# Genetic variation in Greenland halibut, Reinhardtius hippoglossoides, from the St. Lawrence system and the northwest Atlantic

par

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**RÉSUMÉ**

Une étude de la variabilité des allozymes a été réalisée dans le but de déterminer si les flétans du Groenland de la région du golfe du Saint-Laurent appartiennent à des populations génétiquement différenciées de celles de la région du nord-ouest de l'Atlantique. La variabilité génétique a été étudiée pour 13 loci codant pour 10 protéines enzymatiques. Le faible degré de différenciation génétique observé chez cette espèce ne permet pas de conclure que les populations de golfe du Saint-Laurent sont différenciées génétiquement de celles de la côte du Labrador. La fréquence des allozymes diffère peu entre les groupes d'âge étudiés ce qui indique que la structure génétique observée est stable sur une échelle temporelle.

**ABSTRACT**

An allozyme study was conducted to determine if Greenland halibut from the Gulf of St. Lawrence and the northwest Atlantic area belong to genetically differentiated populations. Genetic variations were studied at 13 loci coding for 10 proteins. Results show a low degree of genetic differentiation in this species. Genetic differentiation among age groups within sampling sites is also weak, suggesting that the observed structure is temporally stable.

**INTRODUCTION**

The Greenland halibut (Reinhardtius hippoglossoides) is an important commercial fish in the northwest Atlantic and in the Gulf of St. Lawrence. The management of the Gulf fishery has been complicated by the lack of information about the population structure of this species in the Gulf of St. Lawrence and by the fact that the importance of migration between the Gulf and the northwest Atlantic stocks is not well understood.

Fairbairn's (1981) analysis of allozyme variability at PHI (PGI-1* in this study) and PGM* loci indicate that Greenland halibut from the northwest Atlantic area form a single panmictic population that is differentiated but not completely isolated from the population of the Gulf of St. Lawrence.

Other stock identification studies of Atlantic coast Greenland halibut (see Fréchet 1987 for a summary) have shown differences between the Gulf and the Atlantic stocks in meristic characters (Templeman 1970; Misra and Bowering 1984; Bowering 1988), in population biological parameters such as fecundity and age at maturity (Bowering 1980; 1983), in the rate of infection by blood protozoa (Khan et al. 1982) as well as in the properties of the phosphoglucomutase enzyme (Dey 1982).

Tagging experiments carried out along the coast of Newfoundland and Labrador have shown that there is no migration of adult individuals between the Atlantic and the Gulf stocks (Bowering 1984).

Despite these studies, the contribution of the northwest Atlantic stock to Gulf stock production is not well understood. It has been hypothesized that substantial recruitment to the fishery in the Gulf of St. Lawrence originates from the Labrador stock (Bowering 1982). According to this hypothesis, young fish, larvae or eggs migrate or are passively transported into the Gulf, possibly through the strait of Belle Isle and, as they reach their sexual maturity, they migrate out of the Gulf of St. Lawrence to reproduce. This hypothesis is supported by the synchronism of high recruitment between the Gulf and the Labrador coast stocks as well as by the absence of large individuals in the Gulf (Bowering 1982). However, there are indications that spawning is taking place in the Gulf of St. Lawrence. Indeed, the presence of individuals in spawning condition has been reported in southwest Newfoundland (Templeman 1970, 1973; Tremblay and Axelsen 1981; Bowering 1982) and larvae, although in reduced number, were also observed on the west coast of Newfoundland and in the St. Lawrence Estuary (de Lafontaine 1980). The presence of these larvae in the Gulf could, however, result from their transportation from the Atlantic coast spawning grounds as well as from the spawning of the local stock.

The objective of the present study is to describe the genetic variability of Greenland halibut in the St. Lawrence system and the northwest Atlantic and to determine if the patterns observed support the hypothesis that a genetically differentiated population is present in the Gulf of St. Lawrence.

Greenland halibut is also present in the Saguenay Fjord (Drainville 1970), where the population may be isolated. Samples from this environment were also included to determine if the physical characteristics of the fjord represent an effective barrier to gene flow between the St. Lawrence Estuary and the Fjord stock.

This work is complementary to the study of Greenland halibut parasites conducted by R. Arthur of the Parasitology Section at the Maurice Lamontagne Institute and was coordinated with it.

**MATERIALS AND METHODS**

A) Sampling

Sampling sites located in the Estuary and the Gulf of St. Lawrence, and in the northwest Atlantic (Fig. 1) were visited during the annual research groundfish survey conducted in August 1990 and the shrimp survey conducted off the Labrador coast in July 1990. Greenland halibut in spawning condition were also collected during the winter groundfish survey (January 1990). A sample from Cumberland Sound was obtained in February 1990. Specimens from the Saguenay Fjord were collected during a summer cruise in 1990 and during the winter sport fishery in 1991.

At the sites Estuary, Sept-Iles, Esquiman Channel, Hawke Channel and Hopedale area, specimens belonging to three different size-age groups were collected to assess the temporal variability of the observed genetic structure (Table 1). The homogeneity of Group C regarding the age and size composition is lower than for groups A and B. Where possible, 50 males and females were collected in each size group.

During cruises, fish were measured and samples of liver and muscle were collected and kept frozen on dry ice or in liquid nitrogen. At the laboratory the tissue samples were transferred to a freezer and held at -80°C until analysis.

B) Electrophoretic analysis

Homogenates were prepared according to the procedure described in Roby et al. (1991). The enzymatic systems studied are listed in Table 2. The gene nomenclature for protein-coding loci follows the nomenclature recommended by Shaklee et al. (1990). Staining of the enzymes was as described by Murphy et al. (1990). All enzymes were assayed on cellulose acetate gels using the technique of Hebert and Beaton (1989) except for esterases which were studied on discontinuous polyacrylamide slab gels (Ornstein 1964) and

isocitrate dehydrogenase, which was separated by isoelectric focusing on polyacrylamide slab gels (5% polyacrylamide, 3.0% ampholyte; pH range 3-10). Individuals of known genotype were run on each gel to facilitate identification of alleles. Uncommon alleles at each locus were rerun simultaneously to ascertain their classification.

C) Statistical analysis.

Statistical analyses were carried out in part with the Biosys-1 computer program (Swofford and Selander 1989). Samples were tested for deviations from Hardy-Weinberg expectations using the chi-square test for goodness of fit. Allelic frequency differences among groups within sites and among sampling sites were tested for significance with the G test of heterogeneity. It was necessary to group uncommon alleles into a single class as recommended when expected frequencies of some classes are low (Sokal and Rohlf 1981).

Differentiation among populations was estimated using Cavalli-Sforza and Edwards' genetic distance (1967). A principal coordinate analysis on which a minimum spanning tree was superimposed was computed from the resulting matrix using NTSYS, version 1.40 (Rohlf 1988).

Gene flow was qualitatively evaluated using the method of rare alleles (Slatkin 1985). Gene flow and the number of migrants were also estimated from Wright's fixation index according to the formula:

$$F_{ST} = 1/(1 + 4N_e m)$$

where m = migration rate and $N_e$ = effective number of individuals (Wright 1969).

**RESULTS**

The samples analyzed are described in Table 1. Allelic frequencies and observed and expected heterozygosities measured at the 13 polymorphic loci studied in the muscle or the liver (Table 2) are presented in Table 3. PGM* and PGI-1* are the only two loci studied by Fairbairn (1981) and by Riget et al. (1992) that were also included in the present work. ADA* , PGI-1*, ADHP* and MDH* were studied by Riget et al. (1992). MPI*, G3PDH-1*, G3PDH-2*, LDH*, EST-1* and EST-2* were not scored in previous studies.

Differences were observed in the number of alleles detected at some of the loci that were the object of previous studies. Fairbairn (1981) detected a total of six alleles at the PGM* locus in the northwest Atlantic and the Gulf of St. Lawrence compared to five in the present study. Riget et al. (1992) detected five at this locus in the Newfoundland and Davis Strait samples. Five, three and six alleles were detected at the PGI-1* locus by

Fairbairn (1981), Riget et al. (1992) and the present study, respectively. Two alleles were found at the MDH* loci in the northwest Atlantic by Riget et al. (1992) compared to five in this study. Three, four and seven alleles were detected at the loci GPI-2*, IDHP* and ADA* by Riget et al. (1992) and in this study.

The observed numbers of genotypes were in conformance to Hardy-Weinberg expectations for most loci in the different age groups and for most age groups pooled. Statistically significant excess of homozygotes ($P<0.05$) was observed at the locus ADA* for the age groups B, C and the age group pooled for the site Estuary. Excess of homozygotes was also observed at the locus EST-1* for all the sites and age groups except for the site Estuary (groups B and C), Esquiman (group B) and Hawke Channel (group B). A deficit in heterozygotes was also detected at the GPI-1* for age group C and G3PDH-2* for Group B at the site Sept-Iles and G3PDH-1* for the group B at the site Esquiman Channel. Excess of homozygotes was also observed at the IDDH* locus for the Saguenay Fjord sample, for the site Estuary (Groups B, C and pooled), for the site Sept-Iles (groups A, B and pooled), for the site Esquiman (groups A and B), for the spawning group, for Hawk Channel (groups C and pooled) and Hopedale area (Groups B, C and pooled). Excess of homozygotes was also observed at the IDHP* locus in Hawk Channel sample (Age group A) and Hopedale area (Group A) and at the PGM* locus for the site Estuary (group B and pooled).

The results of the heterogeneity tests for the comparison of allelic frequencies among the three age groups of the sites Estuary, Sept-Iles, Esquiman Channel, Hawke Channel and Hopedale area are presented in Table 4. Statistically significant changes in allelic frequency with age were observed at the loci ADA* (Estuary), GPI-1* (Esquiman Channel) and EST-1* (Esquiman Channel, Hawke Channel and Hopedale area).

Geographic differences in allelic frequencies are generally weak and the results of the comparisons made within and between the Gulf of St. Lawrence and the Atlantic regions are presented Table 5. Significant differences among sites within the Gulf were detected at the loci EST-1* in group B and for the pooled sample and at the locus IDDH* in group B. Differences among the Atlantic sites were found at the locus ADA* in the pooled sample, at the EST-1* locus in groups B and C and for the pooled sample and at the IDDH* locus in group c. Differences between the Gulf and the Atlantic regions were significant at the loci EST-1* (groups A and C), GPI-1* and IDDH* (group A). No difference could be detected for group B and for the pooled samples at any locus (Table 5).

Comparisons of allelic frequencies were also made between the samples collected in the Saguenay Fjord and those of the Estuary to evaluate the importance of migration across this potential ecological barrier. Differences were observed at the PGM* ($G=36.56$, 3df, $P < 0.001$) and EST-1* ($G=11.460$, 4df, $P < 0.05$).

The matrix of genetic distance of Cavalli-Sforza and Edwards for pooled samples presented in Table 6 is represented in the ordination of Figure 2. The ordinations of genetic distance matrices calculated for the three age groups of Table 1 are also represented in Figure 2. The position of the groups differs with age and it is worth noting that the groups are not separated according to the main region: Gulf vs Atlantic. For the pooled samples, Sept-Iles occupies a central position while Cumberland Sound stands apart.

The values of the number of migrants calculated from Wright's fixation index (Table 7) indicate that gene flow is important in Greenland halibut. This observation is in agreement with the high level of gene flow indicated by the relationship of conditional average frequency of alleles and their incidence in Greenland halibut sampling sites (Fig. 3).

**DISCUSSION**

The present work covers a large geographic area within the distribution of the Greenland halibut, including regions not sampled before. A large number of loci were examined, including those described by Fairbairn (1981) and by Riget et al. (1992) and others not described in earlier studies. Our results are in general agreement with those of Fairbairn (1981) and Riget et al. (1992). Indeed, the observed frequencies of the most common alleles segregating at the GPI-1* and PGM* loci in the present study are very similar to the frequencies detected by Fairbairn (1981) at the same loci almost 10 years earlier and to those obtained by Riget et al. (1992). Small discrepancies in allelic frequencies and in the number of alleles detected can most likely be attributed to differences in the techniques used (starch in the studies of Riget et al. (1992) and Fairbairn (1981), in sample size and in the age groups studied.

The analysis of the genetic variation detected in the present study reveals a low level of genetic differentiation, indicating that a high gene flow is taking place across the studied area. Indeed, the presence of alleles of low frequency at several sampling sites from the Saguenay to Cumberland Sound as well as the important number of migrants estimated from Wright's fixation index are indications of the importance of gene flow in this species. Differences between sampling sites within and between regions were detected only at some loci and for specific age groups.

The statistically significant geographical differences in allelic frequencies observed are largely the result of differences observed at the loci ADA* and EST-1, although differences were also observed at a few other loci (Table 5). It is interesting to note that most of the variations in allelic frequency among age groups were also detected at those loci (Table 4). Kirpichnikov (1992) has attributed changes in allelic frequencies with age to the influence

of environmental factors. If selection is acting on some of the loci used in this study, the apparent geographic differentiation observed could be inflated.

The apparent differentiation of Cumberland Sound Greenland halibut from the other populations of the Atlantic region and the Gulf is interesting because this sample is comprised of large size females only. However, preliminary analysis did not reveal important differences in allelic frequencies between sexes.

The importance of gene flow observed in this study from the number of migrants calculated from Wright index and described in the conditional average frequency graph (Fig. 2) is in agreement with the results obtained by Riget et al. (1992) in their study of Greenland halibut from Greenland and Denmark and with those Fairbairn (1981), who concluded that some migration takes place between the Gulf of St. Lawrence and the northeastern Newfoundland populations even though they belonged to separate breeding areas. Differences in allelic frequencies among the sampling sites of the Atlantic and the Gulf of St. Lawrence are as important as the differences observed between the Atlantic and the Gulf regions. This may be an indication that local differentiation is taking place. A recent study (Arthur and Albert, 1993) in which parasites were used as biological tags has shown that it was possible to differentiate adult Greenland halibut of the Gulf of St. Lawrence from those of adjacent areas of the Saguenay Fjord and the Atlantic Ocean. This study indicates that little mixing of adults and sub-adults is taking place between areas. Furthermore, tagging experiments carried out along the coast of Newfoundland and Labrador have shown that larger individuals do not enter the Gulf of St. Lawrence (Bowering 1984). Since the present study indicates that little genetic differentiation has taken place within the study area and that gene flow is important, it is likely, as has been suggested by Bowering (1982), that migration is taking place during the early phases of the life cycle of this species. The shallow waters in the Belle Isle Strait probably represent an effective barrier to migration of larger animals, as do the shallow sill at the entrance of the Saguenay Fjord.

## CONCLUSIONS

Gene flow is apparently high between Greenland halibut stocks from the Gulf of St. Lawrence and those of the northwest Atlantic. Local differentiation, as indicated by changes in allelic frequencies with age, seems to take place despite this gene flow.

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Table 1. Description of the samples analyzed.

| SAMPLING SITES | SAMPLING DATES | GROUPS | | | | | | SAMPLING DEPTH (M) |
|---|---|---|---|---|---|---|---|---|
| | | A | | B | | C | | |
| | | SIZE(mm) | AGE(y) | SIZE(mm) | AGE(y) | SIZE(mm) | AGE(y) | |
| SAGUENAY FJORD | JUNE 90 FEB. 91 | | | | | MAX:720 CV:15.6 MIN:407 AVG:513 N=99 | MAX:13 CV:20.3 MIN:6 AVG:8.34 N=94 | 250 |
| ESTUARY | AUGUST SEPT. 90 | MAX:180 CV:4.1 MIN:160 AVG:167 N=68 | MAX:2 CV: 0 MIN:2 AVG:2 N=68 | MAX:300 CV:5.2 MIN:250 AVG:277 N=58 | MAX:4 CV:14.0 MIN:3 AVG:3.35 N=58 | MAX:660 CV:15.3 MIN:400 AVG:501 N=28 | MAX:11 CV:20.7 MIN:4 AVG:7.82 N=28 | 268 |
| SEPT-ILES | AUGUST SEPT. 90 | MAX:230 CV:1.3 MIN:140 AVG:178 N=122 | MAX:3 CV:11.8 MIN:1 AVG:1.95 N=121 | MAX:340 CV:5.7 MIN:260 AVG:302 N=97 | MAX:5 CV:9.1 MIN:3 AVG:4.07 N:87 | MAX:650 CV:13.0 MIN:350 AVG:464 N=48 | MAX:10 CV:13.1 MIN:5 AVG:7.12 N=46 | 293 |
| ESQUIMAN CHANNEL | AUGUST SEPT. 90 | MAX:240 CV:12.6 MIN:150 AVG:205 N=24 | MAX:3 CV:25.8 MIN:1 AVG:2.48 N=24 | MAX:340 CV:7.8 MIN:250 AVG:298 N=60 | MAX:5 CV:14.8 MIN:3 AVG:4.2 N=59 | MAX:650 CV:14.3 MIN:360 AVG:516 N=53 | MAX:12 CV:18.8 MIN:5 AVG:8.1 N=48 | 246 |
| SPAWNERS | JANUARY 90 | | | | | MAX:650 CV:11.7 MIN:350 AVG:459 N=234 | MAX:11 CV:13.8 MIN:6 AVG:7.53 N=97 | 325 |
| HAWKE CHANNEL | JULY 90 | MAX:200 CV:6.0 MIN:170 AVG:183 N=28 | MAX:3 CV:20.1 MIN:2 AVG:2.34 N=28 | MAX:340 CV:12.3 MIN:250 AVG:291 N=19 | MAX:6 CV:13.2 MIN:4 AVG:4.4 N=19 | MAX:840 CV:12.6 MIN:350 AVG:454 N=88 | MAX:14 CV:14.7 MIN:5 AVG:7.28 N=88 | 364 |
| HOPEDALE CHANNEL | JULY 90 | MAX:200 CV:6.1 MIN:160 AVG:186 N=71 | MAX:3 CV:16.0 MIN:2 AVG:2.13 N=71 | MAX:340 CV:9.8 MIN:250 AVG:294 N=96 | MAX:5 CV:15.8 MIN:3 AVG:4.25 N=96 | MAX:630 CV:13.6 MIN:350 AVG:446 N=126 | MAX:11 CV:19.8 MIN:5 AVG:7.01 N=126 | 470 |
| CUMBERLAND SOUND | FEBRUARY 90 | | | | | MAX:945 CV:11.9 MIN:485 AVG:715 N=134 | MAX:15 CV:17.1 MIN:8 AVG:10.9 N=23 | 600 |

Table 2. Description of the enzymatic systems studied. M = muscle; L = liver; IEF = isoelectric focusing; CA = cellulose acetate electrophoresis; P = polyacrylamide gel electrophoresis.

| Enzyme | EC. No. | No. of loci | No. of alleles | Tissue used | Method |
|---|---|---|---|---|---|
| Adenosine deaminase (ADA) | 3.5.4.4 | 1 | 8 | M | CA |
| Esterase (EST) | 3.1.1.- | 2 | EST-1: 7<br>EST-2: 2 | M | P |
| Glucose-6-phosphate isomerase (GPI) | 5.3.1.9 | 2 | GPI-1: 6<br>GPI-2: 3 | M | CA |
| Glycerol-3-phosphate dehydrogenase (G3PDH) | 1.1.1.8 | 2 | G3PDH-1: 3<br>G3PDH-2: 4 | M, L | CA |
| L-Iditol dehydrogenase (IDDH) | 1.1.1.14 | 1 | 4 | L | CA |
| Isocitrate dehydrogenase (IDHP) | 1.1.1.42 | 1 | 4 | L | IEF |
| L-Lactate dehydrogenase (LDH) | 1.1.1.27 | 1 | 3 | M | CA |
| Malate dehydrogenase (MDH) | 1.1.1.37 | 1 | 5 | M | CA |
| Mannose-6-phosphate dehydrogenase (MPI) | 5.3.1.8 | 1 | 3 | L | CA |
| Phosphoglucomutase (PGM) | 5.4.2.2 | 1 | 5 | L | CA |

Table 3. Allele frequencies and observed (Hobs) and expected (Hobs) heterozygosities for the loci studied in all groups pooled (N = sample size).

| Locus | Population | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Saguenay Fjord | Estuary | Sept-Iles | Spawners | Esquiman Channel | Hawke Channel | Hopedale Channel | Cumberland Sound |
| ADA | | | | | | | | |
| (N) | 99 | 150 | 260 | 233 | 136 | 128 | 294 | 133 |
| *A | .056 | .050 | .042 | .032 | .059 | .043 | .049 | .034 |
| *B | .384 | .360 | .433 | .459 | .364 | .445 | .372 | .410 |
| *C | .247 | .253 | .263 | .232 | .276 | .324 | .287 | .237 |
| *D | .056 | .053 | .052 | .034 | .029 | .039 | .049 | .075 |
| *E | .253 | .247 | .185 | .223 | .243 | .145 | .201 | .214 |
| *F | .005 | .000 | .006 | .006 | .000 | .000 | .020 | .000 |
| *G | .000 | .037 | .019 | .011 | .026 | .004 | .019 | .030 |
| *H | .000 | .000 | .000 | .002 | .004 | .000 | .002 | .000 |
| Hobs | .727 | .620 | .669 | .648 | .750 | .641 | .694 | .639 |
| Hexp | .721 | .739 | .704 | .683 | .728 | .672 | .733 | .722 |
| EST-1 | | | | | | | | |
| (N) | 96 | 151 | 217 | 232 | 136 | 131 | 273 | 134 |
| *A | .016 | .000 | .005 | .011 | .004 | .004 | .002 | .007 |
| *B | .245 | .215 | .251 | .231 | .265 | .233 | .176 | .362 |
| *C | .349 | .298 | .311 | .267 | .401 | .427 | .353 | .354 |
| *D | .240 | .245 | .270 | .280 | .221 | .214 | .280 | .250 |
| *E | .135 | .232 | .161 | .207 | .107 | .118 | .172 | .022 |
| *F | .016 | .010 | .002 | .004 | .004 | .004 | .013 | .004 |
| *G | .000 | .000 | .000 | .000 | .000 | .000 | .004 | .000 |
| Hobs | .552 | .636 | .530 | .547 | .566 | .366 | .491 | .358 |
| Hexp | .742 | .751 | .741 | .754 | .709 | .703 | .736 | .680 |
| EST-2 | | | | | | | | |
| (N) | 95 | 148 | 216 | 232 | 136 | 131 | 266 | 134 |
| *A | 1.000 | .993 | .998 | .996 | 1.000 | 1.000 | .998 | 1.000 |
| *B | .000 | .007 | .002 | .004 | .000 | .000 | .002 | .000 |
| Hobs | 0 | .014 | .005 | .009 | 0 | 0 | .004 | 0 |
| Hexp | 0 | .013 | .005 | .009 | 0 | 0 | .004 | 0 |
| GPI-1 | | | | | | | | |
| (N) | 102 | 153 | 260 | 232 | 139 | 131 | 292 | 133 |
| *A | .725 | .712 | .723 | .711 | .727 | .683 | .685 | .718 |
| *B | .074 | .065 | .054 | .060 | .036 | .046 | .057 | .079 |
| *C | .186 | .199 | .213 | .207 | .223 | .256 | .245 | .188 |
| *D | .010 | .010 | .002 | .009 | .011 | .008 | .005 | .004 |
| *E | .005 | .013 | .004 | .013 | .000 | .004 | .009 | .011 |
| *F | .000 | .000 | .004 | .000 | .004 | .004 | .000 | .000 |
| Hobs | .451 | .477 | .404 | .453 | .403 | .466 | .459 | .421 |
| Hexp | .433 | .448 | .429 | .447 | .421 | .466 | .468 | .443 |
| GPI-2 | | | | | | | | |
| (N) | 102 | 153 | 260 | 231 | 139 | 131 | 292 | 133 |
| *A | 1.000 | 1.000 | .994 | .998 | .996 | 1.000 | 1.000 | .996 |
| *B | .000 | .000 | .004 | .002 | .004 | .000 | .000 | .004 |
| *C | .000 | .000 | .002 | .000 | .000 | .000 | .000 | .000 |
| Hobs | 0 | 0 | .012 | .004 | .007 | 0 | 0 | .008 |
| Hexp | 0 | 0 | .011 | .004 | .007 | 0 | 0 | .007 |
| G3PDH-1 | | | | | | | | |
| (N) | 102 | 153 | 265 | 236 | 138 | 131 | 290 | 132 |
| *A | .799 | .846 | .779 | .833 | .812 | .790 | .778 | .765 |
| *B | .201 | .154 | .221 | .166 | .188 | .210 | .217 | .235 |
| *C | .000 | .000 | .000 | .000 | .000 | .000 | .005 | .000 |
| Hobs | .284 | .268 | .328 | .275 | .261 | .313 | .355 | .348 |
| Hexp | .321 | .260 | .344 | .279 | .306 | .332 | .348 | .359 |

Table 3 (continued).

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| G3PDH-2 | | | | | | | | |
| (N) | 98 | 149 | 262 | 234 | 135 | 132 | 293 | 132 |
| *A | .980 | 1.000 | .992 | .998 | .993 | .992 | .998 | .992 |
| *B | .010 | .000 | .000 | .002 | .000 | .004 | .000 | .004 |
| *C | .010 | .000 | .002 | .000 | .004 | .004 | .002 | .004 |
| *D | .000 | .000 | .006 | .000 | .004 | .000 | .000 | .000 |
| Hobs | .041 | 0 | .008 | .004 | .015 | .015 | .003 | .015 |
| Hexp | .040 | 0 | .015 | .004 | .015 | .015 | .003 | .015 |
| IDDH | | | | | | | | |
| (N) | 69 | 137 | 229 | 216 | 126 | 128 | 240 | 51 |
| *A | .203 | .223 | .199 | .181 | .202 | .227 | .179 | .137 |
| *B | .326 | .292 | .312 | .190 | .306 | .387 | .352 | .343 |
| *C | .297 | .292 | .264 | .389 | .262 | .184 | .250 | .363 |
| *D | .174 | .193 | .225 | .241 | .230 | .203 | .219 | .157 |
| Hobs | .435 | .526 | .563 | .491 | .579 | .602 | .604 | .431 |
| Hexp | .734 | .743 | .743 | .722 | .744 | .724 | .734 | .707 |
| IDHP | | | | | | | | |
| (N) | 89 | 134 | 249 | 229 | 130 | 130 | 277 | 131 |
| *A | .152 | .112 | .141 | .151 | .108 | .123 | .123 | .080 |
| *B | .848 | .877 | .857 | .849 | .885 | .873 | .872 | .912 |
| *C | .000 | .000 | .000 | .000 | .000 | .000 | .005 | .008 |
| *D | .000 | .011 | .002 | .000 | .008 | .004 | .000 | .000 |
| Hobs | .281 | .231 | .261 | .240 | .200 | .208 | .199 | .160 |
| Hexp | .257 | .218 | .245 | .256 | .206 | .223 | .225 | .161 |
| LDH | | | | | | | | |
| (N) | 102 | 153 | 270 | 235 | 139 | 131 | 292 | 135 |
| *A | .995 | 1.000 | 1.000 | .998 | .996 | 1.000 | 1.000 | .996 |
| *B | .005 | .000 | .000 | .002 | .000 | .000 | .000 | .004 |
| *C | .000 | .000 | .000 | .000 | .004 | .000 | .000 | .000 |
| Hobs | .010 | 0 | 0 | .004 | .007 | 0 | 0 | .007 |
| Hexp | .010 | 0 | 0 | .004 | .007 | 0 | 0 | .007 |
| MDH | | | | | | | | |
| (N) | 99 | 150 | 269 | 234 | 136 | 132 | 292 | 132 |
| *A | .995 | .993 | .989 | .998 | .989 | .996 | .995 | .996 |
| *B | .000 | .000 | .002 | .000 | .004 | .000 | .000 | .000 |
| *C | .005 | .000 | .006 | .002 | .007 | .004 | .005 | .004 |
| *D | .000 | .003 | .004 | .000 | .000 | .000 | .000 | .000 |
| *E | .000 | .003 | .000 | .000 | .000 | .000 | .000 | .000 |
| Hobs | .010 | .013 | .022 | .004 | .022 | .008 | .010 | .008 |
| Hexp | .010 | .013 | .022 | .004 | .022 | .008 | .010 | .008 |
| MPI | | | | | | | | |
| (N) | 89 | 148 | 266 | 229 | 134 | 131 | 286 | 123 |
| *A | 1.000 | 1.000 | .998 | .998 | 1.000 | .996 | .990 | 1.000 |
| *B | .000 | .000 | .000 | .002 | .000 | .004 | .010 | .000 |
| *C | .000 | .000 | .002 | .000 | .000 | .000 | .000 | .000 |
| Hobs | 0 | 0 | .004 | .004 | 0 | .008 | .021 | 0 |
| Hexp | 0 | 0 | .004 | .004 | 0 | .008 | .021 | 0 |
| PGM | | | | | | | | |
| (N) | 99 | 150 | 272 | 233 | 136 | 132 | 292 | 132 |
| *A | .783 | .770 | .778 | .766 | .824 | .777 | .801 | .864 |
| *B | .157 | .150 | .149 | .161 | .140 | .163 | .147 | .095 |
| *C | .051 | .057 | .051 | .067 | .029 | .049 | .041 | .034 |
| *D | .005 | .023 | .020 | .006 | .007 | .008 | .010 | .008 |
| *E | .005 | .000 | .002 | .000 | .000 | .004 | .000 | .000 |
| Hobs | .364 | .440 | .371 | .382 | .316 | .356 | .312 | .258 |
| Hexp | .360 | .381 | .370 | .383 | .301 | .368 | .334 | .244 |

Table 4. Test values (G-tests) for heterogeneity of allelic variation among groups within five sampling sites. Degrees of freedom are in parentheses (* = P<.05).

| Locus | Sampling Sites | | | | |
|---|---|---|---|---|---|
| | Estuary | Sept-Iles | Esquiman Channel | Hawke Channel | Hopedale Channel |
| ADA | 18.400(10)* | 8.784 (12) | 6.865 (10) | 1.955 (8) | 5.702 (12) |
| EST-1 | 9.300 (6) | 10.3912 (8) | 211.116 (6)* | 14.661 (6)* | 26.310 (8)* |
| GPI-1 | 2.219 (6) | 6.618 (6) | 9.590 (4)* | 5.006 (6) | 8.710 (6) |
| G3PDH-1 | 1.924 (2) | 0.851 (2) | 1.612 (2) | 0.902 (2) | 1.487 (2) |
| IDDH | 10.390 (6) | 5.733 (6) | 5.777 (6) | 1.443 (6) | 5.984 (6) |
| IDHP | 3.705 (2) | 0.934 (2) | 2.998 (2) | 1.913 (2) | 2.874 (2) |
| PGM | 5.654 (6) | 4.996 (6) | 6.722 (2) | 2.304 (4) | 4.719 (6) |

Table 5. Test values (G) for heterogeneity of allelic frequencies among sites for Greenland halibut of groups A, B and C and for pooled samples[1]. Gulf = Estuary, Sept-Iles and Esquiman Channel; Atlantic = Hawke Channel, Hopedale Channel and Cumberland Sound. Degrees of freedom are in parentheses;(* = P < .05; ** = P < .01; *** = P < .001).

| LOCUS | COMPARISON | GROUP A | GROUP B | GROUP C | POOLED[1] |
|---|---|---|---|---|---|
| ADA | Gulf | 11.534 (8) | 13.346 (10) | 5.508 (12) | 19.819 (15) |
| | Atlantic | 8.415 (4) | 0.689 (4) | 17.627 (10) | 26.020 (10)* |
| | Gulf x Atlantic | 9.775 (6) | 4.012 (5) | 4.383 (6) | 10.452 (7) |
| EST-1 | Gulf | 6.517 (8) | 23.196 (6)*** | 13.723 (12) | 29.408 (12)* |
| | Atlantic | 2.710 (3) | 12.080 (3)** | 66.444 (6)*** | 76.822 (10)* |
| | Gulf x Atlantic | 12.056 (4)* | 3.248 (4) | 16.862 (5)** | 9.500 (5) |
| GPI-1 | Gulf | 5.107 (4) | 6.973 (6) | 2.852 (6) | 7.034 (9) |
| | Atlantic | 0.489 (2) | 1.044 (3) | 6.878 (6) | 4.386 (6) |
| | Gulf x Atlantic | 8.632 (3)* | 1.613 (3) | 1.414 (4) | 6.044 (4) |
| G3PDH-1 | Gulf | 0.652 (2) | 3.566 (2) | 7.241 (3) | 5.851 (3) |
| | Atlantic | 0.390 (1) | 0.015 (1) | 0.173 (2) | 0.484 (2) |
| | Gulf x Atlantic | 0.003 (1) | 0.151 (1) | 1.618 (1) | 2.511 (1) |
| IDDH | Gulf | 3.853 (6) | 12.799 (6)* | 6.023 (9) | 3.810 (9) |
| | Atlantic | 0.942 (3) | 3.412 (3) | 13.036 (6)* | 5.376 (6)* |
| | Gulf x Atlantic | 7.947 (3)* | 4.394 (3) | 2.409 (3) | 7.076 (3) |
| IDHP | Gulf | 1.214 (2) | 0.948 (2) | 5.503 (3) | 2.148 (3) |
| | Atlantic | 0.509 (1) | 0.065 (1) | 5.821 (2) | 3.221 (2) |
| | Gulf x Atlantic | 0.123 (1) | 4.708 (1) | 7.857 (1) | 1.571 (2) |
| PGM | Gulf | 3.751 (4) | 7.360 (4) | 5.698 (6) | 6.174 (6) |
| | Atlantic | 1.562 (2) | 0.408 (2) | 9.581 (6) | 7.973 (6) |
| | Gulf x Atlantic | 1.781 (3) | 0.624 (3) | 3.127 (3) | 2.866 (3) |

[1] Pooled samples represent all the individuals within each region regardless of age group, e.g. Gulf (Saguenay, Estuary, Sept-Iles, Esquiman Channel), Atlantic (Hawke Channel, Hopedale Channel and Cumberland Sound).

Table 6. Cavalli-Sforza & Edwards (1967) genetic distances for pooled samples.

| Population | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| 1 SAGUENAY FJORD | ***** | | | | | | | |
| 2 ESTUARY | .069 | ***** | | | | | | |
| 3 SEPT-ILES | .056 | .052 | ***** | | | | | |
| 4 SPAWNERS | .058 | .057 | .053 | ***** | | | | |
| 5 ESQUIMAN CHANNEL | .063 | .063 | .048 | .069 | ***** | | | |
| 6 HAWKE CHANNEL | .055 | .069 | .052 | .075 | .052 | ***** | | |
| 7 HOPEDALE CHANNEL | .060 | .060 | .051 | .060 | .062 | .057 | ***** | |
| 8 CUMBERLAND SOUND | .072 | .088 | .074 | .085 | .070 | .079 | .081 | ***** |

Table 7. Fst indices for each locus and estimates of the number of migrants ($N_em$) per generation for pooled samples.

| Locus | F(ST) | $N_em$ |
|---|---|---|
| ADA | .005 | 50 |
| EST-1 | .013 | 19 |
| EST-2 | .003 | 83 |
| GPI-1 | .002 | 125 |
| GPI-2 | .002 | 125 |
| G3PDH-1 | .004 | 50 |
| G3PDH-2 | .004 | 62 |
| IDDH | .011 | 22 |
| IDHP | .004 | 62 |
| LDH | .002 | 125 |
| MDH | .002 | 125 |
| MPI | .005 | 50 |
| PGM | .004 | 62 |
| **Mean** | **.007** | 35 |

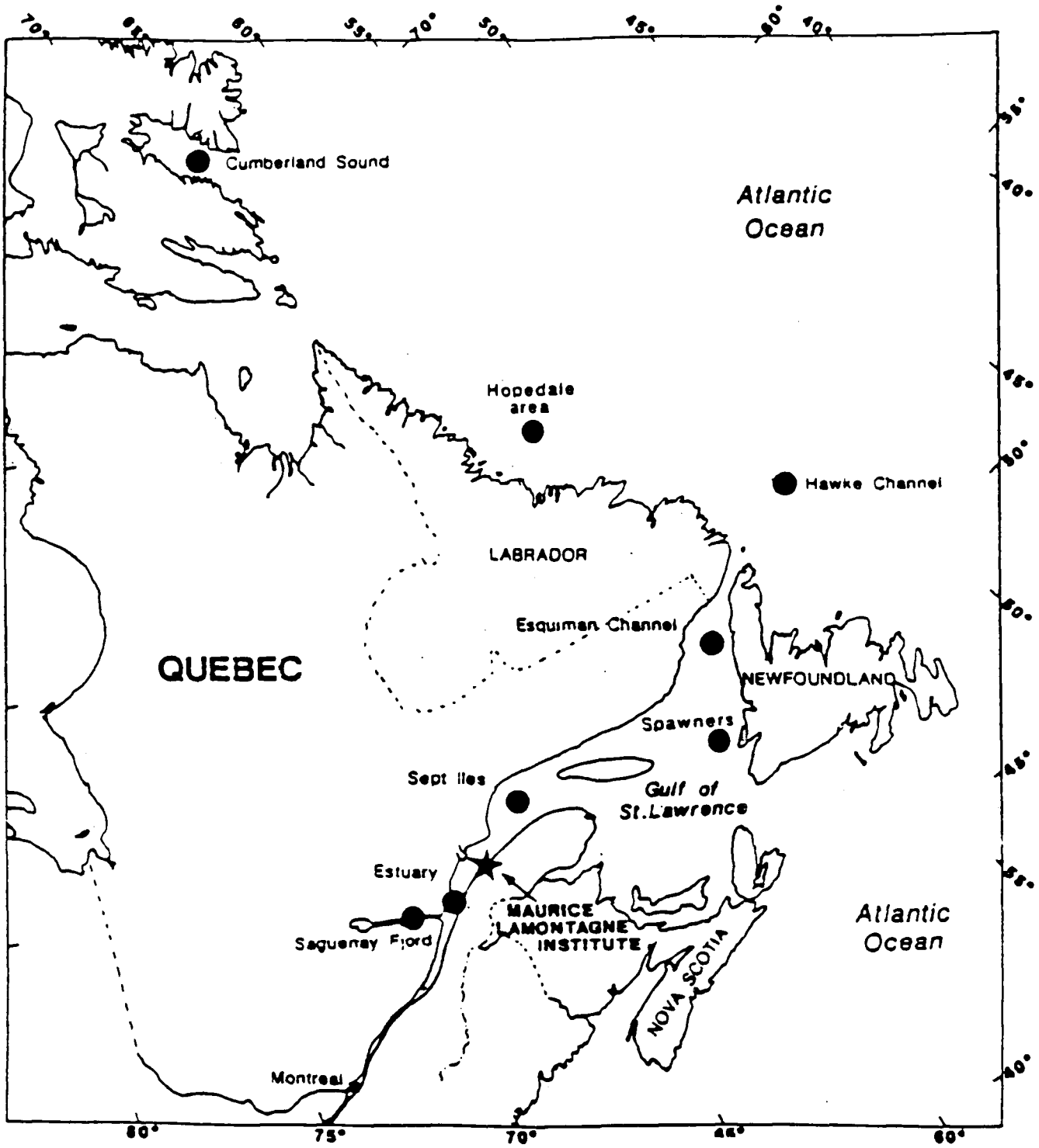


Figure 1. Map of Eastern Canada showing the sampling sites for Greenland halibut.

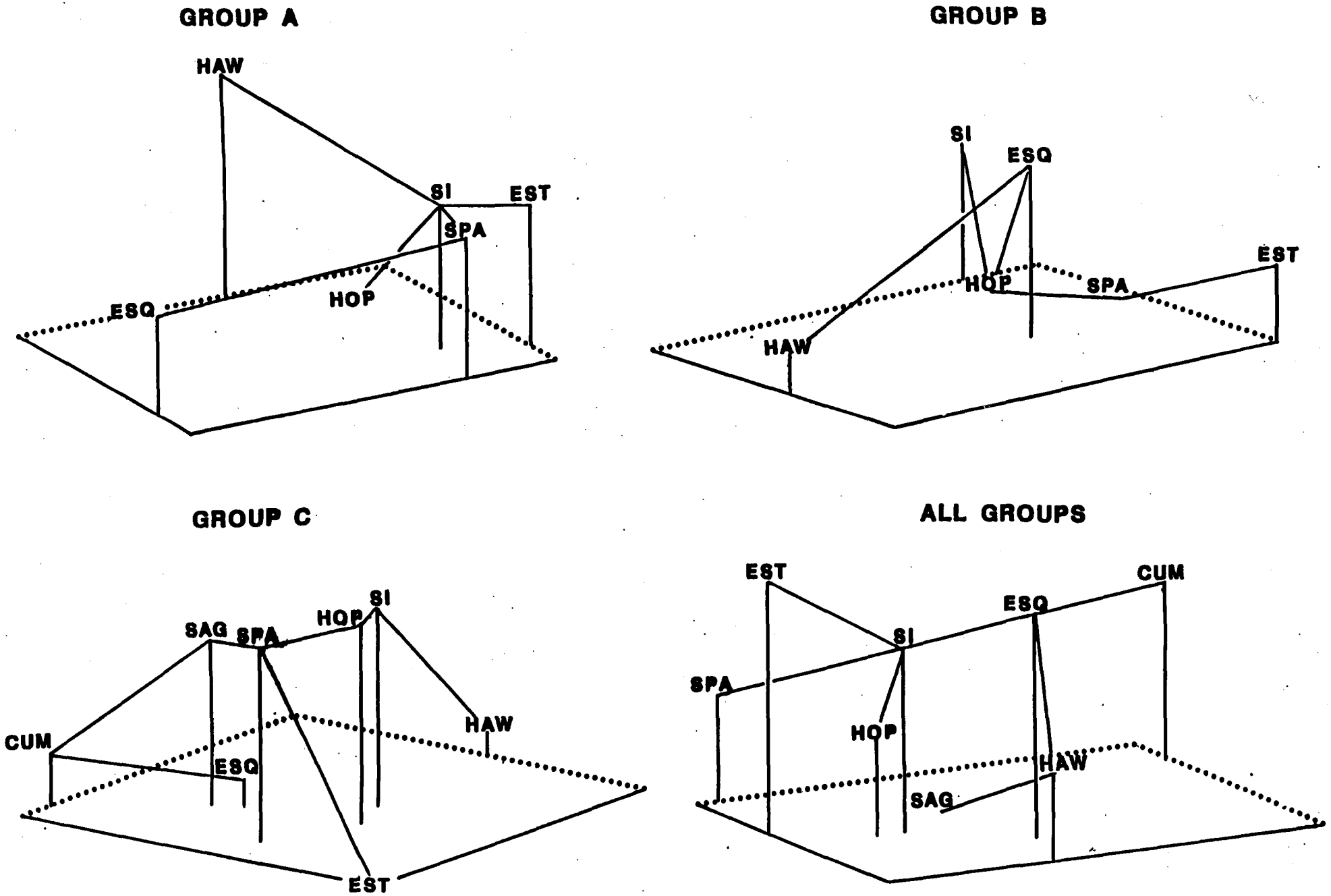


Figure 2. Principal coordinate and minimum spanning tree based on Cavalli-Sforza and Edwards'genetic distances for the different age groups and for all the age groups pooled (SAG = Saguenay Fjord; EST = Estuary; SI = Sept-Iles; ESQ = Esquiman Channel; HAW = Hawke Channel; HOP = Hopedale Channel; CUM = Cumberland Sound; SPA = spawning individuals.

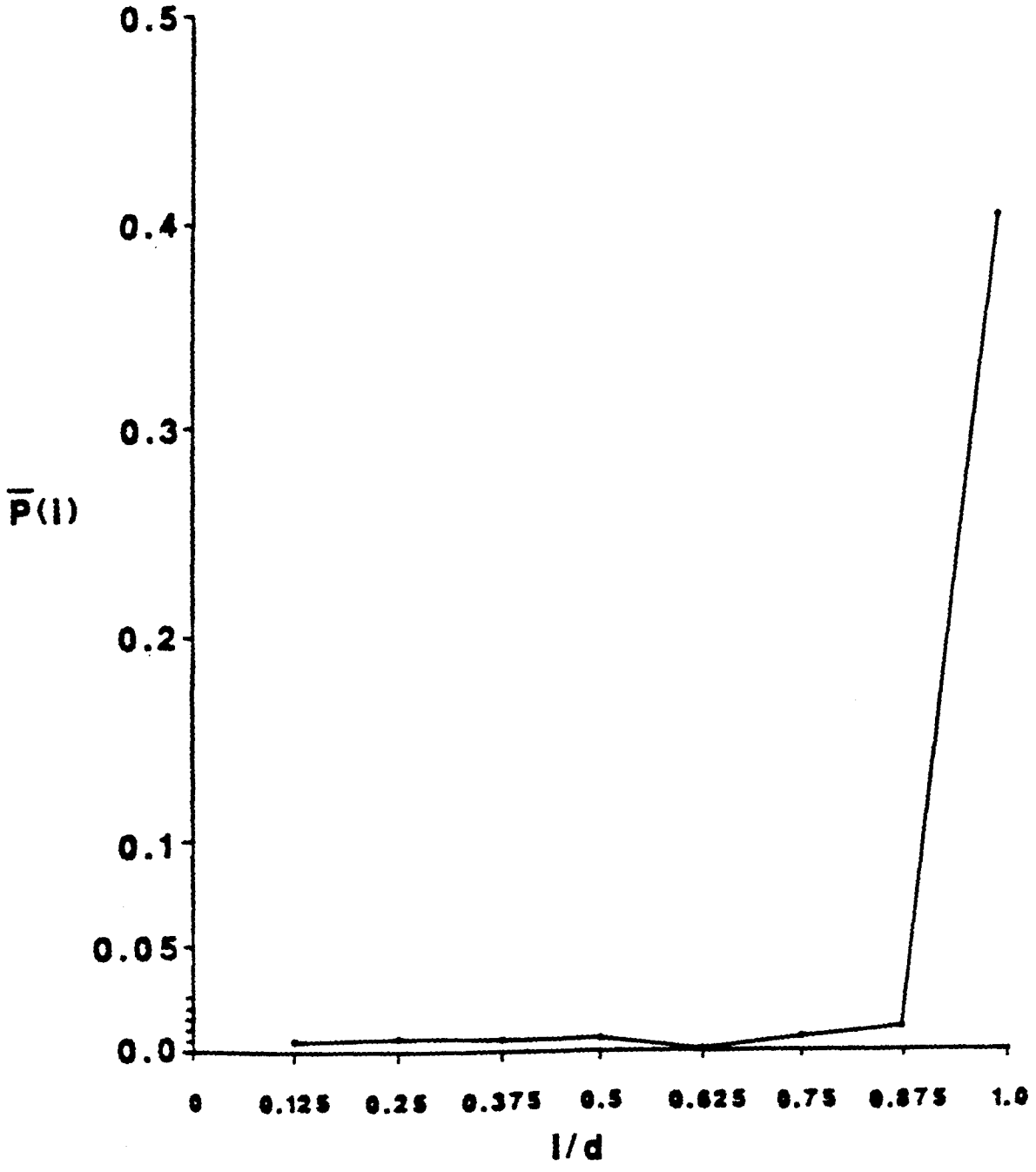


Figure 3. Conditional average frequencies for Greenland halibut (all age groups pooled).