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The Population Structure of Ten Newfoundland Outports

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Abstract Island populations are most informative in the study of the genetic structure of human aggregates. These populations are often of small size, thus violating the Hardy-Weinberg assumption of infinite size. Some geographically isolated island populations are further subdivided by religion, ethnicity, and socioeconomic factors, reducing their effective sizes and facilitating genetic changes due to stochastic processes. Because of extreme geographic and social isolation, fishing communities or outports of Newfoundland have been investigated for genetic microdifferentiation through the founder effect and genetic drift (Crawford et al. 1995). The purpose of this paper is to examine the population structure of 10 Newfoundland outports using the allelic frequencies derived from 12 red cell antigens. To achieve this goal, first we calculated gene frequencies using maximum-likelihood estimation procedures. Second, we used ***R***-matrix methods to explore population differentiation. Third, we regressed mean per-locus heterozygosity on genetic distance from the gene frequency centroid to identify the most isolated populations. On the basis of this information, the three outports of Seal Cove, Island Harbor, and Tilting were found to be genetically differentiated from the other small populations. Moreover, religious and geographic subdivisions appear to explain the observed genetic variation.

Newfoundland's history of settlement and small population size provided the impetus to assess the genetic isolation of its communities (Bear et al. 1987). Although some research on the genetics of Newfoundland focused initially on the presence of rare medical genetic conditions (Buehler et al. 1975; Spiro et al. 1999), several later studies examined its genetic variation and population structure (Newton 1975; Carter et al. 1976, 1978; Devor et al. 1983; Bear et al. 1987; Koertvelyessy et al. 1988, 1989; Crawford et al. 1995). The first

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study, conducted by Buehler et al. (1975), screened three communities in western Newfoundland for genetic mutations. However, they also collected data on blood marker variation and compared them to data from a population from southern England (Newton 1975). The second study, conducted by Bear and colleagues (1987), examined outports from western and southern Newfoundland using historical pedigrees reconstructed from parish records. These data were used to assess the degree of genetic isolation of various communities. The third study, conducted by Crawford and colleagues (1995), examined the genetic structure of Burgeo and Ramea (in the south) and Fogo Island in northern Newfoundland (Devor et al. 1983; Koertvelyessy et al. 1988). The latter study demonstrated that outport populations of Fogo Island had differentiated genetically from each other. To date, all of the investigations of population structure of Newfoundland outports have focused on specific geographic regions. No study has simultaneously compared the population differentiation based on gene frequency data of multiple geographical regions of Newfoundland outport populations.

The purpose of this study was to examine the population structure of Newfoundland using 12 red cell antigens from 10 Newfoundland outports. In addition to the outports of Ramea, Burgeo, and Fogo Island previously examined by Crawford and colleagues (1995), two other regions were analyzed. To achieve this goal, we first calculated gene frequencies using maximum likelihood estimation procedures. Second, we used ***R***-matrix methods to ascertain the scaled variance-covariance matrix of population similarity. Third, we regressed mean per-locus heterozygosity on genetic distance from the gene frequency centroid to further identify population differentiation. Through these analyses, we were able to explore the relationship among outport populations of Newfoundland.

Materials and Methods

Population. Newfoundland, an area of premiere cod fishing, is located off the east coast of Canada. According to archaeological evidence, at least three native groups inhabited Newfoundland: the Beothuk Native Americans, Maritime Archaic Indians, and Paleo Eskimos (Rowe 1980). However, these populations did not, to our knowledge, establish colonies that persisted to the present day. The Irish and Norse also established contact, yet no permanent settlements remain (Rowe 1980). Although Cabot first reached Newfoundland in 1497, the British did not establish colonies until 1610, and these first colonies were seasonal due to the difficult northern winters. In the early 18th century, the Irish began a large-scale emigration to Newfoundland. Because of the massive Irish migration, outports became overcrowded and migration began to more distant outports in a west and northwest direction. Since Newfoundland was a source of great economic wealth because of its fishing in-

dustry, England restricted migration to the island. Although the majority of residents are of English or Irish origin, some French and Basque descendants currently inhabit southern Newfoundland.

Traditionally, Newfoundland has been characterized by low population density, population dispersion along the coast, and limited means of transportation. However, when Newfoundland became a province of Canada in 1949, Newfoundland embarked on a program of economic development and modernization. This program involved industrial development, increased spending on education, transportation, communication, health services, financial support of the fishing industry, and development of hydroelectric power. Although many of these programs failed, they still had an impact on the integration of Newfoundland outports. Newfoundland is still primarily composed of small coastal communities (outports); however, the improvements in transportation and centralization of education have reduced the degree of isolation that Newfoundland outports previously experienced (Koertvelyessy et al. 1989).

Data Collection. The personnel of the Canadian Red Cross Blood Transfusion Services of St. John's collected blood samples from participants in a screening program. The primary goal of this program was to identify familial blood type variants that could be used in transfusions (Devor et al. 1983; Koertvelyessy et al. 1988, 1989). Crawford, Koertvelyessy, and Uttley collected information on the donors' birthplace, current residence, genealogical data, and religious affiliation. The red cell antigens (ABO, Rhesus, MNS, Kell, Kp, Lutheran, P, Lewis, Kidd, Duffy, Wright, and Gerlich) were typed at the Red Cross Laboratory in St. John's, Newfoundland. Blood samples were collected from volunteers residing in each of 10 outports: Burgeo, Seal Cove, Gaultois, Tilting, Island Harbour, Joe Batt's Arm, Seldom, Fogo, Hermitage, and Ramea. Figure 1 displays the geographical location of each of these outports. Initial data on religious affiliation were collected at the village clinics during the blood screening survey. In addition, church registers for all outports were used to verify the stated religious affiliation of all participants.

In addition to these 10 outports, several other populations were considered for comparative purposes: western Newfoundland, England, and Dublin City (Ireland). Newton (1975) published the gene frequency data for the communities of western Newfoundland. We used the gene frequencies from his "rest" category, which consisted of 849 individuals from three western Newfoundland communities. The gene frequency data for England were compiled from Mourant et al. (1976). The late Don Tills provided the gene frequencies for Dublin City.

Analytical Methods. Three analytical methods were used to reconstruct the population structure of the Newfoundland outports. First, the gene frequencies were estimated by the method of maximum likelihood, using the computer

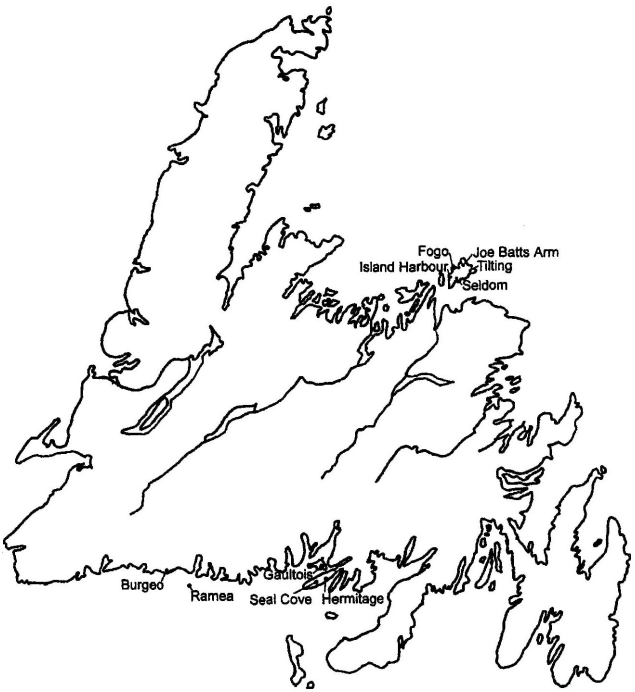

Figure 1. A map of Newfoundland illustrating the location of the outports examined.

program MAXIM. Chi-square statistics (χ^2) were calculated to test whether the phenotypic distributions were in Hardy-Weinberg equilibrium. MAXIM uses maximum-likelihood estimation procedures to calculate gene frequencies. Second, a relationship matrix (***R***-matrix) was used to ascertain the scaled variance-covariance matrix of population similarity (Harpending and Jenkins 1973). ***R***-matrix is a multivariate statistical method of providing measures of genetic similarity within and between populations:

$$\boldsymbol{R} = \begin{bmatrix} e_{1i} & e_{2i} & e_{3i} \\ e_{1j} & e_{2j} & e_{3j} \\ e_{1k} & e_{2k} & e_{3k} \end{bmatrix} \quad \begin{bmatrix} \lambda_1 & 0 & 0 \\ 0 & \lambda_2 & 0 \\ 0 & 0 & \lambda_3 \end{bmatrix} \quad \begin{bmatrix} e_{1i} & e_{1j} & e_{1k} \\ e_{2i} & e_{2j} & e_{2k} \\ e_{3i} & e_{3j} & e_{3k} \end{bmatrix}$$

The ***R***-matrix was reduced through least squares and all axes were examined to determine their information content. Informative axes were used to create a two-dimensional plot of the eigenvalue scaled by the square root of the eigenvector, which displayed population affinities. In addition to ***R***-matrices, ***A***-matrices were also plotted. An ***A***-matrix is the scaled matrix of covariances among allele frequencies (Harpending and Jenkins 1973).

Third, heterozygosity was regressed on the genetic distance from the gene frequency centroid (Harpending and Ward 1982). This method assumes a linear relationship between the genetic distance of a subpopulation from the centroid's gene frequencies and the relative homozygosity if external gene flow is equal in all subdivisions. In this model, the interpretation of outliers is the focus—not the fit of the line. Therefore an expected regression line is calculated by the formula

$$y = H_{(\text{overall population mean gene frequencies})}(1 - r_{ij}). \quad (1)$$

Populations below the expected regression line have experienced less external gene flow, whereas populations above the expected regression line would have experienced more external gene flow (Harpending and Ward 1982). In addition, subpopulations that have low mean per-locus heterozygosity and high distance from the centroid of distribution have experienced the effects of stochastic processes.

Results and Discussion

***R*-matrix.** The gene frequencies as estimated by the computer program MAXIM are summarized in Appendices 1–11. Both the Wright and Gerlich systems are monomorphic in all of these outports. The Kidd and Lewis systems were not typed in Seal Cove, Gaultois, or Hermitage.

The patterns of genetic affinities of the populations are difficult to interpret on the basis of matrices of allelic frequencies (Appendices 1–11). Therefore, ***R***-matrix analyses were used to examine population differentiation. Several different ***R***-matrix analyses were performed. The first included only the 10 Newfoundland outports (Figure 2) and used all gene frequency data except Kp. Kp was excluded because it was highly homogeneous between outports and the analysis was not significantly different with the inclusion of this blood group. The first eigenvector explains 38.5% of the variation, while the second eigenvector explains 22.1% of the variation. The first eigenvector (x-axis) displays the separation of Fogo Island outports from the main island outports (i.e., those populations in the north from those in the south). Tilting and Island Harbour (both located on Fogo Island) are separated by the second eigenvector.

Figure 3 is an ***A***-matrix for the plot of the first and second eigenvectors for all alleles, revealing that the primary discriminators of outports are *ABO*A*, *ABO*O*, *P*P1*, and *FY*B*. Comparatively high frequencies of *ABO*A* and *P*P1* are characteristic of outports that segregated to the left on the first eigenvector (i.e., non–Fogo Island outports). In contrast, high frequencies of *ABO*O* and *FY*B* cause segregation to the right (Fogo Island outports). On the second eigenvector, *ABO*A*, *LU*A*, *P*P1*, *RH*r*, and

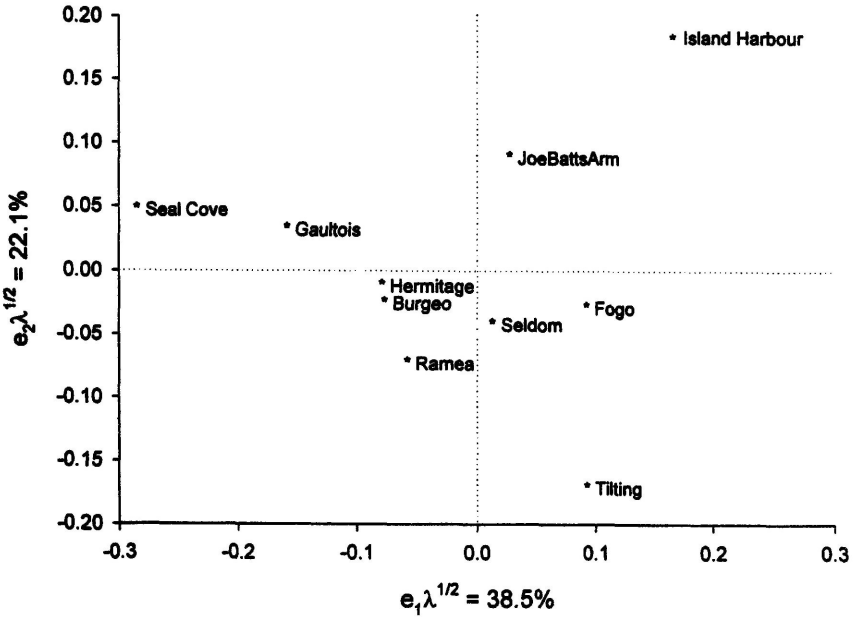

Figure 2. Relationships between outports in Newfoundland plotted using the first two scaled eigenvectors of the ***R***-matrix.

*RH*R2* disperse the outports; *ABO*A, LU*A,* and *RH*r* have a positive value and *P*P1* and *RH*R2* have negative scores.

The overall pattern for the first axis on the ***R***-matrix plot (Figure 2) was a north-south differentiation. Although the northern and southern populations are separated along axis one, the degree of separation is much less than one might expect based on their geographic locations (Figure 1). This suggests that there is less isolation by distance than one would expect from a purely geographical model of population structure. Causes of this reduced separation include common historical origin, limited time depth, and/or frequent migration. Given that these outports were populated primarily by the English and the Irish, the limited differentiation between the north and the south is not surprising. However, other factors may also affect this differentiation. Future studies should address this issue further.

Additionally, the first ***R***-matrix illustrates the differentiation of Seal Cove, Tilting, and Island Harbour from the other outports and each other (Figure 2). Seal Cove is separated by a high frequency of *ABO*A* and *P*P1*, while Island Harbour and Tilting are separated by a high frequency of *ABO*O* and *FY*B* (Figure 3). Tilting is separated on the second eigenvector by a high frequency of *P*P1* and *RH*R2* but a low frequency of *ABO*A, LU*A,* and *RH*r.*

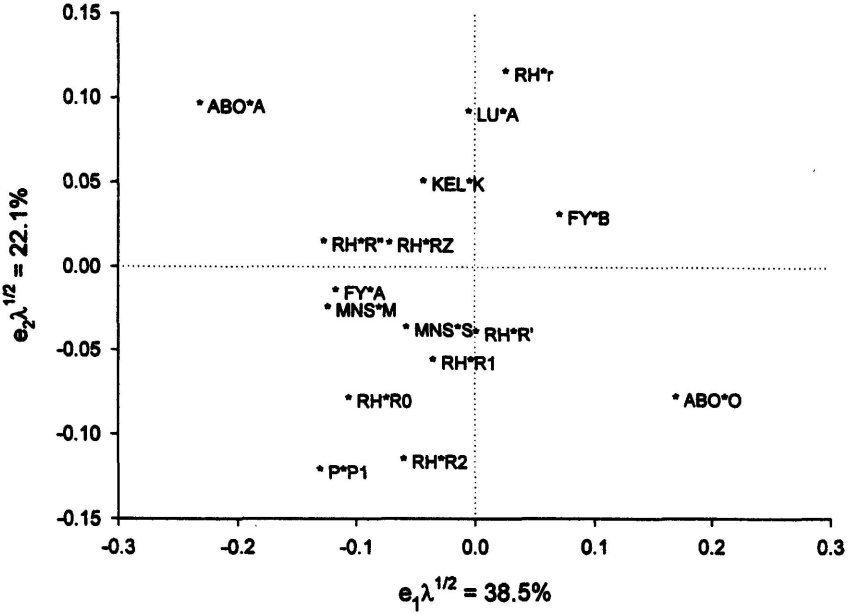

Figure 3. Relationships between the alleles for the Newfoundland outports plotted using the first two scaled eigenvectors of the *A*-matrix.

The differentiation of these three outports may be caused by a complex of interacting factors, such as geographic and social isolation, small size of population, ethnic composition, and religious affiliation. Seal Cove, Island Harbour, and Tilting are located on the end of gravel roads, which limits the amount of contact these populations have with other outports. Indeed, the geographic isolation of these populations is also identified through an examination of migration patterns. Table 1 illustrates the differential migration patterns collected through the comparison of birthplace and current residence. Seal Cove has the lowest frequency of in-migration (11.9) and Island Harbour has the second lowest incidence (16.3). The isolation of Island Harbour and Tilting can also be demonstrated through an examination of the rate of endogamous marriages. Koertvelyessy et al. (1989) demonstrated that Tilting and Island Harbour had the highest rates of endogamous marriages on Fogo Island, suggesting that these were the two most reproductively isolated outports on Fogo Island.

Another factor that may have influenced the population structure of Newfoundland is religious affiliation. Of the residents sampled from Seal Cove, 96% identified themselves as members of the Salvation Army (from now on referred to as Salvationists), whereas 0.46% of the residents outside

Table 1. Percent Exogamy in Newfoundland Outports Based on Birthplace and Current Residence

Outport	*% Exogamy*
Seal Cove	11.9
Island Harbour	16.3
Burgeo	17.7
Tilting	19.4
Joe Batts Arm	25.6
Fogo	45.1
Seldom	45.5
Gaultois	54.4
Ramea	55.7
Hermitage	74.3

of Seal Cove classified themselves as such. Furthermore, 99% of the residents sampled from Tilting identified themselves as Catholic, whereas 7.96% of the residents outside of Tilting classified themselves as such. Therefore, the high frequencies of either Salvationists or Catholics present in Seal Cove and Tilting could serve as isolating factors.

In the second analysis, we added several out-group populations (western Newfoundland, England, and Dublin City) to determine if the population differentiation present in the first analysis could be attributed to migration from these groups. Due to the availability of information the only gene frequencies used were *ABO*A, ABO*B, RH*R1, RH*R2, RH*r, P*P1, FY*A,* and *KEL*K.* The first eigenvector explains 41.0% of the variation, the second eigenvector explains 27.2% of the variation, and the third eigenvector explains 18.8% of the variation. Interestingly, the addition of these out-groups changed the ***R***-matrix only slightly (Figures 4 and 6). Island Harbour, Tilting, and Seal Cove still remained outliers. The differentiation of the outliers was due to two alleles, *ABO*A* and *P*P1* (Figures 5 and 7). However, the differentiation of the Fogo Island outports versus the main island outports was no longer present. All three of the comparative groups clustered close to the centroid. On the first eigenvector, Dublin City (representing Ireland) clusters with Tilting. This is expected because Tilting is primarily Catholic, suggesting an Irish ancestry (Crawford et al. 1995). Given the animosity between the Anglicans and Catholics in this region, our hypothesis was that Tilting was isolated due to religion. The second eigenvector is characterized by the separation of Island Harbour and Tilting. The third eigenvector demonstrates little population substructuring, with only Ramea being an outlier (Figure 6).

Because Crawford et al. (1995) demonstrated that religion influenced the population structure of Fogo Island, we suspected that religion affected the structure of the groups of outports analyzed. Therefore, we subdivided

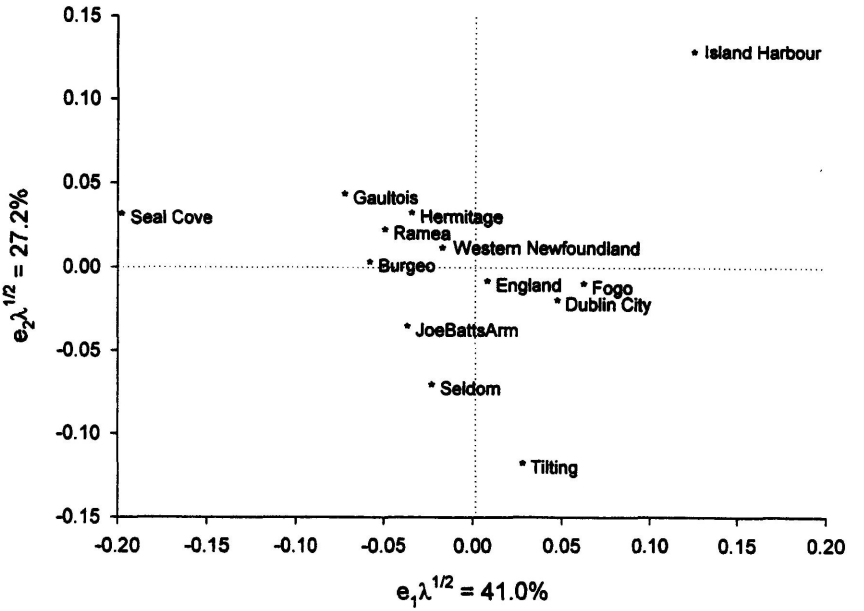

Figure 4. Relationships between outports in Newfoundland, England, Ireland, and western Newfoundland plotted using the first two scaled eigenvectors of the ***R***-matrix.

the data based on five religions, Anglican, Catholic, Evangelical, Protestant, and Salvationist. For this analysis, we used ABO, Duffy, Kell, Kidd, Kp, Lewis, Lutheran, MNS, P, and Rhesus gene-frequency data.

Using religion instead of outport as the unit of subdivision, the first eigenvector explains 72.1% of the variation, while the second eigenvector explains an additional 14.9% of the variation, explaining a total of 87.0% of the variation (Figure 8). The first eigenvector displays the separation of the Salvationists from the others. The alleles responsible for this separation were *FY*B, LE*A,* and *LE*B* (Figure 9). A high frequency of *LE*B* coupled with a low frequency of *FY*B* and *LE*A* is the isolating factor for Salvationists. The second eigenvector separates Evangelicals and Protestants from each other. The alleles responsible for this separation were *FY*B, P*P1, FY*A,* and *RH*R″*.

Heterozygosity versus r_{ii}. Mean per-locus heterozygosity ($\bar{H}$) was regressed on distance from the gene frequency centroid (r_{ii}) for the outports (Figure 10). The expected regression line has been indicated in the plot. The largest deviations from the expected regression line are Seal Cove and Tilting. The position of Seal Cove above the expected regression line suggests that this population has experienced above-average external gene flow. Like-

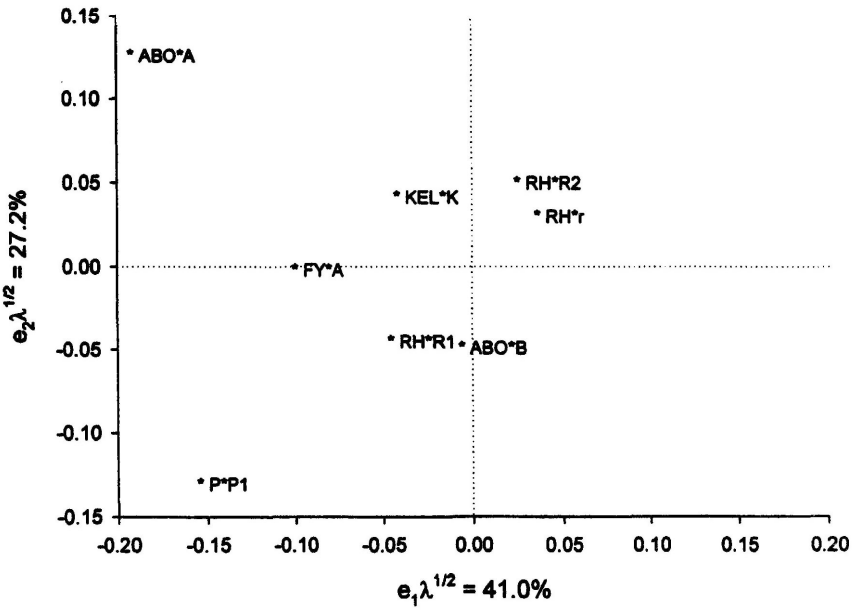

Figure 5. Relationships between alleles for the Newfoundland outports and outgroups plotted using the first two scaled eigenvectors of the *A*-matrix.

wise, the extreme position of Seal Cove in the ***R***-matrix plot (Figure 2) is also consistent with above-average external gene flow, which acts to pull Seal Cove away from the other populations. The inclusion of several external populations (England, Ireland, and western Newfoundland) in Figure 4 does not demonstrate any particular relationship of these populations with Seal Cove, suggesting that there might be another source of gene flow into Seal Cove, possibly Basque or French fishermen contributing to the founding population. As mentioned, 96% of Seal Cove residents identified themselves as Salvationists. Because Salvationists have a strong sense of religious community, perhaps gene flow has occurred between other Salvation Army communities, possibly from Labrador or mainland Canada.

On the other hand, Tilting's position below the expected line suggests that this population has experienced below-average external gene flow. The central position of Tilting in both ***R***-matrix plots (Figures 2 and 4) is consistent with below-average external gene flow, which may be the result of its being primarily a Catholic community (Crawford et al. 1995). Given the animosity between Anglicans and Catholics in this region, our hypothesis is that Tilting was isolated due to religion.

Because religion explained a substantial proportion of the variation using the ***R***-matrix analysis, we also examined mean per-locus heterozygosity

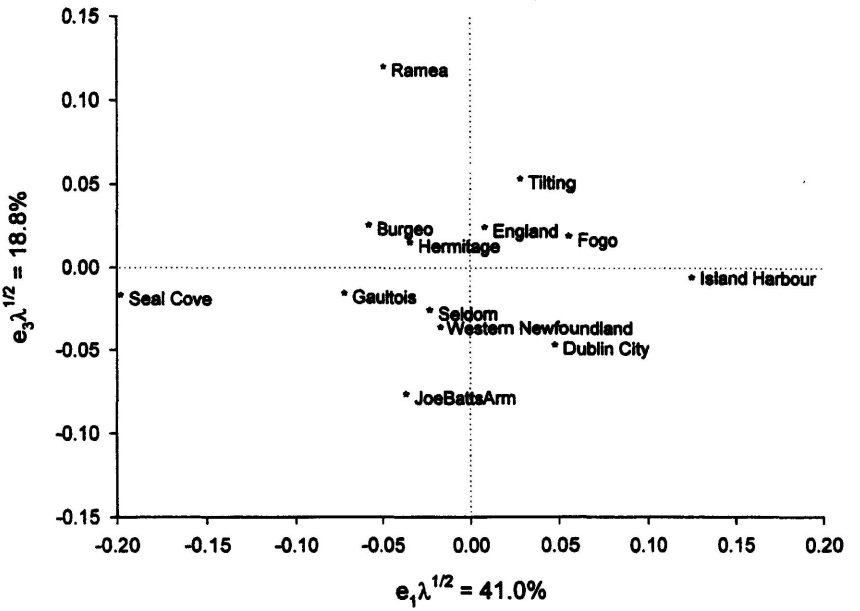

Figure 6. Relationships between outport in Newfoundland, England, Ireland, and western Newfoundland plotted using the first and third scaled eigenvectors of the ***R***-matrix.

regressed against the distance from the gene frequency centroid for religious affiliations (Figure 11). The largest deviations from the expected line are the Protestant and Anglican denominations. The position of Protestants above the expected regression line suggests that this religious group experiences above-average external gene flow. Interestingly, Protestants have a central position in the ***R***-matrix plot for the first eigenvector; however, they are distally located in the second eigenvector (Figure 8). This suggests that although Protestants may be experiencing above-average external gene flow, the flow is not causing a large degree of differentiation, given that Protestants do not separate from other religious denominations in the first ***R***-matrix axis, which explains 72% of the variation.

Like the position of the Protestants, the position of Anglicans above the expected regression line suggests that this religious group experiences above-average external gene flow. In contrast, in the ***R***-matrix plots the Anglicans are positioned centrally, suggesting that Anglicans are experiencing above-average external gene flow, but this is not causing differentiation. Because Anglicanism has been a major religious denomination in England and England has been a historical source of migration into Newfoundland, English migration could be causing this phenomenon.

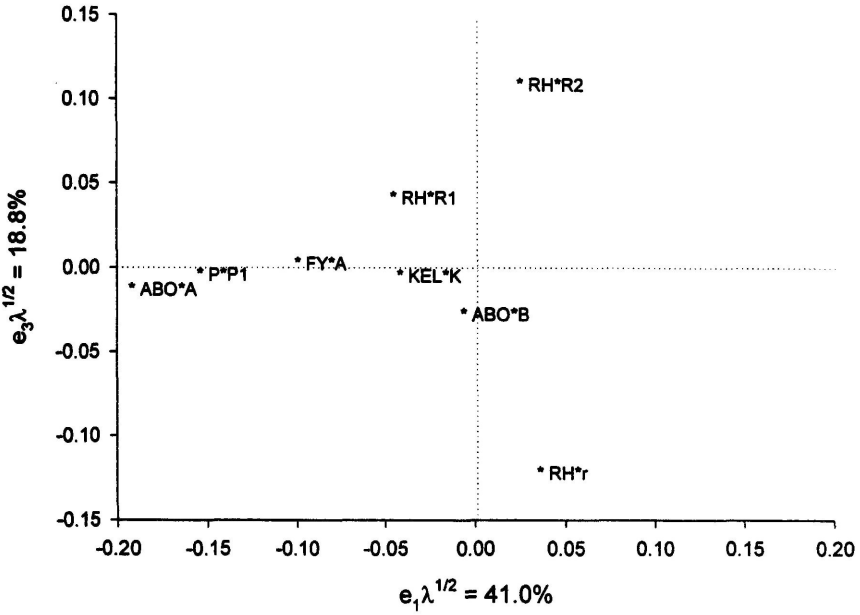

Figure 7. Relationships between alleles for the Newfoundland outports and outgroups plotted using the first and third scaled eigenvectors of the *A*-matrix.

Another interesting feature of the plot of the mean per-locus heterozygosity regressed against the distance from the gene frequency centroid for religious affiliations was the excellent fit of Salvationists to the expected regression line. Given that Seal Cove, which is primarily composed of Salvationists, fell above the regression line, one might expect that the Salvation Army community would mimic the results. However, because the majority of Salvationists are in Seal Cove, Seal Cove and the Salvation Army community contain almost the same sample. Yet in the outport analysis, the groups compared were more similar, as demonstrated by the lower mean per-locus heterozygosities and distance from the centroid. Therefore, the excellent fit of the Salvation Army community to the regression of mean per-locus heterozygosity to distance from the centroid is not inconsistent with the Seal Cove falling above the theoretical regression line.

Conclusions

The medical community has characterized Newfoundland as a genetic isolate. However, the effect of modernization on the population structure of Newfoundland is not well understood. This study examined Newfoundland's

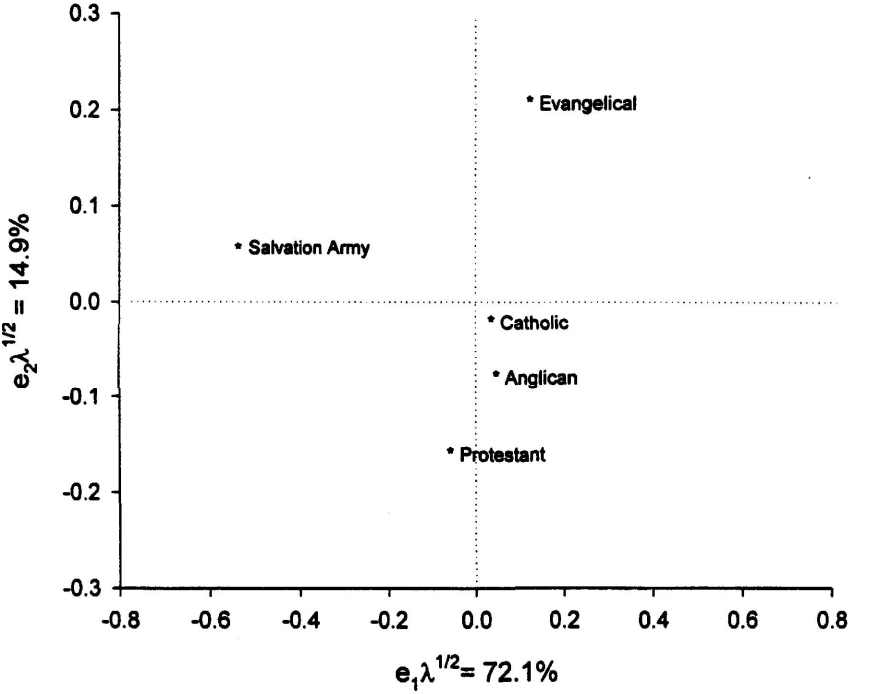

Figure 8. Relationships between the church affiliations plotted using the first two scaled eigenvectors for the ***R***-matrix.

population structure using 12 red cell antigens from 10 outports and several comparative populations. In this study, several main conclusions can be made.

First, we demonstrated that three Newfoundland outports can be considered as genetic isolates. Both ***R***-matrices using outport as a grouping variable identified several populations (Seal Cove, Island Harbour, and Tilting) that have differentiated from the other Newfoundland outports and their parental populations. The heterozygosity-versus-r_{ii} analysis also supports this finding. Both Seal Cove and Island Harbour display low heterozygosities coupled with high r_{ii}, which illustrates their differentiation from the other outports. Tilting has a lower-than-expected heterozygosity for its distance from the gene frequency centroid, illustrating that it is also a genetic isolate.

Second, these analyses have identified religion as an important influence on population differentiation. In the ***R***-matrix analysis using religion as the grouping variable, the first two eigenvectors explained 87.0% of the variation. This differentiation seems to be driven by the uniqueness of the Salvation Army community. This community's high r_{ii} and low $\bar{H}$ values further support this differentiation.

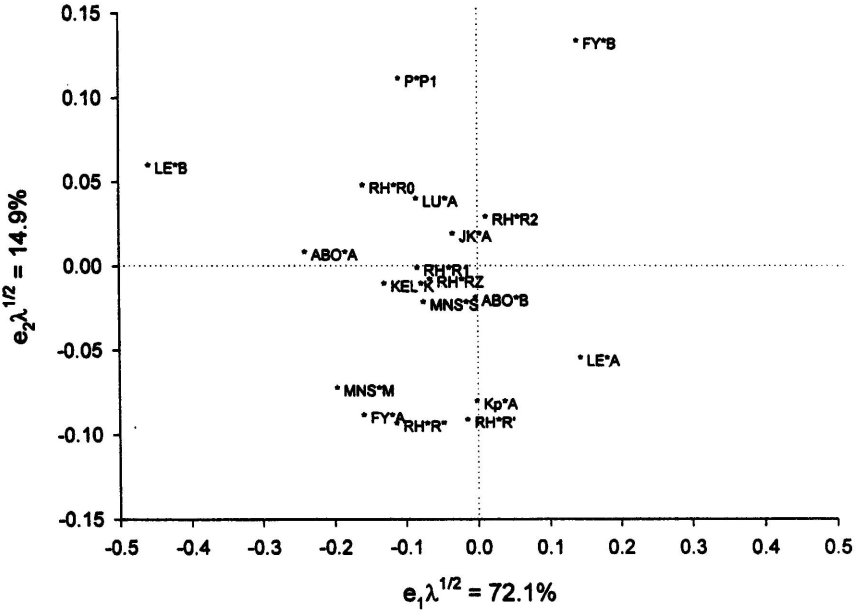

Figure 9. Relationships between alleles for church affiliation plotted using the first two scaled eigenvectors of the A-matrix.

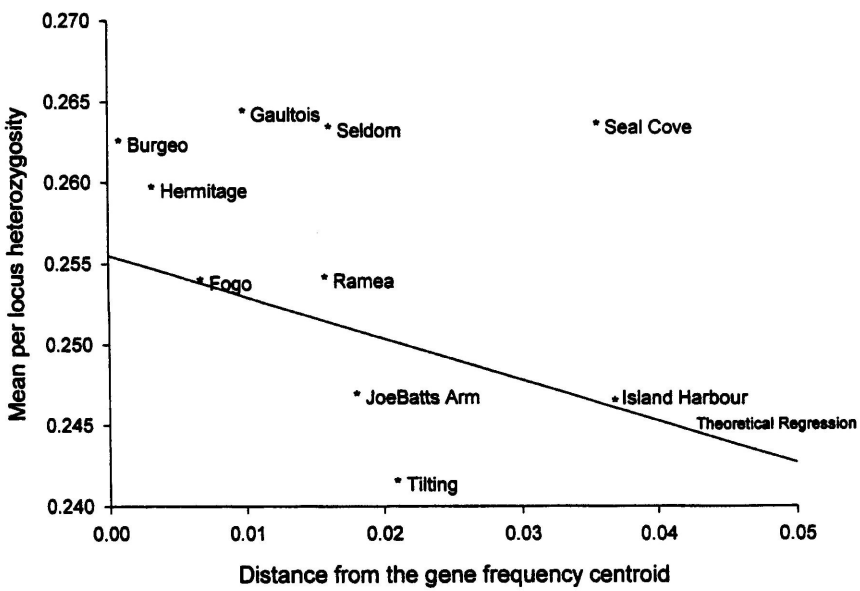

Figure 10. Plot of the mean per-locus heterozygosity against distance from the gene frequency centroid for the Newfoundland outports.

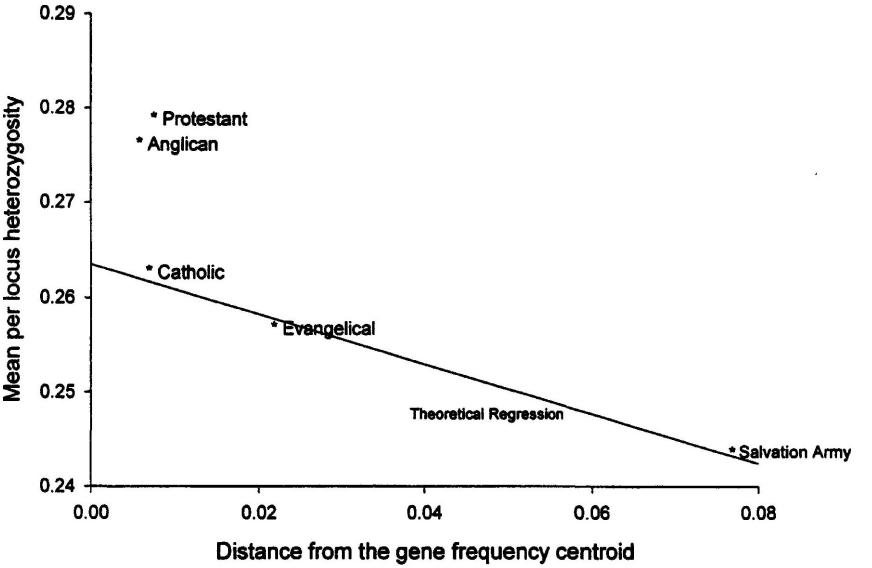

Figure 11. Plot of the mean per-locus heterozygosity against distance from the gene frequency centroid for church affiliations.

In conclusion, we have demonstrated that the population structure of Newfoundland is complex and conditioned by unique historical events, religious affiliation, and geography. Furthermore, several genetic isolates have been identified that may be useful in future studies. The identification of genetic isolates is important because with improvements in transportation during the 20th century, fewer populations can be considered genetic isolates.

As a result of the collapse of the cod fishery outport, Newfoundland is experiencing extensive out-migration. The results of these analyses are thus a snapshot into Newfoundland's ever-changing population structure.

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Appendices

Appendix 1. Gene Frequencies and Hardy-Weinberg Equilibrium of the ABO Blood Group System

	*ABO*A*	*ABO*B*	*ABO*O*	*df*	χ^2
Burgeo	0.331	0.065	0.605	3	0.003
Seal Cove	0.475	0.030	0.495	3	0.292
Gaultois	0.370	0.053	0.577	3	0.089
Tilting	0.070	0.046	0.884	3	0.481
Island Harbour	0.238	0.024	0.738	3	0.643
Joe Batt's Arm	0.266	0.053	0.681	3	0.012
Seldom	0.217	0.087	0.697	3	2.867
Fogo	0.189	0.040	0.771	3	1.793
Hermitage	0.320	0.040	0.640	3	1.746
Ramea	0.340	0.030	0.630	3	2.773

* Significant at $p = 0.10$, ** significant at $p = 0.05$, *** significant at $p = 0.01$.

Appendix 2. Gene Frequencies and Hardy-Weinberg Equilibrium of the MN Blood Group System

	*MNS*M*	*MNS*N*	*df*	χ^2
Burgeo	0.662	0.338	2	0.719
Seal Cove	0.792	0.208	2	0.183
Gaultois	0.648	0.352	2	0.001
Tilting	0.664	0.348	2	0.676
Island Harbour	0.616	0.384	2	0.046
Joe Batt's Arm	0.513	0.487	2	0.227
Seldom	0.555	0.445	2	0.352
Fogo	0.642	0.358	2	0.209
Hermitage	0.681	0.319	2	0.889
Ramea	0.633	0.367	2	0.475

* Significant at $p = 0.10$, ** significant at $p = 0.05$, *** significant at $p = 0.01$.

Appendix 3. Gene Frequencies and Hardy-Weinberg Equilibrium of the S Blood Group System

	*MNS*S*	*MNS*s*	*df*	χ^2
Burgeo	0.322	0.678	2	10.921***
Seal Cove	0.315	0.685	2	0.473
Gaultois	0.409	0.591	2	1.447
Tilting	0.336	0.664	2	0.726
Island Harbour	0.267	0.733	2	0.004
Joe Batt's Arm	0.232	0.768	2	1.442
Seldom	0.391	0.609	2	0.816
Fogo	0.324	0.676	2	1.464
Hermitage	0.289	0.711	2	0.470
Ramea	0.260	0.740	2	1.333

* Significant at $p = 0.10$, ** significant at $p = 0.05$, *** significant at $p = 0.01$.

Appendix 4. Gene Frequencies and Hardy-Weinberg Equilibrium of the Rhesus Blood Group System

	*RH*R2*	*RH*R0*	*RH*R1*	*RH*RZ*	*RH*R'*	*RH*R''*	*RH*r*	*RH*Ry*	*df*	χ^2
Burgeo	0.157	0.061	0.412	0.000	0.010	0.000	0.359	0.000	17	20.622
Seal Cove	0.101	0.089	0.401	0.000	0.000	0.028	0.374	0.007	17	19.330
Gaultois	0.131	0.065	0.351	0.030	0.000	0.021	0.402	0.000	17	20.979
Tilting	0.149	0.088	0.440	0.000	0.000	0.000	0.315	0.008	17	2.667
Island Harbour	0.209	0.000	0.302	0.000	0.000	0.000	0.488	0.000	17	1.753
Joe Batt's Arm	0.077	0.000	0.410	0.000	0.000	0.000	0.513	0.000	17	2.740
Seldom	0.117	0.056	0.357	0.000	0.043	0.019	0.408	0.000	17	8.58
Fogo	0.147	0.039	0.407	0.000	0.025	0.000	0.383	0.000	17	1.851
Hermitage	0.150	0.086	0.365	0.016	0.017	0.011	0.354	0.000	17	31.034**
Ramea	0.271	0.017	0.427	0.000	0.011	0.000	0.274	0.000	17	1.390

* Significant at $p = 0.10$, ** significant at $p = 0.05$, *** significant at $p = 0.01$.

Appendix 5. Gene Frequencies and Hardy-Weinberg Equilibrium of the Lutheran Blood Group System

	*LU*A*	*LU*B*	*df*	χ^2
Burgeo	0.025	0.975	1	0.002
Seal Cove	0.082	0.918	1	0.000
Gaultois	0.029	0.971	1	0.000
Tilting	0.023	0.977	1	0.001
Island Harbour	0.076	0.924	1	0.000
Joe Batt's Arm	0.094	0.906	1	0.000
Seldom	0.056	0.944	1	0.000
Fogo	0.055	0.944	1	0.001
Hermitage	0.023	0.977	1	0.001
Ramea	0.011	0.989	1	0.004

* Significant at $p = 0.10$, ** significant at $p = 0.05$, *** significant at $p = 0.01$.

Appendix 6. Gene Frequencies and Hardy-Weinberg Equilibrium of the P Blood Group System

	*P*P1*	*P*P2*	*df*	χ^2
Burgeo	0.579	0.421	1	0.000
Seal Cove	0.691	0.309	1	0.000
Gaultois	0.523	0.477	1	0.000
Tilting	0.633	0.367	1	0.000
Island Harbour	0.285	0.715	1	0.000
Joe Batt's Arm	0.608	0.392	1	0.000
Seldom	0.643	0.357	1	0.000
Fogo	0.476	0.524	1	0.000
Hermitage	0.507	0.493	1	0.000
Ramea	0.575	0.425	1	0.000

* Significant at $p = 0.10$, ** significant at $p = 0.05$, *** significant at $p = 0.01$.

Appendix 7. Gene Frequencies and Hardy-Weinberg Equilibrium of the Kidd Blood Group System

	*JK*A*	*JK*B*	*df*	χ^2
Burgeo	0.416	0.584	2	0.590
Tilting	0.533	0.467	2	3.501
Island Harbour	0.465	0.535	2	0.034
Joe Batt's Arm	0.485	0.515	2	4.359
Seldom	0.518	0.482	2	0.016
Fogo	0.496	0.504	2	2.514
Ramea	0.488	0.512	2	2.517

* Significant at $p = 0.10$, ** significant at $p = 0.05$, *** significant at $p = 0.01$.

Appendix 8. Gene Frequencies and Hardy-Weinberg Equilibrium of the Lewis Blood Group System

	*LE*A*	*LE*B*	*LE*0*	*df*	χ^2
Burgeo	0.165	0.420	0.415	3	101.51***
Tilting	0.167	0.450	0.383	3	22.02***
Island Harbour	0.063	0.567	0.371	3	7.47*
Joe Batt's Arm	0.100	0.525	0.375	3	9.64**
Seldom	0.092	0.595	0.313	3	16.49***
Fogo	0.166	0.419	0.415	3	29.21***
Ramea	0.217	0.332	0.415	3	54.29***

* Significant at $p = 0.10$, ** significant at $p = 0.05$, *** significant at $p = 0.01$.

Appendix 9. Gene Frequencies and Hardy-Weinberg Equilibrium of the Duffy Blood Group System

	*FY*A*	*FY*B*	*FY*0*	*df*	χ^2
Burgeo	0.419	0.539	0.042	3	1.276
Seal Cove	0.541	0.447	0.013	3	0.029
Gaultois	0.517	0.461	0.022	3	0.086
Tilting	0.438	0.509	0.053	3	0.423
Island Harbour	0.348	0.652	0.000	3	0.025
Joe Batt's Arm	0.359	0.521	0.120	3	1.484
Seldom	0.406	0.594	0.000	3	0.458
Fogo	0.394	0.583	0.023	3	19.760***
Hermitage	0.414	0.562	0.024	3	0.175
Ramea	0.388	0.547	0.065	3	1.760

* Significant at $p = 0.10$, ** significant at $p = 0.05$, *** significant at $p = 0.01$.

Appendix 10. Gene Frequencies and Hardy-Weinberg Equilibrium of the Kell Blood Group System

	*KEL*K*	*KEL*k*	*df*	χ^2
Burgeo	0.075	0.925	2	2.12
Seal Cove	0.125	0.875	2	1.714
Gaultois	0.057	0.943	2	0.318
Tilting	0.075	0.925	2	0.432
Island Harbour	0.116	0.884	2	0.388
Joe Batt's Arm	0.064	0.935	2	0.186
Seldom	0.055	0.945	2	0.181
Fogo	0.054	0.946	2	1.859
Hermitage	0.056	0.944	2	0.532
Ramea	0.054	0.946	2	0.521

Appendix 11. Gene Frequencies and Hardy-Weinberg Equilibrium of the Kp Blood Group System

	*Kp*A*	*Kp*B*	*df*	χ^2
Burgeo	0.005	0.995	1	0.023
Seal Cove	0.006	0.994	1	0.000
Gaultois	0.000	1.000	1	0.000
Tilting	0.000	1.000	1	0.000
Island Harbour	0.000	1.000	1	0.000
Joe Batt's Arm	0.000	1.000	1	0.000
Seldom	0.000	1.000	1	0.000
Fogo	0.020	0.980	1	0.000
Hermitage	0.020	0.980	1	0.000
Ramea	0.020	0.980	1	0.000