Population genetic structure in Atlantic Cod (*Gadus morhua*) from the North Atlantic and Barents Sea: contrasting or concordant patterns in mtDNA sequence and microsatellite data?

Steven M. Carr and Dorothy C. Crutcher
Genetics, Evolution, and Molecular Systematics Laboratory
Department of Biology
Memorial University of Newfoundland
St. John's Newfoundland
Canada

Abstract

We summarize the results of studies of mitochondrial DNA sequence variation in Atlantic cod (*Gadus morhua*) from the North Atlantic and adjacent areas. Population genetic structures in the Northwest and Northeast Atlantic and Barents Sea differ markedly. Whereas all populations from the Northwest Atlantic are dominated by a single common genotype and show low haplotype and nucleotide diversity, samples from Norway and the Barents Sea support multiple genotypes at intermediate frequencies and show much higher genetic diversity. Replicate samples taken in the same year at a single location off Newfoundland, or in different years from the Gulf of Maine and Georges Bank, are as dissimilar as samples taken from opposite sides of the Laurentian Channel. Essentially none of the genetic variance in the Northwest Atlantic is attributable to subdivision among samples, whereas a substantial proportion is attributable to trans-Atlantic differentiation. Re-evaluation of comparable microsatellite data supports the conclusion of extremely limited genetic differentiation among populations in the Northwest Atlantic. The mtDNA data support the hypothesis that cod throughout the Northwestern Atlantic have experienced a bottleneck in population size relative to their source population in the Old World, and show that mtDNA haplotypes are sensitive markers of population structure.

Introduction

Atlantic cod appear to comprise a number of subcomponents that are temporally or spatially separated during part or all of their life cycle, which are therefore regarded as distinct stocks. Fisheries managers have designated eleven such stocks along the North American continental shelf. The original delimitation was based on vertebral counts, although it has long been recognized that there is a substantial degree of overlap in the ranges of vertebral counts in each of the areas (Templeman 1981).

The term "stock" means different things to different people (Booke 1981; Dizon et al. 1997). From a management perspective, stocks are understood to be groups of phenotypically similar individuals whose morphological and meristic homogeneity is due to environmental effects (Templeman 1981). Implied is the idea that a stock could be manageable as a unit. An alternative approach to stock delimitation is genetic. From a population genetic perspective, stocks are equivalent to demes: closed populations that maintain themselves in a given area and are reproductively isolated from other such populations. Morphological differences among groups of genetically homogeneous fish from different areas may simply reflect different environmental conditions. For example, vertebral counts are inversely correlated with water temperature at the time of spawning (Brander 1979).

Our laboratory has taken the genetic perspective in assessing the nature of stock structure in Atlantic cod. Genetic analysis of the DNA sequence of a segment of the mitochondrial cytochrome *b* gene has identified more than 50 genotypes among more than 1,000 cod from more than 30 locations in the North Atlantic (Carr and Marshall 1991a,b; Pepin and Carr 1993; Carr et al. 1995; Crutcher 1996). The bulk of this work has concerned populations in the Northwest Atlantic. Analogous studies with the same genetic locus have been conducted on cod from Iceland, Norway, and the Barents Sea (Árnason 1992; Árnason and Palsson 1996), and from Long Island, Georges Bank, and the Gulf of Maine (T. Kocher, unpubl.). For this conference, we assembled all of the available mtDNA sequence data to examine the degree and distribution of spatial heterogeneity of allele frequencies and genetic variance, in order to address the question: Are there local stocks of cod?

Materials and Methods

To make this comparison, we calculated Rogers's distances (as modified by Wright 1978) among 39 samples (Figure 1), among which 50 genotypes have been identified (Figure 2). We used the matrix of pairwise allele frequency differences, without correcting for pairwise nucleotide differences between haplotypes. Especially in the Northwest Atlantic, nucleotide divergences are very small or negative, which indicates that within-sample divergence is typically greater than that among samples (Carr et al. 1995; Árnason 1996). Rogers Distances were calculated with the NTSYS (v.2.0) program (Rohlf 1992). Neighbor joining and UPGMA cluster analyses of these distances were done with the pre-release version 4 of the PAUP program of Dave Swofford (1998) (versions d59 and subsequent releases). The coancestry coefficient (Θ), which estimates the proportion of the genetic variation due to subdivision among populations and is equivalent to F_{ST} for diploid nuclear loci, was estimated by the HAPLOID program (Weir 1990).

Results

The distance analysis shows that allele frequency distributions of samples from the Northeast Atlantic (Norway and Barents Sea) are sharply differentiated from those in the Northwest Atlantic (Figure 3).

Among samples in the Northwest Atlantic, Flemish Cap is most distinct. This reflects a high frequency of genotype **E** (described in Carr & Marshall 1991a) in this sample, which is otherwise uncommon in the Northwest Atlantic, but which approaches equal frequency with genotype **A** in populations in the Northeast Atlantic. [Genotype **A** occurs at an average frequency of more than 70% in all populations from the Northwestern Atlantic]. Allele frequency distributions in the Northwest Atlantic are otherwise unrelated to geographic distributions. Samples from south of the

Laurentian Channel (Gulf of Maine, Georges Bank, and Bay of Fundy) cluster as closely with samples from north of the channel as they do with each other. Of special interest to the present conference, replicate samples from the Gulf of Maine or the Georges Bank, taken in different years by ourselves and Tom Kocher (pers. com.), are no more similar (or just as dissimilar) to each other than are replicate samples taken in the same year from different locations in Trinity Bay, Newfoundland (NAFO Division 3L) (Carr et al. 1995). Patterns within Norwegian cod are discussed in Árnason and Palsson (1996) and by Einar Árnason as part of this conference. Populations there appear to be much more highly differentiated over much shorter geographic distances than in the Northwest Atlantic. For example, pairwise distances between samples from adjacent fjords along the Norwegian coast (i.e., Varanger *vs.* Porsanger), as well as replicate samples from the Barents Sea, are substantially greater than those between any pair of samples taken in the Northwest Atlantic.

Crutcher (1996) calculated the coancestry coefficient (Θ) for six samples in the Northwest Atlantic, including three samples from south of the Laurentian Channel, plus a sample from Barents Sea, which distribution is therefore comparable to those analyzed in Bentzen et al. (1996). The amount of genetic variation due to subdivision among Northwest Atlantic samples (Θ) is -0.0004 ± 0.0107, that is, not distinguishable from zero. When the Barents Sea sample is included, Θ is positive (0.1155 ± 0.0899), though still within two standard errors of zero. This reflects the high variance of the Barents Sea sample and the low variance of the six northwestern Atlantic samples. When Northwest Atlantic samples are pooled and compared with the Barents Sea sample, is 0.2431.

Discussion

The Utility of Mitochondrial DNA Sequences as Population Markers in Atlantic Cod

The relative utility of mtDNA sequences *versus* other loci such as nuclear RFLPs (Pogson et al. 1995) and particularly nuclear microsatellites (Ruzzante et al. 1996; Bentzen et al. 1996) as tools to investigate stock structure in Atlantic cod has been the subject of some discussion on theoretical and methodological grounds, at this conference and elsewhere. We take this opportunity to state our view of the matter.

Mitochondrial DNA is highly polymorphic. Polymorphism should be distinguished from heterogeneity. The former measures the multiplicity of genotypes within a sample, the latter the probability that two genotypes drawn at random from the sample will be different. Heterogeneity for haploid alleles is analogous to heterozygosity for diploid nuclear alleles. MtDNA in the Northwest Atlantic is highly polymorphic and not very heterogeneous: more than 40 genotypes have been identified at the cytochrome *b* locus, but most of these are rare. By contrast, mtDNA in the Northeast Atlantic and Barents Sea is both highly polymorphic and highly heterogeneous. Multiple genotypes exist at intermediate frequencies. For example, Árnason and Palsson (1996) identified eleven genotypes among 100 Norwegian fish, and a mean heterogeneity h = 0.78, as compared with a mean heterozygosity H = 0.86 for all microsatellites). The microsatellite locus that seems most efficient at discriminating populations (***Gmo132***) showed only 10 alleles and H = 0.369 among 84 fish in the Barents Sea (Bentzen et al. 1996).

Mitochondrial DNA is sensitive to population substructure. Because of the differences in their patterns of inheritance (diploid biparental *versus* haploid maternal), data obtained from the two genomes may be sensitive to different population phenomena. For example, mtDNA heterogeneity

is more sensitive to fluctuations in population size ("bottlenecks" and "founder events") than is nuclear heterozygosity (Wilson et al. 1985). The reduced variability of mtDNA in the Northwest Atlantic is characteristic of an historical bottleneck with respect to its potential source population in the Northeast Atlantic. Because mtDNA is transmitted without recombination, it is possible to reconstruct the matrilineal phylogeny of genotypes, something that is difficult or impossible with nuclear markers such as microsatellite loci. The "star phylogeny" characteristic of a population bottleneck was detected in this way. Nuclear markers fail to give evidence of this important phenomenon in the biology of northern cod.

Mitochondrial DNA provides valuable insights into the population structure (or lack thereof) of Atlantic cod. First principles suggest that the absence of population structure be taken as the null hypothesis (H_o: $F_{ST} = \Theta = 0$). The precautionary approach urged by some fisheries managers is to assume the existence of local stocks, since the potential for overexploitation or extermination of a localized, genetically distinct entity is perceived to have greater consequences for the fishery (Dizon et al. 1997). We favor a precautionary approach to fisheries management. However, we are skeptical of a perspective that assumes, *a priori,* that previously defined management units correspond to distinct stock components.

From such a perspective, it has sometimes been suggested that the mtDNA data "fail to detect population structure" and are therefore not useful as information for managers. In fact, mtDNA data have been used to measure the proportion of the observed genetic variance attributable to among-sample heterogeneity of genotypes. The measured value is essentially zero in the Northwest Atlantic, which indicates that little or none of the observed genetic variance is attributable to among-sample heterogeneity consistent with the notion of "distinct stocks." *Estimation of a parameter as zero is not equivalent to "failure" to detect a positive value of the parameter.* Where such heterogeneity exists, analysis of mtDNA may detect it. A significant proportion of the trans-Atlantic variance *is* attributable to among-sample variation ($\Theta = 0.11$).

The skewed allele frequency distribution within samples, and homogeneity across cod populations from the Northwest Atlantic should be seen as features of their biology. Carr et al. (1995) discussed the contrast between a "deep" structure characterized by an historic bottleneck, possibly associated with Pleistocene glaciation, and a "shallow" structure, characterized by extensive gene flow among contemporary populations.

In the same geographic area, contrasting population structure has been demonstrated in two other marine species. In both cases, the differences can be attributed to differences in dispersal patterns. As assessed with mtDNA sequences, Greenland halibut *(Reinhardtius hippoglossoides)* is a highly polymorphic and heterogeneous species. Like cod, genotype frequencies are uniform throughout the commercial range ($\Theta = 0.00$). Unlike cod, this uniformity extends to populations on both sides of the Atlantic. The difference is attributed to the more benthic distribution of halibut, which allows them to move along transatlantic contours at depths where the continental shelf is continuous (Vis et al. 1997). Harp Seals (*Pagophilus groenlandicus*) are even more polymorphic. Significant stock differentiation ($\Theta = 0.09$) has been detected between breeding grounds in the northwestern Atlantic (Gulf of. St. Lawrence and Newfoundland Shelf) *vs.* those in the Greenland and White Seas. These data are consistent with tagging data that show little or no movement of sexually mature adults between breeding grounds in the northwestern and northeastern Atlantic (Perry et al., in prep.).

Other markers, other interpretations: do nuclear DNA and mitochondrial DNA show contrasting patterns of stock structure?

The major point of contention between mitochondrial *vs.* microsatellite data concerns the degree of population substructure in the Northwest Atlantic, especially north of the Laurentian Channel in the so-called "northern cod stock" of NAFO Divisions 2J3KL. We suggest that the patterns shown by these two aspects of the genome are actually quite similar; it is our respective interpretations that differ. The following patterns appear to us concordant.

i. Both systems indicate significant population substructuring attributable to transatlantic stock differentiation. For comparisons involving individual samples from the Barents Sea and the Northwest Atlantic, $F_{ST} = 0.015$ for microsatellites, compared with $\Theta = 0.11$ for mtDNA. When samples from the Northwest Atlantic are pooled, $F_{ST} = 0.037$ and $\Theta = 0.24$.

Microsatellite loci do not consistently distinguish the Barents Sea sample from those in the Northwest Atlantic, and it seems that the nuclear F_{ST} underestimates the degree of transatlantic differentiation. Bentzen et al. (1996) attribute this to the presumed origin of new microsatellite alleles by convergent and/or parallel step-wise mutation, which would tend to obscure divergence patterns among populations produced by genetic drift. Under such circumstances, "hypervariable microsatellites may not be the markers of choice for broad-scale surveys", such as comparisons across ocean basins.

ii. Both systems indicate that samples taken on the offshore seamount Flemish Cap are distinguishable from those taken on the adjacent continental shelf. In unrooted phenograms of Rogers' distances, the Flemish Cap samples clusters with the Barents Sea apart from the remaining Northwest Atlantic samples (Figure 4 of Bentzen et al. 1996: cf. our Figure 3).

This pattern was first detected in the transferrin electrophoretic data of Cross and Payne (1978), who showed such a separation to be the primary dichotomy in cod populations of the Northwest Atlantic. They attributed the pattern to the glacial history of the continental shelf, during which the vicinity of Flemish Cap may have been the only suitable codfish habitat.

iii. Both systems indicate that samples from south of the Laurentian Channel are not particularly distinct from those north of the Gulf. MtDNA markers indicate that populations south of the Gulf have somewhat higher indices of heterogeneity, but no distinct differences in allele frequencies can be demonstrated. As noted above, samples from south of the Laurentian Channel cluster as closely with samples from north of the channel as they do with each other, and replicate samples from the Gulf of Maine or the Georges Bank are no more similar to each other than are replicate samples from Newfoundland.

For a pool of northern cod *versus* a single population from south of the Gulf (Scotian Shelf), microsatellite data indicate a small but significantly non-zero F_{ST} of 0.003. The Scotian Shelf sample is distinctive because of a group of "rare alleles" at the **Gmo132** locus. However, the Scotian Shelf sample is not a distinct branch in any of the distance analyses, its relationship

with the two pooled subcomponents of Northern Cod being essentially a trichotomy (Figure 4 of Bentzen et al. 1996).

    iv.   What about northern cod?

Based on morphological, meristic, and genetic analysis, Pepin and Carr (1993) concluded that "Adult cod on the northeast Newfoundland shelf exhibit variations in life history features that affect the production of exploitable biomass in the different regions... Thus, geographic complexes of phenotypically homogeneous adult cod can be recognized, and can form the basis for the management of fishing patterns and effort. However, it is essential to recognize that these complexes are not genetically differentiated and thus do not represent distinct populations. The strong correlation of recruitment among Newfoundland cod stocks may represent similar responses to similar environmental conditions... Alternatively, this pattern may also represent spatial variation in reproductive success or failure of a single large population." Carr et al. (1995) recommended an alternative approach to stock assessment, which was "to measure such variation as exists, partition the observed variance among samples drawn from different putative 'stocks', and based on these data to consider the alternate hypothesis that distinct cod stocks do not exist within the complex" (Pepin & Carr 1993).

On the other hand, Bentzen et al. (1996) begin "Genetic differences may also exist between northwestern and southeastern cod aggregations within the northern cod stock complex off Newfoundland," and conclude "We have shown evidence for at least two genetically discernable groups within the northern cod complex, our NORTH and SOUTH pools that correspond to the 2J3K and 3L management divisions... [N]orthern cod are not comprised of a single, panmictic assemblage, but rather appear to be geographically affiliated with spawning area. This suggests that it may be wise to seriously reconsider the current (and historical) management scheme for northern cod, which presumes one stock distributed throughout... NAFO divisions 2J, 3K, and 3L."

This assessment appears to us problematical. First, the "northwestern and southeastern cod aggregations" are not biological entities but rather *a posteriori* statistical pools. The NORTH pool comprises samples from the Hamilton, Belle Isle (both NAFO Division 2J), and Funk Island (Division 3K) banks. The SOUTH pool comprises samples from North Cape, Grand Bank, and Nose of the Bank (Division 3L). Pools were made among samples that were individually indistinguishable. However, a sample from the NE Spur of the Grand Bank (Division 3L) was not pooled with NORTH, even though it is not differentiable from NORTH at any locus (their Table 4, line 2). The correspondence of genetic groups with management divisions seems to be at least in part an artefact of this exclusion.

Second, different microsatellite loci give different results about the structure of these populations. The NORTH and SOUTH assemblages are differentiable at only one microsatellite locus out of six (*Gmo4*). However, that locus fails to differentiate NORTH from any other sample examined, including trans-Laurentian Channel and transatlantic comparisons. The microsatellite marker that otherwise contributes most to the differentiation of samples (*Gmo132*) does not distinguish the NORTH and SOUTH pools. In each of the other nine pairwise comparisons of samples in the northwest Atlantic, only one locus out of six (typically *Gmo132*) differentiates samples (except that SOUTH *and* Flemish Cap are differentiable at two

loci). In only one comparison (SOUTH *versus* Barents Sea) do a majority of loci differentiate the samples.

Finally, "genetically discernable" is evidently not the same as "genetically distinct". The measured F_{ST} for NORTH *versus* SOUTH is 0.000, in agreement with the mtDNA data. Subcomponents of the NORTH and SOUTH pools show F_{ST} values of 0.007 and 0.002, respectively, only the latter of which is significantly non-zero. Both values are on the same order as the difference across the Laurentian channel (0.003) discussed above. We suggest that such small genetic differentiation, even if statistically significant, cannot provide a basis for biologically significant stock differentiation. Ability to detect very small differences among multivariate centroids is to be expected with the relatively large sample sizes employed (an average of 169 for NORTH, SOUTH, and Scotian Shelf) (see Bentzen 1998, this volume). However, reclassification to area of origin for individual cod on the basis of multilocus microsatellites genotypes would be poor.

In summary, we conclude that the mtDNA and microsatellite data confirm the genetic pattern first shown by Cross and Payne (1978) of a primary separation of cod on the Flemish Cap and those elsewhere in the Northwest Atlantic, but that there is otherwise little or no genetic substructuring attributable to genetically distinct stocks in this area. The genetic data support the conclusion of deYoung and Rose (1993) that, due to larval and egg drift, population structure in Northern Cod is insufficiently stable, either geographically or temporally, to allow the development of genetically distinct stocks.

Acknowledgments

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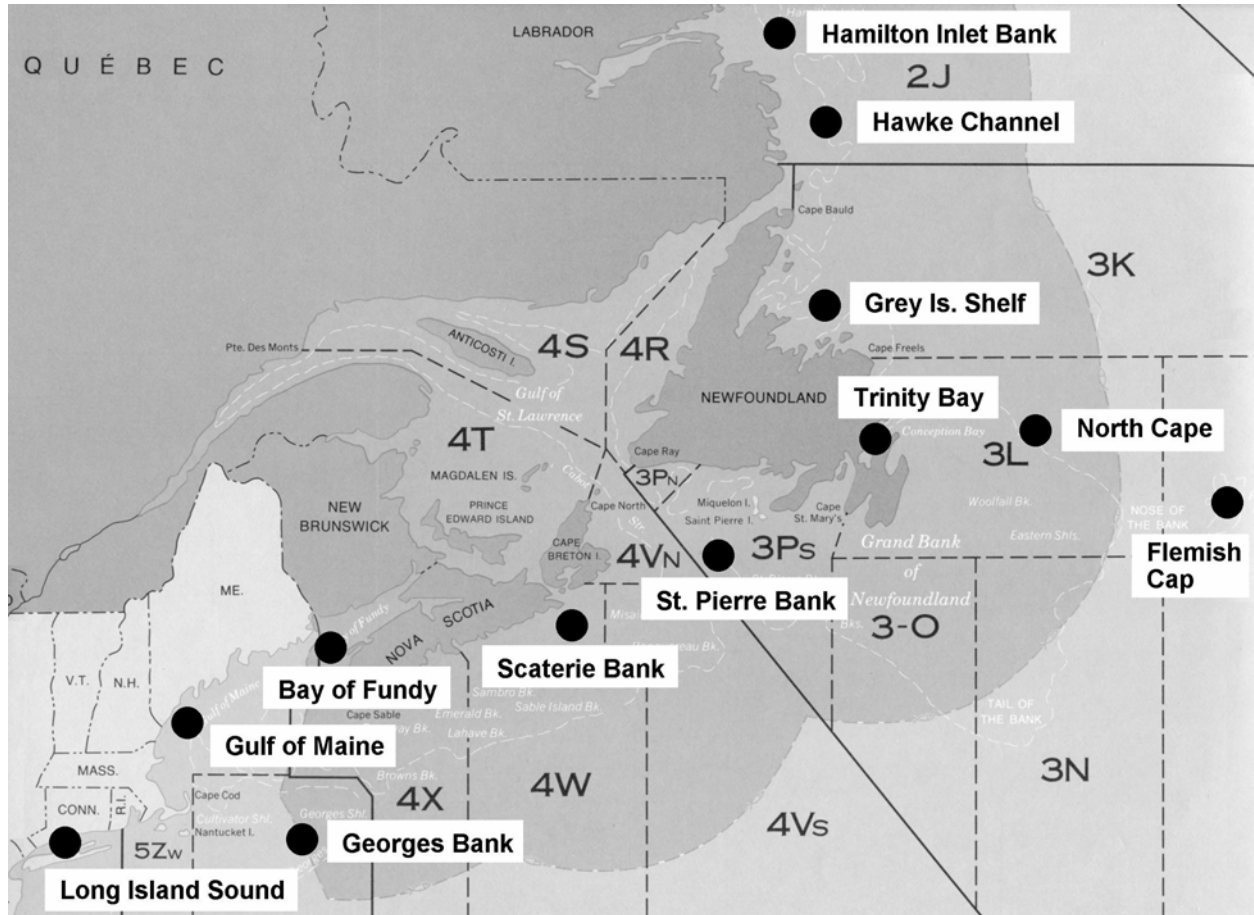
Figure 1. Some of the sample locations of cod populations in the northwest Atlantic that have been examined for mtDNA cytochrome *b* variation (after Crutcher 1996). Samples from the Grey Islands Shelf and St. Pierre Bank are described in Carr and Marshall (1991a). Samples from Hamilton Inlet Bank, Georges Bank, and the Gulf of Maine are from S. M. Carr (unpubl. data). A sample from Long Island Sound and a second sample from the Gulf of Maine are from T. D. Kocher (per. comm.). All other samples shown are described in Crutcher (1996). See also legend to Figure 3; other sample locations not shown here are shown and described in Carr and Marshall (1991a) and Pepin and Carr (1993).
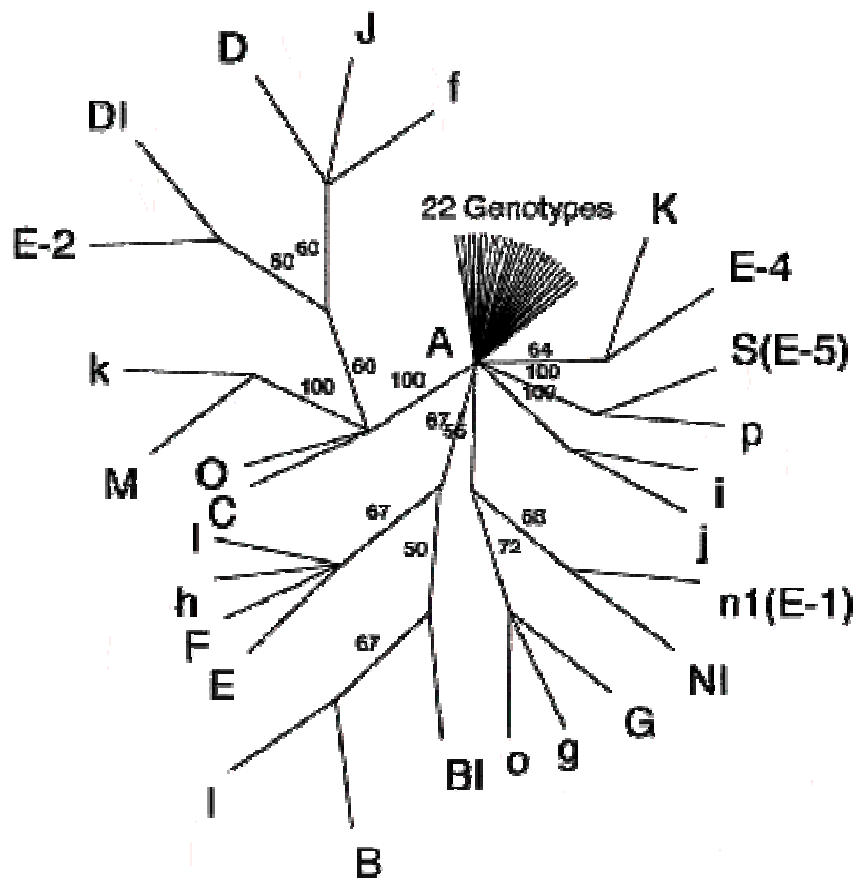
Figure 2. Phylogenetic relationships among 50 mitochondrial cytochrome b haplotypes in Atlantic cod. A majority-rule consensus diagram is shown: numbers on branches indicate the percentage occurrence of that branch in all trees of minimum length =47.
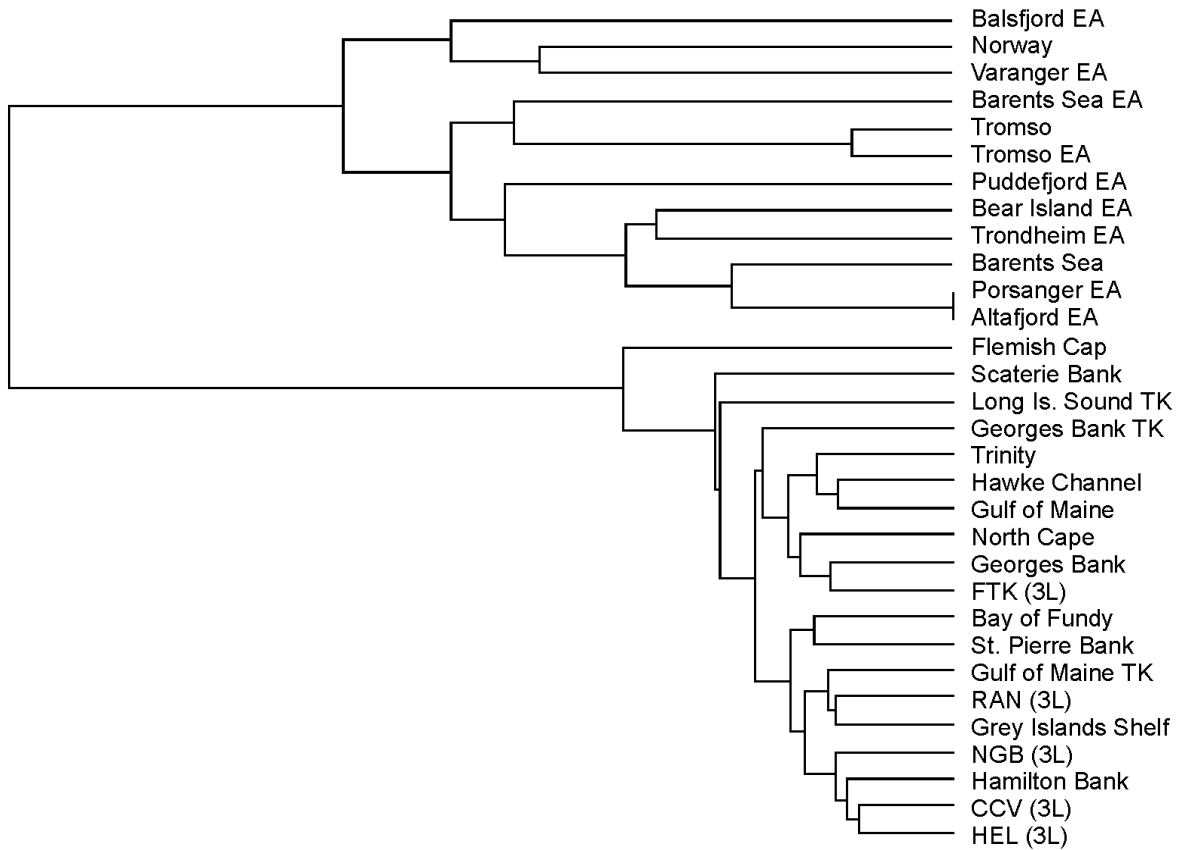
Figure 3. UPGMA distance analysis of Rogers' distance among cod populations in the Northwest and Northeast Atlantic and Barents Sea. Samples marked EA are described in Árnason and Palsson (1996). Samples marked TK are from T. D. Kocher (pers. comm.). The second Tromsö sample is from Carr and Marshall (1991a). Samples marked (3L) were taken in or near Trinity Bay as shown in Figure 1 and are described in Carr et al. (1995). Other samples are described in the legend for Figure 1.