
Spatial Variation of Anthropometric Traits in Ireland

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Abstract To further elucidate the relationship between geography and genetics in Ireland, we considered variation in anthropometric traits of adult males by town using spatial autocorrelation methods. By describing and distinguishing significant patterns of anthropometric variation, we determined whether the anthropometric traits display a simple pattern of spatial variation, as predicted by the isolation by distance model, or other patterns of spatial variation. Several hypotheses were examined, including (1) whether there was spatial patterning of 20 anthropometric phenotypic distributions and 7 principal components of Irish males and (2) if there was, whether these phenotypic distributions could be explained by a simple isolation by distance model. The results of this study can be summarized by several key findings: (1) There is significant spatial patterning among towns, as detected in correlograms of 14 anthropometric traits and 2 principal component factor scores (values of Moran's I ranging from 0.7510 to -0.3616 , $p \leq 0.0071$); (2) 4 spatial patterns were detected, including clinal patterns, long-distance differentiation, distance distinction, and regional patchiness. These results suggest several likely causes of the observed spatial patterns. First, in Ireland patterns of anthropometric variation could not be explained by a single spatial pattern (i.e., isolation by distance). Second, through an examination of the various combinations of statistical homogeneity or heterogeneity, spatial patterning or nonpatterning, and similarity or dissimilarity of spatial patterns, we conclude that several migrational events structured the genetic landscape of Ireland.

The isolation by distance model examines genetic drift, inbreeding, and gene flow among subpopulations separated by geographic distance (Malécot 1968). Although the isolation by distance model has been useful in explaining the structure of several subdivided human populations, it assumes a single, simple underlying spatial pattern of relationships among the sampled populations.

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However, spatial relationships among groups are often more complex (Sokal and Friedlaender 1982; Sokal and Oden, 1978a). A more pragmatic approach to studying biological variation—spatial autocorrelation—has been developed with a different set of assumptions (Sokal and Friedlaender 1982). In this approach the data are examined for groups of patterns of variation, not just for 1 simple spatial pattern (e.g., isolation by distance). Moreover, spatial autocorrelation attempts to describe patterns of variation in a sample over a given geographic area, determining which factors may have brought about these patterns. Specifically, inferences can be made about the impact of the forces of evolution (including gene flow, genetic drift, and natural selection) on population structure through the application of this model. Because of this pragmatic perspective, spatial autocorrelation analysis is a unique approach to the study of population structure that can model the complex biological variation present in human populations.

Previous research has been inconclusive concerning the relationship between geography and genetics of Ireland. Studies of local population subdivisions within a single small region (usually a county), regional population subdivisions (usually a province), and countrywide variation using counties as the unit of analysis have all been conducted. Depending on the level of analysis (e.g., 1 small region or the entire island), different results have been reported. For example, research on the western region of Ireland using anthropometric traits suggested that geographic distance was the major determinant of population structure (Relethford et al. 1980, 1981). Relethford and colleagues used towns as the unit of analysis and included a small subset of the data used here. In contrast, previous research on the entire island, using counties as the unit of analysis and both genetics and anthropometric traits, did not identify geography as the major determinant of population structure (Relethford and Crawford 1995; Tills et al. 1977). However, no studies of the population structure of the entire island of Ireland have used towns as the level of analysis. By focusing on towns as the level of analysis, microdifferentiation may be detected that was not apparent when using aggregate county data.

Our primary objective here is to identify patterns of anthropometric variation in Ireland within their spatial context and to make inferences about the population structure of Ireland through an analysis of these geographic trends. To accomplish this goal, we considered variation in anthropometric traits among towns. Spatial distributions of 20 anthropometric traits and 7 principal components were examined through spatial autocorrelation analysis. Using this methodological approach, we calculated spatial autocorrelation statistics to describe and distinguish significant patterns of variation, as described by Sokal, Harding et al. (1989).

Population

The island of Ireland is composed of 2 countries (the Republic of Ireland and Northern Ireland) that have been distinct political entities since the 1920s.

Ireland covers an area of 32,588 mi², averaging 110 mi from east to west and 220 mi from north to south (Edwards 1981).

Historical Invasions. Archeological evidence suggests that Ireland was inhabited by successive waves of migration beginning in the immediate post-glacial period, as early as 6,000 B.C. (Harbison 1976). After this first initial influx of people, comparatively little immigration to Ireland occurred until the waves of Celtic invasions, starting as early as the 6th century B.C. Later Celtic invaders (of a slightly different ethnic composition, the Gaels) appeared sometime before 150 B.C. (Byrne 1967; Mitchell 1988; Pringle 1985). Until the mid-8th century Ireland was characterized by a high degree of cultural uniformity (Hackett et al. 1956; Pringle 1985). However, in the late 8th century Norse Vikings began to settle Ireland, and this cultural uniformity was disturbed (Chauvire 1956; Sunderland et al. 1973). These invasions forced the Celts inland, and the Vikings established coastal settlements. The next wave of migrants, the Anglo-Normans, invaded Ireland between 1169 and 1300 (Pringle 1985). This conquest was relatively haphazard (Cosgrove 1987). Even so, the Anglo-Normans eventually spread throughout the entire country. Immigration to Ireland continued into the 17th century, with the next wave of migrants coming from Scotland and England (Pringle 1985).

The historical waves of migration to Ireland over the centuries should have resulted in an east-west cline in biological variation because most migration occurred on the east coast of Ireland, with successive groups displacing previous inhabitants to some extent toward the west (Pringle 1985). Moreover, the last group of migrants from England had their greatest influence in the north and east. Indeed, previous research on the population structure of Ireland supports the presence of an east-west cline (Dawson 1964; Hackett et al. 1956; Hooton 1940; Hooton et al. 1955; Relethford 1983; Relethford and Crawford 1995; Tills et al. 1977). However, Relethford and Crawford (1995) suggested that 4 Midland counties were distinct from other Irish counties. Specifically, Relethford and Crawford (1995) proposed that the distinctiveness of these Midland counties relates to a greater genetic impact from Viking admixture.

The Great Famine. The Great Famine of 1846–1850 was a drastic demographic event in the history of Ireland. The population dramatically decreased because of the synergistic effects of famine and disease and massive emigration from Ireland because of almost total crop (potato) failure during a period of 5 years. In fact, an estimated 1 million people died, and over 1.3 million people emigrated during the 5-year period (Kammeyer 1976). However, as could be expected, the impact of the famine on Irish society outlasted this 5-year period of crop failure, and the population size continued to decrease until well into the 20th century (Relethford et al. 1997).

The rapid changes in population size both before the famine and after the famine may have had an impact on the genetic structure of Ireland. Recent research on the local genetic structure in Northern Ireland has revealed a significant genetic impact of the famine (Bittles et al. 1986; Smith et al. 1990; Bittles and Smith 1991, 1994). In contrast, research attempting to quantify changes in migration rates and genetic structure across time in all of Ireland has revealed a minimum impact of the famine on the magnitude of population differentiation (Relethford et al. 1997). However, it is important to note that Relethford et al. used counties as the unit of analysis, whereas Bittles and colleagues used towns as the unit of analysis.

Cultural Influences. Following Relethford (1980), 2 interrelated cultural patterns that may have affected the genetic structure of Ireland, marriage and migration patterns, should be summarized [see Arensberg (1937), Arensberg and Kimball (1968), Byrne (1967), Chauvire (1956), Edwards (1981), and Kennedy (1973)]. The predominant pattern of marriage in Ireland was a contractual agreement (or match) between the families of prospective mates (Arensberg 1937; Connell 1968; Humphreys 1966). Marriage was actually an economic agreement, whereby the families of the males provided land and the families of the females provided dowries (Arensberg and Kimball 1968). Given that land was inherited by 1 chosen son, postmarital residence was patrilocal (Relethford 1980). Although specific data concerning intracounty migration was unavailable, in terms of intercounty transfer migration was usually to the adjacent counties (Relethford 1988; Geary and Hughes 1970).

Not all Irish married (Connell 1968). Although Irish families were large, only 1 of the males and 1 of the females usually married because the family farm was passed down to only 1 son. Basically, there were 2 alternatives for Irish without a prospective mate. The first was to remain unmarried (Arensberg 1937). This option was chosen with a higher frequency by males than by females, and those who remained unmarried often remained celibate (Connell 1968). The second alternative was migration or emigration (Arensberg 1937). This was by far the more popular choice, with emigration more popular than migration. Interestingly, females emigrated at higher rates than males because females were not strongly tied to the land and achieved much greater economic opportunities and higher social status abroad (Kennedy 1973).

Materials and Methods

Data Collection. The data used in this study consist of a series of 20 anthropometric measurements from adult males throughout Ireland. The measurements were weight, stature, acromion breadth, dactylion height, total arm span, biacromial breadth, chest breadth, chest depth, sitting height, head circumference, head length, head breadth, head height, minimum frontal diam-

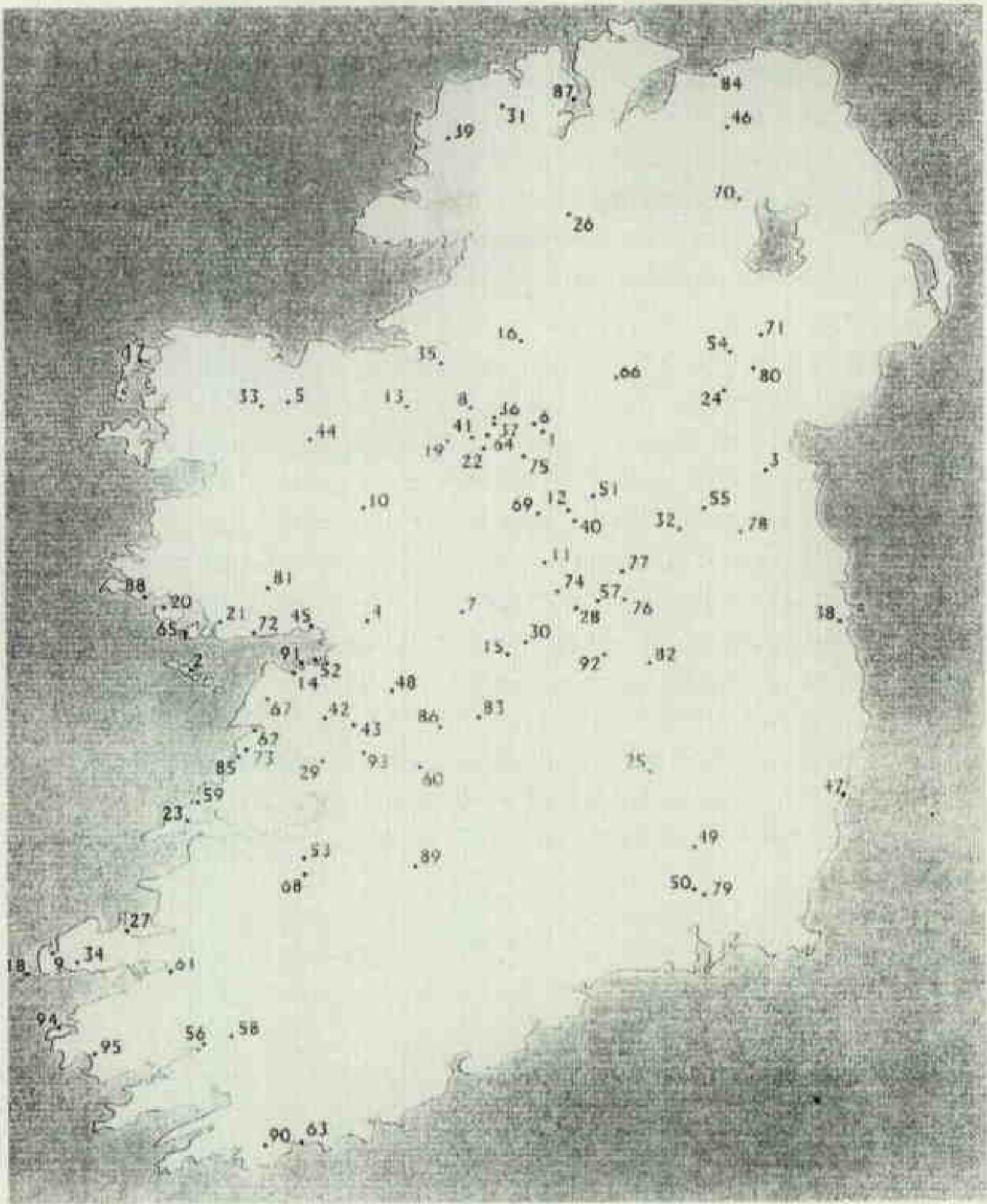


Figure 1. Sample localities for 95 Irish towns.

eter, bizygomatic breadth, bigonial breadth, total facial height, upper facial height, nasal height, and nasal breadth. These data were originally collected by C.W. Dupertuis between 1934 and 1936 as part of an interdisciplinary study of anthropological variation in Ireland by Harvard University. Anthropometric, anthroposcopic, and demographic data were collected on approximately 10,000 males (Hooton and Dupertuis 1951). The basic unit of analysis for this study was town of residence at the time of measurement. The data set was reduced to 95 towns and 3,598 adult males by requiring a minimum sample of 20 or more individuals with no missing data. Figure 1 displays the geographic location of the 95 towns sampled for this study.

Anthropometric measurements were taken in millimeters except weight, which was measured in pounds. All anthropometric measurements were taken in accordance with the methodology described by Hooton [this methodology was later formally described by Hooton (1946)]. The only measurement taken that did not follow the measurement standard of the time was head height, which required a head spanner. Instead, Dupertuis measured head height as is done today, with an anthropometer (Hooton et al. 1955).

Analytical Methods. The pattern of geographic variation of 20 anthropometric traits in Ireland was analyzed using spatial autocorrelation techniques. Spatial autocorrelation analysis is a statistical method that identifies geographic patterning of a variable over space [see Cliff and Ord (1973, 1981), Sokal and Oden (1978a,b), and Sokal and Wartenberg (1981, 1983)]. Spatial autocorrelation is displayed when a variable exhibits a regular pattern over geographic space in which its values at a given set of geographic locations depend on values of the same variable at other locations (Odland 1988). The computation of spatial autocorrelation coefficients requires nonoverlapping sets of localities represented as points on a plane (Griffith 1987). Only 1 value per variable for each geographic point is permitted. Therefore for anthropometric traits mean values are calculated for each locality.

The autocorrelation statistic Moran's I was computed using the formula

$$I = n \sum_{ij} w_{ij} z_i z_j / W \sum_{i=1}^n z_i^2, \quad (1)$$

where n is the number of localities, summation is over all i from 1 to n and over all j from 1 to n ($i \neq j$), w_{ij} is the weighting function given to edges between localities i and j (w_{ij} does not have to equal w_{ji}), $z = Y_i - \bar{Y}$, where Y is the value of a variable Y for locality i and \bar{Y} is the mean of all Y localities, and $W = \sum_{ij} w_{ij}$ is the sum of the matrix weights ($i \neq j$). The expected value of I in the absence of autocorrelation is approximately 0. Values of Moran's I vary from -1 to 1 . Values greater than 0 indicate positive autocorrelation (patterned similarity between localities), and values less than 0 indicate negative spatial autocorrelation (patterned dissimilarity between localities) (Griffith 1987).

Moran's I was calculated for each variable over those points that were considered connected in some sense (Sokal and Friedlaender 1982). Connectedness is expressed by a weighting function that assigns values to pairs of localities to represent their location with respect to one another (Odland 1988). Because these data were separated into towns, we used inverse great circle distance weighting. The great circle distance weighting function measures all distances along great circle routes between localities, assuming a mean radius of 6,371 km for the earth. Latitude and longitude values of each

town were collected from the US Board on Geographic Names (1950) and Geelan and Lewis (1992).

Given these specifications, we computed spatial autocorrelation coefficients (Moran's *I*) for predefined pairs of towns at specified geographic distances. The towns were grouped into categories of specified distances called spatial lags. The lags are spaced so that an equal number of data points contribute to the measure of spatial autocorrelation at each lag. For example, the first spatial lag includes all comparisons of towns between 1 and 79 km apart.

Spatial variation, as detected through the value of Moran's *I* at each lag, was summarized in a spatial correlogram, which plotted Moran's *I* against distance class. The spatial correlogram displays the relationship between pairs of localities as a function of distance between those localities. These correlograms are 1-dimensional because they demonstrate autocorrelation in distance irrespective of geographic direction (north, northwest, etc.).

The spatial correlograms were originally calculated using 6, 8, 10, and 12 spatial lags, as per the standard in most spatial autocorrelation studies (Sokal and Oden, 1978a,b). Experimentation with different correlograms using the same variable but with different numbers of spatial lags did not alter the statistical significance of the correlograms. Therefore the correlograms calculated with 8 spatial lags were selected for further consideration. The last distance class (eighth lag) has not been featured in the analyses presented here because previous research demonstrated that the last lag can be unreliable because of edge effects [for an explanation of edge effects, see Sokal and Oden (1991)]. The upper limits of the distance classes in the analysis by town were 79, 116, 144, 182, 216, 262, and 331 km.

The statistical significance of each autocorrelation was computed under a randomization hypothesis using the SPAC program written by J.T. Williams. For the purpose of this study the Bonferroni method used by Sokal, Harding et al. (1989) was used to test the statistical significance of a correlogram against the null hypothesis of no spatial autocorrelation. All correlograms with 1 or more values of Moran's *I* significant at $p < 0.0071$ ($p = 0.05$ divided by the number of distance classes, 7) were considered significant at $p < 0.05$.

To examine spatial variation of anthropometric traits in Ireland, we used a 3-step statistical method [e.g., Sokal, Jacquez et al. (1989)]. First, homogeneity of localities with respect to the variable under consideration was tested. Using an analysis of variance (ANOVA), we tested the null hypothesis that the variable under consideration was identical in mean for the set of localities being studied (Sokal and Rohlf 1981). Second, spatial autocorrelation was tested for the 20 anthropometric traits and 7 principal components using 95 towns in Ireland. Third, the similarity of correlograms was analyzed to categorize the variables into groups of similar spatial patterns. The Bonferroni significant correlograms were subjected to a nonhierarchical clustering

procedure (a k means cluster analysis) to detect clusters of spatial patterns. The number of clusters to be interpreted was determined following the method of Krzanowski and Lai (1988). This method selects the best cluster partition so that the pooled sum of squares within groups is minimized. Following Sokal, Harding et al. (1989), correlograms allocated to each k means cluster were averaged to provide a summary measure of the spatial patterns in these data.

The computation of the spatial statistics allowed for the development of hypotheses about possible origins of the spatial patterns or about the given population structure. Detailed descriptions of possible interpretations of spatial patterning and their theoretical basis have been offered elsewhere (Sokal and Oden 1978b; Sokal and Wartenberg 1981; Sokal and Jacquez 1991). In brief, homogeneity or heterogeneity, spatial patterning or nonpatterning, and similarity or dissimilarity in the spatial patterns were all considered to generate informed hypotheses concerning microevolutionary patterns [e.g., Sokal, Jacquez et al. (1989)]. Coupled with these considerations, sociocultural, historical, demographic, and environmental factors of the area were reviewed. Through a consideration of all these factors, inferences concerning population structure were made.

Computations. All computations were executed using BMDP (version 1990), SAS (release 6.9), and MINITAB (release 9.1) statistical software. In addition, a program (SPAC) provided by J.T. Williams of the Southwest Foundation for Biomedical Research was used to calculate the spatial autocorrelation statistics.

Results

Homogeneity of Localities. To control for age-related variation, we regressed each anthropometric measurement on age and $\log(\text{age})$ to remove linear and polynomial age effects, and the standardized residuals from these regressions were used in all further analyses. To examine the magnitude of within-group variation, we subjected each anthropometric variable to an ANOVA among towns. Considering all 20 anthropometric traits, the null hypothesis that the variation displayed among towns is what would be expected at random was rejected using Bonferroni protection at $p \leq 0.0025$ ($p = 0.05$ divided by 20, the number of tests). These results suggest differentiation among towns in all anthropometric traits. Therefore further investigation of the nature and cause of this differentiation using all traits was warranted.

Spatial Autocorrelation Analysis. Spatial correlograms for the 20 anthropometric traits using 95 towns were computed. Moran's I coefficients of the 20 correlograms are provided in Table 1. Fifty-four of 140 (39%) I

Table 1. Spatial Autocorrelation Coefficients (Moran's *I*) for 95 Irish Towns

Variable	Significance ^a	Lag 1 (0-79 km)	Lag 2 (80-116 km)	Lag 3 (117-144 km)	Lag 4 (145-182 km)	Lag 5 (186-216 km)	Lag 6 (217-262 km)	Lag 7 (263-331 km)
Weight	S	0.2316	0.0355	0.0042	0.0739 ^b	-0.0232	-0.1473 ^d	-0.1374 ^d
Stature	S	0.0371	0.0077	0.0075	0.0815 ^b	0.0414	-0.0673	-0.1382 ^d
Acromion breadth	S	0.1574	-0.0070	0.0093	0.0571	0.0490	-0.0333	-0.1430 ^d
Dactylion height	S	0.0841	0.0913 ^c	0.0339	0.0302	-0.0277	-0.1879 ^d	-0.1979 ^d
Total arm span	S	-0.1566	0.0098	0.0028	0.1351 ^d	0.0277	-0.0347	-0.1516 ^d
Biacromial breadth	NS	-0.2577	0.0557	0.0046	0.0080	-0.0201	-0.0470	-0.0601
Chest breadth	S	-0.0511	0.1933 ^d	0.1026 ^c	0.0200	-0.0027	-0.2398 ^d	-0.2738 ^d
Chest depth	NS	0.4434	-0.0538	-0.0789	-0.0555	-0.0124	0.0434	0.0388
Sitting height	NS	-0.0334	0.0466	0.0212	0.0178	0.0365	-0.0126	-0.0732
Head circumference	NS	0.0542	-0.0467	0.0003	-0.0339	0.0706 ^b	-0.0250	-0.0317
Head length	NS	0.2757	-0.0119	-0.0398	-0.0544	0.0128	0.0283	-0.0524
Head breadth	S	0.4234	0.1869 ^d	0.1818 ^d	0.1491 ^d	0.0215	-0.1209 ^c	-0.3616 ^d
Head height	S	0.8646	0.1437 ^d	-0.2254 ^d	-0.2120 ^d	-0.1124 ^b	-0.0295	0.0455
Minimum frontal diameter	S	0.7510 ^c	0.3955 ^d	-0.0581	-0.1917 ^d	-0.1561 ^d	-0.3477 ^d	-0.2503 ^d
Bizygomatic breadth	S	0.3189	0.2611 ^d	0.1951 ^d	0.1053 ^c	0.0711 ^b	-0.2083 ^d	-0.3126 ^d
Bigonial breadth	S	0.6194	0.2078 ^d	0.0872 ^b	0.0434	0.0049	-0.1736 ^d	-0.2613 ^d
Total facial height	NS	0.1028	-0.0961 ^b	-0.0772	0.0261	0.0581	-0.0468	-0.0325
Upper facial height	S	0.4818	0.1249 ^d	-0.0920 ^b	-0.2011 ^d	-0.1044 ^b	-0.0098	-0.2360 ^d
Nasal height	S	0.4992	0.0961 ^c	0.0521	-0.0557	0.0236	-0.1185 ^c	-0.2202 ^d
Nasal breadth	S	0.6654	0.0729 ^b	-0.0216	0.1677 ^d	-0.0645	-0.0978 ^b	-0.1962 ^d

a. Overall significance of correlogram using Bonferroni protection at $p \leq 0.0071$ ($p = 0.05/7$). S, significant;

NS, nonsignificant.

b. $0.01 < p \leq 0.05$.

c. $0.001 < p \leq 0.01$.

d. $p < 0.001$.

coefficients were significant at $p \leq 0.05$, indicating considerable spatial structure in these anthropometric variables. By using the Bonferroni criterion, 14 of the 20 correlograms displayed significant spatial patterning across distance at $p \leq 0.0071$ ($p = 0.05$ divided by 7, the number of spatial lags).

Because of the variety of correlograms displayed, it was not informative to make generalizations about all 14 correlograms together. There appears to be no general trend or pattern in these variables; rather, there are several different trends.

A multivariate approach was then used to reduce the 20 anthropometric variables into uncorrelated summary synthetic variables. Principal components analysis was executed using a within-population correlation matrix. Only the first 7 eigenvalues had confidence intervals greater than or equal to 1 and were therefore subjected to spatial autocorrelation analysis. The correlograms of only the first 2 principal component factor scores were significant under Bonferroni protection at $p \leq 0.0071$ ($p = 0.05$ divided by 7, the number of spatial lags) (Table 2). The independence of the 2 principal components was determined using Bartlett's test of sphericity. With a chi-square value of 27.75 and 1 degree of freedom the null hypothesis of sphericity was rejected. Hypothetical orthogonal unit eigenvectors were constructed as a means of interpreting these 2 principal component axes. The first principal component axis appeared to be a size axis. Only upper facial height and head height did not load on this axis (Table 3). The second axis was a contrast axis (Table 3). Loading negatively on the axis were several types of variables, including body length and transverse body, head, and facial measurements. In contrast, loading positively on the axis were a mix of functional factors. Therefore a simple biological explanation of this axis was not plausible.

The correlogram of the first principal component resembled several of the correlograms of variables that were loading onto the axis (i.e., weight, chest breadth, and dactylion height) (Figure 2). Basically, low-order (small) distances displayed positive autocorrelation and high-order (large) distances displayed negative autocorrelation, without necessarily displaying a monotonic decline at intermediate distances. Therefore, according to Sokal, Harding et al. (1989), this correlogram characterizes long-distance differentiation. The long-distance distinction pattern can be explained by different regions at the greatest distances on the map coupled with an absence of clear structure at the intermediate distances. Of course, the terms short and large distance are relative to the analysis being conducted.

The correlogram of the second principal component closely resembled those for upper facial height, which was loading positively on the axis, and head height, which was loading negatively (Figure 2). Again, low-order distances displayed positive autocorrelation with a much faster decline to negative autocorrelation between 140 km and 180 km and then no autocorrelation from about 180–330 km. This correlogram appears to reflect regional patchiness of the surface area (Sokal, Harding et al. 1989). This correlogram pattern

Table 2. Spatial Autocorrelation Coefficients (Moran's *I*) of Principal Components (PC) 1 and 2 for 95 Irish Towns

Variable	Significance ^a	Lag 1 (0-79 km)	Lag 2 (80-116 km)	Lag 3 (119-144 km)	Lag 4 (145-182 km)	Lag 5 (183-216 km)	Lag 6 (217-262 km)	Lag 7 (263-331 km)
PC1	S	0.2067	0.1439 ^d	0.0753	0.1261 ^c	0.0410	-0.1926 ^d	-0.2920 ^d
PC2	S	0.4340 ^b	0.1821 ^d	-0.1925 ^d	-0.3221 ^d	-0.1167 ^c	-0.0031	-0.0981 ^b

a. Overall significance of correlogram using Bonferroni protection at $p \leq 0.0071$ ($p = 0.05/7$). S, significant.

b. $0.01 < p \leq 0.05$.

c. $0.001 < p \leq 0.01$.

d. $p < 0.001$.

Table 3. Summary Description of Anthropometric Variables Positioning on Principal Components 1 and 2^a

<i>Principal Component 1</i>	<i>Principal Component 2</i>		
	<i>Not Loading</i>	<i>Negative Loading</i>	<i>Positive Loading</i>
<i>Loading</i>			
Weight	Upper facial height	Chest depth	Weight
Stature	Head height	Sitting height	Acromion breadth
Acromion breadth		Head height	Chest breadth
Dactylion height		Minimum frontal diameter	Head circumference
Total arm span		Bigonial breadth	Head length
Biacromial breadth		Upper facial height	
Chest breadth		Nasal height	
Chest depth		Nasal breadth	
Sitting height			
Head circumference			
Head length			
Head breadth			
Minimum frontal diameter			
Bizygomatic breadth			
Bigonial breadth			
Total facial height			
Nasal height			
Nasal breadth			

a. These interpretations are made through an examination of the unit eigenvectors and the hypothetical unit eigenvectors.

is consistent with a biological surface on which there are patches or regions of similarity; the regions at intermediate distances are different, but the regions at far distances are not (Sokal, Harding et al. 1989).

There are fewer significant spatial patterns of factor scores because factor scores are linear combinations of characters (a summary of the patterns of variation in all those variables loading on the axes). Therefore these 2 axes presumably represent some underlying developmental or genetic factor (Sokal and Winkler 1987). Consequently, there are at least 2 unique and different spatial patterns in these data.

Similarity of Correlograms. A *k* means cluster analysis was performed on the 14 significant correlograms. Following the method of Krzanowski and Lai (1988), the 7 correlogram partition was selected. Correlograms allocated to each *k* means cluster were averaged and used for all further interpretation of spatial patterning (Sokal, Harding et al. 1989). The results of these summary calculations described 4 distinct spatial patterns.

Cluster 1 yielded an average correlogram with a steep gradient, displaying high positive autocorrelation that monotonically decreased to high negative autocorrelation at the farthest distances (Figure 3). According to

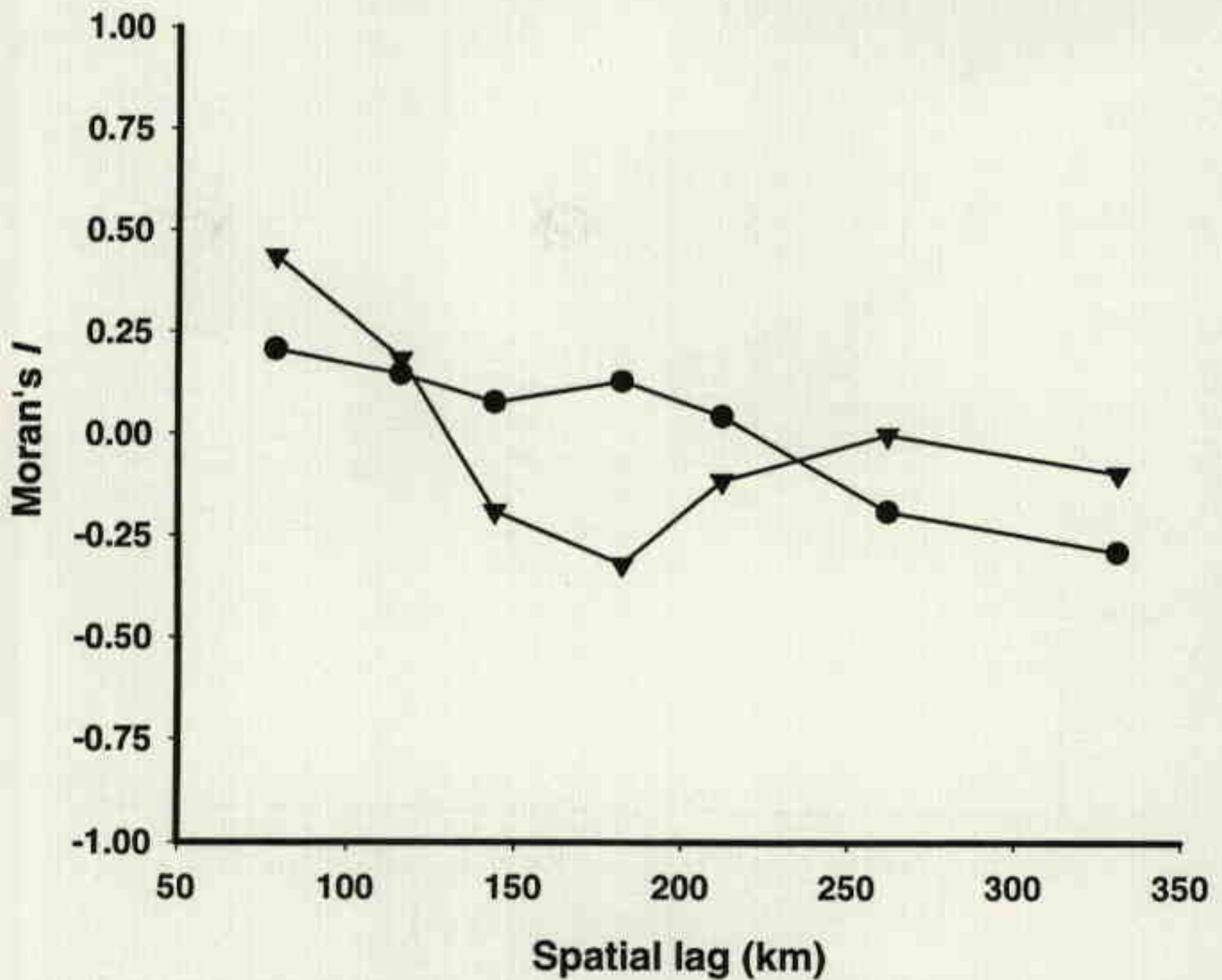


Figure 2. Correlogram of principal component 1 (circles) and principal component 2 (triangles) for 95 Irish towns.

Sokal and Oden (1978a), this pattern is indicative of a clinal distribution. The variables that displayed this clinal pattern were all breadth measurements.

The second spatial pattern indicated significant spatial patterning but only at long distances. Both the correlograms of cluster 2 and cluster 4 showed this spatial structure (Figure 3). Interestingly, both short distances and intermediate distances lacked clear structure. Therefore this pattern revealed no significant relationship in space for all pairs of towns up to 260 km apart. This pattern does not resemble the patterns generally described in the spatial autocorrelation literature and was termed distance distinction.

The third spatial pattern indicated long-distance differentiation (Sokal, Harding et al. 1989). Cluster 3 and singleton clusters of minimum frontal diameter and nasal breadth showed structure with areas of homogeneity up to 115 km and long-distance differentiation at 215 km and beyond (Figure 3).

The fourth spatial pattern was detected in only 1 correlogram, head height. This correlogram displayed a pattern of high positive autocorrelation at the first distance class and negative autocorrelation at the intermediate

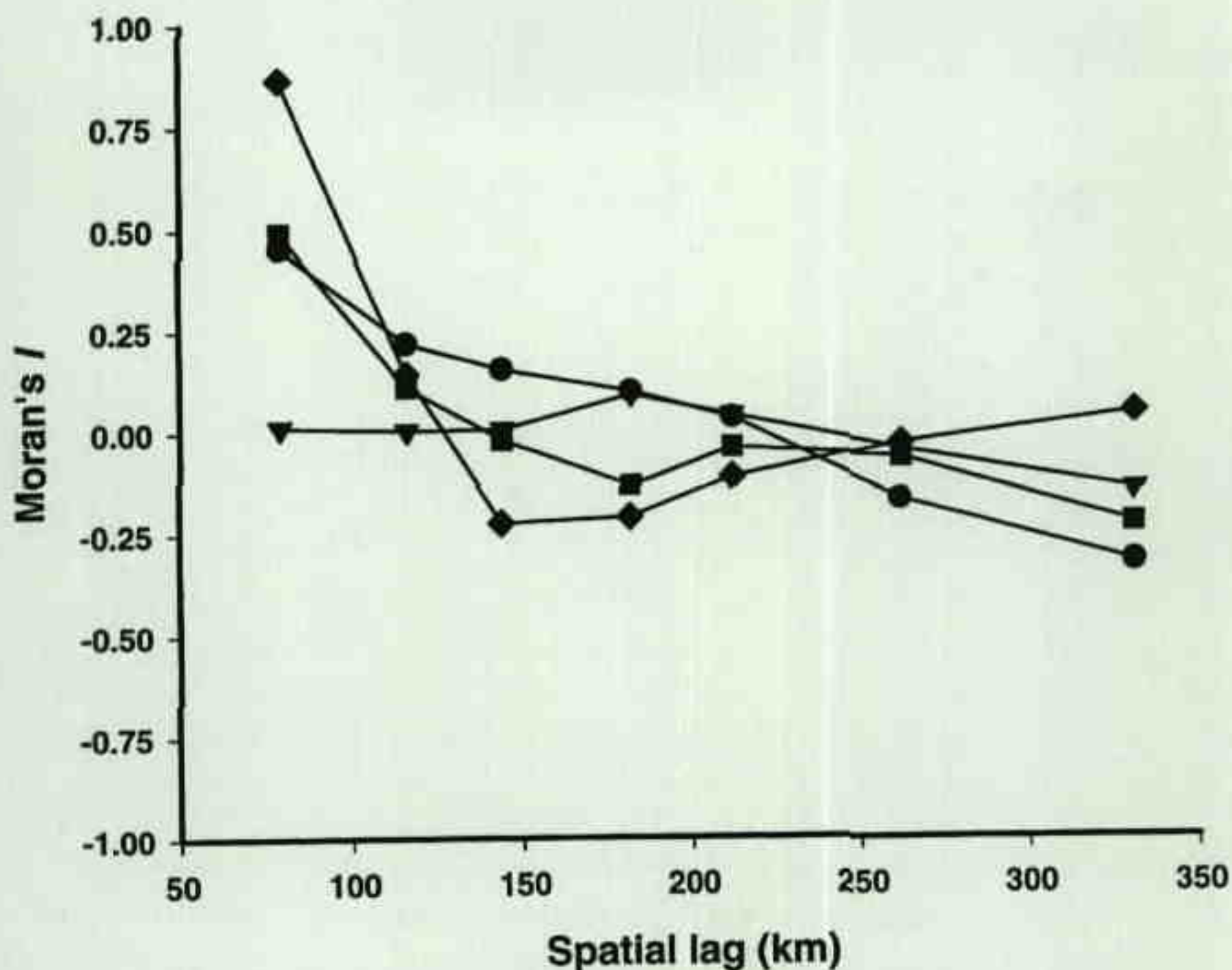


Figure 3. Average correlograms representing the 4 clusters of Moran's *I* correlograms for 95 Irish towns. Circles, pattern 1; triangles, pattern 2; squares, pattern 3; diamonds, pattern 4.

distances, followed by a leveling-out close to 0 autocorrelation in the last lags (Figure 3). This pattern was indicative of regional patchiness (Sokal, Harding et al. 1989).

Although the cluster analysis suggests the presence of 4 distinct spatial patterns, only 2 of the 7 principal component axes displayed significant spatial patterning. According to Sokal and Winkler (1987), "there are fewer significant spatial patterns of factor scores because they represent linear combinations of characters—presumably some underlying developmental trend, rather than the individual variables with specific morphogenetic patterns which are reflected in the *k*-means clusters" (p. 150). Therefore the spatial autocorrelation analyses of anthropometric variation among towns indicates at least 2 (perhaps as many as 4) distinct patterns of spatial variation.

Discussion

The findings of the analyses can be summarized by several key points. (1) There was significant heterogeneity in the means of 20 different anthro-

pometric traits among towns in Ireland. (2) There was significant spatial patterning as detected in correlograms of 14 anthropometric traits and 2 principal component factor scores. (3) Several spatial correlograms are similar and partitioned into clusters. (4) Four spatial patterns were detected, including clinal, long-distance differentiation, distance distinction, and regional patchiness. Therefore spatial variation patterns differed among anthropometric variables. (5) In general, there was significant positive autocorrelation at low-order distances and significant negative autocorrelation at high-order distances.

Inferences Concerning Possible Origins of Spatial Patterning. Based on the results, several suggestions of possible origins of these spatial patterns were made using the approach of Sokal and Wartenberg (1981, 1983). An explanation for the combination of significant heterogeneity of means and the absence of spatial patterning was pertinent. Four of 20 anthropometric variables had significant heterogeneity of means, but the correlograms were not significant. This combination could have resulted from (1) stochastic processes determining these characters in the absence of selection and low levels of migration or (2) the population structure being affected by selective agents that are unpatterned or patterned in components smaller than average inter-locality distance (Sokal and Wartenberg 1981, 1983). In considering these options, it is important to note that only 4 of 20 variables failed to display significant spatial patterning. According to Sokal and Wartenberg (1981), it is impossible for a population to carry with it only several characters and not all the others. Therefore some of the heterogeneity of means (at least these 4 variables) was likely a result of stochastic local differentiation.

Given that there was heterogeneity of means and spatial patterning in these data, the similarity or dissimilarity of patterns of variation and similarity or dissimilarity of correlograms was considered. In these data a combination of different patterns of variation and differing correlograms was detected, possibly indicating differences in the processes producing these patterns. This combination can be generated in populations in which (1) differential selection among various genetic systems occurs or (2) there has been considerable migration at different times, rates, and directions from genetically distinct source populations (Sokal and Wartenberg 1981, 1983).

The first suggestion that the population has been dominated by natural selection with the selective agents patterned differentially in space may be a less likely hypothesis for these data. There were at least 2 distinct patterns (possibly as many as 4) of spatial variation, and it is unlikely that these populations were being selected for all these patterns at once. Indeed, there is little evidence to support a selectionist hypothesis for any of these anthropometric variables in Ireland. Although previous research has suggested that natural selection operates through environmental constraints, such as climatic variables [e.g., O'Rourke et al. (1985) and Suarez et al. (1985)], these findings

have been detected while adopting a continental perspective in the investigation of biological variation. In an area as small as Ireland there is little if any significant climatic (environmental) variation (Edwards 1981). Although there is topographical variation in Ireland, it acts only as an isolating mechanism in small areas along the west coast. Accordingly, for natural selection to be operative in Ireland, another selection regimen would have to be postulated. This postulation would have to encompass "diverse selection regimens for the different clusters, sufficient time for these regimens to operate, and sufficient strength for the selection coefficient to overcome the effects of small population size" (Sokal and Friedlaender 1982, p. 223). Therefore the hypothesis that migration at different times, rates, and directions from genetically distinct source populations has shaped the genetic structure of Ireland was explored further.

To understand how migration has shaped the genetic structure of Ireland, the results of the average correlograms were interpreted through a consideration of the actual population pairs in each distance class. In terms of the first 2 distance classes the populations contributing to the positive autocorrelation were within 116 km of each other. This is what would be expected from an isolation by distance model, where short-range diffusive gene flow modifies local genetic traits varying by genetic drift (Sokal and Friedlaender 1982). The presence of this short-distance positive autocorrelation may also be explained through the populations' mating and migration patterns. In general, migration at marriage was usually to the next village or county and was sufficiently close to maintain family ties (Connell 1968). Moreover, the unmarried males and females generally did not contribute to the gene pool (Relethford 1980). This occurred because unmarried males generally either left the country or remained single and because the unmarried females generally either migrated to the urban centers or emigrated from the country. In addition, there was a low rate of illegitimacy in Ireland because those individuals who remained unmarried were often celibate (Connell 1968). Given these factors and because most comparisons between adjacent towns were within the first spatial lag, the significant positive autocorrelation of the first distance classes can be explained by the mating patterns in Ireland.

In terms of the lags representing the intermediate (and sometimes near) distances, a pattern of long-distance differentiation and distance distinction was identified. This pattern suggests that the relationship between populations at intermediate distances in the long-distance differentiation pattern (and near distances in the distance distinction pattern) was random. It is possible that stochastic local differentiation may have masked the spatial patterning present in these variables. Through the use of simulation studies Fix (1993, 1994) demonstrated that spatial patterning may not be apparent against the background of stochastic noise.

The particular stochastic noise at near and intermediate distances may have been influenced by several historical events in the population history of

Ireland. First, the Great Famine may have had an impact on the local genetic structure of Ireland. For example, current research of the local genetic structure of Northern Ireland has revealed a significant genetic impact of the famine (Bittles et al. 1986; Bittles and Smith 1991, 1994; Smith et al. 1990). In fact, Bittles and colleagues have suggested that the main genetic consequence of the dramatic fluctuations in population size both before and after the famine was an increase in the impact of random genetic drift. It may be that the lack of spatial patterning in some of these variables at near and intermediate distances reflects a swamping of any patterning because of the combination of stochastic processes and different patterns of migration. Second, the multiple settlement patterns of Ireland may have overwhelmed genetic patterning in some areas (e.g., intermediate distances) but not in others. For example, Relethford and Crawford (1995) suggested the uniqueness of 4 Midland counties of Ireland related to a greater genetic impact from Viking invasions. Because comparisons of near and intermediate distances included this Viking cluster and several unrelated counties, considerable stochastic noise could have masked spatial patterning.

In terms of the last 2 lags a pattern of long-distance differentiation and distance distinction was identified. The populations contributing to the last 2 lags include east-west and northeast-west contrasts. This finding is in accordance with previous research of the population structure of Ireland, which has identified an east-west cline of biological variation [e.g., Dawson (1964), Hackett et al. (1956), Hooton (1940), Hooton et al. (1955), Relethford (1983), Relethford and Crawford (1995), and Tills et al. (1977)]. The presence of this cline was attributed to historical patterns of migration and dispersion.

As discussed earlier, the basic east-west gradient in Ireland can be explained by several different migrations. The first well-documented immigration of the Celts to Ireland in the 6th century B.C. reportedly occurred in successive waves, with each successive wave pushing inhabitants further westward (Pringle 1985). In contrast, the Viking invasions, starting in the late 8th century, did not likely contribute to the east-west gradient to a large extent because the Norse established coastal settlements on the west and east coasts of Ireland and forced the Celts inland. Only in the sense that the Celts on the east coast were forced inland (i.e., to the west), could this pattern of migration have contributed to the east-west gradient. The next wave of migrants, the Anglo-Normans, may have had a significant effect on the genetic structure of Ireland. Most of the Norman invasions occurred in the 12th and 13th centuries on the east coast. Immigration to Ireland continued, with the next wave of migrants coming from England, Wales, and Scotland. These migrations occurred because the English tried to gain and maintain political and religious control of Ireland. The English, Scottish, and Welsh migrants settled mostly in northern and eastern regions of Ireland. Indeed, this group of migrants may also have contributed to the east-west gradient of biological variation. More-

over, the English and Scottish migrations may explain the presence of the northeast-west gradient detected in these analyses.

Previous studies do not agree on which of these historical patterns was specifically responsible for the development of the east-west gradient (Relethford and Crawford 1995). Hooton et al. (1955) suggested that the Celtic waves of migration to Ireland, with successive groups pushing previous inhabitants westward, significantly affected the genetic structure. In contrast, Tills et al. (1977) suggested that later patterns of settlement by the Anglo-Normans in the 12th century and the English, Welsh, and Scottish migrations in the 1700s contributed to the east-west gradient. Settlers from England and Wales often settled in the eastern counties and settlers from England and Scotland often settled in the northern counties. *These patterns of settlement displaced the previous inhabitants (Gaelic Irish) and pushed the initial inhabitants of Ireland westward.* Relethford and Crawford (1995) suggested that differential settlement patterns of Ireland, specifically England to the east coast of Ireland, has contributed to the east-west gradient. However, Relethford and Crawford (1995) claimed that any 1 of these patterns of migration could explain the presence of the east-west gradient.

Unfortunately, it is difficult to examine the specific anthropometric traits to ascertain which populations are influenced by which specific group of migrants (Celtic, Norse, Norman, etc.). *Most information about the morphological characteristics of these specific groups of migrants was detailed in the early 20th century using a racial perspective.* Therefore most of the traits that were used to characterize these populations were anthroposcopic. However, 1 of the traits mentioned in previous research using this racial perspective was stature. In an analysis using a subset of the same data used here, Hooton (1940) reported that those populations living in the west of Ireland were taller than those populations living in the east. Hooton claimed that these tall individuals were descendants of the original Celtic invaders that were pushed westward by successive waves of migration through time in Ireland. *This hypothesis is further supported by the fact that the west of Ireland is the only area where the original Gaelic language of Ireland is still spoken today (Tarchetti 1994).* The findings of this study support Hooton's claim.

This research confirms the presence of an east-west gradient. In addition, this research detects a northeast-west pattern of biological variation, possibly reflecting the patterns of English and Scottish immigration to Ireland since the 18th century. In other words, the results of this study support the hypothesis that it is not just the influence of 1 group of migrants in 1 direction. *Rather, these findings suggest that the combination of different migrations from different sources is reflected in the complex spatial patterning of anthropometric traits in Ireland.*

Significance of Findings for Irish Population Structure. As stated previously, the analyses examining the relationship between the geography and

genetics of Ireland have reported differing results. Research in a small region in western Ireland by Relethford (1980, 1982) suggested that geographic distance was the major determinant of population structure. Accordingly, the genetic structure of these local populations was dominated by isolation by distance (Relethford and Crawford 1995). By contrast, in yet another regional study of anthropometric variation in western Ireland, Relethford (1988, 1991) suggested that history, geography, and genetic drift all contributed to population differentiation. In several other studies research of countrywide variation identified historical patterns of settlement and dispersion of populations as the main influence on population differentiation (Dawson 1964; Hackett et al. 1956; Hooton 1940; Hooton et al. 1955; Relethford and Crawford 1995; Tills et al. 1977).

Relethford and colleagues have suggested that these apparent inconsistencies concerning geography and genetics may not be inconsistencies per se. Rather, they have suggested that the level of analysis in these studies may explain differences in results (Relethford and Crawford 1995; Relethford et al. 1997). Indeed, demographic change will have a greater genetic impact on local populations, as opposed to larger regional populations. This occurs because demographic change at a local level may blur population history in a short period of time but could take a longer time to have an impact at the regional level. Therefore studies of microdifferentiation at the local level may reflect short-term changes in the demographic or genetic structure, whereas studies of regions or of all counties may reflect long-term patterning associated with major historical events (Relethford et al. 1997).

The results of this study support this finding. The short-distance significant positive autocorrelation supports the findings of geographic distance being the major determinant of population differentiation for local populations. In addition, the main patternings in these data were long-distance differentiation, distance distinction, and clinal patterns. These patterns may reflect long-term patterning associated with migration, as has been previously suggested. Therefore the answer to the question concerning the relationship between genetics and geography in Ireland is that there is not just 1 answer. Instead, there are several patterns of genetic variation in Ireland, and apparent inconsistencies in results may be related to the level of analysis.

Limitations of the Study. Several caveats should be considered in the interpretation of the results of this study. First, the criterion for the minimum sample size of 20 individuals per town reduces the number of individuals included in the analysis by 1/2. Moreover, this criterion produces a sample of towns with a patchy distribution across Ireland (Figure 1). In other words, several areas of the island are sampled thoroughly (by use of the criteria of 20 individuals), whereas other areas of the island were not examined. This patchy distribution can bias the results of the spatial autocorrelation statistics (Sokal and Oden 1978a,b). Related to this, the means for each town are not

estimated with the same reliability because of differences in sample sizes. This could lead to error in our estimates of the mean, leading to p values that may be biased low. Therefore it is important to interpret the statistical inferences made in this study with caution.

A second limitation of this research concerns the bias introduced into this analysis by using only male anthropometric measurements. Unfortunately, female data spanning the entire island of Ireland were not available. In terms of anthropometric traits males may be more influenced by environmental effects (Hall and MacNair 1972). In addition, males are less migratory than females, and this may introduce a bias into the results. Because of this limitation, it is important to interpret the results of these analyses with caution.

Implications for Future Research. Future research should further investigate the relationship between the level of analysis and discrimination in population studies. This research supports the suggestion that different factors dominate at different levels of analysis (Relethford and Crawford 1995; Relethford et al. 1997). When examining microdifferentiation of the entire island of Ireland, long-term spatial patterning associated with major historical events was detected. However, the short-distance significant positive autocorrelation that we detected suggests that isolation by distance is a major determinant of population differentiation. This hypothesis could be further tested through the use of spatial autocorrelation analysis. Future research could examine local population structure of several different regions of the island using the same data used here. Indeed, spatial autocorrelation analysis could be used to determine what factors dominate the local population structure of Ireland.

Conclusions

The turbulent history of Ireland, with its waves of continuous invasions and immigrations counterbalanced by regional isolation, offers an excellent opportunity to examine the complexity of spatial patterning of biological variation. In this study 3 main conclusions were made. First, we demonstrated that Ireland is not a homogeneous gene pool or a simply structured one in which historical population movements left 1 simple spatial pattern that is independent and diffusive. Rather, we have demonstrated that there is spatial complexity in the phenotypic distribution of anthropometric traits in Ireland.

Second, at least 2 (and maybe more) distinct patterns of spatial variation of anthropometric traits among towns in Ireland were identified. Therefore spatial variation patterns differ among anthropometric variables. Moreover, the patterns of anthropometric variation cannot simply be accounted for by the isolation by distance model.

Third, it can be hypothesized that migration has had an important influence on the spatial patterning of anthropometric characters in Ireland. Indeed,

Irish history, with the blending of different populations following the arrival of group after group of immigrants, has given rise to complex patterns of biological variation. Therefore the combination of many migrational events can be recognized as structuring the phenotypic landscape in Ireland. Furthermore, these analyses support previous research suggesting that population history has been the major determinant of population microdifferentiation.

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