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The Stock Complex of Atlantic Cod (Gadus morhua) in NAFO Divisions 2J, 3K and 3L

by

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INTRODUCTION

The cod populations off southern Labrador and eastern Newfoundland in NAFO Div. 2J, 3K, and 3L (Fig. 1) have been managed as a single stock complex since the implementation of total allowable catches in 1973. The 1973 quota of 575,000 t for 2J3KL cod was agreed upon at the 1972 ICNAF meeting (ICNAF, 1972; Pinhorn 1976). Templeman (1962) formulated the cod stock divisions in the northwest Atlantic and deduced his conclusions mainly on previous studies (Templeman 1953) on migratory routes, growth rates, year-class strength, spawning times and places and times and location of pre-spawning and other concentrations.

Because of a lack of more detailed information, Templeman (1962) did not attempt to define closely the partially separated populations within this large Labrador-Newfoundland stock. The point was made that very likely in the future enough differences would be found to indicate a number of north-south and inshore-offshore sub-stocks of this Labrador-Newfoundland stock which either do not intermingle greatly or separate out at certain seasons. Templeman (1962), however, emphasized several differences in the characteristics of cod within this stock. Differences in growth rate exist throughout the area. For inshore cod the slowest growth of this stock is off Labrador and in the Labrador population there is a slight increase in growth rate from north to south. There was a difference at each size of about 3 cm between inshore coastal cod of the northern ICNAF Div. 2G and 2H and of the more southern Div. 2J (May, 1961). There was also a gradual increase in growth rate southward from Labrador along the east coast of Newfoundland (Fleming 1960). May et al (1965) attributed this clinal increase in growth rate to the varying influence of the Labrador current in terms of increasing surface temperatures and decreasing volume of cold water (less than 0°C) from north to south.

Templeman (1962) also stated that there were considerable differences in the condition of the cod when they arrived in the inshore waters. The cod of the Labrador-Newfoundland stock at the southern end of the range were in excellent condition with fat creamy-white livers when they arrived in June and this condition declined northward until off Labrador the cod arrived on the coast as thin fish with thin brown livers, depleted of fat reserves. Templeman (1962) postulated that each shelf region such as the Bonavista Shelf, Fogo Shelf, and the St. Anthony Shelf, projecting seaward with deep water on each side has a basic stock of its own, some of which it loses temporarily in the summer by coastal or pelagic feeding migrations and in the winter by movements in the deep water, while receiving some migrants from other areas. This hypothesis was supported by retention of a large proportion of the cod close to the tagging area for many years after tagging. It was also supported by the low levels of cod catches and the failure of catches to recover in the Bonavista area, where over-fishing had produced continued low catches in spite of relatively good catches from the Baccalieu region to the south and the Fogo Shelf region to the north (Templeman, 1959; 1960; Fleming, 1959). These conclusions were also supported by tagging studies during 1954-55 and 1962-66 (Templeman 1974,1979) as a result of continued evidence of homing of local populations of cod to original inshore tagging locations along the coast from the Avalon Peninsula to northern Labrador.

May (1966) hypothesized that the cod stock complex was composed of at least three major groups, the distributions of which overlap in summer and tend to be separate in winter. These are as follows:

1) The "Labrador-Newfoundland" stock, which spawns mainly on Hamilton Bank and possibly to a small extent on the Northeast Newfoundland Shelf and is distributed in summer along the coasts of Labrador and Northeastern Newfoundland.

2) The "Northeast Newfoundland" stock, which spawns mainly on Hamilton Bank but also on the Northeast Newfoundland Shelf. Its distribtion in summer extends only along northeastern and eastern Newfoundland. Alternately, two stocks may be involved, one spawning on Hamilton Bank and the other on the Northeast Newfoundland Shelf.

3) "East Newfoundland" stock which spawns on the northern Grand Bank and is distributed in summer mainly along eastern Newfoundland but may extend to northeastern Newfoundland.

The purpose of this paper is to review recent studies on the delineation of the various stock components of NAFO Div. 2J, 3K, and 3L and the biological basis for their separation into the above or similarly related stocks. The cod of Northern Labrador are also part of the Labrador-East Newfoundland stock complex but are usually considered separately for management purposes from the rest of the Labrador-East Newfoundland stock complex because of the effect of the fishery on this part of the complex has been more severe than in the south (Pinhorn 1976).

Biochemical Systematics

Cross and Payne (1978) analyzed the geographic variation in the frequencies of alleles at the Tf locus in Atlantic cod. Their study indicated that it was possible to distinguish three major populations off eastern North America: (1) north of the Laurentian Channel, (2) south of the Laurentian Channel, and (3) Flemish Cap. The data also suggested that the north Laurentian stock could be further subdivided into a northern and southern component. The northern component was comprised of samples from Hamilton Inlet Bank (2J), Domino (2J), Fox Harbour (2J), Belle Isle Bank (2J), NE Newfoundland Shelf (3K), and the northern Grand Bank (3L). The sample from the northern Grand Bank area was obtained during March 1974 at a depth of about 450m. The southern component consisted of samples from St. Pierre and Burgeo banks (3Ps), Rose Blanche Bank (3Pn), Gulf of St. Lawrence (4R), and the northern Grand Bank (3L). The 3L sample in this case was obtained during May 1976 at a depth of about 180m. It is not surprising to find that cod of the northern Grand Bank from different depth zones were of two separate populations. Templeman (1979) found that on 28-29 March, 1961, the cod population (immature and mature) at the shallowest depth (181-183m) had the low vertebral numbers typical of the southern Grand Bank and Avalon stocks. Vertebral numbers increased with depth and at the greatest depths (364-446m) the high vertebral numbers were characteristic of the Labrador-East-Newfoundland stock.

Jamieson (1975) examined population samples of Atlantic cod, collected off the North American coast, for genetic variations at four genetic loci. Of the four genetic loci examined, the frequencies of the transferrin alleles (Tf locus) revealed different genetic sub-populations of cod at North America, and a striking difference between North American cod and cod elsewhere. None of the six Tf alleles, however, were useful to separate cod of northern and eastern Grand Bank from those of Ritu Bank (Funk Island Bank). The frequency of the Tfc allle showed an highly significant difference between cod on Flemish Cap and the northeastern Grand Bank.

Parasites as Biological Tags

Templeman et. al. (1976) examined the gills of about 80,400 Atlantic cod during 1947-70 for the presence of the metamorphosed adult copepod, Lernaeocera branchialis. This parasite lends itself very readily for use as a biological tag since its life appears to be moderately long and even after the parasite has disappeared, the head with the neck protruding can be found at the apex of the gills of the cod. It is very suitable for studies of the relationship of inshore and offshore cod populations (Templeman 1953).

Templeman et al (1976) found that the offshore Labrador and northeast Newfoundland (ICNAF Div. 2J and 3K) cod populations had considerably lower infection rates at the smaller sizes than the inshore populations of these divisions but had approximate equality at the lower infection rates of the larger sizes. If the assumption is valid that the infection usually occurs near the coast, these infection rates indicate that the larger offshore and inshore fish were from the same intermingling population but that the smaller offshore fish did not visit the coast in sufficient numbers to obtain high infection rates. For cod over 30 cm in length, infection rates near the coast were much higher off Newfoundland and off southern Labrador immediately north of the Strait of Belle Isle than further north along the remainder of the Labrador Coast.

The cod of ICNAF Div. 3L from offshore west of 50°W (mainly northwest Grand Bank and slopes and Avalon channel) had high rates of infection, similar to those of inshore cod, at the 21-40 cm range. At all higher length ranges they had lower rates than inshore cod, but higher at all length ranges, especially at 11-40 cm, than cod from east of 50°W. If the parasites were acquired by smaller fish living inshore, apparently the smaller of the offshore cod of Div. 3L west of 50°W visited the shore as much as cod of these sizes taken inshore in 3L. For the larger sizes, however, it was apparent that half of the offshore cod from west of

50°W had migrated from areas where little or no direct infection occurred, such as ICNAF Div. 3L (East of 50°W) and southern Grand Bank (ICNAF Div. 3N and 3O).

The smaller and the larger northern Grand Bank cod, from Div. 3L east of 50°W, had comparatively little infection by the copepod and consequently much less relationship with the coast than fish of intermediate length (41-60cm) which had about half the infection of offshore fish west of 50°W and between one third and one quarter that of the coastal cod of 3L. Templeman et. al. (1976) concluded that the smaller cod east of 50°W are likely to be largely native to the area and many of the larger fish immigrants from the centres of low infection, Div. 3N and 3O.

Another parasite which is useful as a biological tag is the nematode, Phocanema decipiens, (formerly called Porrocaecum decipiens) since it has a long living period and even the dead parasites can be recognized since the cuticle remains (Templeman, 1953). During the period 1947-1953, Templeman et al. (1957) examined over 15,000 cod in the eastern Canadian area to determine the incidence of nematode infections from various areas. It was found that in terms of incidence of infection, expressed in terms of numbers of nemtodes per 100 cod (41 cm and larger) and as the number of nematodes per 100 lbs (45.4kg) of cod fillets, the nematode infection was lowest on the Grand Bank, Flemish Cap, the east coast of Newfoundland, off Labrador, and on the southern part of St. Pierre Bank. There was very little variation in the nematode infection rates of cod (41 cm and larger) in the area from Labrador to the northern Grand Bank as illustrated in the following table extracted from Templeman et al. (1957).

Locality and ICNAF Subdivision	Percentage of cod with nematodes in fillets	No. of Nematodes per 100 cod.	No. of Nematodes per 100 lbs. (45kg) of fillets
Labrador-inshore:2G,2H,2J	4.3	5.1	6.2
Labrador-offshore:2G,2H,2J	3.1	3.4	3.2
NE coast Nfld.-offshore:3K	3.0	3.0	2.1
E coast Nfld.-inshore:3K,3L	3.8	4.6	3.3
St. John's:3L	3.7	4.7	3.1
N.Grand Bank:3L W of 50°W	2.5	2.6	1.2
N.Grand Bank:3L E of 50°W	2.2	2.7	1.5

The infection rates for the northern Grand Bank (offshore 3L) were somewhat lower than those for the more northern areas in 3K and 2J and for inshore 3L. Wells et al. (1985) examined cod from eastern and southern Newfoundland to determine the occurrence and abundance of nematodes in fillets and napes and to compare the results with the earlier study of Templeman et al. (1957). The rates of infection of the present study (Wells et. al. 1985) were not significantly different from those in the earlier study. The patterns of infection among the three NAFO Divisions 2J, 3K, and 3L followed a similar pattern to those of Templeman et al. (1957), i.e. the rate of infection in 3L was lower than those in 2J and 3K.

Khan et al. (1980) initiated a study to ascertain the prevalence of a protozoan parasitic trypanosome Trypanosoma murmanensis in Atlantic cod, especially in relation to the stocks in the Newfoundland area and as an aid in management and conservation. Their study indicated that the highest prevalences were recorded in fish taken off the Labrador coast (ICNAF Div. 2J and 3K, 94 and 90% respectively). Trypanosomes were not as prevalent in fish collected from the northern Grand Bank (46%, Div. 3L) or from the southern Grand Bank (13 and 16%, Div. 3N and 3O, respectively). Fish sampled at inshore localities reflected prevalences corresponding to some extent to offshore localities. Cod taken on coastal Labrador and from northern Newfoundland had a high prevalence of trypanosome infections while in the more easterly bays, intermediate levels occurred. There was an apparent conspicious decrease in prevalence in a sample taken from the most easterly inshore locality (Portugal Cove in Div. 3L).

On the basis of these results, Khan et al. (1980) suggested that cod in the NAFO Div. 2J-3K represented a stock distinct from that in the neighboring Gulf of St. Lawrence (Div. 4R-4S). They stated that the differences recorded between Div. 2J-3K (southerly limit of 50°N latitude) and Div. 3L were sufficient to warrant separation of a northern Grand Bank stock from the Labrador-east Newfoundland stock complex.

Postolaky (1962) found that plerocercoids of the cestode parasite, Pyramicocephalus phocarum occured in 10% of cod examined off southern Labrador (Div. 2J) but in only 4% of the cod examined from the northeastern slope of the Grand Bank (Div. 3L). Anisakis sp. larvae

were found in 37.5% of the cod livers from southern Labrador (2J) but in 54% of cod livers from the northeastern Grand Bank (3L). Clavella uncinata was prevalent on about 38% of buccal cavities of cod examined from southern Labrador and on 62% of buccal cavities of cod from the northeastern Grand Bank. On the gills it was found on about 11% and 20% of the cod from 2J and 3L respectively.

MERISTICS

Templeman (1981) analyzed 416 cod vertebral samples (about 45,000 individual cod) from the Newfoundland and adjacent areas during 1947-71, to determine their utility as an aid for the delineation of cod stocks of the region. It was found that the main portion of the Labrador-East Newfoundland stock (Div. 2G to 3K) was well separated from the southern Grand Bank (Div. 3N and 3O), by the presence in the northern area of high vertebral means and of higher percentages of high vertebral numbers and the lack of low vertebral numbers in the southern area. Cod from the offshore area in Div. 2G to 3K had somewhat higher vertebral numbers than those of the inshore area. The high vertebral count cod of the Labrador-East Newfoundland stock also extended to the northern slopes of the Grand Bank and around the Avalon Peninsula (Div. 3L), but in this area they usually intermingled with cod of the Avalon stock complex and with some migrants from southern Grand Bank as indicated by vertebral means intermediate between the northern and southern extremes. Occasionally, however, relatively unmixed schools of high vertebral-count cod appear to have migrated along the eastern slope of the Grand Bank as far south as 45°30'N (Div. 3N), as evidenced by a sample with a vertebral average of 55.28 (typical of the high vertebral average Labrador-East Newfoundland cod).

Vertebral averages for samples from the western part of the Grand Bank, the Avalon Channel, the Avalon Peninsula, Placentia and Fortune Bays and vicinity were typically intermediate (between 54 and 55). It has been shown from tagging studies (Templeman and Fleming 1962; Templeman 1974, 1979) that the small cod populations in this area (Avalon stock complex) intermingle with each other and also with high and low vertebral-count fish of the Labrador-East Newfoundland and southern Grand Bank stocks, respectively, which migrate to the area.

Lear (1982) analyzed six meristic characters from mature cod collected on spawning, prespawning, or overwintering concentrations from southeastern Hamilton Bank (2J), Funk Island Bank (3K), northwest slope of the Grand Bank (3L) during March 1982 and from the north Cape of the Grand Bank (3L) and the northwestern edge of the Grand Bank (3L) during early May, 1982.

Analysis of variance indicated that all 6 characters from the southeastern Hamilton Bank were significantly higher at the .01 level (except the first anal fin count at the .05 level) than the characters from the other 4 areas. A multiple range test (Kramer 1956) indicated no differences among the other 4 areas for the first dorsal fin ray, the second dorsal fin ray, the third dorsal fin ray, the first anal fin ray and the second anal fin ray averages. For the vertebral averages, the multiple range test indicated that the average from the southeastern Hamilton Inlet Bank was significantly higher than all the others, while that from the eastern edge of the Grand Bank was significantly lower than all the others. The averages from the north cape of the Grand Bank, eastern Grand Bank, and northern Funk Island Bank were not significantly different from each other for any of the six meristic characters analyzed.

The significantly higher meristic counts of the fin rays and vertebrae of the mature cod of the southeastern Hamilton Bank than those from the Funk Island Bank suggest that the Hamilton Bank cod are different from those of the Funk Island Bank and the northeast Newfoundland Shelf. The patterns of tag returns (Lear, 1982, 1984b) from both areas also suggest different summer distributions, although there is some overlapping of the two major groupings.

The homogeneity of the meristic characters from Funk Island Bank, and the northern Grand Bank do not suggest any differences, but the difference in the summer distribution of cod tagged on Funk Island Bank and the north cape of the Grand Bank (Lear 1982, 1984b) suggest that these groups are different in their summer migration pattern. The significantly lower vertebral averages of the cod of the eastern slope of the Grand Bank suggest that the mature cod in this area during the spring are somewhat different from the other groups (Lear, 1982).

Lear and Wells (1984) analyzed the vertebral averages of juvenile cod (ages 0, 1, and 2 years old) from Venison Tickle, Labrador (Div. 2J), eastern Newfoundland (3K) to St. Mary's Bay in southeastern Newfoundland (3L). The vertebral averages from southern Labrador and northeastern Newfoundland were generally of the high or northern type ($\geq$54.8 vertebrae). In southeastern Newfoundland (Div. 3L), particularly around St. Mary's Bay, Trepassey Bay, and Conception Bay, vertebral averages of the 0 and 1-year-old cod were occasionally of the intermediate and rarely of the low type indicative of the Avalon stock complex or intermingling of the Avalon stock and the Labrador-East Newfoundland stock. Low to intermediate values for samples of 2 year old cod from the Avalon Peninsula northward to

Notre Dame Bay may indicate local or late spawning or intermingling with the northern segment of the Avalon stock complex. There was an absence of high vertebral averages of 2 year old cod in the southern areas (St. Mary's Bay to Trinity Bay), with the exception of one sample from Conception Bay. There is a possibility that the 2-year-old juveniles, which were derived from northern spawning, had already migrated northward, by age 2, from their nursery grounds along the southeast coast of Newfoundland, leaving those areas inhabited mainly by 2-year-old juvnile cod of the southern stocks of the Avalon stock complex.

Postolaky (1962) counted the vertebrae of 1655 cod from Div. 2J, 3K, 3L, 3M, 3N, and 30 of which 699 were from Div. 2J, 3K, and 3L. He found that the mean vertebral count of the cod decreased from the north in southern and southwestern directions. No great differences were observed between the mean vertebral counts of the cod of south Labrador (2J), North Newfoundland Bank (3K), and the northern extremity of the Grand Bank (the north cape at about 49°N). In these regions the mean vertebral counts varied from 55.46 to 54.93. In the northeastern (3L) and southeastern part of the Grand Bank, the mean vertebral counts varied greatly from sample to sample (55.10 to 53.42). Postalaky (1962) concluded that on the northeastern slope of the Grand Bank, the cod from the eastern and southeastern coast of Newfoundland apparently intermingled with the cod from Div. 3K and 2J. However, when Postalaky (1962) combined the vertebral counts by Division there were significant differences among the Divisions 2J, 3K, and 3L. In fact they were all different from each other at the .01 level. The combined averages by Div. 2J, 3K, and 3L from Postalaky (1962) are as follows:

Division	Average	Standard Error	S.D.	N
2J	55.31	0.06	1.005	298
3K	54.96	0.08	0.990	143
3L	54.40	0.07	1.095	258

Stanek (1968) counted the rays of the second dorsal fin of 8,616 cod and the vertebrae of 1,781 cod during 1962-65 from Labrador, Newfoundland and Nova Scotia. The numbers of dorsal fin rays were generally higher in 2J and 3K (20.74 to 21.01), than they were on the northern Grand Bank in Div. 3L (19.19 to 20.44). Vertebrae were all generally higher in 2J and 3K (54.83 to 55.34) than they were in 3L although they overlapped somewhat (54.17 to 54.89).

Growth Rates

The slow-growing cod off Labrador (2J) showed distinct differences in growth rate from the Newfoundland east coast (3K) cod which grow somewhat faster. The growth rate of the cod on the north and northeastern part of the Grand Bank (3L) were still more rapid (Templeman, 1953). Since the growth rate studies showed that the Labrador-Newfoundland east coast and northern edge of the Grand Bank cod were distinct enough to show considerable differences, Templeman (1953) concluded that the stocks could not be very greatly intermingled. Fleming (1960) found that there was a general increase in rate of growth in length and weight of cod with decreasing latitude in the eastern part of the Newfoundland-Labrador area, proceeding from Labrador to the southwestern portion of the Grand Bank. In general at about age 6 there was an increase in length at age for cod from inshore Labrador (2G-2J) at 48.8cm, to 51.0 cm inshore on the NE Coast of Newfoundland (3K), 54.8 cm inshore on the SE coast of Newfoundland (3L) and 57.8cm offshore on the northeastern Grand Bank (3L).

The average fork lengths (cm) of the different age groups of cod from Labrador and Eastern Newfoundland, 1947-50 are presented in the following table (from Fleming, 1960):

Age Group	Labrador (2G,2H,2J)	NE Nfld. Coast (3K)	SE Nfld. Coast (3L)	NE Grand Bank (3L)
4	41.1	41.4	43.8	48.0
5	43.6	47.7	47.8	52.7
6	48.8	51.0	54.8	57.8
7	51.8	57.2	59.3	62.2
8	54.2	60.1	62.4	66.2
9	56.2	61.7	63.8	69.5
10	58.4	63.9	65.8	71.0
11	57.8	63.7	66.2	72.9
12	58.5	65.0	67.9	73.1
13	59.0	64.5	71.4	75.3
14	62.2	67.5	75.9	77.1

Postolaky (1962) presented data which showed that both male and female cod of Div. 2J were on the average slightly smaller than those of Div. 3K. For the females of ages 6 to 10 years inclusive, there was an increase in average length of only 0.9 cm from 2J to 3K while for the males there was a corresponding average increase of 2.2 cm. May et al. (1965) reported that the growth rates of cod increased slowly from a very slow rate off Northern Labrador (2H) to a slightly faster rate off Southern Labrador (2J). There was a great increase in growth rate from 2J to 3K in the vicinity of about 10 cm between the areas for ages 10 to 15 years. There was a larger increase in average length at age from 3K to 3L of about 15 to 20 cm for lengths of cod of age 10 to 15 years. May et al. (1965) attributed the variations in growth of cod from northern Labrador to the southern Grand Bank to the varying influence of the Labrador current in terms of increasing surface temperatures and decreasing volume of cold water (less than 0°C) from north to south.

Akenhead et al. (1982) estimated growth of cod of ages 4-8 from the inshore cod trap fishery for each of Div. 2J, 3K, and 3L. The growth increments were calculated by subtracting individual cohort mean lengths from the succeeding year. These values were then averaged to provide an index of annual growth for each area. There were no significant differences observed among mean growth indices of cod from Div. 2J, 3K, and 3L. However, the annual growth indices were not correlated in all cases. The growth indices of cod from Div. 2J and 3L were correlated, but the growth index of cod from Div. 3K was significantly different from the indices in both Div. 2J and Div. 3L. Thus, although the mean growth over the period considered was similar in all areas, the pattern of annual growth was different among areas.

Size and Age at Sexual Maturity

Templeman (1953) indicated that the size at first sexual maturity in the cod of the Labrador area appeared to be small while that on the east coast of Newfoundland and on the northern and western edges of the Grand Bank were intermediate, and that on the southern part of the Grand Bank was the largest of all. Age of cod at first sexual maturity did not show such great differences as did size.

Fleming (1960) found that more cod were sexually mature at the smaller sizes in Labrador than in any other region. In each locality around Newfoundland, all cod were immature at 40cm in length but in Labrador some fish were mature in the 42 to 43cm group, and all were mature at the 52-53cm group. Along the east coast and in the northeast Grand Bank region, considerable numbers of sexually mature fish were found below 60 cm in length and practically all fish were mature at 65cm in the east coast region and 70cm in the northeast Grand Bank. The age at which 50% of the fish in the Labrador area were sexually mature (M_{50}) was about 5.4 years (Fleming, 1960). This was statistically different ($P < .05$) from the comparable ages in samples from other Newfoundland areas sampled. The east coast fish were somewhat later in attaining sexual maturity than the Labrador fish and the age at which 50% were mature was 5.8 from the southeast coast of Newfoundland (3L), and 6.1 from the northeast coast of Newfoundland (3K). On the northeast part of the Grand Bank (3L) 50% were mature at 6.3 years. Sizes and ages of maturity for cod of Div. 2J, 3K, and 3L during recent years are not readily available so it is not possible to tell if these differences still persist, if they have decreased or if the differences have increased or fluctuated over time as a result of the decrease in the cod biomass in the 1970's and the recent increase in the cod biomass. Minet et al. (1980) calculated the lengths and ages at which 50% of the cod of Div. 2J, 3K, and 3L matured but didn't compare for differences among areas.

Spawning Times and Locations

Templeman (1962), in his review of cod stocks in the Northwest Atlantic, conceded that detailed information during the actual spawning season was relatively poor at that time. He indicated that spawning was probably chiefly from April to early June throughout most of the area occupied by the Labrador-Newfoundland stock, at least from southern Labrador and Hamilton Bank southward.

Templeman (1979, 1981) reviewed the earlier studies of Templeman (1964, 1965); Serebryakov (1967); Noskov and Zakharov (1964); Bogdanov et al. (1965); Dias (1965, 1967, 1968, 1971, 1972); Chrzan (1968); Templeman and Fleming (1962); and Monteiro and Dias (1964) on spawning times and locations. The spawning times of cod from northern Labrador (2G and 2H) were inferred from the assumed drift of eggs and larvae found off northern and southern Labrador (Serebryakov 1967). Off Labrador (Subarea 2) cod were presumed to spawn mainly in March-April in deep water on the continental slopes, with most of the remainder spawning in May. There was a small amount of spawning, as late as June, in the colder water channels and slopes closer to the coast.

In Div. 3K off northeast Newfoundland, at least as far south as Funk Island Bank and vicinity, cod spawning begins in March but occurs mainly in April to early May with some spawning continuing to June.

In Div. 3L at the northern slope of the Grand Bank and in the Avalon Channel and on the northwestern slope of the Grand Bank, cod spawn mainly in April-June. Most of the spawning is usually over by June. In the northern part of 3L, however, the mature cod typically lie shallower in winter than in Subarea 2 and Div. 3K and spawning may be delayed in years when unfavorably low temperatures extend deeper than usual. This occurred in 1961 and in 1971 when spawning was delayed, with considerable spawning occurring in June and July. Templeman (1979) was uncertain whether or not the Labrador-East Newfoundland stock spawned in large numbers as far south as the northern Grand Bank (Div. 3L).

RESULTS OF TAGGING STUDIES

Tagging studies provide the most direct methods of obtaining information on the migration of cod populations and the amount of intermingling with neighboring populations. During 1947 and 1948 cod were tagged at Englee in northeastern Newfoundland, Nutak and Domino in Labrador, and at St. John's in southeastern Newfoundland (Templeman and Fleming, 1962).

Of the 226 cod tagged at Nutak on August 12-14, 1948, 15 were recaptured in the tagging area in the month of tagging. There were only two recaptures in the next year, one a short distance south of the tagging area and another about 560 km southward along the Labrador coast.

Of the 505 cod tagged at Domino during July 12-22, 1948, there were 60 recaptures in the tagging area and one a short distance southward along the Labrador coast. In the years following the tagging most recaptures were still near the tagging area but there had been a short movement northward and several fish had moved southward to the northeast coast of Newfoundland.

During September 8-19, 1947, 579 cod were tagged inshore at Englee. In the years following tagging, most of the recaptures were distributed away from the tagging location, over an area extending northward 200 km to the Strait of Belle Isle and southward 300 km to Bonavista. The entire migration was confined to the northeast coast of Newfoundland and the Strait of Belle Isle. From the tagging of 577 cod in the St. John's area during October 5 to November 4, 1948, the recaptures in the following 3 years were restricted coastwise northward as far as Cape Freels and southward and westward to Placentia Bay, but most of the recaptures were not more than 110 km north or south of the tagging area. There were more northward than southward recaptures and few St. John's cod were recaptured west of Cape Race. Recaptures on the northern part of the Grand Bank and in Halibut Channel in deep, warm water below 100 fath (180 m) indicated some overwintering in these areas. Two of the recaptured fish had moved northward several years later about 560 km to the northern tip of the east coast of Newfoundland.

During 1960-62 about 2300 cod were tagged in Div. 2H, 2J, 3K, and 3L (Sidonenko and Postolaky, 1963). Of these there were only 2.3% recaptured during 1960-62. According to the tagging, they concluded that there was a local cod stock in the area of South Labrador (2J) and the North Newfoundland Bank (3K). The cod from these areas migrated from the outer seaward slopes towards the coastal areas of south Labrador and north Newfoundland during summer. In summer the cod of the North Newfoundland Bank (3K) also migrated to the northern Newfoundland coast. Some of the south Labrador cod migrated across the Strait of Belle Isle into the Gulf of St. Lawrence.

Postolaky (1966) reported on the results of the tagging of 22,534 cod in Labrador (Subarea 2) and the north Newfoundland bank (3K) during 1960-64. These cod were tagged on the outer slopes of the continental shelf and the banks presumably during the overwintering period. Of these tagged cod, only 2.6% were recaptured during 1960-64.

From the cod tagged in north Labrador during April 1963, the tag recaptures indicated that the cod migrated after spawning from north Labrador in a southerly direction along the shelf. During June-July the fish tagged in north Labrador were caught by fishermen in the coastal waters of the southern coast of Labrador and the northeastern coast of Newfoundland. The fish that were tagged in south Labrador (2J) and on the north Newfoundland bank (3K) as well as those tagged in north Labrador (2G) were caught on the southern coast of Labrador and northeastern coast of Newfoundland from the middle of June, in July and August.

Templeman (1974) reported on the recaptures of 26% of 18,822 cod, 50 cm or more in length, that were tagged in the feeding season at 13 localities in the Newfoundland area during 1954-55. The cod tagged at the inshore localities at Cape St. Anthony, LaScie in Div. 3K and Bonavista in Div. 3L, intermingled along the east coast and off southern Labrador and with cod of the northern Gulf stock and the Avalon-Burin stock complex, especially during the feeding season in summer and early autumn. Small numbers of cod from these taggings were recaptured usually in late-autumn-winter or early spring, on the Labrador and northeast Newfoundland shelves. Only low percentages of the recaptured cod from these taggings were taken on the Grand Bank.

Tagging at three sites (Fermeuse, Cape Pine, and Cape St. Mary's) off the Avalon Peninsula showed that this group of cod was strongly localized near the Avalon Peninsula during the late spring-summer-autumn feeding season. In each of these three populations tagged, in years after the tagging year there was a strong return to and near the tagging area, showing that there are local differences in migratory behaviour within the intermingling groups of the stock complex. Small percentages (4-11%) of the recaptures were taken on the northern Grand Bank, mainly during April-June. The Avalon-Burin stock complex intermingled with the Labrador-Newfoundland stock especially during the summer-early autumn feeding season and especially during late autumn, winter and spring, with the southern Grand Bank stock. Intermingling with the Labrador-Newfoundland stock complex on the east coast of Newfoundland and on the northern and northwestern slopes of the Grand Bank was greatest for the eastern parts of the Avalon-Burin stock complex and least for the western parts. The St. Pierre Bank cod (part of the Avalon-Burin stock complex) overlapped only slightly at the Avalon Peninsula with the Labrador-Newfoundland stock complex and were not taken on the northern Grand Bank.

Templeman (1974) stated that the cod of the Avalon-Burin stock complex intermingled more with cod of the southern Grand Bank stock than did those of the Labrador-Newfoundland stock complex. Some of the cod, especially those tagged at Fermeuse, remained on the Grand Bank in summer instead of returning to the coast and it was speculated that these were probably fish of the southern Grand Bank stock which had been near the Avalon Peninsula for feeding and had been tagged there.

During 1962-66, 47,560 cod were tagged from inshore and offshore localities in the Newfoundland and adjacent areas of which 32.6% were eventually recaptured and reported (Templeman 1979).

From these taggings inshore at many localities from northern Labrador to the Avalon Peninsula and offshore from Hamilton Bank to the northern Grand Bank, cod of the Labrador-East Newfoundland stock were shown to intermingle and overlap from north to south in their winter-spring spawning areas in deep water on the slopes of the Labrador and Northeast Newfoundland shelves. Cod of this stock tagged offshore in spring on the slopes of Hamilton, Belle Isle, and Funk Island banks mainly migrated in summer to coastal waters from mid-Labrador to the Avalon Peninsula. From coastal taggings along eastern Newfoundland, cod migration to spawning grounds off Labrador was predominantly of the smaller sizes characteristic of mature fish off Labrador, whereas many of the larger cod migrated to the Grand Bank where cod mature at and grow to larger sizes. Cod, tagged in inshore and bank areas impinging on the Avalon and St. Pierre channels and in related channels and bays, intermingled enough in summer-autumn and became separated enough in winter-spring to be considered as the Avalon stock complex, consisting of the following components which are named from their wintering and spawning areas: Placentia Bay, St. Mary's Bay, St. Pierre Bank, Halibut Channel, northwestern slope of Grand Bank, and the Avalon Channel.

The tagging experiments indicated that, in summer-autumn of years after tagging, there was usually considerable homing of local populations of cod, tagged in the summer-autumn feeding season, to and near the original tagging locations.

Templeman (1979) also presented evidence based on spawning places, tagging and migration studies and presumed egg and larval drift to suggest that the main spawning population of cod on the slope of the northern Grand Bank was not a part of the Labrador-East Newfoundland stock.

Lear (1984a) from tagging of adult cod inshore in Conception Bay (3L) during autumn in 1979 and 1980 reported that the main offshore overwintering area of these cod was the northern slope of the Grand Bank and to a lesser extent Funk Island Bank. These cod returned during summer of the following years to the same general areas where they were tagged, confirming Templeman's results of 1974 and 1979.

Adult cod tagged at Exploits and Fortune Harbour (3K) during autumn 1982 were recaptured offshore during January-April mainly on Funk Island Bank and Belle Isle Banks while in summer of following years they returned to the same general feeding areas in which they had been tagged (Lear 1984a).

Adult cod tagged at Orton Island, Nain (2H) during August 1981 were recaptured offshore during winter-spring mainly along the slopes of Hamilton Bank and occasionally as far south as the Belle Isle Bank and Funk Island Bank.

During February-March 1978-81, about 25,000 Atlantic cod ($\geq$45 cm) were tagged from the prespawning concentrations on Hamilton Bank, Belle Isle Bank, Funk Island Bank, and northern Grand Bank (Lear 1984b).

Based upon this tagging there was evidence of a consistent annual pattern of migration to inshore waters during summer and to offshore areas during winter for each group of cod tagged along the outer continental shelf. The Hamilton Bank component evidently contributes to the

southern Labrador and northeast Newfoundland coastal fisheries mainly from Notre Dame Bay northward (Table 1). The Belle Isle Bank component migrates during summer mainly to southern Labrador, Strait of Belle Isle entrance and northeastern Newfoundland as far south as Notre Dame Bay. The pattern of movement is similar to that of the Hamilton Bank component except for a greater proportion in the Strait of Belle Isle. These patterns of migration and summer distribution conform with May's (1966) concept of the "Labrador-Newfoundland" cod stock. High exploitation of the overwintering concentrations in the Hamilton Bank and Belle Isle Bank areas could possibly have adverse effects on the inshore fishery from southern Labrador to Notre Dame Bay. Cod on the northern and northeastern slopes of Funk Island Bank migrate during summer to eastern and southeastern Newfoundland, with smaller proportions going to southern Labrador and the Strait of Belle Isle than from the taggings on Belle Isle Bank. Cod from the southwestern slope of Funk Island Bank contribute mainly to the summer inshore fishery of Notre Dame Bay and Bonavista Bay and in a smaller degree to the fishery in Trinity Bay, Conception Bay, and the eastern part of the Avalon Peninsula. Thus, the components which overwinter and spawn on the northern, eastern, and western slopes of Funk Island Bank collectively form what might best be described as the "Eastern Newfoundland" stock, and the inshore fishery from White Bay to the Avalon Peninsula and to a small extent Labrador would likely be sensitive to changes in the size of this stock. Cod which overwinter on northern Grand Bank migrate southwards across the bank to the Virgin Rocks and to the eastern slope of the bank and to inshore areas. This component contributes mainly to the inshore fishery from Trinity Bay southward to St. Mary's Bay, with little effect on the fishery north of Cape Bonavista.

The evidence from tagging on winter concentrations is that each component contributes to the inshore fishery in specific, although wide overlapping areas.

SUMMARY

1. Analysis of genetic variation in Atlantic cod suggested that there was a northern component from the deep northern slopes of the Grand Bank up to and including Hamilton Bank and a southern component from the shallow areas of the northern Grand Bank, St. Pierre, and Burgeo banks and the Gulf of St. Lawrence north of the Laurentian Channel. The cod of Flemish Cap were significantly different from the population on the northeastern Grand Bank.

2. Studies based upon the use of the adult copepod Lernaeocera branchialis as a biological tag indicated that the offshore Labrador and northeast Newfoundland (Div. 2J and 3K) cod populations had considerably lower infection rates at the smaller sizes than the inshore populations of these divisions but had approximate equality at the lower infection rates of the larger sizes. The cod of Div. 3L from offshore west of 50 W had high rates of infection, similar to those of inshore cod at the 21-40 cm range. Larger cod had lower rates than inshore cod, but the rates were higher at all length ranges, especially at 11-40 cm than cod from east of 50 W. It was apparent that half of the larger offshore cod from west of 50°W had migrated from areas where little or no direct infection occurred, such as Div. 3L (east of 50°W) and southern Grand Bank (Div. 3N and 3O). The smaller and larger northern Grand Bank cod east of 50°W had much less relationship with the coast than fish of intermediate length (41-60 cm) which had about half the infection of offshore cod west of 50°W and between one third and one quarter that of the coastal cod of 3L.

3. There was very little variation in the infection rate with the nematode Phocanema decipiens of cod during 1947-1953 in the area from Labrador to the northern Grand Bank. The infection rates for the northern Grand Bank (offshore 3L) were somewhat lower than those for the more northern areas in 3K and 2J and for inshore 3L. The rate of infection during autumn 1983 was slightly lower in 3L than those in 2J and 3K.

4. On the basis of studies on the prevalence of the protozoan parasitic trypanosome Trypanosoma murmanensis in cod, it was suggested that cod in the NAFO Div. 2J and 3K represented a stock distinct from that in the neighboring Gulf of St. Lawrence (Div. 4R and 4S). Differences in prevalence recorded between Div. 2J-3K (southerly limit of 50°N) and Div. 3L were sufficient to warrant separation of a northern Grand Bank stock from the Labrador-East Newfoundland stock complex.

5. There were differences in the infection rates of the followng parasites of cod between southern Labrador (2J) and the northeastern Grand Bank (3L): (1) plerocercoids of the cestode parasite Pyramicocephalus phocarum, (2) Anisakis sp. and, (3) Clavella uncinata.

6. On the basis of vertebral averages of cod collected during 1947-71, it was found that the main portion of the Labrador-East Newfoundland stock (Div. 2G to 3K) was well separated from the southern Grand Bank (Div. 3N and 3O) by the presence in the northern area of high vertebral means and of higher percentages of high vertebral numbers and the lack of low vertebral numbers in the southern area.

Cod from the offshore area in Div. 2G to 3K had somewhat higher vetebral numbers than those of the inshore area. The high vertebral count cod of the Labrador-East Newfoundland stock also extended to the northern slopes of the Grand Bank and around the Avalon Peninsula (Div. 3L), but in this area they usually intermingled with cod of the Avalon stock complex and with some migrants from southern Grand Bank as indicated by vertebral means intermediate between the northern and southern extremes.

Vertebral averages for samples from the western part of the Grand Bank, the Avalon Channel, the Avalon Peninsula, Placentia and Fortune Bays and vicinity were typically intermediate (between 54 and 55).

7. On the basis of six meristic characters of mature cod collected from spawning or post-spawning concentrations, it was found that the significantly higher meristic counts of the fin rays and vertebrae of the mature cod of the southeastern Hamilton Bank than those from the Funk Island Bank suggest that the Hamilton Bank cod are different from those of the Funk Island Bank and the northeast Newfoundland shelf. The patterns of tag returns from both areas also suggest different summer distributions, although there is some overlapping of the two major groupings.

   The homogeneity of the meristic characters from Funk Island Bank, and the northern Grand Bank do not suggest any differences, but the difference in the summer distribution of cod tagged on Funk Island Bank and the north cape of the Grand Bank suggest that these groups are different in their summer migration pattern. The significantly lower vertebral averages of the cod of the eastern slope of the Grand Bank suggest that the mature cod in this area during the spring are somewhat different from the other groups.

   Other studies on vertebral averages and dorsal fin rays confirmed that meristic characters were generally higher in 2J and 3K than they were in 3L although there was evidence of some overlapping.

8. The cod off Labrador (2J) showed a distinctively slower growth rate, than the cod from the Newfoundland east coast (3K) which grows somewhat faster. The growth rates of the cod of the north and northeastern part of the Grand Bank (3L) showed an even faster growth rate than that of 3K. Based upon the earlier growth rate studies, it has been concluded that since the growth rates of cod of the Labrador-Newfoundland east coast and northern edge of the Grand Bank were distinct enough to show considerable differences, then these stocks could not be very greatly intermingled.

9. Previous studies have shown that the size at first sexual maturity in the cod of the Labrador (2J) area was small, while that on the east coast of Newfoundland (3K) and on the northern and western edges of the Grand Bank (3L) were intermediate, while that on the southern part of the Grand Bank (3NO) was the largest of all.

10. On the basis of earlier studies it has been demonstrated that off Labrador (Subarea 2), cod were presumably spawning mainly in March-April in deep water on the continental slopes, with most of the remainder spawning in May and a small amount in June closer to the coast.

    In Div. 3K off northeast Newfoundland, at least as far south as Funk Island Bank and vicinity, cod spawning begins in March but occurs mainly in April to early May with some spawning continuing to June.

    In Div. 3L at the northern slope of the Grand Bank and in the Avalon Channel and on the northwestern slope of the Grand Bank, cod spawn mainly in April-June. Most of the spawning is usually over by June.

11. Based upon taggings during the 1950's and 1960's inshore at many localities from Labrador to the Avalon Peninsula and offshore from Hamilton Bank to the northern Grand Bank, cod of the Labrador-East Newfoundland stock were shown to intermingle and overlap from north to south in their winter-spring spawning areas in deep water on the slopes of the Labrador and northeast Newfoundland shelf. In the June-September (the main feeding and growing period) in the years after tagging, the most obvious migratory characteristic was the homing of most of the coastally tagged cod to or near the tagging area.

12. Based upon the tagging of about 25,000 Atlantic cod during February-March 1978-81 on the prespawning concentrations on Hamilton Bank, Belle Isle Bank, Funk Island Bank, and northern Grand Bank, there was evidence of a consistent annual pattern of migration to inshore waters during summer and to offshore areas during winter for each group of cod tagged along the outer continental shelf. The Hamilton Bank component (2J) evidently contributes to the southern Labrador (2J) and northeast Newfoundland (3K) coastal fisheries mainly from Notre Dame Bay northward. The Belle Isle Bank component (located mainly in 2J and a small portion in 3K) migrates during summer mainly to southern Labrador (2J), the Strait of Belle Isle entrance (4R) and northeastern Newfoundland as

far south as Notre Dame Bay (3K). The pattern of movement is similar to that of the Hamilton Bank component (2J) except for the greater proportion in the Strait of Belle Isle from the Belle Isle Bank component.

Cod on the northern and northeastern slopes of Funk Island Bank (3K) migrate during summer to eastern (3K) and southeastern Newfoundland (3L), with smaller proportions going to southern Labrador (2J) and the Strait of Belle Isle (4R) than from the taggings on Belle Isle Bank. Cod from the southwestern slope of Funk Island Bank (3K) contribute mainly to the summer inshore fishery of Notre Dame Bay (3K) and Bonavista Bay (3L) and in a smaller degree to the fishery in Trinity Bay, Conception Bay, and the eastern part of the Avalon Peninsula (3L). Thus, the components which overwinter and spawn on the northern, eastern, and western slopes of Funk Island Bank (3K) collectively form what might best be described as the "Eastern Newfoundland" stock, and the inshore fishery from White Bay to the Avalon Peninsula and to a small extent Labrador would likely be sensitive to changes in the size of this stock. Cod which overwinter on northern Grand Bank (3L) migrate southwards across the bank to the Virgin Rocks (3L) and to the eastern slope of the bank and to inshore areas in 3L. This component contributes mainly to the inshore fishery from Trinity Bay southward to St. Mary's Bay, with little effect on the fishery north of Cape Bonavista, i.e. is limited to NAFO Div. 3L.

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Table 1. Percentage distribution of adjusted tag recoveries in inshore areas of Labrador and eastern Newfoundland during the May-December periods to the end of 1982 from 11 tagging operations in offshore areas during the winters of 1978-81. (From Lear 1984b).

Recovery areas	Northeast Hamilton Bank (1981)	Belle Isle Bank (1978)	Northern Funk I. Bank (1978)	Northern Funk I. Bank (1979)	Northern Funk I. Bank (1981)	Eastern Funk I. Bank (1979)	Southeast Funk I. Bank (1980)	Western Funk I. Bank (1980)	Southwest Funk I. Bank (1981)	Northern Grand Bank (1980)
Labrador coast	35.9	35.5	16.0	14.0	19.7	5.6	2.4	1.8	0.0	0.0
Belle Isle Strait	6.3	15.9	10.5	5.8	7.8	2.8	2.0	2.4	2.0	2.0
White Bay	26.4	30.1	26.8	15.9	16.1	4.5	2.2	10.0	5.9	0.0
Notre Dame Bay	9.9	9.8	15.0	13.1	12.5	10.3	12.5	25.9	36.4	1.5
Bonavista Bay	6.8	6.1	11.0	17.4	10.9	25.6	14.5	26.6	28.2	4.4
Trinity Bay	7.7	2.3	5.2	18.9	14.1	22.9	25.9	13.5	12.7	24.6
Conception Bay	2.9	0.0	11.3	4.7	6.2	15.1	5.5	13.3	8.7	21.9
Southeast Avalon	4.1	0.3	2.7	6.5	9.1	4.7	10.8	6.0	2.1	23.3
St. Mary's Bay	0.0	0.0	1.5	3.6	4.1	9.1	24.2	0.7	3.8	24.3
Tag Recoveries	146	304	156	206	169	180	93	307	128	52

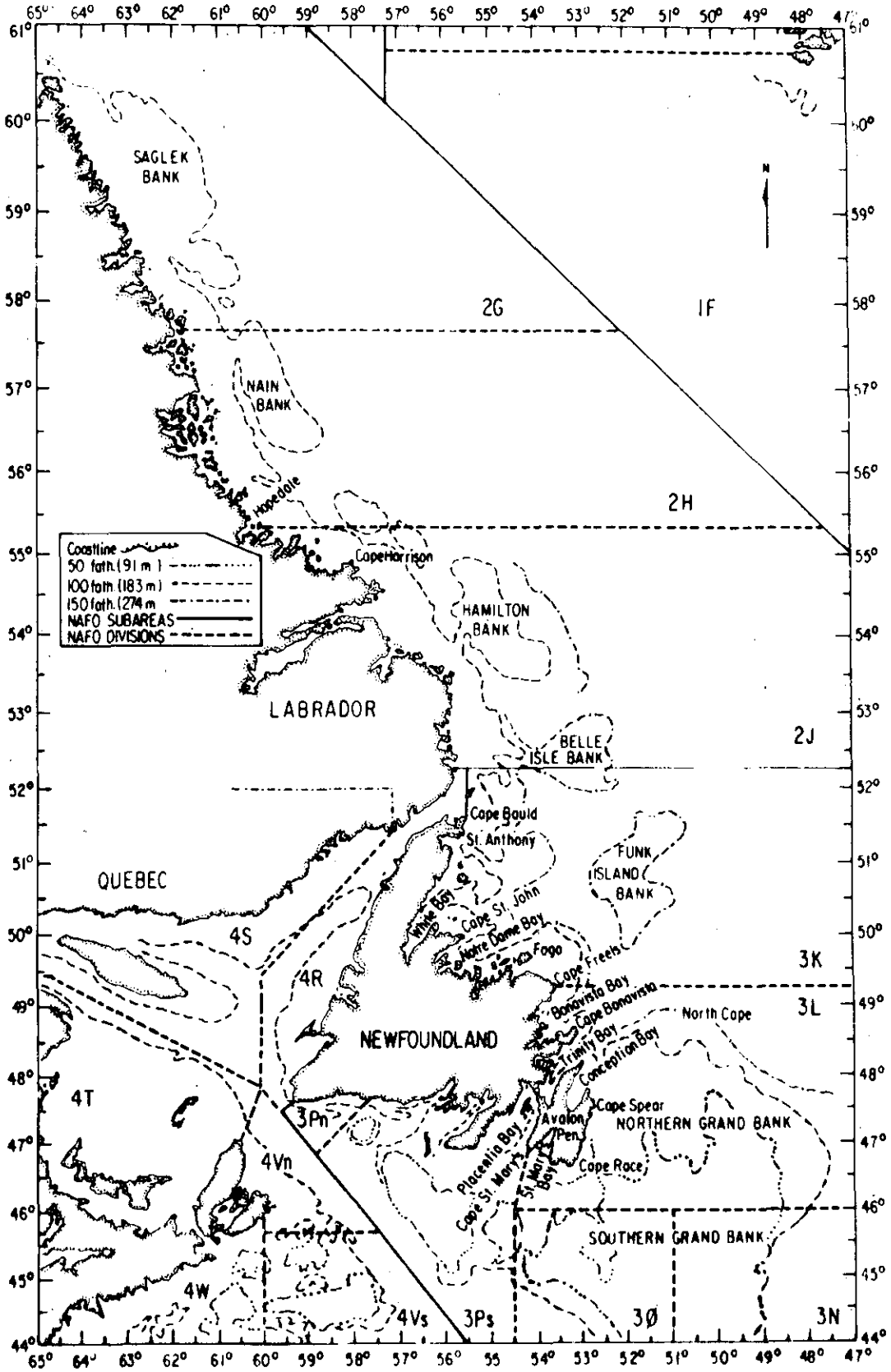

Fig. 1. Area map showing NAFO Divisions, offshore banks and some of the place names mentioned in the text.