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Genetic structure of deep-water redfish, *Sebastes mentella*, populations across the North Atlantic

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Abstract Patterns of genetic diversity of the marine deep-water redfish, *Sebastes mentella* Travin, from 21 sampling locations ($n = 46$ per sample, from 1995 to 1998) were examined throughout its range in the North Atlantic. Eight microsatellite loci were used in order to: (1) define the genetic structure and consider the possible influence of dispersal, geographic distance, oceanic currents and historical factors; and (2) relate the structure to present management units and practices. Three divergent population units (mean $\theta = 0.012$) associated with distinct geographic areas were defined: Eastern (Norway and Barents Sea), Panoceanic and Western (Gulf of St. Lawrence and offshore Newfoundland). The most important observation was the lack of genetic differences (mean $\theta = -0.0004$) and lack of genetic isolation by geographic distance ($r = 0.318$, $P = 0.112$) among samples within the Panoceanic zone, from the Faroe Islands to the Grand Banks (6,000 km). A combination of vicariance, historical introgression with a closely related species, *S. fasciatus*, and contemporary patterns of oceanic circulation are likely to have shaped the observed population structure. These results only partially support current management units, and call for more integrated practices for regulating the exploitation of *S. mentella* throughout its extensive range.

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Introduction

Understanding the patterns of genetic diversity within and among populations is fundamental for sustained exploitation of fishery stocks and sound conservation practices. The genetic characterisation of population structure is challenging for marine organisms with wide early life history vagility (Palumbi 1992, 1994). On the one hand, marine species have been typically characterised by very weak or no obvious genetic population structure over large geographic areas, a feature potentially attributed to large effective population sizes, high potential for dispersal and weak physical barriers to gene flow (Avise et al. 1987; Gold et al. 1994). It is well documented, however, that the dynamic interaction between oceanographic features and specific behavioural characteristics (e.g. homing, vertical migration) may determine the number of distinct populations in marine species (Iles and Sinclair 1982). An apparent lack of genetic structure has often been incongruent with expected population subdivision based on ecological knowledge (e.g. King et al. 1987; Bagley 1999). Consequently, it is often unclear whether apparently weak genetic divergence truly reflects the population structure in marine organisms or is, instead, an artefact of low analytical resolution (Mork et al. 1985; Pogson et al. 1995).

The use of hypervariable genetic markers, such as microsatellite loci, along with the development of new statistical methods, have significantly improved our understanding of genetic population structure in marine organisms. Such studies revealed significant genetic heterogeneity where a lack of structure was previously reported using other markers, such as allozymes or

mitochondrial DNA (e.g. Bentzen et al. 1996; Ruzzante et al. 1999, 2000). Furthermore, population structure revealed by microsatellites was sometimes highly congruent with that expected from the species' ecology and life cycle (e.g. Ruzzante et al. 1996, 1998).

The deep-water redfish, *Sebastes mentella*, is widely distributed throughout the North Atlantic at depths of 300–750 m. It is ovoviviparous and releases pelagic larvae (50,000 female^{-1} year^{-1} on average), which subsequently metamorphose as pelagic juveniles (Moser 1967; Moser et al. 1977). Larvae and juveniles become widely distributed, during the pelagic stage, which lasts from several months to a year, travelling great distances from the epibenthic adult habitats (Moser and Boehlert 1991). In the Gulf of St. Lawrence, copulation probably occurs in autumn, while extrusion of larvae may extend from April to June (St-Pierre and de Lafontaine 1995). In the central North Atlantic, feeding and copulation areas are believed to be along the east coast of Greenland and around Iceland and the Faroe Islands. This implies extensive migration from feeding to larval release areas (Irminger Sea, off southern Iceland) in spring, at least for females, and between nursery and feeding areas for juveniles (Reinert and Lastein 1992). For management purposes, two distinct stocks are recognised over this large area. One comprises the Northeast Arctic with the main range of adults, reproduction and nursery areas lying within the Norwegian zone (regions along the Norwegian coast). The second comprises the waters off the Faroe Islands, Iceland and east Greenland, and is referred to as the Irminger Sea stock complex (Reinert and Lastein 1992). This stock definition has been supported by differences in morphological and meristic traits between fish from the two areas (Reinert and Lastein 1992). In contrast, genetic studies based on either allozymes or haemoglobin revealed low levels of genetic polymorphism within any redfish taxa from the North Atlantic, particularly *S. mentella* (Nedreaas and Naevdal 1989, 1991; Nedreaas et al. 1994; Duschenko 1997). For instance, no difference was observed among *S. mentella* from six locations in the Irminger Sea, based on six allozyme loci, nor among locations off the Norwegian coast, Faroe Islands, Davis Strait east and west Greenland (Nedreaas and Naevdal 1991; Nedreaas et al. 1994). In the Northwest Atlantic (Canadian Atlantic coast and Gulf of St. Lawrence), the attempts to discriminate *S. mentella* from other sympatric taxa (*S. fasciatus* and *S. marinus*) have met with varying degrees of success (Payne and Ni 1982; McGlade et al. 1983; Rubec et al. 1991; Sévigny and de Lafontaine 1992). This has hampered our understanding of these species' ecology, life history and population structure, and has led to the combined management of all taxa as a single "species". The levels of genetic divergence among redfish from eastern, central and western North Atlantic have not been quantified.

The paucity of knowledge on the species' ecology makes a priori predictions about the genetic population structure in *S. mentella* throughout the North Atlantic problematic. Several features of the species' life history are conducive to extensive dispersal, and the generally continuous deep-water habitat (Haedrich 1996) suggests that the genetic structure might be poorly differentiated. Still, population structure could develop as a result of reduced dispersal with geographic distance (Pogson et al. 2001), or as a result of behavioural characteristics regulating vagility at various life history stages (still poorly described), and the strength, direction and variability of oceanic currents. In addition, historical contingency may also have shaped its population structure. For instance, other studies have attributed the occurrence of a genetic discontinuity in other marine species between the East and West Atlantic to such factors (e.g. Avise et al. 1990; Dodson et al. 1991; Bérubé et al. 1998; Rosel et al. 1998).

The objective of the present study was to quantify the distribution of genetic diversity within *S. mentella* throughout its geographic range using highly polymorphic microsatellite loci in order to: (1) assess the degree of dispersal and gene flow in relation to geographic distance, contemporary oceanic currents and historical factors; and (2) compare these patterns against stock structure management practices to contribute to its conservation.

Materials and methods

Redfish sampling and genetic assays

A total of 973 adult redfish (total length > 20 cm) *Sebastes mentella* Travin were collected from 1995 to 1998 by bottom trawls or handlines at 21 sites representing its distribution range in the North Atlantic Ocean (Fig. 1; see Table 1). Most samples were caught outside the extrusion period in spring, except for the Iceland, Irminger Sea and east Greenland samples. Species identification in the Western area was performed by the examination of meristic (anal fin ray count), morphological (gas bladder musculature), and genetic characters (malate dehydrogenase, *MDH*) used for redfish (Ni 1981, 1982; McGlade et al. 1983). To avoid misclassifications, samples were selected when the results of the three methods were concordant. In other regions, redfish were identified using morphological and genetic characters (haemoglobin polymorphism) (Barsukov et al. 1984; Nedreaas and Naevdal 1989). DNA was extracted from muscle tissue, frozen at –80°C or stored in 95% ethanol, using phenol-chloroform (Sambrook et al. 1989) or Chelex (Walsh et al. 1991) methods. Samples were screened for variation at eight specific microsatellite loci, by either the radioactive or the fluorescent labelling PCR method, following Roques et al. (1999a). Allele sizes were determined by reference to internal standards and by comparison with three samples of known allelic sizes that were run on each gel. Samples that were analysed in a previous study (Roques et al. 2001) or in the present study ($n = 433$) are indicated in Table 1. For most of the analyses, 20 samples were used, the small Barents Sea sample being omitted in all cases, except where specified.

Intrapopulation variation

Intrapopulation genetic diversity was estimated from the allelic composition of 20 samples. Estimates of the number of alleles (A), observed heterozygosity (H_o) and unbiased gene diversity (H_e) corrected for sampling bias (Nei 1987) were calculated using the GENETIX program, version 3.0 (Belkhir et al. 1996).

Deviations from Hardy–Weinberg (HW) proportions were examined for a deficit or excess of heterozygotes using the

multisample score test in the GENEPOP program, version 3.1 (Raymond and Rousset 1995). Probabilities of significance (*P*) were computed using the Markov chain method (100 batches, 1,000 iterations) (Guo and Thompson 1992) as implemented in GENEPOP. Multilocus values of significance for HW tests were obtained using Fisher's method (Sokal and Rohlf 1995) to combine proba-

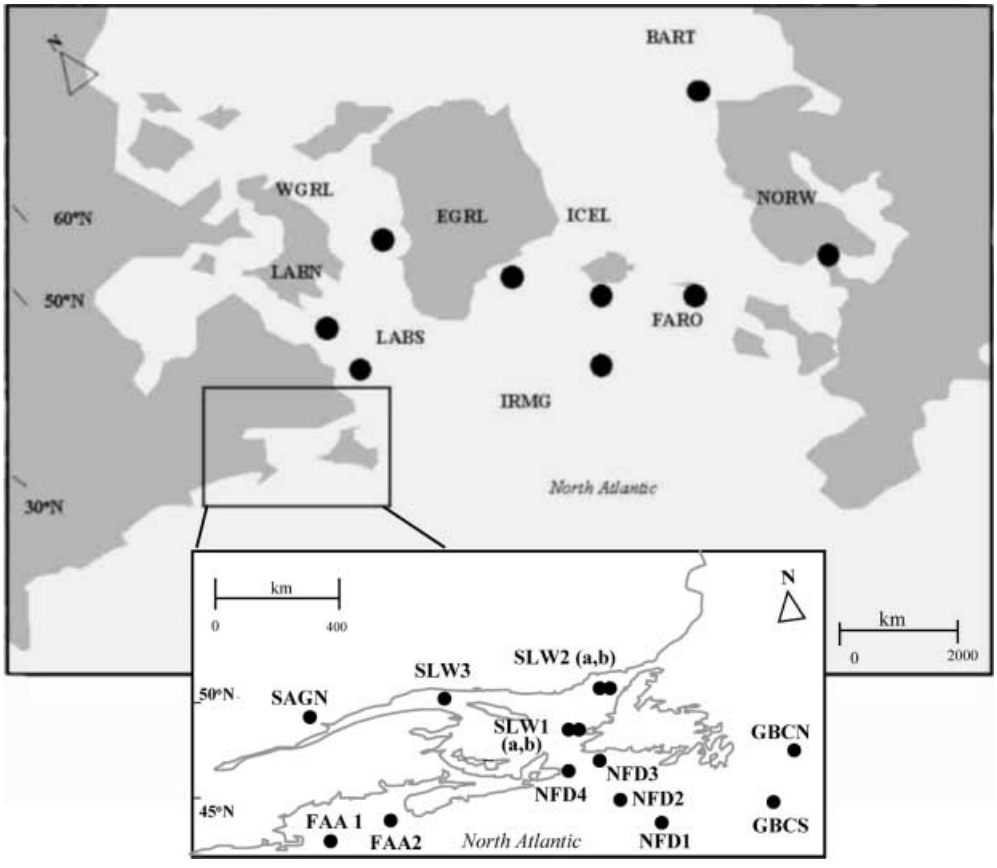

Fig. 1 *Sebastes mentella*. Sampling locations throughout the North Atlantic. Abbreviations correspond to samples detailed in Table 1. Sampling locations for *S. fasciatus* (FAA1, FAA2, in Roques et al. 2001) are also shown

Table 1 *Sebastes mentella*. Geographical origins, collection dates, codes, samples sizes (*n*), total number of alleles (*A*), mean number of alleles per locus (Â), observed (H_o) and expected unbiased (H_e) heterozygosities (±SE), probability of heterozygote deficiency (*P*), *f* values for 21 samples [[a]Present study; [b]Roques et al. (2001); *NA* not available; *ND*: not analysed because of small sample size; **P*-values ≤ 0.01]

Geographical origin	Collection date	Codes	*n*	*A*	Â	H_o	H_e	*P*	*f*
Eastern									
Barents Sea[a]	NA	BART	13	85	11	ND	ND	ND	ND
Norway (Traenaegga)[a]	Oct 1995	NORW	45	135	17	0.777	0.785 (0.012)	0.29	0.012
Panoceanic									
Faroe Islands[a]	Aug 1997	FARO	50	166	21	0.795	0.870 (0.008)	0.00001*	0.087
Iceland (W)[a]	Spring 1995	ICEL	46	150	19	0.742	0.872 (0.008)	0.0001*	0.158
Irminger Sea (NE)[a]	Spring 1996	IRMG	43	154	19	0.834	0.876 (0.008)	0.01*	0.049
Greenland (E)[a]	May 1995	EGRL	44	158	20	0.839	0.878 (0.008)	0.01*	0.049
Greenland (W)[a]	Mar 1993	WGRL	53	170	21	0.827	0.862 (0.008)	0.008*	0.049
Labrador (N)[b]	Oct 1998	LABN	52	168	21	0.872	0.883 (0.008)	0.245	0.049
Labrador (S)[b]	Oct 1998	LABS	52	171	21	0.856	0.890 (0.007)	0.01*	0.049
Grand Bank (N)[b]	Jun 1997	GBCN	44	150	19	0.868	0.843 (0.010)	0.92	0.049
Grand Bank (S)[b]	Jul 1997	GBCS	47	159	20	0.833	0.873 (0.008)	0.005*	0.049
Western									
South Newfoundland[b]	Jul 1996	NFD1	51	153	19	0.848	0.854 (0.009)	0.329	–0.025
South Newfoundland[b]	Jul 1995	NFD2	48	160	20	0.840	0.873 (0.008)	0.024	–0.025
South Newfoundland[b]	Jul 1995	NFD3	51	155	19	0.811	0.848 (0.009)	0.006*	–0.025
South Newfoundland[b]	Jul 1995	NFD4	48	142	18	0.794	0.869 (0.008)	0.00001*	–0.025
St. Lawrence (S)[b]	Aug 1996	SLW1A	49	160	20	0.917	0.895 (0.006)	0.936	–0.024
St. Lawrence (S)[a]	NA	SLW1B	52	155	19	0.861	0.858 (0.009)	0.700	–0.025
St. Lawrence (E)[b]	Aug 1996	SLW2A	48	146	18	0.860	0.882 (0.008)	0.066	–0.025
St. Lawrence (E)[a]	Aug 1996	SLW2B	37	138	17	0.865	0.879 (0.009)	0.228	–0.025
St. Lawrence (W)[b]	Aug 1996	SLW3A	50	149	19	0.847	0.848 (0.009)	0.495	–0.025
Saguenay River[a]	Jan–Mar 1996	SAGN	50	153	19	0.846	0.871 (0.008)	0.045	–0.025

bilities of exact tests. To test whether a particular locus contributed disproportionately to the heterozygote deficits, a Jacknife test was carried out for the calculations of f [Weir and Cockerham's (1984) estimator of F_{is}], using GENETIX. The null hypothesis of no linkage disequilibrium was also tested in all samples, and significance values were computed by unbiased estimates of Fisher's exact tests using the Markov chain method in GENEPOP.

Population differentiation and substructuring

In order to define the main population units among the 20 *S. mentella* samples, we first performed homogeneity tests of allele frequency distribution using GENEPOP. Multiloci values of significance were obtained following Fisher's method to combine probabilities of exact tests. Raw allele frequency data for the eight microsatellite loci are presented in the electronic supplement (Appendix 1, http://dx.doi.org/10.1007/s002270100705). The extent of genetic differentiation among pairwise samples was estimated by the unbiased F_{st} estimator (θ) of Weir and Cockerham (1984), using ARLEQUIN software, version 1.1 (Schneider et al. 1997). Disjunct allelic size distributions, in which alleles were separated by numerous base pairs, were observed for several loci (Roques et al. 1999b), suggesting that they do not follow a strict stepwise mutational model (Di Rienzo et al. 1994; Angers and Bernatchez 1998). Hence, we did not estimate the extent of genetic differentiation based on molecular variance. Probability values were adjusted for multiple test comparisons using sequential Bonferroni corrections (Rice 1989).

To visualise the pattern of genetic differentiation among samples, we conducted a multidimensional scaling analysis (MDS), using the program STATISTICA, version 4.5 (Statsoft 1994). This allowed detection of dimensions that most likely explain the observed dissimilarities among all samples, based on θ-estimates (Ruzzante et al. 1998).

Isolation-by-distance

To examine whether subtle genetic differences had arisen as a result of geographic isolation, we tested the stepping-stone model of isolation-by-distance, which assumes that along a one- or two-dimensional lattice(s), adjacent populations may have greater genetic exchange (Kimura and Weiss 1964). This may well reflect the organisation of marine species, in which dispersal between sites may be correlated to geographic distance (Hellberg 1994). Rousset (1997) showed that a linear relationship is expected in one- or two-dimensional stepping-stone models between geographic separation and $F_{st}/1–F_{st}$. Correlations between the $\log_{10}$ of geographic distance (km) and the $\log_{10}$ of genetic differentiation ($\theta/1–\theta$) were calculated between sample pairs. Distances among samples were measured as the shortest distance between localities on a 1/1,000,000:1 scale map. Since factors determining gene flow may differ with spatial scale, correlations were calculated within and among regions defined as the different population units, for which the null hypothesis of population structure was rejected (see "Results"). The significance of the correlations was assessed using a Mantel test, with 1,000 permutations, in GENETIX.

Genetic distances

Divergence among the 20 samples of *S. mentella* was quantified by Cavalli-Sforza and Edward's (1967) chord distance (D_{ce}). The use of chord distance generally leads to a higher probability of obtaining the correct tree topology under either the infinite allele model (IAM) or single step mutation model (SMM) assumptions (Takezaki and Nei 1996; Angers and Bernatchez 1998). Pairwise distances were used to construct a population tree using the neighbour-joining (NJ) algorithm (Saitou and Nei 1987) in PHYLIP, version 3.5c (Felsenstein 1993). SEQBOOT, GENDIST, NEIGHBOUR and CONSENSE programs were successively used to build the tree. Confidence estimates on tree topology were estimated from 1,000 bootstrap iterations of resampling the allelic frequencies. In order to evaluate the possible impact of introgressive hybridisation on the genetic structure of *S. mentella* throughout its entire distribution range, two *S. fasciatus* samples (FAA1, FAA2) were included, since this species hybridises with *S. mentella* where they co-occur (Roques et al. 2001). The small sample from the Barents Sea (BART) ($n = 13$) was included in this analysis only.

The spatial structure in the tree was further quantified with an analysis of molecular variance (AMOVA) (Excoffier et al. 1992) using ARLEQUIN, version 1.1. Hierarchical analyses were performed to assess the component of genetic variance (based on allelic frequencies) attributable to differences among the main population units and among samples within these groups.

Results

Genetic diversity, HW and linkage equilibrium

All eight microsatellite loci were highly polymorphic in *Sebastes mentella* (Table 1). The mean number of alleles per locus ranged from 17 to 21 and mean expected heterozygosity within samples ranged from 0.7854 to 0.8948.

Departure from HW expectations was detected in nine samples (Table 1). In five cases (FARO, IRMG, WGRL, NFD3, NFD4), no single locus completely caused the deficiency, suggesting that neither a methodological artefact nor null alleles were responsible. Heterozygote deficiencies observed in the Irminger Sea sample may represent intermingling of populations, as this region is known to be a common spawning area for *S. mentella* (Reinert et al. 1992), and, this sample was caught during the extrusion period in spring. Ongoing and pronounced introgression was previously invoked to explain deficit values in NFD3 and NFD4 locations (Roques et al. 2001). Distinguishing among other potential causes with certainty is not possible with the present microsatellite data. The Jacknife procedure, however, indicated that particular loci were responsible for causing the deficits in the other four samples (ICEL, EGRL, LABS, GBCS). For ICEL and EGRL, biological factors appeared the most plausible causes for the observed deficit, since the samples were scored by two different researchers (who agreed on the scoring), and the locus involved (*SEB25*) yielded consistent amplifications and clear patterns. For the other samples (LABS, GBCS), null alleles and/or short allele dominance (Paetkau and Strobeck 1995; Wattier et al. 1998) cannot be ruled out. The loci involved (*SEB33*, *SEB37*, *SEB30*) were the most polymorphic of those examined with the greatest number of alleles. These were often characterised by bimodality in size (a small and a large allele in the same individual); in addition, some individuals were reanalysed at these loci because of non-amplification. There was no evidence of genetic linkage disequilibrium, with ten significant departures from equilibrium (1.7%) ($k = 28$, $\alpha = 0.05/28 = 0.00178$) out of 560 comparisons for the entire data set, a number not exceeding that expected by chance alone.

Population differentiation and substructuring

Overall, the results indicated the occurrence of three main population units among *S. mentella* samples throughout the North Atlantic: Eastern, Panoceanic and Western. The Eastern group was represented by Norway and Barents Sea samples, while the Panoceanic group was composed of most samples from the Grand Banks and Labrador Sea to the Faroe Islands. The Western group included samples from the Gulf of St. Lawrence and offshore Newfoundland regions. Highly significant differences were found between NORW (mean $\theta = 0.0239$) and all other samples (Table 2). Similarly, there was a clear differentiation of the Western samples from all others, with significant differences based on both allele frequencies and θ-values (mean $\theta = 0.0127$). In contrast, all other samples, from Grand Banks to Faroe Islands appeared genetically homogenous (mean $\theta = -0.0004$). Exact tests of allelic frequencies indicated significant differences between the ICEL or EGRL samples and others (Table 2). These differences translated into significant θ-values only between EGRL and WGRL ($\theta = 0.0056$) and EGRL and GBCS ($\theta = 0.0093$) (Table 2) and were supported by all loci, as tested by a Jacknife procedure (results not shown). Few genetic differences were found among the Western samples (mean $\theta = 0.00028$), except for significant θ differences between NFD3, NFD4 and other locations (see Table 2). The differentiation of the former two samples from the others was previously explained as the consequence of variable levels of introgression (Roques et al. 2001). All Western samples were also highly differentiated from those of the Eastern and Panoceanic areas (Table 2).

The MDS applied to θ-values revealed a pattern of genetic differences among populations that was consistent with these results (Fig. 2). Hence, samples from the Eastern, Panoceanic and Western areas were distinct from each other. The first dimension (explaining 22% of the variance) distinguished the Western samples from the others, while the second dimension (explaining 7% of the variance) mainly resulted from the difference between Norway and the other samples. An MDS analysis within the Western and the Panoceanic groups (not shown) revealed no grouping among samples, further supporting the overall lack of population structure within each region.

The NJ tree agreed with previous analyses based on θ estimates, revealing three distinct clusters with high bootstrap values, corresponding to the three main population units (Fig. 3). The Western group was located between *S. fasciatus* and the other groups. Within this group, the NFD4 sample was the most differentiated. A geographic subdivision of two clusters with low support was suggested within the Panoceanic group. One included the three samples from the Eastern-Panoceanic areas (FARO, ICEL, EGRL) and the other included all remaining samples corresponding to Western-Panoceanic regions (WGRL, GBCN, LABN,

Table 2 *Sebastes mentella*. Pairwise sample divergences based on θ estimates (*lower diagonal*) and probabilities of homogeneity of allelic frequencies estimated by Fisher exact tests (*upper diagonal*) at eight microsatellite loci in 20 samples. Codes as in Table 1 [*, *S* significance of pairwise differences following sequential Bonferroni adjustments ($k = 190$, $\alpha = 0.05/190 = 0.00036$); *N* no significant difference; *data in italics* comparisons involving Western samples (see Table 1) versus others]

	NORW	FARO	ICEL	IRMG	EGRL	WGRL	LABN	LABS	GBCN	GBCS	NFD1	NFD2	NFD3	NFD4	SLW1A	SLW1B	SLW2A	SLW2B	SLW3A	SAGN
NORW		N	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
FARO	0.0114*		N	N	N	N	N	N	N	N	S	S	S	S	S	S	S	S	S	S
ICEL	0.0278*	–0.0064		N	N	S	N	S	N	N	S	S	S	S	S	S	S	S	S	S
IRMG	0.0281*	–0.0115	0.0020		N	N	N	N	N	N	S	S	S	S	S	S	S	S	S	S
EGRL	0.0214*	0.0045	–0.0043	–0.0109		S	N	S	S	S	S	S	S	S	S	S	S	S	S	S
WGRL	0.0137*	0.0021	0.0041	–0.0079	0.0056*		N	N	N	N	S	S	S	S	S	S	S	S	S	S
LABN	0.0368*	0.0000	0.0030	–0.0053	0.0037	0.0029		N	N	N	S	S	S	S	N	N	N	N	N	N
LABS	0.0211*	–0.0001	0.0040	–0.0087	0.0013	–0.0002	–0.0006		N	N	S	S	S	S	N	N	N	N	N	N
GBCN	0.0174*	–0.0072	0.0081*	0.0028	0.0016	–0.0071	0.0062*	–0.0008		N	S	S	S	S	S	S	N	N	N	S
GBCS	0.0266*	0.0041	0.0022	–0.0098	0.0093*	0.0026	0.0014	0.0026	–0.0039		S	S	S	S	S	S	S	S	S	S
NFD1	*0.0158**	*0.0103**	*0.0092**	*0.0047*	*0.0124**	*0.0113**	*0.0146**	*0.0118**	*0.0077**	*0.0181**		N	N	S	N	N	N	N	N	N
NFD2	*0.0268**	*0.0146**	*0.0068*	*0.0003*	*0.0143**	*0.0104**	*0.0103**	*0.0125**	*0.0052*	*0.0150**	0.0000		S	S	N	N	N	N	N	N
NFD3	*0.0219**	*0.0162**	*0.0133**	*0.0071**	*0.0223**	*0.0138**	*0.0163**	*0.0158**	*0.0078**	*0.0224**	0.0045	0.0101*		S	S	S	N	N	N	S
NFD4	*0.0316**	*0.0203**	*0.0138**	*0.0116**	*0.0202**	*0.0184**	*0.0213**	*0.0193**	*0.0170**	*0.0274**	0.0094*	0.0098*	0.0186*		S	N	N	S	S	N
SLW1A	*0.0292**	*0.00975*	*0.0038*	*–0.0031*	*0.0078**	*0.0092**	*0.0044*	*0.0082**	*0.0063**	*0.0152**	0.0003	0.0019	0.0093*	0.0095*		N	N	N	N	N
SLW1B	*0.0211**	*0.0104**	*0.0076**	*0.0095**	*0.0091**	*0.0088**	*0.0163**	*0.0123**	*0.0106**	*0.0155**	–0.0019	–0.0012	0.0072*	0.0031	0.0020		N	N	N	N
SLW2A	*0.0321**	*0.0093**	*0.0075**	*0.0014*	*0.0091**	*0.0110**	*0.0090**	*0.0096**	*0.0103**	*0.0154**	0.0017	0.0020	0.0043	0.0036	0.0002	0.0021		N	N	N
SLW2B	*0.0279**	*0.0078**	*0.0091**	*0.0046*	*0.0083**	*0.0095**	*0.0071**	*0.0074**	*0.0102**	*0.0167**	0.0001	0.002	0.0044	0.0067*	–0.0031	0.0034	–0.0036		N	N
SLW3A	*0.0167**	*0.0123**	*0.0142**	*0.0110**	*0.0147**	*0.0109**	*0.0181**	*0.0156**	*0.0101**	*0.0167**	–0.0046	–0.0030	0.0038	0.0057*	0.0010	0.0015	–0.0005	–0.0014		N
SAGN	*0.0275**	*0.0105**	*0.0098**	*0.0019*	*0.0103**	*0.0096**	*0.0097**	*0.0093**	*0.0060**	*0.0145**	0.0015	0.0019	0.0084*	0.0046	0.0000	0.0018	0.0006	–0.0005	–0.0001	

LABS, GBCS, IRMG). This partly agrees with the homogeneity tests of allelic frequencies, which indicated significant differences between ICEL, EGRL and other samples of the central area. Norway (NORW) and Barents Sea (BART) samples formed the third main cluster.

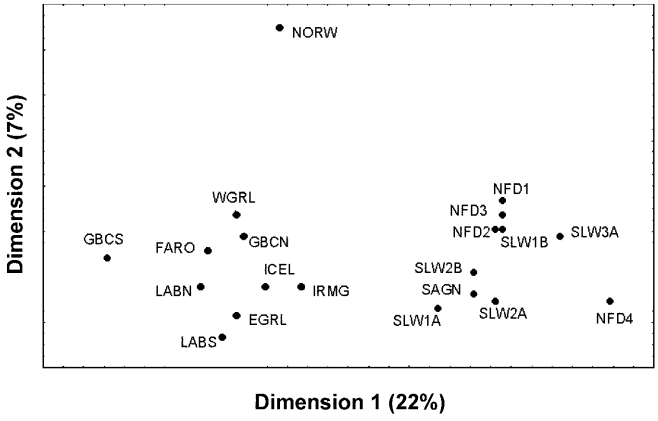

Fig. 2 *Sebastes mentella*. Diagram of the multidimensional scaling analysis showing 20 samples in a multidimensional space defined by the first and second dimensions. Their respective contributions to the groupings are shown as percentages (%)

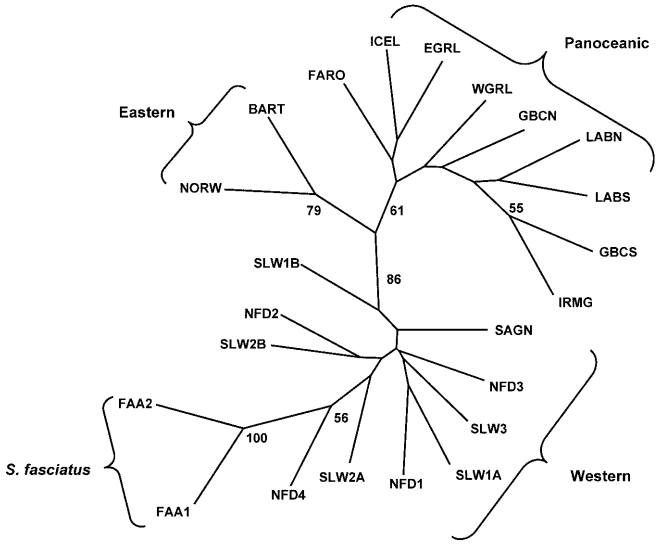

Fig. 3 *Sebastes* spp. Neighbour-joining tree illustrating relationships among 21 transAtlantic samples of *S. mentella* and two of *S. fasciatus* based on pairwise D_{CE} genetic distances. Bootstrap values (in percent) were obtained by 1,000 resamplings over loci

The hierarchical analysis of molecular variance revealed that divergence among the three main sample groups accounted for 1.2% of the total genetic variance (Table 3). In contrast, the amount of genetic variance attributable to genetic differentiation within groups was much lower, being zero in the Panoceanic group (Table 3).

Isolation-by-distance

The relationship between $\theta/1-\theta$ and geographical distance for all population pairs was significant ($r = 0.445$, $P \leq 0.0001$) (Fig. 4a). This pattern of isolation-by-distance, however, was somewhat inconsistent with the previous analyses, since genetic structure according to a stepping-stone model is biologically incompatible with the three discontinuous main population units throughout the North Atlantic (Kimura and Weiss 1964; Rousset 1997). Hence, the overall pattern of isolation-by-distance likely represents a biased effect of the position of the three main groups separated by intermediate geographical distances. This was further supported by the absence of isolation-by-distance within the Panoceanic and Western groups (Fig. 4b, c).

Discussion

Genetic structure of *Sebastes mentella* throughout the North Atlantic

Overall, the analysis of microsatellite variation in *S. mentella* defined three geographically distinct population units in the North Atlantic: Eastern (Barents Sea and Norway), Panoceanic and Western (Gulf of St. Lawrence and Laurentian channel). The most salient finding, however, was the genetic homogeneity within the Panoceanic population over a distance of 6,000 km, from Labrador to the Faroe Islands, which was indicated by few or no genetic differences, and the absence of isolation-by-distance among samples. This evidence that there are only three main populations across the whole North Atlantic is consistent with the hypothesis that the continuous deep-water habitat and the species' high dispersal potential provide little opportunity for physical isolation among populations within this species (Haedrich 1996).

Iles and Sinclair (1982, generalised by Sinclair 1988), developed the "member–vagrant hypothesis" to explain the role of ecological processes in shaping population

Table 3 *Sebastes mentella*. Hierarchical analysis of genetic variance using eight microsatellite loci, with percentages of variation (%), variance components (*Va*) and probability of components being equal to zero (*P*)

	%	Va	*P*
Among groups	1.2	0.03759	< 0.00001
Among samples within groups	0.2	0.00618	< 0.00001
Among samples within Panoceanic	0	0	0.337
Among samples within Western	0.3	0.00951	< 0.00001
Within samples	98.6	3.0329	< 0.00001

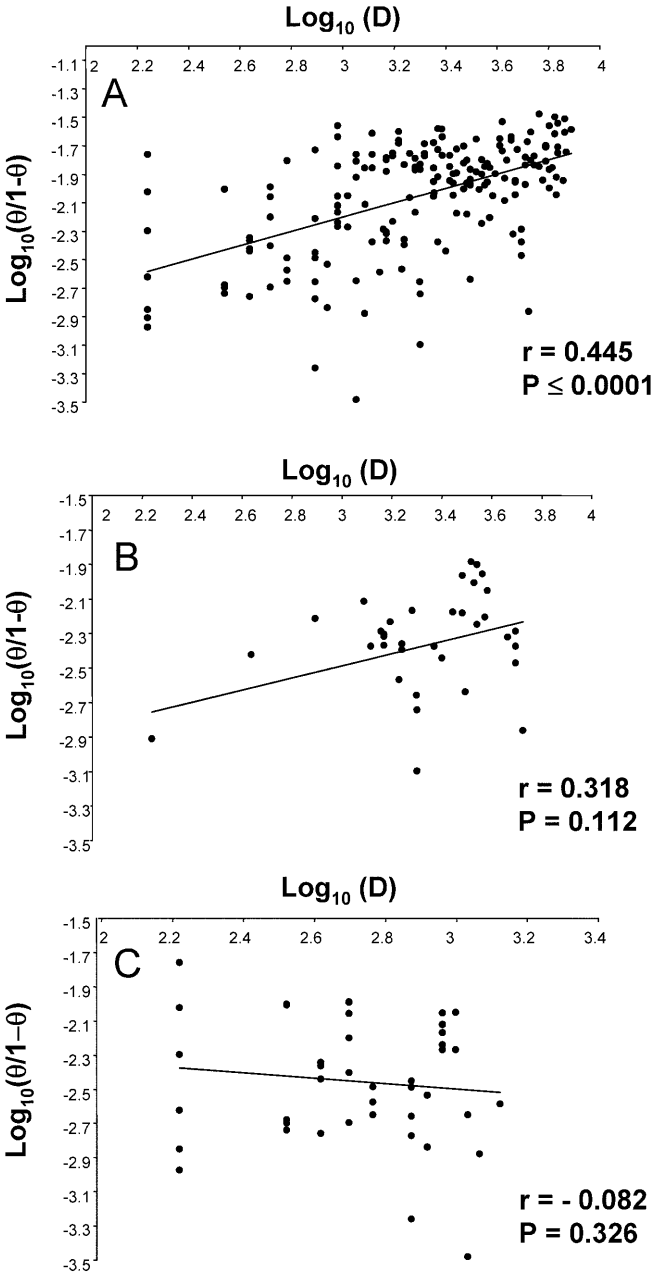

Fig. 4a–c *Sebastes mentella*. Relationships between $\log_{10}(\theta/1-\theta)$ and $\log_{10}$ of geographical distance (km), Pearson correlation coefficients (r) and significance of the correlation (P) using a Mantel test (1,000 permutations) for pairwise comparisons of samples using: **a** complete data set; **b** among samples within the Panoceanic region; **c** among samples within the Western region

structure of marine organisms. They theorised that the number of distinct populations within marine species is mainly determined by the number of environmental settings (oceanographical, physical) that retain young life history stages of the species (larvae, juveniles), and favour their growth and survival. Genetic data have recently supported this prediction in Atlantic mackerel (Nesbo et al. 2000) and cod (Ruzzante et al. 1999, 2000). The larval ecology of *S. mentella* is poorly known. But, the absence of significant genetic discontinuity among *S. mentella* samples in the Panoceanic region suggests a single larval retention zone for this vast area. Several lines of evidence support this possibility. The prevailing surface currents in the central North Atlantic may provide an efficient means of larval retention. The conjunction of the Irminger (west–east axis), Greenland (east–west axis) and Labrador (north–south axis) currents form a cyclonic pattern of water circulation, resulting in horizontal mixing over the whole central North Atlantic basin (Fig. 5) (Couper 1983). Given the duration of the pelagic stage (from several months to a year), *S. mentella* larvae are likely to be widely dispersed within this oceanic current structure (Moser and Boelhert 1991). Surveys in the Central Atlantic also revealed aggregations of adult *S. mentella* within the eastern part of the Irminger Sea during the summer larval release, and large concentrations of larvae were found feeding on zooplankton near the surface (Templeman 1961; Bainbridge and Cooper 1971; Reinert et al. 1992; Magnusson and Magnusson 1995).

Despite the prevailing pattern of genetic homogeneity in the Panoceanic populations, finer genetic structuring cannot entirely be dismissed, since both homogeneity tests of allelic frequencies and the population phenogram were suggestive of modest genetic differences among several Eastern (Iceland, Faroe Islands, east Greenland) and Western (Labrador Sea, Grand Banks, Irminger, west Greenland) samples. More samples will be required to assess whether such differences reflect sampling error (Waples 1998) or genetic structure.

We predict that any genetic differences among redfish within the Eastern and Western regions will be much less important than the observed differences between the Panoceanic and the other two populations, which were highly differentiated. For instance, the amount of genetic divergence between *S. mentella* samples from the Eastern and Panoceanic populations of the Faroe Islands (FARO) was large and highly significant (e.g. $\theta = 0.011$ between NORW and FARO) given their relative geographic proximity (1,000 km). In contrast, samples from the Faroe Islands and Grand Banks, both classified in the Panoceanic population, were almost genetically identical ($\theta = 0.004$) despite a nearly 6,000 km geographical separation. The difference between the Norway sample and all others is congruent with previous morphological and meristic differences between Norway redfish and those from Icelandic waters and the Irminger Sea (Reinert and Lastein 1992).

A relatively strong genetic discontinuity between populations from Norway and Barents Sea and those from more western waters has also been reported for other marine species including capelin (*Mallotus villosus*; Dodson et al. 1991), Atlantic cod (*Gadus morhua*; Bentzen et al. 1996), whales (*Balaenoptera physalus*; Bérubé et al. 1998), halibut (*Hipoglossus hipoglossus*; Foss et al. 1998), Atlantic herring (*Clupea harengus*; Shaw et al. 1999) and hake (*Merluccius merluccius*; Lundy et al. 1999). These patterns have been partly attributed to homing to distinct spawning grounds, or to the existence of a distinct

retention zone created by the Norwegian current (Sinclair 1988; Foss et al. 1998; Shaw et al. 1999). These factors, along with other physical barriers, such as the influence of the North Atlantic current (southwest–northeast axis) (Fig. 5) and the European continental shelf, could also contribute to the isolation of the eastern populations in several species.

In addition to ecological factors, historical events have also been invoked to explain the genetic discontinuity between populations and species distributions in the Barents Sea and/or Norway and more western or southern areas (e.g. Dodson et al. 1991 for capelin; Naranjo et al. 1998 for ascidian species). It is therefore plausible that a combination of both historical vicariance and contemporary ecological factors has effectively isolated redfish from Norway, and possibly other regions of the Northeast Atlantic, from more western populations.

At the end of the range of *S. mentella*, a strong genetic discontinuity was found between Western samples (Gulf of St. Lawrence, southern Newfoundland) and the Panoceanic population. For instance, the amount of genetic divergence between samples of *S. mentella* from south Newfoundland (NFD2, Western population) and the Grand Banks (GBCS, Panoceanic population) was large for microsatellite loci in marine fish ($\theta = 0.015$), despite their geographic proximity (200 km) and a lack of obvious barriers to dispersal (Roques et al. 2001). In contrast, *S. mentella* samples from the Grand Banks and Labrador (LABN) were almost genetically identical ($\theta = 0.0014$), although separated by nearly 2,000 km. The Gulf of St. Lawrence has a complex circulation pattern with low-salinity surface waters, emanating from the St. Lawrence estuary, and deep marine waters brought by the Labrador Current, providing valuable habitat conditions for numerous groundfishes at all life history stages (Dickie and Trites 1983; Drinkwater and Mountain 1997). The high abundance of planktonic copepods (*Calanus* sp.) upon which redfish larvae depend for their growth and survival led Runge and de Lafontaine (1996) to propose that the surface waters of the northern Gulf of St. Lawrence represent a high-quality larval habitat for these species. This almost "enclosed sea" could represent an environment where the species completes all phases of its lifecycle.

We recently documented a zone of introgressive hybridisation between *S. mentella* and *S. fasciatus* in the Gulf of St. Lawrence and south of Newfoundland, where they occur in sympatry (Roques et al. 2001). We showed that pronounced introgression (15%) between the two species was important in shaping redfish genetic diversity, interspecific differences and population structure in this region. Historical episodes of allopatric isolation followed by dispersal and secondary contacts were inferred to explain the observed pattern. Selection was also invoked as a potential cause of the sharp geographic discontinuity between introgressed and non-introgressed samples, despite obvious dispersal and genetic exchanges. In the present study, the close genetic affinity between *S. mentella* and *S. fasciatus* relative to other samples provided further support for the role of introgression in determining the genetic composition of the Western population of *S. mentella*.

Relevance for management and conservation

The genetic structure of *S. mentella* in the North Atlantic only partially supports current management strategies. In the so-called Western regions (Labrador, Grand Bank, regions off Newfoundland, Gulf of St. Lawrence), eight main stock units are defined by the Northwest

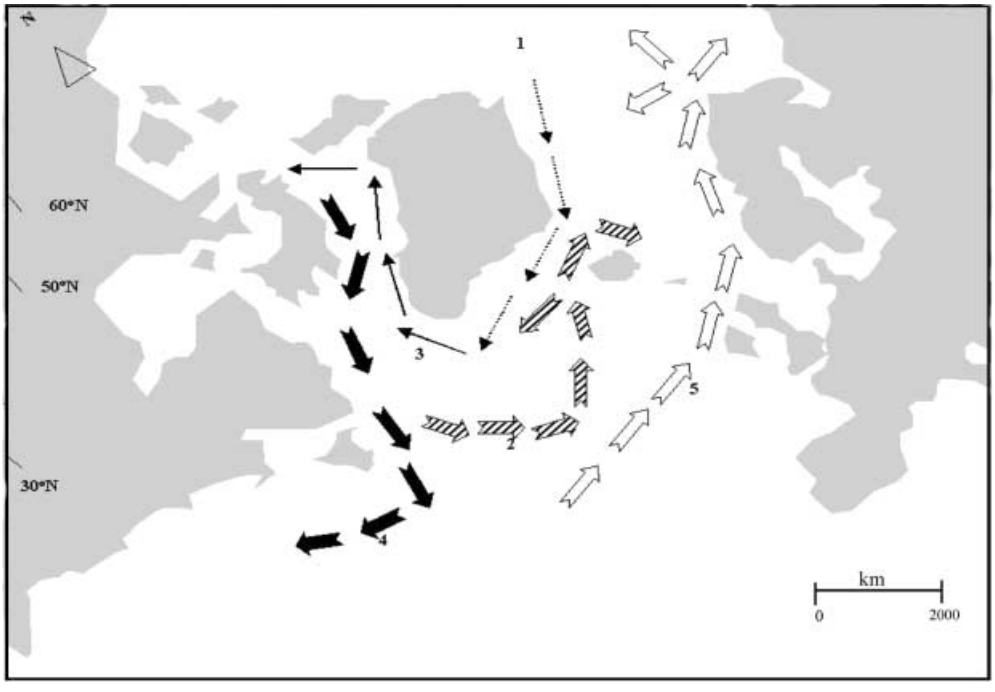

Fig. 5 Main oceanic currents in the North Atlantic (Couper 1983): *1*, *dotted arrow* east Greenland; *2*, *stripped arrow* Irminger Sea; *3*, *thin filled arrow* west Greenland; *4*, *thick filled arrow* Labrador; *5*, *open arrow* North Atlantic

Atlantic Fisheries Organisation on the basis of geographical and fisheries data. Because of the paucity of diagnostic characters, species composition has not been taken into account, and, consequently, management units may include a mixture of more than one redfish species. The potential usefulness and simplicity of redfish species discrimination using microsatellites was recently demonstrated, which could be considered in future management policies for this species complex (Roques et al. 1999b). The almost complete genetic homogeneity observed among samples of the Western population of *S. mentella* does not provide support for separate management by current regional subdivisions. Similarly, the lack of genetic differences between the Grand Banks and Labrador does not support the current management division. In the Eastern regions (from south Greenland to the Barents Sea), management programs based on both biological and geographical considerations commonly divide *S. mentella* into two main stock complexes, one associated with the Northeast Arctic (Norwegian zone) and the other with the Faroe Islands, Iceland and east Greenland regions, commonly referred to as the Irminger Sea stock complex (Reinert et al. 1992). The present study represents the first empirical test for the genetic discreteness of these putative stocks, and supports current management practices. More sampling in these regions is needed for definitive conclusions.

The most important conservation-related observation of this study, however, was the lack of significant genetic differences among samples currently under North American or European management regulations. Although migration rates sufficient to homogenise genetic variance may likely be too low to rapidly rebuild a depleted population (as discussed by Waples 1998), the single nearly panmictic *S. mentella* population extending from Labrador to the Faroe Islands may yet contribute to the fishery of both regions. Overharvesting in either North American (e.g. Labrador) or European (e.g. Irminger Sea) waters may have reciprocal consequences for recruitment and production. Thus, there is a need for more integrated management of the exploitation of *S. mentella* throughout its range in order to conserve this important fishery.

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