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Electrophoretic studies of cod (*Gadus morhua*) from Faroe Bank and Faroe Plateau compared with results found in other distribution areas.

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Abstract

The Faroe Bank covers a relatively small area with water masses fairly well isolated from the water masses on the Faroe Plateau. Individual growth of cod on the Faroe Bank is higher than observed in almost all other areas in the world. It has been shown that there are morpho- and physiological differences between cod from the Faroe Bank and cod on the Faroe Plateau.

In this paper results from electrophoretic studies are presented. In the genetic analyses there were no differences between cod living on the Faroe Plateau and on the Faroe Bank. This genetic similarity is caused by migration between the areas. No differences were detected in allele frequencies neither between the two sexes nor among different year classes neither within nor between the two populations. The results also show that there were no differences in mean size of cod within genotypes or among loci.

Indication of the genetic similarity between cod living on the Faroe Plateau and the Faroe Bank is in agreement with results found in similar investigations of Atlantic cod elsewhere .

Results from electrophoretic investigations of cod stocks in the North Atlantic show great genetic uniformity where local variations within populations often exceed variations between populations.

Keywords: cod; North Atlantic; Faroe Bank; Faroe Plateau; populations; genetic variation; electrophoresis

Introduction

The Faroe Bank is located about 70 km SW of the Faroes and is separated from the Faroe Plateau by the 850 m deep Faroe Bank Channel. The Faroe Bank covers a relatively small area. Inside the 200 m contour the size of the bank is 90 km in the NE-SW direction and 45 km in NW-SE direction. Its shallowest water is less than 100 m deep. The water masses on the Faroe Bank are fairly well isolated from the surrounding area. There is an anticyclonic circulation of the water masses on the Bank (Hansen et al. 1986; Hansen et al. 1991) and the plankton is different from that in the surrounding area (Paulsen 1909; Gaard and Mortensen 1993).

The cod on the Faroe Bank have one of the highest individual growth rate in the world. (Tåning 1943; Jones 1966; Habil et al. 1988). It has also been shown that there are differences between cod from the Faroe Bank and cod on the Faroe Plateau: In a growth experiment with equal environmental conditions Faroe Bank cod grew faster (Fjalsstein & Magnussen. 1996). Schmidt (1930) found differences in the number of vertebrae. The cod on the bank had fewer vertebrae and was more similar to the cod west of Shetland. Sørensen (1988) found that cod on the Faroe Plateau was more infected with parasites than cod on the Faroe Bank and found difference in the composition of parasites . Love et al. (1974) compared cod from the Faroe Bank with cod from 9 other fishing grounds. They found that cod on the Faroe Bank had the lowest water content in the flesh, the lowest post-mortem pH and the lowest heampigmentation in muscle of all cod populations.

Genetic analyses have also shown differences between the cod population on the Faroe Bank and Faroe Plateau. Jamieson and Jones (1967) showed that there were differences in the transferrin composition in the blood and that there was a significant isolation between the two populations. Jamieson and Birley (1989a) showed differences in the haemoglobin composition between the two areas. Their results also showed an imbalance in genotype distribution for the cod of Faroe Bank, and a big temporal variation in the allele frequencies. It has not been possible to discriminate between the two populations in all genetic analysis. Jamieson and Thompson (1972a) investigated the composition of butyric serum esterase in cod in their distribution range, but could not observe any differences between cod on the Faroe Bank and the Faroe Plateau. My genetic analysis is in accordance with this.

Since 1965 the cod stock on the Faroe Bank has been managed as a self-containing population.

The primary purpose of this project was to investigate possible genetic differences between cod on the Faroe Bank an on the Faroe Plateau.

Materials and methods

Blood and muscles used in the electrophoresis were sampled in 1992. The cod were caught by trawl, long-line and by jigging. Cod from the Faroe Bank was caught in the period June 4-11 (n=100). The Faroe Plateau cod was caught on July 24 (n=21) and on October 21 (n=88). The sampling areas are shown in fig 1. The cod from the Faroe Plateau for the most part belonged to the age groups 2-5 years. The average age was 3.2 years and the size 53.9 cm. Most of the Faroe Bank cod belonged to the age groups 5-7 years with an average age and size of 6.0 years and 86.3 cm respectively.

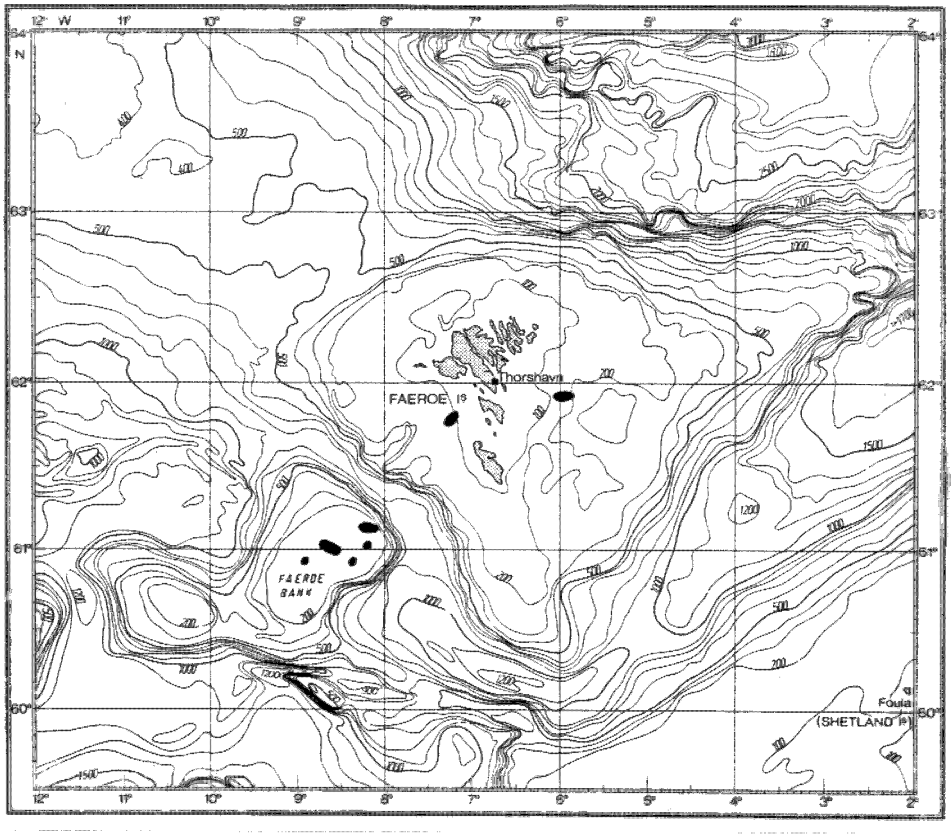

***Figure 1**: Sampling locations on the Faroe Plateau and on the Faroe Bank.*

Analysis of blood and muscle enzymes was done as described in Mork et al. (1982). 9 proteins were analysed: Haemoglobin (HEM), lactate dehydrogenase (LDH-3), glycerol-3-phosphate dehydrogenase (GPD), phosphoglucomutase (PGM-1), phosphogluco isomerase (PGI-1), isocitrate dehydrogenase (IDH-2), malate dehydrogenase (MDH), malic enzyme (ME), glyceraldehydphophate dehydrogenase (GAP).

Hardy-Weinberg proportion was tested with an Haldane's exact test (Haldane 1954). Where more than 3 alleles were observed they were pooled as described in Levene (1949). Comparisons of allele frequencies between areas were done by a χ^2-test. When observed gene frequencies were too low, Fisher's exact test was used as described in Siegel (1956). The genetic distance was measured as described in Nei (1978).

Results

In the genetic analysis 3 of the 9 analysed enzymes were monomorph (MDH, ME and GAP). Only half of the polymorph loci were also polymorph on the 95 % level. On average there were 2.33 and 2.17 alleles pr locus for cod from the two areas respectively. The difference in the allele number is due to lack of the GPD-135 allele on the Faroe Bank. The highest heterozygosity was observed for the LDH-3 locus for cod on the Faroe Plateau. It was 0.551. The average heterozygosity was 0.210 for the cod on the Faroe Plateau and 0.205 for the Faroe Bank cod. All polymorph loci were in Hardy-Weinberg equilibrium (P> 0.068) (Tab. 1). The two samples from the Faroe Plateau also showed Hardy-Weinberg proportion in all genotypes (P = 1.00).

Locus	Area	Genotype distribution						P
HEM		**1**	**1-2**	**2**				
	Faroe Plateau	0 (0,4)	13 (12,3)	93 (93,4)				1,000 N.S
	Faroe Bank	1 (0,6)	14 (14,8)	84 (83,6)				,482 N.S
LDH-3		**70/70**	**70/100**	**100/100**				
	Faroe Plateau	29 (30,7)	58 (54,5)	22 (23,7)				,565 N.S
	Faroe Bank	18 (20,1)	53 (48,8)	27 (29,1)				,421 N.S
GPD		**80/80**	**80/100**	**100/100**	**80/135**	**100/135**	**135/135**	
	Faroe Plateau	0 (0,0)	4 (4,9)	104 (103,1)	1 (0,0)	0 (1,0)	0 (0,0)	,068 N.S
	Faroe Bank	0 (0,0)	1 (1,0)	97 (97,0)	0 (0,0)	0 (0,0)	0 (0,0)	1,000 N.S
PGM-1		**30/30**	**30/100**	**100/100**				
	Faroe Plateau	0 (0,0)	5 (4,9)	104 (104,0)				1,000 N.S
	Faroe Bank	0 (0,1)	5 (4,9)	93 (93,1)				1,000 N.S
PGI-1		**30/100**	**30/150**	**100/100**	**100/150**	**150/150**	**30/30**	
	Faroe Plateau	2 (3,3)	3 (1,6)	45 (46,1)	50 (46,5)	9 (11,5)	0 (0,0)	,677 N.S
	Faroe Bank	3 (5,0)	5 (2,7)	40 (37,0)	37 (41,0)	12 (11,1)	0 (0,1)	,205 N.S
IDH-3		**80/80**	**80/100**	**100/100**				
	Faroe Plateau	0 (0,0)	1 (1,0)	108 (108,0)				1,000 N.S
	Faroe Bank	0 (0,0)	2 (2,0)	96 (96,0)				1,000 N.S

Table 1: *Observed and expected number of genotypes for cod on the Faroe Plateau and Faroe Bank. Observations are tested for Hardy-Weinberg proportion by Haldane's exact test.*

Locus	Area		Homogeneity test		
	Faroe Plateau	Faroe Bank	χ^2	D.F	P
HEM (N)	(106)	(99)	0,592	1	0,442 N.S
1	,061	,081			
2	,939	,919			
LDH-3 (N)	(109)	(98)	2,514	1	,113 N.S
70	,532	,454			
100	,468	,546			
GPD (N)	(109)	(98)	3,217	2	,200 N.S
80	,023	,005			
100	,972	,995			
135	,005	,000			
PGM-1 (N)	(109)	(98)	,029	1	,865 N.S
30	,023	,026			
100	,977	,974			
PGI-1 (N)	(109)	(97)	1,329	2	,515 N.S
30	,023	,041			
100	,651	,619			
135	,326	,340			
IDH-2 (N)	(109)	(98)	,453	1	,501 N.S
30	,005	,010			
100	,995	,990			
Total			8,132	8	0,421 N.S

Table 2: *Allele frequencies for cod caught on the Faroe Plateau and The Faroe Bank. The homogeneity is compared with a χ^2-test. N is the sample size. D.F is the degree of freedom. N.S. is not significant.*

Table 2 shows allele frequencies for cod on the Faroe Plateau and the Faroe Bank respectively. There were no significant differences in the allele frequencies between cod in the two populations (P> 0.113). The difference was highest in the LDH-3 locus. Neither were any significant differences found in allele frequencies between the two samples on Faroe Plateau(P > 0.052).

In table 3 the genotype distribution and the allele frequencies for female and male cod are shown.

Locus	Sex	Genotype					Allele frequencies		
HEM		**1**	**1-2**	**2**			**1**	**2**	
Faroe Plateau	Female	0 (0,3)	9 (8,4)	57 (57,3)			0,068	,932	
	Male	0 (0,1)	4 (3,8)	37 (37,1)			,049	,951	
Faroe Bank	Female	0 (0,2)	6 (5,6)	40 (40,2)			,065	,935	
	Male	1 (0,5)	8 (9,1)	44 (43,5)			,094	,906	
LDH-3		**70/70**	**70/100**	**100/100**			**70**	**100**	
Faroe Plateau	Female	18 (18,5)	35 (33,9)	15 (15,5)			,522	,478	
	Male	11 (12,3)	23 (20,3)	7 (8,3)			,549	,451	
Faroe Bank	Female	6 (7,4)	25 (22,1)	15 (16,4)			,402	,598	
	Male	12 (13,0)	28 (26,0)	13 (13,0)			,500	,500	
GPD		**80/100**	**100/100**	**80/135**			**80**	**100**	**135**
Faroe Plateau	Female	2 (2,9)	65 (64,1)	1 (0,0)			,022	,971	,007
	Male	0 (0,0)	39 (39,0)	0 (0,0)			,000	1,000	,000
Faroe Bank	Female	1 (1,0)	45 (45,0)	-			,011	,989	-
	Male	0 (0,0)	52 (52,0)	-			,000	1,000	-
PGM-1		**30/100**	**100/100**				**30**	**100**	
Faroe Plateau	Female	2 (2,0)	66 (66,0)				,015	,985	
	Male	3 (2,9)	38 (38,1)				,037	,963	
Faroe Bank	Female	1 (1,0)	45 (45,0)				,011	,989	
	Male	4 (3,8)	48 (48,1)				,038	,962	
PGI-1		**30/100**	**30/150**	**100/100**	**150/150**	**100/150**	**30**	**100**	**150**
Faroe Plateau	Female	2 (3,2)	3 (1,6)	27 (27,8)	5 (7,1)	31 (28,1)	,037	,640	,324
	Male	0 (0,0)	0 (0,0)	18 (18,4)	4 (4,4)	19 (18,1)	,000	,671	,329
Faroe Bank	Female	3 (3,1)	2 (1,6)	17 (17,7)	4 (4,9)	20 (18,6)	,054	,620	,326
	Male	0 (1,9)	3 (1,1)	23 (19,5)	8 (6,4)	17 (22,2)	,029	,618	,353
IDH-2		**80/100**	**100/100**				**80**	**100**	
Faroe Plateau	Female	1 (1,0)	67 (67,0)				,007	,993	
	Male	0 (0,0)	41 (41,0)				,000	1,000	
Faroe Bank	Female	0 (0,0)	46 (46,0)				,000	1,000	
	Male	2 (2,0)	50 (50,0)				,019	,981	

Table 3: *Genotype distribution and allele frequencies for female and male cod caught on the Faroe Plateau and the Faroe Bank. The number in parenthesis is the expected value according to the Hardy-Weinberg distribution.*

A comparison between female and male cod on the Faroe Plateau and on the Faroe Bank shows Hardy-Weinberg proportion in all genotypes and no significant sexual differences in the allele frequencies (P>0,168). The largest difference was also in this case in the LDH-3 locus.

The cod used in the genetic analyses are spawned in the period 1982-1990. To test for differences in the allele frequencies of age groups in this period, frequencies were regressed on age (tab.4). HEM, LDH-3, PGM-1 and IDH-2 only have 2 alleles. Because of this the slopes of the lines are equal but with opposite signs and only one is shown in the table. Only for the 30-allele in the PGI-1 locus from Faroe Bank cod, the slope of the regression was significantly different from zero (t = -2.596, P= 0.036) and this may well be spurious in so many regressions. For the Faroe Plateau cod the rare allele in

GPD, PGM-1 and IDH-2 only appears in the youngest age groups. Due to the low heterogeneity in these loci, the sample size is too small to draw any conclusion about selection on these alleles.

Locus		Faroe Plateau			Faroe Bank		
		Slope	t-value	P-value	Slope	t-value	P-value
HEM	1	-0,008649	-0,9899	0,368 N.S	-0,006504	-1,0473	0,330 N.S
LDH-3	100	0,027146	1,1118	0,317 N.S	-0,00996	-0,5682	0,588 N.S
GPD	80	-0,005542	-1,7195	0,146 N.S	-	-	-
	100	0,006618	2,1804	0,081 N.S	-0,006225	-1,0037	0,340 N.S
	135	-0,00107	-1,7506	0,144 N.S	-	-	-
PGM-1	100	0,006608	2,3650	0,064 N.S	0,00019	-0,712	0,945 N.S
PGI-1	30	0,001665	0,1660	0,875 N.S	-,013323	-2,5964	0,036 *
	100	0,033177	1,0488	0,342 N.S	0,009411	0,4759	0,649 N.S
	150	-0,041048	-1,8664	0,121 N.S	0,005044	0,2945	0,777 N.S
IDH-2	100	0,00107	1,7306	0,144 N.S	-0,000431	-0,3646	0,726 N.S

Table 4: *The slope from linear regression of allele frequencies where age of the cod is the independent variable. The slope is tested for deviation from zero. N.S = not significant. * = significant at the 5 % level*

To test for influence on growth rate by genotypes of the loci HEM, LDH-3 and PGI-1, the size of cod of different genotype but within the same locus and age group was compared (tab. 5). The only significant difference in size was in the LDH-3 locus for 4 years old of cod from the Faroe Plateau where the heterozygotes were longest. For the other loci there were no differences in cod size between genotypes within the age groups.

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Age (year)		Faroe Plateau								Faroe Bank			
		2		3		4		5		6		7	
Locus		Length (cm)	Weight (kg)	Length (cm)	Weight (kg)	Length (cm)	Weight (kg)	Length (cm)	Weight (kg)	Length (cm)	Weight (kg)	Length (cm)	Weight (kg)
HEM	1-2	48,3	1,290	-	-	-	-	-	-	-	-	92,0	8,151
	2	45,6	1,060	-	-	-	-	-	-	-	-	91,9	7,766
ANOVA	F	0,238	0,077	-	-	-	-	-	-	-	-	0,011	0,580
	P	0,628	0,783	-	-	-	-	-	-	-	-	0,917	0,451
LDH-3	70/70	44,4	1,014	52,3	1,608	55,0	2,063	64,5	2,873	-	-	90,5	7,550
	70/100	45,9	1,057	53,8	1,765	61,0	2,405	64,2	2,938	88,4	7,337	93,1	8,144
	100/100	47,5	1,214	51,0	1,433	-	-	-	-	86,8	7,008	91,3	7,572
ANOVA	F	1,494	0,580	0,484	0,033	6,521	0,012	0,004	0,162	1,194	0,596	1,046	1,122
	P	0,235	0,990	0,624	0,968	0,034 *	0,915	0,951	0,694	0,243	0,451	0,362	0,337
PGI-1	100/100	46,4	1,111	54,9	1,822	-	-	62,2	2,636	87,5	6,872	93,0	8,288
	150/150	-	-	-	-	-	-	-	-	-	-	90,4	7,840
	100/150	45,5	1,076	50,4	1,473	-	-	65,4	3,077	87,7	7,574	91,4	7,412
ANOVA	F	0,233	0,079	3,464	0,005	-	-	0,548	0,034	0,015	2,746	0,718	2,351
	P	0,793	0,924	0,081	0,945	-	-	0,473	0,857	0,904	0,117	0,495	0,110

***Table 5**: The average length and weight for 2 to 5 year old cod from the Faroe Plateau and for 6 and 7 years old cod from the Faroe Bank. A "-" indicates fewer than 4 specimens in the group. The results are compared by an ANOVA test. * = significant at the 5 % level.*

Historic tagging data

Table 6 shows the results from historic tagging experiments of cod on the Faroe Plateau and the Faroe Bank in the period 1909-1963. The figures in brackets are reported by the crewmembers of the catching vessels, the remaining tags were found in later stages of handling after fish had been landed, when it is often difficult to ascertain exactly the position of recapture. The calculated migration rates are also presented in the table

Year	Number tagged		Number recaptured			References	Migration rate	
	Faroe Plateau	Faroe Bank	Faroe Plateau	Faroe Bank	Other areas		Pl-->FB	FB-->Pl
1909-1913	3.501	585	1.572 2	85	1	Strubberg 1916	0	0,0230
1922-1927	1.871		488	1	1	Strubberg 1933	0,0020	
1932-1939	895		162	1		Tåning 1940	0.0061	
1952-1956	523		92	1	1	Joensen 1956	0,0106	
1959-1963	3.026	1.134	805 12(6)	18 (6) 197		Jones 1966	0,0073	0,0287
Total	9.816	1.719	3.119 8	9 282	3		0,0029	0,0276

Table 6*: Results from tagging experiments on cod from the Faroe Plateau (PL) and Faroe Bank (FB) in the period 1909 - 1963.*

The results show that the migration rate from the Faroe Plateau to the Faroe Bank in this period has varied from 0 to 0.0106 and that the migration from the bank to the plateau from 0.0230 to 0.0287. If all tagging experiments are pooled the, 95 % confidence interval for the migration rate from Faroe Plateau to Faroe Bank was between 0.10 % and 0.48 % pr generation and the migration rate from Faroe Bank to Faroe Plateau between 0.87 % and 4.56 % pr generation. Knowing the population sizes it can be calculated that the migration in absolute numbers between Faroe Plateau and Faroe Bank was 45,000 - 220,000 cod pr generation and between Faroe Bank and Faroe Plateau 13,000 - 74,000 pr generation. Based on Wrights island model the migration between the two areas is estimated to be approximately 80 cod pr generation.

Discussion

Enzyme polymorphism

In the present study, 6 of the 9 analysed enzymes were polymorph. The loci, which were polymorph for the two cod stocks in the Faroese area, are also polymorph in other cod stocks (see appendix). Me, MDH and GAP that are monomorph for the Faroese cod are polymorph in other areas (Mork et al. 1982; Mork et al. 1985; Grant & Ståhl 1988) .

Hardy-Weinberg proportion

The distributions of genotypes for the Faroe cod stocks were consistent with the Hardy-Weinberg (H-W) expectation (Tab. 1). This is also the case in most electrophoretic analysis made on cod. (Møller 1968; Mork et al. 1984b; Mork & Sundnes 1985a; Jørstad & Nævdal 1989; Gjøsætter et al. 1992). In an area with a mixed population the Wahlund effect will occur and there will be an excess of homozygous. This is the case in the middle of the Baltic Sea (Sick 1965b). Mork et al. (1985) investigated 13 loci from 9 areas and found H-W proportion for all loci except PGI-1 in cod from the Barents Sea. In an investigation

of cod in the White Sea H-W proportion didn't occur for HEM (Karpov 1984 et al.). Mork et al. (1987b) observed in one sample from cod in the Trondheim fjord that there was an excess of homozygous. Møller's (1968) investigation of cod in Northern Norway showed an excess in homozygous for most of the samples. The reason for the excess of the homozygous was the Wahlund effect. The sampling was done in the spawning period when cod from the Barents Sea and the Norwegian coast are mixed in a common spawning area.

Homogeneity between the Faroe Plateau and Faroe Bank
My investigation show no significant differences in the allele frequencies between the cod on the Faroe Plateau and Faroe Bank (tab.2) or between the two samples from the Faroe Plateau. This is in accordance with the findings of Jamieson & Thomson (1972a). This genetic homogeneity between Faroe Plateau and Faroe Bank cod is in accordance with the results found in most protein electrophoretic analyses of cod in other areas. The results show that the cod populations in the North Atlantic genetically are relatively homogeneous where local variation within populations in many cases is greater than variation between populations.

Global variation in allele frequencies
The most comprehensive genetic study of cod in the North Atlantic was done by Mork et al. (1985). In a study of ocean-wide genetic structure of Atlantic cod populations 13 of 19 loci were polymorph. Of this there where only 3 cases of significant differences in the allele frequencies among areas: LDH-3 and PGI-1 on the 1 % level and IDH-3 on the 5 % level. Also in the White Sea, cod populations seem to be genetically homogeneous (Karpov et al. 1984).

Jørstad (1984) found differences between Arctic and Norwegian coastal cod. He also found what appear to be local populations in some of the Norwegian fjords, but in his statistical analysis he compares the genotypes instead of the alleles. Jørstad & Nævdal (1989) have continued their genetic investigation of cod in Norwegian fjords. They collected samples from 28 areas. They do not present any statistical analysis of the material, but the conclusion was "*The G-test clearly showed heterogeneity in the material*" (Jørstad & Nævdal 1989). They also compare the genotypes. The variation found in Jørstad (1984) and Jørstad & Nævdal (1989) is on the same level as found by Mork et al. (1985) but they were not able to prove any differences. Gjøsæter et al (1992) have studied the cod in the Skagerrak. They compare their results with Jørstad (1984) and Jørstad & Nævdal (1989). Their conclusion was that investigation of muscle enzyme does not clearly show whether there are subpopulations of cod along the Norwegian coast or not.

The cod in the Baltic Sea
In many respects the cod in the Baltic Sea is different from Atlantic cod (Svetovidov 1948). Genetically cod in the Baltic Sea also is different from cod living in other areas (Mork et al. 1985; Grant & Ståhl 1988). Because of the low salinity, the Baltic Sea is an exceptional area, and many of the organisms living there are influenced by this (Muus 1979). Using LDH-3 and IDH-1 Moth-Poulsen (1982) divided Danish cod in to 4 populations. Comparing allele frequencies among areas, a clear change for both loci were showed along a transect. The allele frequency of the 70-allele in LDH-3 changed from 0.430 in Skagerrak to 0.140 at Gotland and the frequency of the 135-allele in IDH-1 changed from 0,140 in Skagerrak to 0,347 in the area around Bornholm. Haemoglobin also showed differences in the allele frequencies along the transect (Sick 1965b). Christiansen & Frydenberg (1974b) observed the same phenomena in *Zoarces viviparus* in the Baltic Sea and the Danish sounds.

Variation among populations
Genetic analyses have shown that most of the genetic variation in cod is within populations. Mork et al. (1985) found that only 2.1 % of the genetic variation of cod in the North Atlantic was between areas. Of this, half of the variation came from the Baltic Sea cod. Based on size variation in mtDNA fragments Árnason & Rand (1992) found 80 % of the genetic variation was on the individual level, 8 % between cod within populations and only 12 % among populations. Carr & Marshall (1991b) found from DNA-sequencing of cod in North America that more than 75 % of the genotypes were the same. In the rest

there were 24 base substitutions, of which most occur only once and none had frequencies higher than 3 %.

Local variations in allele frequencies
In electrophoretic analysis of cod, LDH-3 and PGI-1 have shown the highest variation. Mork et al. (1985) found that in the whole distribution range, excluding the Baltic Sea, the 100-allele in LDH-3 varied between 0.555 and 0.634 and of PGI-1 between 0.459 and 0.687. Other analyses have shown that local temporal variation is of the same order of magnitude and in some cases exceeds this. In 5 measurements of cod in Flødevig in the period 1989-1990 the frequencies of the100-allele in LDH-3 varied between 0.55 and 0.65 and of PGI-1 between 0.62 and 0.70 (Gjøsæter et al. 1992). In 4 measurements in the period 1989-1990 the frequencies of the 100-allele in LDH-3 for cod in Risør varied between 0.59 and 0.64 and between 0.65 and 0.69 of PGI-1. For cod in Stålvikbotn in Northern Norway the frequencies of the 100-allele in LDH-varied between 0.500 and 0.676 and in PGI-1 between 0.614 and 0.668 (Jørstad & Nævdal 1989). In the same analysis the frequencies of the 100-allele in LDH-3 in cod in the Balsfjord varied between 0.524 and 0.653 and between 0.647 and 667 of PGI-1.

Genetic distances
Nei's genetic distance between cod on the Faroe Plateau and Faroe Bank was 0.00161 while it was 0.00452 between the two samples of cod from the Faroe Plateau. These genetic distances are very small but are on the same level as found in other areas. In Mork et al. (1985) the largest genetic distance was observed between cod in the Baltic Sea and cod on the west coast of the Atlantic. It was about 0.001. Between cod on Georges Bank and the Baltic Sea, Grant & Stål (1988) found the genetic distance to be 0.0022. From RFLP DNA-analysis Árnason et al. (1992) found the genetic distance between cod in North America and Northern Norway to be 0.00839. The average genetic distance among cod from 6 areas around Iceland was 0.00286 (Àrnason et al. 1992). For comparison the genetic distance between Atlantic and Pacific cod is 0.390 (Grant 1987).

Variation in age classes and size
In my analysis there were no differences in allele frequencies among age groups or in mean size of cod among genotypes. This is in agreement with other investigations. (Mork et al. 1982; Gjøsæter et al. 1992; Svåsand et al. 1990a; Jørstad 1986). With the same way of comparing, Gjøsæter et al. (1992) found a significant difference in 2 out of 11 samples in mean length among HEM genotypes and in one sample for LDH-3.

Migration
The degree to which a population can be delimited from other populations depends on the level of gene-flow between them. An assumption for a genetic divergence caused by genetic drift only is that the migration between populations is less than 1 fish pr generation (Árnason et al. 1992). As pointed out earlier the genetic differences among cod populations in the North Atlantic seem to be small. This genetic homogeneity is due to migration among populations. In spite of the low migration rates between Faroe Bank and Faroe Plateau the absolute number is high because of size of the populations. The two methods used in estimating migration rates give very different results but both methods give migration values that are big enough to prevent the divergence, which would occur if the two areas were completely isolated. In addition to the migration between Faroe Bank and Faroe Plateau there are migrations from areas around the Faroes. Jones (1966) assumed the immigrations of cod to the Faroese area to be less than 1 % each year.

Tagging experiments on fish do not give a complete pattern of migration. The tagged fish are in most experiments adults and therefore do not tell anything about the migration of the youngest fish.

Haemoglobin
Of the loci used in genetic analysis of cod, haemoglobin has shown most variation. Haemoglobin polymorphism was fist described by Sick (1965). Since then several investigations have been done. In the table below the main results are summarised:

Area		Allele frequencies
Norwegian cod	Barents Sea	0,03 - 0,21
	Northern coast	,10 - ,41
	Southern coast	,36 - ,52
East Baltic Sea		,01 - ,05
Danish channels		,57 - ,64
North Sea		,55 - ,72
Faroes		,04 - ,10
Greenland and Island		,01 - ,02
North America	Newfoundland	,04
	Golf of Main	,07

Haemoglobin-1 allele frequencies for cod in the North Atlantic. (Sick 1965a; Sick 1965b; Frydenberg et al. 1965; Møller 1968)

Haemoglobin polymorphism in cod seems to be based on selective mechanisms. In a genetic investigation of cod Frydenberg et al. (1965) observed a decrease in HEM-1 frequencies along the Norwegian coast from being 0.7 in Skagerrak to 0.1 in the Barents Sea. Sick (1965a) observed the same phenomenon on the American East coast. Later Karpov & Novikov (1980) have shown that the oxygen affinity in haemoglobin is temperature dependent. HEM-(1/1) genotype was fairly stable while the affinity of HEM-(2/2) declines with increased temperature.

Karpov et al. (1984) found the HEM allele frequencies for cod caught in deep water in the White Sea to be lower than for cod caught in the shallower warmer water. Møller (1968) observed the same for Norwegian cod. For cod caught in shallow water the HEM-1 allele frequency was 0.32 while it was 0.14 for cod caught at 100-200 m depth. There are also observed temporal changes in the HEM allele frequencies. Gjøsæter et al. (1992) observed a HEM-1 allele frequencies of 0.65 while Frydenberg et al. (1965) observed 0.60. Jørstad & Nævdal (1989) and Mork et al. (1984c) found the same allele frequencies for cod in Northern Norway and in Trondheimsfjord as in Møller (1968) and Frydenberg (1965) respectively.

Haemoglobin for cod around the Faroes

The HEM allele frequency for cod on the Faroe Plateau seams to be stable. Sick (1965a) found the mean HEM-1 to be 0.06 and Jamieson & Birley (1989a) found it to vary between 0.06 and 0.09. In my analyses it was 0,06.

For cod on the Faroe Bank it was different. In my analyses it was 0.081. Jamieson & Birley (1989a) found in two samples the mean allele frequency to be 0.19. In this analysis there was a big temporal variation in the frequency; in May it was 0.08 while in November same year it was 0.68. Moreover the population was in Hardy-Weinberg imbalance. The results in November seem to be unrealistic. In the paper only the genotype distribution for the pooled data is presented. Knowing the allele frequencies and the sample size the expected distribution can be calculated:

Observed			Expected genotype distribution		
	N	q_1	1/1	½	2/2
May 1971	102	0,08	0,7	15,0	86,3

November 1971	21	0,68	9,7	9,1	2,2
Total for May and November Observed			10,4 11	24,1 25	88,5 87

The total of the expected genotypes in May and November is in agreement with the observations. Jamieson & Birley (1989a) have probably collected cod from two populations each having Hardy-Weinberg proportions which are distorted when pooled The high allele frequencies in November indicate that the collected cod could have their origin from the area west of Scotland where cod have similar allele frequencies (Jamieson & Thomson 1972b; Jamieson & Birley 1989a). As the ICES area Vb2 covers more than the Faroe Bank, the cod can be caught within ICES area Vb2 but not on the Faroe Bank.

As pointed out earlier the HEM-1 allele frequency increased with increasing water temperature. Thus the higher water temperature on the Faroe Bank compared to the Faroe Plateau is reflected in the differences in the allele frequencies for cod living in the two areas (Lastein 1992).

In spite of the correlation between HEM allele frequencies and the water temperature, this can not explain the big difference between allele frequency on the east and west coast of the North Atlantic. A linear regression based on allele frequencies and water temperature (T) in Karpov & Novikov (1980) gave the relationship:

$$[\text{HEM-1 allele frequency}] = 0.06579*T - 0.12565, \quad r = 0.90$$

Based on this equation the allele frequency for cod around the Faroe should be about 0.4. When these low allele frequencies exist in all cod populations on the western side of the North Atlantic there are probably also other selection mechanisms than temperature operating on haemoglobin.

Transferrin
Jamieson & Jones (1967) found differences in the transferrin composition between cod on the Faroe Bank and on the Faroe Plateau. They also found the difference between samples collected in May 1966 and Marts 1967 to be of the same order of magnitude as the difference between the populations.

Experience in using transferrin in genetics analysis of populations shows that the method is doubtful. By modifying the analytical method, Jamieson & Turner (1978) found a considerable change in the results. In the spawning period Mork (pers. com.) found an increased amount of bonds in the serum. These bonds interfere with the transferrin and make it difficult to distinguish the alleles. Because of this the genetic differences measured by Jamieson & Jones (1967) could be artefacts.

Genetic analyses of fish around the Faroes
Also other fish in the Faroe area appear to be genetically equal with fish in the surrounding areas. Lush (1970) found no difference in LDH frequencies in saithe (*Pollachius virens*) around the Faroes, Iceland, and the area west of Scotland. Fevolden & Haug (1988) analysed isoenzymes in halibut (*Hippoglossus hippoglossus*) caught around the Faroes, West Greenland and Norway, but found no differences between populations. In investigations by Jamieson & Birley (1989b), haddock (*Melanogrammus aeglefinus*) around the Faroes was not found to be an independent genetic population. Based on meristic and morphological methods (Reinert & Lastein 1992) redfish populations in the North Atlantic were separated. This separation could not be confirmed genetically (Nedreaas & Nævdal 1991).

Conclusions

In the genetic analyses there were no differences observed between cod living on the Faroe Plateau and on the Faroe Bank. This genetic homogeneity is caused by migration between the areas. Neither were any differences detected in allele frequencies between the two sexes or among year classes neither within nor between the two populations.

Genetic homogeneity between cod living on the Faroe Plateau and the Faroe Bank is in agreement with results found in similar investigations of cod elsewhere within the distribution range.

Cod populations in the North Atlantic are genetically relatively similar with local variations within populations often exceed by variations between populations

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