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ISOLATION BY DISTANCE IN THE ATLANTIC COD, *GADUS MORHUA*, AT LARGE AND SMALL GEOGRAPHIC SCALES

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Abstract.—Genetic isolation by distance (IBD) has rarely been described in marine species with high potential for dispersal at both the larval and adult life-history stages. Here, we report significant relationships between inferred levels of gene flow and geographic distance in the Atlantic cod, *Gadus morhua*, at 10 nuclear restriction-fragment-length-polymorphism (RFLP) loci at small regional scales in the western north Atlantic region (< 1600 km) that mirror those previously detected over its entire geographic range (up to 7300 km). Highly significant allele frequency differences were observed among eight northwestern Atlantic populations, although the mean F_{ST} for all 10 loci was only 0.014. Despite this weak population structuring, the distance separating populations explained between 54% and 62% of the variation in gene flow depending on whether nine or 10 loci were used to estimate *Nm*. Across the species' entire geographic range, highly significant differences were observed among six regional populations at nine of the 10 loci (mean $F_{ST} = 0.068$) and seven loci exhibited significant negative relationships between gene flow and distance. At this large geographic scale, natural selection acting in the vicinity of one RFLP locus (GM798) had a significant effect on the correlation between gene flow and distance, and eliminating it from the analysis caused the coefficient of determination to increase from 17% to 62%. The role of vicariance was assessed by sequentially removing populations from the analysis and was found to play a minor role in contributing to the relationship between gene flow and distance at either geographic scale. The correlation between gene flow and distance detected in *G. morhua* at small and large spatial scales suggests that dispersal distances and effective population sizes are much smaller than predicted for the species and that the recent age of populations, rather than extensive gene flow, may be responsible for its weak population structure. Our results suggest that interpreting limited genetic differences among populations as reflecting high levels of ongoing gene flow should be made with caution.

Key words.—*Gadus morhua*, gene flow, isolation by distance, nuclear restriction-fragment-length-polymorphism loci, population structure.

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Although it is widely accepted that gene flow plays a fundamental role in affecting a number of evolutionary and ecological characteristics of species (Endler 1977; Slatkin 1985), the true extent of gene flow that occurs among natural populations of many species remains unclear. This uncertainty arises from a variety of sources. First, direct measures of gene flow are rarely attempted and, when successful, provide measures that are relevant over ecological but not necessarily evolutionary time scales (Slatkin 1985). Second, dispersal capability does not always match the levels of gene flow inferred from indirect methods (where the parameter F_{ST} is used to infer *Nm*, the number of migrant individuals entering a population each generation). This mismatch has been noted in several marine species where the magnitude of gene flow predicted from larval developmental mode or time spent in the plankton does not always conform to the observed population structure (see Burton 1983; Hedgecock 1986; Palumbi 1994; Shulman and Bermingham 1995). Third, the use of indirect methods requires many assumptions that are unlikely to be met in the majority of cases (see recent discussions in Bossart and Prowell 1998; Waples 1998; Whitlock and McCauley 1999). The ability of indirect methods to provide meaningful estimates of contemporary gene flow has also recently been questioned, irrespective of whether F_{ST} or coalescent-based approaches are used to estimate *Nm*, because of the overriding effects that population history can exert on existing population structure (Barton and Wilson 1995; Bossart and Prowell 1998; however, see Templeton et al. 1995; Neigel 1997; Bohonak 1999). Verifying assumptions of models represents an important challenge in all studies attempting to indirectly estimate gene flow.

One critical assumption is that the populations under study are at, or near, an equilibrium between the processes of random drift and migration. Assessing the validity of this equilibrium assumption is extremely difficult, if not impossible, under the island model. However, under the stepping-stone model of population structure, where gene flow occurs only among adjacent populations, the attainment of migration-drift equilibrium may under some conditions produce genetic isolation by distance (IBD; Wright 1943; Kimura and Weiss 1964; Slatkin 1993). Although the approach to migration-drift equilibrium is similar for both island and stepping-stone models, the latter will generate greater population differentiation making the signal of IBD easier, in principle, to detect (Wright 1943; Crow and Aoki 1984). The magnitude and spatial scale over which IBD occurs may also provide insights into the species effective neighborhood size, whether dispersal occurs in primarily one or two dimensions, and whether it has experienced recent range expansions or vicariance events (Slatkin 1993; Hellberg 1995).

Recent studies have documented significant associations between gene flow and geographic distance in nearly all major groups of organisms including plants (e.g., Kaufman et al. 1998; Raspe and Jacquemart 1998), insects (e.g., Britten

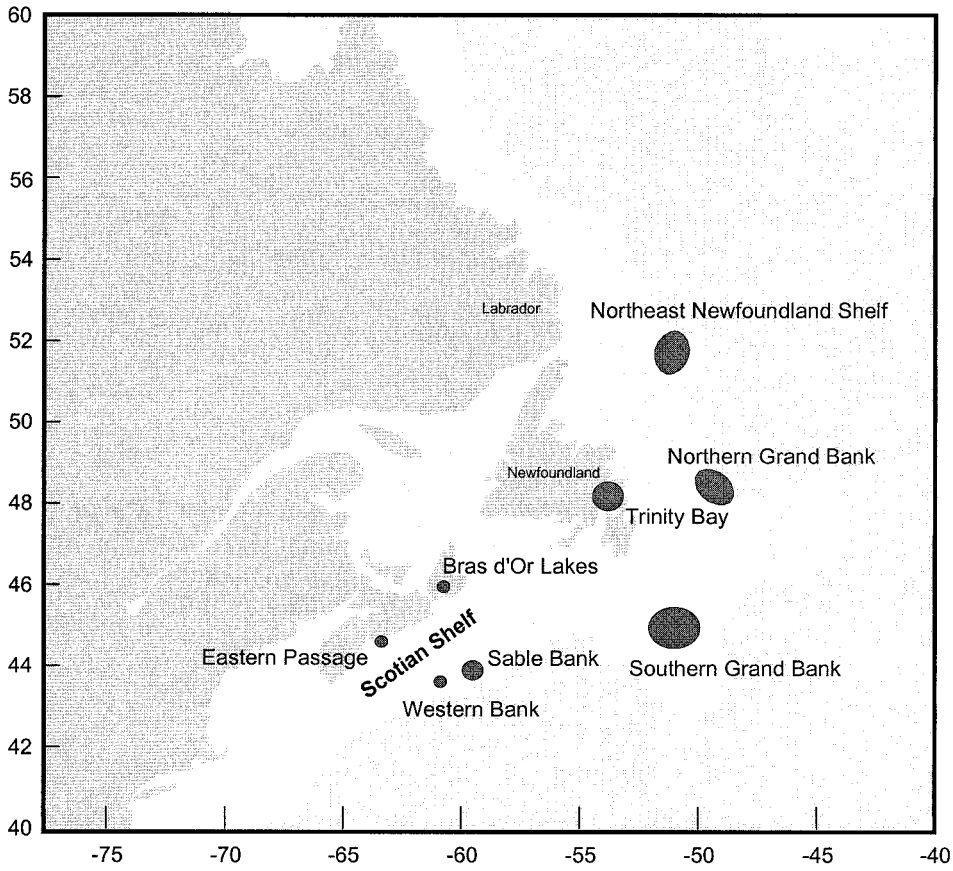

FIG. 1. Locations of *Gadus morhua* samples collected in the northwest Atlantic region.

et al. 1995; Armbruster et al. 1998), marine invertebrates (e.g., Benzie et al. 1994; Johnson and Black 1995; Lavery et al. 1995; Palumbi et al. 1997), freshwater and marine fishes (e.g., Planes et al. 1996; Gold and Richardson 1998; Hansen and Mensberg 1998), amphibians (e.g., Barber 1999; Storfer 1999), birds (e.g., Martinez et al. 1999; McDonald et al. 1999), and mammals (e.g., Burland et al. 1999; von Segesser et al. 1999). However, many studies have not detected relationships between gene flow and distance in species exhibiting substantial degrees of population structuring and, presumably, limited dispersal capacities (e.g., Baer 1998; Kim et al. 1998; Franceschinelli and Kesseli 1999). In studies failing to detect correlations between gene flow and distance, it is unclear whether this is attributable to the inappropriateness of the stepping-stone model, the presence of nonequilibrium conditions, or to the sampling of populations at incorrect spatial scales (see Ruckelshaus 1998). At present, little is known about the prevalence of IBD in different species groups and how variation in gene flow and dispersal distances might affect its expression at different geographic scales.

The objective of the present study was to examine the effect of geographic scale on IBD in the Atlantic cod, *Gadus morhua.* In an earlier study, a highly significant relationship between gene flow and distance was observed at 17 nuclear restriction-fragment-length-polymorphism (RFLP) loci among six populations of *G. morhua* sampled throughout its entire geographic range (Pogson et al. 1995). The DNA markers also revealed much stronger correlations between gene flow and distance than 10 allozyme loci suggesting some role of selection in affecting one or both sets of markers. To examine the relationship between gene flow and distance at smaller geographic scales, we scored 10 nuclear RFLP loci in 840 individuals sampled from eight populations distributed over the continental shelf and inshore areas of Newfoundland and Nova Scotia in the northwest Atlantic. We predicted that if IBD occurred at this finer spatial scale it should be weaker than that detected at the transoceanic scale. Contrary to our expectations, a highly significant relationship between gene flow and distance was observed in the northwest Atlantic that was qualitatively and quantitatively similar to that found at the larger geographic scale. Our results suggest that the weak population structure in *G. morhua* does not result from extensive gene flow per se but to the recent age of populations throughout the entire north Atlantic region.

MATERIALS AND METHODS

Samples

Samples were collected from the northwest Atlantic between the period of October 1991 and January 1993 (Fig. 1). All offshore samples were collected by otter trawls at depths ranging between 300 m and 1000 m. Inshore samples were collected by otter trawls, cod traps, gillnets, or handlines.

The sample from the northeast Newfoundland shelf (51° 05′W, 51°65′N) was pooled from individuals collected from prespawning cod aggregations on the Funk Island Banks in January 1992 ($n = 30$) and January 1993 ($n = 90$). The sample from the northern Grand Banks (49°06′W, 48°33′N) was obtained from the northern shelf break in January 1992. An inshore sample (53°79′W, 48°16′N) was pooled from 71 individuals captured in Trinity Bay and 21 individuals collected in Notre Dame Bay between May and September 1992. The southern Grand Banks sample (50°95′W, 44°94′N) was pooled from two samples collected in November 1992. The Bras d'Or Lakes sample from the Cape Breton region of Nova Scotia (60°80′W, 45°85′N) was obtained in November 1991. From the Scotian Shelf region, the Western Bank sample (61°04′W, 44°10′N) was captured in November 1991 and the Sable Bank sample (59°60′W, 44°09′N) was collected in June 1992. An inshore Nova Scotia was sample was obtained from Eastern Passage near Halifax (63°50′W, 44°50′N) in October 1992. Note that the Nova Scotia sample reported in Pogson et al. (1995) is equivalent to the Western Bank sample of the present study; the Newfoundland sample in Pogson et al. (1995) was the southern Grand Bank sample plus an additional 59 individuals not included in this report. The remaining samples from the eastern north Atlantic have been described by Pogson et al. (1995).

Restriction-Fragment-Length-Polymorphism Analyses

Total DNA was isolated from EtOH-preserved blood samples as described by Pogson et al. (1995). About 100–150 μg of high-molecular-weight DNA was typically obtained from 200 μl of initial material. With the exception of GM615, all cDNA clones used as hybridization probes in the present study, were also used by Pogson et al. (1995). However, unlike the previous study, only a single restriction site polymorphism was scored by each cDNA clone. To maintain consistency in the published nomenclature, each RFLP ''locus'' is synonymous with the name of the cDNA clone used to score the polymorphism. DNA concentrations were determined by measuring absorbance at 260 nm on a Hewlett-Packard 8452 Diode Array spectrophotometer. Total DNA samples (7 μg) were digested with four restriction endonucleases (*Pvu*II, *Dra*I, *Taq*I, and *Pst*I) and electrophoresed for 18–20 h on 0.8% agarose gels in 1× TBE buffer. The digested DNA was transferred to nylon membranes, fixed, and hybridized with dixoxegenin-11-dUTP labeled cDNA clones as described in Pogson et al. (1995). DNA samples digested with *Pvu*II were probed with cDNA clones GM309, GM867, and GM307. Clones GM842, GM860, and GM727 were used to probe samples digested with *Dra*I. Samples digested with *Taq*I were probed by cDNA clones GM777, GM738, and GM865, and clone GM798 was hybridized against DNA digested by *Pst*I. Prior to subsequent hybridizations of the same filter by different probes, membranes were stripped with boiling 0.2× SSC, 0.2% SDS. DNA size-standards (BRL 1-kb ladder) were run in the two outside lanes of each gel and restriction fragment sizes were estimated by unweighted linear regression.

Data Analyses

Allele frequencies, observed and expected heterozygosities, and genetic distances were estimated using the BIOSYS-1 program (Swofford and Selander 1989). Estimates of F_{ST} (i.e., G_{ST}) were obtained from BIOSYS-1 and θ was estimated by the FSTAT (ver. 1.2) program of Goudet (1995). Estimates of θ were tested for significance by randomly permuting both alleles and genotypes among samples using the FSTAT program with 5000 permutations. Tests for deviations from Hardy-Weinberg equilibrium and differences in RFLP allele frequencies among populations were performed using exact probability tests implemented by the GENEPOP (ver. 1.3) program (Raymond and Rousset 1995a).

Relationships between inferred levels of gene flow and the geographic distance separating populations at different spatial scales were examined following the approach of Slatkin (1993) using the ISOLDE subprogram of GENEPOP. Estimates of gene flow (log [Mhat]) were regressed against log (geographic distance), which was estimated as the shortest marine route between samples. F_{ST}, rather than θ, was used to estimate gene flow because the latter occasionally gave negative values (particularly at the smallest geographic scales) and simulations by Hellberg (1995) have shown that F_{ST} produces less biased slopes when gene flow is expected to be high. Analyses were performed both including and excluding the GM798 or pantophysin (*Pan*I) locus (previously called the synaptophysin, or *Syp*I, locus by Fevolden and Pogson 1997). The *Pst*I restriction site polymorphism scored by this cDNA clone exists in strong linkage disequilibrium with a region of the pantophysin gene for which amino acid and nucleotide sequence data strongly supports the action of natural selection (Pogson 2001). The GM798 locus was included in the analyses to assess its effects relative to the other DNA markers for which neutrality is not an issue. All relationships between gene flow and distance were tested for significance by Mantel tests (5000 permutations).

In the northwest Atlantic, analyses were performed separately for the four Nova Scotia populations, the four Newfoundland populations, and then for all eight populations. When comparing the relationship between gene flow and geographic distance in the northwest Atlantic to that detected across the entire species range, the four populations from Nova Scotia and the four from Newfoundland were pooled to create two large northwest Atlantic populations. This was done to prevent biases caused by the overrepresentation of samples from the northwest Atlantic region. To assess the role of vicariance in contributing to the correlation between gene flow and distance, we examined the effect of removing one population at a time from the regression analyses. As before, tests for vicariance were performed both including and excluding the GM798 locus.

RESULTS

A total of 1174 individuals were scored for their genotypes at 10 nuclear RFLP loci. The majority ($n = 840$) were collected from eight populations distributed over the continental shelf and inshore areas of Newfoundland and Nova Scotia in the northwest Atlantic. The remainder ($n = 334$) were captured from four northeast Atlantic populations as described

in a previous report (Pogson et al. 1995). Table 1 summarizes the levels of variability found in the 12 populations and the Appendix provides a listing of allele frequencies. A total of 139 alleles were detected at the 10 loci in the total sample, but only 20 were present in all populations. The remainder were either private variants restricted to a single population (n = 65, mean frequency = 0.0063) or low-frequency alleles present in two or more samples (n = 43 having frequencies below 0.015 in any sample). Rare and private alleles were scattered randomly among populations with little tendency to vary across geographic regions (i.e., northeastern versus northwestern Atlantic). Sample size correlated significantly with the number of rare alleles observed in a sample (r = 0.845, P = 0.0082), but not with the number of private alleles detected (r = 0.196, P = 0.642). As expected, this large pool of low-frequency alleles had little effect on total heterozygosity levels that were similar in all populations. An excellent fit to Hardy-Weinberg proportions was observed at all loci in all populations. The exact test of Rousset and Raymond (1995) found only four loci to exhibit significant departures from Hardy-Weinberg equilibrium (three showing deficiencies and one showing an excess of heterozygotes; Appendix). Out of 120 individual tests, this number is less than expected by chance alone.

To examine the extent of differentiation among populations of *G. morhua* at different geographic scales, we estimated both F_{ST} (by the method of Nei 1977) and θ (Weir and Cockerham 1984) at four sampling levels and tested for allele frequency differences using two approaches. The first was to perform exact probability tests on the allele frequencies using the Markov chain procedure described by Raymond and Rousset (1995b). The results of these tests are shown in Table 2 alongside the estimates of F_{ST}. The second approach was to test whether the estimates of θ differed significantly from zero by randomly permuting alleles among samples by the FSTAT program of Goudet (1995). Small but significant differences were detected among Nova Scotia and Newfoundland populations of *G. morhua* by both permutation and exact tests even though in both regions less than 1% of the total allelic variation was attributable to differences among populations. When all eight northwest Atlantic populations were considered as a group, highly significant differences were observed at three RFLP loci (GM860, GM865, and GM798), but the mean F_{ST} increased to only 1.4%. When populations from the entire north Atlantic were compared, nearly all loci exhibited highly significant differences by both testing procedures, but the among-population component of the total allelic variance remained less than 7%.

In the Nova Scotia region, eight loci exhibited negative correlations between gene flow and geographic distance (Fig. 2), but Mantel tests indicated that the patterns were significant at only three (Table 3). Averaging over all 10 loci, the relationship was not significant even though 77.2% of the variation in gene flow could be accounted for by the distance separating the populations. When the *Pan*I (GM798) locus was excluded the relationship between gene flow and distance became significant and r^2 increased to 0.92. Figure 3 shows that the association between gene flow and distance was less pronounced in the Newfoundland region: only four loci had negative slopes and none were significant (Table 3). Exclud-

TABLE 1. Comparison of levels of genetic variation among cod populations in the northwest and northeast Atlantic regions.

Population	n	No. of alleles			Mean no. of alleles per locus	H_o	H_e	F_{IS}
		Private	Rare	Total				
Northwest Atlantic								
Newfoundland								
Northeast Newfoundland Shelf	120	10	32	54	5.4	0.346	0.336	−0.023
Grand Bank N	144	9	26	48	4.8	0.344	0.341	0.007
Grand Bank S	72	6	20	43	4.3	0.364	0.347	−0.044
Trinity Bay	92	2	19	40	4.0	0.336	0.342	0.023
Pooled	428	28	39	88	8.7	0.345	0.341	−0.004
Nova Scotia								
Bras d'Or Lakes	43	6	10	33	3.3	0.340	0.365	0.065
Western Bank	138	4	27	48	4.8	0.340	0.331	−0.014
Eastern Passage	122	4	22	44	4.4	0.325	0.317	−0.030
Sable Bank	109	5	23	44	4.4	0.341	0.346	0.022
Pooled	412	20	39	80	7.9	0.335	0.334	−0.002
Northeast Atlantic								
Iceland	84	5	27	47	4.8	0.357	0.346	−0.034
North Sea	81	4	17	39	4.0	0.340	0.343	0.001
Balsfjord	87	3	15	38	3.8	0.382	0.365	−0.041
Barents Sea	82	7	19	41	4.1	0.344	0.325	−0.034

TABLE 2. Comparison of levels of genetic differentiation among populations of *Gadus morhua* at different geographic scales. See text for details.

	Nova Scotia region		Newfoundland region		Pooled northwest Atlantic region		Entire north Atlantic region	
Locus	F_{ST}	θ	F_{ST}	θ	F_{ST}	θ	F_{ST}	θ
GM309	0.002	−0.001	0.006	0.006	0.005	0.002	0.011***	0.004**
GM867	0.001	−0.003	0.009	0.007*	0.007	0.003	0.034***	0.036***
GM777	0.018**	0.008*	0.003	−0.002	0.010*	0.002	0.046***	0.064***
GM842	0.008	0.006*	0.003	−0.001	0.007	0.003	0.017***	0.015***
GM860	0.011	0.007	0.001	−0.003	0.020***	0.022***	0.013**	0.019***
GM307	0.006	0.004	0.004	0.001	0.007*	0.005*	0.045***	0.031***
GM738	0.023*	0.013*	0.008	0.006	0.016**	0.007*	0.142***	0.220***
GM865	0.007	0.001	0.006	0.002	0.021***	0.024***	0.018***	0.030***
GM727	0.006*	0.003	0.001	−0.003	0.009*	0.003	0.008	0.007***
GM798	0.011***	0.012*	0.008*	0.006	0.027***	0.034***	0.237***	0.164***
Mean	0.008***	0.004**	0.006*	0.003*	0.014***	0.012***	0.068***	0.065***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

ing the GM798 locus weakened the relationship between gene flow and geographic distance in Newfoundland, although the slope and intercept of the regression became similar to that seen in Nova Scotia.

A highly significant negative relationship was observed between gene flow and geographic distance among the eight northwest Atlantic populations (Fig. 4). The three loci largely responsible for producing this result (GM860, GM865, and GM798) also strongly differentiated populations from both regions (see Table 2). Unlike the results for the Nova Scotia and Newfoundland populations analyzed separately, removal of the GM798 locus had a minimal effect on the relationship between gene flow and distance in the northwest Atlantic (Table 4). The slope of the regressions between log (Mhat) and log (geographic distance) in this region were intermediate between those expected for a one-dimensional stepping-stone model (slope = −1.0) and a two-dimensional model (slope = −0.5).

A significant association between gene flow and distance was also detected across the entire north Atlantic Ocean (Fig. 5). Eight of the 10 loci exhibited negative slopes that Mantel tests confirmed were significant at seven (Table 4). At this largest geographic scale, two RFLP loci (GM798 and GM738) exhibited considerably higher F_{ST}-values than the others. Only the GM798 locus, however, was found to have a pronounced effect on the relationship between gene flow and distance. Excluding the GM798 locus resulted in the slope of the regression of log (Mhat) and log (geographic distance) to approximate that expected under a linear stepping-stone model and r^2 increased from 0.17 to 0.62 (Table 4). In contrast, the GM738 locus had a minor effect on the relationship between gene flow and distance, although removing both it and GM798 caused r^2 to decline slightly to 0.511 (not shown). The strong influence of the GM798 locus at this oceanwide scale is also evident in the UPGMA trees shown in Figure 6. Not including GM798 in the estimation of genetic distance had a small effect on the clustering of populations from the northwest Atlantic with the exception of the Bras d'Or sample. However, in the northeast Atlantic branch lengths were dramatically shortened and the North Sea sample clustered with the Barents Sea sample instead of the Balsfjord sample when the GM798 locus was excluded.

The role of vicariance in contributing to the relationship between gene flow and distance at different geographic scales was examined by removing one population at a time from the regression analyses (Table 5). No single population was found to exert a significant effect on the correlation between gene flow and distance observed at small or large geographic scales. Without exception, slopes remained negative when individual populations were excluded, although the statistical significance of the relationships was generally weakened—apparently by reducing the number of populations compared. Again, the GM798 locus had a major effect on these analyses only at the largest geographic scale. Evidence for a minor effect of vicariance was also present at this oceanwide scale because removal of either Nova Scotia or Newfoundland resulted in the relationship between gene flow and distance no longer being significant.

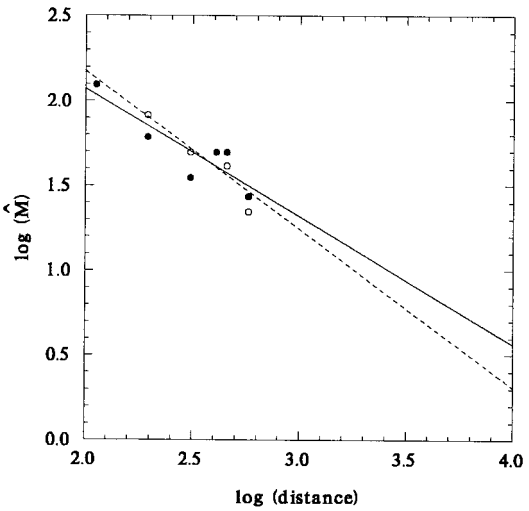

FIG. 2. Relationships between log (Mhat) and log (geographic distance) among the four Nova Scotia populations. Regressions are presented for all 10 restriction-fragment-length-polymorphism loci (closed circles, solid line) and for nine loci (open circles, dashed line) excluding GM798. Open circles that are not visible fall within closed symbols.

TABLE 3. Isolation by distance (IBD) among the Nova Scotia and Newfoundland populations of *Gadus morhua* in the northwest Atlantic.

	Nova Scotia populations				Newfoundland populations			
Locus	IBD slope	IBD intercept	r^2	P	IBD slope	IBD intercept	r^2	P
GM309	0.083	2.043	0.007	0.469	0.034	1.801	0.000	0.658
GM867	0.161	1.952	0.120	0.844	0.970	−0.708	0.033	0.540
GM777	−1.844	6.049	0.756	0.164	0.123	1.924	0.002	0.538
GM842	−0.648	3.356	0.243	0.290	−1.754	6.777	0.492	0.088
GM860	−1.336	5.001	0.617	0.117	0.042	2.238	0.001	0.503
GM307	−0.091	2.211	0.004	0.620	−0.565	3.858	0.027	0.591
GM738	−2.083	7.022	0.575	0.041	−2.022	7.229	0.240	0.503
GM865	−1.563	5.776	0.885	0.047	−2.961	9.808	0.556	0.088
GM727	−0.885	4.093	0.443	0.040	0.294	1.565	0.069	0.678
GM798	−0.221	2.210	0.022	0.629	−0.666	3.586	0.023	0.455
Mean								
10 loci	−0.755	3.582	0.772	0.086	−0.681	3.635	0.699	0.125
9 loci[1]	−0.934	4.044	0.917	0.003	−1.111	4.907	0.224	0.164

[1] Excluding GM798.

DISCUSSION

Our study has revealed a significant relationship between gene flow and geographic distance at 10 nuclear RFLP in the Atlantic cod, *G. morhua*, in the northwestern Atlantic ocean (< 1600 km) that is similar to that detected previously across the species' entire geographic range (up to 7300 km) by Pogson et al. (1995). The magnitude of population differentiation and the number of loci that contribute to the relationship between gene flow and distance both increase with increasing spatial scale. In the northwest Atlantic only 1.4% of the total allelic variance was attributable to differentiation among populations and three of the 10 loci contributed significantly to the relationship between gene flow and distance. In contrast, over the entire north Atlantic region the mean F_{ST} increased to 0.068 and seven loci contributed significantly to the decline in gene flow with distance. At both spatial scales, the geographic distance separating populations explained between 50% and 60% of the variation in gene flow estimated to occur among the populations. Sampling artifacts or vicariance events appear unlikely to explain these observations because mean heterozygosity levels were similar for all populations (Table 1), IBD slopes and intercepts were comparable at all geographic scales (Tables 3, 4), and sequentially excluding populations one at a time from the analyses failed to identify any outliers (Table 5).

The relationship between gene flow and distance observed in *G. morhua* is unlikely to have been produced by natural selection acting at or in the vicinity of the DNA markers scored. Evidence consistent with the neutrality of the RFLP loci has been discussed in previous reports (see Pogson et al. 1995; Pogson and Fevolden 1998) with the notable exception of GM798. This locus was previously identified as encoding a synaptic vesicle membrane protein called syn-

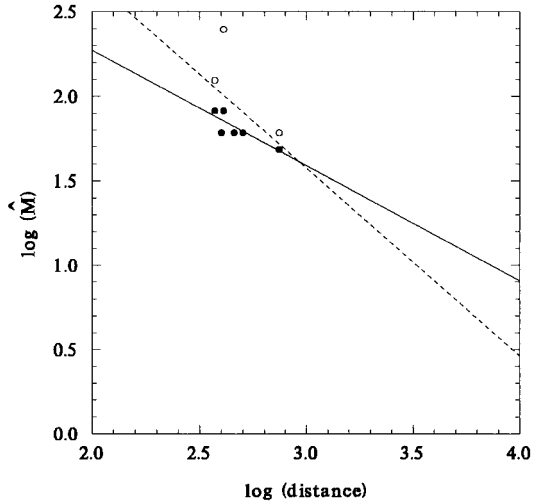

FIG. 3. Relationships between log (Mhat) and log (geographic distance) among the four Newfoundland populations. Regressions are presented for all 10 restriction-fragment-length-polymorphism loci (closed circles, solid line) and for nine loci (open circles, dashed line) excluding GM798. Open circles that are not visible fall within closed symbols.

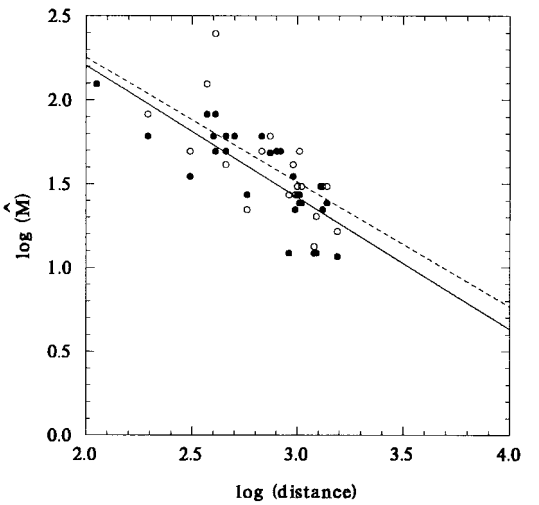

FIG. 4. Relationships between log (Mhat) and log (geographic distance) among the eight northwest Atlantic populations. Regressions are presented for all 10 restriction-fragment-length-polymorphism loci (closed circles, solid line) and for nine loci (open circles, dashed line) excluding GM798. Open circles that are not visible fall within closed symbols.

TABLE 4. Isolation by distance (IBD) among eight northwest Atlantic populations and six north Atlantic populations of *Gadus morhua* that cover its entire geographic range.

	Northwest Atlantic populations				North Atlantic populations			
Locus	IBD slope	IBD intercept	r^2	P	IBD slope	IBD intercept	r^2	P
GM309	−0.208	2.678	0.027	0.139	0.317	0.826	0.046	0.954
GM867	−0.187	2.604	0.010	0.409	−0.862	4.358	0.306	0.049
GM777	0.085	1.672	0.002	0.789	−1.032	4.796	0.403	0.026
GM842	−0.088	2.134	0.008	0.500	−0.805	4.435	0.437	0.039
GM860	−1.137	4.827	0.274	0.019	−0.213	2.509	0.024	0.240
GM307	0.015	1.939	0.001	0.679	−0.929	4.533	0.404	0.029
GM738	−0.486	3.207	0.066	0.116	−2.167	8.619	0.555	0.018
GM865	−1.492	5.782	0.582	0.002	−0.559	3.617	0.139	0.004
GM727	−0.445	3.223	0.075	0.072	−0.432	3.416	0.178	0.003
GM798	−1.101	4.537	0.323	<0.001	0.170	−0.209	0.012	0.511
Mean								
10 loci	−0.787	3.781	0.621	<0.001	−0.338	2.022	0.171	0.021
9 loci[1]	−0.743	3.740	0.543	<0.001	−1.055	4.869	0.619	0.008

[1] Excluding GM798.

aptophysin (Fevolden and Pogson 1997), but is more likely to represent a recently discovered cellular isoform called pantophysin. Frequencies of the polymorphic *Pst*I site scored by the GM798 clone differ markedly among populations of *G. morhua* except in the northwest Atlantic region, where recombination has reduced the extent of linkage disequilibrium between the variable *Pst*I site and a recent amino acid replacement mutation (Pogson 2001). Although the nucleotide and amino acid differences detected between *Pan*I alleles strongly suggests the action of selection, this locus had a minor effect on the relationship between gene flow and distance except at the largest geographic scale. This is attributable to the substantial differences in *Pan*I allele frequencies among populations in the northeast Atlantic (Appendix) and removing it from the analysis at the largest spatial scale caused r^2 to increase from 0.17 to 0.62 (Table 4). A second locus (GM738) also exhibited a much higher F_{ST} than the other DNA markers, but, unlike GM798, did not exert a strong effect on the relationship between gene flow and distance.

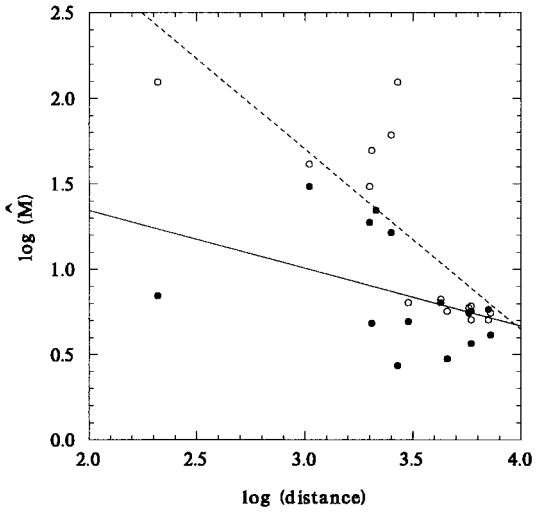

FIG. 5. Relationships between log (Mhat) and log (geographic distance) among the six north Atlantic populations. Regressions are presented for all 10 restriction-fragment-length-polymorphism loci (closed circles, solid line) and for nine loci (open circles, dashed line) excluding GM798.

The significant association between gene flow and geographic distance observed in a highly mobile species like the Atlantic cod is unexpected. In a recent review by Peterson and Denno (1998) on allozyme-generated IBD in phytophagous insects, only four of the 24 studies detecting significant relationships between gene flow and geographic distance had r^2-values exceeding 0.50 and more than half (13) had r^2-values below 0.20. Peterson and Denno (1998) also found a significant effect of population number; only 36% of the studies with less than 15 populations found significant relationships between gene flow and distance compared to 71% of studies including at least 15 populations. The present study involved comparisons among only four to eight populations at various spatial scales yet frequently yielded r^2-values exceeding 0.50. Remarkably, geographic distance explained the greatest proportion of the variation in gene flow among the four Nova Scotia samples that are separated by less than 600 km. In this region r^2 was 0.77 for all 10 loci and increased to 0.92 if the GM798 locus was excluded from the estimation of gene flow (Table 3). Two factors may account for the more pronounced expression of the relationship between gene flow and distance in *G. morhua* compared to insects: habitat structure and marker type. Crow and Aoki (1984) have shown that stepping-stone models with narrow linear habitats (e.g., spawning banks along continental shelf margins) can produce much greater divergence among populations than area models that allow gene flow to occur in many directions simultaneously (e.g., insect populations dispersed over large areas). It is also possible that the DNA markers used in our study are more accurate indicators of population structure than allozymes. Although few studies have compared protein and DNA markers in this context, several have found that the relationship between gene flow and distance expressed at allozymes to be much less pronounced, or absent entirely, compared to DNA markers (Pogson et al. 1995; Raybould et al. 1997).

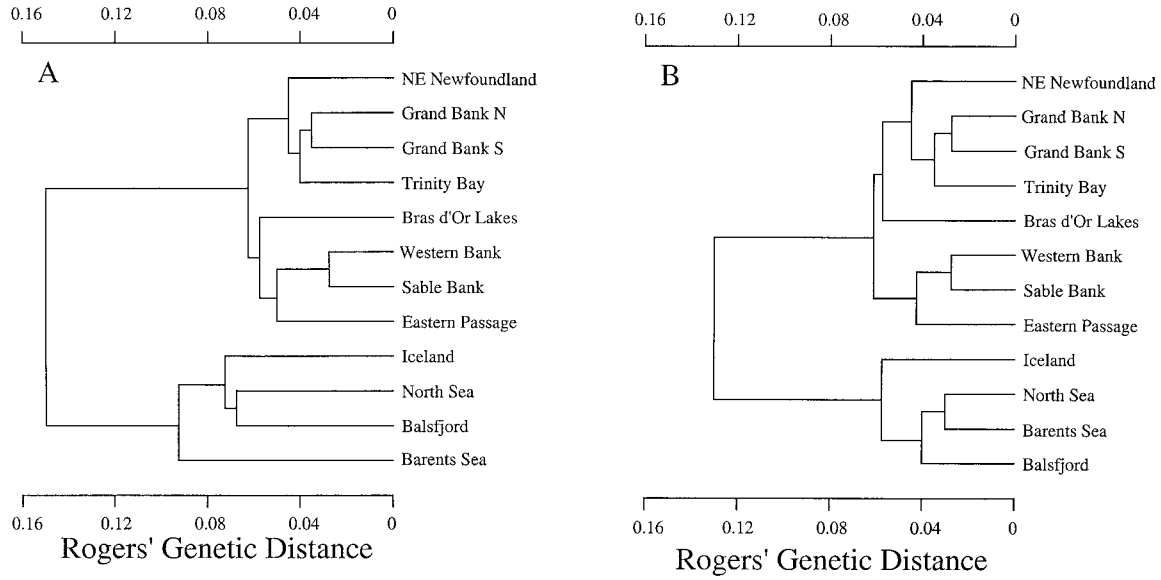

FIG. 6. UPGMA dendograms based on Rogers' genetic distance. Trees are presented for (A) all 10 restriction-fragment-length-polymorphism loci and (B) nine restriction-fragment-length-polymorphism loci excluding GM798.

When relationships between gene flow and distance have been documented in marine species with high dispersal potential, they have typically been described over large geographic areas. For example, Palumbi et al. (1997) reported highly significant associations between gene flow and distance in four *Echinometra* species at large geographic scales across the Indo-Pacific (5000–10,000 km) but not at scales of 2500–5000 km. However, the decline in gene flow with distance observed in *Echinometra* was likely caused by the reduction in genetic diversity that occurs from the center to

TABLE 5. Effect of removing populations one at a time on the relationships between gene flow and geographic distance observed among *Gadus morhua* populations at different geographic scales. IBD, isolation by distance.

Population excluded	10 loci				9 loci (excluding GM798)			
	IBD slope	IBD intercept	r^2	P	IBD slope	IBD intercept	r^2	P
Newfoundland								
Northeast Newfoundland	−1.075	4.701	0.910	0.332	−3.128	10.312	0.466	0.490
Grand Bank N	−0.509	3.154	0.968	0.328	−0.408	2.881	0.967	0.337
Grand Bank S	−1.238	5.065	0.571	0.344	−2.952	9.599	0.571	0.323
Trinity Bay	−0.608	3.438	0.652	0.511	−1.085	4.915	0.222	0.670
Nova Scotia								
Bras d'Or Lakes	−1.251	4.662	1.000	0.169	−0.904	3.964	0.988	0.166
Western Bank	−0.462	2.773	0.229	0.503	−1.339	5.091	0.803	0.335
Eastern Passage	−0.680	3.493	0.995	0.333	−0.757	3.653	0.993	0.161
Sable Bank	−0.608	3.207	0.687	0.174	−1.104	4.466	0.918	0.174
Northwest Atlantic								
Northeast Newfoundland	−0.785	3.753	0.585	<0.001	−0.761	3.777	0.504	0.003
Grand Bank N	−0.701	3.522	0.574	<0.001	−0.638	3.396	0.645	0.001
Grand Bank S	−0.770	3.677	0.698	<0.001	−0.680	3.509	0.665	0.004
Trinity Bay	−0.677	3.479	0.616	<0.001	−0.631	3.432	0.496	0.003
Bras d'Or Lakes	−0.816	3.857	0.635	<0.001	−0.816	3.955	0.621	0.002
Western Bank	−0.982	4.337	0.570	<0.001	−0.963	4.385	0.510	<0.001
Eastern Passage	−0.773	3.808	0.694	<0.001	−0.717	3.729	0.557	0.001
Sable Bank	−0.936	4.215	0.680	<0.001	−0.927	4.281	0.540	0.001
Entire North Atlantic								
Newfoundland	−0.186	1.495	0.068	0.057	−0.980	4.704	0.591	0.104
Nova Scotia	−0.166	1.412	0.044	0.114	−0.943	4.550	0.496	0.107
Iceland	−0.292	1.811	0.185	0.106	−1.006	4.717	0.640	0.046
North Sea	−0.246	1.725	0.160	0.050	−0.982	4.514	0.859	0.018
Balsfjord	−0.912	3.996	0.477	0.091	−1.488	6.396	0.570	0.018
Barents Sea	−1.175	5.081	0.741	0.061	−1.372	5.917	0.711	0.020

the periphery of the species' distributions. In marine fishes, negative relationships between gene flow and distance have been found in anadromous species (Chenoweth et al. 1998; Olsen et al. 1998) or those dependent on estuaries for some phase of their life history (Gold and Richardson 1998; Maltagliati 1999), but have not been widely documented in mobile demersal species like *G. morhua.* The decline in gene flow with distance in *G. morhua* is also unusual in its similarity at small and large geographic scales. This contrasts sharply with marine species with limited dispersal capabilities, which often show pronounced relationships between gene flow and distance at small but not at large spatial scales (e.g., Hellberg 1994; Johnson and Black 1998; Todd et al. 1998).

The significant association between gene flow and distance detected in *G. morhua,* particularly at small geographic scales, appears difficult to reconcile with many aspects of its biology. In general, the genetic process of IBD is expected to operate in species with limited dispersal capabilities, small effective population sizes, and ones that are at, or near, migration-drift equilibrium (Wright 1943; Slatkin 1993). At face value, none of these conditions would appear to be met by the Atlantic cod. Gene flow can readily occur among cod populations either by the passive transport of eggs or larvae in surface waters or by the active movement of juvenile or adult fish. In the northwest Atlantic, long-term tagging studies have demonstrated this potential for gene flow. During the periods of 1954–1955, 1962–1966, and 1978–1991, hundreds of thousands of cod were tagged in the Newfoundland region and approximately 0.50%, 0.35%, and 0.09% of recaptures from those periods, respectively, were reported from the Scotian Shelf region (Taggart et al. 1995). Larvae may also be transported great distances in surface currents in the western Atlantic. Templeman (1981) estimated that cod larvae spawned off northern Labrador in March or April would take 50–60 days to hatch at surface temperatures of -1.5°C to 0°C. During this period, the developing larvae could be transported by the Labrador current as far south as Trinity Bay and the northern Grand Bank area. With this high potential for gene flow at all life-history stages, there would appear to be little opportunity for genetic differentiation to develop among populations of *G. morhua* either within or among coastal shelf regions in the northwestern Atlantic.

The possibility that *G. morhua* possesses a small effective population size (N_e) also appears difficult to reconcile with their large census populations that have supported important commercial fisheries for centuries. Large discrepancies have been noted between census and effective population sizes in Atlantic cod (see Arnason and Palsson 1996; Ruzzante et al. 1996) as they have for most other species (Frankham 1995). However, small N_e-values are not consistent with the high level of allozyme heterozygosity exhibited by *G. morhua* (mean $H = 0.114$ based on the 43 loci; Grant and Stahl 1988), which is nearly double the mean of 57 marine species reviewed by Ward et al. (1994). High levels of variability at the nuclear DNA level are also evident at the RFLP loci scored in the present study and at six highly polymorphic microsatellite loci (Bentzen et al. 1996; Ruzzante et al. 1996, 1998). On the basis of mitochondrial cytochrome *b* sequence variation, Arnason and Palsson (1996) have estimated the effective number of breeding females in *G. morhua* populations from the northeast Atlantic region to be approximately 150,000. However, this must underestimate N_e because the large excess of low frequency RFLP alleles detected in *G. morhua* strongly suggests that populations are significantly displaced from mutation-drift equilibrium, which is an assumption made in obtaining this estimate (see discussion in Pogson et al. 1995).

Finally, the requirement for *G. morhua* populations to be at migration-drift equilibrium appears to be compromised by the recent ages of populations throughout the north Atlantic. Without exception, the locations of populations sampled in our study were covered by ice sheets 15,000 years ago (see Ruddiman and McIntyre 1981). Assuming a mean generation time for *G. morhua* of five to six years and that extant populations were established 10,000–12,000 years ago, the relationship between gene flow and distance detected in our study must have formed within approximately 2000 generations. This number of generations is too low for populations to reach mutation-drift equilibrium, but may have allowed F_{ST} to approach migration-drift equilibrium provided that migration rates and effective population sizes are both sufficiently small (Crow and Aoki 1984; Whitlock 1992).

The weak population structure and gene flow–distance relationship detected in *G. morhua* in the northwest Atlantic suggests not only that migration-drift equilibrium has been achieved but also that temporally stable microgeographic differentiation exists among populations in this region. This fine-scale structure must have developed following a late Pleistocene range expansion in which *G. morhua* colonized the continental margins and nearshore areas in the northwest Atlantic and the remainder of its present range. We propose that after this initial colonization period gene flow has slowed considerably among extant populations. This recent reduction in gene flow would have had a minimal effect on the overall genetic diversity exhibited by *G. morhua* (which would reflect historical levels). The magnitude of genetic differentiation among the recently formed populations will be low and indirect estimates of gene flow correspondingly high. However, these indirect estimates of gene flow will overestimate the true levels by a large, but unknown, degree because they represent averages over many thousands of generations. This scenario can explain the simultaneous presence of weak population structure, comparable relationships between gene flow and distance at small and large geographic scales, and the large number of low frequency RFLP alleles that are distributed randomly among populations (Appendix). It also suggests that vicariance may have contributed to relationship to gene flow and distance as the species formed microgeographic structure in different regions. A weak effect of vicariance is indeed evident among the Nova Scotia and Newfoundland populations (where the three loci that most strongly distinguish populations from these regions also contribute most strongly to the relationship between gene flow and distance) as well as between populations from the northwest and northeast Atlantic (where removal of either northwest Atlantic populations eliminates the significance of the relationship between gene flow and distance).

Two conditions must be met for genetic differences to develop and persist among populations of *G. morhua* at small

spatial scales in the northwest Atlantic. First, eggs and larvae must be retained in coastal areas and on different offshore banks by oceanographic features such as large, gyrelike eddies. Second, when individuals mature they must return to spawn on natal banks or coastal bays with a high degree of fidelity. Evidence for a substantial degree of spawning site fidelity is supported by tagging studies that have suggested limited dispersal across deep ocean channels (Frank 1992; Taggart 1997) and in more confined coastal regions (Taggart et al. 1998). Support also exists for the first requirement, particularly in the Nova Scotia region where temporal differences in spawning times are well documented (Brander and Hurley 1992; Frank et al. 1994) and the bathymetric features of the Scotian Shelf are conducive to formation of persistent retention systems (see discussions in Sanderson 1995; Taggart et al. 1996; Ruzzante et al. 1998). Genetic evidence corroborating microgeographic structuring of populations on the Scotian Shelf has also been obtained by recent studies using five or six highly variable microsatellite loci (Ruzzante et al. 1996, 1998). For example, Ruzzante et al. (1996) found that a large cohort of larvae sampled from Western Bank was more similar genetically to an adult sample collected two years later from the same bank than it was to an adult sample collected on an adjacent bank 150 km away. Significant differences have also been detected among three banks on the Scotian Shelf by Ruzzante et al. (1998). The 10 RFLP loci characterized in the present study produce results that are generally consistent with the microsatellites. However, the microsatellites do not reveal the same magnitude of population differentiation in this region as the RFLPs, nor do they reveal strong associations between gene flow and distance across the entire nothwest Atlantic. This may be attributable to problems associated with the extremely high heterozygosities of the cod microsatellites (see Hedrick 1999) or to their high mutation rates, which might have obscured the geographic patterns of gene flow detected by the RFLPs.

In summary, our study has detected significant relationships between gene flow and geographic distance at both small and large geographic scales in a highly mobile marine fish species exhibiting extremely weak population structuring. The association between gene flow and distance in *G. morhua* at small geographic scales in the northwest Atlantic region suggests that gene flow and effective population sizes are both much lower than expected and that populations are close to migration-drift equilibrium despite their young age and clear departure from mutation-drift equilibrium. Our results suggest that high potential for dispersal does not translate into high gene flow per se and that the interpretation of limited genetic differences among populations of any species as reflecting high levels of ongoing gene flow should be made with caution.

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APPENDIX

Frequencies and sizes of alleles (in kb) at the 10 restriction-fragment-length-polymorphism loci in 12 populations of *Gadus morhua.*

Locus	Allele size	Population											
		NE Nfld	Grand Bank N	Grand Bank S	Trinity Bay	Bras d'Or	Western Bank	Eastern Passage	Sable Bank	Iceland	North Sea	Balsfjord	Barents Sea
GM309	13.30	—	0.003	—	—	—	—	0.004	—	—	—	—	0.006
	11.11	0.008	0.007	0.007	—	—	—	—	—	—	—	0.011	0.006
	10.51	0.404	0.309	0.333	0.348	0.349	0.366	0.303	0.335	0.214	0.370	0.391	0.323
	10.26	0.008	—	0.014	0.005	—	—	—	—	—	0.006	—	0.006
	9.27	—	—	—	—	—	0.004	—	—	—	—	0.006	—
	8.92	—	—	—	0.005	—	0.004	—	—	0.018	—	—	—
	8.35	—	—	—	—	—	—	—	—	0.006	0.012	—	—
	8.20	0.550	0.670	0.625	0.609	0.628	0.605	0.660	0.642	0.726	0.605	0.586	0.622
	8.05	0.004	—	—	0.016	—	—	0.004	—	—	—	—	0.006
	7.78	0.004	—	0.007	0.005	—	0.007	0.004	—	—	—	—	—
	7.41	—	—	—	—	—	—	—	—	0.012	—	—	0.012
	7.14	0.004	—	—	—	—	—	—	—	—	—	—	—
	6.34	—	0.003	—	—	0.012	—	—	0.005	—	0.006	—	0.012
	5.97	0.004	—	—	—	—	—	—	—	—	—	—	—
	5.58	—	—	—	—	—	—	—	0.005	0.006	—	—	—
	3.98	0.008	0.007	0.007	0.011	0.012	0.011	0.020	0.014	0.006	—	0.006	—
	3.49	0.004	—	0.007	—	—	0.004	—	—	0.012	—	—	0.006
	1.79	—	—	—	—	—	—	0.004	—	—	—	—	—
	H_o	0.525	0.424	0.583	0.522	0.488	0.536	0.500	0.569	0.488	0.494	0.563	0.476
	H_e	0.536	0.457	0.581	0.511	0.489	0.502	0.474	0.477	0.429	0.500	0.506	0.511
	F_{IS}	0.021	0.073	−0.165	−0.022	0.002	−0.069	−0.055	−0.193	−0.140	0.012	−0.113	0.070
GM867	9.18	—	—	—	—	—	—	—	—	—	0.006	—	—
	4.95	—	—	—	—	—	0.004	—	—	—	—	—	—
	4.76	—	—	—	—	—	—	—	—	—	0.006	—	—
	4.28	—	—	—	—	—	—	—	—	—	—	0.006	—
	3.42	—	0.003	—	—	—	0.004	—	0.014	0.012	0.012	0.006	0.006
	3.05	—	0.003	—	—	—	0.004	—	—	—	—	—	—
	2.83	—	—	—	—	—	—	0.004	—	—	—	0.006	—
	2.51	—	—	0.007	—	—	0.004	—	—	—	—	—	—
	2.48	0.533	0.493	0.528	0.418	0.535	0.522	0.566	0.523	0.714	0.728	0.626	0.689
	2.42	—	0.003	—	—	—	—	—	—	—	—	—	—
	2.34	0.004	—	—	—	—	—	—	0.005	0.006	—	—	—
	2.21	0.463	0.490	0.458	0.582	0.465	0.460	0.426	0.454	0.268	0.247	0.356	0.305
	2.17	—	0.007	0.007	—	—	0.004	0.004	—	—	—	—	—
	1.91	—	—	—	—	—	—	—	0.005	—	—	—	—
	H_o	0.600	0.597	0.611	0.511	0.326	0.558	0.541	0.523	0.369	0.432	0.483	0.463
	H_e	0.502	0.519	0.515	0.489	0.503	0.518	0.500	0.522	0.420	0.411	0.483	0.435
	F_{IS}	−0.192*	−0.151	−0.189	−0.044	0.356*	−0.078	−0.081	−0.001	0.123	−0.052	0.001	−0.066
GM777	5.20	—	—	—	—	—	—	0.004	—	—	—	—	—
	4.70	—	—	—	0.005	—	—	—	—	—	—	—	0.012
	3.96	0.004	—	—	—	—	—	—	—	—	—	—	—
	3.72	—	—	—	—	—	0.011	—	—	—	—	—	—
	3.26	0.004	—	—	—	—	—	—	—	—	—	—	—
	3.19	0.904	0.917	0.896	0.935	0.977	0.902	0.926	0.881	0.845	0.741	0.690	0.726
	3.11	0.004	—	—	—	—	—	—	—	—	—	—	—
	2.98	—	—	—	—	—	0.007	—	—	0.006	0.006	—	—
	2.82	—	—	—	—	—	—	—	—	—	—	—	0.006
	2.67	0.004	—	0.007	—	—	—	—	—	0.006	—	0.006	—
	2.59	0.067	0.063	0.083	0.049	—	0.072	0.057	0.096	0.131	0.228	0.282	0.207

APPENDIX. Continued.

Locus	Allele size	Population: NE Nfld	Grand Bank N	Grand Bank S	Trinity Bay	Bras d'Or	Western Bank	Eastern Passage	Sable Bank	Iceland	North Sea	Balsfjord	Barents Sea
	2.50	—	—	—	—	—	0.004	—	—	—	—	—	—
	2.43	—	—	—	—	—	—	—	0.005	—	—	—	—
	2.34	0.004	—	0.007	0.011	0.023	0.004	0.004	0.014	—	—	—	—
	2.12	—	—	—	—	—	—	—	0.005	—	—	—	—
	2.00	—	—	—	—	—	—	—	—	—	—	—	0.006
	1.85	0.008	0.014	0.007	—	—	—	0.008	—	0.012	0.025	0.023	0.043
	1.50	—	0.003	—	—	—	—	—	—	—	—	—	—
	1.13	—	0.003	—	—	—	—	—	—	—	—	—	—
	H_o	0.175	0.146	0.208	0.109	0.047	0.167	0.148	0.165	0.286	0.407	0.437	0.427
	H_e	0.179	0.156	0.192	0.124	0.046	0.181	0.139	0.216	0.270	0.401	0.447	0.431
	F_{IS}	0.020	0.066	−0.087	0.126	−0.012	0.081	−0.060	0.236*	−0.059	−0.016	0.023	0.010
GM842	4.60	—	—	—	—	—	—	—	—	0.006	—	—	—
	3.96	0.075	0.097	0.069	0.103	0.058	0.036	0.053	0.096	—	0.006	—	—
	3.66	0.004	—	—	—	—	—	—	0.005	—	—	0.006	—
	3.43	—	—	—	—	—	—	—	0.009	—	—	—	—
	3.23	0.825	0.851	0.882	0.837	0.814	0.866	0.877	0.794	0.905	0.901	0.948	0.933
	3.16	—	—	—	—	—	—	—	0.005	0.006	0.006	—	—
	3.06	0.004	0.014	0.007	0.005	0.012	0.011	0.016	0.018	0.018	0.025	0.006	0.018
	2.94	0.063	0.035	0.035	0.054	0.105	0.065	0.041	0.055	0.012	0.012	0.011	0.012
	2.88	0.004	—	—	—	—	—	—	—	—	—	—	—
	2.81	0.004	—	—	—	—	0.004	0.004	—	—	—	—	—
	2.71	—	—	—	—	0.012	—	—	—	—	—	—	—
	2.67	0.021	—	0.007	—	—	0.011	0.004	0.014	0.042	0.037	0.017	0.037
	2.62	—	—	—	—	—	—	0.004	—	0.006	—	0.006	—
	2.56	—	—	—	—	—	0.007	—	—	—	0.006	—	—
	2.39	—	—	—	—	—	—	—	—	—	—	0.006	—
	2.31	—	0.003	—	—	—	—	—	—	—	—	—	—
	2.20	—	—	—	—	—	—	—	—	—	0.006	—	—
	2.05	—	—	—	—	—	—	—	0.005	0.006	—	—	—
	H_o	0.317	0.292	0.236	0.293	0.256	0.246	0.238	0.367	0.190	0.173	0.103	0.134
	H_e	0.311	0.266	0.218	0.287	0.327	0.245	0.227	0.359	0.180	0.187	0.101	0.129
	F_{IS}	−0.020	−0.095	−0.086	−0.021	0.219*	−0.005	−0.048	−0.023	−0.058	0.074	−0.027	−0.043
GM860	8.73	—	0.003	—	—	—	—	—	—	—	—	0.006	—
	8.14	0.004	—	—	—	—	—	—	—	—	—	—	—
	6.21	—	—	—	—	—	—	—	—	0.006	—	—	—
	5.69	0.488	0.510	0.514	0.538	0.465	0.384	0.320	0.413	0.423	0.543	0.517	0.482
	3.95	—	0.007	—	—	—	—	—	—	—	—	—	—
	3.33	0.004	—	—	—	—	—	—	—	—	—	—	—
	3.12	—	—	—	—	—	—	0.004	—	—	—	—	—
	2.77	—	—	—	—	—	0.004	—	0.005	—	—	—	—
	2.16	—	0.003	—	—	—	0.007	—	—	—	0.006	—	—
	1.86	—	0.003	—	—	—	—	—	—	—	—	—	—
	1.70	—	—	—	—	—	—	—	—	—	—	—	0.006
	1.58	0.004	—	—	0.005	—	—	—	—	—	—	—	—
	1.44	0.500	0.472	0.479	0.457	0.535	0.605	0.676	0.583	0.571	0.451	0.477	0.506
	1.30	—	—	—	—	—	—	—	—	—	—	—	0.006
	1.07	—	—	0.007	—	—	—	—	—	—	—	—	—
	H_o	0.483	0.507	0.444	0.522	0.465	0.493	0.418	0.431	0.560	0.494	0.563	0.622
	H_e	0.514	0.518	0.510	0.505	0.503	0.488	0.442	0.492	0.498	0.505	0.508	0.515
	F_{IS}	0.061	0.022	0.129	−0.034	0.077	−0.010	0.055	0.125	−0.125	0.022	−0.110	−0.209

APPENDIX. Continued.

Locus	Allele size	Population: NE Nfld	Grand Bank N	Grand Bank S	Trinity Bay	Bras d'Or	Western Bank	Eastern Passage	Sable Bank	Iceland	North Sea	Balsfjord	Barents Sea
GM307	9.62	—	0.003	—	—	—	—	—	—	—	—	—	—
	8.64	0.004	0.014	0.028	0.011	—	0.011	0.012	—	0.006	0.012	—	—
	7.60	—	—	—	—	—	—	—	—	—	—	—	0.006
	7.04	0.075	0.128	0.097	0.103	0.081	0.058	0.102	0.050	0.006	—	—	—
	6.70	0.908	0.854	0.868	0.864	0.907	0.913	0.873	0.936	0.982	0.975	1.000	0.988
	5.35	0.004	—	—	—	0.012	0.014	0.012	0.009	—	—	—	—
	3.88	—	—	—	0.005	—	—	—	—	—	—	—	—
	3.52	0.004	—	—	0.011	—	0.004	—	0.005	—	0.012	—	—
	3.34	0.004	—	—	—	—	—	—	—	—	—	—	—
	3.13	—	—	—	—	—	—	—	—	—	—	—	0.006
	2.81	—	—	—	—	—	—	—	—	0.006	—	—	—
	2.66	—	—	—	0.005	—	—	—	—	—	—	—	—
	1.73	—	—	0.007	—	—	—	—	—	—	—	—	—
	H_o	0.167	0.222	0.236	0.250	0.140	0.174	0.238	0.128	0.036	0.049	0.000	0.024
	H_e	0.170	0.255	0.238	0.244	0.173	0.163	0.228	0.122	0.036	0.049	0.000	0.024
	F_{IS}	0.019	0.127	0.007	−0.026	0.194	−0.066	−0.042	−0.051	−0.006	−0.013	0.000	−0.003
GM738	4.80	—	—	—	—	—	—	—	—	0.006	—	—	—
	4.09	0.004	—	—	—	—	—	—	0.005	—	—	—	—
	3.42	—	—	—	—	—	—	—	0.005	—	—	—	—
	2.73	0.921	0.851	0.854	0.880	0.779	0.895	0.906	0.881	0.518	0.481	0.500	0.482
	2.53	—	—	—	0.005	—	—	—	—	0.006	—	—	—
	2.36	0.008	0.014	—	0.011	—	—	0.004	—	—	—	—	—
	2.11	—	—	0.007	—	—	—	—	—	—	—	—	—
	1.86	0.067	0.135	0.139	0.103	0.221	0.105	0.090	0.110	0.470	0.519	0.500	0.518
	H_o	0.142	0.229	0.236	0.217	0.395	0.181	0.189	0.202	0.488	0.469	0.586	0.524
	H_e	0.148	0.259	0.253	0.215	0.348	0.189	0.172	0.213	0.514	0.502	0.503	0.502
	F_{IS}	0.044	0.114	0.067	−0.010	−0.137	0.040	−0.095	0.053	0.050	0.067	−0.167	−0.044
GM865	3.38	—	—	—	—	0.012	—	—	—	—	—	—	—
	2.42	—	—	0.014	—	—	—	—	—	—	—	—	—
	2.02	—	0.003	0.007	0.005	—	0.004	—	—	—	—	0.006	0.006
	1.81	0.613	0.663	0.708	0.647	0.709	0.779	0.811	0.771	0.607	0.654	0.569	0.610
	1.76	0.383	0.333	0.271	0.348	0.279	0.217	0.189	0.229	0.375	0.346	0.414	0.378
	1.68	—	—	—	—	—	—	—	—	0.012	—	0.011	—
	1.62	0.004	—	—	—	—	—	—	—	0.006	—	—	0.006
	H_o	0.458	0.486	0.444	0.402	0.349	0.341	0.295	0.349	0.595	0.420	0.506	0.573
	H_e	0.480	0.451	0.428	0.463	0.424	0.347	0.307	0.355	0.494	0.455	0.508	0.488
	F_{IS}	0.045	−0.079	−0.040	0.132	0.179	0.019	0.040	0.018	−0.208	0.078	0.004	−0.175
GM727	8.56	—	—	—	—	0.012	—	—	—	—	—	—	—
	6.70	—	0.003	—	—	—	—	—	—	0.006	—	—	—
	5.61	—	—	—	—	—	—	0.008	—	—	—	—	—
	5.20	—	0.003	—	—	—	—	—	0.005	—	—	—	—
	3.48	0.933	0.917	0.924	0.924	0.837	0.895	0.906	0.867	0.929	0.938	0.960	0.951
	3.34	—	—	—	—	0.012	—	0.004	—	—	0.012	—	—
	2.93	—	0.003	—	0.005	—	0.014	0.012	—	—	—	—	—
	2.79	0.054	0.066	0.049	0.054	0.105	0.083	0.057	0.115	0.036	0.037	0.023	0.043
	2.21	0.013	0.007	0.028	0.016	0.035	0.004	0.012	0.014	0.030	0.012	0.017	0.006
	1.40	—	—	—	—	—	0.004	—	—	—	—	—	—
	H_o	0.133	0.153	0.153	0.141	0.326	0.188	0.180	0.229	0.143	0.123	0.080	0.098
	H_e	0.126	0.156	0.145	0.144	0.290	0.193	0.177	0.236	0.136	0.119	0.078	0.094
	F_{IS}	−0.056	0.020	−0.055	0.018	−0.124	0.022	−0.021	0.029	−0.048	−0.040	−0.026	−0.039

APPENDIX. Continued.

Locus	Allele size	Population											
		NE Nfld	Grand Bank N	Grand Bank S	Trinity Bay	Bras d'Or	Western Bank	Eastern Passage	Sable Bank	Iceland	North Sea	Balsfjord	Barents Sea
GM798	10.16	—	—	—	—	0.035	—	—	—	—	—	—	—
	7.50	—	—	—	—	—	—	—	—	—	—	0.006	—
	7.01	0.004	—	—	—	—	—	—	0.005	—	—	—	—
	6.49	0.004	—	—	—	—	—	—	—	—	—	—	—
	5.92	0.254	0.236	0.333	0.310	0.395	0.395	0.488	0.349	0.613	0.821	0.523	0.055
	5.75	—	—	—	—	—	—	—	—	—	—	—	0.006
	5.54	—	—	0.007	—	—	—	—	—	—	—	—	—
	4.87	—	—	—	—	—	—	—	—	0.006	—	—	—
	4.70	—	—	—	—	0.012	—	—	—	—	—	—	—
	4.48	—	—	—	—	—	—	—	—	—	0.006	—	—
	4.07	—	0.003	—	—	—	—	—	—	—	—	—	—
	3.63	—	0.003	—	—	—	—	—	—	—	—	—	—
	2.91	—	—	—	0.005	—	—	0.004	—	—	—	—	—
	2.40	0.738	0.757	0.646	0.685	0.547	0.605	0.508	0.647	0.381	0.173	0.460	0.939
	2.29	—	—	0.007	—	—	—	—	—	—	—	0.011	—
	1.74	—	—	—	—	0.012	—	—	—	—	—	—	—
	1.60	—	—	0.007	—	—	—	—	—	—	—	—	—
	H_o	0.458	0.382	0.486	0.391	0.605	0.514	0.500	0.450	0.417	0.333	0.494	0.098
	H_e	0.393	0.373	0.475	0.437	0.550	0.480	0.506	0.462	0.482	0.298	0.518	0.116
	F_{IS}	−0.167	−0.025	−0.024	0.106	−0.101	−0.073	0.012	0.028	0.136	−0.120	0.046	0.159

* $P < 0.05$.