Molecular Ecology (1998) **7**, 1663–1680

A nuclear DNA basis for shelf- and bank-scale population structure in northwest Atlantic cod (*Gadus morhua*): Labrador to Georges Bank

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Abstract

Variation at five microsatellite DNA loci scored in ≈ 1300 individuals provided evidence of genetic structure among 14 cod (*Gadus morhua*) populations spanning the range of the species in the northwest (NW) Atlantic. Using D_A and D_{SW} measures of genetic distance, as well as F_{ST} and R_{ST} measures of population structure, differences are revealed among populations at continental shelf scales (NE Newfoundland Shelf, Grand Banks, Flemish Cap, Scotian Shelf, Georges Bank) where regions are separated by submarine saddles, channels and trenches. However, we also provide evidence of genetic structure at spawning-bank scales consistent with variation in oceanographic features and in the spatiotemporal distribution of spawning, each of which may represent barriers to gene flow among geographically contiguous populations inhabiting a highly advective environment. The differences described are consistent with postdispersal spawning fidelity to natal areas, a behaviour that may be facilitated by topographically induced gyre-like circulations that can act as retention mechanisms. Significant degrees of substructure among neighbouring and contiguous cod populations may be most easily explained by the associated oceanographic features and processes that conceivably form the template for the evolution of the structure. We suggest that bathymetric and hydrodynamic structure represents a rational starting point for developing hypotheses to examine the processes that lead to the genetic structuring of marine fish species.

Keywords: bank-scale population structure, cod, *Gadus morhua*, genetic distance, genetics, indel mutation, microsatellite

Received 6 January 1998; revision received 4 June 1998; accepted 17 June 1998

Introduction

Marine fish typically exhibit high dispersal rates and low levels of population structure, whereas freshwater fish show the opposite pattern, and anadromous fish or those with less distinct barriers to movement show intermediate levels of both dispersal and structure (Ward *et al*. 1994; Stabile *et al*. 1996). Very abundant migratory marine fish species with broad and continuous geographical distributions can exhibit significant and persistent levels of population subdivision if the species also exhibit postdispersal spawning fidelity (i.e. homing) to natal areas. Homing may be facilitated by the retention of individuals during early development (eggs, larvae, juveniles) at a variety of geographical scales defined by oceanographic structure. Thus, genetic structure should be apparent at scales that are compatible with oceanographic structure. Postdispersal fidelity to natal spawning areas is apparent for most salmon species, as well as for sturgeon (Stabile *et al*. 1996) and for several eel species. Similar evidence in highly exploited groundfish species is rare. Nevertheless, spawning fidelity to natal grounds is evident in Greenland–Iceland cod (*Gadus morhua* L.) stock interactions and it is hypothesized for Scotian Shelf haddock,

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and in both cases oceanographic phenomena appear to play a significant role (see review in Frank 1992). Such phenomena have important demographic consequences and may provide more information on the processes that determine population genetic structure.

Atlantic cod is a typically abundant migratory marine fish species with a broad geographical distribution over a wide range of oceanographic structures. Populations in the northwest (NW) Atlantic range along the continental shelf from the northeast (NE) Newfoundland Shelf off Labrador (≈ 63°N) to Cape Hatteras (≈ 35°N). Across this 3000 km range the distribution is essentially continuous with different regions encompassing populations, stocks, or stock complexes that are recognized as explicit management units generally defined by latitude and bathymetry. Spawning areas among regions are relatively discrete, temporally stable and isolated at shelf-wide and Atlantic basin scales (Frank *et al*. 1994; Nakken 1994; Serchuk *et al*. 1994; Shopka 1994; Taggart *et al*. 1994). These stocks also reveal substantial differences in productive capacity related to temperature as well as stock-specific growth characteristics (Brander 1994) and therefore maturity schedules. However, whether they constitute reproductively isolated or genetically structured populations remains uncertain and subject to debate. Thus, cod in the NW Atlantic represents a model marine species for addressing population genetics questions within an oceanographic framework. The questions and the approach taken in addressing them should be applicable to a range of marine species, and perhaps most importantly to those undergoing exploitation.

Genetic stock identification in cod: questions, techniques and resolution

Different genetic markers vary in their power to resolve genetic differences among cod populations. Variations in blood proteins (allozyme loci) show differences among populations (Møller 1968; Jamieson 1975; Cross & Payne 1978; Dahle & Jørstad 1993) that become less apparent when a larger number of allozyme loci are used (Mork *et al*. 1985). Mitochondrial DNA variations show limited or no population differentiation throughout most of the species' range (Smith *et al*. 1989; Carr & Marshall 1991; Árnason & Rand 1992), or within smaller geographical and management regions (Árnason & Pálsson 1996; Carr & Marshall 1991; Pepin & Carr 1993; Carr *et al*. 1995). Nuclear DNA restriction fragment length polymorphism (RFLP) loci and microsatellite loci reveal population structure in cod at ocean basin scales as well as at continental shelf scales in the NW Atlantic (Bentzen *et al*. 1996; Pogson *et al*. 1995). Furthermore, microsatellite loci reveal population structure among inshore and offshore cod populations in the Newfoundland (Ruzzante *et al*. 1996b, 1997) and Labrador (see preliminary results in Taggart *et al*. 1998) regions.

In this study we examine microsatellite DNA variation among cod populations in relation to oceanographic features and variation in the spatiotemporal distribution of spawning, each of which has the potential to act as a barrier to gene flow. We examine populations across the latitudinal range of the species in the NW Atlantic from the NE Newfoundland Shelf to Georges Bank (Fig. 1). Using D_A (Nei *et al*. 1983) and D_{SW} (Shriver *et al*. 1995) measures of genetic distance and F_{ST} (Wright 1951) and R_{ST} (Slatkin 1995) measures of population structure, significant differences are revealed among populations on the major continental shelves and frequently among populations on neighbouring banks that are separated by deep channels and/or are characterized by gyre-like circulations (eddies) that are hypothesized to act as retention mechanisms for cod eggs and larvae.

Materials and methods

Sampling

Between January 1992 and December 1995 ≈ 1300 cod from pre- and postspawning aggregations were collected from 25 locations ranging from the NE Newfoundland Shelf in the north to the Bay of Fundy and Georges Bank in the south (Table 1, Fig. 1). Offshore bank-scale collections were made using an otter trawl deployed to the bottom at depths ranging between 35 and 500 m in waters at temperatures between 1.6 °C and 13 °C (Table 1). Inshore bay-scale collections were made using handlines, gillnets or otter trawl at depths between 15 and 275 m and in waters as cold as – 1.4 °C. The large range in size of cod within and among samples reflects a wide variation in ages (many estimated from age-at-length relationships) ranging from 1 to 11 years (Table 1). In some samples (e.g. Georges Bank) all individuals were classified as mature (spawning, or immediately pre- or postspawning), while in others (e.g. Grand Bank) none were mature (Table 1). Several of these samples were examined in previous studies (Bentzen *et al*. 1996; Ruzzante *et al*. 1996a, 1997) and those that are analysed here for the first time (a total of 578 fish) are marked with an asterisk in Table 1 (see also the Results).

Tissue collections and DNA extraction

Cod blood (≈ 1 mL) was the primary source of nuclear DNA and was collected from live or recently dead cod (details in Bentzen *et al*. 1996; Ruzzante *et al*. 1996a,b, 1997) and was preserved immediately in ≈ 5 mL of 95% ethanol. When blood was unavailable we employed soft muscle tissue taken from the posterior of the tongue and preserved in 95% ethanol.

DNA was extracted using a procedure designed for nucleated blood cells. An aliquot of blood/alcohol

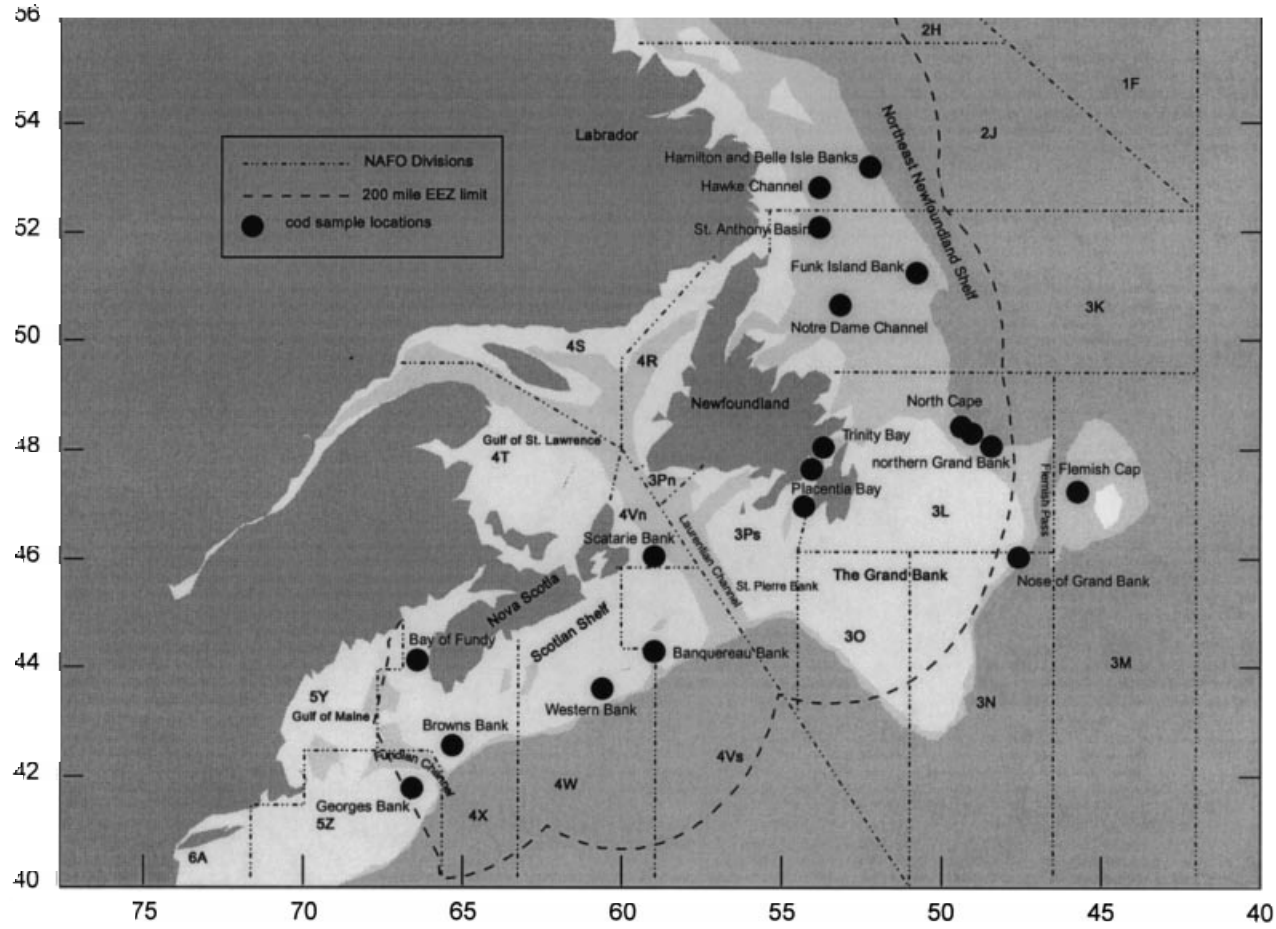

Fig. 1 Bathymetric chart of the NW Atlantic region from Labrador to Georges Bank showing major submarine banks, basins and channels, the major NW Atlantic Fisheries Management Organization (NAFO) Divisions and the sampling locations for cod used in the microsatellite analyses.

equivalent to approximately 75 μL of blood was washed in high TE (100 mM Tris-HCl pH 8.0, 40 mM NaCl). The pellet of cells was resuspended in 200 μL of lysis buffer (10 mM Tris-HCl, 1 mM EDTA, 200 mM LiCl, pH 8.0, 0.8% SDS) containing 250 μG/mL proteinase K. The sample was then incubated at 45 °C for 15 min, vortexed and again incubated until all cells were digested (nominally 15 min). The digest was diluted with 500 μL of TE (10 mM Tris-HCl, 0.1 mM EDTA) and precipitated by the addition of 750 μL of isopropanol. The DNA precipitate was washed with cold 70% EtOH, air-dried and resuspended in 100 μL of TE.

PCR amplification of five microsatellite loci, Gmo2, Gmo132, Gmo145 (Brooker *et al*. 1994), Gmo4 (Wright 1993), and Gmo120 (Ruzzante *et al*. 1996a) was accomplished using a modification of the procedure described by Brooker *et al*. (1994). One primer was labelled at the 5′ end with [γ^{32}P]-ATP (18.5 kBq/10 pM primer) using 2.5 units of T4 polynucleotide kinase. PCR was carried out in a 96-well plate format, in a MJ PTC-100 thermal cycler. The standard reaction contained 15 ng of template DNA, 0.6 mM of each unlabelled primer, 0.06 mM ^{32}P-labelled primer, 10 mM Tris-HCl at pH 8.3, 50 mM KCl, 0.01% gelatin, 1 mM $MgCl_2$ (1.5 mM $MgCl_2$ for Gmo120), 0.1% Tween 20, 65 mM each dNTP and 0.05 units of *Taq* polymerase in a 5-mL reaction volume. We used a multistage program for amplification: six cycles for 1 min at 94 °C, 30 s at the appropriate annealing temperature, and 30 s at 72 °C followed by 35 cycles during which the denaturation temperature was reduced to 90 °C for 30 s with the remaining steps as above. Stop-dye (5 mL of 10 mM NaOH, 99% deionized formamide, 0.1% bromophenol blue and 0.1% xylene cyanol green) was added to the reaction and the samples were denatured for 15 min at 94 °C. A volume of 3.5 mL of the reaction was subjected to electrophoresis in a 5.8% denaturing acrylamide gel and sized relative to a size standard generated from M13 mp18 sequence (Yanisch-Perron *et al*. 1985) and by comparison to a suite of standard samples.

Table 1 Summary statistics for Atlantic cod (*Gadus morhua*) used in microsatellite DNA analysis of population structure showing sample size (*N*) for number of individuals, latitude, longitude, depth and water temperature range at the capture location, length and age averages and ranges and the proportion of mature individuals in each sample, as well as the average number of alleles per locus and the observed (H_O) and expected (H_E) heterozygosity and heterozygote deficiency (*D*). HWE, loci out of Hardy–Weinberg equilibrium ($P < 0.05/5 = 0.01$) with either or both goodness-of-fit and log-likelihood ratio tests. Samples that are analysed for the first time are marked with the symbol §

Group	Geographic location and collection date	*N*	Latitude	Longitude	Depth range (m)	Mean temp range (°C)	Mean (range) length (cm)	Mean (range) age (years)	Proportion mature	Mean alleles per locus	H_O	H_E	*D*	HWE
NORTH	Hamiton, Belle Isle Banks, Jan 1992, 1993	38	53.15	–52.21	296–445	3.0–3.6	34.6 (25–48)	2.9 (2–4)	0.50	17	0.854	0.857	< 0.001	None
N = 174	Funk Island Bank, Jan 1992	30	51.25	–50.51	316–518	3.4–3.8	41.0 (28–51)	3.2 (2–5)	0.57	16	0.845	0.867	–0.022	
	Funk Island Bank, Jan 1993	58	51.22	–50.76	390–500	2.7–3.7	33.6 (21–48)	2.4 (1–4)	0.25	20.2	0.915	0.863	0.064	
	Hawke Channel, Jun 1994 (§)	48	52.81	–53.83	477–485	2.4–2.4	35.8 (29–50)	NA	0.38	19.4	0.903	0.864	0.042	
SAND	St. Anthony Basin, Jun 1994 (§)	48	52.07	–53.78	401–401	2.3–2.3	30.7 (25–47)	NA	0.96	19.4	0.882	0.862	0.020	None
N = 96	Notre Dame Channel, Jun 1994 (§)	48	50.66	–53.13	448–448	2.6–2.6	30.9 (23–43)	NA	0.06	19	0.890	0.849	0.050	
SOUTH	North Cape, Jan 1992	83	48.49	–49.46	439–482	2.8–3.8	53.9 (40–75)	4.9 (3–8)	0.84	21.4	0.825	0.878	–0.059	Gmo4 Gmo145
N = 249	North Cape 1993	30	48.38	–49.51	380–380	2.8–2.8	34.3 (21–47)	2.4 (1–4)	0.23	18	0.887	0.861	0.033	
	North Cape, Jun 1994 (§)	48	48.30	–49.10	416–436	2.5–2.5	33.3 (21–48)	NA	0.25	18.6	0.851	0.872	–0.023	
	Grand Bank, Jan 1992	60	48.11	–48.50	462–462	3.5–3.5	39.1 (24–63)	3.3 (2–6)	0.00	20.2	0.857	0.868	–0.012	
	Nose Grand Bank 1993	30	46.09	–47.59	391–391	1.6–1.6	30.1 (23–69)	2.1 (1–7)	0.03	15.8	0.904	0.868	0.039	
TRINITY														
N = 303	Trinity Bay high antifreeze, Jun 1992,Apr–Jun 1993, Jun 1992–94	122	48.03	–53.89	15–275	– 1.4–0.9	45.7 (24–80)	NA	0.03	25.2	0.878	0.874	< 0.001	Gmo2
	Trinity Bay, April 1995	100	48.18	–53.80	150–154	–0.99-(–0.97)	57.4 (45–85)	NA	0.70	23.8	0.877	0.870	0.006	
	Trinity Bay, Dec 1995	50	48.15	–53.82	44–46	NA	56.9 (52–65)	NA	1.00	19.6	0.862	0.852	0.002	
	Trinity Bay, farm-held cod	30	48.03	–53.63	NA	NA	64.8 (48–71)	6.9 (6–9)	1.00	16.8	0.879	0.856	0.028	
	Flemish Cap, Jul 1993	51	47.25	–45.75	316–366	NA	60.1 (38–94)	6.1 (3–11.5)	0.06	20.8	0.900	0.868	0.035	None
	Placentia Bay–North Harbour, Mar 1995 (§)	50	47.78	–54.08	68–68	NA	66.8 (54–86)	7.4 (5–11)	1.00	20.8	0.913	0.845	0.089	Gmo120 Gmo145
	Placentia Bay, St. Brides, Fox Harbour, Jun -Jul 1995 (§)	50	46.96	–54.30	34–40	NA	61.9 (43–74)	6.5 (5–9)	0.96	18.6	0.910	0.866	0.051	Gmo4 Gmo120 Gmo145
	Placentia Bay, Feb – Apr 1995 (§)	46	47.67	–54.08	46–275	NA	57.7 (36–83)	NA	0.63	18	0.900	0.867	0.037	Gmo4
	Scatarie Bank, Jul 1994 (§)	48	46.06	–59.00	84–154	0.5–3.6	46.2 (31–61)	5.3 (2–8)	0.71	19.8	0.849	0.853	–0.012	Gmo145
	Banquereau Bank, Jul 1994 (§)	48	44.31	–59.02	62–223	2.2–5.6	39.5 (23–77)	4 (2–8)	0.70	18	0.899	0.885	0.013	Gmo4
	Western Bank, Jul 1994 (§)	48	43.64	–60.65	34–88	1.3–11.3	38.2 (26–59)	4.1 (2–7)	0.94	18.8	0.840	0.854	–0.014	Gmo4
	Browns Bank, Jul 1994 (§)	48	42.60	–65.37	58–181	5.6–12.7	45.5 (32–62)	3 (2–5)	0.60	22	0.937	0.892	0.051	Gmo4 Gmo120 Gmo145
	Georges Bank, Feb 1995 (§)	48	41.83	–66.66	62–81	NA	59.9 (52–73)	NA	1.00	22.8	0.937	0.892	0.051	Gmo4 Gmo145
	Bay of Fundy, Jul 1994 (§)	48	44.16	–66.45	71–194	8.6–9.5	46.7 (31–63)	2.6 (2–4)	0.64	22.2	0.871	0.876	–0.007	Gmo4 Gmo120

$D = (H_O\text{-}H_E)/H_E$ averaged over loci. The mean *D* value was calculated by averaging over *D*-values for individual loci.

Data analysis

We tested for the probability of homogeneity of allele frequency distributions, for departures from Hardy–Weinberg (HWE) equilibrium, and for gametic linkage disequilibrium between two loci using χ^2 pseudoprobability contingency tests following Weir (1996). All tests were conducted using SPLUS© (MathSoft Inc. 1996). Tests of homogeneity were performed by randomization of alleles across individuals and populations (1000 bootstrap samples, Manly 1991). Tests of HWE were performed with both goodness-of-fit and log-likelihood ratio tests and were conducted by randomization of alleles within populations. Tests of linkage disequilibrium were carried out by permutation of alleles across individuals for the entire data set as well as within populations to test for the possibility of disequilibrium due to drift. Estimates of subpopulation structure were obtained using F_{ST} (Wright 1951) and R_{ST} (Slatkin 1995). F_{ST} was estimated following Weir & Cockerham (1984). Because estimates of gene flow obtained with this method are biased upward when the true level of gene flow is much higher than one (Nm » 1, Slatkin & Barton 1989), we also calculated gene flow with Nei's (1973) G_{ST} estimator where appropriate. Nei's G_{ST} generally gives estimates of gene flow that are smaller than the true value (Slatkin & Barton 1989). Thus actual values of gene flow should be somewhere between those derived from the G_{ST} and F_{ST} estimates. R_{ST} was calculated following Goodman (1997; see also Michalakis & Excoffier 1996) to minimize the variance due to differences in sample size (see Ruzzante 1998). Prior to estimation, allele sizes were standardized across the entire data set (Goodman 1997; eqn 3) to prevent differential influence among loci. Significance for both structure measures was estimated in two ways: first, by bootstrapping genotypes; and second, by bootstrapping alleles. In both cases bootstrapping was conducted across individuals and populations and for each locus separately. As the results were qualitatively similar with both methods of resampling for both F_{ST} and R_{ST} estimates (e.g. the difference in P-value between the two methods of resampling for all $R_{ST} > 0$ was: median = 0.0005; mean = 0.009), we only present results obtained by bootstrapping genotypes. Multilocus estimates of F_{ST} and R_{ST} were calculated by first averaging variance components across loci, as suggested by Weir & Cockerham (1984), Slatkin (1995), and Goodman (1997), rather than averaging single-locus R_{ST} or F_{ST} estimates over loci. Upper and lower 95% confidence limits for F_{ST} and R_{ST} were obtained by adding to, and substracting from, the corresponding estimate, the 97.5th and the 2.5th percentile of the empirical distribution of 1000 bootstrap samples. Pairwise genetic distances among populations based on the stepwise mutational model (SMM) were estimated using D_{SW} (Shriver *et al*. 1995). For comparative purposes we also estimated D_A (Nei *et al*. 1983), a non-SMM estimate of genetic distance with low variance relative to other non-SMM measures (Takezaki & Nei 1996; see also Ruzzante 1998). Significance for both distance measures was estimated in two ways: by bootstrapping genotypes (10 000 resampling trials with replacement) across individuals and populations for each locus separately; and also by bootstrapping over loci (100 resampling trials) to produce the relational phenograms (trees). UPGMA trees for both distance estimates were produced using standard SPLUS (MathSoft Inc. 1996) code ('hclust' with method 'average'), and values on nodes represent the percentage of tree configurations constructed with bootstrapped data (over loci) that showed the particular node. We also used multidimensional scaling analysis of the D_{SW} genetic distance matrix to illustrate relationships among populations in more than the two dimensions permitted by UPGMA. In all cases significance levels were adjusted for multiple comparisons using the sequential Bonferroni approach (Rice 1989). All statistical tests and analyses of genetic distances and population structure were conducted using SPLUS (MathSoft Inc. 1996) standard code or functions written by D. E. Ruzzante.

Results

Variation within and among samples and single-locus statistics

The average number of alleles per locus per cod sample ranged from 16 to 25 (Table 1). Observed and expected heterozygosities per sample ranged from 0.825 and 0.845 to 0.942 and 0.897, respectively (Table 1). The total number of cod analysed per locus ranged from 1205 (Gmo120) to 1273 (Gmo2) and the number of alleles per locus for the whole data set ranged from 24 for Gmo132 to 61 for Gmo145.

We pooled samples collected within the northern cod stock complex to facilitate statistical analyses (Table 1). Pairwise comparisons using single-locus χ^2 pseudoprobability contingency tests were conducted first among temporally spaced samples from the same location, and then among geographically related locations. Significant ($\alpha < 0.05/K$, where $K = 15$) differences in allele frequencies was found in one locus (Gmo4, $P < 0.001$) out of 15 single-locus χ^2 contingency tests involving comparisons among the 1992, 1993 and 1994 offshore samples from Hamilton/Belle Isle and Funk Island Banks and Hawke Channel. As sample sizes and the number of alleles per locus in our samples were relatively large we expected some heterogeneity between temporally spaced samples even though the cause may be drift alone (Waples & Teel 1990). As we found no evidence of population structure among these samples representing the northern reaches of northern cod using R_{ST} (= – 0.00008), although there was weak evidence for it using F_{ST} (= 0.005, $P = 0.006$), we grouped the Hamilton, Belle Isle, and Funk Island Banks

and Hawke Channel samples into a single pool referred to as NORTH (N = 174, Table 1). This is consistent with Bentzen *et al*. (1996) who examined all but the Hawke Channel sample. When these samples were compared to those from St Anthony Basin and Notre Dame Channel differences in allele frequency distributions ($P \leq 0.001$ for loci Gmo4 and Gmo120) and population subdivision became evident using F_{ST} (= 0.004, P = 0.004) and were marginal using R_{ST} (= 0.005, P = 0.088). In contrast, no significant differences in allele frequencies ($P > 0.124$) were found between cod from St Anthony Basin and Notre Dame Channel and R_{ST} and F_{ST} between these two samples were nil ($R_{ST} = -0.001$, $F_{ST} = -0.002$). Accordingly, the samples from the St Anthony Basin and Notre Dame Channel were pooled separately and are referred to as SAND (N = 96; Table 1).

There were differences in allele frequency distributions for only one (Gmo145, P = 0.005) of the five microsatellite loci among samples collected from the southern reaches of the northern cod stock complex on the Grand Bank (Table 1: North Cape, Grand Bank and the Nose of the Grand Bank) and the R_{ST} and F_{ST} estimates among these samples were either nil ($R_{ST} = -0.0001$) or low and non-significant (F_{ST} = 0.001, P = 0.170). We therefore pooled these samples and they are referred to as SOUTH (N = 249, Table 1). This is also consistent with Bentzen *et al*. (1996) who examined all but the 1994 samples from the North Cape.

Ruzzante *et al*. (1996b, 1997) demonstrated that cod overwintering in the inshore area of Trinity Bay between 1992 and 1995 were largely indistinguishable from each other and were genetically different from offshore overwintering cod. Therefore, all inshore samples from Trinity Bay were pooled and are referred to as TRINITY (N = 303; Table 1). As all of the remaining samples came from different geographical locations and/or differed genetically from each other, they were treated separately in the following analyses which consider a total of 14 different populations (Tables 1, 2, and 3).

Linkage and Hardy–Weinberg equilibrium

Pseudoprobability χ^2 tests indicated that there was no evidence ($P \geq 0.023$, $\alpha = 0.05/10 = 0.005$) of linkage disequilibrium for any of the 10 pairwise combinations of loci when the entire data set was considered. When individual populations were considered, one population, Flemish Cap, exhibited ($P \leq 0.002$) evidence of linkage in two pairwise combinations of loci, and marginal evidence (P = 0.078) in a third combination. Three other populations exhibited marginal ($0.020 < P < 0.090$) evidence of linkage in at least one (maximum four) pairwise combination of loci; these were Placentia–North Harbour (four combinations), the Bay of Fundy (two combinations), and Western Bank (one combination). Linkage among loci in these populations but absence of it in the entire data set suggests that linkage is caused by drift, an observation that is consistent with the fact that cod from Flemish Cap, Placentia–North Harbour, and the Bay of Fundy are genetically distinguishable (and thus somewhat isolated) from neighbouring populations (see below). Note, however, that none of these linkage disequilibrium tests in individual populations is significant when the sequential Bonferroni correction for multiple tests is applied. Tests of HWE were conducted for each of the 14 populations or regional pools. Populations and loci not in HWE are listed in Table 1.

Multilocus analysis of population structure

F_{ST}. A hierarchical analysis of F_{ST} revealed evidence of population genetic structure at several geographical scales (Table 2a). At continental shelf scales, cod north of the Laurentian Channel (N = 1055) were genetically distinguishable from those south of the Laurentian Channel (N = 288; F_{ST} = 0.008, $P < 0.001$, 95% CI: 0.007–0.008; Table 2a). This level of genetic differentiation was similar to that exhibited among all 14 populations considered separately (F_{ST} = 0.0084, $P < 0.001$, 95% CI: 0.0078–0.0091; Table 2a, lines 1 and 7). In both cases the genetic differentiation was largely dependent on locus Gmo132 and to a lesser degree on loci Gmo145 and Gmo4 (Table 2a). Genetic differentiation increased moderately if populations were pooled into six shelf-scale groups: northern cod, Flemish Cap, south Newfoundland, Scotian Shelf, Georges Bank, and Bay of Fundy (F_{ST} = 0.011, $P < 0.001$, 95% CI: 0.0002–0.0015; Table 2a, line 2). F_{ST} estimates within the northern cod complex (bank-scale), although relatively low, were significant whether cod aggregations off the southern coast of Newfoundland were included or not (F_{ST} = 0.001–0.002, 95% CI: 0.0016–0.0031; Table 2a, lines 3 and 4). Consequently the number of migrants (Nm) between components was between 124 and 250 individuals per generation depending on the number of components considered (Table 2a, lines 3 and 4). Nm was considerably lower when derived from G_{ST}: between 50 and 163 individuals per generation (again depending on the number of components considered). Bank-scale population structure was also evident among the three offshore banks on the Scotian Shelf (F_{ST} = 0.004, P = 0.019, 95% CI: 0.001–0.007; Table 2a, line 5), and this level of genetic differentiation increased almost threefold when cod from Georges Bank and the Bay of Fundy were included in the analysis (F_{ST} = 0.011, $P < 0.001$, 95% CI: 0.009–0.014; Table 2a, line 6). In the last two comparisons the structure was primarily dependent upon the Gmo132 and Gmo145 loci.

Table 2 Single and multilocus (a) F_{ST} and (b) R_{ST} estimates (P-values) of genetic structure among Atlantic cod (*Gadus morhua*) populations from the NW Atlantic.

Population	Gmo2	Gmo4	Gmo120	Gmo132	Gmo145	Over all loci	CI	*Nm*
(a) F_{ST}								
North vs. South of Laurentian Channel	0.001 (0.135)	0.001 (0.073)	0.000 (0.258)	0.041 (< 0.001)	0.001 (0.008)	0.008 (< 0.001)	0.007–0.008	32.2
NW Atlantic 6 groups*	0.002(0.062)	0.001 (0.028)	0.000 (0.273)	0.057 (< 0.001)	0.002 (0.001)	0.011 (< 0.001)	0.010–0.012	22.3
Northern cod, 4 components†	–0.001 (NA)	0.001 (0.026)	0.000 (0.153)	0.002 (0.075)	0.001 (0.019)	0.001 (0.023)	0.0002–0.0015	249.8
Northern cod, 8 components‡	–0.001 (NA)	0.001 (0.061)	0.001 (0.128)	0.010 (< 0.001)	0.002 (0.001)	0.002 (< 0.001)	0.0016–0.0031	124.8
Scotian Shelf, offshore§	0.004 (0.212)	–0.002 (NA)	0.001 (0.369)	0.014 (0.020)	0.004 (0.070)	0.004 (0.019)	0.001–0.007	62.3
Scotian Shelf–Fundy–Georges Bank¶	0.004 (0.125)	–0.000 (NA)	–0.001 (NA)	0.056 (< 0.001)	0.003 (0.057)	0.011 (< 0.001)	0.009–0.014	22.5
NW Atlantic, 14 populations	<0.001 (0.306)	0.001(0.035)	0.001 (0.165)	0.043 (< 0.001)	0.003 (< 0.001)	0.0084 (< 0.001)	0.0078–0.0091	29.4
(b) R_{ST}**								
North vs. South of Laurentian Channel	–0.001 (NA)	–0.000 (NA)	–0.001 (NA)	0.270 (< 0.001)	0.009 (0.010)	0.091 (< 0.001)	0.090–0.094	1.2
NW Atlantic 6 groups*	–0.000 (NA)	0.015 (< 0.001)	0.007 (0.009)	0.263 (< 0.001)	0.010 (0.001)	0.089 (< 0.001)	0.084–0.089	2.1
Northern cod, 4 components†	–0.001 (NA)	0.009 (0.006)	0.005 (0.028)	– 0.000 (NA)	0.015 (< 0.001)	0.006 (< 0.001)	0.004–0.008	32.3
Northern cod, 8 components‡	–0.001 (NA)	0.013 (< 0.001)	0.009 (0.001)	0.013 (< 0.001)	0.016 (< 0.001)	0.011 (< 0.001)	0.006–0.011	20.2
Scotian Shelf, offshore banks§	0.020 (0.047)	–0.005 (NA)	0.011 (0.183)	0.038 (0.013)	–0.005 (NA)	0.012 (0.026)	0.0045–0.024	14.0
				0.038 (0.005)		0.012 (0.033)	0.0046–0.023	14.1
Scotian Shelf; Fundy–Georges Bank¶	0.018 (0.029)	0.005 (0.265)	–0.000 (NA)	0.180 (< 0.001)	0.020 (0.036)	0.045 (< 0.001)	0.040–0.055	4.2
				0.161 (< 0.001)		0.041 (< 0.001)	0.036–0.051	4.6
NW Atlantic, 14 populations	< 0.001 (0.150)	0.017 (< 0.001)	0.008 (0.001)	0.245 (< 0.001)	0.023 (< 0.001)	0.073 (< 0.001)	0.069–0.074	2.9
				0.212 (< 0.001)		0.063 (< 0.001)	0.058–0.064	3.5

CI, 95% confidence intervals, these were obtained as the 2.5th and the 97.5th percentile of the empirical distribution of 1000 bootstrap samples. *Nm*, number of migrants.

*Northern cod, Flemish Cap, South Newfoundland, Scotian Shelf, Georges Bank, Bay of Fundy.

†NORTH, SAND, TRINITY, SOUTH.

‡NORTH, SAND, TRINITY, SOUTH, Placentia North Harbour, Placentia St. Brides, Placentia Feb-Apr. 1995, Scatarie Bank. The Scatarie sample was included in this comparison because analysis based on D_A and D_{SW} suggested that these cod were indistinguishable from some of the samples from NE Newfoundland.

§Banquereau, Western, and Browns Banks.

¶Banquereau, Western, Browns, and Georges Bank and Bay of Fundy.

**The columns Gmo132, Over all loci, CI, and *Nm* contain two estimates for tests involving cod south of the Laurentian channel; the second estimate was obtained after subtracting flanking sequences, which for Gmo132 differed depending on whether alleles were longer or shorter than 128 bp. Alleles longer than 128 bp only occurred south of the Laurentian Channel (see the Results).

Table 3 Estimates of genetic distance: D_A (Nei *et al*. 1983), above the diagonal, and D_{SW} (Shriver *et al*. 1995), below the diagonal between Atlantic cod (*Gadus morhua*) aggregations from 14 locations in the NW Atlantic. For D_{SW} values within parentheses in columns containing two numbers refer to estimates corrected for indel mutation in one of the flanking regions of locus Gmo132 (i.e. after subtraction of flanking region of Gmo132). Columns containing a single value reflect comparisons where there was no change with or without subtraction of the flanking region of Gmo132. Significance values were estimated using the sequential Bonferroni approach for multiple tests (Rice 1989) with initial number of simultaneous tests $K = 91$. A total of 10 000 bootstrap simulations were performed for each distance measure

Population	NORTH	SAND	SOUTH	TRINITY	Placentia North Harbour	Placentia St Brides	Placentia Feb-Apr 1995	Flemish Cap	Scatarie Bank	Banquereau Bank	Western Bank	Browns Bank	Georges Bank	Bay of Fundy
NORTH	–	0.052	0.037	0.036	**0.109**	0.092	0.080	**0.100**	0.078	0.079	0.098*	**0.110**	**0.141**	**0.159**
SAND	**0.054**	–	0.044	0.047	0.101	0.107*	0.094	0.094	0.083	0.091	0.110*	**0.120**	**0.152**	**0.168**
SOUTH	**0.048**	0.037*	–	0.032*	**0.108**	**0.097**	0.079	**0.097**	0.072	0.080	**0.102**	**0.101**	**0.135**	**0.152**
TRINITY	**0.032**	–0.002	0.016*	–	**0.104**	0.088*	0.080	**0.096**	0.062	0.078	**0.099**	**0.103**	**0.134**	**0.147**
Placentia North Harbour	**0.176**	**0.143**	**0.255**	**0.172**	–	0.145*	0.147*	0.140	0.139*	**0.145**	**0.164**	**0.187**	**0.204**	**0.226**
Placentia St Brides	0.068*	**0.185**	**0.165**	**0.155**	0.130*	–	0.128	0.124	0.141*	0.140*	0.138*	**0.159**	**0.183**	**0.211**
Placentia Feb-Apr. 1995	0.019	–0.011 (–0.007)	–0.008 (–0.001)	–0.016	**0.160**	0.116*	–	0.140*	0.115	0.109	0.129	**0.139**	**0.179**	**0.167**
Flemish Cap	**0.100**	**0.120**	**0.184**	**0.125**	**0.186**	**0.145**	0.113*	–	**0.149**	0.130*	0.133*	**0.168**	**0.185**	**0.202**
Scatarie Bank	0.016	<< 0.001	0.041	– 0.003	**0.096**	**0.140**	– 0.012	**0.145 (0.144)**	–	0.112	0.120	0.118	**0.150**	**0.161**
Banquereau Bank	**0.099 (0.093)**	**0.102 (0.096)**	0.043 (0.037)	**0.072 (0.066)**	**0.352 (0.346)**	**0.270 (0.264)**	0.047 (0.041)	**0.184 (0.178)**	0.094* (0.091)	–	0.115	0.129	0.141*	**0.149**
Western Bank	**0.091 (0.071)**	**0.153 (0.133)**	**0.097 (0.077)**	**0.118 (0.098)**	**0.339 (0.319)**	**0.229 (0.209)**	0.088 (0.068)	**0.191 (0.170)**	0.103* (0.089)	0.004 (0.001)	–	0.097	0.124	0.118
Browns Bank	**0.135 (0.096)**	**0.212 (0.173)**	**0.151 (0.111)**	**0.172 (0.134)**	**0.405 (0.365)**	**0.238 (0.198)**	**0.152 (0.112)**	**0.286 (0.247)**	**0.148 (0.118)**	0.094* (0.081)	0.007 (0.006)	–	0.118	0.136*
Georges Bank	**0.566 (0.391)**	**0.610 (0.435)**	**0.582 (0.408)**	**0.583 (0.411)**	**0.770 (0.595)**	**0.746 (0.571)**	**0.573 (0.398)**	**0.744 (0.569)**	**0.484 (0.329)**	**0.457 (0.344)**	**0.269 (0.169)**	**0.139 (0.095)**	–	0.116
Bay of Fundy	**0.678 (0.444)**	**0.745 (0.511)**	**0.629 (0.395)**	**0.688 (0.456)**	**1.028 (0.793)**	**0.892 (0.656)**	**0.660 (0.426)**	**0.879 (0.646)**	**0.624 (0.414)**	**0.426 (0.262)**	**0.263 (0.150)**	**0.175 (0.101)**	0.036 (0.039)	–

Bold text: $P < 0.05 / K = 0.0005$ (max $K = 91$).
*$P \leq 0.0020$.

Stepwise mutational model (SMM). The degree of population subdivision inferred from employing SMM-derived measures relies on the assumption that changes in allele length result from stepwise mutations within the repetitive array (see Slatkin 1995). However, length variation in the Gmo132 microsatellite is also a function of a mutation involving the indel of a 6-bp sequence in one of the flanking regions (D. Cook, unpublished). The frequency distribution of alleles at this locus is markedly bimodal in cod populations south of the Laurentian Channel where all alleles > 128 bp primarily result from changes in the flanking sequence but differ from each other in the length of the repetitive array. These large alleles increase in frequency with decreasing latitude south of the Laurentian Channel and are found at maximum frequency (≈ 55%) in Georges Bank cod. Estimates of genetic distances that do not correct for the difference in the length of the flanking sequence may be inflated, particularly among populations where these alleles occur frequently. Conversely, correcting for the difference in the length of the flanking sequence brings alleles from the two modes of the distribution closer together than would be expected given their different origins. Thus, estimates of structure and distances after correction for differences in the length of the flanking region are probably underestimates. We therefore conducted our analyses of SMM-related measures by first ignoring the differences in length of the flanking region of Gmo132, and then by subtracting the length of the flanking region for this locus. The true estimates of population subdivision using SMM-derived measures should logically lie somewhere in between the two estimates.

R_{ST}. Hierarchical analysis of R_{ST} also provided evidence of population structure at several scales. At the shelf-scale, cod north of the Laurentian Channel (N = 1015) were genetically distinguishable from cod south of the Laurentian Channel (N = 288; R_{ST} = 0.091, $P < 0.001$, 95% CI: 0.090–0.094; Table 2b, line 1) and this level of structure was largely dependent on differences in the Gmo132 allele frequencies and to a lesser degree in Gmo145. However, unlike the F_{ST} results above, this level of genetic differentiation was 20–30% higher than that exhibited among all 14 populations considered separately (Table 2b, lines 1 and 7). Furthermore, structure was apparent in four of the five microsatellite loci. There was again evidence of population structure within the northern cod complex, whether cod from southern Newfoundland and the Scatarie areas were included or not (Table 2, lines 3 and 4) and this structure was due primarily to differences in allele frequencies at Gmo145, Gmo120, and Gmo4, and to Gmo132 when the latter samples were included (Table 2b). However, regardless of the number of components, the R_{ST} estimates for northern cod were much lower than in the shelf-scale comparison involving the 14 populations north and south of the Laurentian Channel. There was also evidence of bank-scale population subdivision among the samples collected on the Scotian Shelf (R_{ST} = 0.012, $P \leq 0.033$, 95% CI: 0.0045–0.024; Table 2b, line 5) and the degree of population subdivision increased nearly fourfold when cod from the Bay of Fundy and Georges Bank were included in the analysis ($0.041 \leq R_{ST} \leq 0.045$, $P < 0.001$, 95% CI: 0.036–0.055; Table 2b, line 6). These differences were due mainly to variation in the Gmo132, Gmo145, and Gmo2 loci.

The results of the repeated analyses after correcting for the indel mutation in the Gmo132 locus (see above) are displayed in the columns labelled 'Gmo132', 'Over all loci', and '*Nm*', in Table 2b. In all cases the reduction in the magnitude of population subdivision was minimal or nil and there was no major change in the statistical significance for any of the R_{ST} estimates, or in the number of migrants per generation (Table 2b).

Genetic distance measures

D_A *and* D_{SW}. The two measures of genetic distance, D_A and D_{SW}, were highly correlated (Table 3) before and after the estimates for D_{SW} were corrected for the mutation in the flanking region of Gmo132 (r = 0.826 and r = 0.804, respectively; n = 91). We first describe the similarities between the two measures and then focus on their differences. Inspection of Table 3 reveals five important features of cod population structure in the NW Atlantic:

(i) Cod from Georges Bank and the Bay of Fundy are genetically distinct from all other populations with both measures of genetic distance and they appear marginally distinct from each other (D_{SW} = 0.036, 95% CI: 0.008–0.101; D_A = 0.116, 95% CI: 0.036–0.244 ($P \leq 0.10$, uncorrected, Table 3).

(ii) Cod from three known spawning banks on the Scotian Shelf (Banquereau, Western, and Browns) are largely genetically distinct from components of the northern cod complex (Table 3). Most of the nonsignificant comparisons involve cod from Banquereau Bank, i.e. the Scotian Shelf bank nearest to the Grand Banks and the NE Newfoundland Shelf (Fig. 1). The genetic differences between Scotian Shelf cod and northern cod increase with geographical distance (Table 3).

(iii) Cod from the Flemish Cap are genetically distinguishable from most other cod samples within the northern cod stock complex as well as from all populations collected elsewhere (Table 3).

(iv) Cod collected in inner Placentia Bay at North Harbour and Saint Brides are genetically distinguishable from most other populations as well as from each other (Table 3).

(v) Cod collected in Placentia Bay between February and April 1995 (Table 3, column and line 7) and cod collected on

the opposite side of the Laurentian Channel on Scatarie Bank in July 1994 (Table 3, column and line 9), are genetically indistinguishable from most other samples within the northern cod stock complex as well as from each other.

Inspection of Fig. 2a,b reveals a number of important differences in the average linkage (UPGMA) phenograms for D_A and D_{SW}. For example, a highly supported group in the D_A tree (SAND, NORTH, SOUTH, TRINITY; bootstrap = 96%) falls apart (bootstrap = 22%), and includes other populations in the other tree. Similarly, the differences between the Georges Bank/Bay of Fundy samples and the other samples is supported at 70% in the D_{SW} tree, but only at 42% in the D_A tree (Fig. 2). Most other differences between the trees involve nodes with low bootstrap values. For example, where D_{SW} shows Banquereau, Western, and Browns Banks on the Scotian Shelf grouped together and separate from the nearest cluster of northern cod components (Fig. 2b), D_A shows Banquereau Bank cod more closely associated with neighbouring Scatarie Bank cod and with components of northern cod than with Western and Browns Bank cod (Fig. 2a) (see the Discussion). Thus, the difference in tree topologies is due primarily (although not exclusively) to the relatively large variance of the two measures of genetic distance together with the fact that the magnitude of the genetic differences among most of these populations is small.

Multidimensional scaling analysis (MDSA)

A MDSA applied to the D_{SW} genetic distance matrix revealed a pattern of differences among populations (Fig. 3) that is largely consistent with the tree topologies above. A scattergram of the relation between dimension 1 (explaining 47% of the variance) and dimension 2 (29% of variance) reveals that cod from Georges Bank and from the Bay of Fundy are distinct from each other and from all other populations (Fig. 3a). The samples from the North Harbour region of Placentia Bay are also somewhat distinct from the rest, although not to the same extent as those from Georges Bank and the Bay of Fundy. The scattergram also indicates a clinal structure in dimension 1 along the Scotian Shelf from Browns Bank through to Western and Banquereau Banks (Fig. 3a). The scattergram of dimension 1 in relation to dimension 3 (10% of variance; Fig. 3b) indicates that cod in the Saint Brides region of Placentia Bay differ from all other populations along dimension 3, while dimension 1 in relation to dimension 4 (5% of variance; Fig. 3c) indicates that Flemish Cap cod and the SOUTH component of northern cod differ from each other as well as from all others along dimension 4. Some added information from the scattergram of dimension 2 vs. dimension 3 (Fig. 3d) indicates that there are differences among the four pooled samples representing northern cod (NORTH, SAND, TRINITY, and SOUTH). Finally, the relationship between dimension 1 of the MDSA and geographical distance from the north reveals a complex pattern of genetic differences among these samples: Georges Bank and the Bay of Fundy at one extreme showing the largest differences from other samples; a pattern of isolation by

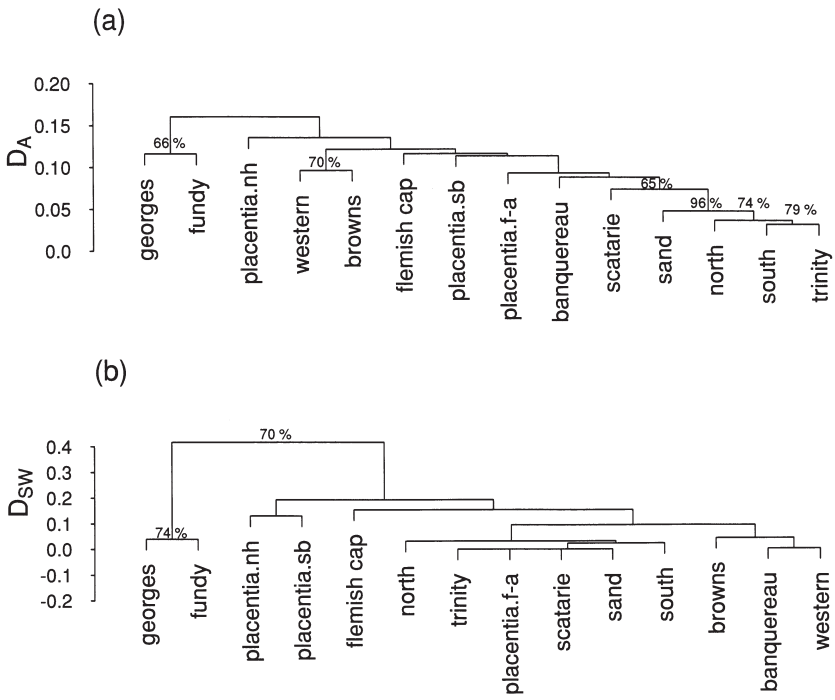

Fig. 2 UPGMA phenogram depicting genetic distance relationships among 14 Atlantic cod populations. (a) D_A (Nei *et al*. 1983) distance; and (b) D_{SW} distance (Shriver *et al*. 1995). Phenograms were constructed using standard SPLUS (Mathsoft Inc. 1996) code ('hclust' with method 'average'). Values on the nodes represent the percentage of bootstrap (over loci) samples ($N = 100$) showing the particular nodes, only those with values > 50% are reported (Majority rule). Terminal branches are all of an arbitrary and equal length; information is contained in the height of the nodes with respect to zero.

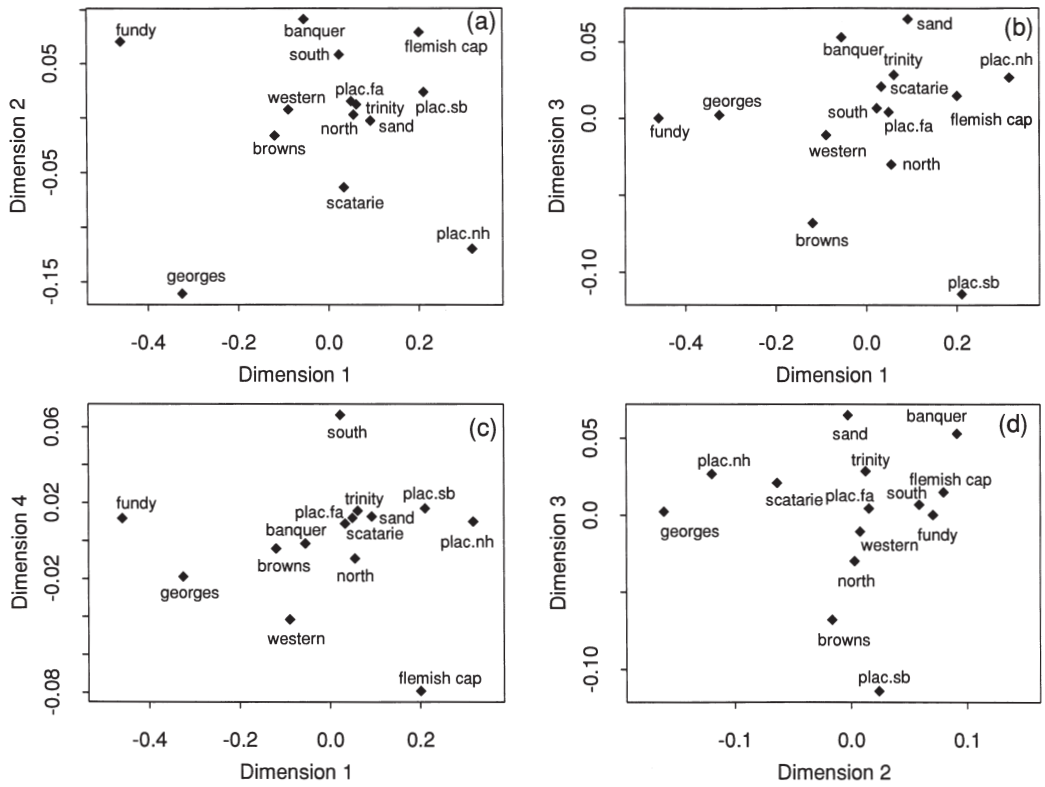

Fig. 3 Scattergram of a multidimensional scaling analysis applied to the D_{SW} matrix of genetic distances among all 14 Atlantic cod populations. (a) Dimension 1 vs. dimension 2; (b) dimension 1 vs. dimension 3; (c) dimension 1 vs. dimension 4; and (d) dimension 2 vs. dimension 3. See text for explanation.

distance among the Scotian Shelf samples of Browns, Western, Banquereau and Scatarie Banks; a complex mosaic of relatively minor differences in this dimension among the northern cod samples; and finally Flemish Cap cod lying at the opposite extreme to Georges Bank (Fig. 4). MDSA based on the D_A distance matrix revealed a pattern largely consistent with the preceding analysis (not shown).

Discussion

Polymorphism at five microsatellite loci provides clear evidence of genetic structure among cod populations in the NW Atlantic over a 3000-km range from Hamilton Bank in the north to Georges Bank in the south. We detected differences among cod populations at continental shelf scales involving the NE Newfoundland Shelf,

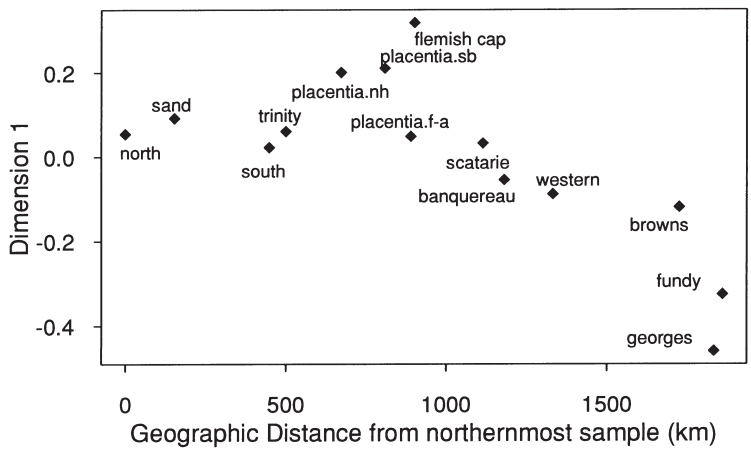

Fig. 4 Scatterplot of dimension 1 of multidimensional scaling analysis (ordinate) vs. geographical distance from the northernmost sampling location (abscissa). See text for explanation.

the Grand Banks, the Flemish Cap, the Scotian Shelf, and Georges Bank; each separated from the next by a series of submarine saddles, channels or trenches. We also found evidence of genetic structure in cod populations at spawning bank scales that can be characterized by distinct oceanographic features. These results suggest that oceanographic features and the known spatiotemporal variation in spawning may represent sufficient barriers to gene flow among otherwise geographically contiguous cod populations inhabiting a highly advective environment in the NW Atlantic.

The largest degree of gene flow, as determined under the infinite island model using F_{ST} and R_{ST} estimates, was detected among the four pools of samples of northern cod on the NE Newfoundland Shelf, where the number of migrants among components was estimated to be between 32 and 250 individuals depending on the method of estimation (Table 2). We stress that such high levels of migration from an evolutionary point of view (sufficient to prevent genetic differentiation of local populations; see Slatkin 1985, 1987; Lande & Barrowclough 1987; Mills & Allendorf 1996) are probably low in the context of cod population sizes and cod population dynamics at shorter timescales. This is because they are unlikely to prevent the different local populations from experiencing their own more or less independent recruitment dynamics and there is little evidence of recruitment synchrony in cod populations at distances > 500 km (Myers *et al*. 1995). We also stress, however, that any interpretation of gene-flow estimates derived from F_{ST} and R_{ST} assumes that the populations are in equilibrium, probably an invalid assumption given the extreme fluctuations in population sizes that have occurred under intense exploitation over the last four decades. Thus, it is essential to assess the results in comparison to other known biological aspects of the populations and their associated oceanographic features. We discuss three examples, northern cod, Flemish Cap cod, and cod from Georges and Browns Banks and the Bay of Fundy.

NE Newfoundland Shelf, northern Grand Bank and offshore–inshore northern cod

Cod collected in the northern range of northern cod (NORTH) were genetically distinct from cod collected in the southern range (SOUTH), and both of these groups were genetically distinguishable from inshore overwintering cod from the Trinity Bay area. Are these results consistent with known biological aspects of the species in this area and with associated oceanographic features?

Following offshore spawning in the late Winter, adult northern cod have historically been known to migrate inshore to the summer feeding grounds of coastal Newfoundland and to return offshore in late autumn, early winter (review in Taggart *et al*. 1994). Tagging studies provide clear evidence of spawning fidelity at offshore bank scales (Templeman 1979; Lear 1984; Taggart *et al*. 1995; Taggart 1997), as well as at inshore bay scales (Taggart *et al*. 1995; Wroblewski *et al*. 1996), which is remarkably similar to that observed in Gulf of Maine cod (Perkins *et al*. 1997). This kind of evidence, together with that based on the bank-scale spatial and temporal differences in spawning (Hutchings *et al*. 1993; Myers *et al*. 1993) and on variation in vertebral counts (Templeman 1981; Lear & Wells 1984), is consistent with the northern cod stock being a complex of distinct spawning components as indicated by the genetic analyses presented here.

The regular occurrence of juvenile and adult northern cod overwintering in coastal regions (Goddard *et al*. 1992, 1994; Wroblewski *et al*. 1994) coupled with evidence of inshore spawning (Wroblewski *et al*. 1996; Smedbol & Wroblewski 1997) suggests that inshore bay-scale population structure is to be expected (see Templeman 1966), as was recently demonstrated and tested for the Trinity Bay region (Ruzzante *et al*. 1996b, 1997). The larger and more diverse collection of samples in this study have provided generally consistent results. However, the TRINITY cod were not distinct from the cod collected in the St Anthony Basin and in the Notre Dame Channel (SAND) in the Summer of 1994. This latter finding may be a function of: (i) postspawning summer intermingling of populations as the SAND samples were collected in June; or (ii) a disruption of normal population dynamics (distribution and/or migration) caused by the recent and extensive collapse of northern cod (Hutchings 1996; Taggart 1997); or (iii) oceanographic processes that might be consistent with a north–south coastal delineation of genetically distinct inshore cod hypothesized decades ago by Templeman & Fleming (1953; reproduced in Fig. 11 in Halliday & Pinhorn 1990) and Templeman (1962).

Our genetic results that describe the NORTH pool of samples as a genetically distinguishable group are not entirely consistent with existing models of drift and retention patterns in the northern range of northern cod, which indicate that spawning products could be dispersed southward onto the northern portion of the Grand Bank (Davidson & deYoung 1995; Pepin & Helbig 1997). The conclusions of these modelling studies are difficult to reconcile with: (i) the empirically derived spatially and temporally disjoint spawning distribution of cod in this region (Hutchings *et al*. 1993; Myers *et al*. 1993); (ii) the clear evidence of bank-scale spawning fidelity in migratory northern cod; and (iii) the clearly disjoint offshore distribution of NE Newfoundland Shelf cod and northern Grand Bank cod during the winter spawning period (Taggart 1997).

Two-dimensional surface current models probably inadequately capture eddy-scale water mass dynamics relevant to egg and larval cod persistence and/or retention

in these regions. In addition, neither of the modelling studies included the potential influence of egg buoyancy or larval behaviour on their vertical distribution dynamics in a flow-structured water column, either of which can influence downstream transport variations (Anderson & deYoung 1994, 1995) and local retention (e.g. Sclafani *et al*. 1993).

These limitations aside, we note that the circulation modelling results are not entirely inconsistent with the genetic results as the level of genetic differentiation, although significant, is small and the number of effective migrants presumed to occur per generation is considerable (Table 2).

Flemish Cap

Bathymetry and oceanographic features as well as differences in spawning time may also be associated with the marked genetic distinctiveness of cod on the Flemish Cap. Cod in this region differ from cod elsewhere on the basis of allozyme loci (Cross & Payne 1978), the cytochrome *b* gene of mitochondrial DNA (Crutcher & Carr 1997), and microsatellite DNA (Bentzen *et al*. 1996; this study). The Flemish Cap is isolated from the NE Newfoundland Shelf and the Grand Bank by the Flemish Pass, a deep submarine trench (Fig. 1). The dispersal of eggs and larvae from the Flemish Cap is probably limited (see Templeman 1976; Kudlo *et al*. 1984) by anticyclonic gyral circulations frequently observed during summer (e.g. Colbourne 1993; Sheng & Thompson 1996 and references therein) and winter (Akenhead 1986; but see Hayes *et al*. 1977). Tagging studies (Taggart *et al*. 1995) indicate that for migratory adult cod the Flemish Cap is virtually isolated. Finally, the spawning time for cod on the Flemish Cap is anomalously early relative to all other cod on the NE Newfoundland Shelf and the Grand Banks (Myers *et al*. 1993).

Browns Bank, the Bay of Fundy, and Georges Bank

We have described significant genetic differences among cod from Georges Bank, Browns Bank, and the Bay of Fundy, as well as lower levels of differentiation among cod aggregations on the eastern (Scatarie, Banquereau and Western Banks) and western (Browns Bank) Scotian Shelf. The bathymetry and oceanography of the Scotian Shelf, as well as the spatiotemporal distribution of spawning, are all consistent with cod from the various banks experiencing independent population dynamics. The different banks of the eastern Scotian Shelf are relatively shallow (crests sometimes < 40 m deep) in comparison to the NE Newfoundland shelf and they are associated with cod spawning activity and persistent egg and larval concentrations (Gagné & O'Boyle 1984; O'Boyle *et al*. 1984; Campana *et al*. 1989; Suthers *et al*. 1989; Frank *et al*. 1994). In particular, high concentrations of cod larvae have been observed on Western Bank (Taggart *et al*. 1996) within well-defined kilometre-scale gyre-like circulation systems (Sanderson 1995). Furthermore, three-dimensional, time-varying shelf circulation models (that also include a real time-varying wind component) for the Scotian Shelf (Cong *et al*. 1996) describe variable but persistent retention areas in the vicinities of Banquereau, Western, and other banks.

Spawning time differs among regions of the Scotian Shelf (Colton *et al*. 1979; Sherman *et al*. 1984; Hurley & Campana 1989) with egg concentrations appearing first on Georges Bank (January–February), then on Browns Bank (March–April), and finally on the banks to the east in April and May and in the autumn on Western Bank (see Brander & Hurley 1992; review in Frank *et al*. 1994).

The largest genetic differentiation among neighbouring cod populations occurs between Georges Bank and Browns Bank. Georges Bank and Browns Bank are bathymetrically separated by a distance of ≈ 80 km by the Fundian Channel and each is characterized by distinct and relatively persistent gyre-like circulations. Juvenile and adult cod migration as well as mixing of spawning products between these banks are thought to be low or negligible (Campana *et al*. 1989; Suthers & Frank 1989), but not absolutely so (Townsend & Pettigrew 1996). The evidence thus suggests that retention mechanisms resulting from topographically induced eddies act to minimize the dispersal of ichthyoplankton among these banks (Loder *et al*. 1988; Smith 1989a,b; for Browns Bank; Hopkins & Garfield 1981; Smith & Morse 1985; Loder *et al*. 1988; Werner *et al*. 1993; for Georges Bank; Iles & Sinclair 1982; O'Boyle *et al*. 1984; review in Frank *et al*. 1994), and/or to allow for sufficient imprinting necessary for subsequent spawning on natal banks.

To summarize, the geographically and temporally disjoint distribution of spawning, variation in vertebral count (McKenzie & Smith 1955), tag recovery data (McKenzie 1956), and the general bathymetry and oceanography of the region south of the Laurentian Channel all suggest the existence of at least three different populations: one on Georges Bank, one on the western Scotian Shelf (Browns Bank and the Bay of Fundy), and one on the eastern Scotian Shelf (Frank *et al*. 1994). Our data suggest the existence of further genetic differences between cod on Browns Bank and the Bay of Fundy and also between Banquereau and Western Bank cod, although the temporal stability of these genetic differences (see Ruzzante *et al*. 1996a) should be tested.

NW Atlantic cod stock structure and management implications

Determining whether the extent of gene flow among stock components in a marine fishery is sufficiently high

to warrant management of a stock complex as a panmictic unit, or low enough to warrant the separate management of the components, is essential for an appropriate analysis of population and recruitment dynamics. For natural populations under exploitation, incorrect assumptions regarding genetic structure, or exploitation patterns that ignore structure can easily lead to overexploitation and the erosion of genetic resources via the depletion of the constituent spawning components. This problem is exacerbated in exploited marine fish species which are frequently managed under the critical assumption of panmixia. If the assumption is invalid within management units then the stock components most readily exploited are also those most readily eliminated. This is detrimental to the stock because of the direct negative effects on recruitment potential; it is detrimental to the species because it leads to depleted genetic resources (diversity) that provide resilience; and it is inconsistent with the principles of resource conservation.

At continental shelf scales our results are consistent with contemporary stock structure management, but they also suggest the existence of significant genetic differences among populations within current management units at bank and bay scales. Such evidence suggests that oceanographic features (e.g. gyre-like eddies) and known spatiotemporal differences in spawning time may act as barriers to gene flow between and among neighbouring cod aggregations in the NW Atlantic. For northern cod and neighbouring regions a conservative approximation suggests that the most appropriate stock structure is one comprising: (i) a nonmigratory Flemish Cap component; (ii) a cross-shelf migrant component with spawning (winter) fidelity to the various banks on the NE Newfoundland Shelf; (iii) a cross-shelf migrant component with spawning (winter) fidelity to the northern Grand Bank region; and (iv) an along-shelf migrant component that has inshore or nearshore winter and spawning fidelity along coastal Newfoundland. This latter group may exhibit structure at the scale of neighbouring bays, although such structure may be ephemeral.

For the southern coast of Newfoundland, a conservative approximation suggests inner-bay resident populations (at least Placentia Bay) that seasonally intermingle with offshore migrants from St Pierre and Burgeo Banks and elsewhere from the west and the northeast. For the Scotian Shelf, our results suggest genetic differentiation among cod on Western Bank and Banquereau Bank although these regions are managed as a single component on the eastern Scotian Shelf. The genetic differentiation in our offshore samples for the Scotian Shelf was minor. However, these samples were collected in June (1994), when the cod would be in a more disaggregated and postspawning state. Thus, these relatively minor genetic differences may be amplified if measured using spawning individuals from the two regions. Although Bay of Fundy and Browns Bank cod on the western Scotian Shelf are managed as a single unit our results show that these two regions may have genetically distinct populations. Finally, Georges Bank cod appear to be the most distinct of all populations that we have examined thus far and, although they are considered a unit stock, they are exploited by both Canada and the US who have no formal cooperative management scheme.

We have shown that there are significant differences in genetic composition among cod populations in the NW Atlantic. The genetic composition of populations vary with latitudinal separation at continental shelf and bank scales. Such differences are also consistent with postdispersal spawning fidelity to natal areas (i.e. homing), a behaviour that may be facilitated by topographically (bank) induced gyre-like circulations (eddies) that have been shown to act as retention mechanisms for eggs, larvae, and juveniles. The extent of gene flow among cod stock components is sufficiently low to warrant separate management schemes more or less as currently practised at the largest scales. We suggest that the substructure apparent at smaller spatial scales may be most easily explained by the associated oceanographic features and processes that conceivably form the template for the evolution of the structure. Thus, we further suggest that bathymetric and hydrodynamic structure represents a rational starting point for constructing hypotheses designed to examine genetic structuring of marine fish species. From a pragmatic perspective, the same oceanographic structures could equally serve as a template for conserving genetic resources and population diversity. Dismissal of genetic structure in any marine species along the lines that we have defined, particularly in highly mixed-population fisheries, is prone to risk and may lead to the differential depletion of stock components with negative consequences for the stock and the species as a whole.

Acknowledgements

For assistance in securing cod tissue samples we thank the Captains and crews of the vessels Wilfred Templeman, Gadus Atlantica, Alfred Needler, Shamook and Lady Kenda, and the support staff and Observers in the Canada Department of Fisheries and Oceans (DFO) at the Northwest Atlantic Fisheries Centre, the St Andrews Biological Station, and the Bedford Institute of Oceanography. We thank E. Árnason, S. Carr, P. Bentzen, and G. Pogson for useful discussions. We are particularly grateful to P. Avendano, W. Bailey, W. Edison, C. George, J. Hunt, G. Rose, and J. Wroblewski for assistance in sample collections, and J. Berthier, L. Bussey, S. Lang, J. McPhail, S. Neale, A. Pickle, P. Simard, and K. Spence for help in the laboratory. Funding to C.T.T. for this research was provided by the Ocean Production Enhancement Network (OPEN) through the Interim Funding Research Program (IFRP) which was supported by the

Government of Canada and by the Canada/Newfoundland and Canada/Nova Scotia COOPERATION agreements, by the DFO northern Cod Science Program and by The Canadian Centre for Fisheries Innovation.

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The work presented in this study is part of a research programme to describe the genetic structure of cod in the NW Atlantic. The research was conducted in the Marine Gene Probe Laboratory and the Departments of Oceanography and Biology at Dalhousie University. Daniel Ruzzante is an Adjunct Professor in the Deptartment of Biology; his interests are in the area of evolutionary and population genetics of fish. Christopher Taggart is Associate Professor in the Department of Oceanography and his interests are in the area of fisheries oceanography and physical–biological interactions in fish and zooplankton. Doug Cook is the Manager of the Marine Gene Probe Laboratory and his interests are in the area of molecular evolution.
