Greenland halibut (*Reinhardtius hippoglossoides*) in the North Atlantic are genetically homogeneous

Morgan L. Vis, Steven M. Carr, W.R. Bowering, and William S. Davidson

Abstract: Greenland halibut (*Reinhardtius hippoglossoides*) have become of great importance to the Canadian fishery since the moratorium on northern cod (*Gadus morhua*), and an understanding of stock relationships among populations at the northern and southern extremes of their commercial range is crucial for proper management. We compared mitochondrial DNA sequence variation among fish taken from thoughout the Northwest Atlantic (Flemish Pass, the Grand Banks, Davis Strait, and Northwest Greenland) with samples from the Gulf of St. Lawrence, Iceland, and Norway. Within a 401 base pair portion of the cytochrome *b* gene, 22 genotypes were identified. Three of these occur at frequencies >10% and in the same relative abundances in all samples (except the Gulf of St.Lawrence). Genotype proportions do not differ significantly among samples, and genetic subdivision among samples (measured by the coancestry coefficient θ) is nil. Genetic distances among samples are not related to geographic distribution: pairwise differences between the Gulf sample and other western Atlantic samples exceed those for trans-Atlantic comparisons. These data suggest that there is sufficient mixing of Greenland halibut, not only within the NAFO regulatory area, but among sites in the North Atlantic generally, to prevent the development or maintenance of genetically independent stocks.

Résumé : Le flétan du Groenland (*Reinhardtius hippoglossoides*) est devenu une espèce très importante pour la pêche canadienne depuis que le moratoire a été décrété sur la pêche à la morue (*Gadus morhua*) et, pour assurer la bonne gestion de cette espèce, il est indispensable de connaître les relations entre les populations occupant les extrémités nord et sud de l'aire de répartition commerciale de l'espèce. Nous avons comparé la variation de la séquence d'ADN mitochondrial chez des poissons capturés dans l'Atlantique Nord-Ouest (col Flemish, talus continental au nord-est de Terre-Neuve, détroit de Davis et au nord-ouest du Groenland) avec des échantillons provenant du golfe du Saint-Laurent, d'Islande et de Norvège. On a identifié 22 génotypes dans un segment de 401 paires de bases du gène du cytochrome *b*. Trois de ces génotypes ont une fréquence >10% et présentent les mêmes abondances relatives dans tous les échantillons (sauf pour les poissons du golfe du Saint-Laurent). Les proportions génotypiques n'ont pas différé de manière statistiquement significative entre les échantillons. La subdivision génétique entre les échantillons était nulle et les distances génétiques parmi les échantillons n'étaient pas liées à la répartition géographique : les différences touchant les paires entre les échantillons du golfe et d'autres échantillons de l'Atlantiqe Ouest étaient supérieures à celles que l'on a observées dans les comparaisons transatlantiques. Ces données indiqueraient qu'il y a suffisamment de mélange chez le flétant du Groenland, non seulement pour ce qui est de l'ensemble de l'Atlantique Nord-Ouest, mais dans les différents sites situés dans l'Atlantique Nord de façon générale, pour empêcher la constitution ou le maintien de stocks génétiquement indépendants.

Introduction

Greenland halibut (*Reinhardtius hippoglossoides*) in the Northwest Atlantic are widely distributed from high in the Arctic between Canada and Greenland to as far south as the Scotian Shelf; they are most abundant from the eastern Grand Bank and Flemish Cap well beyond the Canadian 200-mile (1 mile = 1.609 km) limit and north (Bowering and Brodie 1995) (Fig. 1). It is a deepwater species with higher densities occurring in depths of about 500–1200 m along the edge of the continental slope and the channels running between the fishing banks of the continental shelf as well as the deep inshore bays of eastern Newfoundland and the fjords of Greenland and Baffin Island. In recent years, with advances in modern fishing technology, it has been found to be commercially abundant in some areas as deep as 1500–1800 m, particularly in the proximity of the Sackville Spur and Flemish Pass, immediately east of the Grand Banks (Bowering and Brodie 1995) and has been caught in longline investigations as deep as 2200 m off West Greenland (Boje and Hareide 1993) and the Flemish Cap (de Cardenas et al. 1996). The species is also of commercial importance in the Gulf of St. Lawrence and exists in limited quantities along the south Newfoundland coast, Fortune Bay, and in the Laurentian Channel.

Stock structure of Greenland halibut in the Northwest Atlantic has been studied using a variety of methods (e.g., protein electrophoresis (Fairbairn 1981), parasites (Khan et al. 1982; Arthur and Albert 1993), morphometrics (Bowering 1988),

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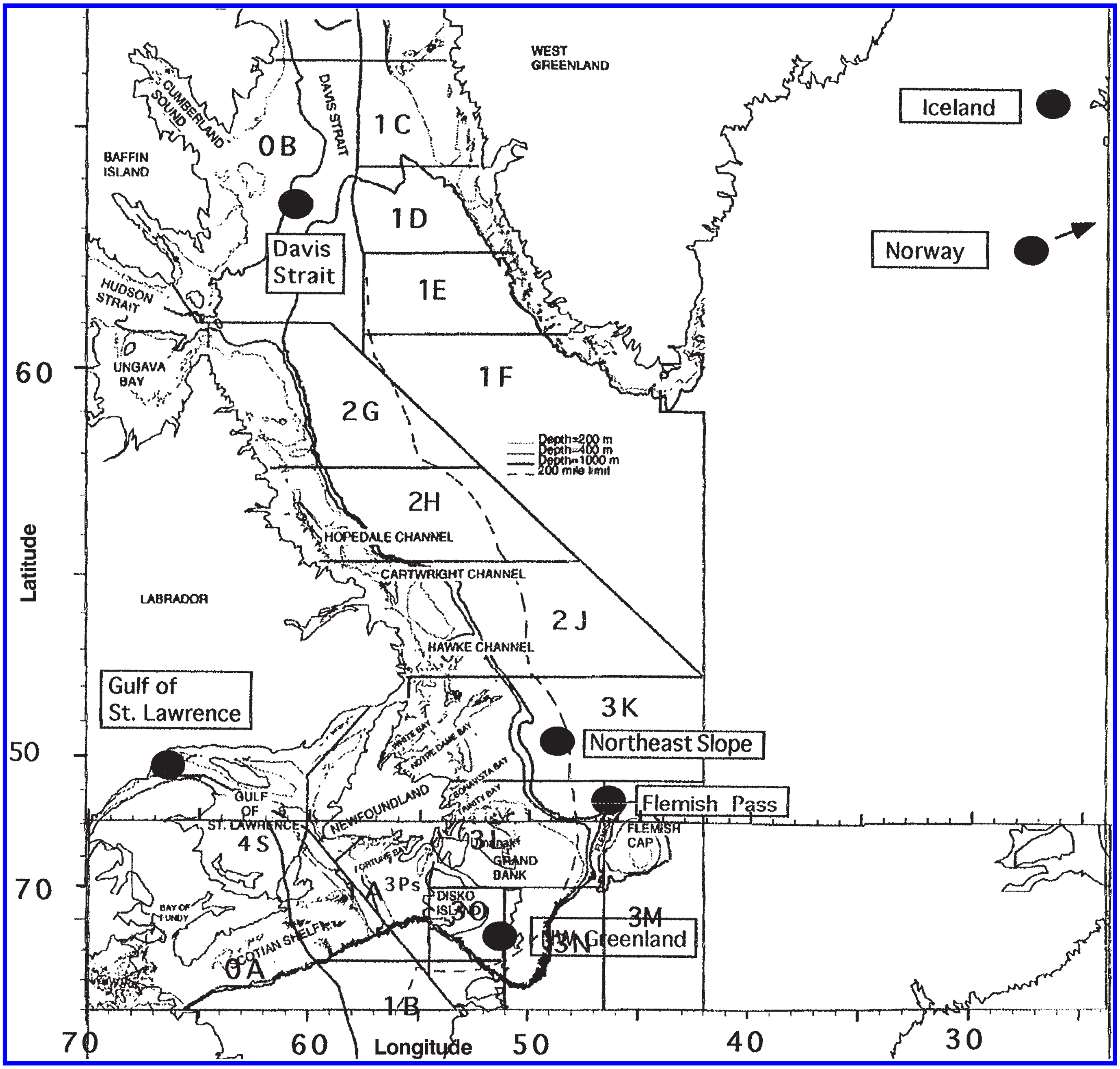
Fig. 1. Sampling locations from which Greenland halibut were collected. Northwest Atlantic Fisheries Organization (NAFO) divisions, depth contours, and the 200-mile Canadian economic limit are shown for reference. The base map is taken from Bowering and Brodie (1995).



meristics (Misra and Bowering 1984; Riget et al. 1992), and tagging (Bowering 1984; Riget and Boje 1989)). These data suggest that Greenland halibut comprise a single self-sustaining stock from Davis Strait to the Grand Bank and Flemish Cap (Bowering and Chumakov 1989). Greenland halibut in the Gulf of St. Lawrence are believed to be a separate, relatively small, self-sustaining stock, which receives migrants from the Labrador area through the Strait of Belle Isle between Quebec and the island of Newfoundland (Bowering 1982). The major spawning location of Greenland halibut in the western Atlantic is in the deep slope area of Davis Strait along the boundary between Canada and Greenland (Smidt 1969; Templeman 1973; Chumakov 1975; Bowering 1983). However, with research activity on Greenland halibut expanding to very deep water, complemented by commercial fishing operations, additional information on spawning locations is becoming available. Fish in spawning condition have recently been reported from the deep slope area off the coasts of Labrador and northeastern Newfoundland by domestic gillnetters (Morgan and Bowering 1996) to as far south as Flemish Pass (Junquera and Zamarro 1994; Morgan and Bowering 1996). It is not clear whether this is a change in behaviour or a typical behaviour that has not been previously observed, although major shifts in Greenland halibut distribution have been recorded in recent years (Anonymous 1995). Apparent changes in behaviour have been reported also for other flatfish species in this area such as witch flounder (Bowering 1995) and American plaice (*Hippoglossoides platessoides*) (Bowering et al. 1995*a*, 1996, 1997; Brodie et al. 1995). The extent of Greenland halibut spawning in the area of the continental slope off eastern Canada has been discussed in Morgan and Bowering (1997).

As a result of the massive increase in fishing effort by foreign vessels directed towards Greenland halibut in the Northwest Atlantic Fisheries Organization (NAFO) Regulatory Area during the 1990s, annual catches in this area alone have nearly doubled the highest catch ever recorded in traditional fisheries since the Greenland halibut fishery began more than 30 years ago (Bowering and Brodie 1995). Annual catches from West Greenland to the Flemish Pass averaged about 85 000 t during 1990–1994, making it the largest groundfish fishery in the Northwest Atlantic (Anonymous 1995). As a consequence of the collapse of the West Greenland cod fishery and most other Canadian Atlantic groundfish fisheries, the offshore fishery for Greenland halibut in the Davis Strait in the 1990s has also increased substantially (Jørgensen and Boje 1995).

Several disturbing trends have accompanied these new fisheries. There have been steep systematic declines in estimates of stock size from Davis Strait to the Grand Bank and Flemish Pass (Bowering and Brodie 1995). Canadian catches of Greenland halibut have declined dramatically in traditional fishing areas and effort has been moving progressively deeper throughout the distribution range. Finally, Greenland halibut of commercial size have virtually disappeared in traditional midshore areas despite no apparent decline in recruitment (Bowering et al. 1995*b*).

In consequence of its change in status from an “underutilized species” to the major groundfish fishery in the western Atlantic, Greenland halibut have received a very high public profile. A serious international dispute regarding the fishery arose between Canada and the European Union during 1995, which received much attention at the United Nations Conference on High Seas Fishing. This level of interest will likely continue until a more conclusive evaluation of stock structure is available. In common with other fisheries, Greenland halibut in the Northwest Atlantic are regulated according to a system of statistical subareas and divisions established by NAFO (cf. Fig. 1). Fish stocks that fall within the 200-mile economic zone are typically managed unilaterally by Canada, whereas stocks that occur outside or overlap that limit fall under the multinational control of the NAFO Fisheries Commission. Canadian managers are particularly concerned about the relationship of Greenland halibut outside the 200-mile economic limit on the Grand Banks of Newfoundland and adjacent waters (NAFO Subarea 3) to those within the Canadian economic zone as far north as Davis Strait. They ask whether Greenland halibut outside the 200-mile limit on the Grand Banks and adjacent waters constitute a separate stock, or do they instead comprise an extension of the distribution from Davis Strait southward along the deep edge of the continental slope, as currently believed? Are the newly found spawning fish in the deepslope areas of the NAFO Regulatory Area migrants from the Canadian zone? The implications for fisheries management can be quite complex considering the possible scenarios for stock structure. Prior to 1995, Greenland halibut in the far north in the Davis Strait and northwestern Greenland (NAFO Subareas 0 and 1) were managed bilaterally between Canada and Greenland as a single unit, while those further south along the Labrador and northeastern Newfoundland continental shelf (NAFO Subarea 2 and Divisions 3KL) were regulated by Canada within its 200-mile limit. The fishery for Greenland halibut beyond the 200-mile limit south of this area (NAFO Divisions 3LMNO) was unregulated. In 1995, based on the advice of the NAFO Scientific Council, the inshore area of northwestern Greenland (Division 1A) began to be regulated separately from the offshore areas, and all of the Greenland halibut south of the Davis Strait (NAFO Subareas 2 and 3) began to be regulated as a single unit under the management of the multinational NAFO Fisheries Commission. These changes were prompted by conservation concerns. For example, if the entire resource were a single biological unit, intense fishing effort in areas of localized abundance could cause significant damage to the resource as a whole. It is critical, therefore, that the stock structure in the Northwest Atlantic be elucidated as conclusively as possible.

Stock structure of Greenland Halibut in the Northeast Atlantic is less well understood. It has been assumed that a single stock resides in the waters around Iceland and the nearby Faeroe Islands (Sigurdsson 1981). Fish are found from the west side of the island around to the northern and southeastern coasts; the absence of Greenland halibut on the southern coast is associated with elevated water temperatures (Nizovtsev 1970). Spawning usually occurs in winter in the northwest, and along the continental slope of east Greenland at depths to 1000 m (Sigurdsson 1977). Juvenile (0-group) Greenland halibut have been caught from western Iceland to the southern tip of Greenland, with higher catches taken on the east Greenland continental shelf (Sigurdsson 1980). Postspawning fish undertake a spring feeding migration back to northern and eastern Iceland; by September the main feeding migration is over and they return west for spawning (Nizovtsev 1970). Research vessel surveys in 1992 and 1993 confirmed this pattern and suggest that the highest commercial densities are located to the west of Iceland (E. Hjörleifsson, Marine Research Institute, Reykjavik, Iceland, personal communication). The range of Greenland halibut in the Northeast Atlantic extends along the northwest shores of Spitsbergen northeast to the coast of Novaya Zemlya (Sorokin 1967) and along the entire White Sea

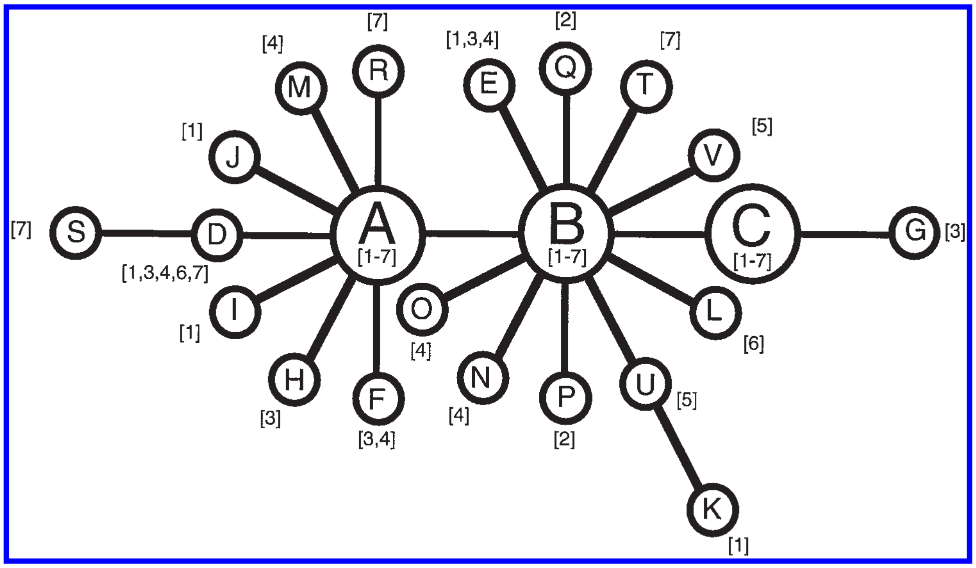


Fig. 2. Phylogenetic relationships of 22 genotypes among seven sample locations of Greenland halibut. A maximum parsimony network is shown; a single nucleotide substitution occurs along each network branch. Distributions of genotypes among regions are summarized from Table 1. Genotypes A, B, and C occur in all seven samples; the remaining genotypes occur in the samples indicated in brackets: [1] Northeast Slope; [2] Gulf of St. Lawrence; [3] Iceland; [4] Davis Strait; [5] Flemish Pass; [6] Norway; and [7] Northwest Greenland.

and Norwegian Atlantic coasts as far south as Bergen (Hognestad 1969). Recent research vessel surveys have captured Greenland halibut as deep as 1500 m off Norway (Anonymous 1996). The spawning area for Greenland halibut in the Northeast Atlantic may extend as far south as Traena Bank (66°N) and northward to southwestern Spitsbergen (Godo and Haug 1987).

A key component of the unit stock concept is that, to be treated as separate populations, fish stocks must be genetically as well as ecologically distinct (Ovenden 1990; Utter 1991; Dizon et al. 1992). Genetic differentiation in marine fish species has been examined by direct analysis of mitochondrial DNA (mtDNA) sequences, amplified in vitro by the polymerase chain reaction (PCR) (Carr and Marshall 1991*a*, 1991*b*; Bartlett and Davidson 1991; Pepin and Carr 1993; Carr et al. 1995). Here, we extend this analysis to Greenland halibut in the North Atlantic.

Materials and methods

Greenland halibut were collected by personnel of the Canadian Department of Fisheries and Oceans (DFO) and colleagues in Denmark (Greenland), Iceland, and Norway. Spawning aggregations of Greenland halibut are difficult or impossible to sample: known sites are usually ice-covered during spawning, and in the eastern Atlantic, spawning times and locations are largely unknown. We therefore choose a series of geographically isolated sites where Greenland halibut were known to be commercially abundant. Samples were collected from the northeastern Newfoundland continental shelf (hereinafter referred to as the Northeast Slope) (NAFO Division 3K), the estuary of the Gulf of St. Lawrence (Division 4S), Flemish Pass (Divisions 3LM), Davis Strait (Division 0B), northwestern Greenland at Jakobshavn fjord (Division 1A), western Iceland (65°16′N, 28°18′W), and Bear Island north of Norway (hereinafter referred to as Norway) (73°17′N, 14°47′W) (Fig. 1).

DNA was extracted from frozen muscle tissue as described by Carr and Marshall (1991*a*) or Bartlett and Davidson (1992). Forty fish were examined from each locality. A portion of the mitochondrial genome including a 401 base pair (bp) region at the 5′ end of the cytochrome *b* sequence was amplified by PCR, substantially as described by Carr and Marshall (1991*a*, 1991*b*). The oligonucleotides L14724, (5′-CGAAGCTTGATATGAAAAACCATCGTTG-3′; Irwin et al. 1991) and H15149 (5′-GCCCCTCAGAATGATATTTGTCCTCA-3′; Kocher et al. 1989) were used as primers for both amplification and sequencing. DNA sequencing was accomplished using fluorescent dye-terminator chemistry and an Applied Biosystems 373A automated DNA sequencer (Carr and Marshall 1991*b*). All sequences are given as their coding-strand equivalents.

Sequences were analysed and prepared for publication with the help of ESEE (version 3.00) (Cabot and Beckenbach 1989). Genetic heterogeneity within samples was estimated by the nucleon diversity (*h*) index for nonselfing populations and nucleotide diversity (π) index of Nei and Tajima (1981) as calculated by the Restriction Enzyme Analysis Package (REAP) (McElroy et al. 1991) from the pairwise haplotype divergences obtained using the Molecular Evolutionary Genetics Analysis (MEGA) program (Kumar et al. 1993). Genetic heterogeneity among samples was tested with the Monte Carlo χ^2 test of Roff and Bentzen (1989) from REAP; 5000 resamplings of the data matrix were used. The coancestry coefficient θ was calculated with the HAPLOID program (Weir 1990) to determine the proportion of genetic diversity attributable to subdivision among samples. The degree of gene flow among samples was estimated using the program of M. Slatkin (Department of Integrative Biology, University of California, Berkeley, CA 94729, U.S.A.). Pairwise Rogers' genetic distances (Rogers 1972) among populations were calculated by the NTSYS program of Rohlf (1992). Cluster analyses by the UPGMA and neighbor joining algorithms were performed with the Phylogenetic Analysis Using Parsimony (PAUP) program of Swofford (1993).

Results

Within the 401-bp region examined, 20 variable sites were identified among the 280 fish sampled (Fig. 2). All but two of the observed substitutions occur in the third codon position and would not result in an amino acid substitution. The other two substitutions were first position transitions that exchange valine for isoleucine. These variable sites define 22 genotypes

Table 1. Distribution of mtDNA genotypes of Greenland halibut among seven sampling locations in the North Atlantic and adjacent waters.

		mtDNA genotype																					
Locality	*n*	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V
Northeast slope	40	16	11	8	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gulf of St. Lawrence	40	12	18	5	1	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Iceland	40	17	14	7	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Davis Strait	40	18	10	4	2	1	1	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0
Flemish Pass	40	18	16	4	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Norway	40	20	10	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	0	0
Nortwestern Greenland	40	16	12	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1
Totals	280	117	91	42	6	3	2	1	1	1	1	1	1	1	2	1	1	1	1	1	2	2	1

that differ by one to five nucleotide substitutions (Table 1). These sequences have been submitted to the Genome Sequence Data Base and assigned the accession numbers L77930–L77951. Genotype A is the most common genotype in all samples except that from the Gulf of St. Lawrence (overall mean 41.8%, range 30.0–50.0%); the most common alternative genotypes (B and C) also occur in all samples, at overall frequencies of 32.5% (range 25.0–45.0%) and 15.0% (range 10.0–22.5%), respectively. In the Gulf of St. Lawrence sample, genotype B is more abundant than A. Genotype D occurs in 2.5% of fish and in all samples except Flemish Cap and northwestern Greenland. The remaining genotypes typically occur only in one or two samples in one or two individual fish.

The Monte Carlo χ^2 test indicates no significant differences of genotype distributions among the seven samples ($\chi^2 = 138.03$, df = 126, $P > 0.10$). There are no significant differences if the Gulf of St. Lawrence sample is removed from the analysis ($\chi^2 = 98.06$, df = 90, $P > 0.15$) or if that sample is compared with a pool of the remaining samples ($\chi^2 = 25.91$, df = 42, $P > 0.26$). There are no significant differences if the western and eastern Atlantic populations are pooled separately and compared (Iceland and Norway versus all others, $\chi^2 = 17.20$, df = 16, $P > 0.35$). There are no significant differences if fish from the northern and southern extremes of the Northwest Atlantic are pooled and compared (Davis Strait and Northwest Greenland versus Northeast Slope and Flemish Pass, $\chi^2 = 11.88$, df = 14, $P > 0.75$). There are no significant differences if fish from within the 200-mile limit are pooled and compared with those outside the limit in the western Atlantic (Davis Strait and Northeast Slope versus Northwest Greenland and Flemish Pass, $\chi^2 = 19.08$, df = 14, $P > 0.068$).

The nucleon diversity (h) and nucleotide diversity (π) indices within samples are given in Table 2. The mean nucleon diversity is 0.69, which indicates that the probability that any two fish chosen at random will have different genotypes is about 70%. The Flemish Pass and adjacent Northeast Slope samples have the smallest and largest nucleon diversity, respectively. The nucleotide diversity calculation corrects the nucleon diversity index for the actual number of nucleotide substitutions between any two genotypes; for a 400-bp molecule, the mean value of 0.0025 indicates that any two fish chosen at random differ on average by about one nucleotide substitution in the gene region examined (i.e., $400 \times 0.0025 = 1.0$).

Nucleotide diversity and Rogers' distance between samples are given in Table 3. Calculation of the former includes a correction for nucleotide diversity within samples: a negative value indicates that the average within-sample variation is greater than the between-sample difference. This is the case for 13 of 21 pairwise comparisons. Rogers' distance describes the difference between populations as the pairwise Euclidean distance between haplotype frequencies. UPGMA cluster analysis will represent these differences among multiple samples on the assumption that genetic distance accumulates linearly with respect to time; neighbor joining analysis does not make this assumption. Both UPGMA (Fig. 3) and neighbor joining (Fig. 4) analyses of Rogers' distance indicate that such genetic differences as exist among Greenland halibut populations are not related to their geographic distribution. The relative distinctness of the Gulf of St. Lawrence sample reflects the reversal in relative frequency of the two most abundant genotypes. Otherwise, samples from opposite sides of the Atlantic are typically more similar than are geographically contiguous samples from the Northwest Atlantic.

Table 2. Haplotype (h) and nucleotide (π) diversity indices within samples of Greenland halibut from the North Atlantic and adjacent waters.

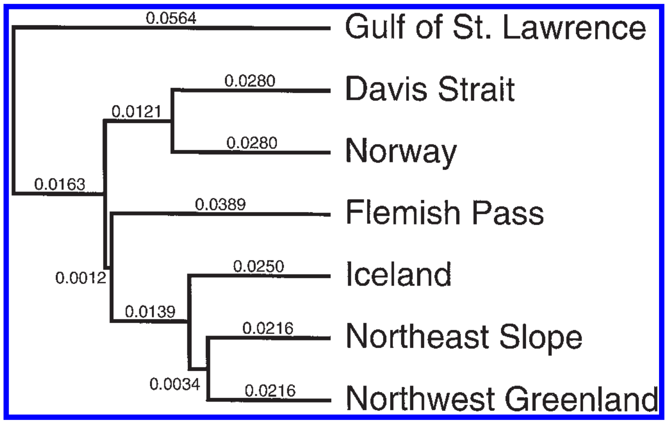
Population	Haplotype diversity	Nucleotide diversity
Northeast Slope	0.7304	0.002 799
Gulf of St. Lawrence	0.6975	0.002 516
Iceland	0.6734	0.002 391
Davis Strait	0.7266	0.002 969
Flemish Pass	0.6342	0.001 986
Norway	0.6759	0.002 558
Northwestern Greenland	0.7051	0.002 500
Mean	0.6919±0.000 16	0.002 531

The coancestry coefficient θ over the seven samples is -0.0033 ± 0.0072, that is, not significantly different from zero. This result also indicates that the proportion of genotypic differentiation attributable to subdivision among samples is negligible (Weir 1990). Slatkin and Maddison's (1989) estimate of $N_e m$ is based on a count of the minimum number of migration events (S) necessary to account for the observed distribution of genotypes among multiple populations. For example, the occurrence of a genotype in n samples requires a minimum of $S = n - 1$ events. From the phylogenetic relationships shown in Fig. 4 and the sample sizes and distribution of the 22 genotypes among the seven samples given in Table 1, S was calculated to be 26 (25 from the occurrence of genotypes in multiple populations, plus 1 from the distribution of genotype K with respect to genotype U), from which $N_e m$ was estimated as 0.8 (95% confidence interval 0.5–1.1).

Table 3. Nucleotide divergences (below the diagonal) and Rogers' distances (above the diagonal) among samples of Greenland halibut from the North Atlantic and adjacent waters.

	Northeast slope	Gulf of St. Lawrence	Iceland	Davis Strait	Flemish Pass	Norway	Northwest Greenland
Northeast Slope	—	0.111 80	0.050 00	0.068 47	0.090 14	0.075 00	0.043 30
Gulf of St. Lawrence	–0.000 002	—	0.088 39	0.132 29	0.086 60	0.146 84	0.110 40
Iceland	–0.000 051	–0.000 028	—	0.075 00	0.053 03	0.075 00	0.050 00
Davis Strait	0.000 002	0.000 035	–0.000 007	—	0.088 39	0.055 90	0.088 39
Flemish Pass	–0.000 005	–0.000 027	–0.000 033	–0.000 009	—	0.088 39	0.090 14
Norway	0.000 004	0.000 057	–0.000 002	–0.000 038	0.000 003	—	0.086 60
Northwest Greenland	–0.000 033	–0.000 024	–0.000 036	0.000 060	0.000 000	0.000 062	—

Fig. 3. UPGMA cluster analysis of Rogers' distances among Greenland halibut populations.

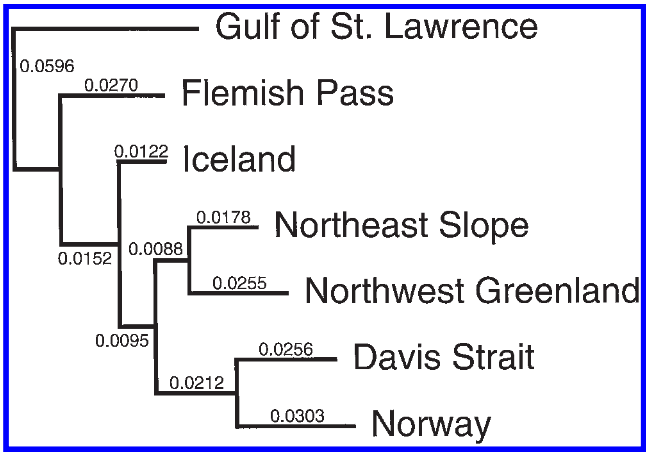


Discussion

Comparison of mtDNA sequence variation in Greenland halibut throughout the North Atlantic identifies extensive polymorphism (22 genotypes) and genetic diversity (global $h = 0.69$, global $\pi = 0.0025$). However, genotype proportions are not significantly differentiated among samples. Three major genotypes are present at approximately equal frequencies in all populations, except that the relative abundances of the two major genotypes are reversed in the Gulf of St. Lawrence sample (the difference is not statistically significant). There is no indication that such genetic variation as exists is subdivided among geographic samples: $\theta \simeq 0.0$, and cluster analysis does not identify any structure consistent with geographical stocks. Intermixing among Greenland halibut, between the northern and southern extremes of the commercial range in the western Atlantic, inside and outside the 200-mile Canadian economic zone, and between samples on either side of the Atlantic, appears to be sufficient to produce a single genetically homogeneous population in the North Atlantic.

Substantially identical results were obtained by Fairbairn (1981), who studied Greenland halibut populations in the Northwest Atlantic and Gulf of St. Lawrence with protein electrophoretic markers. She found that neither of two polymorphic loci was significantly differentiated among samples from Labrador to the Northeast Slope, and that the Gulf sample, although somewhat different in allele frequencies, was not significantly differentiable from the Atlantic samples. Fairbairn (1981) concluded that the Northwest Atlantic populations were a single interbreeding stock, whereas the Gulf population was a separate breeding area. (Fairbairn (1981) emphasized the presence of an essentially private allele at the *PHI1* locus in the Gulf sample. She pooled rare alleles for her χ^2 test and found no significant difference between the pool of Northwest Atlantic samples and the single Gulf sample. We re-analyzed her data by the Monte Carlo χ^2 test, which does not require pooling, and found this comparison to be significantly differentiated ($\chi^2 = 18.87$, df = 4, $P < 0.003$).) Data from the cytoplasmic and nuclear genomes are thus in agreement as to the absence of significant stock structure in the Northwest Atlantic and the relative distinctiveness of the Gulf population.

Fig. 4. Neighbor-joining analysis of Rogers' distances among Greenland halibut populations. The network was rooted with the Gulf of St. Lawrence sample specified as the outgroup, as indicated by the UPGMA analysis in Fig. 3.



The genetic structure of Greenland halibut differs markedly from that in Atlantic cod (*Gadus morhua*), which has been studied with the same genetic marker in the same general area of the North Atlantic (Carr and Marshall 1991*a*, 1991*b*; Pepin and Carr 1993; Carr et al. 1995; Crutcher 1996). Cod in the western Atlantic are also highly polymorphic (more than 40 genotypes), but all populations are dominated by a single genotype at high mean frequency. In contrast, cod in the eastern Atlantic show multiple alleles at moderate frequencies. The distribution of genotype proportions is uniform among populations in the western Atlantic, whereas populations on either side of the Atlantic are significantly differentiated (Carr and Marshall 1991*b*). Pairwise genetic distances among cod samples from Norway and the Barent's Sea are more than twice those of sample pairs drawn from anywhere in the commercial range of cod in the western Atlantic (Crutcher 1996). The same is true for Icelandic versus Norwegian cod (Árnason and Pálsson 1996). The pattern of reduced variation in the western North Atlantic has been interpreted as the result of bottleneck(s) subsequent to the colonization from the eastern North Atlantic, possibly during the most recent glaciation (Carr et al. 1995; cf. Cross and Payne 1978).

The differences in genetic patterns between the two species may be attributable to differing life-history characters. Greenland halibut, the more bathypelagic species, may have been less affected by glaciation if they remained at greater depths. As noted, they are commercially abundant to depths of 1800 m (Bowering and Brodie 1995) and have been caught as deep as 2200 m at western Greenland (Boje and Hareide 1993) and in the Flemish Pass (de Cardenas et al. 1996). Because the slope of the entire North Atlantic continental shelf is continuous at these depths (Fig. 1), the potential for extensive mixing exists along the slope contour. Atlantic cod, on the other hand, are generally confined to the more shallow banks of the continental shelf, which are separated by deep channels that this species is less likely to cross. As well, Greenland halibut larvae remain pelagic for an unusually long time and are more readily dispersed by current-driven drift (Templeman 1973) than are Atlantic cod. Tagging studies indicate that a substantial degree of mixing in Greenland halibut may result from long-distance movement of reproductive adults among populations, which is less extensive in cod (Lear 1984). It is known that Greenland halibut migrate between eastern Newfoundland waters and the Davis Strait area (Bowering 1984). Boje (1993) reported that fish tagged at southwestern Greenland have been recaptured at eastern Greenland, and Sigurdsson (1981) reported incidental recaptures of fish tagged in northern Iceland from as far east as the Faroe Islands and Bear Island and as far northeast as the Russian coast. The direction of movement may not be uniform: fish tagged off Newfoundland in southern areas have never been recaptured further north in the inshore areas of western Greenland (Bowering 1984), and there are no published reports of recaptures made west of the tagging sites in the eastern Atlantic. It must be remembered that a level of movement among populations that would be regarded as quite small from a tag-return perspective can lead to substantial gene flow and homogenization of allele frequencies. For haploid genetic markers such as mtDNA, the exchange of a single breeding female per pair of populations per generation is sufficient to prevent divergence of selectively neutral alleles (Slatkin 1985).

Based on meristic and morphometric characters, previous studies of stock structure in Greenland halibut have identified distinguishable groups of adult fish that are geographically localized. The present analysis suggests that such phenotypic differences likely reflect environmental influences rather than genotypic differences among isolated gene pools. Contrasting patterns of meristic or morphological versus genetic variation have been found in other marine teleost species (Leslie and Grant 1990; Roby et al. 1991; Pepin and Carr 1993). Spawning in marine fish species generally occurs over a broad geographic area, and extensive egg and larval drift across management unit boundaries may limit their genetic differentiation, despite differences in subsequent environmental histories that may affect phenotypic features (Sinclair 1988). Some degree of mixing through egg and larval flow is likely in Greenland halibut, particularly in areas such as the Gulf of St. Lawrence. Attempts to define "stocks" based on differences in meristic or morphological features must be supported by genetic evidence to confirm that the former differences reflect some degree of reproductive isolation rather than simply environmental distinctiveness (Pepin and Carr 1993). Studies of the distribution of local components of Greenland halibut for management purposes may find traditional methods helpful but must now recognize that extensive gene flow occurs among populations throughout the North Atlantic.

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