

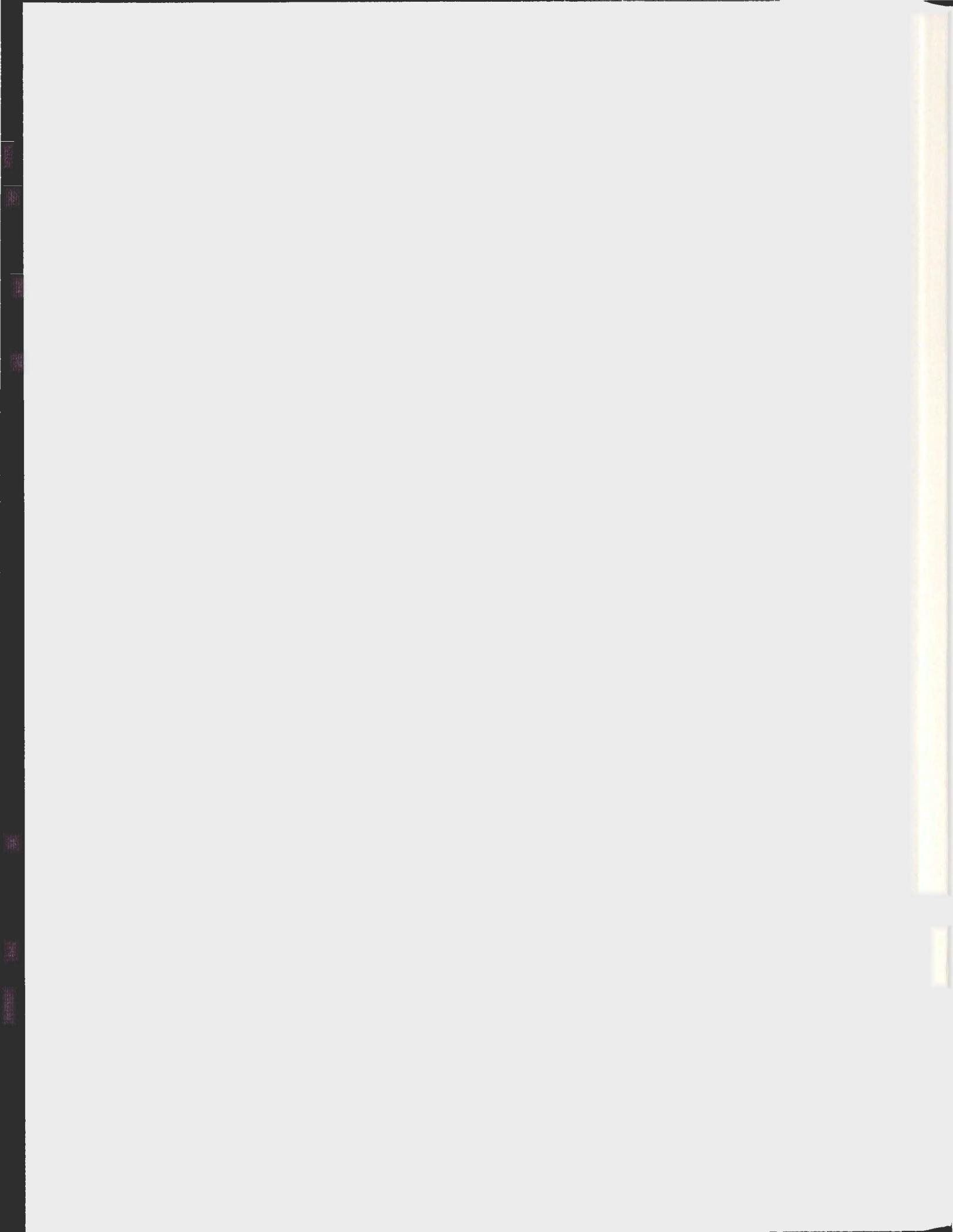
**CERTAIN BIOLOGICAL CHARACTERISTICS OF
GREENLAND HALIBUT IN THE NORTHWEST
ATLANTIC AND THEIR SIGNIFICANCE
FOR STOCK IDENTIFICATION**

CENTRE FOR NEWFOUNDLAND STUDIES

**TOTAL OF 10 PAGES ONLY
MAY BE XEROXED**

(Without Author's Permission)

WM. RAYMOND BOWERING



CERTAIN BIOLOGICAL CHARACTERISTICS OF GREENLAND HALIBUT
IN THE NORTHWEST ATLANTIC AND THEIR SIGNIFICANCE
FOR STOCK IDENTIFICATION

by



W. R. Bowering, B.Sc.

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science

Department of Biology
Memorial University of Newfoundland
July 1982

St. John's

Newfoundland

ABSTRACT

Greenland halibut (Reinhardtius hippoglossoides, (Walbaum)) are distributed throughout the Canadian Northwest Atlantic from Baffin Bank to the northern Grand Bank and into the Gulf of St. Lawrence. Larger older fish are found in deeper waters than the smaller fish and are more abundant in the more northerly areas. Analysis of growth rates indicated that the largest size at age for Greenland halibut is in the Gulf of St. Lawrence with the smallest size at age associated with Baffin Bank. Average sizes at age for intervening areas were generally similar. Probit analysis on female maturity indicated that fish in the Gulf of St. Lawrence mature at a much smaller size than other areas. In the Labrador area size at 50% maturity decreased progressively moving northward. Fish fecundity was also found to be significantly higher for the same size fish in the Gulf of St. Lawrence compared with those of southern Labrador. Tagging studies in eastern Newfoundland inshore indicate that Greenland halibut migrate towards deeper water and northward to Davis Strait. Young Greenland halibut move towards the coastal areas in summertime as part of a feeding migration. Based on the analyses of these biological characteristics, two separate spawning stocks of Greenland halibut are identified. One stock is comprised of fish from the northern Grand Bank to Davis Strait where spawning occurs, the second in the northern Gulf of St. Lawrence with spawning occurring southwest of St. George's Bay in the Laurentian Channel.

ACKNOWLEDGEMENTS

The author wishes to thank Dr. R.L. Haedrich, Department of Biology for his guidance and assistance during the supervision of this project and Drs. J. Carscadden, W. Templeman, R.A. Khan, and J.M. Green for their helpful comments and suggestions.

Thanks are also extended to the scientific and technical staff of the Groundfish Management Program of the Department of Fisheries and Oceans particularly the research technicians of the Flatfish Section who assisted in the collection and preparation of much of the samples. A special thanks to Messers. C. Butt, C.A. Rose, and A. Pitcher for this.

I would also like to express a sincere thanks to Messers. W.B. Brodie and J.M. Baird for their advice and assistance in some of the statistical analyses.

TABLE OF CONTENTS

	<u>PAGE</u>
ABSTRACT	iii
ACKNOWLEDGEMENTS	iii
LIST OF TABLES	vi
LIST OF FIGURES	vii
INTRODUCTION	1
MATERIALS AND METHODS	
Distribution	
A. Geographic distribution and relative abundance	7
B. Length frequency distribution by depth zone	9
C. Average size and sex ratios by depth zone	9
Age and Growth	
A. Age composition	10
B. Growth curves from empirical data	10
C. Back-calculated growth	11
Sexual Maturity	
A. Maturity curves	12
B. Probit analysis	13
Fecundity	
A. Collection of ovaries and counting of ova	14
B. Statistical analyses	16
Migrations	17
RESULTS	
Distribution	
A. Distribution and relative abundance	18
B. Length frequency distribution by depth zone	30
C. Average lengths and sex ratios of catch by depth zone	40
Age and Growth	
A. Age composition	40
B. Growth curves from empirical data	47
C. Back-calculated growth curves	50

Sexual Maturity	
A. Maturity curves	56
B. Probit analysis	61
Fecundity	
A. Fecundity vs. fish length	64
B. Fecundity vs. fish age	65
C. Fecundity vs. fish length and fish age	72
Migrations	
A. White Bay Tagging	74
B. Trinity Bay Tagging	81
C. Funk Island Bank Tagging	82
DISCUSSION	
Distribution	82
Age and growth	87
Sexual Maturity	92
Fecundity	95
Migrations	99
SUMMARY AND CONCLUSIONS	102
LITERATURE CITED	107

LIST OF TABLES

<u>TABLE</u>		<u>PAGE</u>
1	Sex ratios and mean lengths by depth for male and female Greenland halibut for the Gulf of St. Lawrence (Divisions 4RST).	41
2	Weighted average length (cm) of Greenland halibut by depth (m) and area in the Northwest Atlantic.	42
3	Sex ratio of Greenland halibut by depth in the Northwest Atlantic.	43
4	Summary of statistics for empirical growth equations ($y=a+bl_{nx}$ where y =length and x =age) for Greenland halibut.	49
5	Summary of adjusted means (intercepts) and regression coefficients (slopes) for back-calculated growth equations ($y=a+bl_{nx}$ where y =length and x =age) for Greenland halibut.	54
6	T-test matrix for adjusted group means for back-calculated growth curves.	55
7	Results of probit analyses of sexual maturity data, by area, with results of χ^2 tests for acceptability of the fitted lines to the observed data.	62
8	Matrix of t-values for paired comparisons of sexual maturity data for Greenland halibut.	63
9	Regression constants and tests for significance of correlations of fecundity with length and age for Greenland halibut; M = slope and log K = intercept of fitted log-log straight lines.	70
10	Summary of covariance analysis for regressions of fecundity against length and age for Greenland halibut.	71
11	Summary of statistics for multiple correlation of fecundity, age and length of Greenland halibut. X_1 - log fecundity, X_2 - log length and X_3 - log age. Estimating equation $X_1 = a_{1.23} + b_{12.3} X_2 + b_{13.2} X_3$.	73

LIST OF FIGURES

<u>FIGURE</u>		<u>PAGE</u>
1	Map of study area with corresponding major place names mentioned in text	4
2	Average catch of Greenland halibut (kilograms whole weight) by $1/2^{\circ}$ lat. 1° long. rectangles per 30-min. otter trawling set of the research vessel <u>Cryos</u> in the Baffin Island Area.	19
3	Average catch of Greenland halibut (numbers) by $1/2^{\circ}$ lat. 1° long. rectangles per 30-min otter trawling set of the research vessel <u>Cryos</u> in the Baffin Island Area.	20
4	Number of successful otter-trawling sets by the research vessel <u>Cryos</u> in the Baffin Island Area.	21
5	Average catch of Greenland halibut (kilograms whole weight) by $1/2^{\circ}$ lat. 1° long. rectangles per 30-min otter trawling set of the research vessel <u>Gadus Atlantica</u> in the Labrador-eastern Newfoundland area.	23
6	Average catch of Greenland halibut (numbers) by $1/2^{\circ}$ lat. 1° long. rectangles per 30-min otter-trawling set of the research vessel <u>Gadus Atlantica</u> in the Labrador-eastern Newfoundland area.	24
7	Number of successful otter trawling sets by the research vessel <u>Gadus Atlantica</u> in the Labrador-eastern Newfoundland area.	25
8	Average catch of Greenland halibut (kilograms whole weight) by $1/2^{\circ}$ lat. 1° long. rectangles per 30-min otter-trawling set of the research vessel <u>Gadus Atlantica</u> in the northern Gulf of St. Lawrence.	27
9	Average catch of Greenland halibut (numbers) by $1/2^{\circ}$ lat. 1° long. rectangles per 30-min otter-trawling set of the research vessel <u>Gadus Atlantica</u> in the northern Gulf of St. Lawrence.	28
10	Number of successful otter-trawling sets by the research vessel <u>Gadus Atlantica</u> in the Northern Gulf of St. Lawrence.	29

11	Length frequency distribution by depth (m) of male and female Greenland halibut in the Baffin Bank Area (NAFO Division OB).	31
12	Length frequency distribution by depth (m) of male and female Greenland halibut in the Saglek Bank Area (NAFO Division 2G).	32
13	Length frequency distribution by depth (m) of male and female Greenland halibut in the Nain Bank Area (NAFO Division 2H).	34
14	Length frequency distribution by depth (m) of male and female Greenland halibut in the Hamilton Bank area (NAFO Division 2J).	35
15	Length frequency distribution by depth (m) of male and female Greenland halibut in the Northeast Newfoundland Shelf area (NAFO Division 3K).	37
16	Length frequency distribution by depth (m) of male and female Greenland halibut in the northern Grand Bank (NAFO Division 3L)	38
17	Length frequency distribution by depth (m) of male and female Greenland halibut in the northern Gulf of St. Lawrence (NAFO Divisions 4RST).	39
18	Age composition of male and female Greenland halibut by area from Baffin Bank (NAFO Division OB) southward to the northern Grand Bank (NAFO Division 3L) inclusive.	45
19	Age composition of male and female Greenland halibut from the Northern Gulf of St. Lawrence.	46
20	Empirical growth curves of male and female Greenland halibut from seven areas of the Canadian Northwest Atlantic.	48
21	Scatter plot and linear least squares regression for total fish length against total otolith length of Greenland halibut.	51

22	Back-calculated growth curves (ages 1-5) of male and female Greenland halibut from seven areas of the Canadian Northwest Atlantic.	52
23	Comparisons of back-calculated growth curves (ages 1-5) of Greenland halibut, sexes combined, from seven areas of the Canadian northwest Atlantic.	53
24	Sexual maturity ogives of female Greenland halibut from six areas of the Canadian Northwest Atlantic.	57
25	A comparison of sexual maturity ogives of female Greenland halibut from six areas of the Canadian Northwest Atlantic.	58
26	Sexual maturity ogives of female Greenland halibut from the Hamilton Bank Area (NAFO Division 2J) for September and November-December.	59
27	A comparison of sexual maturity ogives of female Greenland halibut from the Hamilton Bank area (NAFO Division 2J) for September and November-December.	60
28	Relationship of fecundity to length for Greenland halibut from southern Labrador 1976-77.	66
29	Relationship of fecundity to age for Greenland halibut from southern Labrador 1976-77.	67
30	Relationship of fecundity to length and age for Greenland halibut from Southeastern Gulf of St. Lawrence, 1978.	68
31	A comparison of the relationships of log-fecundity to log-length and log-age for Greenland halibut of southern Labrador in 1976 and 1977.	69
32	Comparison of fecundity-length relationships for Greenland halibut from southern Labrador and southeastern Gulf of St. Lawrence	75
33	Greenland halibut tagging positions in White Bay, Newfoundland in October-November, 1969.	76

34	Greenland halibut tagging positions in Trinity Bay, Newfoundland in October-November, 1971.	77
35	Site of tagging operations and positions of tag returns for Greenland halibut in the Funk Island Bank area tagging experiment March, 1979.	78
36	Chart showing the Greenland halibut tag returns for the White Bay tagging experiment October-November, 1969.	79
37	Chart showing the Greenland halibut tag returns for the Trinity Bay tagging experiment October-November, 1971.	180
38	Suggested migratory routes of Greenland halibut in the Northwest Atlantic.	106

INTRODUCTION

Greenland halibut are found in both the North Atlantic and North Pacific Oceans but absent from intervening Arctic waters (Hubbs and Wilimovsky 1964, Atkinson et al. 1981). Based on meristic and morphometric characters, Hubbs and Wilimovsky (1964) concluded that there is one species found in both oceans, not two as previously thought (Andriyashev 1954).

In the Northwest Atlantic, Greenland halibut are widely distributed along the West Greenland Coast and in the Davis Strait and are reported as far north as Smith Sound (78° latitude) by Smidt (1969) and Templeman (1973). In the Canadian far north they are found in abundance in the Baffin Island area (Templeman 1973; Bowering 1978c, 1979a) and extend in the Hudson Strait to Ungava Bay (Dunbar and Hildebrand 1952). They are most prevalent in deeper waters from northern Labrador to the deeper waters of the northern Grand Bank (Templeman 1973; Bowering 1977, 1978d, 1979b, 1980b; Bowering and Brodie 1981) with small numbers recorded in the vicinity of the Flemish Cap (Bowering and Baird 1980). Greenland halibut are found incidentally on St. Pierre Bank with a small localized concentration located in Fortune Bay (Bowering 1978b). Earlier investigations by Templeman (1973) indicated that Greenland halibut were found in the northern Gulf of St. Lawrence in relatively small numbers. More recent investigations (Bowering 1979d, 1980a, 1981b) have shown that Greenland halibut have become commercially abundant in this area with very

little occurrence on the Scotian Shelf. The most southerly occurrence in Canadian waters was reported by Barrett (1969) in March 1968 in the Bay of Fundy where he caught two Greenland halibut 27 and 42 cm in length. Subsequent to this Templeman (1973) reported catches as far south as the southern tip of the Scotian Shelf.

In the Northwest Atlantic, spawning is believed to take place in spring in the Davis Strait area. It occurs in deep warm water to the south of the Greenland-Canadian cascade located between Greenland and Baffin Island at about 67°N latitude (depths down to 675 m) (Smidt 1969). The eggs and small larvae are found in depths of 600-1000 m. However, the larvae later rise to the surface waters where they are taken by currents to and along the west coast of Greenland to the northern part of Davis Strait. Here the current turns and larvae are likely transported southward to the banks of Baffin Island (Atkinson et al. 1981). Templeman (1973) hypothesized that larvae caught in the current off Baffin Island drift to the south and colonize the banks off Labrador and eastern Newfoundland. Chumakov (1975) suggested that as Greenland halibut in the Labrador, eastern Newfoundland and the northern Grand Bank region approach maturity, they migrate north from the banks and slope into deeper water for spawning. This would suggest that most Greenland halibut in the Northwest Atlantic form one continuous stock (Zilanov 1976; Bowering 1977). Lear (1970) and Templeman (1970) suggested that the Greenland halibut in the Gulf of St. Lawrence may be a separate stock; however, Bowering (1980a, 1981b) suggested that while the Gulf of St.

Lawrence may support a separate stock of Greenland halibut there appears to be mixing of stocks in this area. This could result from immigration from the Labrador region through the Strait of Belle Isle.

Commercial landings of Greenland halibut in the Northwest Atlantic during the last several years averaged about 60,000 mt annually making it one of the most important groundfish species in the Northwest Atlantic. The Greenland halibut resource in the Northwest Atlantic is now managed as three separate stocks; 1) The Gulf of St. Lawrence stock (NAFO Div. 4RST), 2) the Labrador-Eastern Newfoundland stock (NAFO Subarea 2 and Div. 3KL), and 3) the Baffin Island-West Greenland stock (NAFO Subareas 0 and 1) (Fig. 1). The implications of management strategy by three separate compartments with regard to the accuracy of international fish stock assessment of this species in these areas have recently become a contentious issue. This is the result of recent hypotheses that the stock complex from Davis Strait to the northern Grand Bank (Chumakov 1975; Bowering 1977) is a single population not two, as well as the evidence for two populations in the Gulf of St. Lawrence (Bowering 1979d, 1980b, 1981b) not one as previously thought. The management bodies of NAFO (Northwest Atlantic Fisheries Organization) and CAFSAC (Canadian Atlantic Scientific Advisory Committee) have therefore recommended considerable research effort be placed into the accurate delineation of Greenland halibut stocks in Canada's far north, to provide for effective biological management of this very valuable resource.

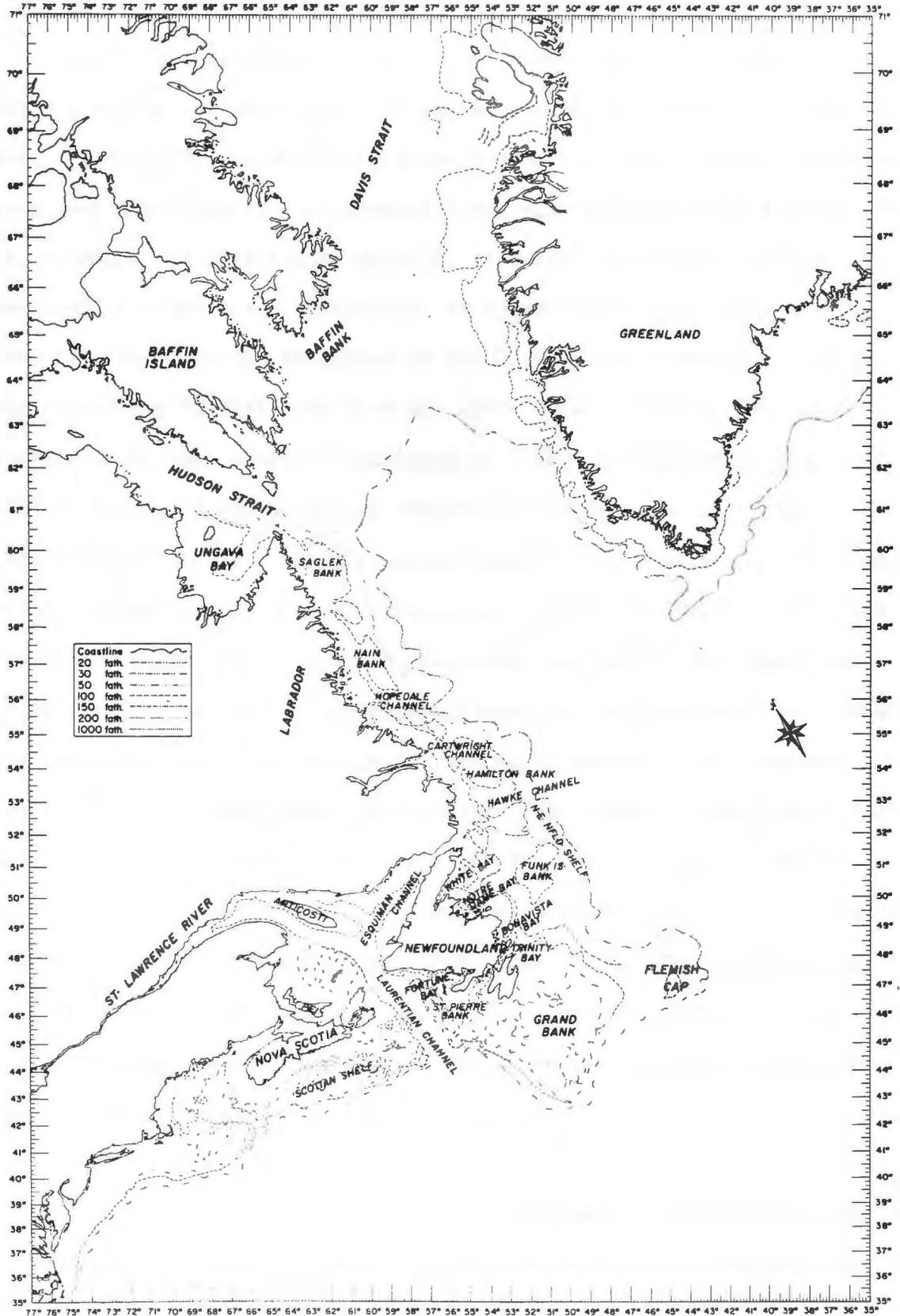


Fig. 1. Map of study area with corresponding major place names mentioned in text.

The first investigation into stock identification of Greenland halibut in the Northwest Atlantic was published by Templeman (1970). He analysed meristic characters of Greenland halibut from samples collected from West Greenland to the southern Grand Bank and the northern Gulf of St. Lawrence. A statistical analysis of vertebral numbers averages revealed no significant differences throughout the range under investigation with the exception of the Gulf of St. Lawrence. This area was significantly different from all other areas. He concluded that vertebral averages were not particularly useful in separating Greenland halibut stocks of the Northwest Atlantic apart from the possible separation of the Gulf of St. Lawrence population. Laboratory experiments on the deformation of meristic characters by Gabriel (1944), Heuts (1949) and Tåning (1944, 1952), however, suggested that while the numbers of vertebrae and fin rays in teleostean fishes may be genotypically selected, the individual phenotype may be influenced by external environmental factors such as temperature and salinity. The phenocritical period during which the final numbers of vertebrae and fin rays are determined in teleostean fishes has consequently been the subject of much discussion and scientific investigations. These investigations have produced varied results for different species (summarized in Templeman and Pitt 1961). The conclusions of Templeman (1970) therefore are at best inconclusive even though they may be entirely accurate.

Khan et al. (1981) studied stock delineation of Greenland halibut in the Northwest Atlantic by analysing the prevalence of trypanosome and

piroplasm infections as biological tags. Results from the study suggested that Greenland halibut from the Davis Strait, northern Labrador and the northern Grand Bank form a single stock. The southern Labrador data were different from the other areas and might represent an isolated population, but the authors concluded it was part of a cline in the prevalence data. The Gulf of St. Lawrence data were distinct from that of all other areas north and east of Newfoundland and was considered as evidence of a separate stock there. While studies of this nature may enhance the solution to stock identification, definitive stock delineation is difficult for two main reasons. Firstly, little is known about the accurate distribution of the parasites studied and secondly, it is not known exactly when the infection occurs in the fish sampled. Therefore, if the Gulf of St. Lawrence is colonized from immigration through the Strait of Belle Isle and the parasitic infection occurs after entry into the area, then these incidence of infection may appear upon analysis, significantly different from those of the Labrador area, but are actually from the same population.

Fairbairn (1981) investigated allele and genotype frequencies at 16 electrophoretically detectable protein loci, from tissue samples of Greenland halibut throughout the range from Davis Strait to the northern Grand Bank. Her analysis suggested that Greenland halibut from the Northwest Atlantic area form a single genetically homogenous stock. She concluded that Greenland halibut in the Gulf of St. Lawrence form a separate stock from the eastern Newfoundland area although this stock

was not completely isolated since it showed similarities to the Labrador areas. Her conclusions are probably most accurate with particular reference to the Gulf of St. Lawrence since most fish from this area were found to be genetically different. However, while the population of Greenland halibut from Davis Strait to the northern Grand Bank appears to be genetically homogeneous it cannot be concluded on the strength of this evidence alone that it is a single spawning unit.

Since most of the previous stock identification studies have been inconclusive, the purpose of this study is to evaluate the distribution and abundance, age and growth, sexual maturity, fecundity and migratory patterns of Greenland halibut from these areas. These biological characteristics are examined for their significance as to stock identification of Greenland halibut in the Northwest Atlantic.

MATERIALS AND METHODS

DISTRIBUTION

a) Geographic distribution and relative abundance

In October 1977 a stratified-random biomass survey for groundfish (Pinhorn 1972) was conducted in the Baffin Bank area (NAFO Div. OB) by the French research vessel Cryos to a depth of 900 m (Fig. 4). This

vessel is a stern otter trawler which uses a Lofoten bottom otter trawl with a 5 mm small mesh liner in the codend. All sets were of 30 min duration during daylight hours at a towing speed of 3.5-4.0 knots. Sets in which the fishing gear was badly damaged or other reasons considered to interfere with normal retention of the catch were not used in any of the calculations. For each set the total weight and numbers of Greenland halibut caught was obtained on board.

Biomass surveys for groundfish using a similar stratified-random survey design have been conducted in the Hamilton Bank area (NAFO Div. 2J) since 1977 and in the Northeast Newfoundland Shelf (NAFO Div. 3K), the northern Grand Bank (NAFO Div. 3L) (Fig. 7) and the northern Gulf of St. Lawrence areas (NAFO Div. 4RST) since 1978 by the Canadian research vessel Gadus Atlantica (Fig. 10). The Gadus Atlantica is a large stern trawler which used an Engels high-rise bottom otter trawl with a 30-mm small mesh nylon liner in the codend. All sets were of 30 min duration and fishing was carried out on a 24 hr basis. The maximum depth fished ranged from 400 m in NAFO Div. 3L to 1200 m in NAFO Div. 2J and 3K depending upon the availability of deeper water in the area or the accessibility of the deeper water to the fishing gear.

Two biomass surveys for groundfish have been conducted in the Saglek Bank (NAFO Div. 2G) and Nain Bank areas (NAFO Div. 2H) since 1978 by the research vessel Gadus Atlantica (Fig. 7). However, both surveys were not of the stratified-random survey design as in the other areas. These two

surveys were conducted using fixed stations at particular depths down to 1200 m. The stations were entirely exploratory and were not made at positions selected for the abundance of any particular groundfish species. Other than the survey design, all other aspects of the survey techniques were similar to those of other areas.

b) Length frequency distribution by depth zone

For each individual catch of Greenland halibut during the surveys, the length (cm) of each fish was measured from the tip of the snout to the fork of the caudal fin. The length compositions were compiled for 100 m depth intervals from 101 to 500 m with two additional intervals of 500-750 m and greater than 750 m where available, except for the Gulf of St. Lawrence area where the survey area was stratified in fathoms rather than meters. The depth zones for this area when converted to metres are 185-275 m, 276-366 m and greater than 366 m.

c) Average size and sex ratios by depth zone

For each area and depth zone where length frequencies were available, average lengths for males and females were calculated. These averages were weighted by the numbers caught at each 2-cm length group. Similarly, the percentages of males and females caught were calculated.

AGE AND GROWTH

a) Age composition

Age frequencies were compiled for males and females separately for each NAFO Div. from Div. OB (Baffin Bank) southward to Div. 3L (northern Grand Bank) inclusive and for Div. 4RST (Gulf of St. Lawrence). The distributions were calculated as numbers per thousand at age for fish caught in selected groundfish surveys conducted at approximately the same time of year with the exception of Div. 4RST. The ages were determined from the left sacculus otolith. In the case of Greenland halibut these were most suitable for age determination since the annuli were spaced more evenly and were more distinct than those of the right otolith (Lear and Pitt 1975). Otoliths were ground on the convex surface to expose the center more clearly and were placed in a black watch glass containing ethanol. Ages were read using validation procedures described by Lear and Pitt (1975).

b) Growth curves from empirical data

Growth is expressed in terms of semi-logarithmic curves ($y = a + b \ln x$) (Roff 1980) of length on age since the data were highly correlated by this method and did not appear to fit the traditional von Bertalanffy growth equation (Bowering 1978b). This linearized

expression also allowed for easy statistical comparisons. Growth curves were computed separately by sex for samples collected from groundfish surveys in each of the seven areas previously described. The growth curves were weighted by the number of observations at each age since many of the older age groups were based upon as little as one observation and the age reading of very old large fish is often questionable (Lear and Pitt 1975).

C) Back calculated growth

Otoliths from 30 males and 30 females of the 1972 year-class were selected from surveys in all seven areas described in the previous section and examined to back-calculate length at age. In order to standardize the number of ages for consideration, calculations were only made up to age 5. Otoliths were measured by means of a drawing tube attached to a binocular microscope using a technique similar to that described by Moores and Winters (1978). An annulus was considered to be the width described by an opaque (summer) zone and a translucent (winter) zone accounting for a growth increment in a particular year. The ratio of otolith length to total fish length was used to back-calculate the average length at each age using the direct proportionality method described by Lea (1919). Subsequently, semilogarithmic curves were fitted to the data points. In order to validate the direct proportionality method as it applied to Greenland halibut, a linear least squares regression was performed on a random sample of 123 measurements of total fish length to total otolith

length (3 measurements per 1-cm group from 10-50 cm).

A covariance analysis (Zar 1974) was performed on males versus females in order to determine if there were significant differences among the regression coefficients (slopes) or the adjusted means (y-intercepts). Where no differences between the sexes occurred the sexes were combined for each of the areas for further analysis. A covariance analysis was performed on these combined data to determine if there were any significant differences in the slopes of the fitted lines. Among the different areas, for areas where significant differences did not occur, the analysis was continued using paired comparisons by t-tests to determine if differences occurred between the adjusted means (y-intercepts).

SEXUAL MATURITY

a) Maturity curves

Due to the difficulty and uncertainties connected with the determination of sexual maturity in male Greenland halibut, only sexual maturity data on female Greenland halibut were used. During all survey cruises, observations on sexual maturity of Greenland halibut were obtained from random samples collected for age reading and other purposes. The percentages mature at each length group were calculated for each of

six different areas: Baffin Bank (0B), Saglek Bank (2G), Nain Bank (2H), Hamilton Bank (2J), Northeast Newfoundland Shelf (3K), and the Gulf of St. Lawrence (4RST). These data were plotted and curves were drawn through the data points. Since sexual maturity data for the northern Grand Bank area were so sparse, these were not included. Except for the Gulf of St. Lawrence data, only data collected during the same time of year were used to generate the curves. Maturity curves were also generated for the Hamilton Bank area from data collected at two different times in the year for comparative purposes.

b) Probit analysis

The age or length when equal numbers of fish are mature and immature is known as the 50% maturity level or more commonly M_{50} . In assessing the effects of various dosages of poisons and vitamins on animals Bliss (1952) devised a probit analysis method for calculating the 50% lethal dosage level (LD_{50}) which is the level where 50% of the animals are dead. Fleming (1960), Pitt (1964) and Bowering (1976) applied the same probit analysis method to determine the length at 50% maturity for cod, American plaice and witch flounder, respectively. The only difference was that in fitting the provisional line (Bliss 1952) a closer fit was obtained by using log dosage which in the latter studies were the percentages of mature fish plotted against log length on probability paper. This modified probit analysis method was applied to the female Greenland

halibut sexual maturity data from each of the six areas individually where data were available. It was also applied to the second set of data from the Hamilton Bank area collected at a different time of year than the others. Chi-square analyses were then carried out in order to determine the acceptability of the fitted lines to the observed data at the 5% level. The ages at M_{50} were calculated by applying the length at M_{50} to age-length relationships for the respective areas.

In order to test hypotheses about equality among the population regression coefficients (slopes) of the fitted lines, paired comparisons were made involving the use of Student's t-test in a manner analogous to that of testing the difference between two population means (Zar 1974). Where paired comparisons indicated that the regression coefficients were not statistically different a t-test procedure applicable to testing the hypothesis that the elevations (y-intercepts) of the fitted lines are equal was applied using the "common" or "weighted" regression coefficients as defined by Zar (1974).

FECUNDITY

a) Collection of ovaries and counting of ova

All ovaries were collected late enough in the maturity cycle to enable separating the present generation ova from second generation ova

(Bowering 1978a). Ovaries which contained clear ova were rejected since it was probable that some of such ova had already been extruded. All material was collected at sea during regular random stratified groundfish surveys by Canadian research vessels. The samples collected are presented according to area, date collected and number collected as follows:

<u>Area</u>	<u>Date collected</u>	<u>No. collected</u>
Southern Labrador (NAFO Div. 2J-3K)	Oct.-Nov. 1976	47
Southern Labrador (NAFO Div. 2J-3K)	Nov. 1977	66
Southeastern Gulf of St. Lawrence (NAFO Div. 4R-3Pn)	Jan. 1978	40

Otoliths and fork lengths to the nearest centimeter were obtained from all fish sampled for ovaries. The ovaries after extraction were cut longitudinally and placed in jars of Gilson's fluid, which causes breakdown of connective tissue after several weeks without damage to the ova (Simpson 1951). When the connective tissue was sufficiently broken down, the contents of the jars were washed through a series of fine screens of varying mesh sizes until the present generation ova could be separated from all other material. After cleaning, the ova were stored in a solution of 2-ethoxyethanol for several days before counting. This solution allows the ova to harden and prevents clumping by breaking down any greasy or fatty material. The ova were then dried on blotter paper with particular care taken so that none clumped. Fecundity was subsequently determined using an electronic DECCA batch counter (Boyar and

Clifford 1967). For each sample the ova were counted twice to check for variations by the counting device. In all cases the difference between the two counts was less than 1%.

b) Statistical analyses

For analyses, the data were organized into two geographically separate groups: (1) southern Labrador (NAFO Div. 2J-3K) and (2) southeastern Gulf of St. Lawrence (NAFO Div. 4R-3Pn). All data were fitted by least squares regressions using log-log (base $_{10}$) transformations which gave higher correlations than arithmetic or semi-log plots. Relationships of fecundity to length and age for the southern Labrador and southeastern Gulf of St. Lawrence were calculated as well as between years comparisons for the southern Labrador data.

Covariance analyses (Zar 1974) were conducted for both between areas and between years for the southern Labrador data. A multiple correlation analysis was performed on both the southern Labrador data and the southeastern Gulf of St. Lawrence data separately in order to determine the relative contributions of length and age to variation in fecundity.

MIGRATIONS

The migratory patterns of Greenland halibut were investigated by means of tagging studies. Three different tagging studies were conducted in the eastern Newfoundland areas: a) White Bay - Oct.-Nov. 1969 using longlines, b) Trinity Bay - Oct.-Nov. 1971 using longlines, and c) offshore Funk Island Bank - April 1979 using bottom otter trawls.

The longlining tagging was carried out on board the Canadian research vessel Marinus, a small wooden side trawler using 3-5 tubs of longline gear. Each tub contained eight 100-m lines with hooks 2 m apart. The hooks were baited with frozen capelin obtained from a cold storage plant and were placed near the sea bottom at 300-350 m for a maximum of 2-4 hr.

The bottom otter trawl tagging was conducted by the Canadian research vessel Gadus Atlantica using commercial size gear to allow for the escapement of smaller fish and invertebrates which could damage the catch.

Sets ranged from 10-30 min duration at depths of 350-450 m depending upon the abundance of Greenland halibut in the area. For both types of experiments, a canvas recovery tank with running sea water was placed near where the specimens would come on board ship and the fish were immediately placed in the tank. Only fish in good condition were tagged and those damaged or with excessive scale loss were discarded.

The fish were tagged with 1 cm diameter Peterson discs. These were attached 2-4 cm below the dorsal fin near the head by means of 0.32 mm diameter stainless steel wire. After tagging the fish were placed in a recovery tank until they appeared in active condition after which they were returned to the sea. Totals of 266, 410 and 2976 Greenland halibut were tagged in the White Bay, Trinity Bay and the Funk Island Bank tagging studies respectively.

RESULTS

DISTRIBUTION

a) Distribution and relative abundance

Baffin Bank (Division OB): Survey results show that Greenland halibut are generally distributed throughout the survey area (Fig. 2 and 3) of Div. OB. The average weights (kg) per 30-min set (Fig. 2) indicate that the larger catches by weight were taken in the deeper waters near the continental slope in the middle to northern part of the division. The larger catches by number per set (Fig. 3) were taken more towards the coastal area of Baffin Island. Fish were generally much more abundant in the northern part of the division. In the most southerly portion of the division where waters of the Hudson Strait run into the Atlantic the abundance of Greenland halibut was much less in both average weights and numbers per set. Survey coverage is shown in Fig. 4.

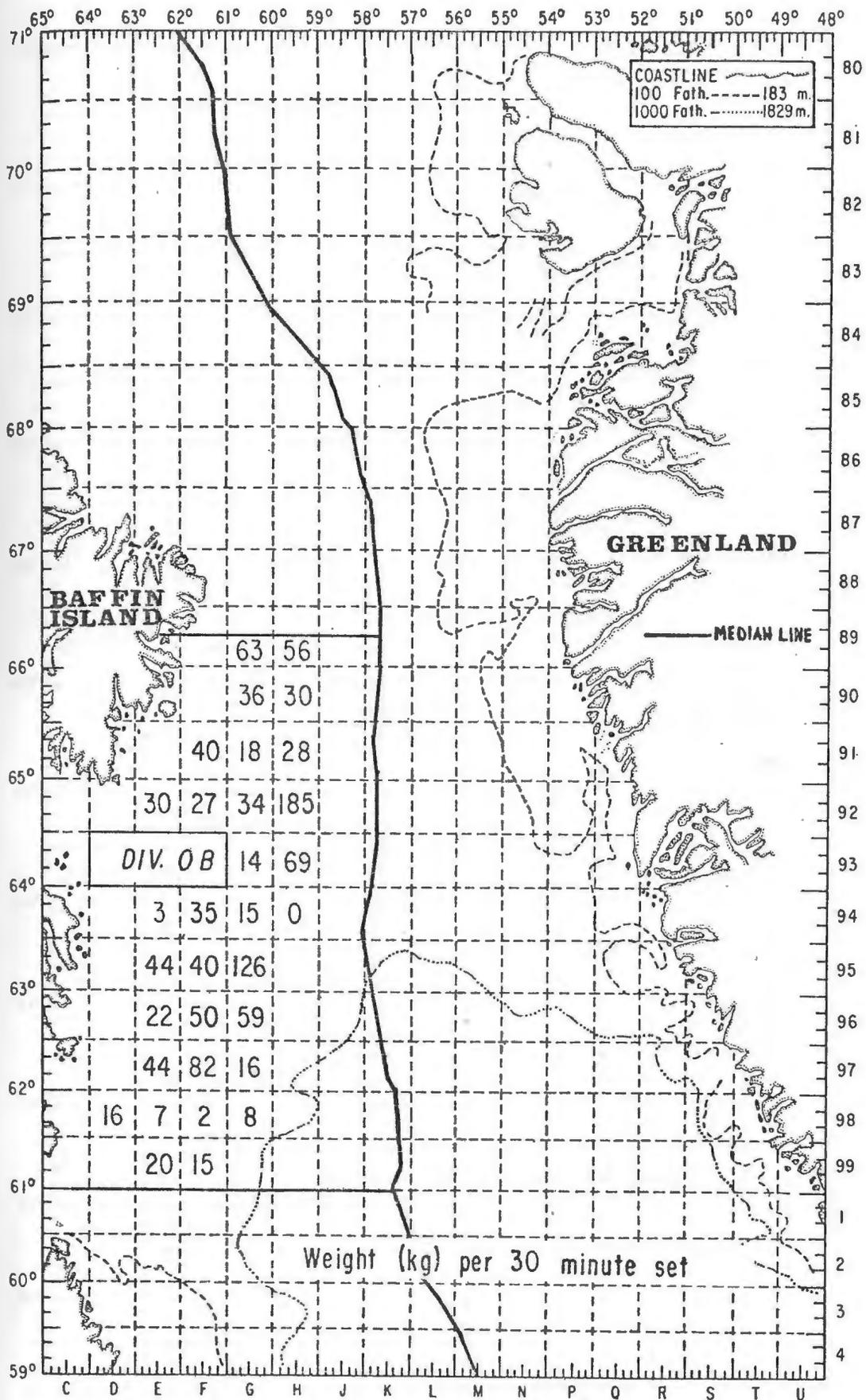


Fig. 2. Average catch of Greenland halibut (kilograms whole weight) by $\frac{1}{2}^{\circ}$ lat. 1° long. rectangles per 30-min otter trawling set of the research vessel CRYOS in the Baffin Island area.

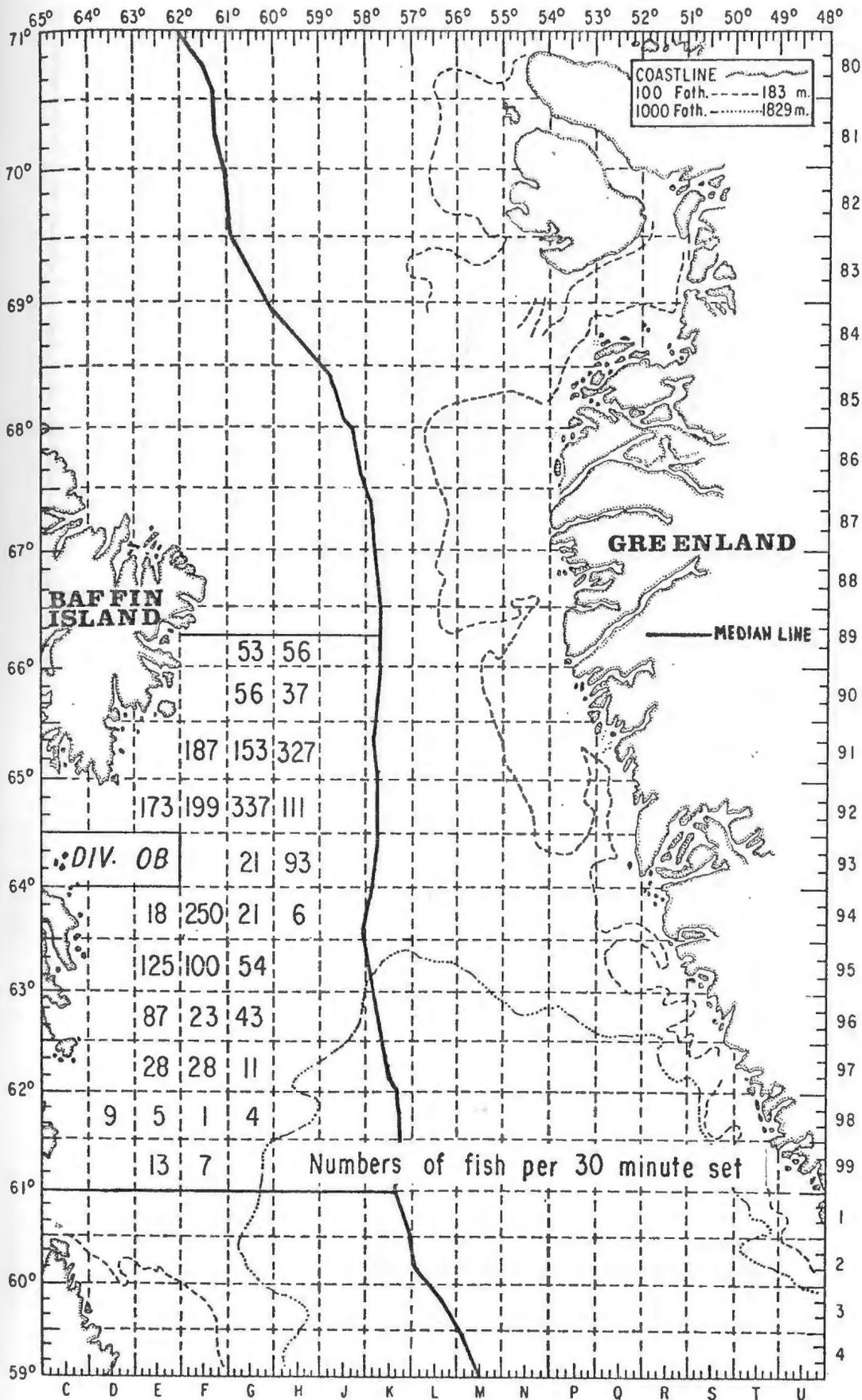
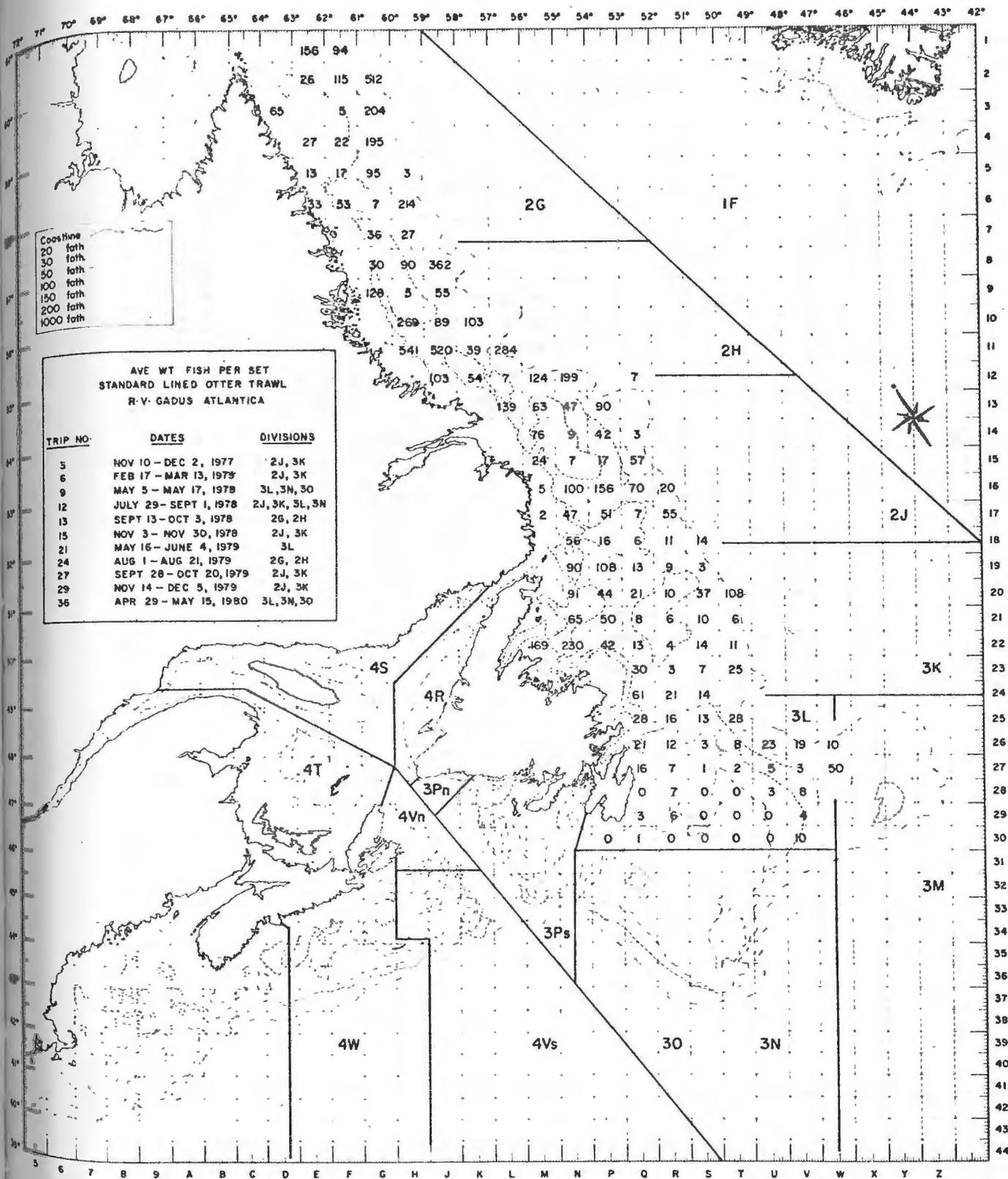


Fig. 3. Average catch of Greenland halibut (numbers) by $\frac{1}{2}^{\circ}$ lat. 1° long. rectangles per 30-min otter trawling set of the research vessel CRYOS in the Baffin Island area.

Labrador and eastern Newfoundland (Division 2G, 2H, 2J, 2K, and 3L):

Results of research vessel surveys throughout the entire area (Fig. 5 and 6) indicate that Greenland halibut are found in abundance from the latitude of Cape Chidley (the most northerly tip of the Labrador coast) to the deeper waters on the northern slope of the Grand Bank (Fig. 5 and 6) with no apparent break in continuity of the distribution. In Div. 2G the highest catches are found near the continental slope for both average weights and average numbers per set (Fig. 5 and 6) with smaller catches associated with the shallower waters of Saglek Bank. Large catches were experienced throughout Div. 2H with the exception of the shallow water directly on the top of Nain Bank. Large average catches in excess of 360 kg/set and 192 fish per/set were associated with the deep eastern slope of Nain Bank with the largest average catches throughout the entire range taken just to the south of Nain Bank in the Hopedale Channel area. At this location depths reach 600 m and some unit areas produced average catches in excess of 500 kg/set and 400 fish/set. The average catches were also high at the southern limits of Div. 2H, particularly in Cartwright Channel eastward to the edge of the continental shelf.

Greenland halibut were abundant on both the inner and outer slopes of Hamilton Bank in Div. 2J. However, the area of highest concentration (> 100 kg/set and 130 fish/set) appeared in Hawke Channel, a trough of deep water up to 600 m in depth extending between the south end of Hamilton Bank and the north slope of Belle Isle Bank (Fig. 5 and 6). Areas of high abundance in Div. 3K were generally connected with the



Coastline
 20 fath
 30 fath
 50 fath
 100 fath
 150 fath
 200 fath
 1000 fath

AVE WT FISH PER SET
 STANDARD LINED OTTER TRAWL
 R-V GADUS ATLANTICA

TRIP NO.	DATES	DIVISIONS
3	NOV 10 - DEC 2, 1977	2J, 3K
6	FEB 17 - MAR 13, 1978	2J, 3K
9	MAY 5 - MAY 17, 1978	3L, 3N, 3O
12	JULY 29 - SEPT 1, 1978	2J, 3K, 3L, 3N
13	SEPT 13 - OCT 3, 1978	2G, 2H
15	NOV 3 - NOV 30, 1978	2J, 3K
21	MAY 16 - JUNE 4, 1979	3L
24	AUG 1 - AUG 21, 1979	2G, 2H
27	SEPT 28 - OCT 20, 1979	2J, 3K
29	NOV 14 - DEC 5, 1979	2J, 3K
36	APR 29 - MAY 15, 1980	3L, 3N, 3O

Fig. 5. Average catch of Greenland halibut (kilograms whole weight) by $\frac{1}{2}^{\circ}$ lat. 1° long. rectangles per 30-min. otter trawling set of the research vessel Gadus Atlantica in the Labrador-eastern Newfoundland area.

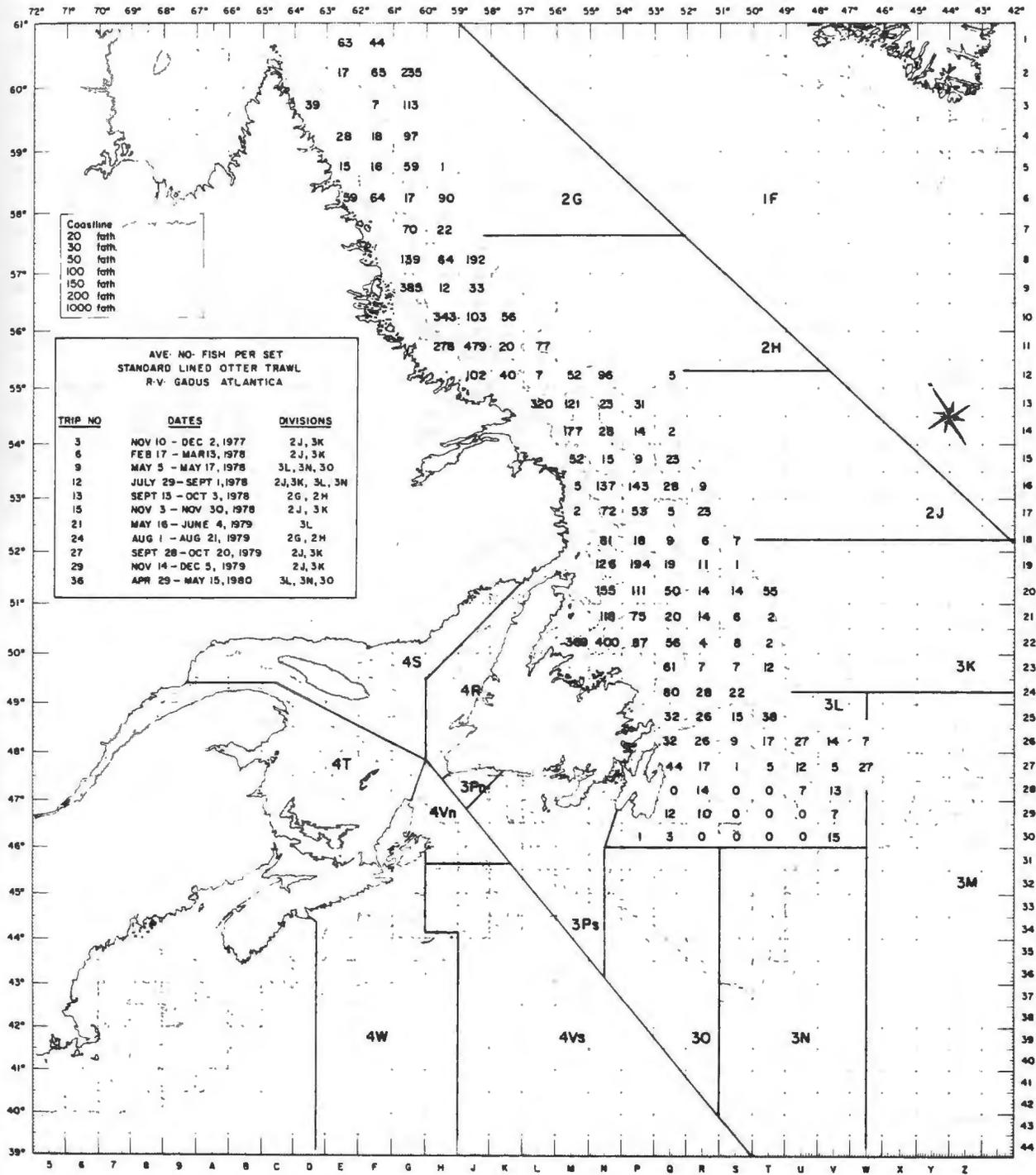


Fig. 6. Average catch of Greenland halibut (numbers) by $\frac{1}{2}^{\circ}$ lat. 1° long. rectangles per 30-min otter trawling set of the research vessel Gadus Atlantica in the Labrador-eastern Newfoundland area.

channels of deep water running and around Funk Island Bank and south of Belle Isle Bank where catches were between 40-100 kg/set and 50-200 fish per set (Fig. 5 and 6). The highest concentration was found in the Notre Dame Channel area extending into the Notre Dame Bay region where catches exceeding an average of 200 kg/set and 40 fish per set were experienced. In the southern portion of Div. 3K the abundance of Greenland halibut began to diminish, with most catches less than 20 kg per set and less than 15 fish per set. Catches in Div. 3L were similar to those of southern 3K and catches in this division were mainly confined to the northern slopes of the Grand Bank. Substantial portions of Div. 3L yielded no catch, particularly in the shallower waters of the Grand Bank (Fig. 5 and 6). Survey coverage for these areas are shown in Fig. 7.

Gulf of St. Lawrence (Division 4RST): Greenland halibut were found in relatively low abundance throughout the area (less than 10 kg/set and less than 10 fish per set) with the exception of the area to the south of St. George's Bay and Port-aux-Basques (Fig. 8 and 9). In the deepest waters of the Laurentian Channel are found, average catches were as high as 115 kg or 69 fish per set. Where the channel runs into the estuary of the St. Lawrence River, Greenland halibut were found in slightly higher abundance than the surrounding area (Fig. 8 and 9), however, these were still low in comparison to the southeastern Laurentian Channel. Survey coverage for the Gulf of St. Lawrence is presented in Fig. 10.

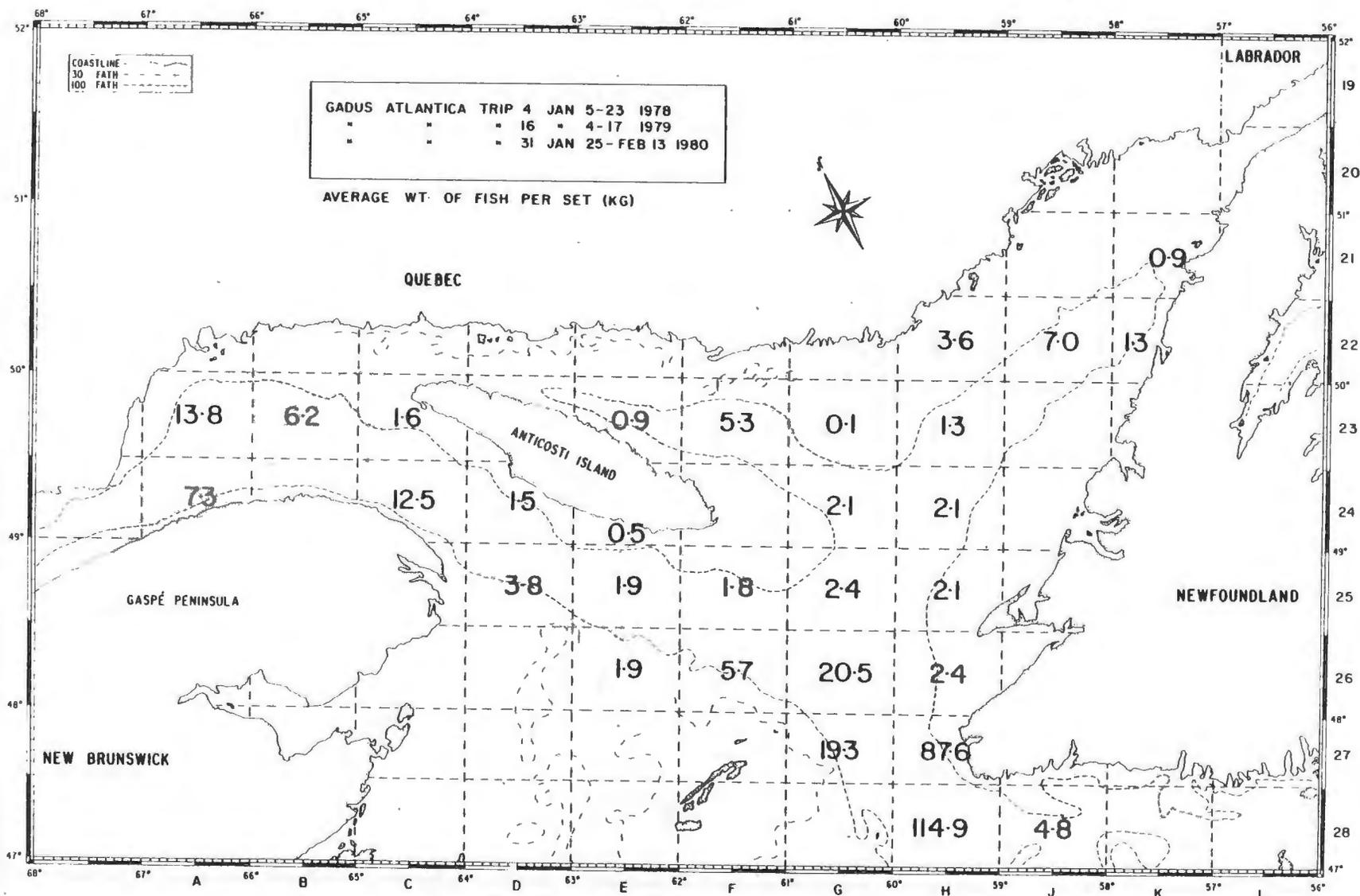


Fig. 8. Average catch of Greenland halibut (kilograms whole weight) by $\frac{1}{2}^{\circ}$ lat. 1° long. rectangles per 30-min otter-trawling set of the research vessel Gadus Atlantica in the northern Gulf of St. Lawrence.

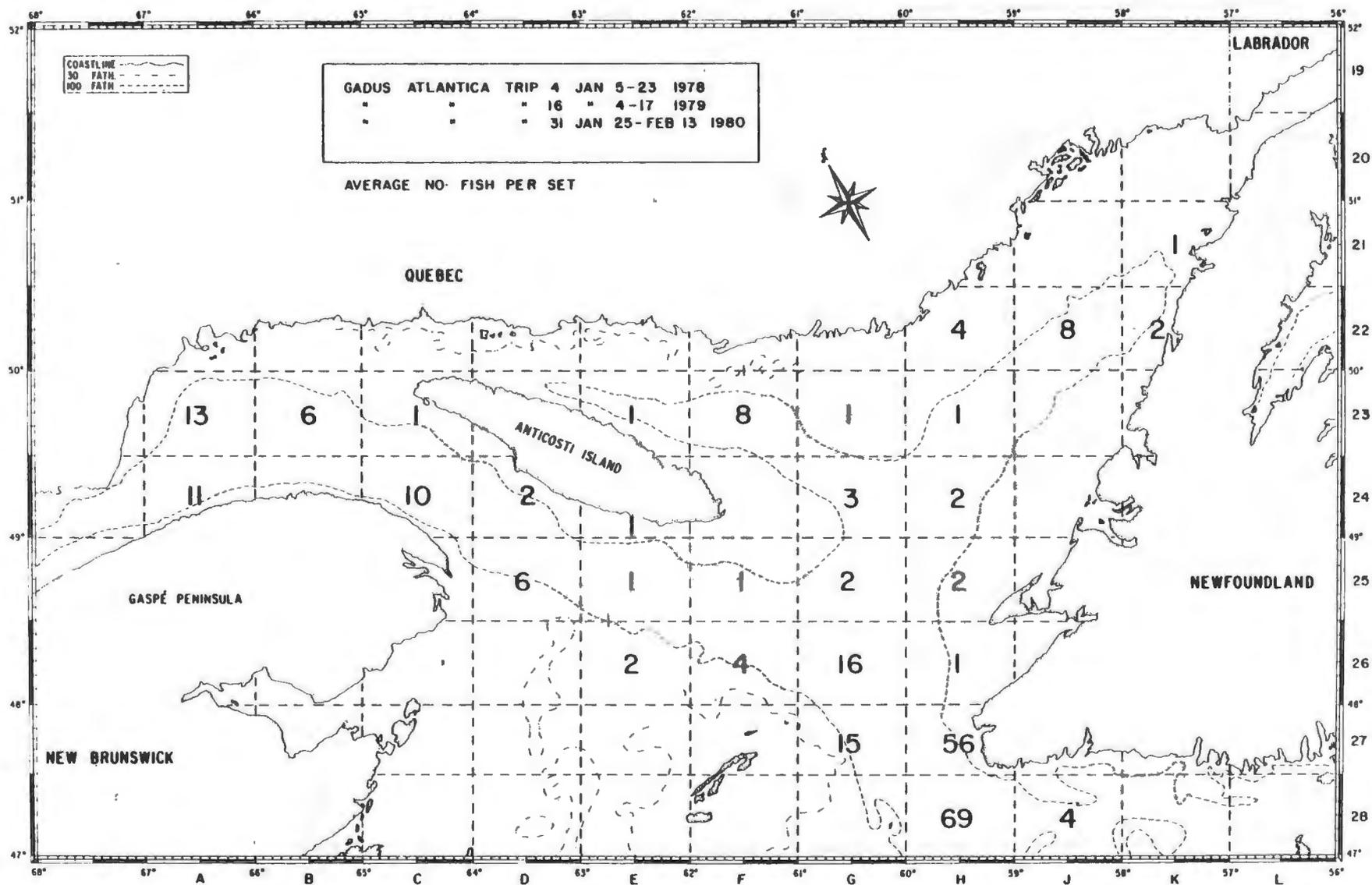


Fig. 9. Average catch of Greenland halibut (numbers) by $\frac{1}{2}^{\circ}$ lat. 1° long. rectangles per 30-min otter-trawling set of the research vessel *Gadus Atlantica* in the northern Gulf of St. Lawrence.

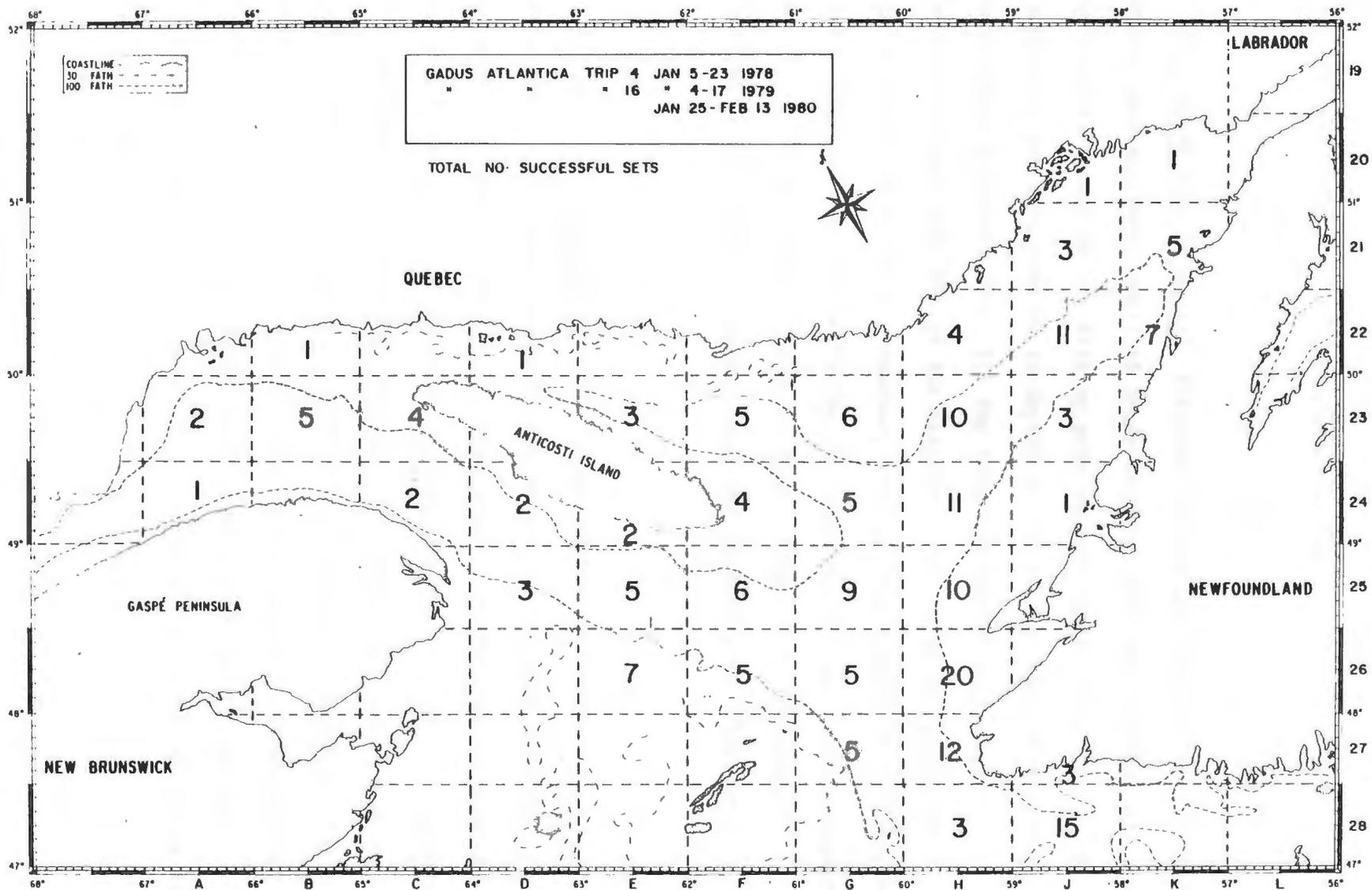


Fig. 10. Number of successful otter-trawling sets by the research vessel *Gadus Atlantica* in the northern Gulf of St. Lawrence.

b) Length frequency distribution by depth zone

Divison OB (Baffin Bank): Although fishing was conducted to 900 m the catches were extremely small at great depths. This was probably due to the ineffectiveness of the fishing gear at such depths therefore length frequencies are only used up to depths of 500 m. For each of the three depth ranges presented (Fig. 11) the length frequency distributions are similar with more than 85% of the catches in the 15-30 cm range with a peak at the 10-14 cm range. However, although the numbers of fish caught beyond 40 cm were negligible in the shallower depths, substantial numbers were caught in the 45-70 cm range in deeper water. The frequency distribution for males and females were not particularly different.

Division 2G (Saglek Bank): The length frequency distributions for depths of 101-300 m were relatively similar with the higher proportions of the catch less than 50 cm in length particularly in the 201-300 m range where about 50% of the catches were less than 34 cm (Fig. 12). From 301-500 m depth on the other hand, there were no catches of fish less than 36 cm in length with very high proportions in the 50-70 cm range. The distributions for males and females were of much the same pattern except there were no males caught at any depth beyond 72 cm length whereas females were caught up to a length of 94 cm in 101-200 m and to 110 cm in length at a depth of 401-500 m.

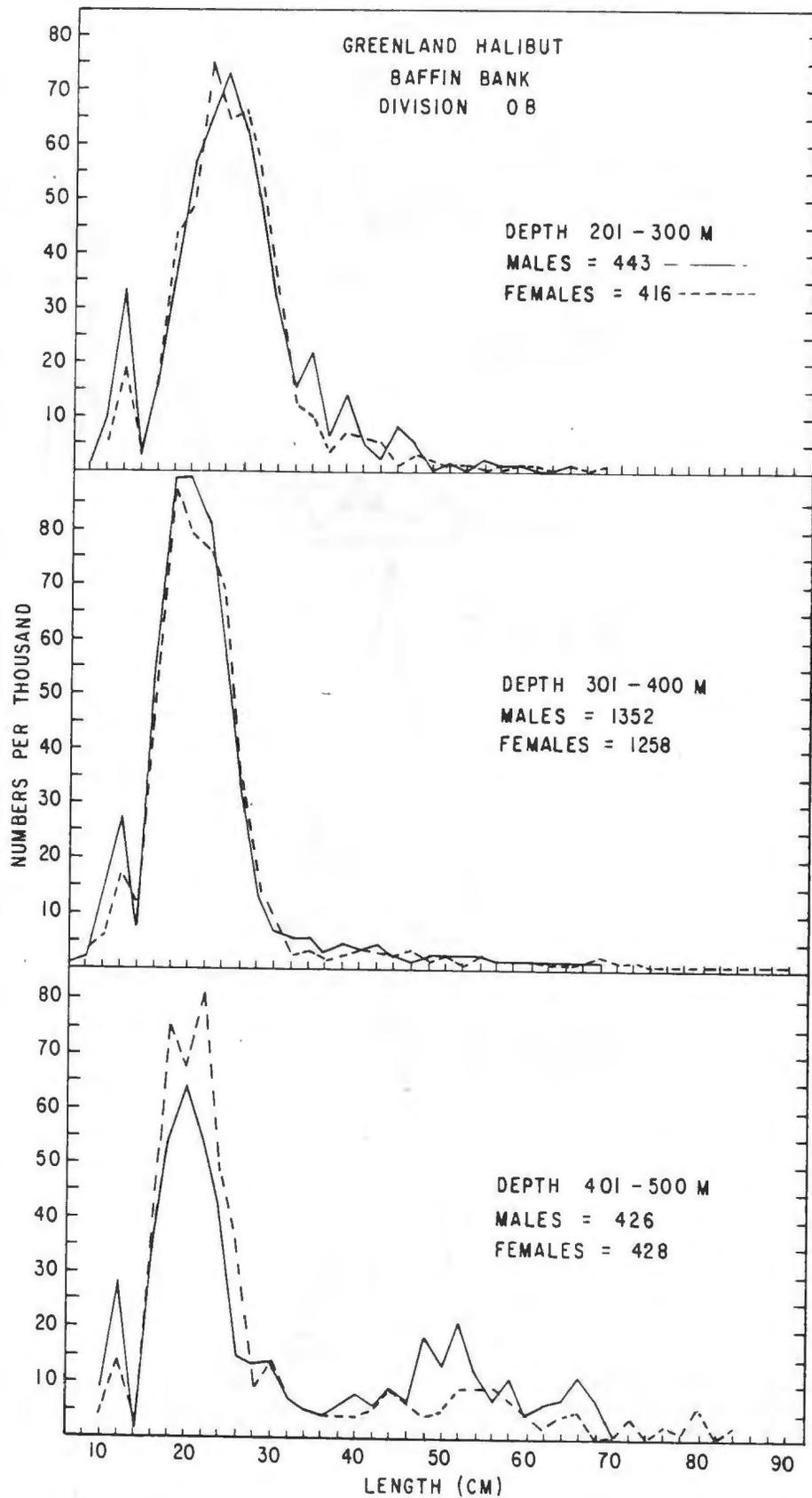


Fig. 11. Length frequency distribution by depth (m) of male and female Greenland halibut in the Baffin Bank area (NAFO Division 0B.)

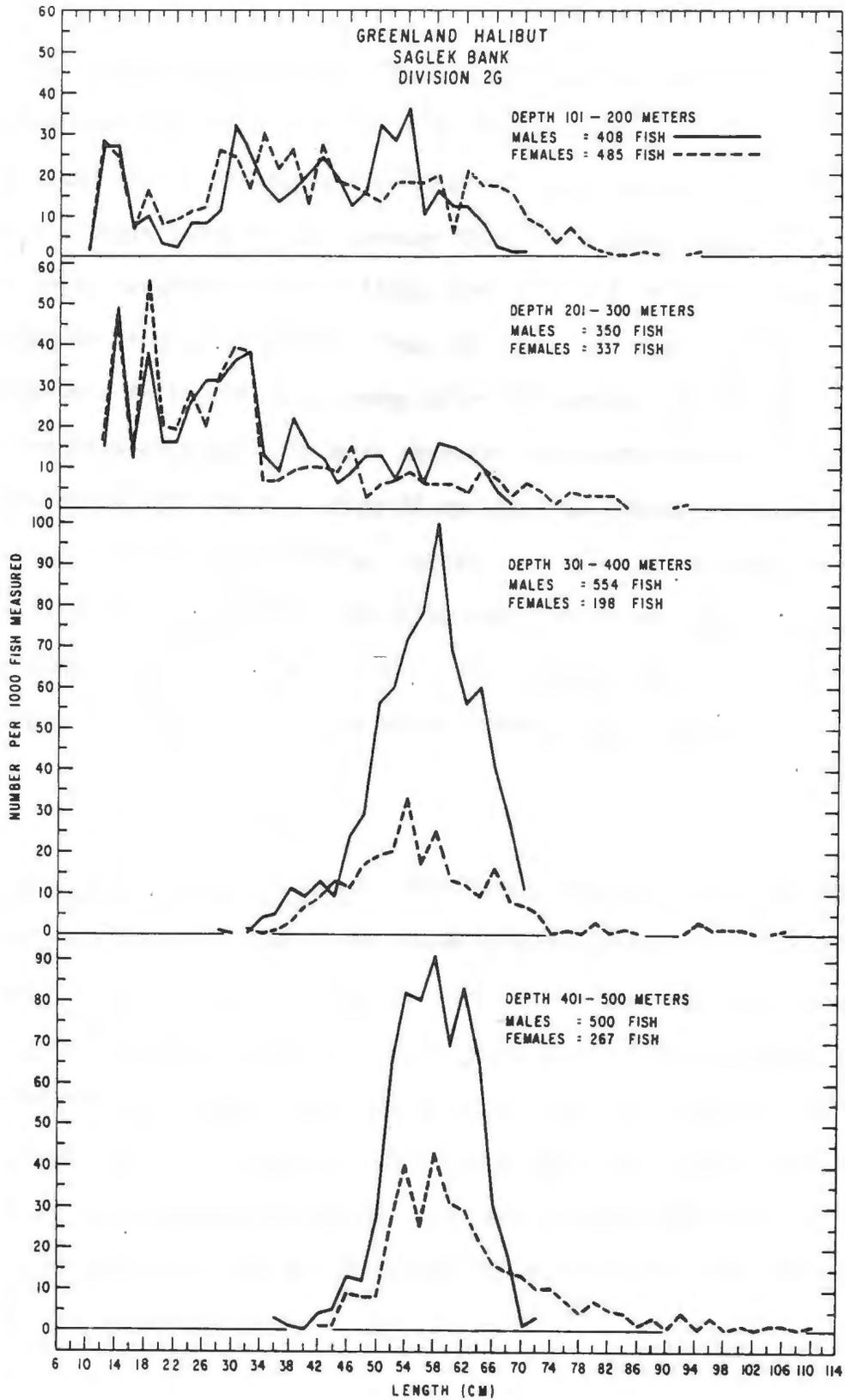


Fig. 12. Length frequency distribution by depth (m) of male and female Greenland halibut in the Saglek Bank area (NAFO Division 2G)

Division 2H (Nain Bank): The length frequency distributions for this Division were available from 101 m to greater than 750 m (Fig. 13). There was a clear change in the length frequency distribution going from the 101-200 m depth range to the greater than 750 m depth range. In the 101-200 m depth range there was a large peak at 10-14 cm which quickly disappeared at greater depth. From 201-500 m the major portion of the catches were in the 18-36 cm range with the numbers of fish beyond this size becoming progressively more abundant in greater depths. Beyond 501 m the abundance of fish less than 36 cm began to decrease and were essentially absent beyond 750 m. On the other hand, the numbers beyond 36 cm in depths greater than 750 m became increasingly more abundant. Large females particularly beyond 70 cm in length were very high in abundance in relative terms for depths greater than 750 m.

Division 2J (Hamilton Bank): The length frequency distributions for Div. 2J were also available from 101 m to greater than 750 m (Fig. 14). The results were similar to that for Div. 2H in that the proportions of the larger Greenland halibut increased over depth. The greatest transition in the length frequency distribution (as with Div. 2H) was going from 501-750 m to greater than 750 m where the length frequency distribution in the 501-750 depth range was largely comprised of fish less than 40 cm in length and depths beyond 750 m, fish less than 40 cm in length were virtually absent.

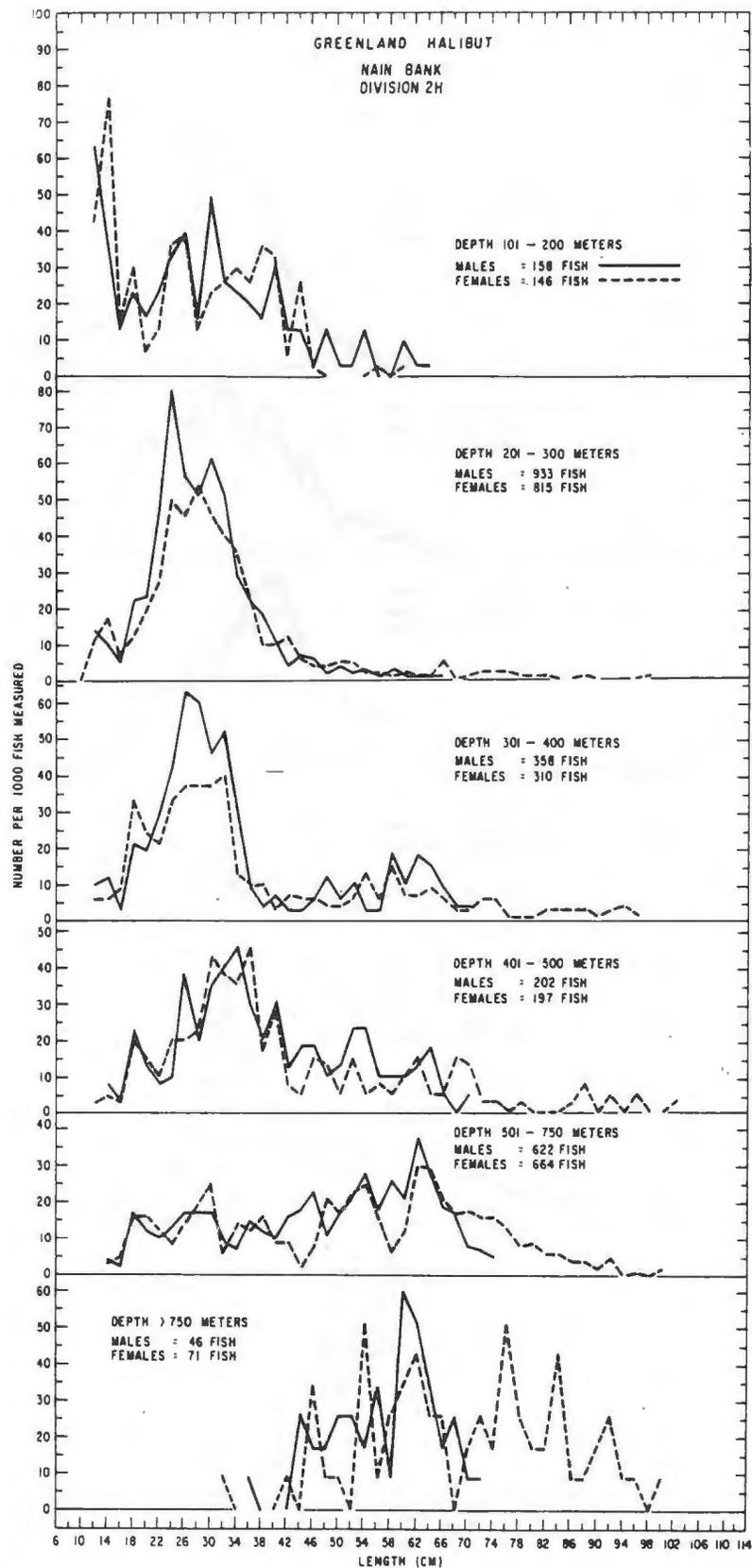


Fig. 13. Length frequency distribution by depth (m) of male and female Greenland halibut in the Nain Bank area (NAFO Division 2H).

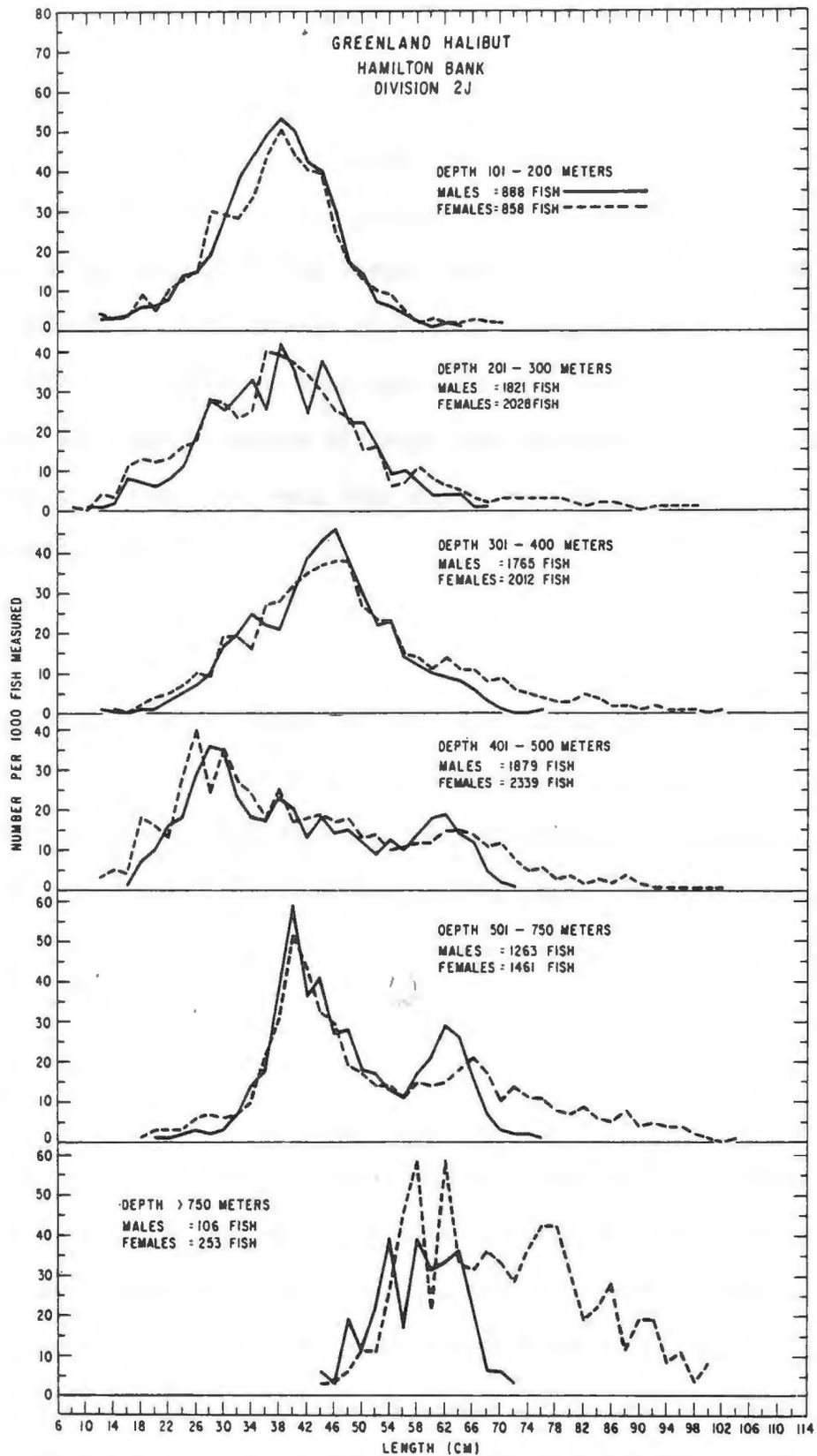


Fig. 14. Length frequency distribution by depth (m) of male and female Greenland halibut in the Hamilton Bank Area (NAFO Division 2J)

Division 3K (Northeast Nfld. Shelf): The length frequency distributions for this area are mostly for depth zones up to 400 m with a small frequency distribution for greater than 750 m depth (Fig. 15). There is a slight change in the length frequency distribution from 201-300 m to 301-400 m. The absence of fish less than 40 cm in length in depths greater than 750 m is once again apparent in Div. 3K, however, while there are higher numbers of large females beyond 70 cm in length in this deeper zone they are much less abundant proportionately than in the more northerly areas.

Division 3L: Length frequency distributions were available for depths less than 101 m up to 400 m (Fig. 16). The major proportions of each frequency distribution were the same over all depths. However, there was a substantial increase in the numbers of fish beyond 50 cm in length going from 201-300 m depth to 301-400 m depths particularly in females greater than 62 cm in length.

Division 4RST: Length frequency distributions for three depth zones from 185 m to greater than 366 m followed the same pattern as found throughout the other divisions (Fig. 17). In this case, however, there were very few fish less than 30 cm in length found in any depth zone throughout the division. There was a change from a peak of 40-48 cm in length in 185-275 m depth to 44-56 cm in length in 276-366 m depth. Beyond 366 m depth there appeared to be fewer females smaller than 50 cm than in the shallower depths.

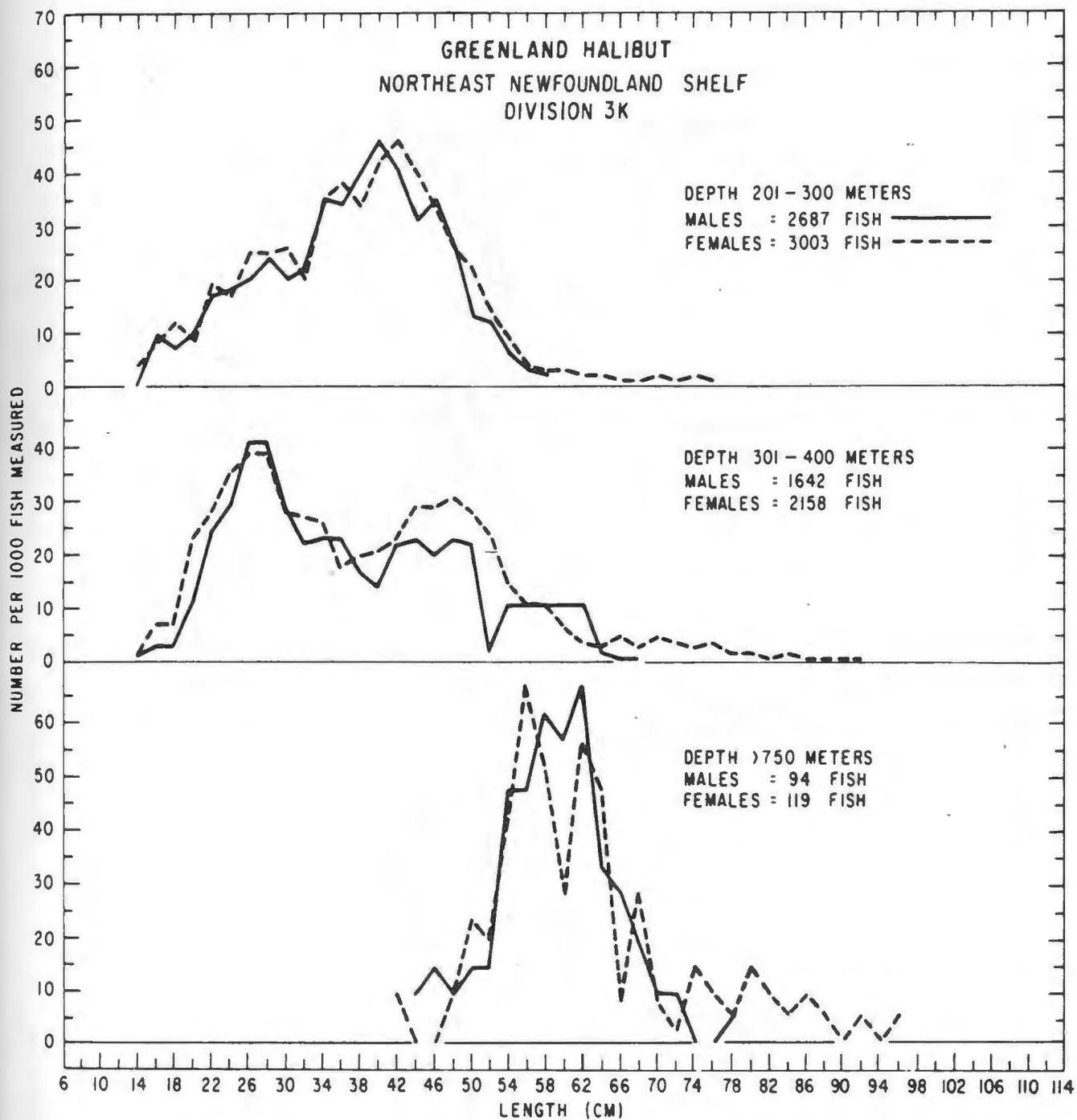


Fig. 15. Length frequency distribution by depth (m) of male and female Greenland halibut in the Northeast Newfoundland shelf area (NAFO Division 3K).

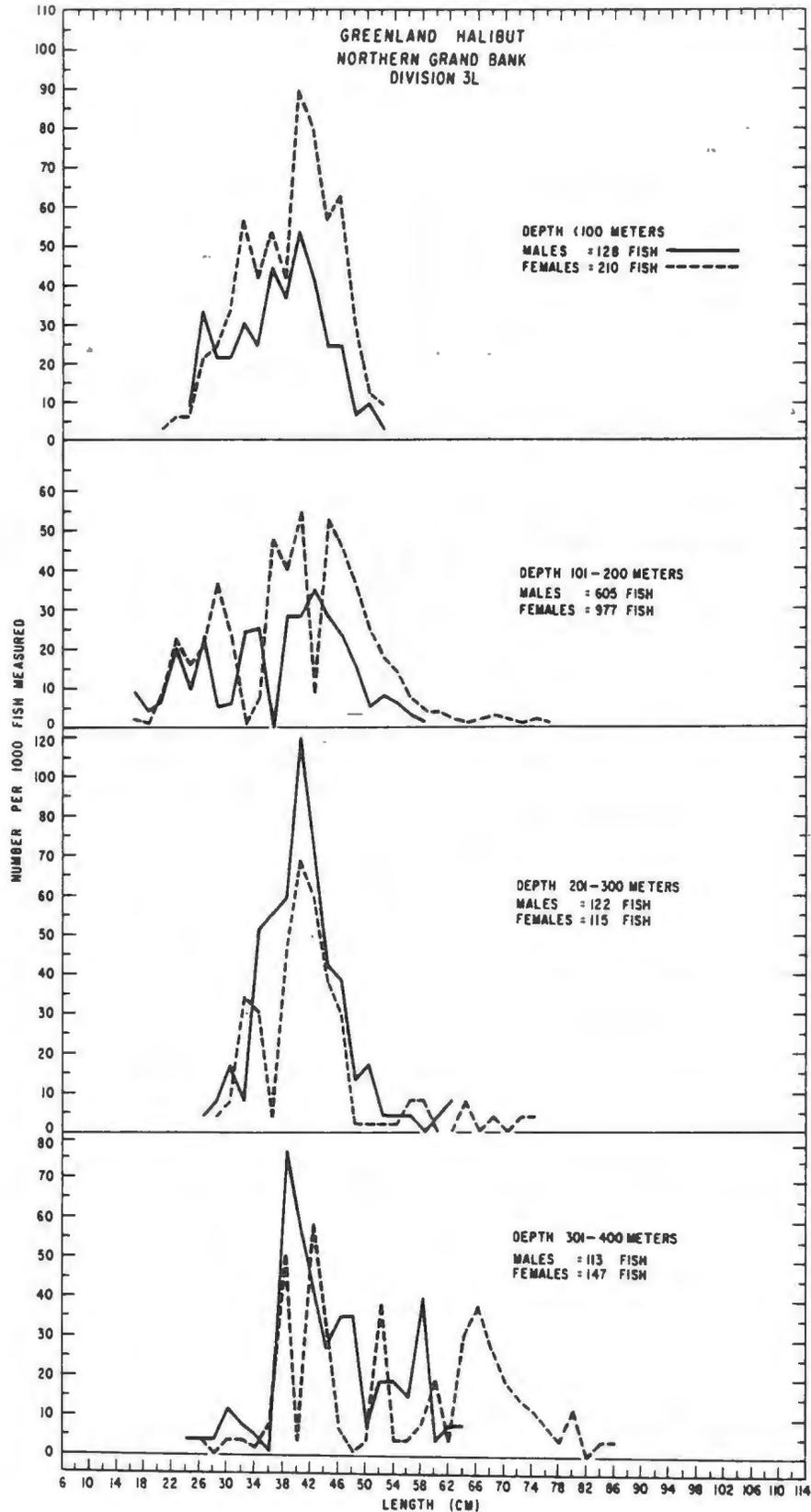


Fig. 16. Length frequency distribution by depth (m) of male and female Greenland halibut in the northern Grand Bank area (NAFO Div. 3L).

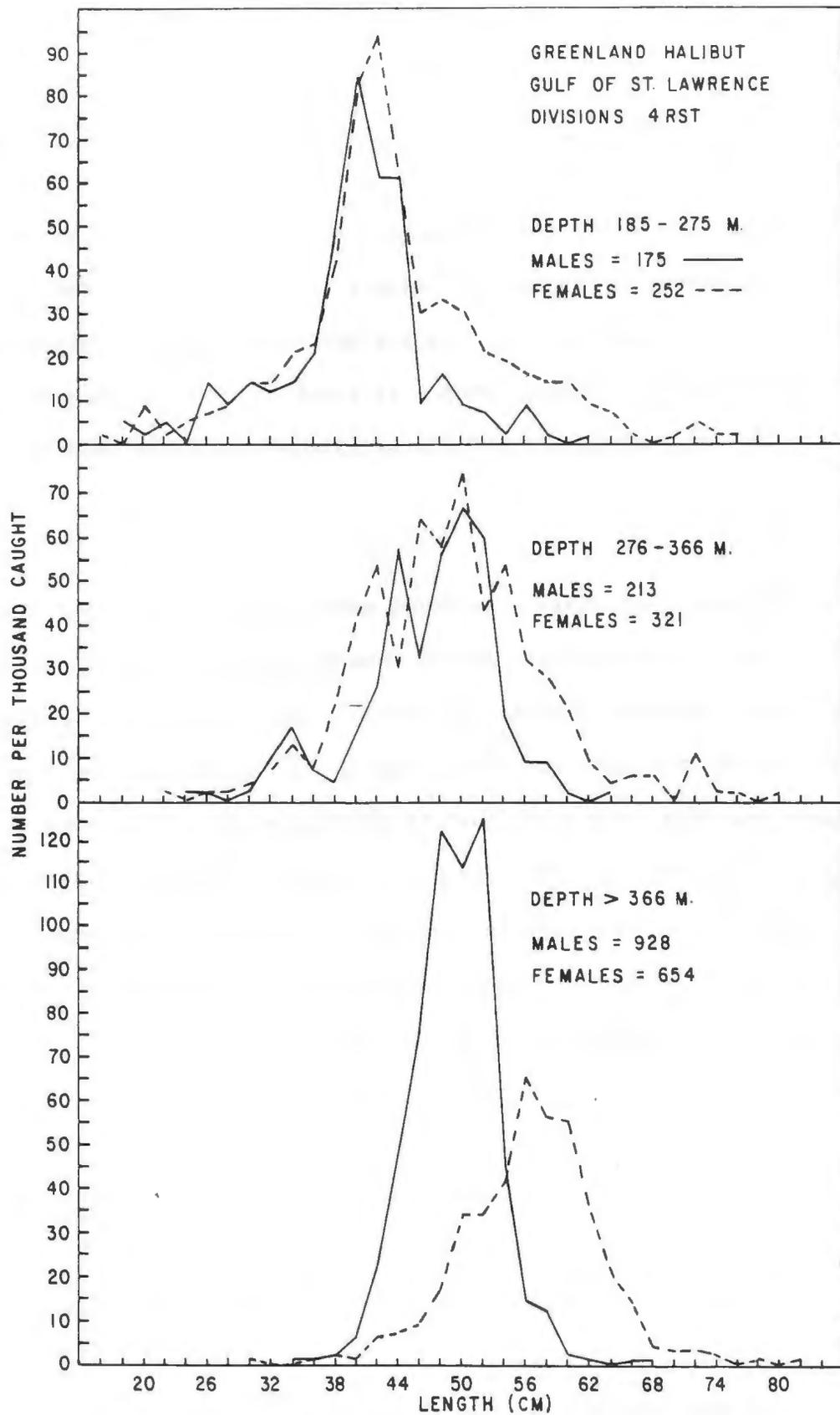


Fig. 17. Length frequency distribution by depth (m) of male and female Greenland halibut in the northern Gulf of St. Lawrence (NAFO Divisions 4RST).

c) Average lengths and sex ratios of catch by depth zone

The average lengths of catch by depth zone for males and females (Table 1 and 2) are relatively similar throughout the range up to 400 m depth however, in most cases the average size increases in the deeper zones. Beyond 400 m depth there is a considerable increase in the average length of both males and females in all areas as depth increases (Tables 1 and 2).

For areas where samples were relatively large the proportion of either sex in the catch was between 40-60% particularly in the 201-500 m depth range with no apparent trend in proportions of males versus females (Tables 1 and 3). Beyond 500 m depth, with the exception of Div. 0B where samples were small, the proportion of females in the catch was always higher than that of the males (Tables 1 and 3). This was particularly apparent in the deepest zones of Div. 2J and 2H. In Div. 4RST, on the other hand, there was a strong shift from a predominance of females in the shallower depths to a predominance of males in the deeper zones.

AGE AND GROWTH

a) Age composition

Age compositions of Greenland halibut from Baffin Bank in October 1977, showed a predominance of younger age-groups particular

Table 1. Sex ratios and mean lengths by depth for male and female Greenland halibut for the Gulf of St. Lawrence (Divisions 4RST).

Depth zone (m)	Sex ratio		Mean length	
	Males	Females	Males	Females
185-275	40.98	59.02	40.32	44.15
276-366	60.11	39.89	47.24	51.46
>366	58.66	41.34	49.76	56.88

Table 2. Weighted average length (cm) of Greenland halibut by depth (m) and area in the Northwest Atlantic.

Depth (m)	Northern Grand Bank (3L)		NE Nfld. Shelf (3K)		Hamilton Bank (2J)		Nain Bank (2H)		Saglek Bank (2G)		Baffin Bank (0B)	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
<100	37.04	38.99										
101-200	36.74	39.82			37.68	38.02	30.03	26.97	39.85	42.19		
201-300	40.91	43.63	37.40	38.47	39.18	40.48	28.85	31.26	33.49	33.12	25.24	25.40
301-400	43.47	51.90	36.49	39.79	44.77	48.16	34.46	38.02	56.64	57.48	22.01	22.49
401-500			34.13	37.88	41.05	43.57	39.20	41.60	58.12	62.94	31.27	28.61
501-750					48.66	54.51	47.75	52.04			46.18	47.80
>750			59.52	58.70	56.05	71.10						

Table 3. Sex ratio of Greenland halibut by depth in the Northwest Atlantic.

Depth (m)	Northern Grand Bank (3L)		NE Nfld. Shelf (3K)		Hamilton Bank (2J)		Nain Bank (2H)		Saglek Bank (2G)		Baffin Bank (0B)	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
<100	37.81	62.13										
101-200	38.24	61.76			50.86	49.14	51.96	48.04	45.55	54.45		
201-300	51.48	48.52	52.78	47.22	47.31	52.69	53.44	46.56	48.85	51.15	51.57	48.43
301-400	43.46	56.54	43.21	56.79	46.73	53.27	53.85	46.15	73.82	26.18	51.80	48.20
401-500			40.24	59.76	44.55	55.45	50.54	49.46	65.17	34.83	49.88	50.12
501-750					46.37	53.63	48.21	51.79	44.48	55.52	61.72	38.28
>750			44.13	55.87	29.53	70.47	39.21	60.79				

3-5-yr-old for both males and females (Fig. 18). Although fish were present in the catches up to age 14 for males and age 18 for females, very few fish were present beyond 8 years old. In Saglek Bank area, the opposite was the case with a strong predominance of fish beyond 5-yr-old although fish in the 3-5-yr-old range were well represented (Fig. 18). The age compositions for Greenland halibut from the Nain Bank, Hamilton Bank and Northeast Newfoundland Shelf areas were relatively similar with an abundance of fish in the 2-8-yr-old range for both sexes (Fig. 18). Although older fish were present in the catches, the abundance of the older fish decreased moving progressively southward. This is particularly evident considering the age composition from the northern Grand Bank data where males beyond 9 yr old and females beyond 12 yr old did not appear in the catches (Fig. 18). Age 2 fish were virtually absent from the northern Grand Bank although they occurred in moderate to high abundance in the adjacent areas to the north.

Age compositions for the Gulf of St. Lawrence data indicated very few fish less than age 4 for either sex (Fig. 19) with males absent beyond age 10 and females absent beyond age 12. The predominant age groups were 5-7 yr olds for males and 6-9 yr olds for females, all year-classes of the early 1970's.

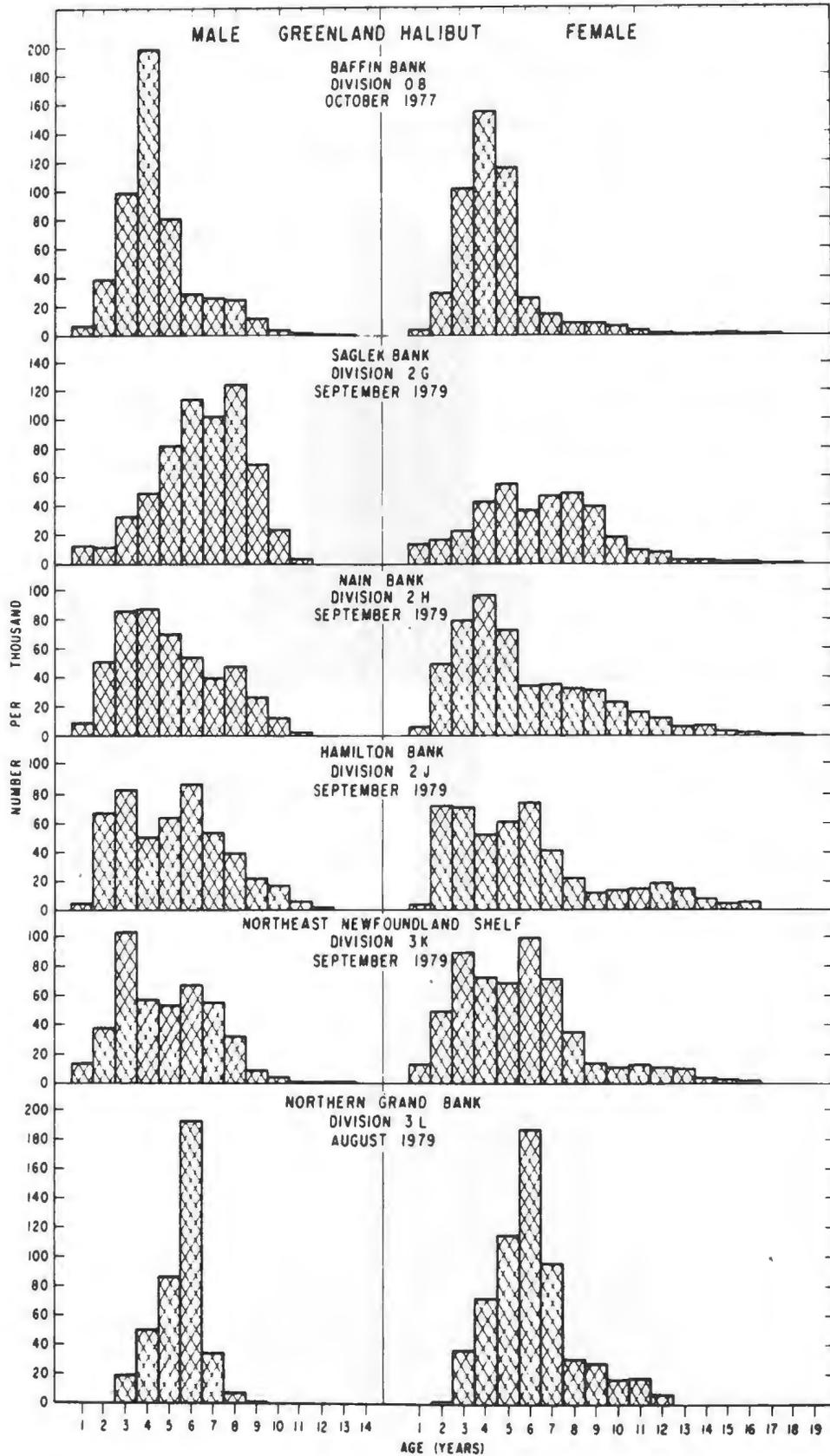


Fig. 18. Age composition of male and female Greenland halibut by area from Baffin Bank (NAFO Division 0B) southward to the northern Grand Bank (NAFO Div. 3L) inclusive.

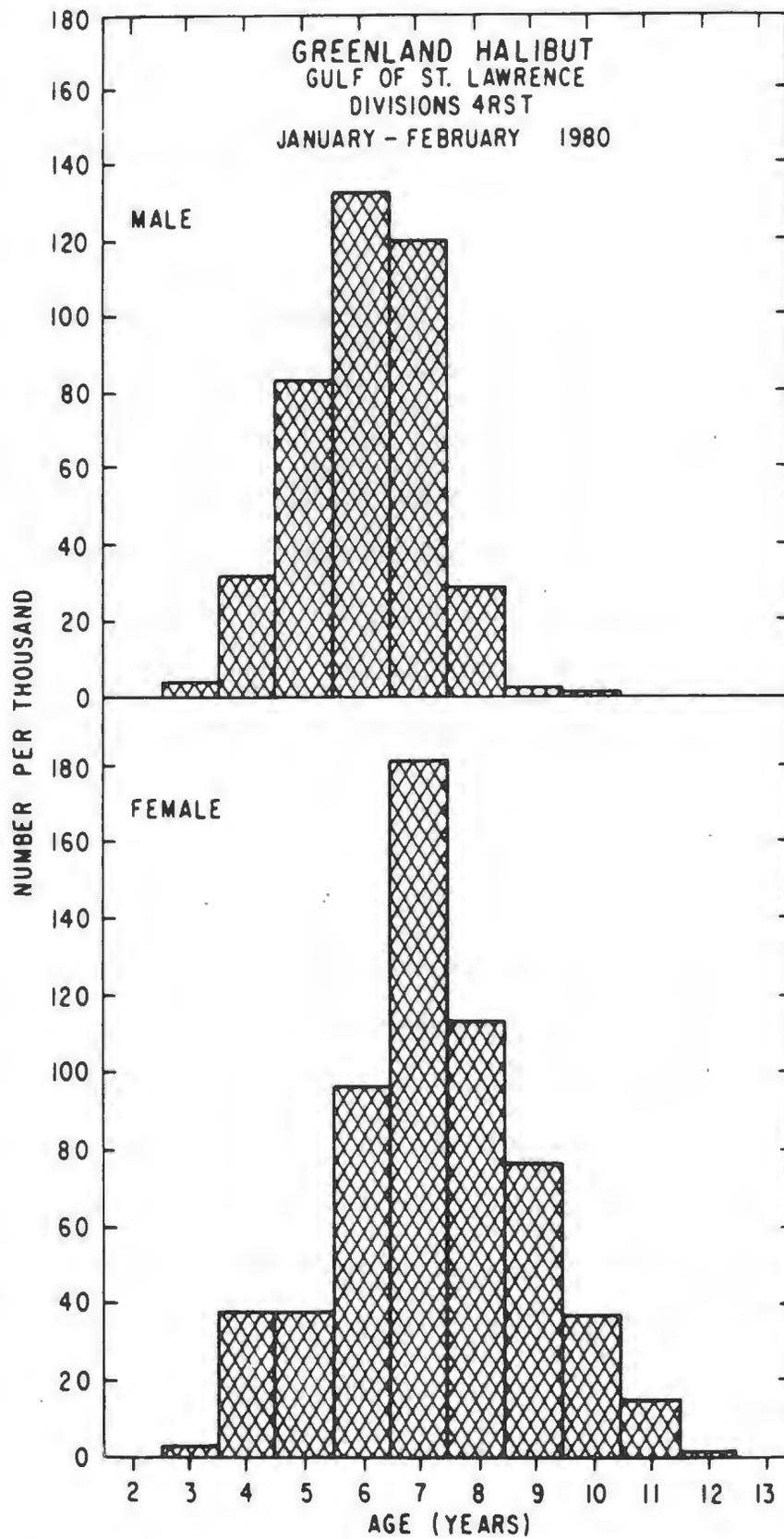


Fig. 19. Age composition of male and female Greenland halibut from the northern Gulf of St. Lawrence.

b) Growth curves from empirical data

It appears from the growth curves shown in Fig. 20 that the males attain a larger size at age in the first 3-5 yrs but the females appear to grow faster in the older age groups. This becomes evident from the slopes of the curves presented in Table 4 where the slopes of the curves for the females are higher in all cases than for the males. It is also suggested by the upper extremes of the growth patterns that the life span of females is larger than that of males. The number of age groups comprising the females are greater by 2 for the Gulf of St. Lawrence to as much as 8 for Saglek Bank.

While the curves do not appear to fit the data points very well because of the weighting procedure, the correlation coefficients (r) were all greater than $r = 0.92$ and were all highly significant (Table 4). In almost all cases the data points for the older ages are above the fitted lines. This would suggest that if the observations were more numerous in the older ages, the computed growth rates may be higher than appear here since more weight would be given statistically to these points.

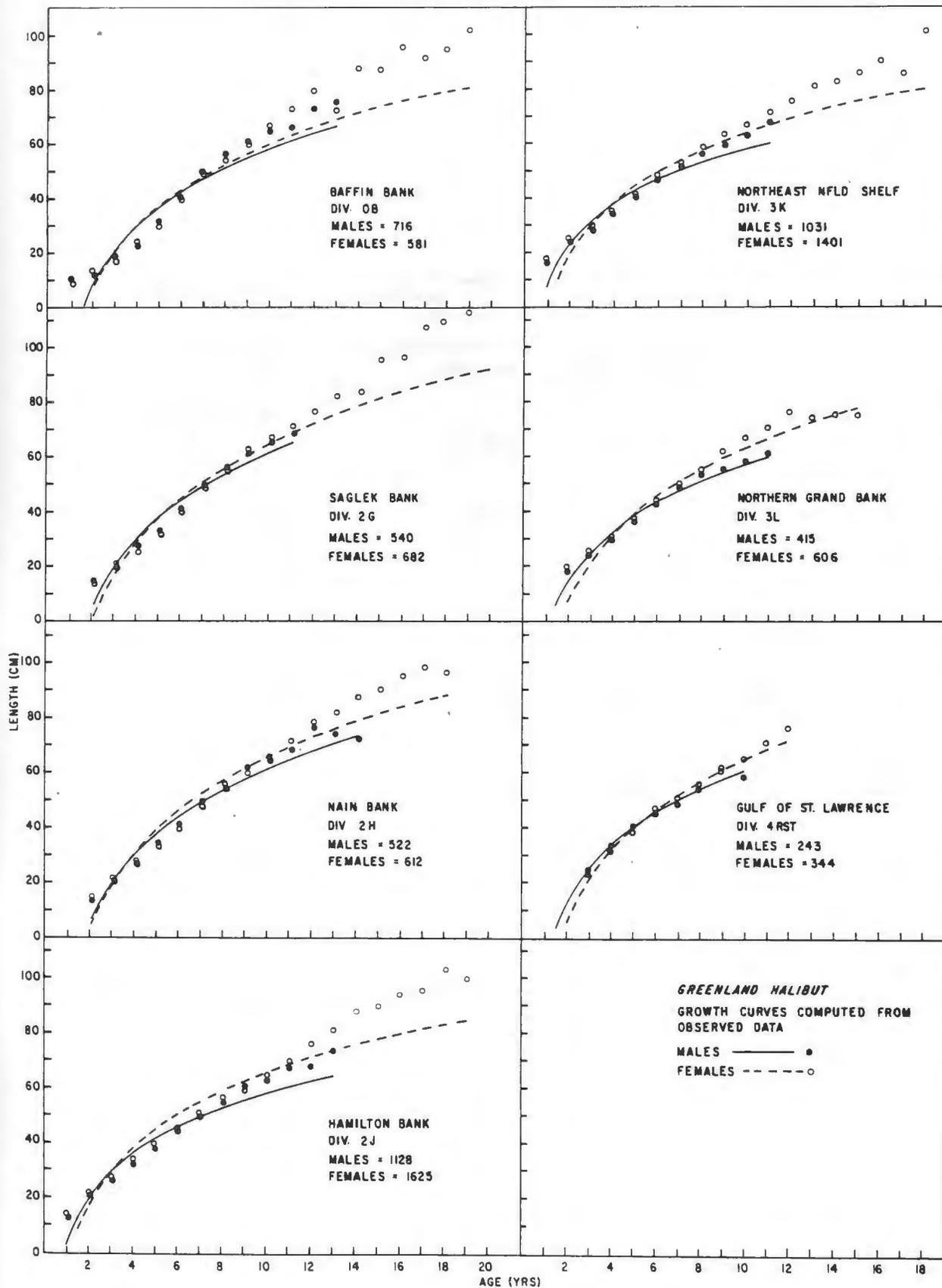


Fig. 20. Empirical growth curves of male and female Greenland halibut from seven areas of the Canadian Northwest Atlantic.

Table 4. Summary of statistics for empirical growth equations ($y = a + b \ln x$ where y = length and x = age) for Greenland halibut.

Area	Adj. mean	Regre. coeff.	r	t-value for r
Baffin Bank (0B)				
Male	-11.9946	30.2943	0.9381	72.3507
Female	-14.4133	32.0104	0.9292	60.4914
Saglek Bank (2E)				
Male	-17.6947	34.3366	0.9705	93.4232
Female	-25.6599	39.2109	0.9647	95.5000
Nain Bank (2H)				
Male	-16.8360	34.1269	0.9787	108.7012
Female	-21.9547	38.2450	0.9738	105.7064
Hamilton Bank (2J)				
Male	2.7669	24.1810	0.9622	118.5710
Female	-4.0089	30.3923	0.9473	119.1077
NE Nfld. Shelf (3K)				
Male	5.5334	22.0822	0.9704	128.9849
Female	-1.9794	28.0902	0.9609	129.8013
Northern Grand Bank (3L)				
Male	-6.4826	27.3112	0.9829	108.4079
Female	-18.5227	35.2007	0.9708	99.4724
Gulf of St. Lawrence (4RST)				
Male	-8.0324	29.8902	0.9909	114.0783
Female	-18.8768	36.1907	0.9906	134.0496

c) Back-calculated growth curves

For validation of the direct proportionality technique, a fit was obtained which was highly significant ($P < 0.05$) with an $r = 0.98$ (Fig. 22). Back-calculated growth curves up to age 5 of the 1972 year-class show very close agreement between males and females particularly for the more southerly areas where the curves essentially coincide (Fig. 21 and Table 5). A covariance analysis of males vs. females indicated no significant difference in the males and females for both the regression coefficients (slopes) or adjusted means (y-intercepts) throughout the range under consideration ($P = 0.44$). The sexes therefore were combined. A covariance analysis on the slopes of the fitted lines for the sexes combined was performed and indicated that with the exception of the Baffin Bank (OB) data the regression coefficients (slopes) were equal ($P < 0.16$), indicating that the growth rates in these areas were similar. Paired comparisons using t-tests to test for differences between the adjusted means indicated that both the Gulf of St. Lawrence (4RST) data and the Nain Bank (2H) data were significantly different from those of all other areas (Table 6). The Saglek Bank (2G) data differed from those of the Northeast Newfoundland Shelf (3K) but did not differ from either the Hamilton Bank (2J) data or the northern Grand Bank (3L) data. There was no significant difference amongst the adjusted means of the Hamilton Bank (2J), Northeast Newfoundland Shelf and the northern Grand Bank data (Table 6). The combined back-calculated growth curves (Fig. 23) shows the Baffin Bank (OB) growth rate to be the slowest with a considerably

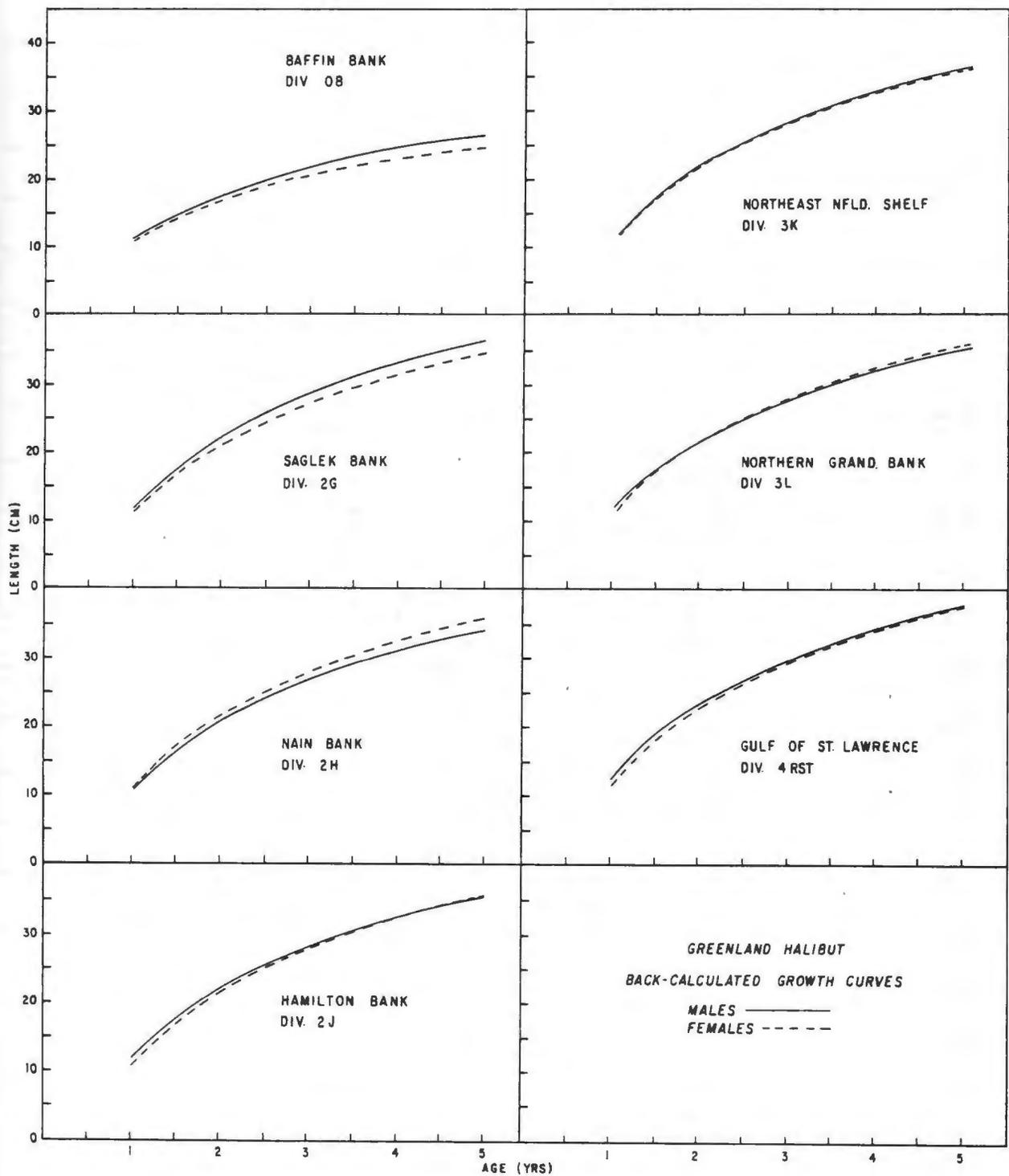


Fig. 21. Back-calculated growth curves (ages 1-5) of male and female Greenland halibut from seven areas of the Canadian Northwest Atlantic.

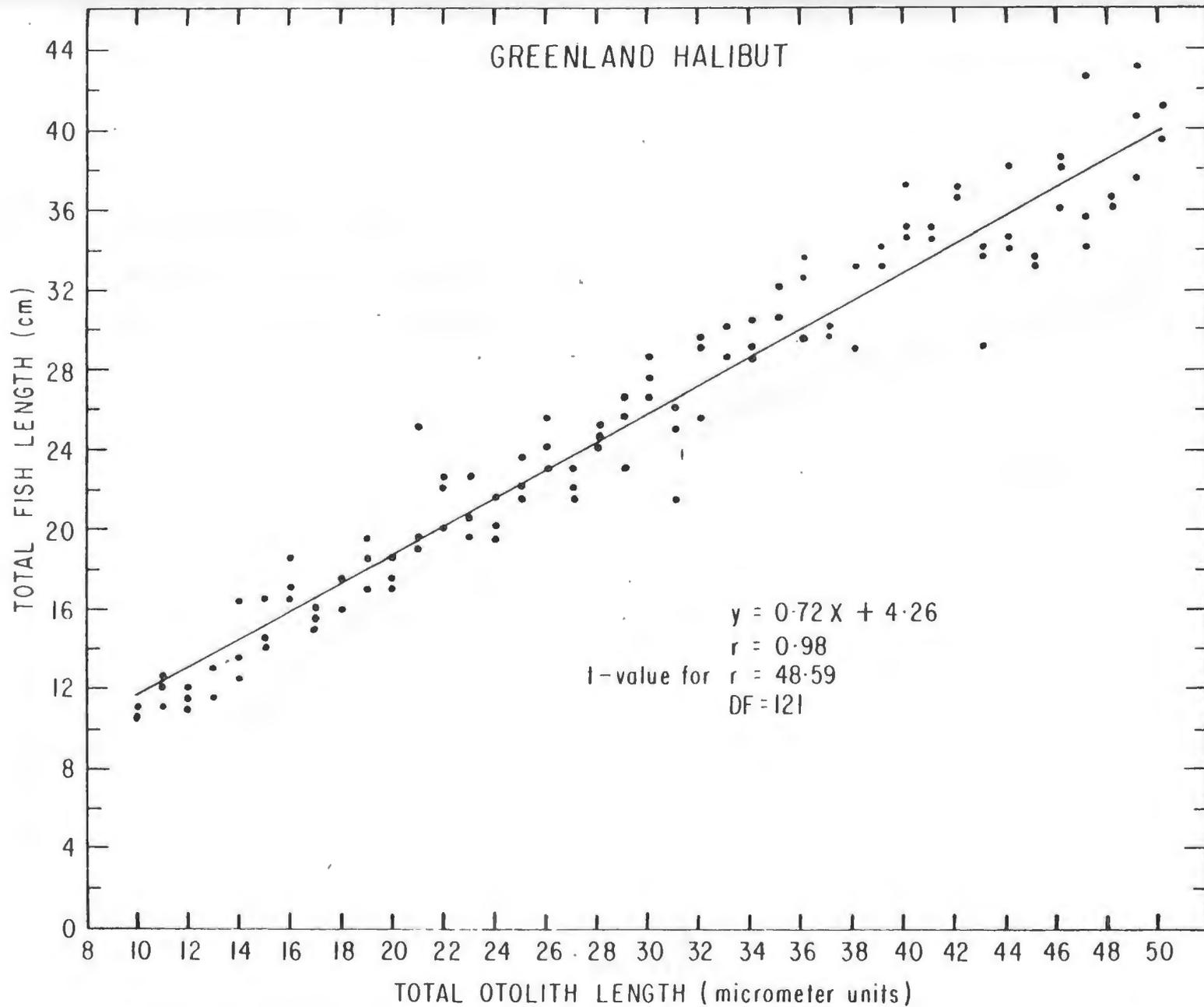


Fig. 22. Scatter plot and linear least squares regression for total fish length against total otolith length of Greenland halibut

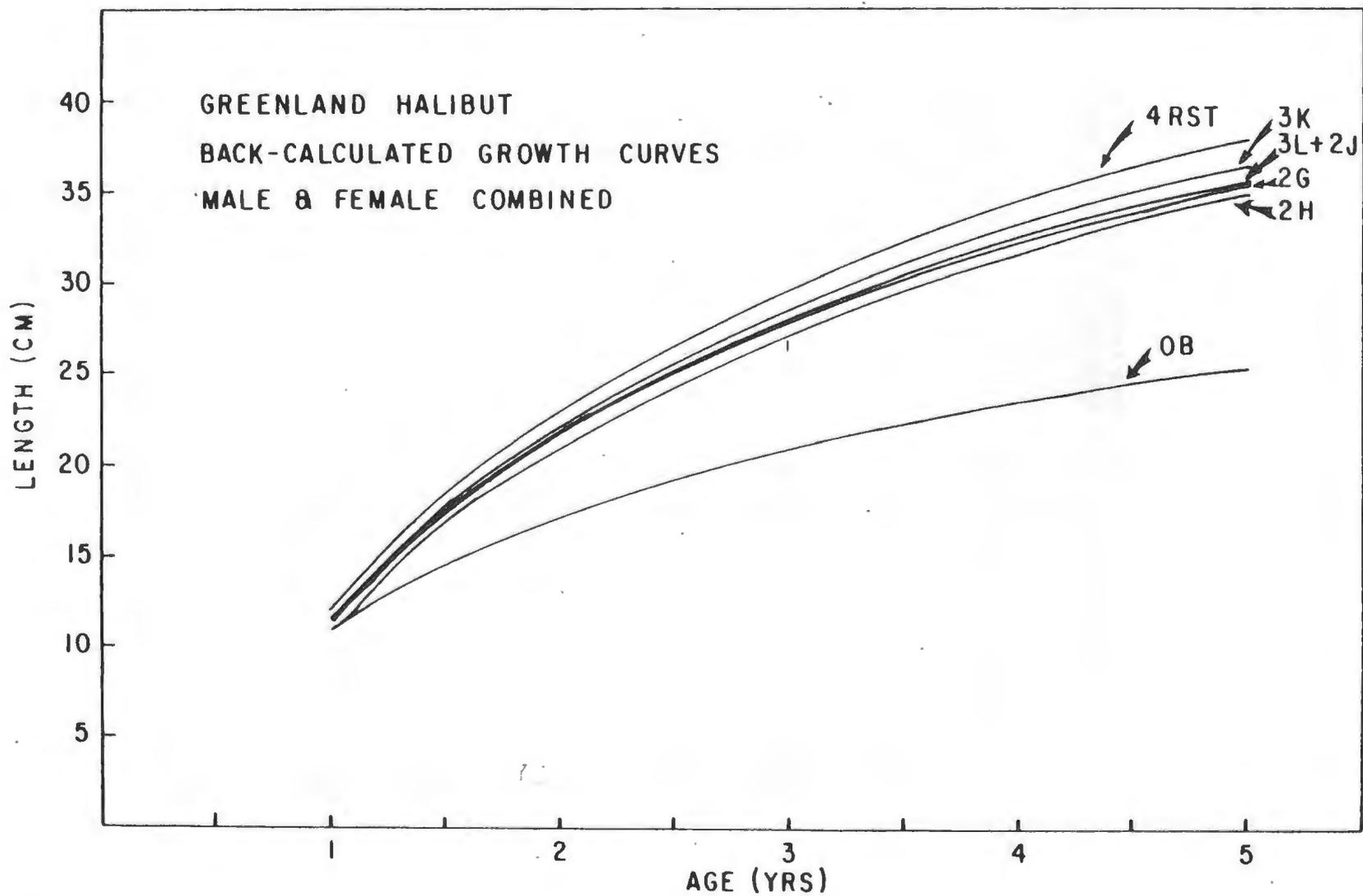


Fig. 23. Comparisons of back-calculated growth curves (ages 1-5) of Greenland halibut, sexes combined, from seven areas of the Canadian northwest Atlantic.

Table 5. Summary of adjusted means (intercepts) and regression coefficients (slopes) for back-calculated growth equations ($y = a+blnx$ where y = length and x = age) for Greenland halibut.

Area	Adjusted mean	Regression coefficient
Baffin Bank (0B)		
Male	10.9818	9.4920
Female	10.7557	8.5236
Total	10.8734	9.0385
Saglek Bank (2G)		
Male	11.6394	15.3603
Female	10.9514	14.6399
Total	11.3008	15.0058
Nain Bank (2H)		
Male	10.6006	14.5811
Female	10.7914	15.4339
Total	10.6944	15.000
Hamilton Bank (2J)		
Male	11.9195	14.7988
Female	10.8376	15.5281
Total	11.3872	15.1577
NE fld. Shelf (3K)		
Male	11.2684	15.8019
Female	11.3186	15.6316
Total	11.2943	15.7142
Northern Grand Bank (3L)		
Male	11.7141	14.7185
Female	11.1423	15.4794
Total	11.4141	15.1177
Gulf of St. Lawrence (4RST)		
Male	12.4891	15.8638
Female	11.3576	16.3780
Total	11.8513	16.1536

Table 6. T-test matrix for adjusted group means for back-calculated growth curves.

NAFO areas	NAFO areas				
	2G	2H	2J	3K	3L
2G					
2H	-2.0878				
2J	0.7976	2.8790			
3K	2.3387	4.4309	1.5319		
3L	0.7519	2.8171	-0.0392	-1.5588	
4RST	5.4818	7.4573	4.7117	3.2846	4.7140

Probabilities for t-values above

2G					
2H	0.0370*				
2J	0.4253	0.0041**			
3K	0.0195*	0.0001**	0.1258		
3L	0.4523	0.0050**	0.9687	0.1193	
4RST	0.0000**	0.0000**	0.0000**	0.0011*	0.0000*

** significant at the 1% level

* significant at the 5% level

smaller size at age. The largest size at age is found in the Gulf of St. Lawrence (4RST) with all other areas in the mid-range.

SEXUAL MATURITY

a) Maturity curves

The maturity curves and data points for female Greenland halibut are presented in Fig. 24 for the six areas where data were available. For all areas, the data points followed a sigmoid pattern with all points reasonably close to the curves. When the curves for the six areas are superimposed (Fig. 25) there is a clear clinal shift to the right in the curves going from northern Labrador to southern Labrador with the Northeast Newfoundland Shelf and southern Labrador curves approximately the same. The curve for the Baffin Bank area falls near the middle close to that of Nain Bank area. The Gulf of St. Lawrence curve, however, is well to the left (Fig. 25) and appears nearly isolated from all others. For Hamilton Bank data (Div. 2J) where two sets of data are presented, both sets follow a similar pattern with data points close to the curves (Fig. 26). Both appear to be in close agreement with each other as shown in Fig. 27.

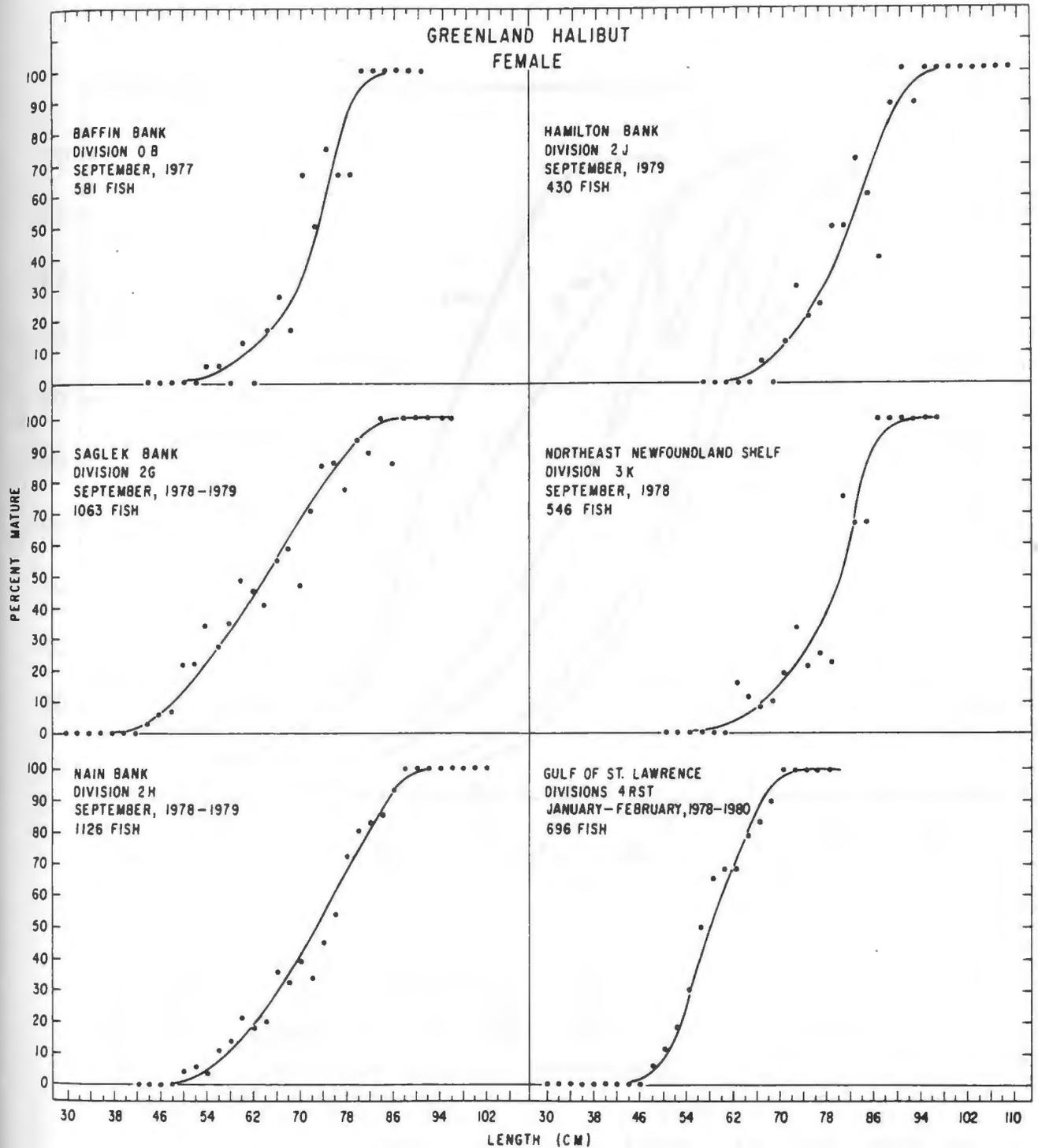
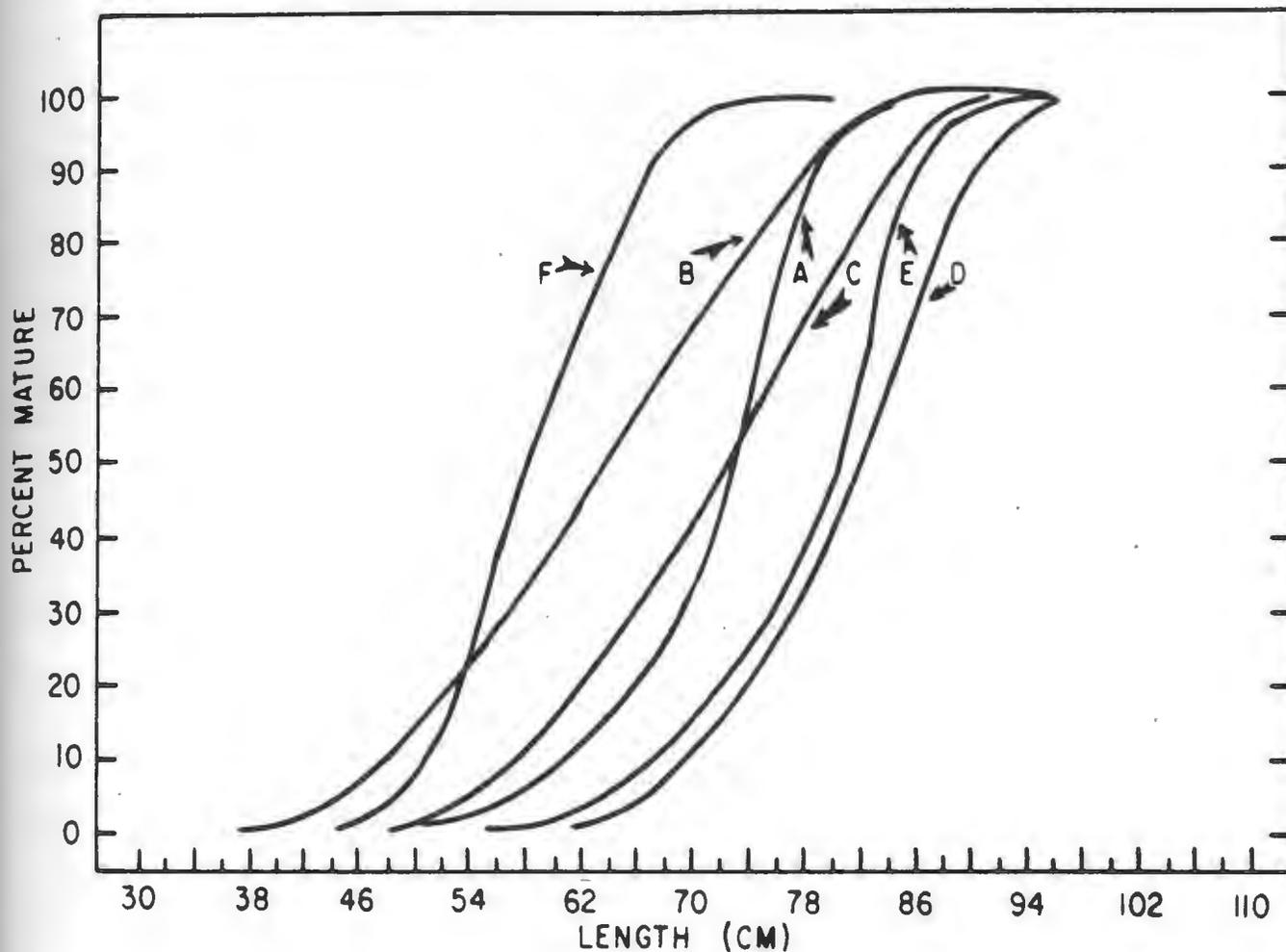


Fig. 24. Sexual maturity ogives of female Greenland halibut from six areas of the Canadian Northwest Atlantic.



- A — BAFFIN BANK DIV 0B SEPT 1977
 B — SAGLEK BANK DIV 2G SEPT 1978-79
 C — NAIN BANK DIV 2H SEPT 1978-79
 D — HAMILTON BANK DIV 2J SEPT 1979
 E — NORTHEAST NFLD. SHELF DIV 3K SEPT 1978
 F — GULF OF ST. LAWRENCE DIV'S 4RST JAN - FEB 1978-80

Fig. 25. A comparison of sexual maturity ogives of female Greenland halibut from six areas of the Canadian Northwest Atlantic.

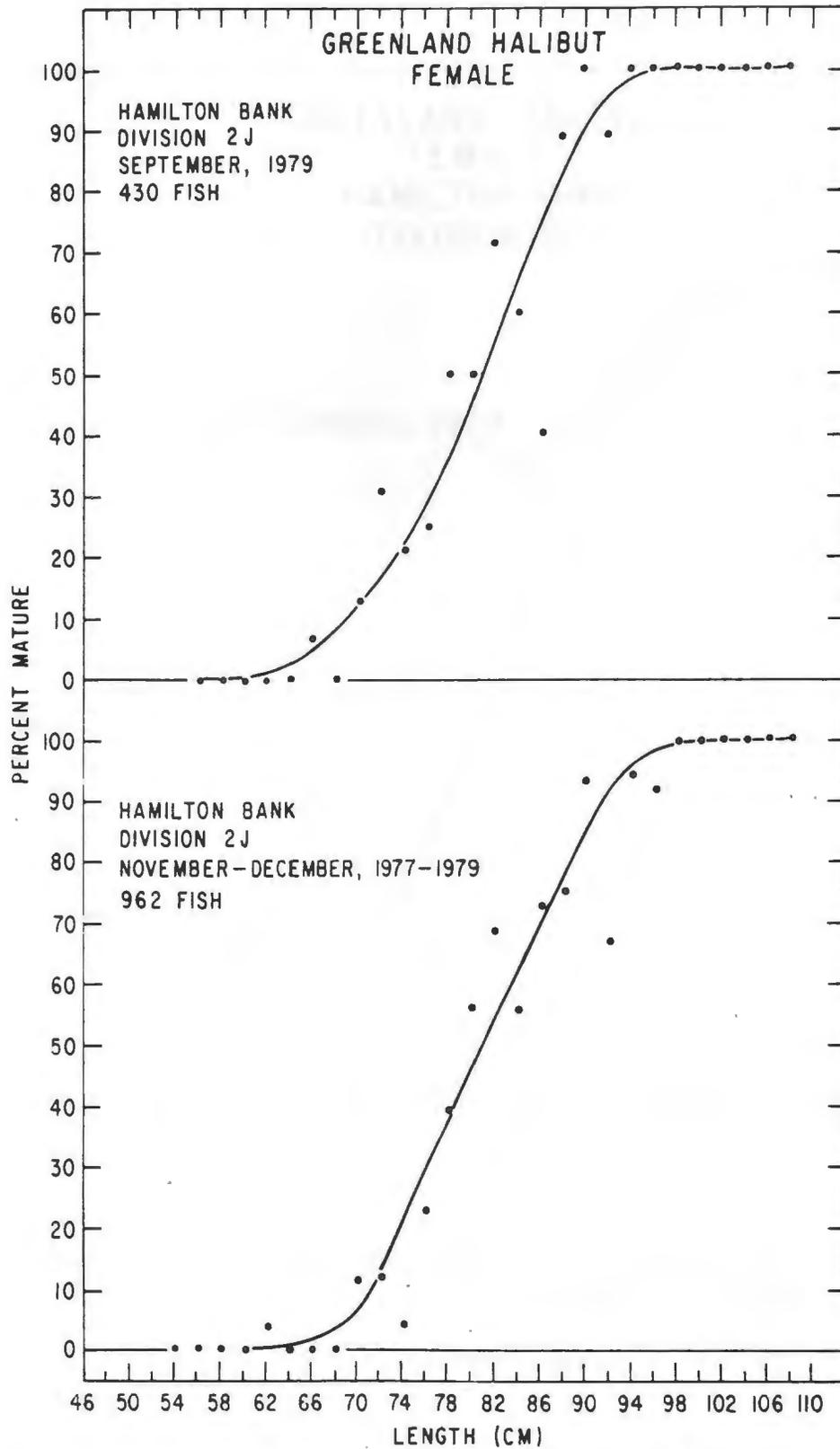


Fig. 26. Sexual maturity ogives of female Greenland halibut from the Hamilton Bank Area (NAFO Division 2J) for September and November-December.

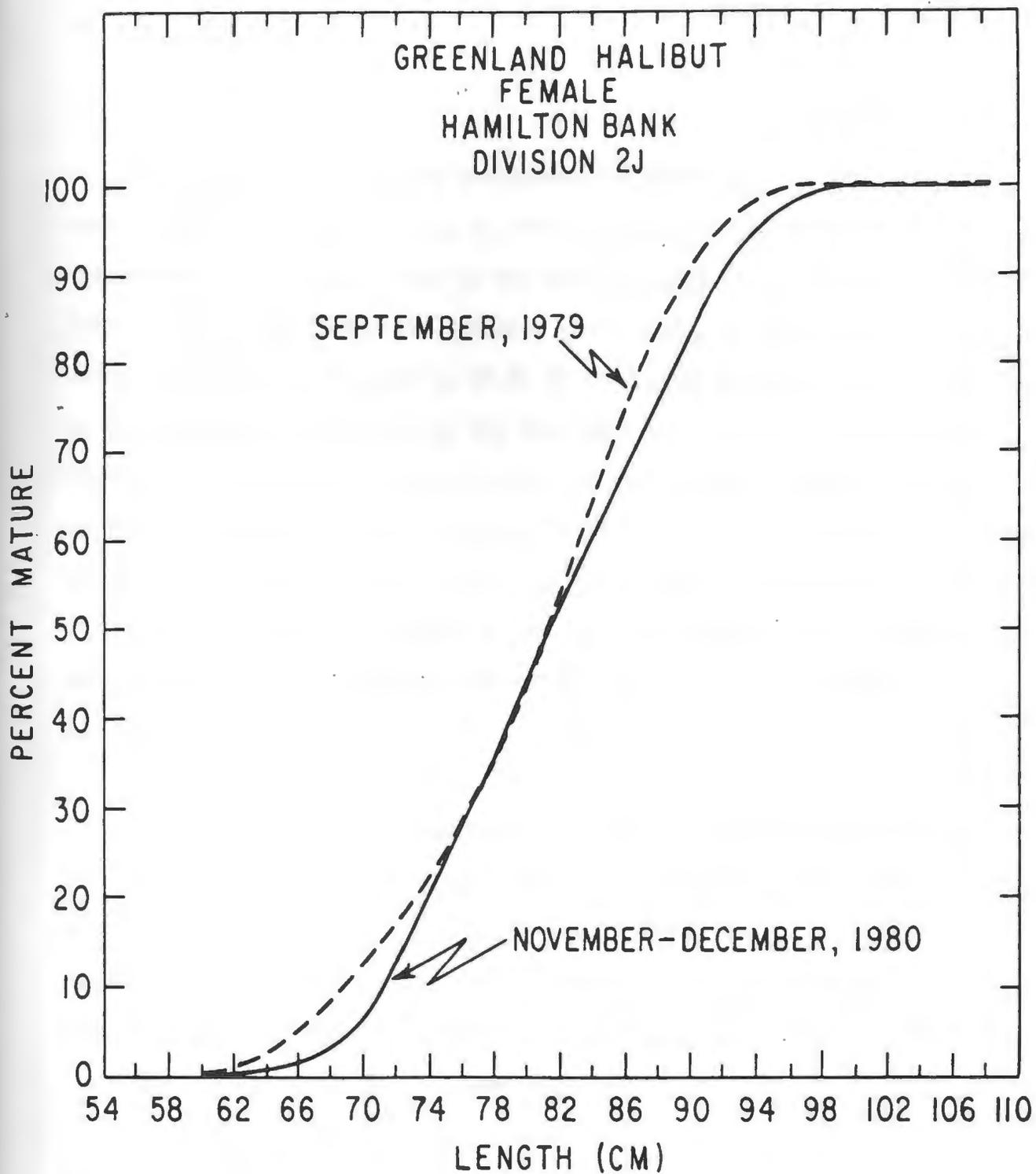


Fig. 27. A comparison of sexual maturity ogives of female Greenland halibut from the Hamilton Bank Area (NAFO Division 2J) for September and November-December.

b) Probit analysis

The results of the probit transformation analysis of sexual maturity data by area are shown in Table 7. All chi-square tests indicate acceptance of the fitted lines to the observed data at the 5% significance level. The length at the 50% maturity level or M_{50} decreased from 71.76 cm in Baffin Bank area to 64.80 in the Saglek Bank area. The length at M_{50} increased to 73.05 cm in the Nain Bank area and then to 80.86 cm in the Hamilton Bank area for the September-October data. The M_{50} value for Northeast Newfoundland shelf area was 79.58 cm, very similar to the Hamilton Bank value. The difference in the two sets of data for Hamilton Bank was 1.24 cm with the larger M_{50} of 82.10 cm coming in the November-December data set. The lowest value of M_{50} was 57.83 cm for the Gulf of St. Lawrence.

The ages at M_{50} calculated from the growth equations (Table 4) showed the same trends as did the lengths at M_{50} . The lowest age at M_{50} was 8.3 yrs for the Gulf of St. Lawrence data to a maximum of 18.2 yrs for the Northeast Newfoundland shelf. A value of 17.0 yrs however was calculated for the November-December data set compared to 16.3 yrs for the September-October data set from Hamilton Bank.

The results of the covariance analyses for testing the regression coefficients (slopes) and elevations (y-intercepts) of the fitted lines are shown in Table 8. The slope of the Baffin Bank data differed from

Table 7. Results of probit analyses of sexual maturity data, by area, with results of χ^2 tests for acceptability of the fitted lines to the observed data.

Statistical parameter	NAFO division						
	OB	2G	2H	Sept.-Oct. 2J	Nov.-Dec. 2J	3K	4RST
Slope	0.1574	0.0733	0.0864	0.1118	0.1220	0.1016	0.1574
Y int.	-6.297	0.250	-1.312	-4.043	-5.014	-3.086	-4.101
Len. M_{50}	71.76	64.80	73.05	80.86	82.10	79.58	57.83
A (ΣX^2)	698.88	29002.42	21570.79	2719.69	7168.01	2643.90	5588.90
B (ΣXY)	110.00	2125.88	1863.72	304.06	874.50	268.62	879.69
C (ΣY^2)	21.14	175.39	172.49	45.80	125.05	32.43	148.37
χ^2 (Res. SS)	3.830	19.565	11.460	11.806	18.358	5.141	9.906
\bar{x}	70.57	60.70	69.82	78.85	81.19	72.52	56.07
SE m_{50}	0.2048	0.0613	0.0681	0.1237	0.0847	1.7904	0.0684
SE m	0.0267	0.0058	0.0053	0.0208	0.0135	0.0127	0.0127
N	10	22	21	12	16	14	13
Age M_{50}	14.8	10.0	12.0	16.3	17.0	18.2	8.3

Table 8. Matrix of t-values for paired comparisons of sexual maturity data for Greenland halibut.

	Saglek Bank Area 2G		Nain Bank Area 2H		Hamilton Bank Area 2J (Sept.-Oct.)		Hamilton Bank Area 2J (Nov.-Dec.)		NE Nfld. Shelf Area 3K		Gulf of St. Lawrence Areas 4RST		
	Slope	Int.	Slope	Int.	Slope	Int.	Slope	Int.	Slope	Int.	Slope	Int.	
Baffin Bank (ØB)	t												
	df												
		2.404*	N/A	2.455*	N/A	1.154	-2.977**	0.889	0.109	1.959	-10.748**	-0.0001	-11.484**
		28		27		18	19	22	23	20	21	19	20
Saglek Bank (2G)	t												
	df			1.634	8.311**	1.877	14.947**	3.496**	N/A	1.586	13.824**	5.905**	N/A
				39	40	30	31	34		32	33	31	
Nain Bank (2H)	t												
	df					1.394	10.775**	2.747**	N/A	1.008	7.958**	5.604**	N/A
						29	30	33		31	32	30	
Hamilton Bank (2J) (Sept.-Oct.)	t												
	df							0.404	2.914**	0.426	-4.619**	1.918	-6.643**
								24	25	22	23	21	22
Hamilton Bank (2J) (Nov.-Dec.)	t												
	df									0.943	-8.213**	1.866	-9.451**
										26	27	25	26
NE Nfld. Shelf (3K)	t												
	df											2.923**	N/A
												23	

* indicates rejection of H_0 at $\alpha = 0.05$ ** indicates rejection of H_0 at $\alpha = 0.01$

that of Saglek Bank and Nain Bank but not from those of any other areas. The slope of the fitted lines for Saglek Bank, Nain Bank, Hamilton Bank (Sept.-Oct) and Northeast Newfoundland Shelf did not differ significantly. The slope of the Gulf of St. Lawrence data differed significantly from those of all areas except Hamilton Bank and Baffin Bank.

For paired comparisons which did not yield significant differences between the slopes of the fitted lines, statistical treatment of the elevations (y-intercepts) indicated highly significant differences between the intercepts for all pairs at the 1% significance level (Table 8) with the exception of the Hamilton Bank (Nov-Dec data set) and Baffin Bank.

FECUNDITY

a) Fecundity vs. fish length

Analysis of the combined data for 1976 and 1977 for the southern Labrador area suggested that fecundity is related to length according to the relationship:

$$\log F = 3.082 \log L - 1.205$$

where F = fecundity (number of eggs) and L is fish length (cm). Fecundity related to fish length for the southeastern Gulf of St. Lawrence is represented by the equation:

$$\log F = 4.264 \log L - 3.152$$

Plots of the fecundity-length data and the arithmetic forms of the relationships are shown in Fig. 28 and 30 respectively for the southern Labrador and southeastern Gulf of St. Lawrence areas. For both cases, the correlation coefficient differed significantly from zero (Table 9).

An analysis of covariance of the fecundity length data for southern Labrador in 1976 and 1977 (Table 10 and Fig. 31) indicated that there were no significant differences in either the regression coefficients (slopes), the rate of egg production, or the adjusted means (y-intercepts), the quantity of eggs produced. The results of a similar analysis for fecundity-length relationships of the southern Labrador (1976-77 combined) and the southeastern Gulf of St. Lawrence (Table 10, Fig. 32) indicated that the difference between the regression coefficients was significant at the 5% level. The difference between the adjusted means was significant at the 1% level.

b) Fecundity vs fish age

For the southern Labrador area, analysis of the 1976 and 1977 combined data indicated that fecundity is related to age according to the relationship:

$$\log F = 1.571 \log A + 3.032$$

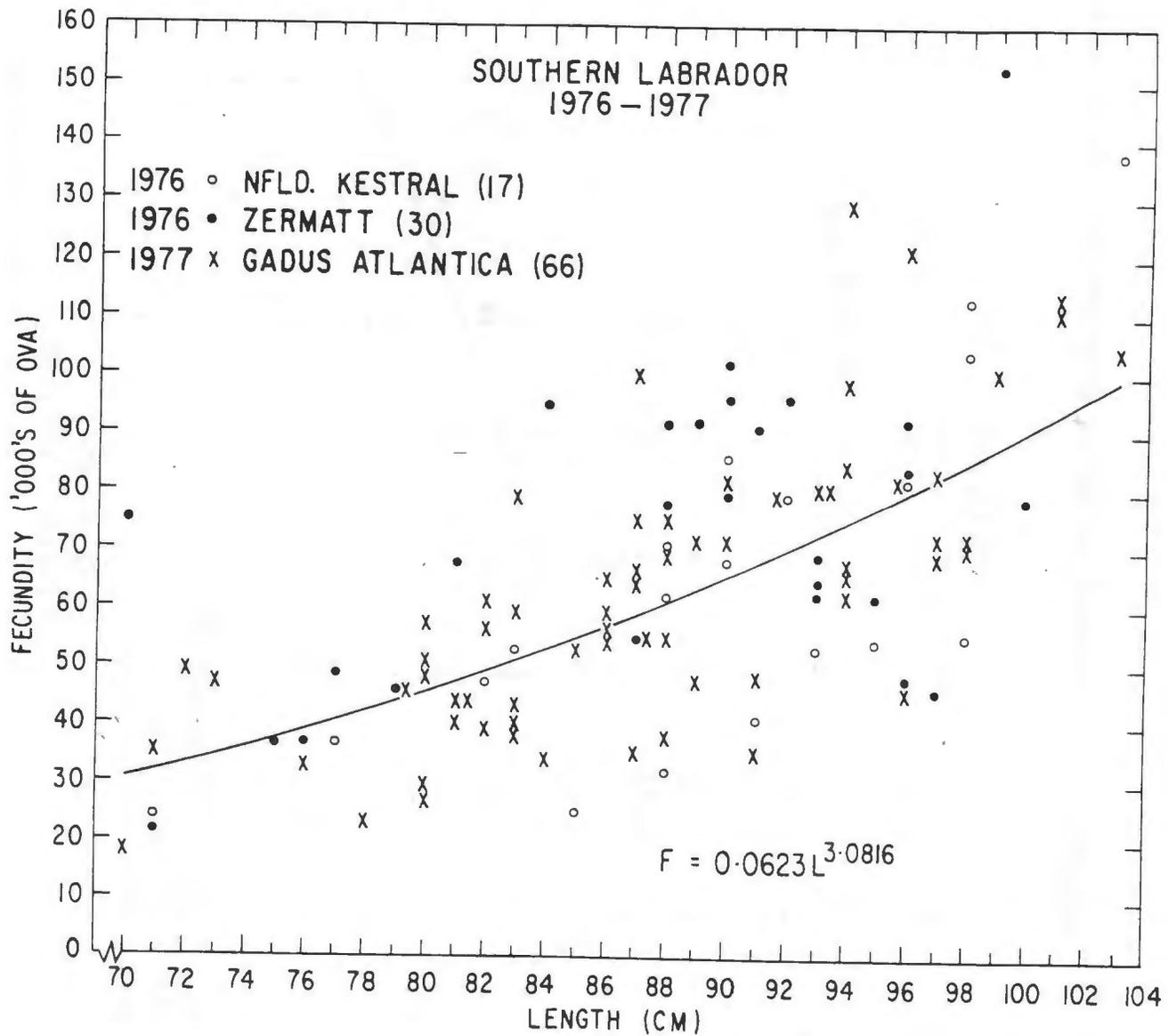


Fig. 28. Relationship of fecundity to length for Greenland halibut from southern Labrador 1976-77.

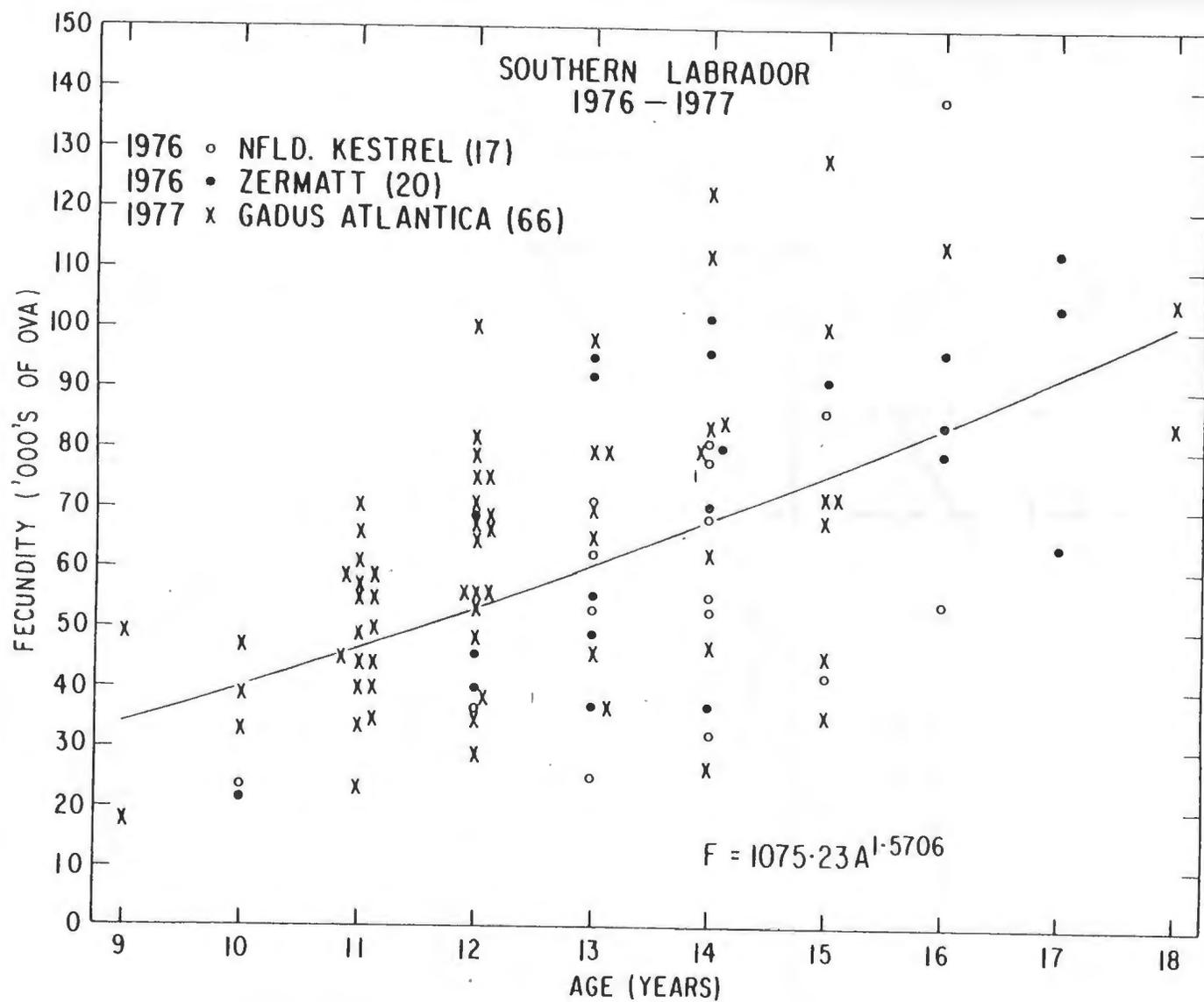


Fig. 29. Relationship of fecundity to age for Greenland halibut from southern Labrador 1976-77.

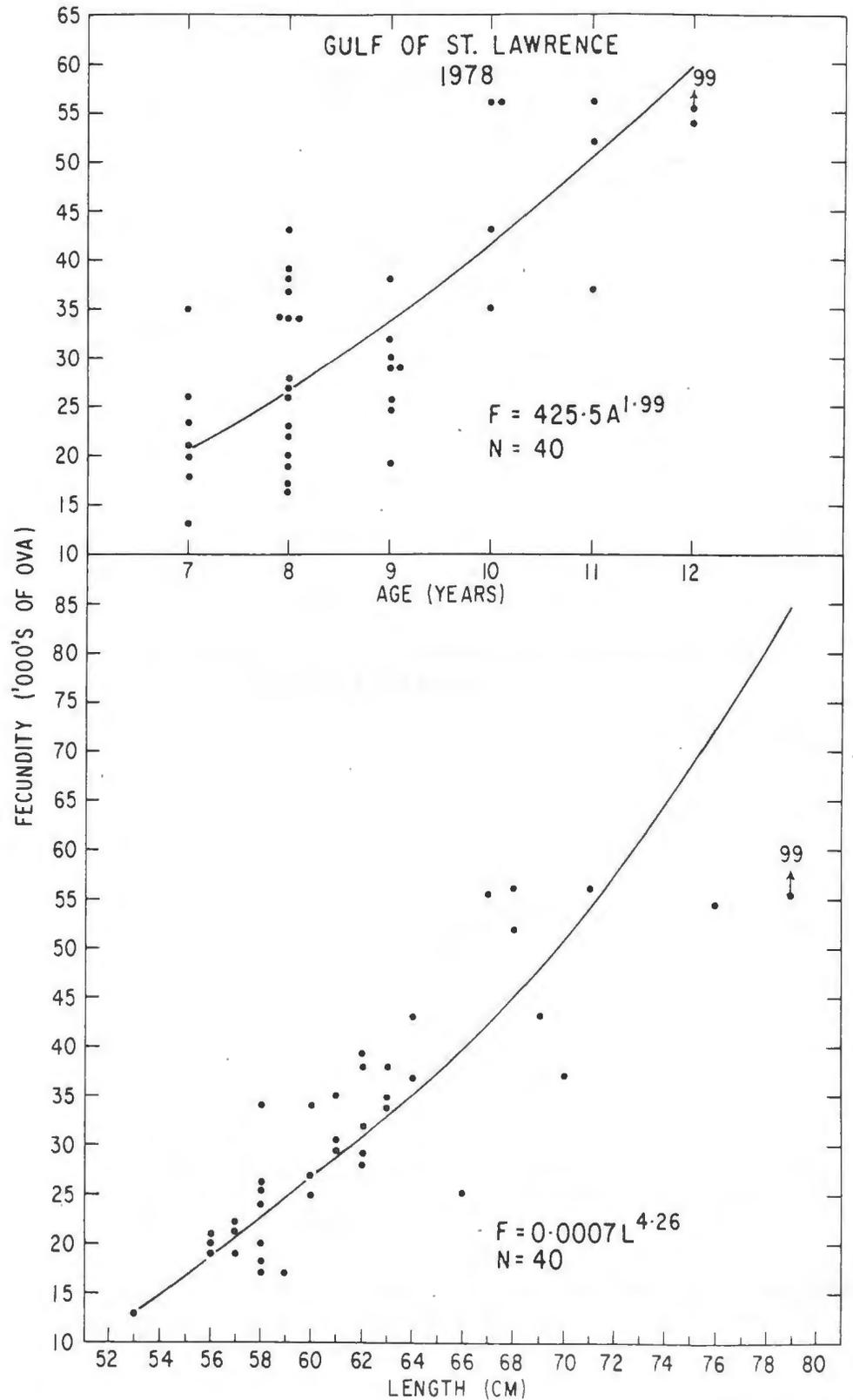


Fig. 30. Relationship of fecundity to length and age for Greenland halibut from Southeastern Gulf of St. Lawrence, 1978.

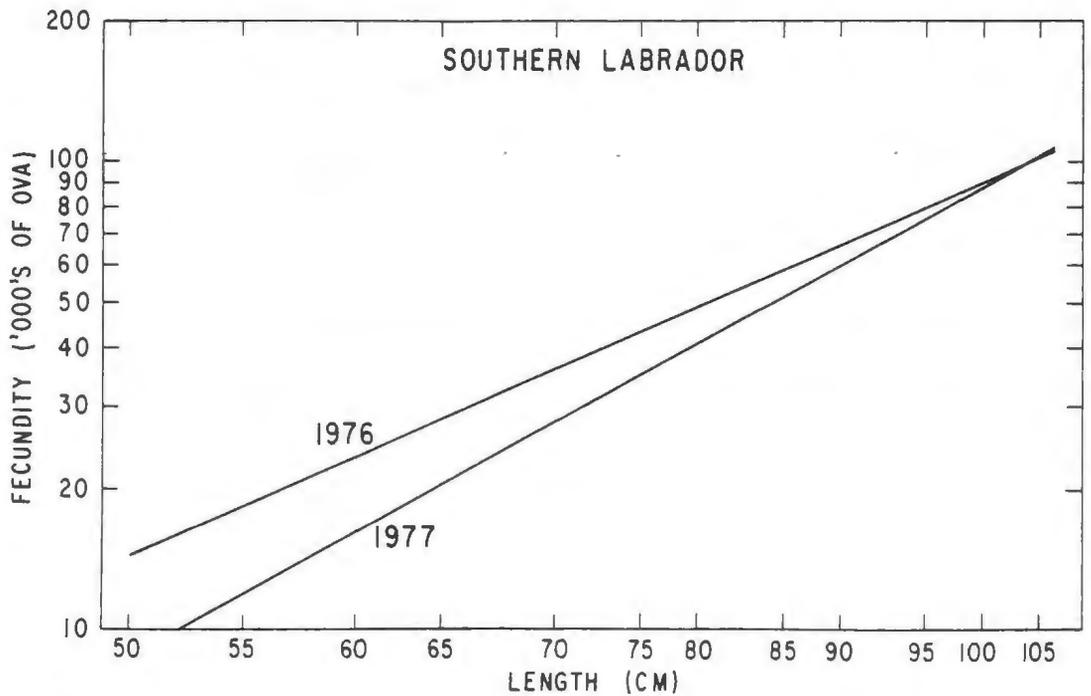
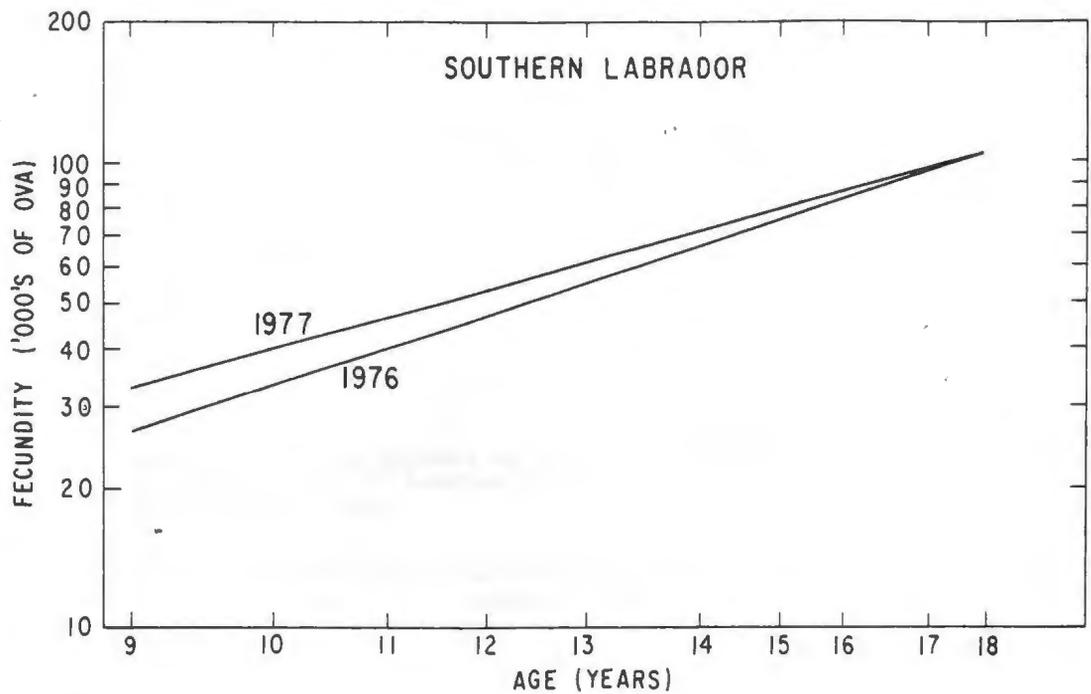


Fig. 31. A comparison of the relationships of log fecundity to log-length and log-age for Greenland halibut of southern Labrador in 1976 and 1977.

Table 9. Regression constants and tests for significance of correlations of fecundity with length and age for Greenland halibut; M = slope and log k = intercept of fitted log-log straight lines.

	Area	Number of fish	M	Log k	r	t	P
Length	Southern Labrador 1976	47	2.667	-0.380	0.594	4.946	<0.01
	Southern Labrador 1977	66	3.398	-1.833	0.733	8.614	<0.01
	Southern Labrador 1976-77	113	3.082	-1.205	0.669	9.505	<0.01
	Southern Gulf of St. Lawrence 1978	40	4.264	-3.152	0.888	11.904	<0.01
Age	Southern Labrador 1976	38	2.010	2.506	0.579	4.262	<0.01
	Southern Labrador 1977	66	1.548	3.072	0.544	5.188	<0.01
	Southern Labrador 1976-77	104	1.571	3.032	0.547	6.597	<0.01
	Southern Gulf of St. Lawrence 1978	40	1.989	2.629	0.721	6.420	<0.01

Table 10. Summary of covariance analysis for regressions of fecundity against length and age for Greenland halibut.

	Areas	Tested	Mean squares		F	P	Mean squares		F	P
			within regression samples	coefficients			common adjusted regression means			
Length 1)	Southern Labrador Southern Gulf of St. Lawrence	1976-77	0.016	0.059	3.72	0.052	0.016	0.342	21.15	<0.001
		1978								
2)	Southern Labrador Southern Labrador	1976 1977	0.019	0.024	1.27	0.261	0.019	0.029	1.55	0.213
Age 1)	Southern Labrador Southern Gulf of St. Lawrence	1976-77	0.022	0.021	0.96	0.669	0.022	0.007	0.03	0.853
		1978								
2)	Southern Labrador Southern Labrador	1976 1977	0.024	0.017	0.72	0.598	0.024	0.046	1.94	0.164

where F = fecundity and A is age (years). For the southeastern Gulf of St. Lawrence the relationship between fecundity and fish age is indicated by the expression:

$$\log F = 1.989 \log A + 2.629$$

Plots of the data and the arithmetic forms of the equations are shown in Fig. 29 and 30 respectively for the southern Labrador area and the southeastern Gulf of St. Lawrence area. The correlation coefficients (r) for both relationships are significant at the 1% level although the correlation coefficients are lower than in the fecundity-length relationship (Table 9).

Analysis of covariance for the 1976 and 1977 fecundity-age data for southern Labrador yielded no significant difference between the regression coefficients or between the adjusted means (Table 10; Fig. 31). A similar analysis of the fecundity-age relationships for southern Labrador in 1976-77 combined and for the southeastern Gulf of St. Lawrence, 1978 also produced no significant difference between the regression coefficients or between the adjusted means.

c) Fecundity vs fish length and fish age

Since the fecundity of Greenland halibut appears to be related to both length and age, a multiple correlation analysis was performed in order to determine the relative contributions of length and age to

Table 11. Summary of statistics for multiple correlation of fecundity, age and length of Greenland halibut. X_1 - log fecundity, X_2 - log length and X_3 - log age. Estimating equation $X_1 = a_{1.23} + b_{12.3} X_2 + b_{13.2} X_3$.

		Area	
		Southern Labrador 1976-77	Southern Gulf of St. Lawrence 1978
Number of fish	N	104	40
Coefficient of determination for X_1 and X_2	r_{12}^2	0.522	0.789
Correlation coefficient for X_1 and X_2	r_{12}	0.723	0.888
Coefficient of determination for X_1 and X_3	r_{13}^2	0.299	0.520
Correlation coefficient for X_1 and X_3	r_{13}	0.547	0.721
Coefficient of multiple determination	$r_{1.23}^2$	0.523	0.791
Coefficient of multiple correlation	$r_{1.23}$	0.723	0.889
Coefficient of partial determination	$r_{13.2}^2$	0.002	0.009
	t for $r_{13.2}^2$	0.450	0.580
	P for $r_{13.2}^2$	0.60-0.70	0.50-0.60

variation in fecundity. For data from both geographical areas, the coefficients of determination for log-fecundity and log-length (r^2) are considerably greater than those for log-fecundity and log-age (r_{13}^2) (Table 11). However, when log-length and log-age are considered together in relation to log-fecundity, the coefficients of multiple determination ($r_{1.23}^2$) for both areas are only slightly greater than the simple coefficients for log-fecundity and log-length (r_{12}^2). To determine whether these slight increases were significant, t-tests were applied to the coefficients of partial determination ($r_{13.2}$) which in both cases were not found to be significantly different from zero (Table 11). It was considered therefore that variation in fecundity of Greenland halibut may be adequately explained in terms of length alone.

MIGRATIONS

a) White Bay Tagging

From 266 Greenland halibut tagged in 1969, 41 tags have been returned for a total of 15% return. Of the 41 tag returns, 1 was returned during the same fishing season, 19 in 1970, 13 in 1971, 6 in 1972, 1 in 1974, and 1 in 1976. Almost half of the returns came from the White Bay Area, near the site of the tagging operations (Fig. 33 and 36). Many others were taken eastward in the deep waters of the Notre Dame Channel and Funk Island Deep with the most southerly recapture taken in Trinity Bay

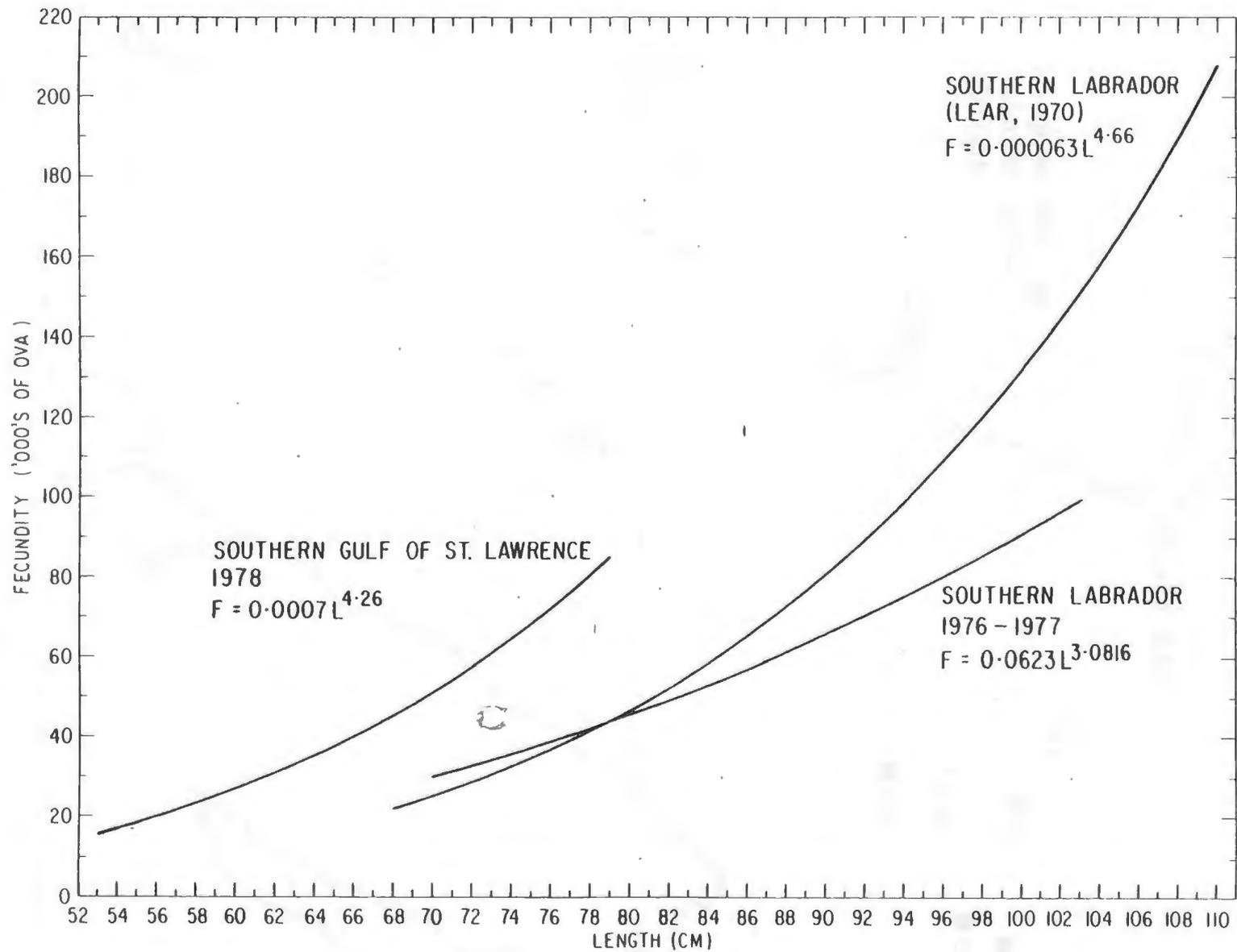


Fig. 32. Comparison of fecundity-length relationships for Greenland halibut from southern Labrador and southeastern Gulf of St. Lawrence.

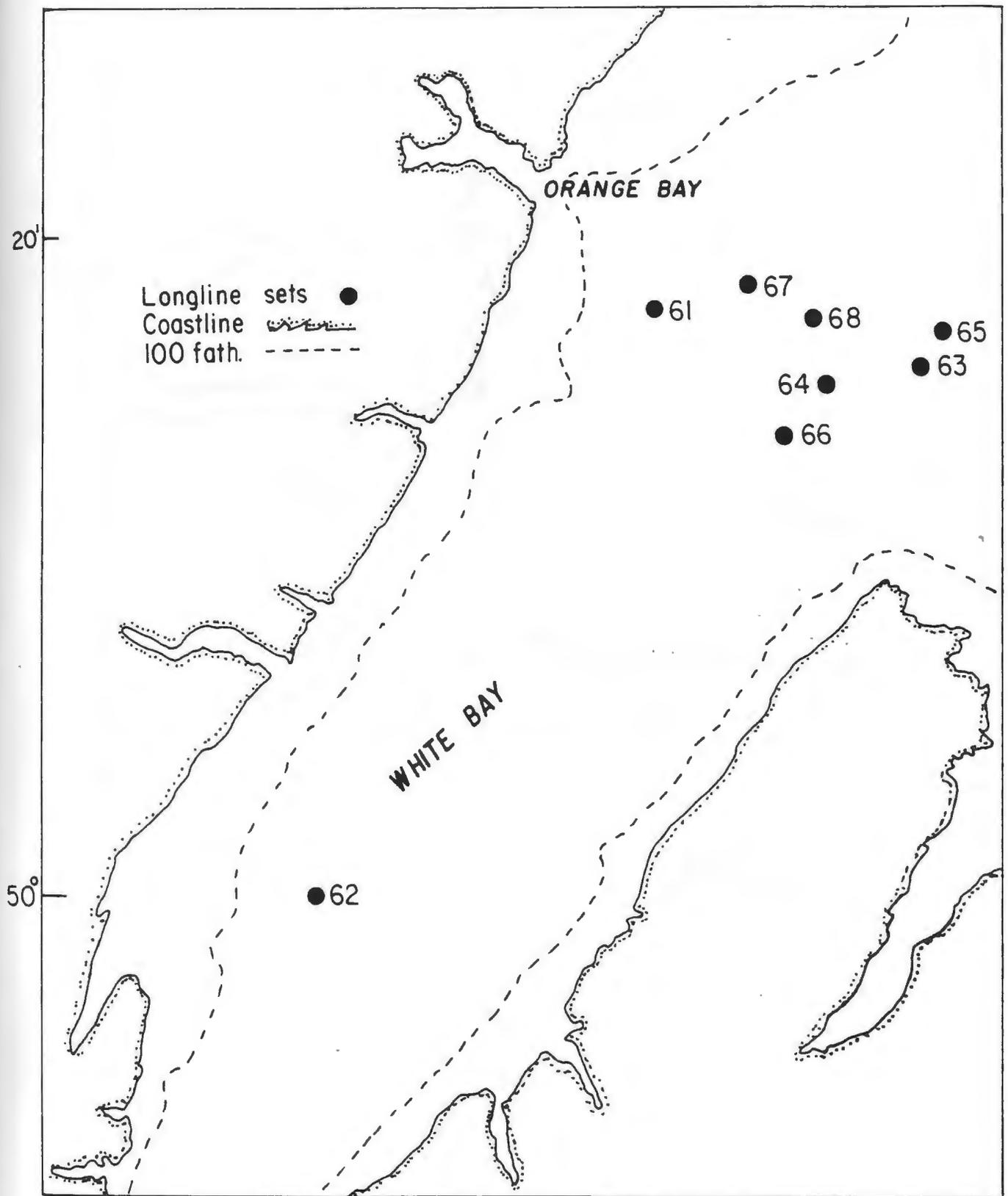


Fig. 33. Greenland halibut tagging positions in White Bay, Newfoundland in October-November, 1969.

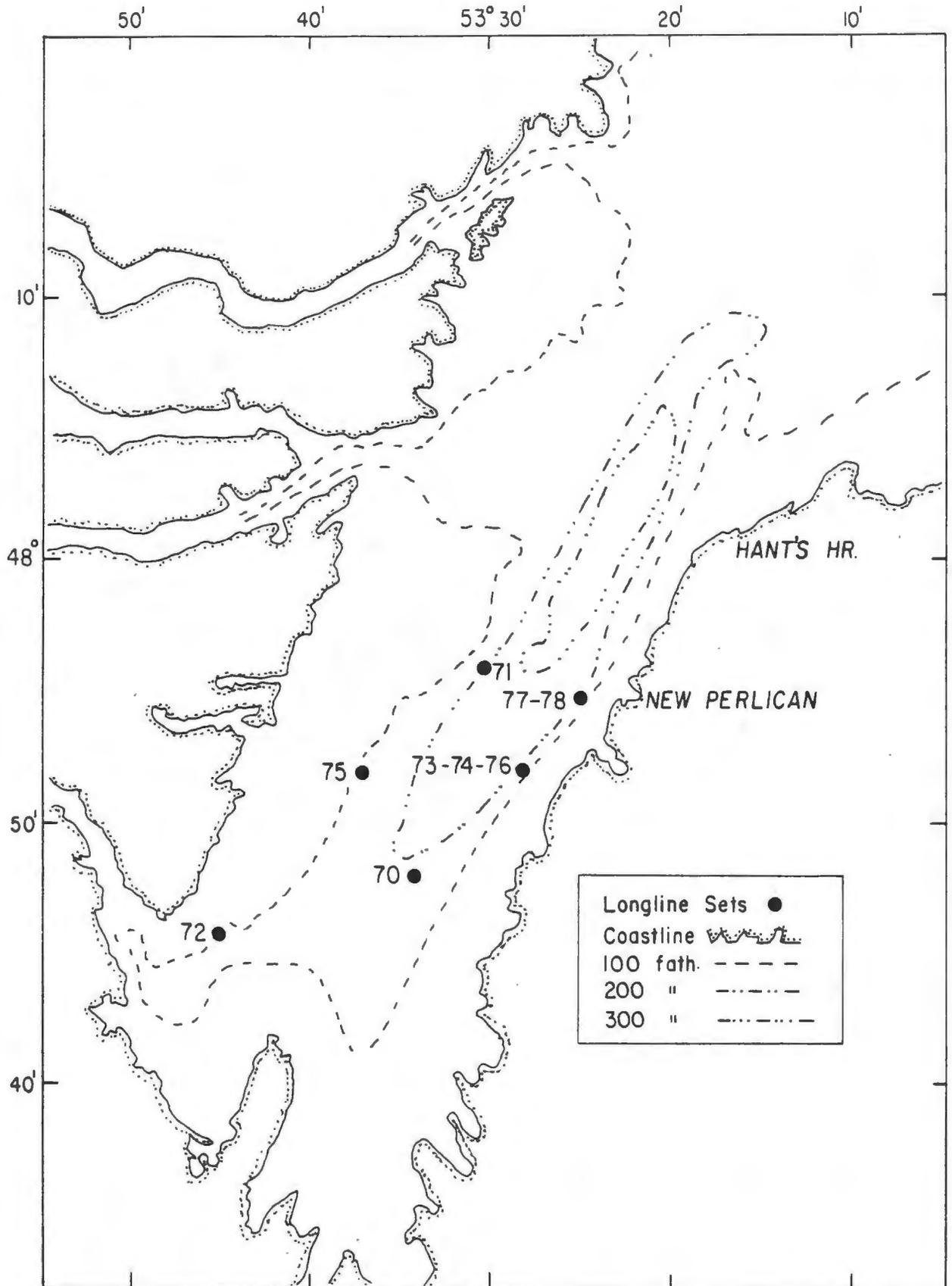


Fig. 34. Greenland Halibut tagging positions in Trinity Bay, Newfoundland in October-November, 1971.

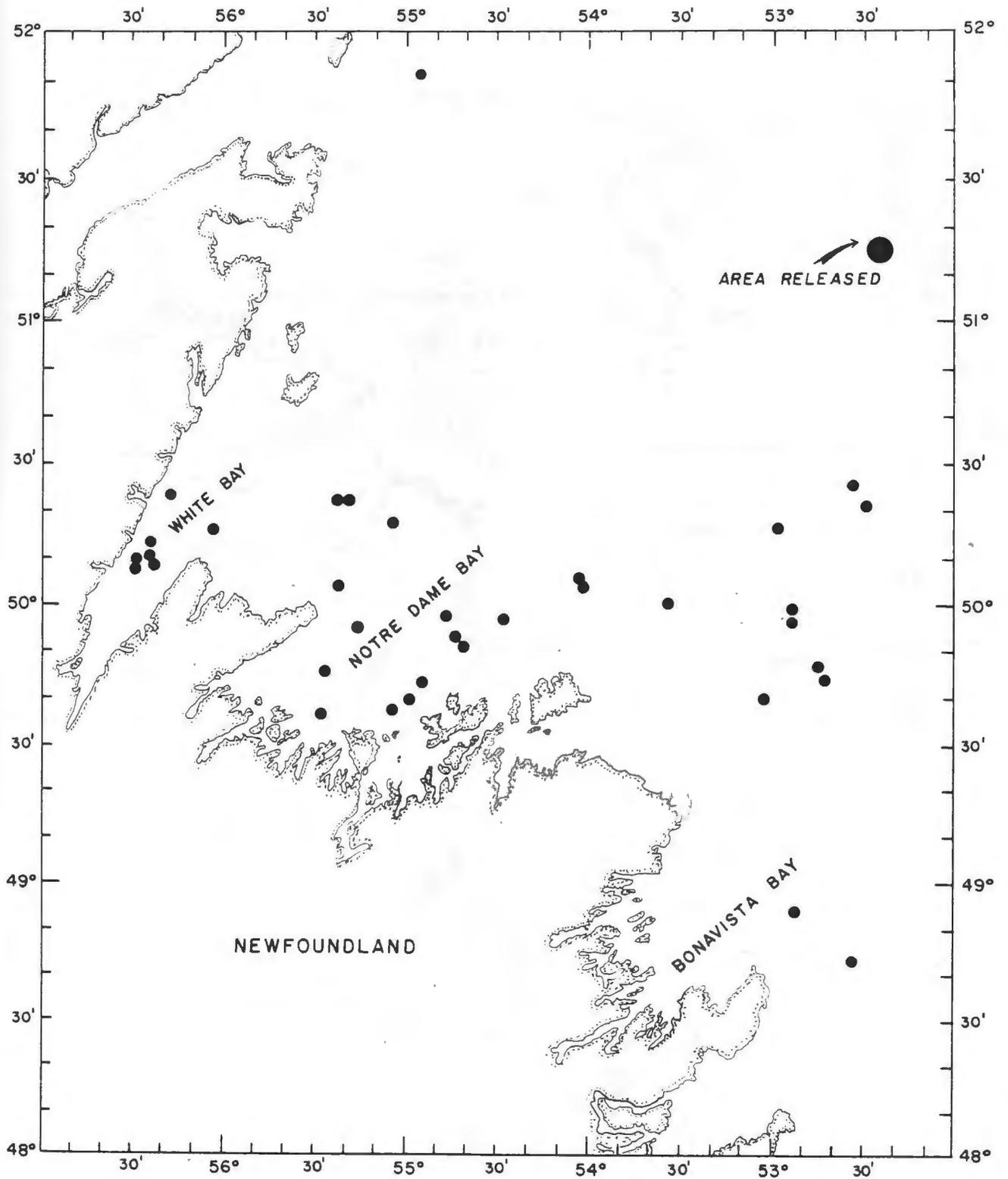


Fig. 35. Site of tagging operations and positions of tag returns for Greenland halibut in the Funk Island Bank area tagging experiment.

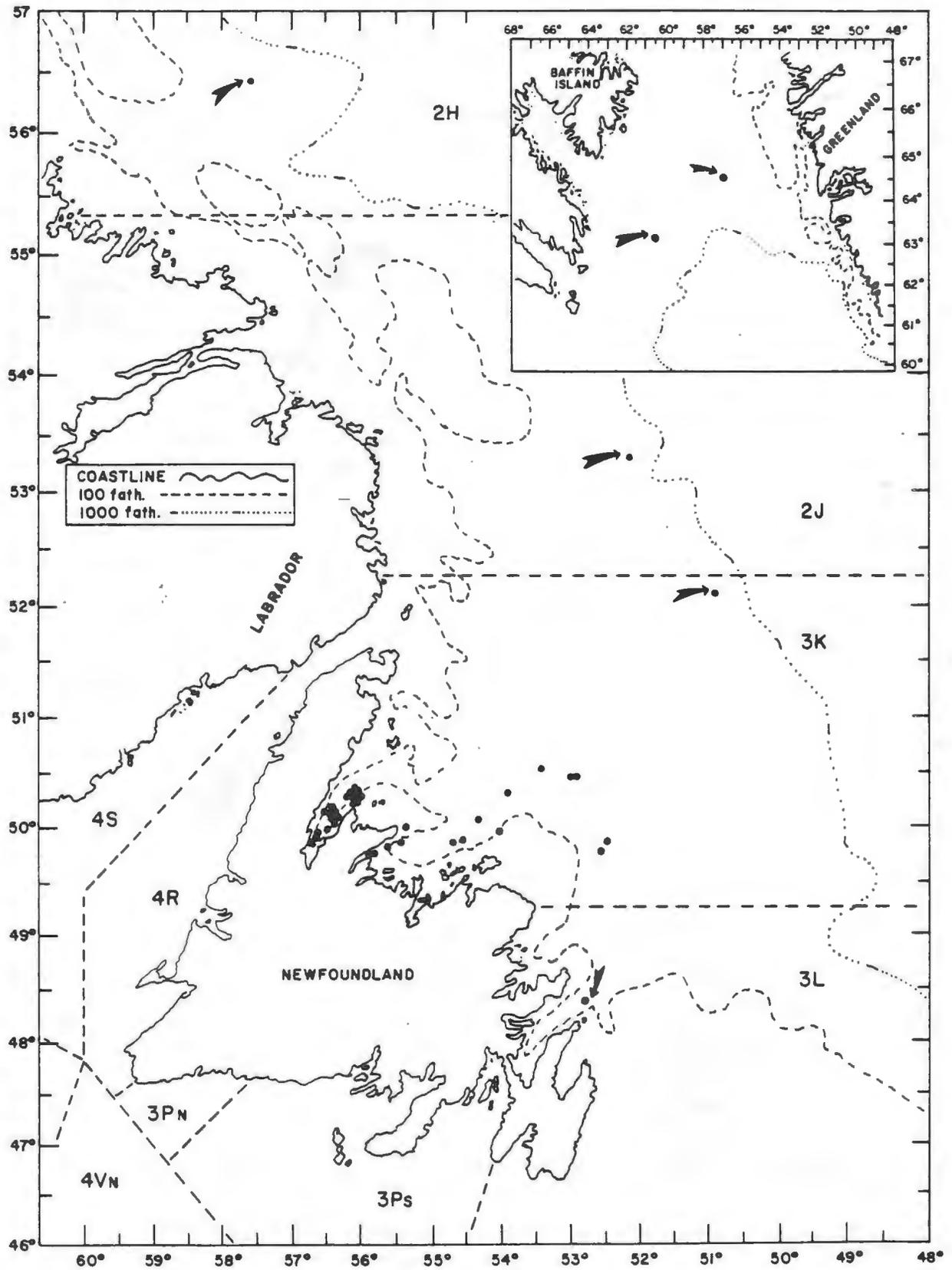


Fig. 36. Positions of the Greenland halibut tag returns for the White Bay tagging experiment October-November, 1969.

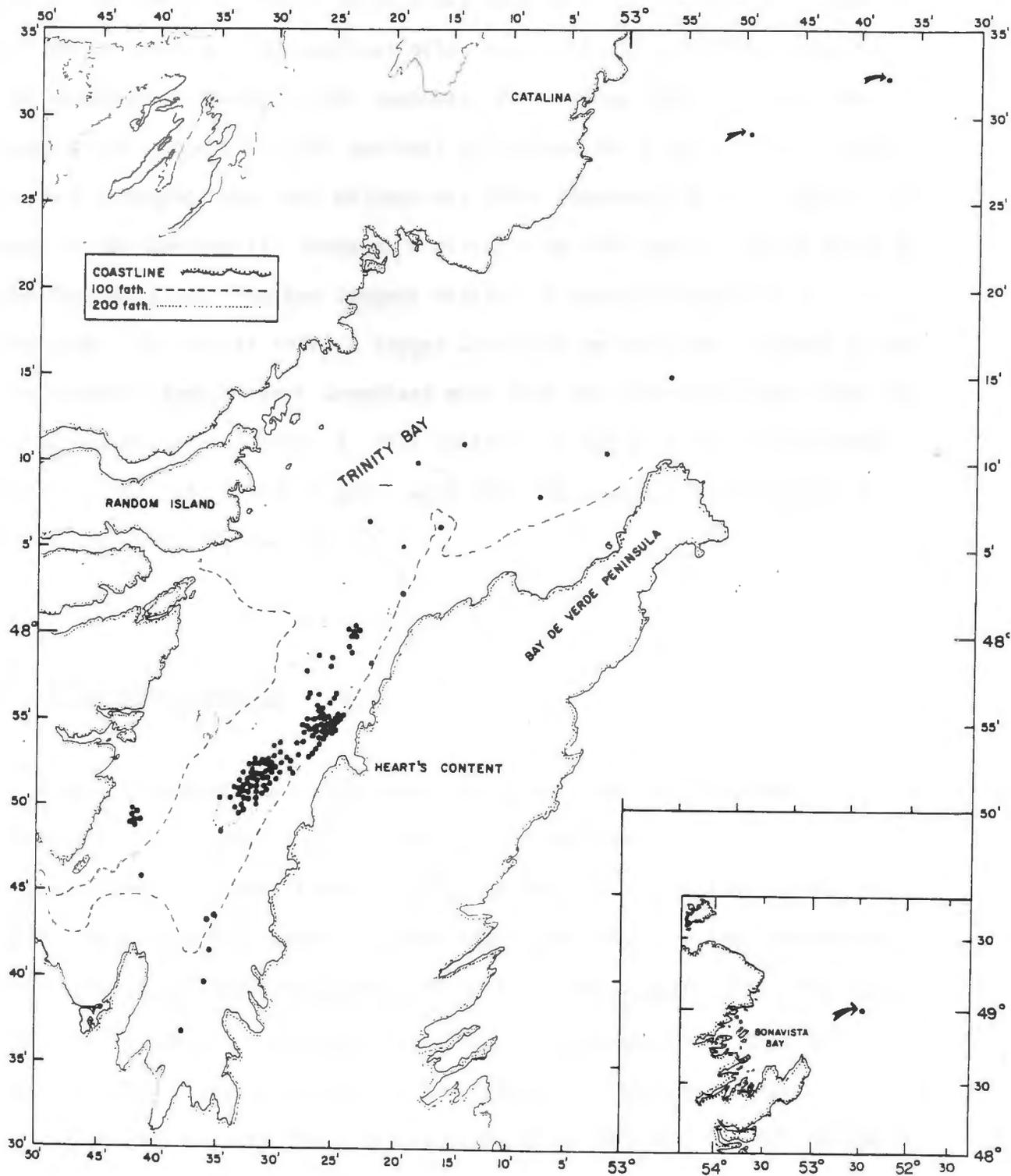


Fig. 37. Positions of the Greenland halibut tag returns for the Trinity Bay tagging experiment October-November, 1971.

2 yrs after being released (Fig. 36), a distance of about 240 nautical miles. On April 2, 1972 a capture was made near the continental slope at 52° north latitude, 230 nautical miles north east of White Bay. Another was captured on March 7, 1971 southeast of Hamilton Bank also near the continental slope about 250 nautical miles from White Bay. In the spring of 1974 a tagged Greenland halibut was taken southeast of Nain Bank at the edge of the continental slope at a distance of 370 nautical miles north of the tagging site. The two longest distance migrations occurred in 1971 and 1976. In July of 1971, a tagged Greenland halibut was captured on the continental slope of West Greenland more than 850 nautical miles north of White Bay while on October 2, 1976 another was taken at the continental slope of the Baffin Bank region, more than 780 nautical miles north of White Bay (Fig. 36, see inset).

b) Trinity Bay tagging

Of 410 Greenland halibut tagged in Trinity Bay in 1971, 145 recaptures were reported for a total of 35% returned (Fig. 37). Of the 145 recaptures, 62 were taken in 1972, 68 in 1973, 14 in 1974, and 1 in 1975. None have been reported since that time. Most of the recaptures from this study were taken within 50 miles of the tagging site with only 3 tag returns reported outside Trinity Bay. These were less than 100 nautical miles from the tagging site (Fig. 37). The most distant recapture from the tagging site was reported on October 10, 1972 at the mouth of Bonavista Bay at 49° north latitude.

c) Funk Island Bank tagging

There were 2976 Greenland halibut tagged during this study and only 37 have yet been returned for a total of just over 1% (Fig. 35). Of these, 23 tags were returned in 1979 and 14 returned in 1980. Most of these returns were taken in the near shore gillnet fishery of White Bay, Notre Dame Bay, Funk Islands east with two recaptured in the Bonavista Bay area in July 1979 and October 16, 1980. The most northerly recapture was just east of Belle Isle on October 26, 1979. There were no reported tag returns east or northeast of the tagging site.

DISCUSSION

DISTRIBUTION

Baffin, Labrador, and eastern Newfoundland

The Greenland halibut is widely distributed along the Baffin Coast, Labrador and eastern Newfoundland to the northern slopes of the Grand Bank. The areas of highest abundance are generally associated with the deeper waters along the continental slope as well as the deep channels running between the fishing banks. The areas of greatest abundance were found in the northern Labrador areas of Hopedale Channel and Cartwright Channel (Fig. 1). Bowering and Parsons (1981) associated these areas of

high abundance of Greenland halibut with the main fishing grounds of the pink shrimp (Pandalus borealis) on which these fish were feeding heavily. Jensen (1935) and Smidt (1969) also found this to be the case for the West Greenland area where the pink shrimp is the most important food item in the diet of Greenland halibut. They found that high abundance of Greenland halibut was always associated with high abundance of pink shrimp. The Greenland halibut is also prevalent in the Hawke Channel area of southern Labrador which is also the locality of a commercial concentration of pink shrimp (Parsons et al. 1981) although to a lesser extent than the more northerly areas. The highest abundance in the more southerly area occurred in White Bay and Notre Dame Bay. In this area the main food item in the diet of Greenland halibut is the capelin (Mallotus villosus) (Lear MS 1970) and areas of high abundance may be associated with the large concentrations of capelin in these areas as reported by Pinhorn (1976). Greenland halibut abundance diminishes very quickly near the Grand Bank area particularly in the shallow waters at the top of the bank where bottom temperatures are often less than -1°C . Templeman (1965, 1973) reported that large numbers of Greenland halibut were killed in Trinity Bay in 1964 and suggested that they probably died while pursuing capelin into waters of intermediate depths where temperatures were below -1°C . If this is the case, it is unlikely Greenland halibut would inhabit the Grand Bank at such low temperatures.

Bowering (1977), Chumakov (1975) and Zilanov et al. (1976) found that Greenland halibut inhabiting the continental shelf of Labrador and

eastern Newfoundland and deep bays of eastern Newfoundland were mostly immature. Most mature fish were found further to the north and in deeper water. This would explain why the larger fish in the frequency distributions are found in deeper water and to the north (Fig. 11 to 16) since the larger fish are obviously more likely to be maturing. Spawning concentrations or fully mature fish have not been observed in these southern areas and it has been suggested by these authors that since Greenland halibut inhabiting this portion of the range do not reproduce here, it may be assumed that these fish migrate for spawning to the Davis Strait area when they approach maturity. Jensen (1935) and Smidt (1969) have also found that Greenland halibut in the West Greenland area do not spawn in the fjords or on the fishing banks. They migrate south of the deep ridge between Canada and Greenland at about 67° north latitude where water temperatures are more conducive to spawning (Jensen 1935; Smidt 1969; Templeman 1973). According to Smidt (1969) and Atkinson et al. (1981) 1-yr-old Greenland halibut are very abundant west of Disko Island. The vast shallow areas from 200-250 m northwest and southwest of Disko Bay are regarded as important nursery grounds from where the fish stocks of northern Greenland districts are recruited. Accordingly, large numbers of these young fish probably move south and spend much of their early life in the Baffin Bank area. This would be supported in part by the extremely high abundance of young fish shown in the frequency distributions for Div. 0B (Fig. 11). Bowering (1979a) reported research vessel catches using shrimp trawls in Div. 0B in 1978 where more than 80% of the Greenland halibut catches were comprised of 1-yr-old fish.

It has been hypothesized by Templeman (1973), Chumakov (1975) and Atkinson et al. (1981) that because of the southward movement of the Labrador Current the young Greenland halibut from the north are led into the deep bays along the east coast of Newfoundland and along the continental shelf and slope. The wide continental shelf in the southern Labrador and eastern Newfoundland area which contains many deep channels and these deep east coast Newfoundland bays would be suitable areas for these fish. Bottom temperatures in these areas would be lower than at similar depths along the continental slope due to projections of the cold current. However, it is likely that most maturing fish would migrate from these colder areas northward to the deep warmer waters of the continental slope (Templeman 1973) where temperatures are more suitable for spawning (Jensen 1935; Smidt 1969).

Gulf of St. Lawrence

Greenland halibut are generally distributed throughout the northern portion of the Gulf of St. Lawrence in comparatively small quantities except for the deep area in the southern Esquiman Channel and Laurentian Channel. Since the surveys from which the distribution charts have been constructed are conducted in early winter, these areas of high concentration are assumed to be a spawning concentration. This is similar to that reported in the same area for witch flounder (Glyptocephalus cynoglossus) and cod (Gadus morhua) by Bowering (1978e, 1979c, 1981a), Bowering and Brodie (1980) and Lussia-Berdou (1979). Investigative

surveys carried out during the summer (Tremblay and Axelsen 1980, 1981) have indicated however, that the distribution during summer is considerably different. According to these authors the Greenland halibut re-distribute themselves after spawning to an area along the northern coast of Anticosti Island. High concentrations at this time are also found to the southwest of Anticosti Island substantial quantities found in the mouth of the St. Lawrence River.

It was shown by Bowering (1979d, 1980a, 1981b) that there was a substantial increase in the commercial abundance of Greenland halibut in the Gulf of St. Lawrence over the last several years. He related it to very strong year classes similar to the strong year classes found in the Labrador and eastern Newfoundland areas (Bowering 1980b; Bowering and Brodie 1981). Bowering (1980a) found that there were few small Greenland halibut (less than 26 cm) appearing in the length frequency distributions from the Gulf of St. Lawrence as evidenced in Fig. 19. It was obvious from the frequency distributions from Labrador and eastern Newfoundland however that the research vessel gear could catch small fish (Fig. 18). It was also evident that Greenland halibut disappeared from the length frequency distributions at relatively small sizes in comparison to eastern areas. Because of these factors, Bowering (1980a, 1981b) suggested that the recent high abundance of Greenland halibut may be a result of immigration of these large year classes from the Labrador area to the Gulf of St. Lawrence through the Strait of Belle Isle. It was also suggested that when these immigrants approach maturity they emigrate from the Gulf of St. Lawrence which would explain the disappearance of the older fish

from the Gulf of St. Lawrence area. However, Tremblay and Axelsen (1981) recently indicated from research vessel surveys north of Anticosti Island the presence of a very strong year class at age 1 and have suggested that this might be a nursery area for the Gulf of St. Lawrence. Based upon the distribution patterns it is evident that a self reproducing population of Greenland halibut probably exists in the Gulf of St. Lawrence. Whether immigration to and emigration from the Gulf of St. Lawrence occurs as suggested by Bowering (1980a, 1981b) is still speculative.

AGE AND GROWTH

Age composition

Age composition of Greenland halibut varied throughout the range under consideration. It was evident from the age distribution as with length distribution (since age is a function of length) that the older age fish were predominant in the deeper waters and were more abundant in the more northerly areas. The large numbers of young fish in Baffin Bank area may suggest that this area is a nursery area as previously mentioned. Significant numbers of large Greenland halibut were not encountered in the Baffin Bank survey (probably because of ineffectiveness of fishing gear at great depths). Chumakov (1975), however, found that the oldest

individuals throughout the range were located in continental slope area greater than 800 m in the northern region of Baffin Bank which he considered to be on or near the spawning grounds. Berth et al. (1979) in reporting results of a survey for Greenland halibut throughout the same area in December of 1978 also found that young Greenland halibut increased in abundance with increased distance from the more northerly Labrador area to the eastern Newfoundland area. Consequently, it follows that the abundance of older individuals increased with increased distance from the more southerly areas, results similar to that reported here. Berth (pers. comm.) was also of the opinion that because of this change in age distribution, Greenland halibut migrated northward into the Baffin Island-Davis Strait area for spawning. Subsequently, the pelagic larvae were carried from here by the polar currents to the banks of West Greenland and eastern Canada.

The absence of Greenland halibut less than age 4 from the Gulf of St. Lawrence is difficult to explain. It may be that the young fish move to a different area than that surveyed in winter or for some unknown reason are inaccessible to the fishing gear. If there is immigration into the Gulf of St. Lawrence from outside as suggested by Bowering (1980a, 1981b), it may not occur in the very young age groups. The reporting of numerous very small Greenland halibut in summer of 1980 by Tremblay and Axelsen (1981) may simply be the result of a very strong anomalous year class produced by a small resident population of Greenland halibut within the Gulf of St. Lawrence. Therefore most recruitment would have to come from elsewhere.

GROWTH PATTERNS

Differences in growth rate between males and females are generally the result of genetics which determine the physiology and behaviour of the fish rather than the result of the environment (Alm 1959), since presumably the males and females are subjected to the same set of environmental conditions. These differences are generally the result of a diversion of energy towards the formation of the sex products with less energy available for growth. Bowering (1978b), in studying growth in Greenland halibut, expressed growth in terms of linear least squares regression since most fish in the study were immature and showed little or no diversion in growth patterns of males and females. It was considered that the study only dealt with that section of the growth curve below the inflection point and consequently estimates of L_{∞} for the von Bertalanffy growth equation were not realistic and could not be used. Results of back-calculated growth curves up to age 5 in this study resulted in no statistical difference between males and females (Fig. 22) which in essence would agree with the above statement of Alm (1959) and the findings of Bowering (1978b). On the other hand, there appears to be a divergence of growth pattern between males and females as shown from the growth curves calculated from the empirical observations in Fig. 20 with growth curves of the males lower beyond age 3-5 than females for all areas. However, the unweighted data points indicate that differences would not be readily observed until in the 8-12 yr-old range. While power curves were used to fit these data with high correlations, linear least squares regression performed on the same data resulted in higher

correlations in all cases, except for the Gulf of St. Lawrence data, giving results very similar to that of Bowering (1978b). It would imply that with the possible exception of the Gulf of St. Lawrence data the influence of sexual maturity on growth patterns in these areas was not apparent.

Covariance analyses on the back-calculated data indicated that the growth rate throughout the entire area with the exception of the most northerly Baffin Bank area was the same. The growth rate of the Baffin Bank data was considerably lower than all other areas. Analysis of the adjusted means indicated that the average size at age for the Gulf of St. Lawrence data was significantly higher than all other areas implying a substantially higher growth rate in the first year of life. While the Nain Bank size at age was significantly different from all areas it did not appear to vary greatly from the adjacent Labrador and eastern Newfoundland areas. Since the differences between growth patterns from Saglek Bank to the northern Grand Bank are not totally variable, they may be a result of the location and behaviour of the fish in the first year of life throughout the range.

There are many factors which influence the growth rate of fishes, the most important being food supply (Brown 1957) for only when sufficient food is available can a fish attain its maximum size for existing environmental conditions. Factors such as temperature, density-dependence and abundance of competing species are generally the result of their

effect upon food supply. Since there appears to be a general increase in average size at age from north to south, temperature may be a contributing factor. Templeman (1964) indicated that the volume of warmer water increased from north to south because of the direction of the Labrador current thereby making it possible for water temperature to have an influence on growth pattern (Lear MS 1970). Any influence here however, would have to be particularly related to the first year of life since older Greenland halibut are known to migrate over long distances (Nizovtsev 1970; Chumakov 1970; Sigurdsson 1977) as well as vertically in the water column (Lear MS 1970; de Groot 1970) making them subject to a wide variety of temperatures. When relating growth to environmental conditions other conditions such as reductions or increases in stock size, removal of competing species such as cod and removals of food species such as shrimp and capelin must be considered since any combination of these may affect growth relationships. If the growth patterns presented here had included the mature portion of the populations one may hypothesize that the Gulf of St. Lawrence and Baffin Bank may support separate stocks with a single stock in the Labrador-eastern Newfoundland areas neither of which would necessarily be exclusive of the other. However, differences in growth patterns of the immature individuals alone may simply be a result of the conditions where they grew prior to maturity. Upon approaching maturity they could all still return to a common breeding area and be part of the same original stock.

SEXUAL MATURITY

It has been pointed out in numerous publications (Chumakov 1975; Zilanov et al. 1976; Templeman 1973; Berth et al. 1979; Bowering 1977-81) that the commercial fisheries for Greenland halibut on the banks and slopes in the Northwest Atlantic are mainly comprised of immature fish. The scarcity of mature fish in the commercial as well as research catches led to consideration of the possible misinterpretation of maturity condition of the ovaries, particularly by visual observation. Walsh and Bowering (1981) suggested that recovery from spent condition may have been so rapid that ovaries of previously spawned fish may be designated visually as immature. Since the accuracy of determining maturity stages through field observations is essential to the understanding of the maturation cycle and onset of first maturity, they undertook to compare the observations of oogenesis made in the field with a more accurate analysis based on histological studies. The methods were similar to the methods described by Federov (1968) for Greenland halibut in the Barents Sea. Walsh and Bowering (1981) concluded that while the accuracy of visual observations of sexual maturity of female Greenland halibut may be enhanced by histological analysis, field observations on the onset of first maturity were adequate. Maturity of male Greenland halibut was not included in the analysis here, since it was extremely difficult to determine whether males with growing gonads were maturing for the upcoming spawning season or later. This uncertainty was probably a result of the timing of the surveys when milt was not present in the testes and previously spawned fish may have been fully recovered.

The results of probit transformation analysis here indicated that the 50% maturity level (M_{50}) was reached very quickly for the Gulf of St. Lawrence fish whereas there was a clinal trend of increasing M_{50} particularly for fish from northern Labrador to the southern Labrador-northeast Newfoundland Shelf area. Covariance analysis showed that the rate of approach to sexual maturity did not differ throughout the Labrador-eastern Newfoundland area. The Baffin Bank and Gulf of St. Lawrence data differed from some areas and not from others. The most noticeable results of the analysis were the highly significant differences in the intercepts of the fitted lines which indicated significant statistical differences in the lengths and ages at M_{50} for all areas.

Molander (1925) in studying European plaice and flounder in the Baltic, found that with increased growth rate, maturity appeared at a lower age but at a greater length, implying that maturity was at a greater age when growth rate was poor. Bowering (1976) found similar results for witch flounder in the Northwest Atlantic. Pitt (1975) indicated for American plaice that faster-growing fish matured at an earlier age but all matured at approximately the same size suggesting that sexual maturity is probably dependent on size and indirectly on growth rate rather than age. From experimental research on sexual maturity of fishes, Alm (1959) concluded that "with an initially good growth rate maturity is reached at an earlier age than an initially poor growth rate. The metabolic processes are probably relatively fast with good growth rate. Consequently, differentiation processes in the gonads and maturity apparently occur much earlier, the opposite being the result of poor

growth rate". The results here support in part the conclusions of Alm (1959) where maturity at an earlier age than everywhere else is evident for the Gulf of St. Lawrence data which also exhibits the fastest initial growth rate. The Baffin Bank data on the other hand, exhibits the slowest growth rate and maturity is reached at a much later age than that of the Gulf of St. Lawrence Greenland halibut. The initial growth rate of the Labrador-eastern Newfoundland areas have been shown to be very similar occurring somewhere between those of the Baffin Bank and the Gulf of St. Lawrence. However, the size and age at maturity decrease significantly going from south to north contrary to the above theory. The reason for this may be explained if a spawning migration northward occurs. If this is the case then it would be expected that the proportion of maturing individuals in catches at any particular size up to 100% mature would be greater moving progressively northward. This would result in a shifting of the maturity curve to the left going north and subsequently producing lower values of M_{50} . This would further suggest that in the Labrador area the value of M_{50} for Saglek Bank may be in fact more representative of the entire Labrador-eastern Newfoundland area. The value of M_{50} for Saglek Bank falls between that of the Gulf of St. Lawrence and Baffin Bank data as does the initial growth rate. This would be in agreement with Alm's (1959) theory of the relationship of maturity and initial growth rate.

FECUNDITY

In studying the fecundity of the North Sea plaice (Pleuronectes platessa), Simpson (1951) expressed the relationship between fecundity and length by the "cube law" $F = LK^3$. Other investigators such as Bagenal (1963), Pitt (1964), May (1967) and Bowering (1978a) in studying fecundity of European witch, American plaice, cod and witch flounder, respectively, used this relationship and found that more often than not the exponent of the equation fell between 3 and 4. This was true for both data sets from southern Labrador however the exponent for the southeastern Gulf of St. Lawrence data was 4.26. The exponent for age-fecundity is generally in the vicinity of 2 which is similar to that shown here. Fecundity in Greenland halibut from southern Labrador and southeastern Gulf of St. Lawrence was found to be related more to body length than age, results also similar to fecundity studies of Bagenal (1963), Pitt (1964), May (1967), Hodder (1963) and Bowering (1978a).

Fecundity in fish of the same species has been reported to vary from one geographical area to another. Simpson (1951) found for North Sea plaice of the same body length that the fast-growing fish in the Flamborough area had a higher fecundity than the slow-growing fish from the Southern Bight. Bowering (1978a) also found significant variation in fecundity of witch flounder from three adjacent areas in the Northwest Atlantic (i.e. northern Grand Bank, southern Grand Bank and St. Pierre Bank). The present study shows that the fecundity-length relationship

for Greenland halibut from southern Labrador is significantly different from that for southeastern Gulf of St. Lawrence fish both in terms of the rate of egg production and the total numbers of eggs produced. This is probably due to the variation in the size at maturity, since it has been shown that female Greenland halibut from the Gulf of St. Lawrence mature at considerably smaller sizes than elsewhere. It is also obvious from Fig. 32 that since the fecundity samples from both areas were collected over the entire size range of the mature females in the catches, Greenland halibut mature at smaller sizes in the southeastern Gulf of St. Lawrence than in southern Labrador. Hodder (1963) showed for haddock (Melanogrammus aeglefinus) of the Grand Bank that fecundity increased with the frequency of spawning. This phenomenon was also found to occur in cod (May 1967) and witch flounder (Bowering 1978a). Since Greenland halibut in the Gulf of St. Lawrence mature at an earlier age, it would be expected that within the length range common to the samples from both areas, i.e. 70-78 cm (Fig. 32), the southeastern Gulf of St. Lawrence fish would be more fecund than the southern Labrador fish because the former would have spawned more often. This was found to be the case here.

No statistical difference was found between the fecundity-age relationships of Greenland halibut in the two areas. Fecundity was found to be related more to length than to age, consequently the greater variation within samples resulted in considerably more overlap of the fecundity-at-age data for both areas than was apparent in the fecundity-at-length data. The effect of variation in fecundity within an age

group was investigated and the results shown in Hodder (1963) and Bowering (1978a) for haddock and witch flounder respectively.

Annual fluctuation in fecundity of Greenland halibut was not apparent in this study of fecundity length and fecundity-age relationships for the southern Labrador area in 1976 and 1977. However, such variation has been reported in many studies of this nature, e.g. by Hodder (1963) for Grand Bank haddock, by Pitt (1964) for American plaice from the Grand Bank and by Bowering (1978a) for witch flounder from St. Pierre Bank and the Grand Bank. Bagenal (1963) from a study of witch flounder in the Firth of Clyde attributed annual fluctuations in fecundity to changes in fishing intensity which in turn affect fecundity through variation in food supply. He also indicated that the pattern of fluctuating fecundity for witch flounder was different than that of the European plaice of the same area and concluded that the variation in fecundity was not related to changes in hydrographic conditions. Hodder (1963) on the other hand, related annual fluctuations in haddock with fluctuations in air and water temperatures. He found that years of unusually low temperature were followed by low fish fecundity 2 years later whereas years of unusually high temperatures were followed by high fish fecundity 2 years later. He suggested that years of low temperature caused crowding which resulted in less food per individual and subsequently less growth and probably less fecundity 2 years later, the opposite being the case for years of high temperatures.

Lear (1970) studied fecundity in Greenland halibut off Labrador and eastern Newfoundland from 45 specimens collected in an area extending from the banks off southern Labrador southward to Notre Dame Bay, Bonavista Bay and Trinity Bay. A comparison of the fecundity-length relationship for the southern Labrador area from the present study with that of Lear (1970) indicates that fecundity in fish greater than 80 cm during 1967-69 was higher than in 1976-77, the exponents of the relationships being 4.66 and 3.08 respectively. Since Lear's (1970) sample included specimens beyond the length range of those used in the present study, it was thought that high fecundity estimates of the very large fish may have caused the higher value of the exponent in the 1967-69 fecundity-length relationship. However, an analysis of the 1967-69 data excluding values for lengths beyond the range of the 1976-77 data, resulted in a higher exponent (5.36). These differences are difficult to explain biologically but may be due to the fact that Lear's (1970) data were derived from only 45 specimens, collected over a period of 3 years and a geographical expanse of about 600 nautical miles. With such a small sample over such a large area, the relationship would be very sensitive to minor fluctuations in the data. However, many changes in population structure have occurred over this period of time and their effects upon fecundity should not be overlooked.

MIGRATIONS

The results of the White Bay tagging study suggest that Greenland halibut migrate from the near shore deep bays of the northeast Newfoundland coast to the deep waters outward towards the continental slope as well as northward as far as Baffin Island and West Greenland. Although information on sex and maturity of these tagged fish was not available it is possible that these fish were part of a spawning migration and, if so, would support previous hypotheses of Templeman (1973), Chumakov (1975), Zilanov et al. (1976) and Bowering (1977) of a northward spawning migration. The tag returned from Baffin Bank in fact was taken from a 10 kg Greenland halibut in excess of 1 m in length which would assuredly have been a mature female.

Long distance migrations of Greenland halibut have been reported on various occasions from other areas. One Greenland halibut tagged at north Iceland in July 1973 was captured 4 months later in the Barents Sea (Sigurdsson 1979). Another tagged from a Soviet Union research trawler off the Icelandic east coast on January 1970 was recaptured in the Barents Sea in August 1972 (Nizovtsev 1974). At least two captures were made in the Faroe Islands area from tagging studies off northeast Iceland and one capture in the Shetland Island area range from tagging studies at northeast Iceland (Sigurdsson 1979). One Greenland halibut tagged in Lichtenau Fjord at southwest Greenland in June 1955 was recaptured off Vestfiridir in northwest Iceland in June 1959, the only known data implying

a connection between the stocks at Iceland and West Greenland (Smidt 1969).

Investigations by Kosier (1970), Chumakov (1969) and Sigurdsson (1979) in the Icelandic region have shown through tagging studies that Greenland halibut in that area perform long distance spawning migrations as well as feeding migrations. During the summer feeding period the Greenland halibut remained near the point of release and that a prespawning migration to the west and northwest into the Denmark Strait (the assumed spawning grounds) began at the end of September. Having spawned in April-May, the fish, migrating eastward, returned to their summer feeding grounds north of Iceland. Chumakov (1969) reported dense concentrations of Greenland halibut moving eastward from the deepwater trench between Greenland and Iceland. Catches were found to fluctuate widely because the fish were migrating to the summer feeding grounds and consisted entirely of post-spawning fish.

Jensen (1935) and Smidt (1969) found a similar situation in West Greenland. Maturing Greenland halibut migrate from the fjords of West Greenland to the south of the Davis Strait ridge which extends across from Greenland to Canada. Here they spawn in waters of 600-1000 m in depth. After spawning, there is a migration towards the coast and into the fjords where the summer fishery consists mainly of post-spawning Greenland halibut.

Indications from Bowering (1980a, 1981b) and Tremblay and Axelsen (1980, 1981) suggest a similar occurrence in the Gulf of St. Lawrence. Bowering (1980a, 1981b) found from the commercial Newfoundland trawler fishery and research vessel surveys that a pre-spawning concentration of Greenland halibut occurs in the southeast Laurentian Channel in winter where the Newfoundland trawler fishery is located. Tremblay and Axelsen (1980, 1981) found that in summertime Greenland halibut are more concentrated in the western part of the Gulf of St. Lawrence and are found associated with the shrimp fishery in this area. It is probable that this indicates a feeding migration since Greenland halibut feed heavily on shrimp (Smidt 1969; Bowering and Parsons 1981).

Results from the Trinity Bay tagging study did not yield much in the way of distant migrations with most tags recovered near the tagging site. However, for the three recaptures outside Trinity Bay there was a indication that these fish moved in a northerly direction.

The results of the Funk Island Bank tagging study (the only offshore tagging study) clearly indicate an inward migration from the offshore area to the nearshore deep bays along the northeast Newfoundland coast. Most tag returns were from the summer gillnet fishery for Greenland halibut which occurs in the deep nearshore bays and channels from southern Labrador to Trinity Bay. The inward movement may be a feeding migration similar to that reported for cod in the same area (Templeman 1979). Here both species have been reported to feed heavily on capelin (Lear MS 1970;

Templeman 1979) and to follow them towards coastal areas in summer. Most of the Greenland halibut in this study were relatively small and were not likely to be maturing. Consequently, it is unlikely that they would move further north in a spawning migration at this time. However, the large deep sea offshore fishery in the Labrador area for Greenland halibut has decreased substantially over the past few years (Bowering 1980b; Bowering and Brodie 1981) and any Greenland halibut that may have migrated northward there may well have gone undetected.

SUMMARY AND CONCLUSIONS

Geographically, Greenland halibut in the eastern area are distributed in abundance from Baffin Bank southward to the northern slopes of the Grand Bank with no obvious break in continuity. They are generally associated with the deep channels around the fishing banks and the deeper areas of the continental slope (Fig. 5 and 6). There is a general increase in average size moving from shallower to deeper water and an increase in abundance of larger fish moving progressively northward. In the Gulf of St. Lawrence, they form a prespawning concentration in wintertime south of St. Georges' Bay, apparently followed by a feeding migration in summer to the north of Anticosti Island and in the mouth of the St. Lawrence River (Fig. 8 and 9). Since the maximum depth in the Gulf area is less than 500 m, changes in the distribution of size over depth is not pronounced.

Age composition in the eastern area ranged up to 14 years for males and up to 18 years for females, however, most of the catches were of fish less than 10 years old. There was a predominance of older fish in the more northerly areas as well as in deeper water. This is believed to be related to a northward migration of maturing fish into deeper warmer water. In the Gulf of St. Lawrence, males beyond age 9 and females beyond age 12 were completely absent from the catch. It is not fully clear if this is the result of emigration of older fish from the area or mortality due to early maturity. The empirical growth curves for all areas show females growing faster than the males, particularly in the older ages. This is presumably due to earlier maturity in the males. Unfortunately, statistical comparison of total growth among areas was impossible due to lack of standardization procedures. Statistical treatment of back-calculated growth curves up to age 5 indicated no difference between males and females. No statistical difference was found in the growth rate of fish of the Labrador and eastern Newfoundland areas. However, the Gulf of St. Lawrence fish exhibited the fastest growth rate and Baffin Bank fish the slowest throughout the range, both statistically significant (see Table 6).

Maturity of female Greenland halibut occurred at a much smaller size and faster rate in the Gulf of St. Lawrence than in all other areas. In the Labrador-eastern Newfoundland area the onset of maturity occurred at smaller sizes, moving progressively northward. Since the growth rates of fish throughout this area are the same it is believed that this shift of

the maturity curves is a result of mature fish migrating towards the spawning ground. The Baffin Bank maturity curve on the other hand is similar to that of Nain Bank in the mid-Labrador area. However, since Baffin Bank is so near the presumed spawning ground and heavily influenced by the cold polar current, it is likely that most maturing fish are in deep warmer water outside the fishable range. Consequently, the curve may be biased to the right (see Fig. 25 and Table 8).

Fecundity of Greenland halibut was found to be related to both length and age but could be adequately explained in terms of length alone. Greenland halibut in the Gulf of St. Lawrence were found to be more fecund than those in southern Labrador. They were also found to reproduce at a much smaller size as evident from the maturity curves (Fig. 32).

Tagging studies suggested that Greenland halibut tagged in the eastern Newfoundland inshore eventually migrate towards the edge of the continental shelf and northward as far as Davis Strait (Fig. 36). These fish are in a maturing condition and are migrating to spawning grounds in the Davis Strait area. An offshore tagging study in the same general area showed that Greenland halibut migrate towards shore in summer thought to be a feeding migration similar to that of cod (Fig. 35).

In conclusion, it appears clear that the Gulf of St. Lawrence has a self-sustaining stock of Greenland halibut. This is particularly evident from the fecundity analysis which produced highly significant differences between those fish in the Gulf area compared to those of southern Labrador. This is further supported by significant differences in the size and age at sexual maturity as well as differences in growth patterns. There is however strong evidence, particularly by Fairbairn (1981), that there is a mixture of Greenland halibut in the Gulf of St. Lawrence of those fish originating within the Gulf and those from eastern areas. It was shown, particularly from the age distributions, that this is very likely to be the case; however, from the data presented here, it could not be concluded as to what quantitative extent this mixture occurs. It is considered that only through an intensive tagging study could such a problem be resolved. Based on the evidence presented here, it is also concluded that there is a single interbreeding stock from the Baffin Island-West Greenland area to the northern Grand Bank area. Considering the nature of the distribution patterns, the shifts in the maturity patterns, and information gathered from tag returns, indications are that spawning for this stock occurs in Davis Strait between West Greenland and Baffin Island. The main nursery areas are in the Disko Bay area according to Smidt (1969) and in the Baffin Bank area according to distribution patterns presented here. Young fish are caught in the polar currents to move down the continental shelf of Labrador and eastern Newfoundland where they settle in the deeper waters (Fig. 38). Upon approaching sexual maturity, these fish begin a spawning migration back towards the spawning

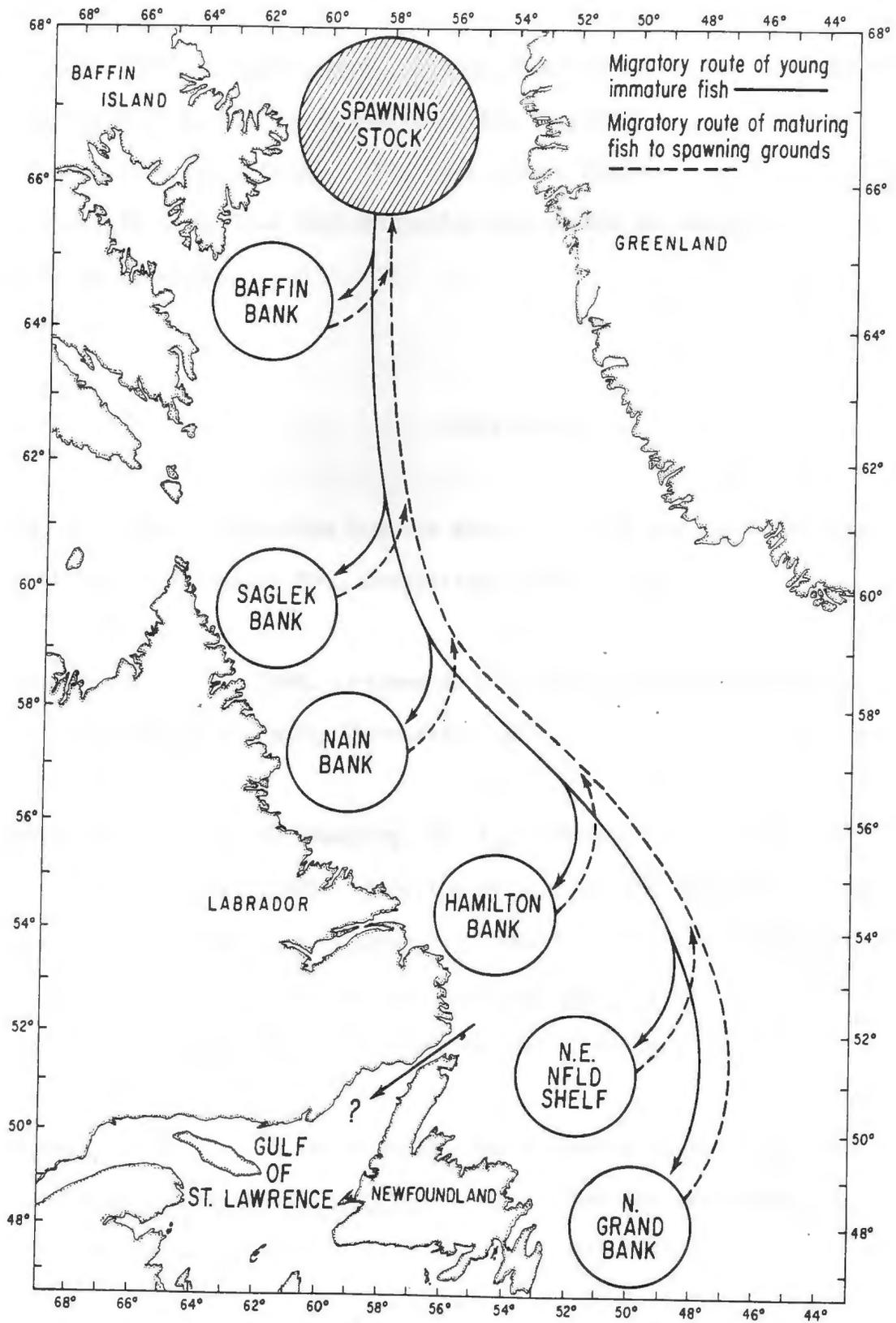


Fig. 38. Suggested migratory routes of Greenland halibut in the Northwest Atlantic.

grounds. This is particularly evident from the increased evidence of maturing fish going from south to north, supported also by the migration inferred from tag returns. It is not known, however, exactly what stage in the life cycle that this migration begins and subsequently how long it takes to complete.

REFERENCES

- Alm, G. 1959. Connection between maturity, size and age in fishes. Rep. Inst. Freshwater Res. Drottningholm 40: 145 p.
- Andriyashev, A. P. 1954. Fishes of the Northern Seas of the USSR. (English Trans. edit. Jerusalem, 1964).
- Atkinson, D. B., W. R. Bowering, Sv. Aa. Horsted, J. P. Minet, and D. G. Parsons. 1981. A review of biology and fisheries of roundnose grenadier (Macrourus rupestris), Greenland halibut (Reinhardtius hippoglossoides) and shrimp (Pandalus borealis) in Davis Strait (NAFO Subareas 0 and 1). NAFO SCR. Doc. 81/VI/22 Ser. No. N290.
- Bagenal, T. B. 1957. The breeding and fecundity of the long rough dab, (Hippoglossoides platessoides (Fabr.)) and the associated cycle in condition. J. Marine Biol. Ass. U.K.; 36: 339-375.

1963. The fecundity of witches in the firth of Clyde. J. Marine Biol. Ass. U.K.; 43: 401-407.
- Barrett, B. E. 1968. First occurrence of Greenland halibut (Reinhardtius hippoglossoides) in the Bay of Fundy. J. Fish. Res. Board Can. 25: 2721-2722.
- Berth, U., N. Shultz, and B. Vaske. 1979. Report on groundfish survey carried out by the RV Ernst Haeckel in statistical Area 0, Subarea 2 and Division 3K during autumn 1978. ICNAF Res. Doc. 79/VI/127, Ser. No. 5523.
- Bliss, E. I. 1952. The statistics of bioassay with special reference to the vitamins. Academic Press, Inc. New York, N.Y. 184 p.
- Bowering, W. R. 1976. Distribution, age and growth, and sexual maturity of witch flounder (Glyptocephalus cynoglossus) in Newfoundland Waters. J. Fish Res. Board Can. 33: 1574-1584.
1977. Trends in the Greenland halibut fishery in Subarea 2 and Divisions 3K and 3L. ICNAF Res. Doc. 77/VI/11, Ser. No. 5031, 14 p.
- 1978a. Fecundity of witch flounder (Glyptocephalus cynoglossus) from St. Pierre Bank and the Grand Bank of Newfoundland. J. Fish. Res. Board Can. 35:1119-1206.

1978b. Age and growth of Greenland halibut (Reinhardtius hippoglossoides (Walbaum)) in ICNAF Subareas 2-4. ICNAF Res. Bull. 13: 5-10.

1978c. The distribution of Greenland halibut in statistical Area "0". ICNAF Res. Doc. 78/VI/38, Ser. No. 5200, 6 p.

1978d. The exploitation of the Greenland halibut stock complex of ICNAF Subarea 2 and Divisions 3KL. ICNAF Res. Doc. 78/VI/39, Ser. No. 5201, 14 p.

1978e. An analytical assessment of the witch flounder stock in the Gulf of St. Lawrence (ICNAF Divisions 4R and 4S). CAFSAC Res. Doc. 78/7, 12 p.

1979a. Recruitment prospects for Greenland halibut in statistical Area 0. ICNAF Res. Doc. 78/VI/60, Ser. No. 5401, 6 p.

1979b. The Greenland halibut fishery on the Continental Shelf of ICNAF Subarea 2 and Divisions 3KL. ICNAF Res. Doc. 79/VI/71, Ser. No. 5413, 14 p.

1979c. Current status of the witch fishery in the Gulf of St. Lawrence (ICNAF Divisions 4RS). CAFSAC Res. Doc. 79/8, 17 p.

1979d. A developing interest for Greenland halibut in the Gulf of St. Lawrence. CAFSAC Res. Doc. 79/9, 12 p.

1980a. The Greenland halibut fishery in the Gulf of St. Lawrence. CAFSAC Res. Doc. 80/24, 18 p.

1980b. Stock assessment and abundance of Greenland halibut in the Canadian North Atlantic (Subarea 2 and Divisions 3K and 3L). NAFO SCR Doc. 80/VI/96, Ser. No. N151, 26 p.

1981a. Witch flounder in the Northern Gulf of St. Lawrence (NAFO Divisions 4RS). CAFSAC Res. Doc. 81/52, 14 p.

1981b. Greenland halibut in the Gulf of St. Lawrence -from Immigrants to Emigrants. CAFSAC Res. Doc. 81/55, 12 p.

Bowering, W. R., and J. Baird. 1980. Greenland halibut and witch flounder on the Flemish Cap (Division 3M). NAFO SCR Doc. 80/VI/85, Ser. No. N139, 11 p.

Bowering, W. R., and W. Brodie. 1980. An evaluation of recent management strategy for witch in the Gulf of St. Lawrence (NAFO Divisions 4RS). CAFSAC Res. Doc. 80/49, 20 p.

1981. Stock assessment of Greenland halibut in NAFO Subarea 2 and Divisions 3K and 3L with projected catches for 1982. NAFO SCR Doc. 80/VI/64, 17 p.
- Bowering, W. R. and D. G. Parsons. 1981. Observations on the relationship between Shrimp (Pandalus borealis) and Greenland halibut (Reinhardtius hippoglossoides) in two Labrador Channels. CAFSAC Res. Doc. 81/5, 23 p.
- Bowering, W. R. and T. K. Pitt. 1975. Yield per recruit assessment of Greenland halibut (Reinhardtius hippoglossoides), ICNAF Subarea 2 and Divisions 3K and 3L. ICNAF Res. Doc. 75/24, Ser. No. 3479, 7 p.
- Boyar, H. C., and R. A. Clifford. 1967. An automatic device for counting dry fish eggs. Trans. Amer. Fish. Soc. 96: 361-363.
- Brown, M. E. 1957. Experimental studies on growth. In Physiology of fishes. Vol. 1 Metabolism. Academic Press, Inc., New York, N.Y. 447 p.
- Chumakov, A. K. 1969. Fishery and marking the Greenland halibut (Reinhardtius hippoglossoides) near Iceland. Problems of Ichthyology, Vol. 9, Issue 6. 909-912.

1970. The Greenland halibut (Reinhardtius hippoglossoides) in the Iceland area - The halibut fisheries and tagging. Tr. Polyarn. Nauchnoissled. Proektn. Inst. Morsk. Rybn. Khoz. 1970.

1975. Localities of Greenland halibut stocks in the northwest Atlantic. Tr. Polyarn. Nauchnoissled. Proektn. Inst. Morsk. Rybn. Khoz. 35: 203-209, 1975.

deGroot, S. J. 1970. Some notes on the ambivalent behaviour of the Greenland halibut (Reinhardtius hippoglossoides (Walb.)) Pices: Pleuronectiformes. J. Fish. Biol. 2: 275-279.

Dunbar, M. J., and H. H. Hildebrand. 1952. Contribution to the study of the fishes of Ungava Bay. J. Fish. Res. Board Can. 9: 83-128.

Fairbairn, D. J. 1981. A biochemical genetic analysis of population differentiation in Greenland halibut (Reinhardtius hippoglossoides, (Walbaum)) from the Northwest Atlantic, Gulf of St. Lawrence and the Bering Sea. Can. J. Fish. Aquat. Sci. 38(7):782-794.

Federov, K. Y. 1968. Oogenesis and sexual maturity of the Greenland halibut. Can. Fish. Aquat. Sci. Transl. No. 4559, 1979.

Fleming, A. M. 1960. Age, growth, and sexual maturity of cod (Gadus morhua L.) in the Newfoundland area 1947-50. J. Fish. Res. Board Can. 17: 775-809.

- Gabriel, M. L. 1944. Factors affecting the number and form of vertebrae in Fundulus heteroclitus. J. Exp. Zool. 95, 1944. p 105-147.
- Heuts, M. J. 1949. Racial divergence in finray variation patterns in Gasterosteus aculeatus. Journal of Genetics, Vol. 49, 1949. 183-191.
- Hodder, V. M. 1963. Fecundity of Grand Bank haddock. J. Fish. Res. Board Can. 20: 1465-1487.
- Hubbs, C. L.; and N. J. Wilimovsky. 1964. Distribution and synonymy in the Pacific Ocean and variation of the Greenland halibut (Reinhardtius hippoglossoides). J. Fish. Res. Board Can. 21: 1129-1154.
- Jensen, A. S. 1935. The Greenland halibut (Reinhardtius hippoglossoides) its development and migrations. K. danske. vidensk. Selsk. Skr. 9 Rk., 6: 1-32.
- Khan, R. A., M. Dawe, R. Bowering, and R. K. Misra. 1981. Blood protozoa as an aid for separating stocks of Greenland halibut (Reinhardtius hippoglossoides) in the northwest Atlantic. ICES C.M.1981/G:40.
- Kosier, A.D.B. 1970. Greenland halibut of the Northeast Atlantic. Technika i Gospodarka Morska Vol. 20, No. 10 (632), 1970, p. 458-460.

- Lea, E. 1919. Report on age and growth of the herring in Canadian waters. Can. Fish. Exped. p. 75-164.
- Lear, W. H. MS 1970. The biology and fishery of the Greenland halibut (Reinhardtius hippoglossoides) in the Newfoundland area. Master's Thesis, Dept. Biol., Memorial University of Newfoundland. 130 p.
1970. Fecundity of Greenland halibut (Reinhardtius hippoglossoides) in the Newfoundland-Labrador area. J. Fish. Res. Board Can. 27: 1880-1882.
- Lear, W. H., and T. K. Pitt. 1975. Otolith age validation of Greenland halibut (Reinhardtius hippoglossoides). J. Fish. Res. Board Can. 32(2): 289-292.
- Lussiaa-Berdou, J. P. 1979. Evaluation recente de la population du Fletan du Groenland (Reinhardtius hippoglossoides) et de sa peche dans le golfe du St. Laurent. CAFSAC Res. Doc. 79/10 : 1-10.
- May, A. W. 1967. Fecundity of Atlantic cod. J. Fish. Res. Board Can. 24: 1531-1551.
- Molander, A. R. 1925. Observations on the witch flounder and its growth. Publ. Circ. Cons. Explor. Mer 85: 15p.

- Moore, J. A., and G. H. Winters. 1978. Growth patterns in a Newfoundland herring stock. CAFSAC Res. Doc. 78/43.
- Nizovtsev, G. P. 1970. Migrations of Greenland halibut (Reinhardtius hippoglossoides (Walbaum)) in Icelandic waters. ICES C.M.1970/F:24.
1974. A Greenland halibut (Reinhardtius hippoglossoides) tagged in eastern Icelandic waters and caught in the Barents Sea. J. Ichthyol. (English translation VOPR. IKHTIOL.) 14(2).
- Parsons, D. G., G. E. Tucker, and P. J. Veitch. 1981. Review of abundance indices and stock assessment for shrimp (Pandalus borealis) in the Labrador channels. CAFSAC Res. Doc. 81/7, 40 p.
- Pinhorn, A. T. 1972. Proposed stratification scheme for ICNAF Subdivision 3Ps. ICNAF Res. Doc. 72/60: 2 p.
1976. Living marine resources of Newfoundland-Labrador: Status and Potential. Bull. Fish. Res. Board Can. No. 194: 64 p.
- Pitt, T. K. 1964. Fecundity of American plaice (Hippoglossoides platessoides (Fabr.)) from Grand Bank and Newfoundland areas. J. Fish. Res. Board Can. 21: 597-612.

- Roff, D. A. 1980. A motion for the retirement of the von Bertalanffy.
Can. J. Fish. Aquat. Sci. 37:127-129.
- Sigurdsson, A. 1977. On the spawning grounds of Greenland halibut in
Icelandic waters. ICES C.M.1977/F:28.
1979. The Greenland halibut (Reinhardtius hippoglossoides (Walb.))
at Iceland. Publ. of the Marine Research Institute, Reykavik, ICELAND,
1979.
- Simpson, A. C. 1951. The fecundity of the plaice. Fish. Invest., Lond.
(2), 17(5), 27 p.
- Smidt, E. 1969. The Greenland halibut (Reinhardtius hippoglossoides),
biology and exploitation in Greenland waters. Medd. Danm. Fisk.
Havunders/g., (N.S.) 6: 79-148.
- Taning, A.V. 1944. Experiments on meristics and other characters in
fishes. Medd. fra. Komm. for Danmarks Fiskeri og Havunders. Bd.
XI, Fiskeri. 1944, 1-66.
1952. Experimental study on meristic characters in fishes.
Biological Reviews, Vol. 27, 1952, 169-193.
- Templeman, W. 1964. Canadian Research Report, 1963. ICNAF Redbook 1964,
pt. 2, p. 3-21.

1965. Mass mortalities of marine fishes in the Newfoundland area presumably due to low temperatures. ICNAF Spec. Publ. No. 6: 137-147.

1970. Vertebral and other meristic characteristics of Greenland halibut (Reinhardtius hippoglossoides) from the Northwest Atlantic. J. Fish. Res. Board Can., Vol. 27, No. 9, p. 1549-1562.

1973. Distribution and abundance of the Greenland halibut (Reinhardtius hippoglossoides (Walbaum)), in the Northwest Atlantic. ICNAF Res. Bull. No. 10: 82-98.

1979. Migration and intermingling of stocks of Atlantic cod (Gadus morhua) of the Newfoundland and adjacent areas in 1962-66. ICNAF Res. Bull. No. 14: 5-50.

Templeman, W. and T. K. Pitt. 1961. Vertebral numbers of Redfish (Sebastes marinus (L.)) in the Northwest Atlantic 1947-1954. Rapp. et Proc.-Verb Vol. 150, 1961 Cons. Internat. Explor. de la Mer.

Tremblay, C.; and F. Axelsen. 1980. Donnees sur la peche du Fletan du Groenland (Reinhardtius hippoglossoides) dans le Golfe du Saint-Laurent. CAFSAC Res. Doc. 80/34.

1981. Analyse de la population de Fletan du Groenland du Nord-ouest du Golfe du Saint-Laurent (4S, 4T). CAFSAC Res. Doc. 81/26.

- Walsh, S. J.; and W. R. Bowering. 1981. Histological and visual observations on Oogenesis and sexual maturity in Greenland halibut off Northern Labrador. NAFO Sci. Coun. Studies, No. 1: 71-75.
- Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall., Englewood Cliffs, N.J., 620 p.
- Zilanov, V. K.; A. A. Stroganov, F. M. Troyanovsky, and A. K. Chumakov. 1976. The results of the study of commercial reserve of Greenland halibut (Reinhardtius hippoglossoides) at the continental slopes in the northwestern Atlantic. ICNAF Res. Doc., No. 110, Ser. No. 3933.

