken at Lofoten (northern Norway). Some of these had begun spawning and all but one were larger than 80 cm; therefore they have not been utilized in the present comparison. Thomson (1962) gives the fecundity-length relationship of Pacific cod as

$$\log F = 3.65 \log L - 0.41.$$

The intercept of Thomson's equation has been adjusted to give fecundity in millions. The above regressions may be compared to that for present material by reference to Fig. 43. Differences in fecundity at length between western and eastern Atlantic cod are quite striking, the latter producing about double the number of eggs of the former at a given length. In fact the numbers produced by northeast Atlantic cod are similar to those produced by the Pacific species (_G. macrocephalus_). On the other hand the relationships for the eastern Atlantic and Baltic cod are very similar, though these are considered subspecies by Svetovidov (1948).

Nikolsky (1953) presents data to show that closely related Atlantic and Pacific species spawning in coastal areas exhibit quite different fecundity, being much less for Atlantic species. He regards the higher egg production of coastal Pacific species as an adaptive response to greater numbers of predators. The related species *G. morhua* and *G. macrocephalus* are included by Nikolsky (1953) in a group of species which do not spawn close to the coast and which exhibit no regular differences in fecundity from Atlantic to Pacific. Sources of data are not given, but for *G. morhua* are presumably from the northeast Atlantic. Considering northwest Atlantic cod as well, Nikolsky's generalization appears to be an oversimplification. In fact it may be an oversimplification to categorize the Pacific species as not spawning close to the coast. They do not undertake extensive spawning migrations (Svetovidov, 1948) as do Atlantic cod, and in fact are classified by Svetovidov (1948) as one of a group of "coastal forms" within the genus *Gadus*. In the eastern Pacific they are distributed in depths shallower than 80 fathoms (Ketchen, 1961) and are known to spawn in coastal areas, e.g. Hecate Strait (Ketchen, 1961).

It is of interest to examine the Pacific material for trans-oceanic differences in fecundity at length. Unfortunately, little is available, but Thomson (1962), comparing his results with fragmentary data for the western Pacific summarized by Moiseev (1953), concludes that the fecundity-length relationship for Pacific cod is constant. The high fecundity of Pacific cod is understandable in purely physical terms since their diameter at fertilization averages about 1 mm (Forrester, 1964) as opposed to 1.5 mm for Atlantic cod. The high fecundity of eastern Atlantic cod is difficult to reconcile.

It is of interest to note that eggs of Pacific cod are demersal (Thomson, 1963) while those of Atlantic cod are buoyant. The demersal quality of Pacific cod eggs is possibly an adaptation to a more coastal-oriented existence.

It was early assumed that fecundity of fishes should vary, as does weight, at a rate proportional to the cube of length (Mitchill, 1913). Simpson (1951) used this so-called "cube law" to describe fecundity of North Sea plaice. Application of the cube law to fecundity-length relationships is presumably based on assumptions that fecundity is related linearly (and arithmetically) to ovary size, and ovary size to the cube of length. Considering the first, Simpson (1951) observes that number of eggs produced may be determined either when new primary oocytes are being formed each year, or when eggs to be released in the next spawning season are separated from the resting oocytes. He futther proposes, with reference to Reibisch

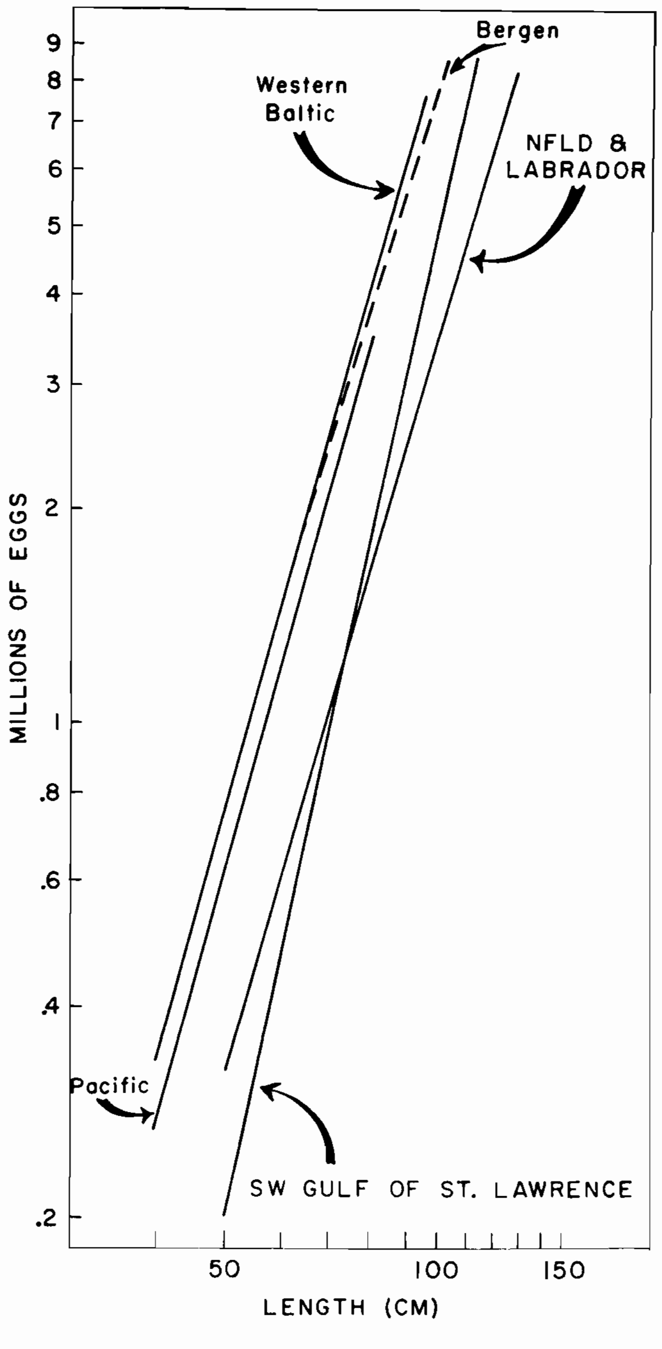

Figure 45. Comparison of fecundity-length regressions for Atlantic and Pacific cod.

(1899) and Franz (1910), that new primary oocytes are probably formed at least 2-3 years before the resulting eggs are released, and that separation from resting oocytes occurs one year before release. Hodder (1963) shows that egg number may well be determined by environmental conditions at either period. While number varies, size of eggs produced does not, at least for marine species (Beverton and Holt, 1957). Very little information is available on the relation of egg number to ovary size _per se_, but Bertin (1958) observes that number of eggs per unit ovary weight declines with size of fish. The same conclusion may be drawn from data of Pitt (1964) who shows that fecundity of american plaice is proportional to the 0.7 power of ovary weight. Considering the second assumption, it might be assumed that since weight of fish often approaches a cube-law relation to length, ovary weight would show a similar relation. Pitt (1964) gives the relation between log ovary weight and log length for american plaice. The estimating equation is not given but inspection of the plot yields a value for slope of 3.8, i.e. ovary weight is related to the 3.8 power of length. It is thus not surprising that fitted fecundity-length regressions seldom approach the cube law very closely. Published values of the exponent range from 1.8 (Nagasaki, 1958) for a small sample of Pacific herring to 5.7 (Hodder, 1963) for a small sample of Grand Bank haddock. However most published values are between 3 and 4. Nagasaki (1958) and Hodder (1963) give more detailed reviews.

## 9. SEASONAL MIGRATION AND STOCK DEFINITION

An extensive cod tagging program was begun by the St. John's Biological Station in 1962. Dr. W. Templeman, Station Director, has kindly permitted the use of data from tagging in the area supposedly occupied by the "Labrador-Newfoundland cod stock". Returns were tabulated from nine selected tagging experiments, covering the area from north to south and both inshore and offshore. These were originally analysed by 3-month periods, i.e. December-February, March-May, etc. This particular combination was chosen to give the best seasonal picture. Returns depend on recaptures by fishing and the offshore fishery is most important during March-May; the inshore fishery during June-August. In fact returns from the other seasonal periods were so few that the data were further combined into 6-month periods for ease of display.

Returns were therefore summarized for December-May and June-November (winter-spring and summer autumn) and are shown for areas of ½-degree latitude by 1-degree longtitude in Figs. 45-54. Areas and dates of tagging are listed below. Returns were tabulated to September 30, 1965, thus should be reasonably complete to the end of August, 1965. They are of course by no means finally complete, especially for the 1964 tagging, but are of sufficient magnitude to allow useful conclusions to be made. Returns from the immediate period of tagging have not been considered and are not included in the figures.

| Area of Tagging | Date | Number Tagged | Figure No. |
|---|---|---|---|
| INSHORE | | | |
| Northern Labrador (Nain) | Aug/62 | 704 | 46 |
| Mid-Labrador (Hopedale) | Aug/62 | 768 | 47 |
| Southern Labrador (Domino) | July/62 | 768 | 48 |
| Northern Nfld (Quirpon) | Aug/62 | 768 | 49 |
| Northeast Nfld (Fogo) | Oct/63 | 1152 | 50 |
| Eastern Nfld (Baccalieu) | Nov/62 | 1152 | 51 |
| OFFSHORE | | | |
| Southern Labrador (Hamilton Inlet Bank) | Sept/62 | 1152 | 52 |
| Northeast Nfld (Funk Island Bank) | May/64 | 384 | 53 |
| Eastern Nfld (Northern Grand Bank) | Apr/64 | 1152 | 54 |

Returns were few from the northern Labrador tagging (Fig. 46) but show dispersion in summer-autumn north and south along the Labrador coast, extending southward to northeast Newfoundland. Winter returns are almost entirely from the offshore area of Hamilton Inlet Bank. Some localization of returns from the area of tagging is noticeable. None of these occurred during the year of tagging. The returns from mid and southern Labrador show very similar trends (Figs. 47-48), with the exception of a few offshore returns from the northeast Newfoundland Shelf and more extensive movement southward in summer and autumn. There is no indication of significant movement into the Gulf of St. Lawrence or to the northern Grand Bank.

The three inshore Newfoundland taggings (Figs. 49-51) exhibit a uniform pattern and may be described as a unit. Each shows a very strong tendency for returns to be concentrated in the locality of tagging. Again the returns from the immediate time of tagging are not included, thus these localized returns occurred in later years. As in the Labrador tagging, offshore returns came mainly from the area of Hamilton Inlet Bank, but the offshore areas of northeast Newfoundland and the northern Grand Bank were also represented. It is particularly evident from the eastern Newfoundland taggings (Figs. 51 and 54) that some fish have moved in summer to the shallow waters of the central Grand Bank rather than inshore. The northern Newfoundland tagging shows a number of returns from the Strait of Belle Isle (Fig. 49) but otherwise no significant connection with the Gulf of St. Lawrence. Thompson (1943) notes the penetration of "Gulf" cod eastward through the Straits in summer. No doubt the cod tagged in the northern Newfoundland tagging included some of these and they show up as returns from the Straits in later years. It is most significant that from all three Newfoundland coastal taggings there are very few recaptures from Labrador.

The offshore Hamilton Inlet Bank tagging (Fig. 52) resulted in a general inshore distribution of returns along the Labrador and northeast Newfoundland coasts, though few from northern Labrador. Offshore returns in later years were concentrated off southern Labrador. The small 1964 tagging off northeast Newfoundland gave similar results (Fig. 53). The 1964 northern Grand Bank tagging has so far resulted in very few winter-spring returns, but those in summer-autumn were concentrated in eastern Newfoundland, with some from northeast Newfoundland and the central Grand Bank, but none from northern offshore regions.

The return of tagged fish depends on the existence of a fishery, and cooperation of fishermen in returning tags. The proportions returned from one area to another will depend on the relative intensity of the fishery. Since there is usually no fishery in Division 2G (northernmost Labrador) few returns are expected. The lack of returns cannot be taken to mean that no tagged fish occurred there. Again the heavy concentration of fishing in Division 2J offshore (Hamilton Inlet Bank) should result in a disproportionately high number of returns from this area. It is curious that while the amounts of cod taken offshore in the area are more than ten times those taken in the small inshore fishery (Fig. 2) the number of returns is usually less offshore. Within these limitations some interesting generalizations may be made.

There is clear indication of movement onshore in spring and summer, offshore in autumn and winter. Hamilton Inlet Bank is a major offshore concentration area from all cod tagging except that on the northern Grand Bank. On the northeast Newfoundland Shelf there is greater concentration in winter offshore from Newfoundland inshore tagging than from Labrador inshore tagging.

There is clear indication of "localization" of returns from the Labrador and Newfoundland coasts. Cod tagged in a particular locality in one year tend to be concentrated around this area in later years. There are two possible causes. Either a number of fish remain in the same coastal area throughout the year, i.e. move in winter to deep water near the coast rather than offshore, or there is a tendency for cod to "home" on the areas to which they drifted as larvae and in which they spent their first few years of life. From the relatively small number of offshore returns the first might be favoured. Two of the Newfoundland taggings were made late in the year, when fish remaining in the area might be expected to be part of a local stock. Also Fleming (1965) shows that concentrated fishing in an area up to 20 miles from the coast can produce evidence of stock depletion. However the second possibility cannot be dismissed out of hand.

It is evident from the foregoing that the "Labrador-Newfoundland cod stock" is in fact a "stock-complex", composed of at least three major groups which overlap in their summer distribution, but tend to separate to some extent in winter. The tag returns suggest the following picture.

(1) There is a "Labrador-Newfoundland" cod stock which spawns mainly on Hamilton Inlet Bank, though possibly to a small extent on the northeast Newfoundland Shelf,

and is distributed in summer on the coasts of Labrador and northeast Newfoundland (Figs. 46, 47, 48 and 52).

(2) There is a "Northeast Newfoundland" cod stock which spawns mainly on Hamilton Inlet Bank but also on the northeast Newfoundland Shelf. Its summer distribution extends only to northeast and eastern Newfoundland (Figs. 49, 50, 51 and 53). Alternatively there are two stocks, one spawning on Hamilton Inlet Bank, the other on the northeast Newfoundland Shelf (Funk Island Bank). This is unlikely however since all winter returns of fish tagged on Funk Island Bank were taken on Hamilton Inlet Bank (Fig. 53).

(3) There is an "East Newfoundland" stock which spawns on the northern Grand Bank and is distributed in summer mainly in eastern Newfoundland, though extending to northeast Newfoundland as well (Fig. 54).

(4) In addition there is evidence of smaller local stocks associated throughout the year with the coastal shelf (Figs, 46-51), and others with the offshore banks, particularly the northern Grand Bank (Figs. 51 and 54).

The picture in northern Labrador is not complete, but reports of spawning cod in spring in Division 2G (Postolaky, 1965) may be indicative of a separate "North Labrador" stock which spawns off northern Labrador and is distributed in summer along the Labrador coast. Several far northern offshore returns (Figs. 47-49) may be evidence of this. Postolaky (1965) proposes that there is a post-spawning migration from northern Labrador to Hamilton Inlet Bank. This appears to be based on returns of two tagged cod which moved from north to south in 20 days. If such a post-spawning migration actually occurs it raises the question as to where the northern coastal cod come from. Do fish which have moved about 400 miles to the south now migrate north again? The inshore appearance of cod is progressively later from south to north, indicating that at least part of the northern summer population may come from southern offshore Labrador. However it seems more likely that the main bulk of these northern spawners are those which occur in summer in coastal northern Labrador, eastern Ungava Bay (Dunbar and Hildebrand, 1952) and possibly in Ungava Bay generally. The foregoing possibilities are summarized diagramatically in Fig. 55

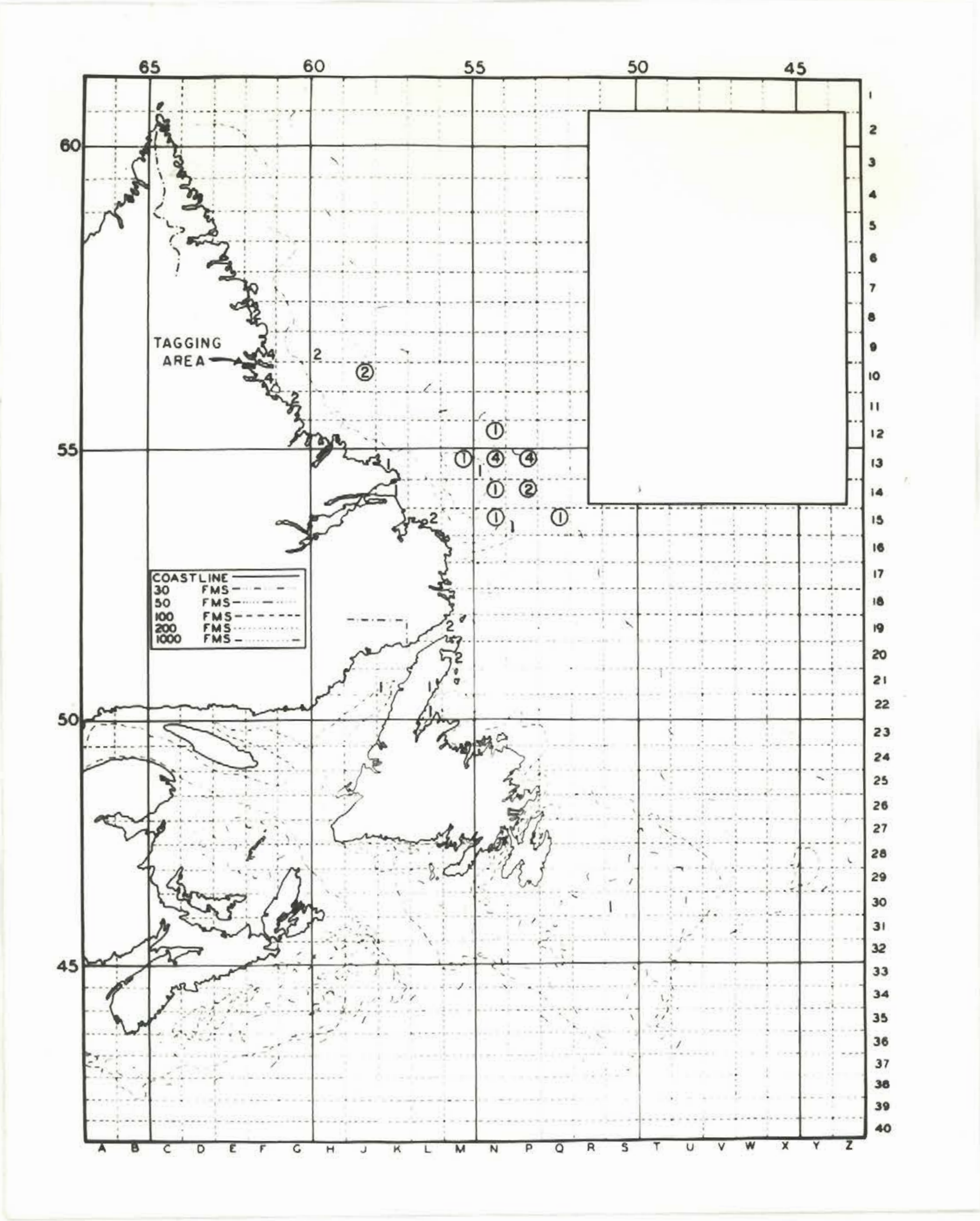

Figure 46. Winter-spring (circled) and summer-autumn tag returns from 704 cod tagged in northern Labrador, August, 1962.

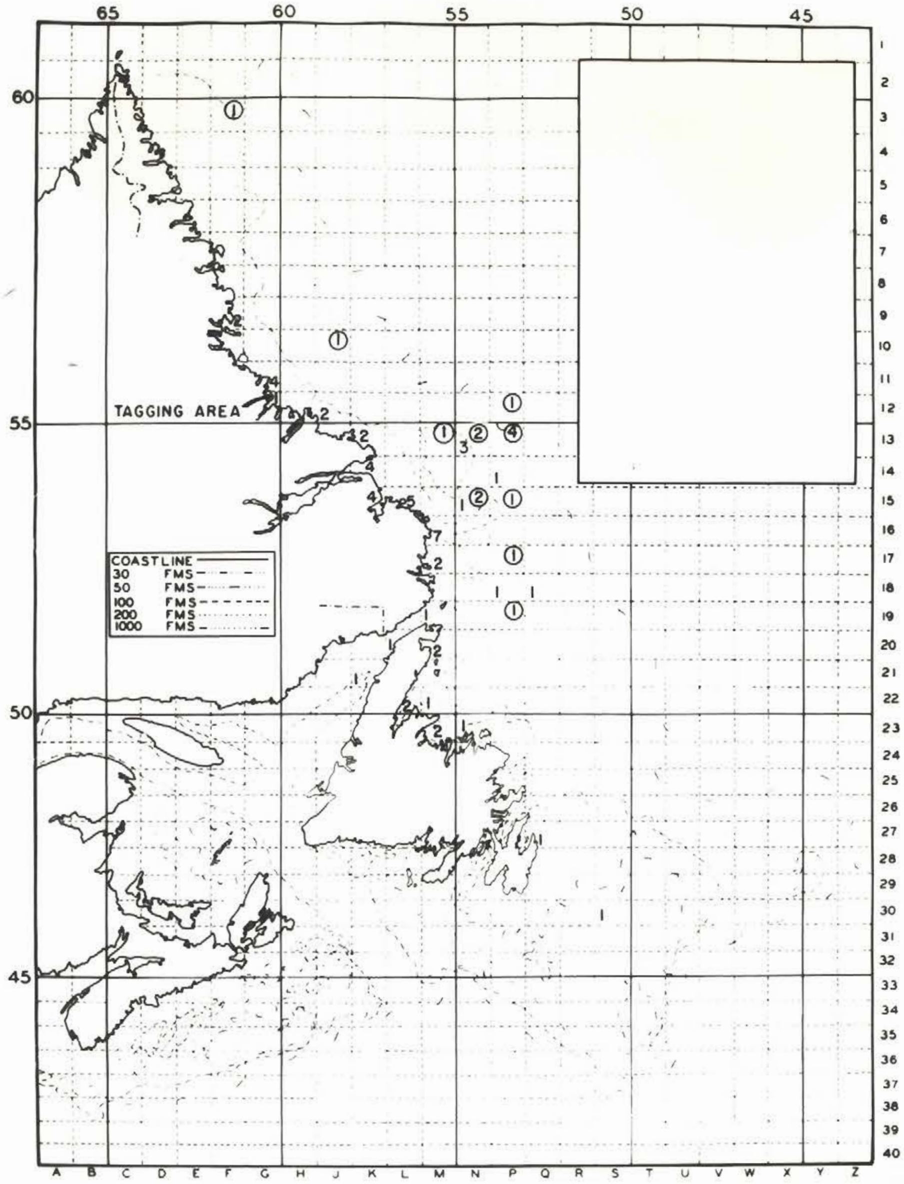

Figure 47. Winter-spring (circled) and summer-autumn tag returns from 768 cod tagged in mid-Labrador, August, 1962

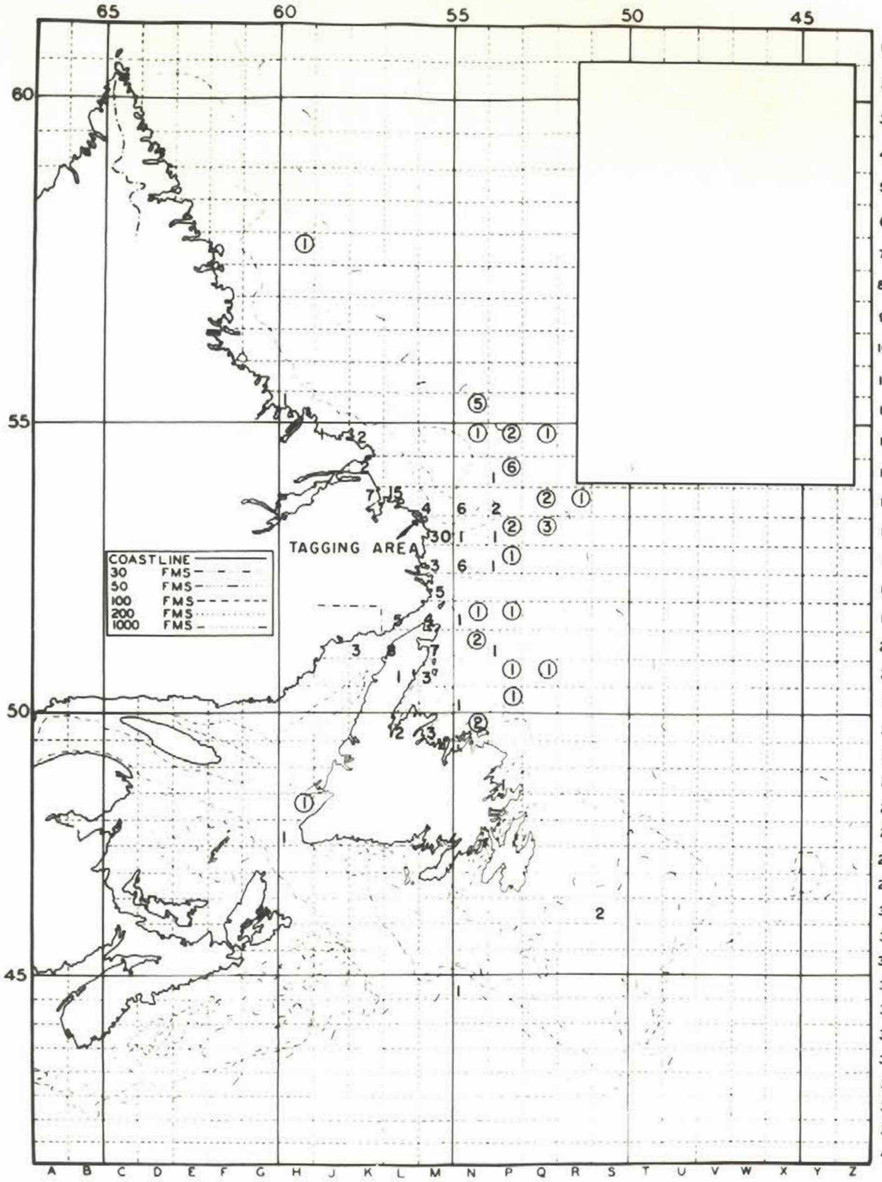

Figure 48. Winter-spring (circled) and summer-autumn tag returns from 768 cod tagged in southern Labrador, July, 1962.

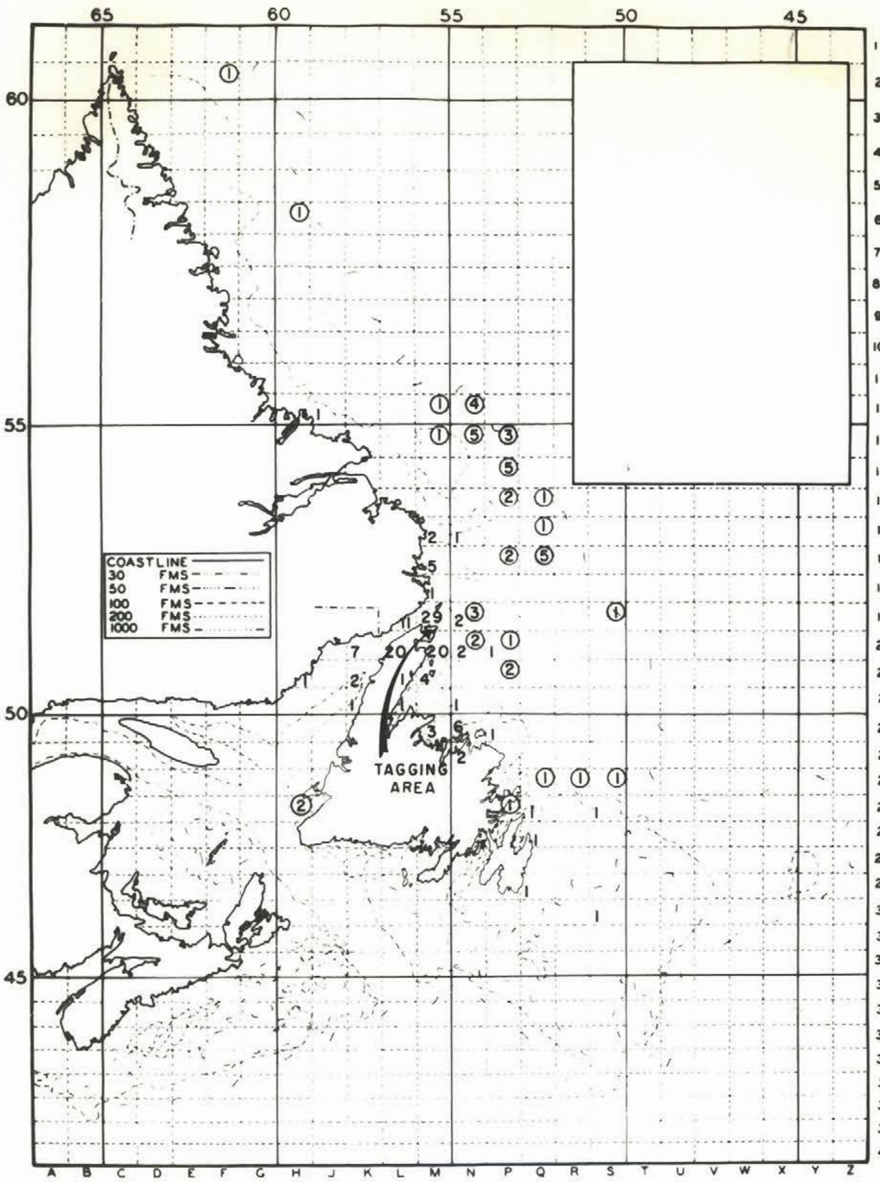

Figure 49. Winter-spring (circled) and summer-autumn tag returns from 768 cod tagged in northern Newfoundland, August, 1962.

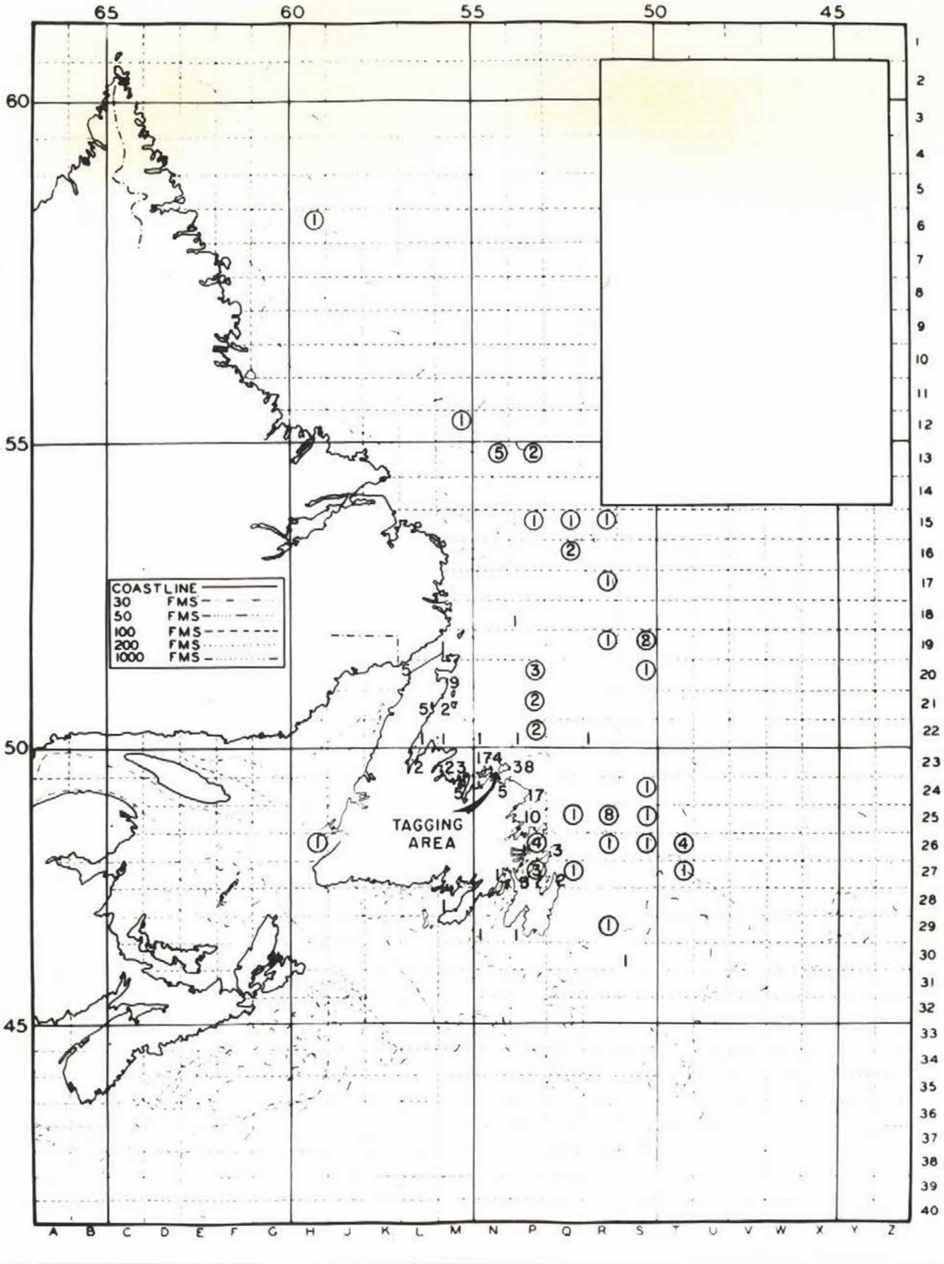

Figure 50. Winter-spring (circled) and summer-autumn tag returns from 1152 cod tagged in northeast Newfoundland, October, 1963.

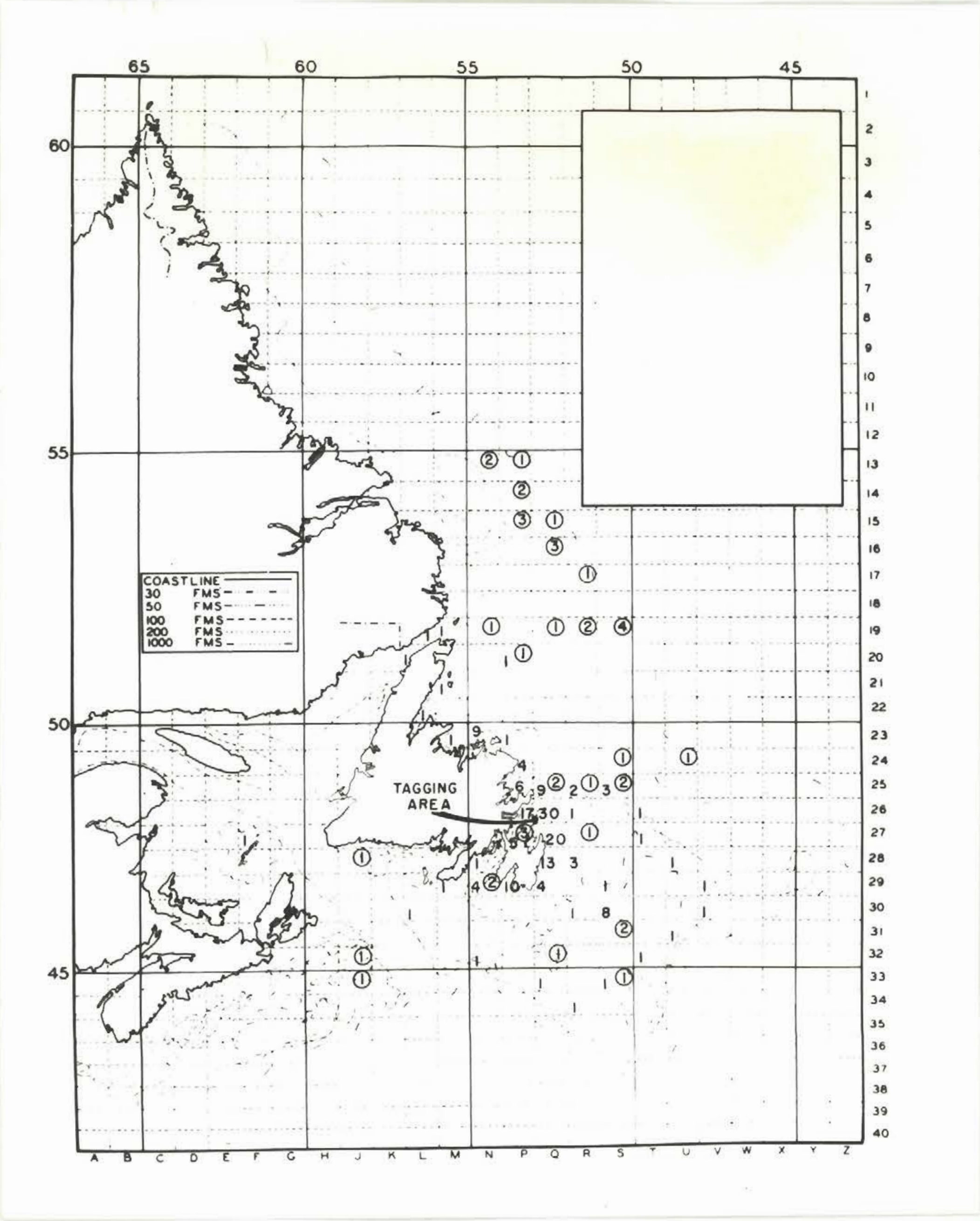

Figure 51. Winter-spring (circled) and summer-autumn tag returns from 1152 cod tagged in eastern Newfoundland, November, 1962

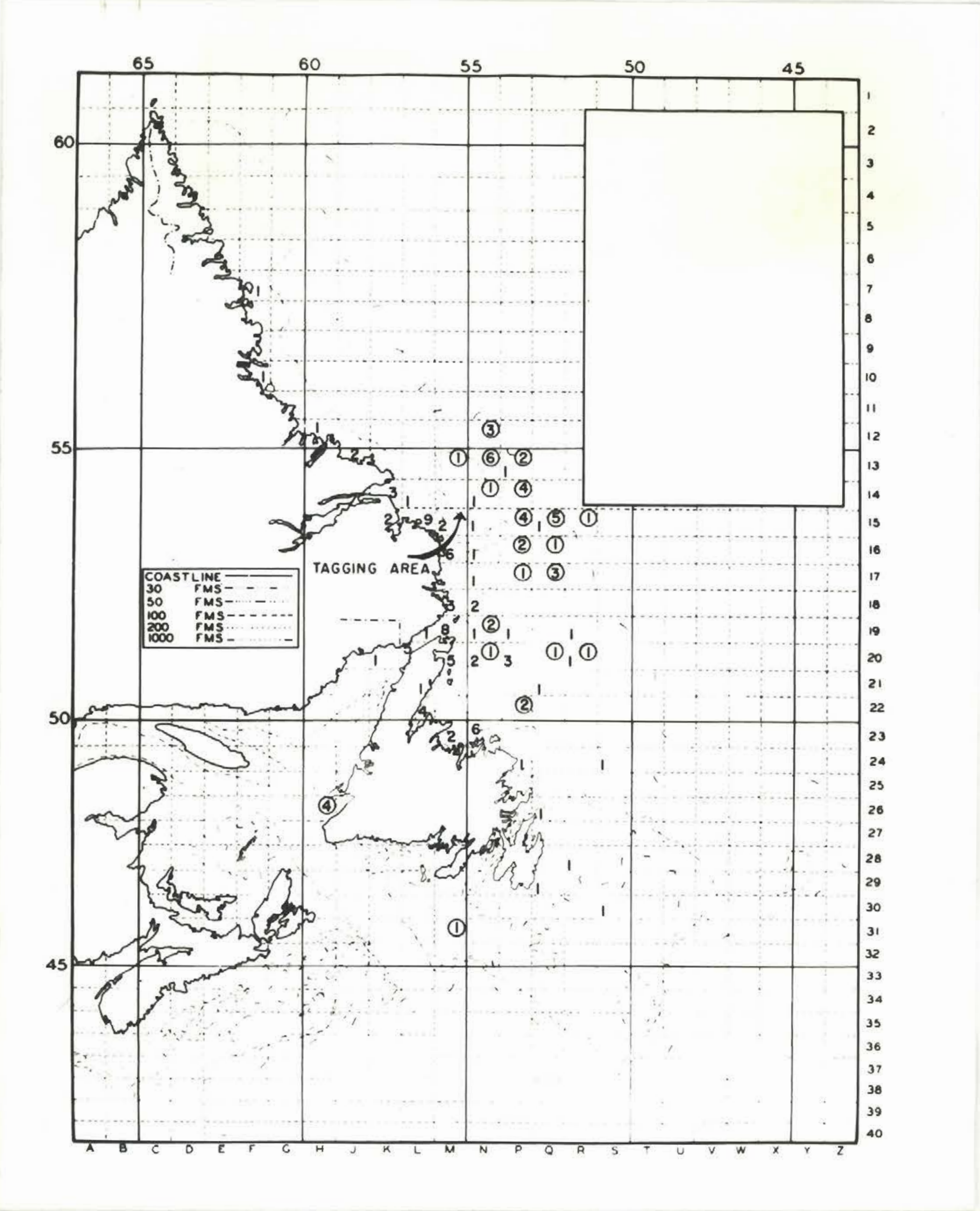

Figure 52. Winter-spring (circled) and summer-autumn tag returns from 1152 cod tagged on Hamilton Inlet Bank, September, 1962.

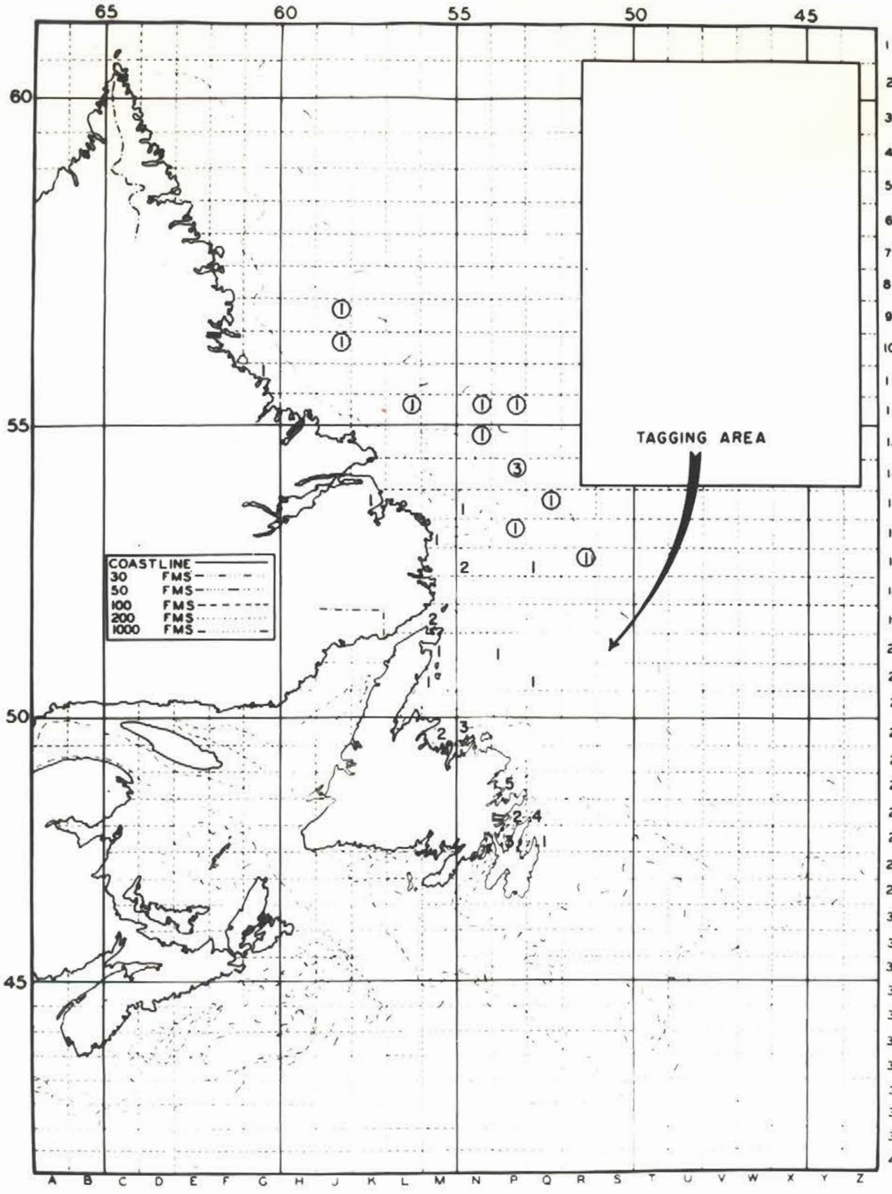

Figure 53. Winter-spring (circled) and summer-autumn tag returns from 384 cod tagged on the northeast Newfoundland Shelf, May, 1964.

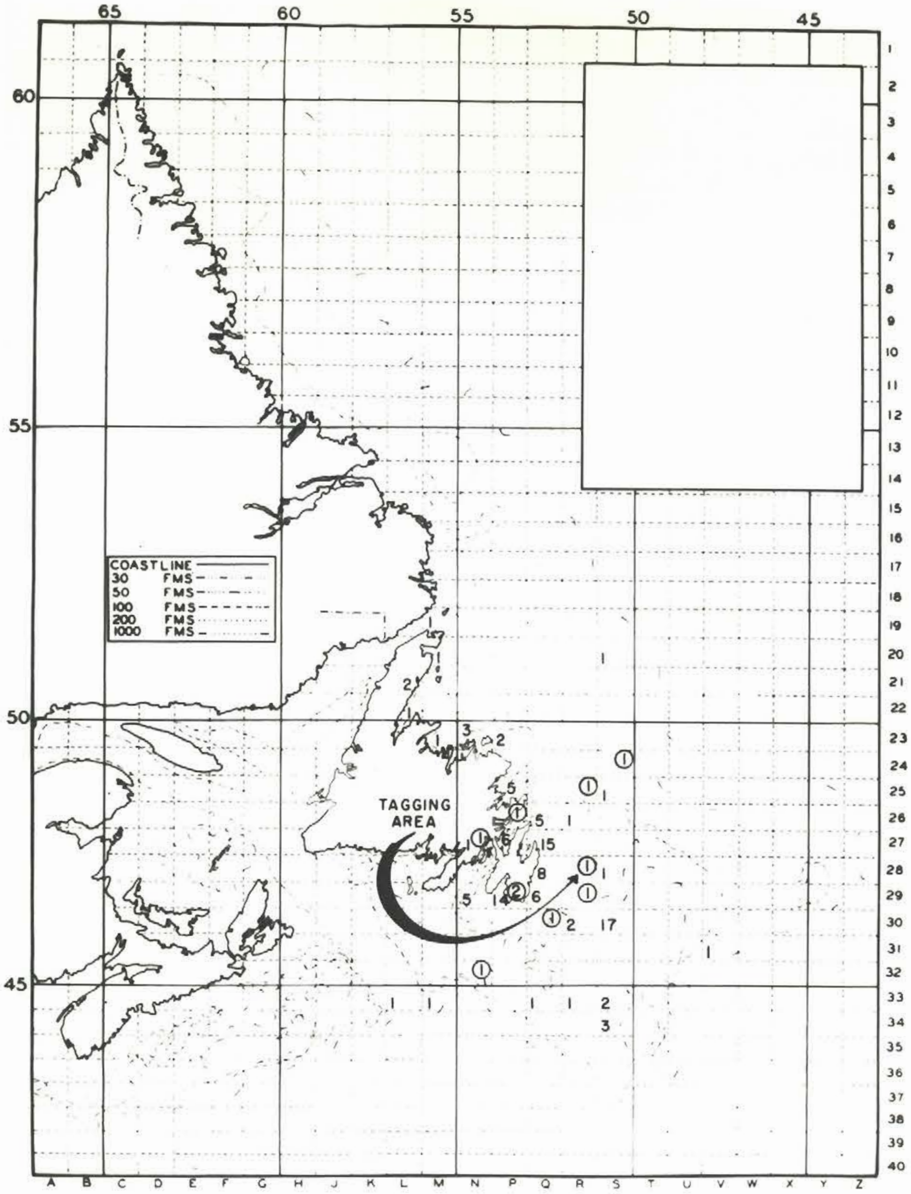

Figure 54. Winter-spring (circled) and summer-autumn tag returns from 1152 cod tagged on the northern Grand Bank, April, 1964.

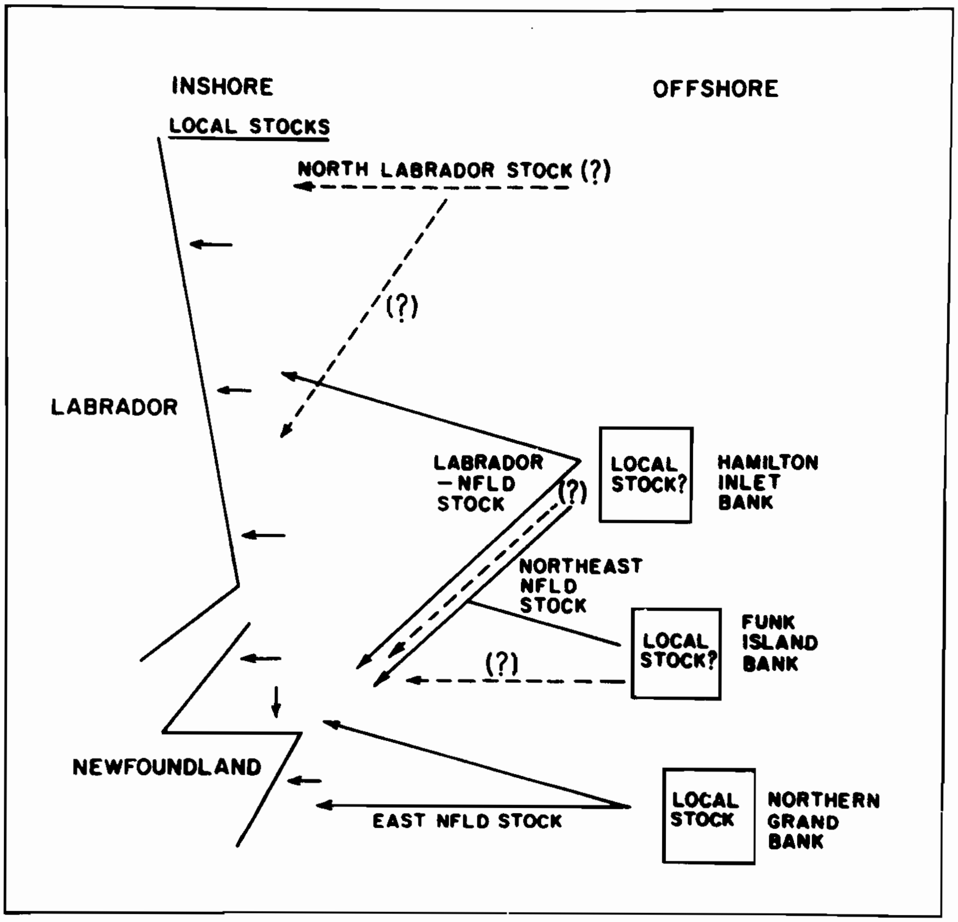

Figure 55. Diagrammatic summary of possible divisions within the Labrador-Newfoundland cod stock complex. The arrows indicate onshore migration in summer.

## 10. SUMMARY AND CONCLUSIONS

Cod inhabiting the area from northern Labrador to the northern Grand Bank are shown to be composed of at least three major groups, possibly four. These move inshore in spring and early summer and their distributions overlap, but there is some tendency to separate during the spawning season, i.e. a tendency for reproductive isolation. There is also evidence of smaller local stocks, exhibiting minimal seasonal movement, associated with the coastal shelves and offshore banks.

Gradients in growth, size and age at maturity and in the fecundity-length relationship exist from north to south. The fact that these are maintained is indicative of incomplete mixing of adults, both inshore and offshore. Increased age at maturity from north to south may have a genetic basis. Growth differences are probably phenotypic, the increased growth in the south being related to generally warmer hydrographic conditions, though the possibility of genetically related differences in growth cannot be ruled out. The tendency to higher fecundity at similar lengths in the north is probably related to the younger age and smaller size at maturity. Vertebral counts throughout the area are similar. This is probably due to similar conditions at the time of egg and larval development.

In the Labrador area there is a possible stock separation from north to south. There is evidence of slight gradients in length and age at maturity, and a recent large increase in growth of older ages in southern Labrador is reflected only to a very slight extent in the north. There appear to be at least two separate offshore spawning areas. One of these, Hamilton Inlet Bank, is shared with at least one other stock from the south. Some cod tagged inshore and on Hamilton Inlet Bank move to the Northeast Newfoundland coast, but very few tagged in the latter area are found in inshore Labrador. It may be supposed that movement of individuals from the main Labrador stocks to northeast Newfoundland is relatively slight. There must then be a separate northeast Newfoundland stock which spawns in offshore Labrador but moves inshore only on the northeast Newfoundland coast.

From the scarcity of larger immature fish it is suggested that those fish which move inshore in summer in the Labrador area are mainly post-spawners. It is further suggested that since few fish below age 3 are found on Hamilton Inlet Bank, since extensive southward larval drift must occur and since large numbers of cod less than age 3 are found inshore, then the inshore areas of southern Labrador and northeast Newfoundland are important "nursery" areas, from which young fish gradually move offshore as size and age increase. Most of these appear to return to Hamilton Inlet Bank to spawn.

Time of spawning is earlier in the north. This is possibly an adaptation to ensure adequate time for larval drift to settlement areas. Fluctuations in year-class survival may be related to the direction and extent of larval drift. The two largest recent year-classes occurred in cold years. These were also years of extensive iceberg drift.

The great increase in offshore fishing since 1959 has produced significant effects. Catch per unit effort inshore has declined greatly. A decline in catch per unit effort offshore has so far been prevented by fishing heavily in spring, rather than in autumn only, but the catch per unit effort in autumn has declined. Growth has increased in those age groups beyond the selection range of the gear, while the younger age groups show a slight decline. The latter may be due to greater abundance of young fish in two recent large year-classes and to lesser predation by older cod. The fishery has had little or no effect on size at maturity, but age at maturity has increased due to slower growth of younger fish. Estimates of mortality were usually unsatisfactory because of variations in year-class survival and overlapping of stocks, but catch curves assumed the typical pattern indicative of increased fishing.

It is evident that it will be difficult to set up mathematical models and to apply population dynamics theory to cod in the Labrador-northeast Newfoundland area. Aside from uncertainties related to the inshore fishery, such as measures of gear selection and relative importance of various gears in the catches, the area as a whole exhibits a wide range in growth and size and age at maturity. The various stocks cannot easily be treated separately since there are usually several occupying an area at a given time, in proportions as yet undetermined on a quantitative basis.

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Table 1. Collections from the Labrador inshore commercial fishery, July-August, 1959-64. (H & L = Hook and Line).

| Year | Area | Gear | Specimens Examined |  |  |
|---|---|---|---|---|---|
|  |  |  | Random | Category | Total |
| 1950 | 2G | Jigger | 240 | - | 240 |
| 1959 | 2G | Jigger | 120 | - | 120 |
|  | 2H | Jigger | 600 | - | 600 |
|  | 2J | Trap | 608 | - | 608 |
|  |  | Jigger | 240 | - | 240 |
|  |  | H&L | 281 | - | 281 |
| 1960 | 2G | Jigger | 316 | - | 316 |
|  | 2H | Jigger | 621 | - | 621 |
|  | 2J | Trap | 1061 | - | 1061 |
|  |  | H&L | 105 | - | 105 |
| 1962 | 2G | Jigger | 200 | 5 | 205 |
|  | 2H | Jigger | 768 | 16 | 784 |
|  | 2J | Trap | 811 | 105 | 916 |
|  |  | Jigger | 120 | - | 120 |
|  |  | H&L | 76 | - | 76 |
| 1963 | 2G | Jigger | 241 | 16 | 257 |
|  | 2H | Jigger | 865 | 72 | 937 |
|  | 2J | Trap | 803 | 69 | 872 |
|  |  | Jigger | 514 | 48 | 562 |
|  |  | H&L | 86 | - | 86 |
| 1964 | 2G | Jigger | 123 | - | 123 |
|  | 2H | Jigger | 256 | 21 | 277 |
|  | 2J | Trap | 137 | 85 | 222 |
|  |  | Jigger | 276 | 93 | 369 |
|  |  | H&L | 42 | - | 42 |

Table 2. Collections from research vessel surveys off Labrador, 1950-64. (B-U = southern Baffin Island and Ungava Bay).

| Year | Month | Area | Range of Depths Sampled (Fms.) | Specimens Examined | | |
|---|---|---|---|---|---|---|
| | | | | Random | Category | Total |
| 1950 | Aug. | 2G | 200 | 112 | - | 112 |
| | Aug. | 2H | 180 | 119 | - | 119 |
| | Sept. | 2J | 122 | 120 | - | 120 |
| 1951 | Sept. | 2J | 98-108 | 232 | - | 232 |
| 1953 | July | 2J | 112-150 | 119 | - | 119 * |
| | Aug. | 2J | 165 | 115 | - | 115 * |
| | Sept. | 2J | 107 | 124 | - | 124 |
| 1954 | Sept. | 2J | 108 | 120 | - | 120 |
| 1958 | June | 2J | 97 | 132 | - | 132 |
| | Aug. | 2J | 148-149 | 160 | - | 160 |
| 1959 | Aug-Sept | B-U | 28-205 | 186 | - | 186 |
| | Sept. | 2G | 155-415 | 43 | - | 43 |
| | Sept. | 2H | 99 | 139 | - | 139 |
| | Sept. | 2J | 117-160 | 21 | - | 21 |
| 1960 | Aug. | 2H | 78-247 | 1178 | 50 | 1228 |
| | Aug. | 2J | 89-305 | 567 | 125 | 692 |
| 1962 | June | 2J | 151-152 | 44 | 4 | 48 |
| | Aug. | 2J | 87-152 | 969 | 44 | 1013 |
| | Sept. | 2J | 96 | 120 | - | 120 |

(continued next page)

* longline catches

Table 2 (continued)

| Year | Month | Area | Range of Depths Sampled (Fms.) | Specimens Examined Random | Specimens Examined Category | Specimens Examined Total |
|---|---|---|---|---|---|---|
| 1963 | Apr. | 2J | 95-247 | 1081 | 247 | 1328 |
| | May | 2J | 112-180 | 901 | 58 | 959 |
| | Sept. | 2J | 122-174 | 222 | 148 | 370 |
| | Oct. | 2J | 77-125 | - | 589 | 589 |
| 1964 | Apr. | 2J | 130-198 | 302 | 169 | 471 |
| | May | 2J | 110-120 | 292 | 121 | 413 |
| | Oct. | 2J | 81-100 | 139 | 30 | 169 |
| | Nov. | 2J | 88-175 | 417 | 34 | 451 |
| | Nov. | 2H | 65-177 | 214 | 5 | 219 |
| | Nov. | 2G | 65-149 | 287 | 1 | 288 |

Table 3. Background data for length distributions of Figures 14 and 15.

| | | RESEARCH | | | COMMERCIAL | | | |
|---|---|---|---|---|---|---|---|---|
| Area | Year | Month | Depth (Fms.) | Mesh Size (mm) | Month | Depth (Fms.) | Mesh Size (mm) | Country |
| Baffin Is. Ungava Bay | 1959 | Aug-Sept | 28-205 | 28.5 | Oct. | 82 | 110 | West Germany |
| 2J | 1960 | Aug. | 89-305 | 28.5 | Aug. | 100-125 | 114 | Portugal |
| 2J | 1962 | Aug. | 87-152 | 28.5 | Aug. | 44-175 | 120 | Spain |
| 2J | 1963 | Apr-May | 95-247 | 28.5 | Apr-May | 102-255 | 110 | USSR |

Commercial data sources - ICNAF Sampling Yearbooks:

Ungava Bay, 1959 - Vol. 4, p. 22 (A. Meyer)

2J, 1960 - Vol. 5, p. 31 (M.J. Ruivo and G.V. Quartin)

2J, 1962 - Vol. 7, p. 20 (O. Rodriguez-Martin and O. Cendrero)

2J, 1963 - Vol. 8, p. 18 (A. Noskov and A.P. Senina).

Table 4. Partial age-length key for collections from Division 2J, April-May, 1963, to illustrate method of adjusting age distributions. The frequency of ages within each length group (whole numbers) is converted to catch by multiplication by the catch to sample ratio. The otolith sample size was 2287. S = sample, A = adjusted.

AGES (to age 21)

| Length (cm) | 2 | | 3 | | 4 | | 5 | | | No. in Sample | No. in Catch | C/S Ratio |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | S | A | S | A | S | A | S | A | | | | |
| 15-17 | 10 | 15.00 | | | | | | | | 10 | 15 | 1.50 |
| 18-20 | 36 | 36.00 | | | | | | | | 36 | 91 | 2.53 |
| 21-23 | 25 | 132.25 | 6 | 31.74 | | | | | | 31 | 164 | 5.29 |
| 24-26 | 5 | 33.75 | 42 | 283.50 | 5 | 33.75 | | | | 52 | 351 | 6.75 |
| 27-29 | | | 35 | 383.60 | 47 | 515.12 | 1 | 10.96 | | 83 | 910 | 10.96 |
| 30-32 | | | 6 | 81.18 | 126 | 1704.78 | 7 | 94.71 | | 139 | 1881 | 13.53 |
| 33-35 | | | 1 | 10.58 | 175 | 1851.50 | 46 | 486.68 | ...... | 227 | 2403 | 10.58 |
| 36-38 | | | | | 59 | 618.91 | 73 | 765.77 | ...... | 151 | 1584 | 10.49 |
| 39-41 | | | | | 7 | 93.45 | 76 | 1014.60 | ...... | 131 | 1749 | 13.35 |
| 42-44 | | | | | 2 | 28.52 | 44 | 627.44 | ...... | 202 | 2881 | 14.26 |
| 45-47 | | | | | | | 18 | 287.10 | ...... | 212 | 3381 | 15.95 |
| 48-50 | | | | | | | 9 | 169.11 | ...... | 183 | 3439 | 18.79 |
| 51-53 | | | | | | | 6 | 100.50 | ...... | 176 | 2948 | 16.75 |
| 54-56 | | | | | | | 4 | 57.00 | ...... | 175 | 2494 | 14.25 |
| (to 109 cm) | | | | | | | | | | | | |
| Totals | | 217.00 | | 790.60 | | 4846.03 | | 3613.87 | ....... | | 28,180 | |
| Percent | | 0.8 | | 2.8 | | 17.2 | | 12.8 | ....... | | 100.0 | |

Table 5. Estimates of total mortality from the catch curves of Figures 20 and 21.

| Curve | Area | Period | Ages | ln $N_t$ | ln $N_{t+r}$ | Z | a(%) |
|---|---|---|---|---|---|---|---|
| 20A | 2H | 1960 | 3-8 | 3.16 | 2.00 | .23 | 20.6 |
| | | | 8-13 | 2.00 | 0 | .40 | 33.0 |
| | | | 14-20 | .30 | -3.50 | .63 | 46.7 |
| 20B | 2J | 1950-58 | 5-9 | 2.92 | 2.48 | .11 | 10.4 |
| | | | 9-18 | 2.37 | -2.45 | .54 | 41.7 |
| 20C | 2J | 1960&62 | 6-9 | 2.35 | 1.35 | .25 | 22.1 |
| | | | 9-15 | 1.28 | -0.05 | .22 | 19.8 |
| | | | 15-18 | .07 | -3.30 | .84 | 56.8 |
| 20D | 2J | 1963-64 | 6-7 | 3.32 | 3.06 | .26 | 22.9 |
| | | | 7-8 | 3.06 | 1.75 | 1.31 | 73.0 |
| | | | 8-9 | 1.75 | .84 | .91 | 59.8 |
| | | | 9-10 | .84 | .38 | .46 | 36.9 |
| | | | 6-10 | Average | | .74 | 52.3 |
| | | | 10-19 | .38 | -3.00 | .38 | 31.6 |
| 21A | 2GH | 1959-60 | 9-13 | 2.72 | 1.87 | .21 | 18.9 |
| | | | 14-18 | 2.12 | -0.80 | .73 | 51.8 |
| 21B | 2GH | 1962-63 | 10-15 | 2.54 | 1.40 | .23 | 20.6 |
| | | | 16-20 | 1.65 | -1.80 | .86 | 57.7 |
| 21C | 2J | 1959-60 | 9-14 | 2.45 | 1.85 | .12 | 11.3 |
| | | | 15-19 | 1.34 | -1.90 | .81 | 55.5 |
| 21D | 2J | 1962-63 | 7-15 | 2.57 | 1.15 | .18 | 16.5 |
| | | | 16-18 | 1.12 | .28 | .42 | 34.3 |

Table 6. Numbers of mature and immature cod collected in random samples from the inshore commercial fishery, 1959-64.

| Area | Year | Number Immature | Number Mature | Total | Percent Immature |
|---|---|---|---|---|---|
| 2G | 1959 | 1 | 119 | 120 | .8 |
| | 1960 | 0 | 316 | 316 | 0 |
| | 1962 | 4 | 196 | 200 | 2.0 |
| | 1963 | 17 | 224 | 241 | 7.0 |
| | 1964 | 0 | 123 | 123 | 0 |
| 2H | 1959 | 26 | 574 | 600 | 4.3 |
| | 1960 | 3 | 618 | 621 | .5 |
| | 1962 | 2 | 766 | 768 | .3 |
| | 1963 | 102 | 763 | 865 | 11.8 |
| | 1964 | 4 | 252 | 256 | 1.6 |
| 2J | 1959 | 22 | 826 | 848 | 2.6 |
| | 1960 | 38 | 1023 | 1061 | 3.6 |
| | 1962 | 80 | 851 | 931 | 8.6 |
| | 1963 | 265 | 1052 | 1317 | 20.1 |
| | 1964 | 49 | 364 | 413 | 11.9 |

Table 7. Comparison of fecundity estimates from a single fish by whirling vessel and **dry weight** methods.

| Sample Number | No. of Eggs | Whirling Vessel | Dry Weights | Difference (d) |
|---|---|---|---|---|
| 1 | 1220 | 1.2200 | 1.3531 | +.1331 |
| 2 | 1204 | 1.2040 | 1.4030 | +.1990 |
| 3 | 1454 | 1.4540 | 1.3943 | -.0597 |
| 4 | 1271 | 1.2710 | 1.3765 | +.1055 |
| 5 | 1380 | 1.3800 | 1.4194 | +.0394 |
| 6 | 1261 | 1.2610 | 1.4602 | +.1992 |
| 7 | 1278 | 1.2780 | 1.4799 | +.2019 |
| 8 | 1304 | 1.3040 | 1.4551 | +.1511 |
| 9 | 1220 | 1.2200 | 1.4491 | +.2291 |
| 10 | 1270 | 1.2700 | 1.4799 | +.2099 |
| N | - | 10 | 10 | 10 |
| $\Sigma X$ | - | 12.8620 | 14.2705 | 1.4085 |
| $\bar{X}$ | - | 1.28620 | 1.42705 | .14085 |
| $\Sigma X^2$ | - | 16.597094 | 20.382409 | .273384 |
| SD | - | .077453 | .044340 | - |
| CV | - | 6.0% | 3.1% | - |

$SE_{\bar{d}}$ = .028867 $t$ = 4.879 df = N-1 = 9 $P < .01$

Table 8. Comparison of fecundity estimates (millions of eggs) by whirling vessel and weight methods for two 1/1000 whirling vessel samples for each of 8 fish. The combined estimate by the weight method is derived from the combined fractions, i.e. it is not the mean value. %D = percent deviation of each pair of estimates from their mean. d = difference between the combined estimates from each method.

| | WHIRLING VESSEL | | | | WEIGHTS | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Fish Length | Fraction 1 | Fraction 2 | %D | Combined | Fraction 1 | Fraction 2 | %D | Combined | d |
| 76 | 1.5590 | 1.4870 | 2.4 | 1.5230 | 1.4266 | 1.4392 | 0.4 | 1.4327 | -.0903 |
| 76 | 1.8440 | 1.8790 | 0.9 | 1.8615 | 1.7818 | 1.7706 | 0.3 | 1.7761 | -.0854 |
| 77 | 1.9920 | 2.0770 | 2.1 | 2.0345 | 2.0224 | 2.1567 | 3.2 | 2.0888 | +.0543 |
| 77 | .8320 | .7020 | 8.8 | .7700 | .7736 | .7662 | 0.5 | .7703 | +.0003 |
| 78 | 1.6310 | 1.8330 | 5.8 | 1.7320 | 1.6605 | 1.7694 | 3.2 | 1.7164 | -.0156 |
| 78 | 1.8460 | 1.5750 | 7.9 | 1.7105 | 1.4907 | 1.5436 | 1.7 | 1.5146 | -.1959 |
| 79 | 2.2730 | 2.3850 | 2.4 | 2.3290 | 2.2274 | 2.1719 | 1.3 | 2.1986 | -.1304 |
| 80 | 2.3260 | 1.9920 | 7.7 | 2.1590 | 1.8981 | 1.9089 | 0.3 | 1.9031 | -.2559 |
| N | | | | 8 | | | | 8 | 8 |
| ≤X | | | | 14.1195 | | | | 13.4006 | -.7189 |
| X̄ | | | | 1.7649 | | | | 1.6751 | -.0899 |
| ≤$X^2$ | | | | 26. 527958 | | | | 23.859282 | .139505 |
| SD | | | | .47935 | | | | .44912 | - |
| CV | | | | 27.2% | | | | 26.8% | - |

$SE_{\bar{d}}$ = .036565 t = 2.46 df = 8-1 = 7 $.05 > P > .02$

Table 9. Regression constants and tests for significance of correlations of fecundity with length, age and weight. m = slope and log k = intercept of fitted log-log straight lines.

| | Area | No. Fish | m | log k | r | t | P | $r^2$ |
|---|---|---|---|---|---|---|---|---|
| LENGTH | 2J-3K | 28 | 3.63 | -0.64 | .940 | 14.11 | <.01 | .884 |
| | 3L | 21 | 2.51 | 1.52 | .729 | 4.64 | <.01 | .531 |
| | 3N | 41 | 3.81 | -1.05 | .871 | 11.06 | <.01 | .759 |
| | 30 | 40 | 3.88 | -1.27 | .834 | 9.24 | <.01 | .696 |
| | All | 130 | 3.42 | -0.30 | .857 | 18.24 | <.01 | .734 |
| AGE | 2J-3K | 26 | 2.24 | 3.85 | .695 | 4.74 | <.01 | .483 |
| | 3L | 21 | 0.96 | 5.34 | .560 | 2.94 | <.01 | .314 |
| | 3N | 41 | 1.93 | 4.42 | .788 | 7.99 | <.01 | .621 |
| | 30 | 40 | 2.48 | 3.84 | .777 | 7.66 | <.01 | .604 |
| | All | 128 | 1.94 | 4.35 | .680 | 10.41 | <.01 | .462 |
| WEIGHT | 2J-3K | 8 | 0.48 | 0.01* | .883 | 4.61 | <.01 | .780 |
| | 3L | 21 | 0.41 | 0.42* | .815 | 6.12 | <.01 | .664 |
| | 3N | 25 | 0.50 | -0.31* | .889 | 9.30 | <.01 | .790 |
| | 30 | 29 | 0.50 | -0.44* | .862 | 8.83 | <.01 | .743 |
| | All | 83 | 0.48 | -0.12* | .862 | 15.27 | <.01 | .743 |

* values of k from arithmetic straight lines.

Table 10. Summary of covariance analyses for regressions of fecundity against length, age and weight. A single asterisk (*) indicates significance at P = .05, a double asterisk (**) significance at P = .01.

| | | Test | MEAN SQUARES | | | MEAN SQUARES | | |
|---|---|---|---|---|---|---|---|---|
| | | | Within Samples | Reg. Coeff. | F | Common Regression | Adjusted Means | F |
| LENGTH | (1) | 3N,1964-3N,1965 | .018935 | .000155 | .01 | .018440 | .014465 | .78 |
| | (2) | 2J,3K-3L-3N-30 | .026374 | .034707 | 1.32 | .026574 | .139329 | 5.24** |
| | (3) | All except 2J,3K | .028512 | .051949 | 1.82 | .028990 | .174391 | 6.02** |
| | (4) | All except 3L | .027663 | .004496 | .16 | .027221 | .166569 | 6.12** |
| | (5) | All except 3N | .030150 | .049538 | 1.64 | .030606 | .224977 | 7.35** |
| | (6) | All except 30 | .018621 | .042120 | 2.26 | .019168 | .035994 | 1.88 |
| | (7) | 3N,1965-30,1965 | .037690 | .004320 | .11 | .037072 | .119003 | 3.21 |
| | (8) | 3N,1964/65-30,1965 | .030762 | .000485 | .02 | .030374 | .136087 | 4.48* |
| AGE | (9) | 2J,3K-3L-3N-30 | .046652 | .143089 | 3.07* | .049004 | .401960 | 8.20** |
| | (10) | All except 3L | .050078 | .038487 | .77 | .049853 | .509351 | 10.22** |
| | (11) | 3N,1964/65-30,1965 | .041996 | .076728 | 1.83 | .042412 | .016280 | .38 |
| WEIGHT | | 2J,3K-3L-3N-30 | .776580 | .185862 | .24 | .753861 | .915333 | 1.21 |

Table 11. Summary of ststistics for multiple correlation of fecundity with age and length. $X_1$ = log fecundity, $X_2$ = log length, $X_3$ = log age.

| | | 2J,3KL | 3NO |
|---|---|---|---|
| Nunber of fish | N | 47 | 81 |
| Coefficient of determination for $X_1$ and $X_2$ | $r^2_{12}$ | .796 | .705 |
| Correlation coefficient for $X_1$ and $X_2$ | $r_{12}$ | .892 | .840 |
| Coefficient of determination for $X_1$ and $X_3$ | $r^2_{13}$ | .325 | .610 |
| Correlation coefficient for $X_1$ and $X_3$ | $r_{13}$ | .570 | .781 |
| Computed value of $X_1$ when $X_2$ and $X_3 = 0$ | $a_{1.23}$ | -.21 | .14 |
| Coefficient of $X_2$ in estimating equation | $b_{12.3}$ | 3.36 | 2.72 |
| Coefficient of $X_3$ in estimating equation | $b_{13.2}$ | .08 | .88 |
| Coefficient of multiple determination. Proportion of $X_1$ variation explained by $X_2$ and $X_3$ | $R^2_{1.23}$ | .797 | .740 |
| Coefficient of multiple correlation | $R_{1.23}$ | .893 | .860 |
| | F for $R^2_{1.23}$ | 9.29 | 10.54 |
| Coefficient of partial determination. Proportion of additional $X_1$ variation, unexplained by $X_2$, which is explained by $X_3$ | $r^2_{13.2}$ | .003 | .120 |
| | t for $r^2_{13.2}$ | .13 | 1.03 |
| | P for $r^2_{13.2}$ | .8-.9 | .2-.3 |
| Coefficient of partial determination. Proportion of additional $X_1$ variation, unexplained by $X_3$, which is explained by $X_2$ | $r^2_{12.3}$ | .699 | .333 |
| | t for $r^2_{12.3}$ | 10.11 | 6.25 |
| | P for $r^2_{12.3}$ | <.01 | <.01 |

Estimating equation: $X_1 = a_{1.23} + b_{12.3}X_2 + b_{13.2}X_3$

Table 12. Fecundity at age versus number of spawning zones. Data from ICNAF Divisions 3N and 3O.

| Age | Number Spawning Zones | Number of Fish | Geometric Mean Length | Geometric Mean Fecundity |
|---|---|---|---|---|
| 9 | 1 | 2 | 92.3 | .946 |
| | 2 | 5 | 82.2 | 1.690 |
| | 3 | 7 | 83.1 | 1.669 |
| | 4 | 4 | 82.7 | 1.725 |
| 10 | 2 | 4 | 91.8 | 2.746 |
| | 3 | 9 | 90.1 | 2.400 |
| | 4 | 1 | 86.0 | 2.537 |
| | 5 | 5 | 93.4 | 2.266 |