Abstract—This study examines genetic variation at five microsatellite loci and at the vesicle membrane protein locus, pantophysin, of Atlantic cod (*Gadus morhua*) from Browns Bank, Georges Bank, and Nantucket Shoals. The Nantucket Shoals sample represents the first time cod south of Georges Bank have been genetically evaluated. Heterogeneity of allelic distribution was not observed ($P>0.05$) between two temporally separated Georges Bank samples indicating potential genetic stability of Georges Bank cod. When Bonferroni corrections ($\alpha=0.05$, $P<0.017$) were applied to pairwise measures of population differentiation and estimates of F_{ST}, significance was observed between Nantucket Shoals and Georges Bank cod and also between Nantucket Shoals and Browns Bank cod. However, neither significant differentiation nor significant estimates of F_{ST} were observed between Georges Bank and the Browns Bank cod. Our research suggests that the cod spawning on Nantucket Shoals are genetically differentiated from cod spawning on Browns Bank and Georges Bank. Managers may wish to consider Nantucket Shoals cod a separate stock for assessment and management purposes in the future.

Manuscript approved for publication 5 November 2003 by Scientific Editor.

Manuscript received 20 January 2004 at NMFS Scientific Publications Office.

Fish. Bull. 102:289–297 (2004).

Genetic differentiation among Atlantic cod (*Gadus morhua*) from Browns Bank, Georges Bank, and Nantucket Shoals

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The Atlantic cod (*Gadus morhua*) is a migratory gadid found on both sides of the North Atlantic. In the Northwest Atlantic, cod are distributed nearly continuously along the continental shelf from Greenland to North Carolina, spawning in relatively discrete, temporally stable areas, and different regions are regarded as different management units defined primarily by latitude and bathymetry (Ruzzante et al., 1998). Atlantic cod historically supported economically important fisheries in the Northwest Atlantic (Halliday and Pinhorn, 1996). In U.S. waters, cod are assessed and managed as two stocks: 1) Gulf of Maine and 2) Georges Bank and southward (including Nantucket Shoals). Growth rates differ between the two stocks; growth is slower in the Gulf of Maine compared to growth in Georges Bank (Pentilla et al., 1989); each stock is exploited by the same gear type and may show similar biological responses towards such gear selection. Although both stocks support important commercial and recreational fisheries, each is overexploited and remains at a low biomass level (Mayo and O'Brien, 1998; O'Brien and Munroe, 2001; Mayo et al., 2002). Overexploitation may result in significant life-history changes such as a decline in time to reproductive maturity which has been observed in Georges Bank cod (O'Brien, 1998); such changes may be a compensatory response to overfishing but may also be influenced by shifts in underlying genetic control (Policansky, 1993).

Commercial fisheries are conducted year round, using primarily otter trawls and gill nets. The Canadian fishery on Georges Bank is managed under an individual quota system. United States cod fisheries are managed under the New England Fishery Management Council's Northeast Multispecies Fishery Management Plan (FMP)[1] as implemented by the U.S. Federal Register, 50 CFR Part 648 (U.S. Federal Register, 2003). Under this FMP, cod are included in a complex of 15 groundfish species managed by time and area closures, trip limits, gear restrictions, minimum size limits, days-at-sea restrictions, and a permit moratorium. The FMP's goal is to reduce fishing mortality to levels that will allow stocks within the complex to initially rebuild above minimum biomass thresholds, and, ultimately, to remain at or near target levels.

When ecological and evolutionary processes are responsible for stock structuring, it is necessary to incorpo-

[1] New England Fishery Management Council. 2003. Northeast Multispecies Fishery Management Plan. NEFMC, 50 Water St., Mill 2, Newburyport, MA, 01950

rate them into strategies designed to manage exploited species (Avise, 1998). High dispersive capabilities of many marine fish often correlate with low levels of population divergence over vast areas (Ward et al., 1994; Graves, 1998) and may be particularly true for species characterized by high fecundity, large population size, and potentially long-distance egg and larval dispersal. Although marine fish predominantly have high dispersal rates and low levels of population structuring, migratory species with continuous distributions may develop and maintain stock structure if they show fidelity to natal spawning sites or limited egg and larval dispersal. Fidelity to natal grounds has been shown in Greenland-Iceland cod (Frank, 1992) and Georges Bank haddock (Polacheck et al., 1992). Genetic divergence between areas originates when populations are formed or through the restriction of gene flow. Cod in some regions are known to migrate long distances, whereas in other regions they are nearly stationary (Lear and Green, 1984). Tagging studies in the Gulf of Maine show little exchange between the region east of Browns Bank and Georges Bank, and the inner Gulf of Maine (Hunt et al., 1999); however exchange has been reported among Bay of Fundy, southern Nova Scotia, Browns Bank, and Georges Bank populations (Klein-MacPhee, 2002). Such exchange among cod from different management areas may be important for stock assessments and management practices. Determining underlying genetic structure of spawning stocks is paramount to the conservation and management of overexploited species.

In the last 30 years the use of molecular-based studies in fisheries science has become common (Shaklee and Bentzen, 1998). In cod, a number of studies have used allozymes (Moller, 1968; Jamieson, 1975; Cross and Payne, 1978; Dahle and Jorstad, 1993), but their use and sensitivity are limited because of weak statistical power resulting from low levels of polymorphism and because of processes of balancing selection (Mork et al., 1985; Pogson et al., 1995). Mitochondrial DNA (mtDNA) characterization among Northwest Atlantic cod indicates that there is limited, albeit significant, population structuring throughout most the species' range (Smith et al., 1989; Carr and Marshall, 1991; Pepin and Carr, 1993; Carr et al., 1995; Arnason and Palsson, 1996). Genetic divergence at the vesicle membrane protein locus, pantophysin (*Pan*I), originally called *GM*798 and identified as synaptophysin (*Syp*I) (Fevolden and Pogson, 1997), has been reported among populations of cod from the Northwest Atlantic (Pogson, 2001; Pogson et al., 2001), Norway and the Arctic (Fevolden and Pogson, 1997), and Iceland (Jonsdottir et al., 1999, 2002). High levels of variation have been reported at nuclear RFLP loci (Pogson et al., 1995; Pogson et al., 2001), and especially at microsatellite loci (Bentzen et al., 1996; Ruzzante et al., 1996a, 1996b, 1997, 1998; Beacham et al., 1999; Miller et al., 2000; Ruzzante et al., 2000, 2001). By using microsatellites, significant genetic structuring has been detected among cod populations on major continental shelves and on neighboring banks that are separated by deep channels and have gyre-like circulation patterns hypothesized to act as retention mechanisms for eggs and larvae (Ruzzante et al., 1998). Although both Browns and Georges Bank maintain persistent gyre-like circulation patterns that may act to retain eggs and larvae, they are separated by the Fundian Channel (>260 m) which may pose a barrier to juvenile and adult migration (Klein-MacPhee, 2002). Evaluation of Northwest Atlantic haddock by using microsatellites showed similarly significant stock structuring from Newfoundland to Nantucket Shoals (Lage et al., 2001). Current assessment and management of cod in U.S. waters combine Georges Bank with the regions to its south including Nantucket Shoals. This study investigates genetic stock structure among cod from this region and provides additional insight for scientists and managers.

Materials and methods

Sampling

Samples of adult cod were collected through the U.S. National Marine Fisheries Service and the Canadian Department of Fisheries and Oceans groundfish surveys between 1994 and 2000. Adult cod were obtained from each of the following spawning grounds (Fig. 1): Browns Bank (July 1994, n=30), Georges Bank (March 1994, n=48; March 1999, n=96; Σn=144), and Nantucket Shoals (March 2000, n=97). Blood or tissue (or both) was obtained from individual fish and preserved in 95% ethanol for subsequent DNA extraction.

DNA extraction, amplification, and visualization

DNA was extracted by using either a Qiamp DNA Mini Kit (Qiagen Inc., Valencia, CA) or by following a published protocol designed for nucleated blood cells (Ruzzante et al., 1998). Five microsatellite loci—*Gmo*1, *Gmo*132 (Brooker et al., 1994), *Gmo*8, *Gmo*19, *Gmo*34 (Miller et al., 2000), and the pantophysin locus, *Pan*I (Fevolden and Pogson, 1997; Pogson, 2001)—were used to evaluate genetic diversity. Polymerase chain reactions (PCR) of all loci were performed in an Eppendorf Mastercycler Gradient thermal cycler. Final concentrations of reagents in a 25 μL PCR cocktail were as follows: ~10 ng of genomic DNA, 1×PCR buffer pH 9.5 [10 mM KCl, 20 mM Tris-HCl pH 8.3, 10 mM $(NH_4)_2SO_4$], 1.5 mM $MgCl_2$, 200 μM each dNTP, 0.15 μM forward primer, 0.15 μM reverse primer (unlabeled for the *Pan*I locus and 5′-labeled with a TET, FAM, or HEX ABI dye for all microsatellite loci), and 0.75 units of Taq DNA polymerase. PCR conditions were as follows: initial 5 min at 95°C, 30 cycles of denaturing at 95°C for 1 min, annealing at 50°C (*Gmo*8, *Gmo*19, and *Gmo*34), 55°C (*Pan*I), and 57°C (*Gmo*1 and *Gmo*132) for 1 min 30 s, and extending at 72°C for 1 min 30 s with a final extension of 72°C for 10 min. *Gmo*19 and *Gmo*34, as well as *Gmo*1 and *Gmo*132, were multiplexed in two 25 μL PCR reactions. Flourescent microsatellite PCR products were visualized on an ABI377 automated DNA sequencer (Perkin-Elmer Corporation, Foster City, CA) and were analyzed by using GeneScan (vers. 2.1) and Genotyper (vers. 2.1) software programs (Perkin-Elmer Corporation, Foster City, CA). *Pan*I PCR

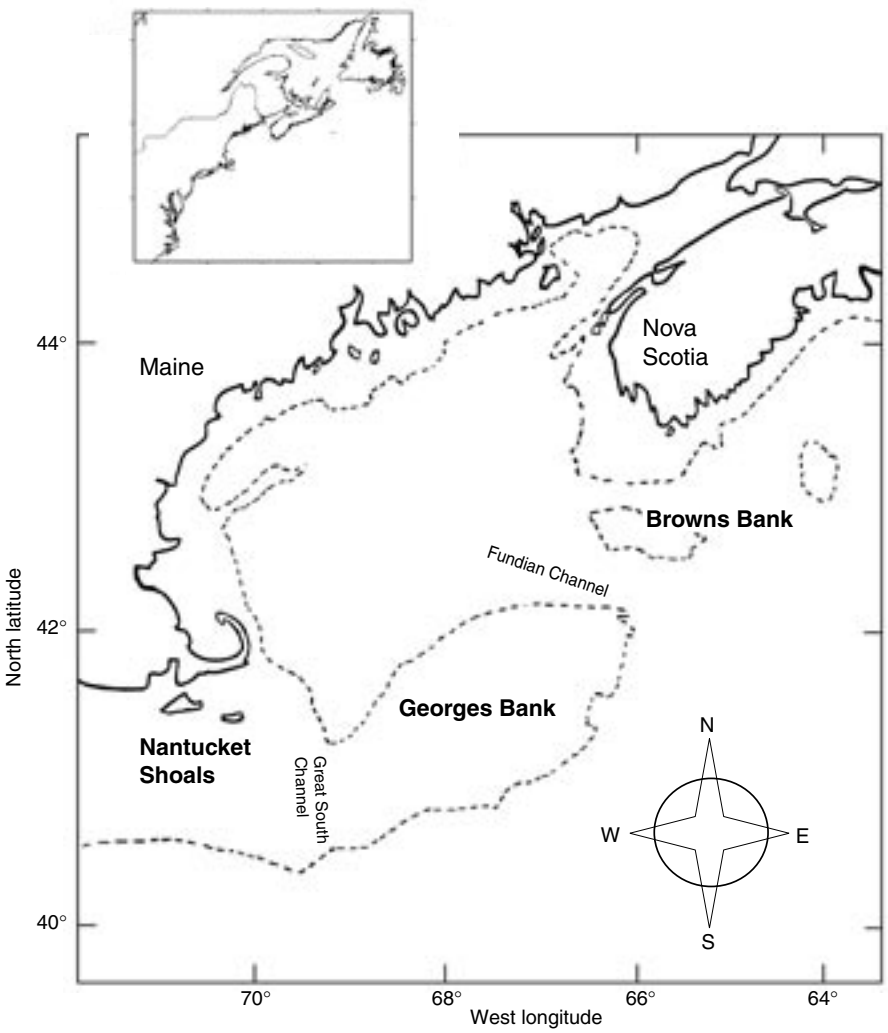

Figure 1

Map of Northwest Atlantic sampling regions for Atlantic cod (*Gadus morhua*). Dashed lines indicate the 100-m isobath.

products were digested with the restriction endonuclease *Dra*I for at least 2 hours at 37°C and visualized on 2% agarose gels to determine presence of *Pan*I^{A} or *Pan*I^{B} (or both) allelic variants.

Genetic analyses

Samples were tested for conformation to Hardy-Weinberg equilibrium (HWE) expectations by the Markov chain method (Guo and Thomson, 1992) by resampling 2000 iterations per batch for 200 batches with GENEPOP vers. 3.1d (CEFE/CNRS, Montpelier, France; available at http://www.cefe.cnrs-mop.fr/) (Raymond and Rousset, 1995); the null hypothesis tested was random union of gametes within a population. All loci were tested for genotypic disequilibrium across the entire data set, as well as for individual populations by using Markov chain resampling with 2000 iterations per batch for 200 batches in GENEPOP vers. 3.1d; the null hypothesis tested was that the genotypes at one locus are independent from genotypes at the other locus.

Tests of allelic and genotypic differentiation among and between population samples were conducted by using FSTAT 2.9.1 (UNIL, Lausanne, Switzerland; available at http://www.unil.ch/izea/softwares/fstat.html) (Goudet, 1995); the null hypothesis tested was homogeneous distributions across samples. Because alleles can be considered as independent when samples conform to HWE, it is valid to permute alleles among samples to test for population differentiation. On the other hand, when HWE is rejected within samples, alleles within an individual cannot be considered independent, and thus permuting genotypes among samples is the only valid permutation scheme. In both cases, contingency tables were generated and classified by using the log-likelihood statistic G (Goudet et al, 1996). Estimates of among- and between-sample F_{ST}'s were generated according to Weir and Cocherham (1984) with FSTAT vers. 2.9.1 and GENETIX vers. 4.04 (available

Table 1

Genetic variation in sampled populations of Atlantic cod (*Gadus morhua*) and *P*-value (in parentheses) for among sample population differentiation. n = observed number of alleles; H_0 = observed heterozygosity; F_{ST} = the among-sample *P*-value); bp = base pairs; * = significant deviation from HWE (α=0.05, P<0.0083); † = P <0.05; ‡ P= ≤0.001

			Browns Bank		Georges Bank		Nantucket Shoals			
Locus	Σn	Allelic range	H_0	n	H_0	n	H_0	n	F_{ST}	Differentiation
*Pan*I	2	*Pan*I^A/*Pan*I^B	0.0385	2	0.0397	2	0.0222	2	–0.0052 (0.767)	0.7820
*Gmo*1	5	96–110 bp	0.1000	4	0.1319	5	0.1505	5	0.0019 (0.307)	0.3210
*Gmo*8	23	118–201 bp	0.8929	17	0.8370	19	0.8444*	20	0.0001 (0.437)	0.5200
*Gmo*19	26	120–237 bp	0.8846	17	0.8148*	25	0.7975*	23	–0.0021 (0.857)	0.8320
*Gmo*34	11	82–120 bp	0.7778	5	0.5683	11	0.6630	7	–0.0033 (0.797)	0.8400
*Gmo*132	21	105–155 bp	0.8333	13	0.8214	17	0.7727	16	0.0255 (0.000)‡	0.0010‡
All loci	88	—	—	—	—	—	—	—	0.0047 (0.001)‡	0.0240†

at http://www.univ-montp2.fr/~genetix/genetix/genetix.htm) (Belkhir et al.[2]). Significance of F_{ST} estimates was determined with 2000 randomizations. Tests of population differentiation and estimations of F_{ST} were calculated at each locus individually and at all loci combined. To correct for simultaneous comparisons, standard Bonferroni corrections were applied by using a global significance level of 0.05 (Rice, 1989).

Results

Genetic variation

Observed numbers of alleles, allelic ranges, heterozygosities, and deviations from HWE are presented in Table 1. All tests of genotypic linkage disequilibrium were nonsignificant at the global and population levels. When Bonferroni corrections for multiple tests were applied to tests of HWE (α=0.05, P<0.0083), the pooled Georges Bank sample deviated significantly at *Gmo*19, and the Nantucket Shoals sample deviated at *Gmo*8 and at *Gmo*19. Interestingly, these two loci have the greatest variation based on number of alleles and heterozygosity. In each case, the cause of deviation was due to an excess of homozygotes. Population samples that generally conform to expectations of random mating but show a lack of concordance to HWE at one or more loci may be due to a number of processes including null alleles, genetic drift, admixture, selection, and insufficient sampling (e.g., Ruzzante, 1998). Possible explanations of homozygote excess include sample admixture (Wahlund effect) or drift; however these explanations are unlikely because one would expect to see similar results at all loci. More likely explanations are the presence of null alleles or selection. Deviations of HWE at *Gmo*8 and *Gmo*19 were not observed in all population samples, indicating that null alleles were not present at a global-level but may be present at the population-level for these two loci. Subsequently, any significant population structuring observed at these loci should be viewed with caution (see below).

Population structure

Tests of population structure are shown in Table 2. Although *Gmo*8 and *Gmo*19 showed significant deviations from HWE, they did not support any significant population structuring even when tests of population differentiation were performed without assuming conformation to HWE (i.e., permuting among genotypes rather than alleles). Heterogeneity of allelic distribution was not observed (P>0.05) between the 1994 and 1999 Georges Bank samples at each locus individually and at all loci combined, thus indicating potential genetic stability of Georges Bank cod. These samples were subsequently pooled to form a single Georges Bank population sample to facilitate statistical analyses by allowing for better estimations of allele frequencies and by reducing the number of pairwise tests. Tests of population differentiation among samples showed significant divergence at *Gmo*132 (P<0.01) and at all loci combined (P<0.05). When Bonferroni corrections were applied to pairwise measures of divergence (α=0.05, P<0.017), significance was observed between Nantucket Shoals and Georges Bank at *Gmo*132 and at all loci combined, and also between Nantucket Shoals and Browns Bank at *Gmo*132. No significant differentiation was observed between individual or pooled Georges Bank samples and the Browns Bank sample.

Significant among-population F_{ST} values were estimated at *Gmo*132 (0.0255, P<0.001) and at all loci combined (0.0047, P<0.01). When Bonferroni corrections were applied, significant pairwise-population F_{ST} values were estimated between Nantucket Shoals and Browns Bank at *Gmo*132 (0.0624, P<0.001) and at all loci combined

[2] Belkhir K., P. Borsa, L. Chikhi, N. Raufaste, and F. Bonhomme. 2002. GENETIX 4.04, logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome, Populations, Interactions, CNRS UMR 5000, Université de Montpellier II, Montpellier (France).

Table 2

Genetic structuring in sampled populations of Atlantic cod (*Gadus morhua*): Above diagonal are *P*-values for pairwise differentiation. Below diagonal are pairwise F_{ST} values; upper values are for all loci combined; lower values are for *Gmo*132. * = P <0.0167 (α=0.05 for three comparisons); ** = P ≤0.001.

	Browns Bank	Georges Bank	Nantucket Shoals
Browns Bank	—	0.5440	0.2970
	—	0.1120	0.0020*
Georges Bank	0.0012	—	0.0030*
	0.0124	—	0.0010**
Nantucket Shoals	0.0114*	0.0045*	—
	0.0624**	0.0226**	—

(0.0114, P<0.017), and between Nantucket Shoals and Georges Bank at *Gmo*132 (0.0226, P<0.001) and at all loci combined (0.0045, P<0.017). Estimates of F_{ST} values between Browns Bank and Georges Bank samples were all nonsignificant. No significant genetic structuring was observed in any comparison when *Gmo*132 was excluded from the analysis.

Discussion

Georges Bank, a large, shallow offshore bank located along the southern edge of the Gulf of Maine off the U.S. and Canadian coasts (Fig. 1), supports a large fish biomass. High primary productivity and tightly bound system energetics on the bank result in relatively stable levels of overall biomass and total fish production, although major shifts in species composition routinely occur (Fogarty and Murawski, 1998). The largest spawning aggregation of cod on Georges Bank is found on the Northeast Peak, a gravel region that is an important habitat for the early demersal phase of cod, and may represent a limiting resource for this stock (Lough and Bolz 1989; Langton et al., 1996). The bank maintains its own circulation pattern in a slow clockwise gyre which may act as a transportation and retention mechanism for planktonic eggs and larvae (Smith and Morse, 1984; Lough and Bolz, 1989). There may be exchange of biota among regions by episodic fluxes of shelf water carrying eggs and larvae away from the Scotian Shelf and Browns Bank onto Georges Bank (Cohen et al., 1991; Townsend and Pettigrew, 1996; Bisagni and Smith, 1998). Once on Georges Bank, planktonic eggs and larvae may, depending on depth, be entrained and transported to gravel settlement sites along the western edge of Georges Bank (Smith and Morse 1984; Lough and Bolz, 1989; Werner et al., 1993). However, wind-driven advection may cause egg and larval loss from the Northeast Peak and southern flank of Georges Bank (Lough et al., 1989). Cod spawned in the Gulf of Maine usually drift southeasterly towards Georges Bank because of the counterclockwise Gulf of Maine gyre, but the extent of egg and larval exchange between these regions is unknown (Serchuk et al., 1994).

Cod have been found from the surface to depths greater than 450 meters; however few cod proximate to the Gulf of Maine occur deeper than 180 meters (Klein-MacPhee, 2002). Browns Bank and Georges Bank are bathymetrically separated by the relatively deep (>260 meters) Fundian Channel which may act as a barrier to adult migration, whereas Georges Bank and Nantucket Shoals are separated by the relatively shallow (<100 meters) Great South Channel. Although the latter channel is probably not a significant barrier to adult migration, it is an area of strong recirculation towards Georges Bank and could limit egg and larval dispersal. Tagging studies show little exchange of adults between the inner Gulf of Maine and the region east of Browns Bank and Georges Bank (Hunt et al., 1999), but limited exchange has been reported among the Bay of Fundy, southern Nova Scotia, Browns Bank, and Georges Bank (Klein-MacPhee, 2002).

The likelihood of determining correct population structure increases when population differentiation is stable over time (Waples, 1998). Results from this study are concordant with observations of temporal stability of microsatellite variation observed in Atlantic cod (Ruzzante et al., 1996a, 1997, 2001). Tests of population differentiation and subdivision cannot reject the maintenance of genetic homogeneity among Georges Bank cod from 1994 to 1999 and thus may indicate some degree of temporal genetic stability among adult Georges Bank cod.

Our results indicate that cod from Nantucket Shoals are genetically distinct from those from Browns Bank and Georges Bank, and cod from the two Banks are more genetically similar. The observed lack of heterogeneity between Browns Bank and Georges Bank is consistent with gene flow — perhaps due to episodic larval transport and some level of limited adult exchange. Nantucket Shoals cod may be genetically distinct because of egg and larval isolation by entrainment in the Georges Bank gyre or because of limited movement of adults between regions (or a combination of both). Eggs and larvae spawned on Nantucket Shoals most likely do not enter the Georges Bank gyre system; these early life history forms may be retained on the shoals or transported to the southwest by prevailing circulation (Fogarty and Murawski, 1998). Some North Atlantic cod stocks have shown substantial differences in

growth rate, reproductive capacity, and maturity schedules related to temperature (Brander, 1994). Cod within our study zone generally avoid water temperatures greater than 10°C, but Nantucket Shoals cod are abundant in temperatures as warm as 15°C (Klein-MacPhee, 2002). This differential thermal tolerance may support genetic structuring of Nantucket Shoals cod by selecting against individuals from other areas.

Closely related gadid species such as cod and haddock may exhibit similar patterns of population genetic structuring associated with similar life histories, selective pressures, and ecological constraints. Our results are concordant with a previous study suggesting that haddock from Browns Bank and Georges Bank are genetically similar and that haddock from Nantucket Shoals are distinct (Lage et al., 2001). However, Ruzzante et al. (1998) observed significant genetic differentiation between cod from Browns Bank and Georges Bank. Our results do not agree with this previously observed heterogeneity between Browns Bank and Georges Bank and may be due to the examination of different loci, different sampling comparisons, or small sample sizes used in both studies (or to a combination of these variables) (Ruzzante, 1998; Smouse and Chevillon, 1998).

Among loci, the greatest genetic differentiation was observed at locus *Gmo*132. Indeed, observed statistical significance of population differentiation and F_{ST} depends entirely on *Gmo*132. Length variation at *Gmo*132 is a function of mutations in the repetitive array and of an indel in a flanking region (Ruzzante et al., 1998) causing bimodal allele distributions in some populations. When compared to other microsatellite loci, *Gmo*132 has shown the greatest differentiation among other Northwest Atlantic cod populations (Bentzen et al., 1996; Ruzzante et al., 1998, 2001) and among Northwest Atlantic haddock populations (Lage et al., 2001) by an order of magnitude. Other loci examined have not shown similarly strong measures of population structuring. Observed genetic structuring may be due to forces currently determining regional larval and adult distributions, including bathymetry and oceanographic patterns. However, because similar genetic structuring is not observed at all loci, another potential explanation is that structuring at *Gmo*132 is due to forces that acted during the formation of populations rather than to forces presently maintaining strong reproductive isolation. Once genetic structure was generated during the formation of these populations subsequent to the last ice age, biological and oceanographic forces may have maintained such structure; other loci may show an absence of structure simply because it may not have been present when populations were formed. Pogson et al. (2001) reported that the recent age of populations, rather than extensive gene flow, may be responsible for weak population structure in Atlantic cod, and that interpreting limited genetic differences among populations as reflecting high levels of ongoing gene flow should be made with caution. This suggests that the observed lack of heterogeneity between Browns Bank and Georges Bank may not be due to high levels of ongoing gene flow, but to similarities between recently generated populations maintained by small but adequate levels of gene flow.

Alternatively, significant structuring associated with *Gmo*132 in both cod and haddock may suggest that selection is acting at this or at a linked locus. Although microsatellites themselves may be generally considered neutral, there is, in theory, potential for physical linkage or drift-generated linkage disequilibrium between microsatellite and functional loci. There is however, recent evidence of selection acting directly on microsatellite loci in tilapia in high-salinity environments. Streelman and Kocher (2002) found a strong functional genotype-environment interaction and suggested that microsatellite repeats of varying length might induce promoter conformations that differ in their capacity to bind transcriptional regulators. A potential selective mechanism to support the observed genetic structuring of Nantucket Shoals cod (and haddock) may be differential thermal tolerance, although this hypothesis remains untested.

There is strong evidence for an unusual mix of balancing and directional selection at the pantophysin (*Pan*I) locus in cod but no evidence of stable geographically varying selection among North Atlantic populations (Pogson, 2001; Pogson et al., 2001). In the present study, the *Pan*I locus showed little variation and no significant genetic structuring (Table 1). The observed lack of geographic structuring at *Pan*I provides no evidence for local adaptation. However, our observations may be due to strong balancing selection among the geographically proximate populations examined or, if *Pan*I is not under selection, insufficient variation to resolve genetic structure. Alternatively, this observed lack of genetic divergence at *Pan*I could be due to similarities among recently generated populations of North Atlantic cod.

Our research suggests that the cod spawning on Nantucket Shoals are genetically differentiated from cod spawning on Browns Bank and Georges Bank. Managers may wish to consider Nantucket Shoals cod as a separate stock for assessment and management purposes in light of current practices that combine Georges Bank with regions to the south as one management unit. Cod from within the Gulf of Maine can potentially migrate along the coast to Nantucket Shoals where there is little geographic barrier to adult movement. If this is true, the Nantucket Shoals sample that we analyzed may actually be representative of a mixed Gulf of Maine and Nantucket Shoals population. Additional analyses are needed to evaluate the hypothesis that Nantucket Shoals cod are genetically distinct from cod spawning within the Gulf of Maine. Further studies should address the issues of temporal stability and robust sampling and should incorporate cod samples from within the Gulf of Maine.

Acknowledgments

We thank three anonymous reviewers for their insightful comments. We thank the captains, crews, and scientists from the Canadian Department of Fisheries and Oceans and the United States. National Marine Fisheries Service. In particular, we would like to thank Chris Taggart, Nina Shepard, and Holly McBride for assistance in obtaining

samples. IK thanks Maryhaven for support. This work was funded by OCE9806712 from the U.S. National Science Foundation.

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