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No. 87

Population genetics of cod (*Gadus morhua* (L.)), haddock (*Melanogrammus aeglefinus* (L.)), whiting (*Merlangius merlangus* (L.)) and saithe (*Pollachius virens* (L.))

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CONTENTS

1. Introduction

Electrophoretic techniques have been used successfully to separate 'stocks' of fish. This report describes a series of population genetic studies made on four commercially important gadoid species — cod, haddock, whiting and saithe.

The concept of the 'unit stock' is fundamental to fisheries management. However, there are several different interpretations of what is meant by a 'stock' of fish. A synthesis of the definitions given by the International Commission for the North-West Atlantic Fisheries (ICNAF) (Anon., 1960), Beverton and Holt (1957) and Cushing (1981) describes a unit stock as a self-contained population with a single spawning ground. There are negligible changes in composition either by immigration or emigration and the stock is maintained in a steady state with adults returning annually to spawn. This description is essentially a Mendelian population which has been described as a large random-breeding group of a species in which changes by immigration, emigration, selection and mutation are negligible.

In practice, a stock defined for fisheries management purposes may not conform to these strict limitations. A typical stock description may simply relate to an aggregation of fish within a certain geographical area, determined to a great extent, by physical factors such as substrate and hydrography. Whilst recruitment to the stock is an essential factor in its maintenance, the origins of the recruits may not be known with certainty and, as a consequence, the genetic integrity of such a unit stock may be in doubt.

Several parameters have been used to distinguish fish stocks. These include the comparison of continuous morphometric characteristics such as growth rate (as revealed by age/length keys) and body proportions and comparisons of discrete meristic characters such as the numbers of fin rays or vertebrae. Morphometric variations were used by Yarrell (1836) and Day (1880-1884) to differentiate North Sea cod. Schmidt (1930) showed that there were variations in the numbers of 2nd dorsal fin-rays and in the numbers of vertebrae in North Atlantic cod. Variations in the relative rates of growth between year classes of herring. (*Clupea harengus* L.) were used to distinguish between three stocks in the North Sea (Cushing and Bridger, 1966).

Stocks have been identified by similarities in the patterns of annual rings laid down in the otoliths (Rollefsen, 1934; Trout, 1957; Holden, 1960). The amount of growth, estimated as the distance between the otolith nucleus and the first annual ring (L_1) can be used to distinguish between regional stocks of mackerel (*Scomber scombrus* L.) (Dawson, 1983).

All of these methods may be usefully employed to differentiate between spatially separated groups of fish. However, discrimination of the stocks is more likely to be based on their response to the environment at crucial stages in their development rather than on any genetic differences.

Tagging data have been used extensively to distinguish fish stocks. However, tagging is subject to a number of important constraints. Fish cannot be marked until they have reached a certain size. Eggs and larval fish cannot be studied by this method and it is, therefore, not possible to monitor the early life histories of the species. Tagging returns give a measure of the migration patterns of a species and supply information on longevity but they are subject, to a considerable extent, to the vagaries of fishing intensity and to the whims of the fishing fraternity. A number of species suffer high mortalities due to tagging, imposing practical limitations on the method.

The distribution of fish species infested with certain parasites has also been used to describe stocks (Kabata, 1958, 1967; Hislop and MacKenzie, 1976). The records are often confined to older fish whilst ignoring the early stages. It is highly likely that the information obtained describes the distribution of intermediate host species and the extent to which these species are associated with the species being studied. For example, Kabata (1958) reported that the parasite, *Lernaeocera* was absent in specimens of haddock captured at Faroe but was common in haddock from the northern North Sea. This distribution was found to be linked with the distribution of the parasite's intermediate host, the lemon sole (*Microstomus kitt).*

There can be no doubt that the above methods each contribute to the definition of fish stocks but, nevertheless, they play a limited part in the definition of a particular stock as a genetic entity. A genetic stock has been described as "any discrete breeding unit showing genetic variation" (Jamieson, 1974). In contrast to the previously described ecotypic characteristics, the genetic identity of an individual is determined at the moment of zygote formation and remains unchanged throughout its life. Modern techniques allow analysis of all stages of the fish's life cycle, including eggs and larvae.

The advantages of biochemical genetic analysis in stock identification were recognized by Cushing (1952), Marr and Sprague (1963) and Parrish (1964). Early results of electrophoretic analysis were presented at a special ICES meeting in Dublin in 1969 (de Ligny, 1971). Since then, a vast amount of information has been produced describing the genetics of populations of many species. Despite many advances in protein sequencing methodology and deoxyribonucleic acid (DNA) analysis, electrophoretic separation and histochemical staining of structural proteins and enzymes still provides the simplest method of analysing the gene products of an individual.

The search for electrophoretically-detectable polymorphic loci is generally made by utilising previously published methods and observations. In many fish species, variants at the transferrin and haemoglobin loci and polymorphic enzymes such as glucose phosphate isomerase *(GPI)*, phosphoglucomutase *(PGM)*, several dehydrogenases and esterases have proved to be useful in population studies. Samples from the areas of interest are analysed and the observed numbers of phenotypes are tested against the expected numbers determined from the genetic model known as the Hardy-Weinberg equilibrium. The results of this comparison show whether the population sample is representative of a random-breeding population. Deviations from the predictions of this genetic model may indicate population sub-division. For example, an excess of homozygotes could result from the mixing of two or more sub-populations. It may indicate that the sample contains different age groups having different gene frequencies due to variation in selective forces, or it may show the occurrence of different gene frequencies between male and female fish within the population. It is, thus, important to obtain as much biological information as possible, relating to the sample, before attempting to interpret the results. In the absence of deviations from genetic equilibrium, it may be possible to show that there are significant differences between samples from different areas which may indicate isolated populations of the species in question. Sample size is an important factor in population genetics since the variance of the gene frequency estimates is a function of 1/2N where N is the sample size. It is possible to obtain quite large differences in gene frequency between small samples and this random sampling error must be taken into account when interpreting the results of a population analysis.

Whilst significant differences between the gene frequencies of individual samples indicate a degree of stock differentiation, similarities between samples are more difficult to interpret. Such similarities may be due to a stable, balanced polymorphism which is entirely coincidental, so it is important to analyse as many different gene loci as possible in the study of population variation.

Much of the early work on fish population genetics was carried out on gadoids. Sick (1961a,b) analysed haemoglobin gene frequencies in cod and whiting. No significant differences were found at this locus between samples of either species in the North Sea. Jamieson (1970) and Jamieson and Thompson (1972a,b) studied variation at the haemoglobin, transferrin, lactate dehydrogenase *(LDH)* and butyric esterase loci in North Sea cod. Their results showed that there was no significant variation between cod samples in the North Sea. Dando (1974) described the *GPI* locus in cod. It was shown by Cross and Payne (1976, 1978) that there was some variation at this locus between cod from the east and west Atlantic Ocean. Lactate dehydrogenase isozymes have been studied in a number of gadoid species. Lush (1970), Odense *et al* (1969), Jamieson (1975) and Cross and Payne (1976) reported polymorphism at the *LDH-B* locus in cod. They found little variation in gene frequencies at this locus over the entire North Atlantic range of species. Lush (1970) and Odense *et al.* (1971) reported variation at two *LDH* loci in the saithe. Odense and Leung (1975) found evidence of polymorphism in haddock.

This report contains the results of analyses of *GPI* and *LDH* in cod, *GPI* and *LDH* in haddock, *PGM* and *GPI* in whiting and *LDH* and *GPI* in saithe.

2. Materials and methods

2.1 Sample collection

2.1.1 Cod—North Sea

The sampling sites are shown in Figure 1 and the sampling details (sample size, date and research vessel used) are given in Table 1.
Samples from the International Council for the Exploration of the Sea (ICES) statistical rectangles 34F1, 33F1 and 30F1 were 1-group cod caught in trawls from chartered vessels. The

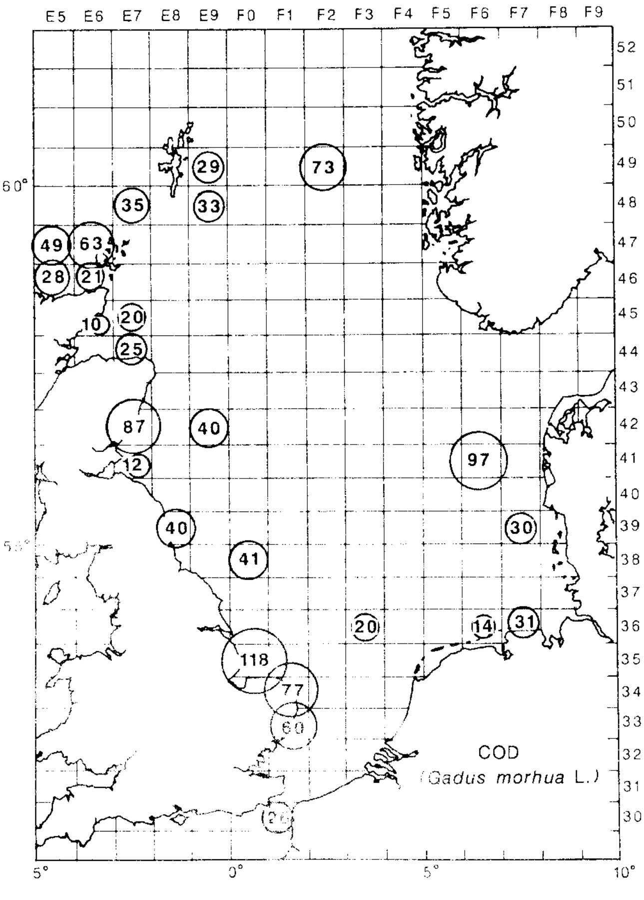

Figure 1 The distribution of sampling sites and the number of individual 0-group cod sampled at each site.

Note: Enzyme loci are referred to as italisised abbreviations e.g. *PGM*. Where there are multiple loci with different tissue distribution, the locus is given as uppercase descriptor e.g. *LDH-A* and *LDH-B*. Multiple allelic forms are numbered with a superscript according to the relative mobilities of the different isozymes coded. For example, the most common *LDH-B* allele is numbered $LDH\text{-}B^{100}$; a second hypothetical allele coding for an isozyme with twice the electrophoretic mobility would be designated $LDH\text{-}B^{200}$.

Table 1 Sampling details for cod, haddock, whiting and saithe

Species	Area	Sampling site[1] (ICES rectangle)	Specimens in sample	Age[2]	Vessel[3]	Date
Cod	North Sea	49E9	29	0	JH	1977
		49F2	73	0	EXP	1978
		48E7	35	0	COR	1978
		48E9	33	0	JH	1977
		47E5	49	0	EXP	1979
		47E6	63	0	COR	1978
		46E5	28	0	EXP	1979
		46E6	21	0	EXP	1979
		45E6	10	0	EXP	1977
		45E7	20	0	COR	1978
		44E7	25	0	EXP	1979
		42E7	87	0	COR	1978
		42E9	40	0	COR	1977
		41E7	12	0	COR	1977
		41F6	97	0	TRI	1977
		39E8	40	0	COR	1977
		39F7	30	0	CLI	1980
		38F0	41	0	COR	1977
		36F3	20	0	CIR	1980
		36F6	14	0	CLI	1980
		36F7	31	0	CLI	1980
		35F0	118	0	CHA	1980
		34F1	77	1	CHA	1980
		33F1	60	1	CHA	1980
		30F1	26	1	CHA	1977
	Irish Sea	35E4	31	0	CLI	5/1979
		38E5	37	0	CLI	5/1979
		37E5	55	1	CLI	5/1980
		37E6	26	1	CLI	5/1980
		36E4	20	1	CLI	5/1980
		35E6	27	1	CLI	5/1980
		34E3	22	1	CLI	5/1980
		37E5	40	1	COR	9/1980
		35E6	40	1	COR	9/1980
		33E3	50	1	COR	9/1980
Haddock	North Sea	51F1	20	0	EXP	1979
		50F1	20	0	EXP	1979
		50F3	11	0	JH	1979
		48F0	10	0	JH	1979
		47E7	20	0	CIR	1979
		47E7	20	0	EXP	1979
		46F0	20	0	CIR	1979
		45F4	48	0	CIR	1979
		42E8	20	0	CIR	1979
		42F2	20	0	CIR	1979
		41F0	20	0	CIR	1979
		41F5	20	0	JH	1979
Whiting	North Sea	47E8	40	1	CIR	8/1981
		45E7	40	1	CIR	8/1983

Table 1 Continued

Species	Area	Sampling site[1] (ICES rectangle)	Specimens in sample	Age[2]	Vessel[3]	Date
Whiting	North Sea	43E9	40	1	CIR	8/1983
		41E9	16	1	CIR	3/1983
		41F5	90	1	CIR	3/1983
		40E8	24	1	CIR	3/1983
		40F1	43	1	CIR	3/1983
		39F0	47	1	CIR	3/1983
		39F6	40	1	CIR	8/1981
		38F5	63	1	CIR	3/1983
		38F6	40	1	CIR	8/1983
		37F1	49	1	CIR	3/1983
		35F0	56	1	CIR	3/1983
		35F1	11	1	CIR	3/1983
		35F2	40	1	CIR	8/1983
		34F0	50	1	CHA	9/1979
		34F0	40	1	CHA	5/1980
		33F1	50	1	CHA	5/1980
		33F1	35	1	CIR	3/1983
Saithe	W. Ireland	38E0	39	–	CIR	7/1980
	S. Minch	42E2	13	–	CIR	7/1980
	S. Minch	42E2	9	–	CIR	3/1981
	W. Hebrides	43E0	24	–	CIR	3/1981
	Rockall	43D5	30	–	GAR	11/1981
	North Sea	51E8	49	–	CIR	3/1981
		51F0	33	–	CIR	3/1981
		49E8	9	–	CIR	3/1981
		49F0	16	–	CIR	8/1980
		47E8	8	–	CIR	8/1980
		47F0	22	–	CIR	8/1980
		47F2	43	–	CIR	8/1980
		45F4	22	–	CIR	8/1980

[1] ICES rectangles are statistical divisions of the sea areas as shown in the Figures

[2] 0=Spawned in the calendar year; 1=Spawned in the previous year; –=Age not determined

[3] CIR =RV CIROLANA, MAFF   GAR=RV G. A. REAY, MAFF-Torry*
COR =RV CORELLA, MAFF*   JH =RV JOHAN HJORT, Norway
CLI =RV CLIONE, MAFF*   TRI =RV TRIDENS, Holland
EXP =RV EXPLORER, DAFS   CHA =Chartered vessels

* Indicates research vessels in use at the time of the investigations but since withdrawn from service.

remaining samples were 0-group pelagic larvae collected with an International Young Gadoid Trawl (IYGT) during ICES sampling exercises between 1977 and 1980.

2.1.2 Cod—Irish Sea

0-group cod were collected in 1979 from two areas of larval concentration in the Solway Firth and off the east coast of Ireland. Both of these samples were caught using a Lowestoft frame trawl. 1-group cod were collected in 1980 using a Granton trawl. Sampling sites (Figure 2) and sampling details (Table 1) are given.

2.1.3 Haddock—North Sea

0-group specimens were collected using an IYGT in 1979. Sampling sites (Figure 3) and sampling details (Table 1) are given.

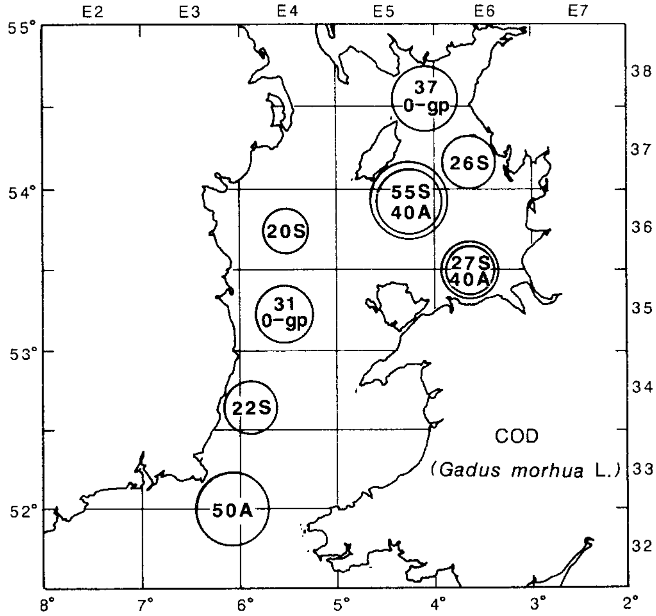

Figure 2 The distribution of sampling sites and the number of individuals sampled at each site. The two samples of 0-group cod (0-gp) were collected in the spring of 1979; the remaining samples of 1-group cod were collected in the spring (S) or autumn (A) of 1980.

2.1.4 Whiting — North Sea

1-group whiting were collected over the period 1979-1983 using commercial trawls. Sampling sites (Figure 4) and sampling details (Table 1) are given.

2.1.5 Saithe

Samples of saithe (not aged) between 30-70 cm in length were collected using commercial trawls. Specimens collected in the North Sea comprised pooled samples from blocks of four ICES statistical rectangles. Sampling sites (Figure 5) and sampling details (Table 1) are given.

2.2 Sample preservation and analysis

Whole fish, or blocks of skeletal muscle (saithe), were blast-frozen on the research vessel and transported (frozen) to the laboratory where they were stored at −20°C.

Samples were prepared for analysis by macerating a small amount of skeletal muscle (0.25g) in 0.2 cm^3 of 30% dimethylsulphoxide in 0.05M Tris/HCl buffer at pH 7.8 (modified from Dando, 1974).

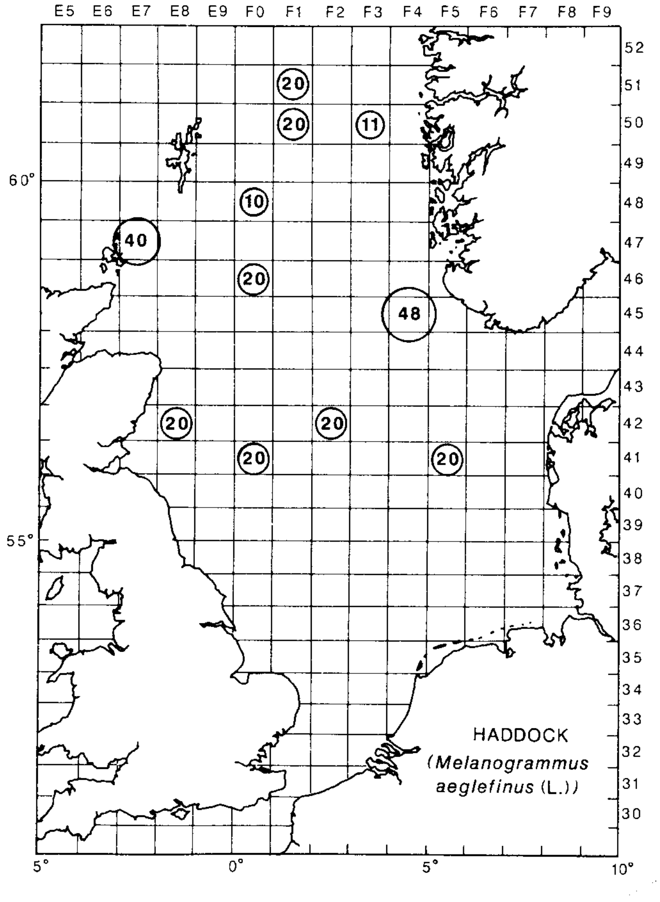

Figure 3 The distribution of sampling sites and the number of individual 0-group haddock sampled at each site.

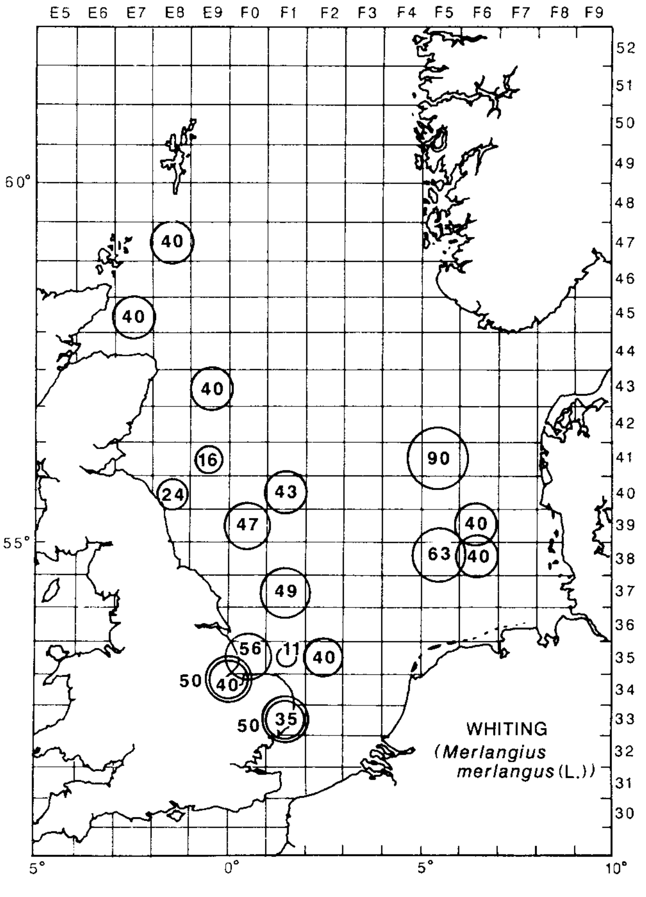

Figure 4 The distribution of sampling sites and the number of individual 1-group whiting sampled at each site. Two samples were collected from ICES rectangles 33F1 and 34F0 (see Table 1).

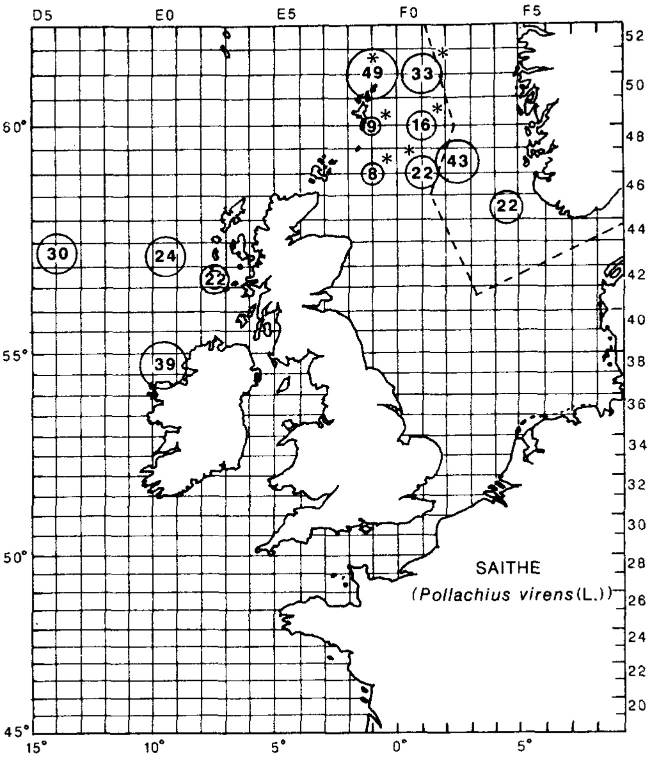

Figure 5 The distribution of sampling sites and the number of individual saithe sampled at each site. Two samples were collected from ICES rectangle 42E2 (see Table 1); circles marked with an asterisk are drawn in the centre of a block of four ICES rectangles from which the sample was taken; the dashed line shown in the North Sea represents the boundary between the EC and Norwegian Territorial Waters (see Subsection 3.5.3).

The supernatant was absorbed onto 5mm × 5mm squares of Whatman 3M filter paper which were inserted into 13% starch gels, prepared using a discontinuous buffer system (Ridgway *et al.*, 1970):

vessel buffer: 0.1M lithium hydroxide/0.24M boric acid;
gel buffer: 0.03M Tris/0.005M citric acid.

Gels were cut in half horizontally and the cut surfaces were stained for the appropriate enzyme. Enzyme staining methods were as described in Harris and Hopkinson (1976) with slight modifications. Staining solutions were modified by the replacement of phenazine methosulphate (PMS) with 0.2 cm^3 Meldola's Blue solution (0.4% in distilled water) in 25 cm^3 staining solution (Turner and Hopkinson, 1979). Meldola's Blue has the advantage over PMS in eliminating the blue background staining which occurs when PMS is exposed to light.

2.3 Statistical analysis

The numbers of each phenotype were tabulated and the gene frequencies of each allele were calculated. The expected numbers of each phenotype were estimated from the gene frequencies according to the Hardy-Weinberg model.

The observed numbers of homozygotes and heterozygotes were tested against the expected numbers for heterogeneity. The heterogeneity X^2 with N-2 degrees of freedom was found by subtracting the sum of individual X^2 values obtained for N samples from the X^2 value obtained for the population total. This X^2 value tests the null hypothesis that all samples are in genetic equilibrium.

Tests for contingency of allele distribution were made by calculating the expected numbers of alleles in each sample from the row (r) and column (c) totals and estimating the X^2 value with (r−1)(c−1) degrees of freedom by comparison with the observed numbers of alleles in each sample. This X^2 value estimates the probability that all samples are representative of a single population.

All calculations were performed using a Fortran 77 program (HGENE2) written by the author.

3. Results and discussion

3.1 Cod populations in the North Sea

Samples from 24 sites were analysed at the *GPI-B* locus and samples from 21 sites were analysed at the *LDH-B* locus.

3.1.1 Glucose phosphate isomerase (GPI-B: EC 5.3.1.9) analysis

This locus coded for dimeric codominant alleles. Isozyme activity was observed and was assumed to be controlled by three alleles $GPI\text{-}B^{142}$, $GPI\text{-}B^{100}$ and $GPI\text{-}B^{60}$.

Observed and expected phenotype numbers are shown in Table 2 together with the estimated allele frequencies. The heterogeneity X^2 test was not significant: $X^2_{22} = 20.057$; $0.7 > P > 0.5$ (Table 3).

The test for contingency of allele distribution was not significant: $X^2_{46} = 51.973$; $0.3 > P > 0.2$ (Table 4).

3.1.2 Lactate dehydrogenase (LDH-B: EC 1.1.1.27) analysis

This locus coded for tetrameric codominant alleles. Isozyme activity was assumed to be controlled by three alleles: $LDH\text{-}B^{117}$, $LDH\text{-}B^{100}$ and $LDH\text{-}B^{60}$.

Observed and expected phenotype numbers and gene frequencies are shown in Table 5. The heterogeneity X^2 test was not significant: $X^2_{19} = 15.165$; $0.8 > P > 0.7$ (Table 6). Phenotypes coded by $LDH\text{-}B^{117}$ were uncommon and in the contingency test these alleles were pooled with $LDH\text{-}B^{60}$ alleles. The contingency X^2 value was not significant: $X^2_{20} = 16.494$; $0.7 > P > 0.5$ (Table 7).

Table 2 Phenotype numbers and allele frequencies at the *GPI-B* locus in North Sea cod. (Expected phenotype numbers are shown in parentheses.)

Sampling Site (ICES rectangle)	Observed phenotypes						N	Allele frequencies		
	142/142	142/100	142/60	100/100	100/60	60/60		142	100	60
49E9	3	11		15			29	0.293	0.707	
	(2.5)	(12.0)		(14.5)						
49F2	4	39	1	27	2	0	73	0.329	0.561	0.021
	(7.9)	(31.2)	(1.0)	(30.9)	(2.0)	(0.0)				
48E7	0	17	0	17	1	0	35	0.243	0.743	0.014
	(2.1)	(12.6)	(0.2)	(19.3)	(0.7)	(0.0)				
48E9	4	17		12			33	0.379	0.621	
	(4.7)	(15.5)		(12.7)						
47E5	9	15	1	24	0	0	49	0.347	0.643	0.010
	(5.9)	(21.9)	(0.3)	(20.3)	(0.6)	(0.0)				
47E6	2	11	0	9	3	0	25	0.300	0.640	0.060
	(2.3)	(9.6)	(0.9)	(10.2)	(1.9)	(0.1)				
46E5	2	11	0	14	1	0	28	0.268	0.714	0.018
	(2.0)	(10.7)	(0.3)	(14.3)	(0.7)	(0.0)				
45E6	1	10	0	7	3	0	21	0.286	0.643	0.071
	(1.7)	(7.7)	(0.9)	(8.7)	(1.9)	(0.1)				
45E7	3	12		5			20	0.450	0.550	
	(4.1)	(9.9)		(6.0)						
44E7	3	14	0	6	2	0	25	0.400	0.560	0.040
	(4.0)	(11.2)	(0.8)	(7.8)	(1.1)	(0.0)				
42E7	2	6		9			17	0.294	0.706	
	(1.5)	(7.1)		(8.5)						
42E9	1	19	0	18	2	0	40	0.262	0.712	0.025
	(2.8)	(15.0)	(0.5)	(20.3)	(1.4)	(0.0)				
41E7	1	3	1	4	0	0	9	0.333	0.611	0.056
	(1.0)	(3.7)	(0.3)	(3.4)	(0.6)	(0.0)				
41F6	11	44	1	41	0	0	97	9.345	0.649	0.005
	(11.6)	(43.5)	(0.3)	(40.9)	(0.6)	(0.0)				
39E8	5	16	1	15	3	0	40	0.337	0.612	0.050
	(4.6)	(16.5)	(1.4)	(15.0)	(2.5)	(0.1)				
39F7	0	11		19			30	0.183	0.817	
	(1.0)	(9.0)		(20.0)						
38F0	5	16	1	16	2	0	40	0.337	0.625	0.038
	(4.6)	(16.9)	(1.0)	(15.6)	(1.9)	(0.1)				
36F3	1	10	0	8	1	0	20	0.300	0.675	0.025
	(1.8)	(8.1)	(0.3)	(9.1)	(0.7)	(0.0)				
36F7	2	7	1	3	1	0	14	0.429	0.500	0.071
	(2.6)	(6.0)	(0.9)	(3.5)	(1.0)	(0.1)				
36F7	4	11	0	14	2	0	31	0.306	0.661	0.032
	(2.9)	(12.6)	(0.6)	(13.6)	(1.3)	(0.0)				
35F0	14	51	4	45	4	0	118	0.352	0.614	0.034
	(14.6)	(51.0)	(2.8)	(44.5)	(4.9)	(0.1)				
34F1	9	34	2	27	5	0	77	0.351	0.604	0.045
	(9.5)	(32.6)	(2.5)	(28.1)	(4.2)	(0.2)				
33F1	3	28	2	27	0	0	60	0.300	0.683	0.017
	(5.4)	(24.6)	(0.6)	(28.0)	(1.4)	(0.0)				
30F1	2	17		6			25	0.420	0.580	
	(4.4)	(12.2)		(8.4)						

Table 3 Heterogeneity X^2 test for North Sea cod at the *GPI-B* locus. (Expected numbers are shown in parentheses.)

Sampling site (ICES rectangle)	Homozygotes	Heterozygotes	N	X^2	Sampling site (ICES rectangle)	Homozygotes	Heterozygotes	N	X^2
49E9	18	11	29	0.147	41E7	5	4	9	0.166
	(16.983)	(12.017)				(4.389)	(4.611)		
49F2	31	42	73	3.372	41F6	52	45	97	0.010
	(38.829)	(34.171)				(52.490)	(44.510)		
48E7	17	18	35	2.312	39E8	20	20	40	0.011
	(21.386)	(13.614)				(19.662)	(20.338)		
48E9	16	17	33	0.263	39F7	19	11	30	0.646
	(17.470)	(15.530)				(21.017)	(8.983)		
47E5	33	16	49	3.844	38F0	21	19	40	0.058
	(26.153)	(22.847)				(20.238)	(19.762)		
47E6	11	14	25	0.399	36F3	9	11	20	0.748
	(12.580)	(12.420)				(10.925)	(9.075)		
46E5	16	12	28	0.014	36F6	5	9	14	0.379
	(16.304)	(11.696)				(6.143)	(7.857)		
46E6	8	13	21	1.190	36F7	18	13	31	0.292
	(10.500)	(10.500)				(16.500)	(14.500)		
45E7	8	12	20	0.882	35F0	59	59	118	0.003
	(10.100)	(9.900)				(59.275)	(58.725)		
44E7	9	16	25	1.330	34F1	36	41	77	0.152
	(11.880)	(13.120)				(37.708)	(39.292)		
42E7	11	6	17	0.272	33F1	30	30	60	0.796
	(9.941)	(7.059)				(33.433)	(26.567)		
42E9	19	21	40	1.712	30F1	8	17	25	3.720
	(23.087)	(16.913)				(12.820)	(12.180)		
					Total	479	477		
						(504.2)	(451.8)		
					Sum of individual X^2_{33}		22.717		
					Total X^2_1		2.661		
					Heterogeneity X^2_{32}		20.057 $0.7 > P > 0.5$		

Table 4 Contingency test of allele distribution at *GPI-B* locus in North Sea cod. (Expected numbers in parentheses are calculated from row and column totals.)

Sampling site (ICES rectangle)	Alleles 142	Alleles 100	Alleles 60	N	X^2	Sampling site (ICES rectangle)	Alleles 142	Alleles 100	Alleles 60	N	X^2
49E9	17	41	0	58	1.956	41E7	6	11	1	18	0.741
	(19.020)	(37.554)	(1.426)				(5.903)	(11.655)	(0.442)		
49F2	48	95	3	146	0.099	41F6	67	126	1	194	3.159
	(47.878)	(94.533)	(3.589)				(63.618)	(125.61)	(4.769)		
48E7	17	52	1	70	2.830	39E8	27	49	4	80	2.276
	(22.955)	(45.324)	(1.721)				(26.234)	(51.799)	(1.967)		
48E9	25	41	0	66	2.213	39F7	11	49	0	60	7.953
	(21.643)	(42.734)	(1.622)				(19.676)	(38.849)	(1.475)		
47E5	34	63	1	98	0.935	38F0	27	50	3	80	0.628
	(32.137)	(63.454)	(2.409)				(26.234)	(51.799)	(1.967)		
47E6	15	32	3	50	2.675	36F3	12	27	1	40	0.142
	(16.396)	(32.374)	(1.229)				(13.117)	(25.900)	(0.983)		
46E5	15	40	1	56	1.105	36F6	12	14	2	28	4.305
	(18.364)	(36.259)	(1.377)				(9.182)	(18.130)	(0.688)		
46E6	12	27	3	42	3.979	36F7	19	41	2	62	0.254
	(13.773)	(27.195)	(1.032)				(20.332)	(40.144)	(1.524)		
45E7	18	22	0	40	3.388	35F0	83	145	8	236	1.639
	(13.117)	(25.900)	(0.983)				(77.391)	(152.810)	(5.801)		
44E7	20	28	2	50	1.867	34F1	54	93	7	154	3.424
	(16.396)	(32.374)	(1.229)				(50.501)	(99.713)	(3.786)		
42E7	10	24	0	34	1.133	33F1	36	82	2	120	0.829
	(11.150)	(22.015)	(0.836)				(39.351)	(77.699)	(2.950)		
42E9	21	57	2	80	1.567	30F1	21	29	0	50	2.873
	(26.234)	(51.799)	(1.967)				(16.396)	(32.374)	(1.229)		
						Total	627	1238	47	1912	
						Contingency $X^2_{46} = 51.973$		$0.3 > P > 0.2$			

Table 5 Phenotype numbers and allele frequencies at the *LDH-B* locus in North Sea cod. (Expected phenotype numbers are shown in parentheses.)

Sampling site (ICES rectangle)	Observed phenotypes					N	Allele frequencies		
	117/100	117/60	100/100	100/60	60/60		117	100	60
49F2			11	23	6	40		0.563	0.438
			(12.7)	(19.7)	(7.6)				
48E7			7	20	7	34		0.500	0.500
			(8.5)	(17.0)	(8.5)				
48E9			5	19	9	33		0.439	0.561
			(6.4)	(16.3)	(10.4)				
47E5			15	20	12	47		0.532	0.468
			(13.3)	(23.4)	(10.3)				
47E6			18	31	14	63		0.532	0.468
			(17.8)	(31.4)	(13.8)				
46E5			6	15	7	28		0.482	0.518
			(6.5)	(14.0)	(7.5)				
46E6	1	0	8	9	3	21	0.024	0.619	0.357
	(0.6)	(0.4)	(8.0)	(9.3)	(2.7)				
45E6			4	4	2	10		0.600	0.400
			(3.6)	(4.8)	(1.6)				
45E7	0	1	3	12	4	20	0.025	0.450	0.525
	(0.5)	(0.5)	(4.0)	(9.5)	(5.5)				
44E7			5	8	3	16		0.563	0.438
			(5.1)	(7.9)	(3.0)				
42E7			30	39	18	87		0.569	0.431
			(28.2)	(42.7)	(16.2)				
42E9			15	18	4	37		0.649	0.351
			(15.6)	(16.9)	(4.6)				
41E7			4	7	1	12		0.625	0.375
			(4.7)	(5.6)	(1.7)				
41F6	1	0	24	37	18	80	0.006	0.538	0.456
	(0.5)	(0.4)	(23.2)	(39.3)	(16.6)				
39E8			14	21	4	39		0.628	0.372
			(15.4)	(18.2)	(5.4)				
38F0	1	0	10	26	5	41	0.012	0.561	0.427
	(0.6)	(0.4)	(12.9)	(19.6)	(7.5)				
36F3			7	9	4	20		0.575	0.425
			(6.6)	(9.8)	(3.6)				
35F0	2	0	35	60	21	118	0.009	0.559	0.432
	(1.2)	(0.9)	(36.9)	(57.0)	(22.0)				
34F1			24	39	14	77		0.565	0.435
			(24.6)	(37.9)	(14.6)				
33F1			26	24	10	60		0.633	0.267
			(24.1)	(27.9)	(8.0)				
30F1			5	17	4	26		0.519	0.481
			(7.0)	(13.0)	(6.0)				

3.1.3 Discussion

Bedford (1966) reported that results from tagging experiments suggested that there were three main areas of cod spawning concentration in the North Sea. He also indicated that mature cod tagged in these areas did not migrate away from them to any significant extent but that, nevertheless, there was some limited mixing outside the spawning season. Holden and Raitt (1974) maintained that the North Sea cod represented the furthest departure from the concept of a unit stock. Basing their observations on tagging results, they suggested that the North Sea cod population was separated into a number of isolated stocks. This opinion was modified by Daan (1978) who stated "although the North Sea is certainly not built up of one homogeneous stock, it makes more sense, from a practical point of view, to consider the North Sea as a unit stock, rather than appoint 'sub-stocks' on the basis of arbitrary boundaries".

Genetic surveys of Sick (1965), Jamieson (1970) and Jamieson and Thompson (1972a, b) were in agreement in suggesting that the North Sea cod population was homogeneous. The results presented in this report on *GPI* and *LDH* confirm these findings and provide further support to the hypothesis that the North Sea cod constitute a single stock.

These results do not necessarily contradict the tagging results, if it is borne in mind that tagging results apply to adult fish. The movements of the pelagic larvae are not known. The wind-driven currents of the North Sea are highly variable and there is considerable mixing of the surface waters (J. N. Carruthers, quoted in Graham *et al.*, 1925). The pelagic phase of larval cod may last for three or more months and during this period it is quite feasible to propose that larvae

Table 6 Heterogeneity X^2 test for North Sea cod at the *LDH-B* locus. (Expected numbers are shown in parentheses.)

Sampling site (ICES rectangle)	Homozygotes	Heterozygotes	N	X^2	Sampling site (ICES rectangle)	Homozygotes	Heterozygotes	N	X^2
49F2	17	23	40	1.098	42E9	19	18	37	0.140
	(20.313)	(19.688)				(20.135)	(16.865)		
48E7	14	20	34	1.059	41E7	5	7	12	0.633
	(17.000)	(17.000)				(6.375)	(5.625)		
48E9	14	19	33	0.912	41F6	42	38	80	0.158
	(16.742)	(16.258)				(40.225)	(39.775)		
47E5	27	20	47	0.986	39E8	18	21	39	0.797
	(23.596)	(23.404)				(20.782)	(18.218)		
47E6	32	31	63	0.009	38F0	15	26	41	3.288
	(31.627)	(31.373)				(20.805)	(20.195)		
46E5	13	15	28	0.148	36F3	11	9	20	0.120
	(14.018)	(13.982)				(10.225)	(9.775)		
46E6	11	10	21	0.002	35F0	56	62	118	0.497
	(11.095)	(9.905)				(59.831)	(58.169)		
45E6	6	4	10	0.256	34F1	38	39	77	0.069
	(5.200)	(4.800)				(39.149)	(37.851)		
45E7	7	13	20	1.830	33F1	36	24	60	1.002
	(10.025)	(9.975)				(32.133)	(27.867)		
44E7	8	8	16	0.004	30F1	9	17	26	2.485
	(8.125)	(7.875)				(13.019)	(12.981)		
42E7	48	39	87	0.610					
	(44.328)	(42.672)							
					Total	446	463		
						(460.6)	(448.4)		

Sum of X^2 = 16.113

Total X^2 = 0.949

Heterogeneity X^2_{19}= 15.165 $0.8 > P > 0.7$

Table 7 Contingency test of allele distribution at the *LDH-B* locus in North Sea cod. (Expected numbers in parentheses are calculated from row and column totals.)

Sampling site (ICES rectangle)	Alleles 100	Alleles 60[1]	N	X^2	Sampling site (ICES rectangle)	Alleles 100	Alleles 60[1]	N	X^2
49F2	45	35	80	0.006	42E9	48	26	74	2.449
	(44.664)	(35.336)				(41.315)	(32.685)		
48E7	34	34	68	0.937	41E7	15	9	24	0.433
	(37.965)	(30.035)				(13.399)	(10.601)		
48E9	29	37	66	3.784	41F6	86	74	160	0.281
	(36.848)	(29.152)				(89.329)	(70.671)		
47E5	50	44	94	0.265	39E8	49	29	78	1.545
	(52.481)	(41.519)				(43.548)	(34.452)		
47E6	67	59	126	0.360	38F0	46	36	82	0.002
	(70.347)	(55.653)				(47.781)	(36.219)		
46E5	27	29	56	1.317	36F3	23	17	40	0.045
	(31.265)	(24.735)				(22.332)	(17.668)		
46E6	26	16	42	0.628	35F0	132	104	236	0.001
	(23.449)	(18.551)				(131.760)	(104.240)		
45E6	12	8	20	0.141	34F1	87	67	154	0.027
	(11.166)	(8.834)				(85.979)	(68.021)		
45E7	19	21	40	1.126	33F1	76	44	120	2.739
	(22.332)	(17.668)				(66.997)	(53.003)		
44E7	18	14	32	0.002	30F1	27	25	52	0.322
	(17.866)	(14.134)				(29.032)	(22.968)		
42E7	99	75	174	0.080					
	(99.145)	(76.855)							
					Total	1015	803	1818	

Contingency X^2_{20} = 16.494 $0.7 > P > 0.5$

LDH-B^{117} pooled with *LDH-B*^{60}

from any number of isolated spawning grounds may be mixed together. The consequences of mixing, in genetic terms, is the production of a homogeneous population. Recruitment to an isolated stock must be from within the stock if it is to maintain its genetic integrity. It is highly unlikely that this condition can be maintained in the North Sea.

3.2 Cod populations in the Irish Sea

Samples collected in the spring of 1979 (2), the spring of 1980 (5) and the autumn of 1980 (3) were analysed for *GPI-B*. The samples collected in the spring of 1979 and the spring of 1980 were also analysed for *LDH-B*.

3.2.1. Glucose phosphate isomerase (GPI-B: EC 5.3.1.9) analysis

Evidence for seven alleles was found at this locus (four of which were uncommon (*)). They were $GPI\text{-}B^{166}$*, $GPI\text{-}B^{142}$, $GPI\text{-}B^{133}$*, $GPI\text{-}B^{109}$*, $GPI\text{-}B^{100}$, $GPI\text{-}B^{65}$*, and $GPI\text{-}B^{60}$ For the calculation of the contingency X^2 the uncommon alleles were combined with the $GPI\text{-}B^{60}$ alleles. Observed and expected phenotype numbers and gene frequencies are shown in Table 8. The heterogeneity test was not significant: $X^2_8 = 11.180$; $0.3 > P > 0.2$ (Table 9). The contingency test of allele distribution was highly significant: $X^2_{18} = 41.423$; $0.01 > P > 0.001$ (Table 10).

The difference in allele distribution for the two 0-group cod samples collected in 1979 was significant: $X^2_2 = 17.973$; $P > 0.001$. The 1-group cod collected in 1980 were compared with each of the 0-group samples and it was found that those cod collected in spring 1980 from the west of the Irish Sea (ICES rectangles 36E4 and 34E3) and from the east of the Isle of Man (ICES rectangle 36E5) were significantly different from the Solway Firth sample. The sample collected off St Bees Head (ICES rectangle 37E6) was significantly different from the Kish Bank 0-group sample off Dublin (ICES rectangle 35E4). The sample from North Wales (ICES rectangle 35E6) was more similar to the Solway Firth population than to the Kish Bank population, although it was not significantly different from either group (Table 11a). None of the samples collected in the autumn of 1980 was significantly different from the Solway Firth sample but the St Bees Head and North Wales samples were both significantly different from the Kish Bank group (Table 11b).

3.2.2 Lactate dehydrogenase (LDH-B: EC 1.1.1.27) analysis

The isozymes observed at this locus were assumed to be controlled by three alleles: $LDH\text{-}B^{117}$, $LDH\text{-}B^{100}$, and $LDH\text{-}B^{60}$. The observed and expected phenotype numbers and the gene frequencies are shown in Table 12. The heterogeneity test was not significant: $X^2_5 = 5.021$; $0.5 > P > 0.3$ (Table 13). The contingency test of allele distribution in which $LDH\text{-}B^{117}$ alleles were combined with $LDH\text{-}B^{60}$ alleles was not significant: $X^2_6 = 5.373$; $0.5 > P > 0.3$ (Table 14).

Table 8 Phenotype numbers and allele frequencies at the *GPI-B* locus in Irish Sea cod. (Expected phenotype numbers are shown in parentheses.)

Sampling site (ICES rectangle)	Season[1] Year Age[2]	Observed phenotypes										N	Allele frequencies						
		166/100	142/142	142/100	142/65	142/60	133/100	109/60	100/100	100/65	100/60		166	142	133	109	100	65	60
38E5	S-79-0		1	16		0			18		2	37		0.243			0.730		0.027
			(2.2)	(13.1)		(0.5)			(19.7)		(1.5)								
35E4	S-79-0		6	16		5			3		1	31		0.532			0.371		0.097
			(8.8)	(12.2)		(3.2)			(4.3)		(2.2)								
37E5	S-80-1		8	29		3	1		11		3	55		0.435	0.009		0.500		0.056
			(10.2)	(23.5)		(2.6)	(0.5)		(13.5)		(3.0)								
37E6	S-80-1		2	11		0			12		1	26		0.288			0.692		0.020
			(2.2)	(10.4)		(0.03)			(12.5)		(0.7)								
36E4	S-80-1		2	11	1	1			4	0	1	20		0.425			0.500	0.025	0.050
			(3.6)	(8.5)	(0.4)	(0.9)			(5.0)	(0.5)	(1.0)								
35E6	S-80-1		5	11					11			27		0.389			0.611		
			(4.1)	(12.8)					(10.1)										
34E3	S-80-1		4	7	0	2	1		5	1	2	22		0.386	0.023		0.477	0.023	0.091
			(3.3)	(8.1)	(0.4)	(1.6)	(0.5)		(5.0)	(0.5)	(1.9)								
37E5	A-80-1		5	12	0	0			20	1	2	40		0.275			0.687	0.013	0.025
			(3.0)	(15.1)	(0.3)	(0.6)			(18.9)	(0.7)	(1.4)								
35E6	A-80-1	1	6	13		1			19		1	40	0.013	0.313			0.650		0.024
		(0.7)	(3.9)	(16.3)		(0.6)			(16.9)		(1.3)								
33E3	A-80-1		4	22		1		1	18		4	50		0.310		0.010	0.620		0.060
			(4.8)	(19.2)		(1.9)		(0.06)	(19.2)		(3.7)								

[1] S = May
A = September

[2] 0 = Spawned in the calendar year
1 = Spawned in the previous year

Table 9 Heterogeneity X^2 for Irish Sea cod at the *GPI-B* locus. (Expected numbers are shown in parentheses.

Sampling site (ICES rectangle)	Season[1] Year Age[2]	Homozygotes	Heterozygotes	N	X^2
38E5	S-79-0	19 (21.919)	18 (15.081)	37	0.954
35E4	S-79-0	9 (13.339)	22 (17.661)	31	2.477
37E5	S-80-1	19 (24.445)	36 (30.555)	55	2.184
37E6	S-80-1	14 (14.635)	12 (11.365)	26	0.063
36E4	S-80-1	6 (8.725)	14 (11.257)	20	1.510
35E6	S-80-1	16 (14.167)	11 (12.833)	27	0.499
34E3	S-80-1	9 (8.705)	13 (13.295)	22	0.017
37E5	A-80-1	25 (21.988)	15 (18.012)	40	0.917
35E6	A-80-1	25 (20.538)	15 (19.462)	40	1.993
33E3	A-80-1	22 (24.830)	28 (25.170)	50	0.641
Total		164 (166.66)	184 (181.4)		

Sum of X^2 Values 11.253
Total X^2 Value 0.073
Heterogeneity X_8^2 = 11.180 0.3 > P > 0.2

[1] S = May
A = September
[2] 0 = Spawned in the calendar year
1 = Spawned in the previous year

Table 10. Contingency test of allele distribution at the *GPI-B* locus in Irish Sea cod. (Expected numbers in parentheses are calculated from row and column totals.)

Sampling site (ICES rectangle)	Season[1] Year Age[2]	Alleles 142	100	60[3]	N	X^2
38E5	S-79-0	18 (26.368)	54 (43.698)	2 (3.934)	74	6.035
35E4	S-79-0	33 (22.092)	23 (36.612)	6 (3.296)	62	12.665
37E5	S-80-1	48 (39.195)	55 (64.957)	7 (5.848)	110	3.731
37E6	S-80-1	15 (18.529)	36 (30.707)	1 (2.764)	52	2.711
36E4	S-80-1	17 (14.253)	20 (23.621)	3 (2.126)	40	1.443
35E6	S-80-1	21 (19.241)	33 (31.888)	0 (2.871)	54	3.070
34E3	S-80-1	17 (15.678)	21 (25.983)	6 (2.339)	44	6.797
37E5	A-80-1	22 (28.506)	55 (47.241)	3 (4.253)	80	3.128
35E6	A-80-1	26 (28.506)	51 (47.241)	3 (4.253)	80	0.888
33E3	A-80-1	31 (35.632)	63 (59.052)	6 (5.316)	100	0.954
Total		248	411	37	696	

Contingency X_{18}^2 = 41.423 0.01 > P > 0.001

[1] S = May
A = September
[2] 0 = Spawned in the calendar year
1 = Spawned in the previous year
[3] *GPI-B*^{166}, *GPI-B*^{133}, *GPI-B*^{109} and *GPI-B*^{65} pooled with *GPI-B*^{60}

3.2.3 *Discussion*

The results presented for the Irish Sea cod show that, in June 1979, there was evidence for two populations of larval 0-group cod represented by samples from the Solway Firth and the eastern coast of Ireland. These samples were genetically distinct. Further sampling, in the early summer of the following year, revealed that the sample from the eastern Irish Sea had similar gene frequencies to the Solway Firth larval sample and that the sample from the western Irish Sea had similar gene frequencies to the 1979 Irish sample. These findings suggest that the two populations remained isolated over this period.

The results obtained from samples collected in the autumn of 1980 were less conclusive and it is possible that, by this time, the older fish had moved away from their nursery grounds and mixed with cod from elsewhere as suggested by Brander (1975).

The distribution of larval cod in the Irish Sea for June 1979 is shown by Brander and Symonds (1984). The contours drawn (Figure 225 of Brander and Symonds, 1984) indicate that all of the larvae caught by the MAFF research vessel CLIONE, which made up the two samples analysed here, originated from spawning grounds off Carlingford Lough, Northern Ireland. K. Brander (personal communication) has suggested that two genetically isolated groups could be present on these grounds. If this is correct, then it is necessary to explain the mechanism by which individuals of one population, with predominantly *GPI-B*^{142} genotypes, tended to drift southwards and those of the other population, with predominantly *GPI-B*^{100} genotypes, drifted eastwards. A simpler explanation would be to suggest that the Solway Firth larvae were spawned in the eastern Irish Sea on the St Bees ground and the western Irish Sea larvae were spawned on the Irish coastal ground. The results, from the survey by the French research vessel THALLASA in June 1979, showed

Table 11 Comparison of *GPI-B* allele numbers for 0-group Irish Sea cod collected from Solway Firth and Kish Bank in spring 1979 with 1-group cod collected in spring (a) and autumn (b) in the following year (1980). Each 1-group cod sample is compared with each of the two 0-group samples in a 3 × 2 contingency test. X^2 values with two degrees of freedom are given together with the probability estimate for each comparison.

Area	Sampling site (ICES rectangle)	Alleles 142	100	60	X^2_2	*P*	Area	Sampling site (ICES rectangle)	Alleles 142	100	60	X^2_2	*P*
0-group cod (spring 1979) Solway Firth	38E5	18	54	2			Kish Bank	35E4	33	23	6		
a. 1-group cod (spring 1980)													
E. Isle of Man	37E5	48	55	7	9.75	0.01-0.001		37E5	48	55	7	2.81	0.3-0.2
W. Irish Sea	36E4	17	20	3	6.27	0.05-0.02		36E4	17	20	3	1.66	0.5-0.3
S.E. Ireland	34E3	17	21	6	9.54	0.01-0.001		34E3	17	21	6	2.22	0.5-0.3
St Bees Head	37E6	15	36	1	0.38	0.9-0.8		37E6	15	36	1	12.40	0.01-0.001
N. Wales	35E6	21	33	0	4.28	0.2-0.1		35E6	21	33	0	5.10	0.1-0.05
b. 1-group cod (autumn 1980)													
E. Isle of Man	37E5	22	55	3	0.367	0.9-0.8		37E5	22	55	3	14.40	<0.001
N. Wales	35E6	25	52	3	1.170	0.7-0.5		35E6	25	52	3	11.36	0.01-0.001
S.E. Ireland	33E3	15	20	3	5.026	0.1-0.05		33E3	15	20	3	2.38	0.5-0.3

Table 12 Phenotype numbers and allele frequencies at the *LDH-B* iocus in Irish Sea cod. (Expected phenotype numbers are shown in parantheses)

Sampling site (ICES rectangle)	Season[1] Year Age[2]	Observed phenotypes 117/100	100/100	100/60	60/60	N	Allele frequencies 117	100	60
38E5	S-79-0		11 (10.3)	17 (18.5)	9 (8.3)	37		0.527	0.473
35E4	S-79-0		8 (11.5)	22 (16.0)	3 (5.5)	33		0.591	0.409
37E5	S-80-1	1 (0.5)	9 (12.6)	33 (26.5)	11 (14.0)	54	0.009	0.482	0.509
37E6	S-80-1		5 (6.0)	15 (13.0)	6 (7.0)	26		0.481	0.519
36E4	S-80-1		7 (7.8)	11 (9.4)	2 (2.8)	20		0.625	0.375
35E6	S-80-1		9 (9.5)	14 (13.0)	4 (4.5)	27		0.593	0.407
34E3	S-80-1		4 (4.6)	12 (10.9)	6 (6.5)	22		0.455	0.545

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[1] S = May
A = September

[2] 0 = Spawned in the calendar year
1 = Spawned in the previous year

Table 13 Heterogeneity X^2 test for Irish Sea cod at the *LDH-B* locus. (Expected numbers are shown in parentheses.)

Sampling site (ICES rectangle)	Season[1] Year Age[2]	Homo-zygotes	Hetero-zygotes	N	X^2
38E5	S-79-0	20	17	37	0.226
		(18.554)	(18.446)		
35E4	S-79-0	11	22	33	4.191
		(16.879)	(16.121)		
37E5	S-80-1	20	34	54	3.668
		(27.037)	(26.963)		
37E6	S-80-1	11	15	26	0.627
		(13.019)	(12.981)		
36E4	S-80-1	9	11	20	0.530
		(10.625)	(9.375)		
35E6	S-80-1	13	14	27	0.138
		(13.963)	(13.037)		
34E3	S-80-1	10	12	22	0.216
		(11.091)	(10.909)		
Total		94	125		
		(109.8)	(109.2)		

Sum of X^2 value = 9.597
Total X^2 value = 4.576
Heterogeneity X_6^2 = 5.021 $0.5 > P > 0.3$

[1] S = May
A = September
0 = Spawned in the calendar year
1 = Spawned in the previous year

Table 14 Contingency test of allele distribution at the *LDH-B* locus in Irish Sea cod. (Expected numbers in parentheses are calculated from row and column totals.)

Sampling site (ICES rectangle)	Season[1] Year Age[2]	Alleles 100	Alleles 60[3]	N	X^2
38E5	S-79-0	39	35	74	0.00004
		(39.027)	(34.973)		
35E4	S-79-0	38	28	66	0.619
		(34.808)	(31.192)		
37E5	S-80-1	52	56	108	0.914
		(56.959)	(51.041)		
37E6	S-80-1	25	27	52	0.454
		(27.425)	(24.575)		
36E4	S-80-1	25	15	40	1.529
		(21.096)	(18.904)		
35E6	S-80-1	32	22	54	0.921
		(28.479)	(25.521)		
34E3	S-80-1	20	24	44	0.937
		(23.205)	(20.795)		
Total		231	207	438	

Contingency X_6^2 = 5.373 $0.5 > P > 0.3$

[1] S = May
[2] 0 = Spawned in the calendar year
1 = Spawned in the previous year
[3] *LDH-B* pooled with *LDH-B*^{60}

Table 15 Phenotype numbers and allele frequencies at the *GPI-A* locus in North Sea haddock. (Expected phenotype numbers are shown in parentheses.)

Sampling site (ICES rectangle	Observed phenotypes 100/100	Observed phenotypes 100/96	Observed phenotypes 96/96	N	Allele frequencies 100	Allele frequencies 96
50F1	4	3	3	10	0.550	0.450
	(3.0)	(4.9)	(2.0)			
50F3	5	5	1	11	0.682	0.318
	(5.1)	(4.8)	(1.1)			
48F0	4	6	0	10	0.700	0.300
	(4.9)	(4.2)	(0.9)			
47E7	7	11	2	20	0.625	0.375
	(7.8)	(9.4)	(2.8)			
46F0	7	8	5	20	0.550	0.450
	(6.0)	(9.9)	(4.1)			
45F4	16	27	5	48	0.615	0.385
	(18.1)	(22.7)	(7.1)			
42E8	7	13	0	20	0.675	0.325
	(9.1)	(8.8)	(2.1)			
42F2	7	8	5	20	0.550	0.450
	(6.0)	(9.9)	(4.1)			
41F0	7	9	4	20	0.575	0.425
	(6.6)	(9.8)	(3.6)			
41F5	4	8	7	20	0.421	0.579
	(3.4)	(9.3)	(6.4)			

Table 16 Heterogeneity X^2 test for haddock at the *GPI-A* locus. (Expected numbers are shown in parentheses.)

Sampling site (ICES rectangle)	Homozygotes	Heterozygotes	N	X^2
50F1	7	3	10	1.521
	(5.050)	(4.950)		
50F3	6	5	11	0.019
	(6.227)	(4.773)		
48F0	4	6	10	1.330
	(5.800)	(4.200)		
47E7	9	11	20	0.530
	(10.625)	(9.375)		
46F0	12	8	20	0.722
	(10.100)	(9.900)		
45F4	21	27	48	1.517
	(25.260)	(22.740)		
42E8	7	13	20	3.625
	(11.225)	(8.775)		
42F2	12	8	20	0.722
	(10.100)	(9.900)		
41F0	11	9	20	0.120
	(10.225)	(9.775)		
41F5	11	8	19	0.336
	(9.737)	(9.263)		
Total	100	98		
	(102.3)	(95.7)		

Sum of X^2 values = 10.442
Total X^2 value = 0.104
Heterogeneity X_8^2 = 10.338 $0.3 > P > 0.2$

concentrations of larvae off the Cumbrian coast and off the Irish coast. The distribution is given by Brander and Symonds (1984).

It is apparent from the results of the biochemical analysis that two genetically distinct populations remained separated for at least one season. They may then disperse and mix but if, as suggested by Brander (1975) the adult cod return to their original spawning grounds, then this could result in continued genetic isolation. Brander (1975) showed, from tagging experiments, that there is a degree of isolation between western and eastern Irish Sea cod. He also described some genetic variation at the haemoglobin locus, although the findings were thought to be inconclusive.

The results presented in this paper are for one season only and the opportunity to sample further larval concentrations has not arisen since. It would be essential to carry out further analyses to confirm these findings.

3.3 Haddock populations in the North Sea

Samples of 0-group haddock were collected from eleven sites in the North Sea. Ten samples were analysed for *GPI* and eight for *LDH*.

3.3.1 Glucose phosphate isomerase (GPI-A: EC 5.3.1.9) analysis

Isozymes observed at this locus were assumed to be controlled by two alleles: $GPI\text{-}A^{100}$ and $GPI\text{-}A^{96}$. The observed and expected phenotype numbers and the gene frequencies are shown in Table 15. The heterogeneity test and the contingency test were not significant: $X^2_8 = 10.338$; $0.3 > P > 0.2$ and $X^2_9 = 8.591$; $0.5 > P > 0.3$ respectively (Tables 16 and 17).

3.3.2 Lactate dehydrogenase (LDH-A: EC 1.1.1.27) analysis

Isozymes observed at this locus were assumed to be controlled by three alleles: $LDH\text{-}A^{262}$, $LDH\text{-}A^{192}$ and $LDH\text{-}A^{100}$. The observed and expected phenotype numbers and the gene frequencies are shown in Table 18. Neither the heterogeneity test nor the contingency test were significant: $X^2_6 = 0.946$; $P > 0.99$ and $X^2_{14} = 13.156$; $0.7 > P > 0.5$ respectively (Tables 19 and 20).

3.3.3 Discussion

The results presented in this report suggest that the North Sea haddock may consist of a single homogeneous stock. However, as stated in Section 1, observations showing similarities at particular loci do not prove that the stock is homogeneous. Studies on the variations at the transferrin locus in haddock (A. Jamieson and R.J. Turner, personal communication) suggest that there might be genetic variation between haddock found to the west and east of the Greenwich meridian.

3.4 Whiting populations in the North Sea

Samples collected from 19 sites in the North Sea were analysed for *PGM* and *GPI-A*.

3.4.1 Phosphoglucomutase (PGM: EC 2.7.5.1) analysis

This locus codes for monomoric codominant alleles. The isozymes observed at this locus were assumed to be controlled by three alleles: PGM^{122}, PGM^{100} and PGM^{76}. The observed and expected numbers of phenotypes and the gene frequencies are shown in Table 21. The tests for heterogeneity and contingency of allele distribution were not significant: $X^2_{17} = 17.926$; $0.5 > P > 0.3$ and $X^2_{36} = 36.992$; $0.5 > P > 0.3$ respectively (Tables 22 and 23).

3.4.2 Glucose phosphate isomerase (GPI-A: EC 5.3.1.9) analysis

The isozymes observed at this locus were assumed to be controlled by four alleles: $GPI\text{-}A^{108}$, $GPI\text{-}A^{104}$, $GPI\text{-}A^{100}$ and $GPI\text{-}A^{79}$. The observed and expected phenotype numbers and gene frequencies are shown in Table 24.

Table 17 Contingency test of allele distribution at the *GPI-A* locus in haddock. (Expected numbers in parentheses are calculated from row and column totals.)

Sampling site (ICES rectangle)	Alleles		N	X^2
	100	96		
50F1	11 (11.818)	9 (8.182)	30	0.138
50F3	15 (13.000)	7 (9.000)	22	0.752
48F0	14 (11.818)	6 (8.182)	20	0.985
47E7	25 (23.636)	15 (16.364)	40	0.192
46F0	22 (23.636)	18 (16.364)	40	0.277
45F4	59 (56.727)	37 (39.273)	96	0.223
42E8	27 (23.636)	13 (16.364)	40	1.170
42F2	22 (23.636)	18 (16.364)	40	0.277
41F0	23 (23.636)	17 (16.364)	40	0.042
41F5	16 (22.455)	22 (15.545)	38	4.535
Total	2340	162	396	

Contingency $X^2_9 = 8.591$ $0.5 > P > 0.3$

Table 18 Phenotype numbers and allele frequencies at the *LDH-A* locus in haddock. (Expected phenotype numbers are shown in parentheses.)

Sampling site (ICES rectangle)	Observed phenotypes					N	Allele frequencies		
	262/192	262/100	192/192	192/100	100/100		262	192	100
51F1	0	1	0	7	12	20	0.025	0.175	0.800
	(0.2)	(0.8)	(0.6)	(5.6)	(12.8)				
50F1	1	3	1	3	12	20	0.100	0.150	0.750
	(0.6)	(3.0)	(0.5)	(4.5)	(11.3)				
47E7	0	2	0	1	17	20	0.050	0.025	0.925
	(0.0)	(1.9)	(0.0)	(0.9)	(17.1)				
47E7	0	2	0	2	16	20	0.050	0.050	0.900
	(0.1)	(1.8)	(0.0)	(1.8)	(16.2)				
46F0	1	2	0	2	15	20	0.075	0.075	0.850
	(0.2)	(2.6)	(0.1)	(2.6)	(14.5)				
42E8	0	1	0	4	15	20	0.025	0.100	0.875
	(0.1)	(0.9)	(0.2)	(3.5)	(15.3)				
42F2	0	1	0	3	16	20	0.025	0.075	0.900
	(0.1)	(0.8)	(0.1)	(2.7)	(16.2)				
41F0	0	1	0	4	15	20	0.025	0.100	0.875
	(0.1)	(0.9)	(0.2)	(3.5)	(15.3)				

Table 19 Heterogeneity X^2 test for haddock at the *LDH-A* locus. (Expected numbers are shown in parentheses.)

Sampling site (ICES rectangle)	Homozytgotes	Heterozygotes	N	X^2
51F1	12	8	20	0.460
	(13.425)	(6.575)		
50F1	13	7	20	0.251
	(11.900)	(8.100)		
47E7	17	3	20	0.013
	(17.175)	(2.825)		
47E7	16	4	20	0.030
	(16.300)	(3.700)		
46F0	15	5	20	0.027
	(14.675)	(5.325)		
42E8	15	5	20	0.079
	(15.525)	(4.475)		
42F2	16	4	20	0.035
	(16.325)	(3.675)		
41F0	15	5	20	0.079
	(15.525)	(4.475)		
Total	119	41		
	(120.0)	(40.0)		

Sum of X^2 values = 0.974
Total X^2 value = 0.028
Heterogeneity $X^2_6 = 0.946$ $P = 0.99$

Table 20 Contingency test of allele distribution at the *LDH-A* locus in haddock. (Expected numbers in parentheses are calculated from row and column totals.)

Sampling site (ICES rectanlgle	Alleles			N	X^2
	262	192	100		
51F1	1	7	32	40	3.389
	(1.875)	(3.750)	(34.375)		
50F1	4	6	30	40	4.315
	(1.875)	(3.750)	(34.375)		
47E7	2	1	37	40	2.225
	(1.875)	(3.750)	(34.375)		
47E7	2	2	36	40	0.829
	(1.875)	(3.750)	(34.375)		
46F0	3	3	34	40	0.829
	(1.875)	(3.750)	(34.375)		
42E8	1	4	35	40	0.436
	(1.875)	(3.750)	(34.375)		
42F2	1	3	36	40	0.635
	(1.875)	(3.750)	(34.375)		
41F0	1	4	35	40	0.436
	(1.875)	(3.750)	(34.375)		
Total	15	30	275	320	

Contingency $X^2_{14} = 13.168$ $0.7 > P > 0.5$

Table 21 Phenotype numbers and allele frequencies at the *PGM* locus in whiting. (Expected phenotype numbers are shown in parentheses.)

Sampling site (ICES rectangle	Observed phenotypes						N	Allele frequencies		
	122/122	122/100	122/76	100/100	100/76	76/76		122	100	76
47E8	10	19		11			40	0.488	0.513	
	(9.5)	(20.0)		(10.5)						
45E7	12	19		9			40	0.538	0.462	
	(11.6)	(19.9)		(8.6)						
43E9	5	21		14			40	0.387	0.613	
	(6.0)	(19.0)		(15.0)						
41E9	5	7		4			16	0.531	0.469	
	(4.5)	(8.0)		(3.5)						
41F5	19	30		28			90	0.450	0.550	
	(18.2)	(31.4)		(27.2)						
40E8	9	7		8			24	0.521	0.479	
	(6.5)	(12.0)		(5.5)						
40F1	17	17	0	8	1	0	43	0.593	0.395	0.012
	(15.1)	(20.2)	(0.0)	(6.7)	(0.4)	(0.0)				
39F0	15	20		12			47	0.532	0.468	
	(13.3)	(23.4)		(10.3)						
39F6	11	20	1	7	1	0	40	0.538	0.438	0.025
	(11.6)	(18.8)	(1.1)	(7.7)	(0.9)	(0.0)				
38F5	15	30		18			63	0.476	0.524	
	(14.3)	(31.4)		(17.3)						
38F6	8	23		14			40	0.488	0.512	
	(9.5)	(20.0)		(15.0)						
37F1	14	25	0	9	1	0	49	0.541	0.449	0.010
	(14.3)	(23.8)	(0.5)	(9.9)	(0.4)	(0.0)				
35F0	18	16		22			56	0.464	0.536	
	(12.1)	(27.9)		(16.1)						
35F1	3	5		3			11	0.500	0.500	
	(2.8)	(5.5)		(2.8)						
35F2	12	21		7			40	0.563	0.437	
	(12.7)	(19.7)		(7.7)						
34F0	11	26	1	11	1	0	50	0.490	0.490	0.020
	(12.0)	(24.0)	(1.0)	(12.0)	(1.0)	(0.0)				
34F0	13	15	0	11	1	0	40	0.513	0.475	0.012
	(10.5)	(19.5)	(0.5)	(9.0)	(0.5)	(0.0)				
33F1	15	20		15			50	0.500	0.500	
	(12.5)	(25.0)		(12.5)						
33F1	5	17	1	12	0	0	35	0.400	0.586	0.014
	(5.6)	(16.4)	(0.4)	(12.0)	(0.6)	(0.0)				

Table 22 Heterogeneity X^2 test for whiting at the *PGM* locus. (Expected numbers are shown in parentheses.)

Sampling site (ICES rectangle)	Homozygotes	Heterozygotes	N	X^2	Sampling site (ICES rectangle)	Homozygotes	Heterozygotes	N	X^2
47E8	21 (20.013)	19 (19.987)	40	0.098	38F6	17 (20.013)	23 (19.987)	40	0.908
45E7	21 (20.113)	19 (19.687)	40	0.172	37F1	23 (24.214)	26 (24.786)	49	0.120
43E9	19 (21.012)	21 (18.988)	40	0.406	35F0	40 (28.143)	16 (27.857)	56	10.043
41E9	9 (8.031)	7 (7.969)	16	0.235	35F1	6 (5.500)	5 (5.500)	11	0.091
41F5	47 (45.450)	43 (44.550)	90	0.107	35F2	19 (20.313)	21 (19.688)	40	0.172
40E8	17 (12.021)	7 (11.979)	24	4.132	34F0	22 (24.030)	28 (25.970)	50	0.330
40F1	25 (21.849)	18 (21.151)	43	0.924	34F0	24 (19.537)	16 (20.463)	40	1.992
39F0	27 (23.596)	20 (23.404)	47	0.986	33F1	30 (25.000)	20 (25.000)	50	2.000
39F6	18 (19.238)	22 (20.762)	40	0.153	33F1	17 (17.614)	18 (17.386)	35	0.043
38F5	33 (31.571)	30 (31.429)	63	0.130					
					Total	425 (403.0)	379 (411.0)		

Sum of X^2 values = 22.948
Total X^2 value = 5.022
Heterogeneity X^2_{17} = 17.926 $0.5 > P > 0.3$

Table 23 Contingency test of allele distribution at the *PGM* locus in whiting. (Expected numbers in parentheses are calculated from row and column totals.)

Sampling site (ICES rectangle)	Alleles 122	100	76	N	X^2	Sampling site (ICES rectangle)	Alleles 122	100	76	N	X^2
47E8	39 (39.705)	41 (39.902)	0 (0.393)	80	0.436	38F6	39 (39.705)	41 (39.902)	0 (0.393)	80	0.436
45E7	43 (39.705)	37 (39.902)	0 (0.393)	80	0.878	37F1	53 (48.639)	44 (48.880)	1 (0.482)	98	1.436
43E9	31 (39.705)	49 (39.902)	0 (0.393)	80	4.376	35F0	52 (55.587)	60 (55.862)	0 (0.550)	112	1.088
41E9	17 (15.882)	15 (15.961)	0 (0.157)	32	0.294	35F1	11 (10.919)	11 (10.973)	0 (0.108)	22	0.109
41F5	81 (89.337)	99 (89.779)	0 (0.885)	180	2.610	35F2	45 (39.705)	35 (39.902)	0 (0.393)	80	1.701
40E8	25 (23.823)	23 (23.941)	0 (0.423)	48	0.331	34F0	49 (49.631)	49 (49.877)	2 (0.491)	100	4.655
40F1	51 (42.683)	34 (43.894)	1 (0.423)	86	4.254	34F0	41 (39.705)	38 (39.902)	1 (0.393)	80	1.070
39F0	50 (46.654)	44 (46.885)	0 (0.462)	94	0.879	33F1	50 (49.631)	50 (49.877)	0 (0.491)	100	0.494
39F6	43 (39.705)	35 (39.902)	2 (0.393)	80	7.444	33F1	28 (34.742)	41 (34.914)	1 (0.344)	70	3.620
38F5	60 (62.536)	66 (62.845)	0 (0.619)	126	0.880						
						Total	808	812	8	1628	

Contingency X^2_{36} = 36.992 $0.5 > P > 0.3$

Table 24 Phenotype numbers and allele frequencies at the *GPI-A* locus in whiting. (Expected phenotype numbers are shown in parentheses.)

Sampling site (ICES rectangle)	Observed phenotypes										N	Allele frequencies			
	108/108	108/104	108/100	108/79	104/104	104/100	104/79	100/100	100/79	79/79		108	104	100	79
47E8					2	17	4	15	2	0	40		0.313	0.613	0.074
					(3.9)	(15.4)	(1.9)	(15.0)	(3.6)	(0.2)					
45E7					4	18	0	17	1	0	40		0.325	0.663	0.012
					(4.2)	(17.2)	(0.3)	(17.6)	(0.7)	(0.0)					
43E9	0	0	1	0	3	14	1	19	2	0	40	0.012	0.262	0.688	0.038
	(0.0)	(0.3)	(0.7)	(0.0)	(2.8)	(14.4)	(0.8)	(18.9)	(2.1)	(0.1)					
41E9					3	5	2	6	0	0	16		0.406	0.531	0.063
					(2.6)	(6.9)	(0.8)	(4.5)	(1.1)	(0.1)					
41F5	0	1	2	0	6	37	8	29	7	0	90	0.017	0.322	0.578	0.083
	(0.0)	(1.0)	(1.7)	(0.3)	(9.3)	(33.5)	(4.8)	(30.0)	(8.7)	(0.6)					
40E8					4	7	2	9	2	0	24		0.354	0.563	0.083
					(3.0)	(9.6)	(1.4)	(7.6)	(2.2)	(0.2)					
40F1					2	21	5	16	1	0	45		0.333	0.600	0.067
					(5.0)	(18.0)	(2.0)	(16.2)	(3.6)	(0.2)					
39F0	0	1	1	0	2	22	3	15	4	0	48	0.021	0.313	0.594	0.073
	(0.0)	(0.6)	(1.2)	(0.1)	(4.7)	(17.8)	(2.2)	(16.9)	(4.2)	(0.3)					
39F6	0	3	0	0	10	10	0	13	4	0	40	0.038	0.375	0.500	0.087
	(0.1)	(1.1)	(1.5)	(0.3)	(5.6)	(15.0)	(2.6)	(10.0)	(3.5)	(0.3)					
38F5					5	24	7	24	3	0	63		0.325	0.595	0.079
					(6.7)	(24.4)	(3.3)	(22.3)	(6.0)	(0.4)					
38F6	0	0	1	0	7	15	1	16	0	0	40	0.012	0.375	0.600	0.012
	(0.0)	(0.4)	(0.6)	(0.0)	(5.6)	(18.0)	(0.4)	(14.4)	(0.6)	(0.0)					
37F1					6	24	3	14	2	0	49		0.398	0.551	0.051
					(7.8)	(21.5)	(2.0)	(14.9)	(2.8)	(0.1)					
35F0					8	31	4	12	1	0	56		0.455	0.500	0.045
					(11.6)	(25.5)	(2.3)	(14.0)	(2.5)	(0.1)					
35F1					1	3		7			11		0.227	0.733	
					(0.6)	(3.9)		(6.6)							
35F2	0	1	0	0	4	20	1	14	0	0	40	0.012	0.375	0.600	0.012
	(0.0)	(0.4)	(0.6)	(0.0)	(5.6)	(18.0)	(0.4)	(14.4)	(0.6)	(0.0)					
34F0	0	2	3	0	9	22	0	11	2	0	49	0.050	0.430	0.500	0.020
	(0.1)	(2.1)	(2.5)	(0.1)	(9.1)	(21.1)	(0.8)	(12.3)	(1.0)	(0.0)					
34F0	0	0	1	0	9	19	0	10	1	0	40	0.013	0.463	0.513	0.011
	(0.0)	(0.5)	(0.5)	(0.0)	(8.6)	(19.0)	(0.4)	(10.5)	(0.5)	(0.0)					
33F1					2	17	3	24	2	2	50		0.240	0.670	0.090
					(2.9)	(16.1)	(2.2)	(22.5)	(6.0)	(0.4)					
33F1	0	1	2	0	0	16	2	13	1	0	35	0.043	0.271	0.643	0.043
	(0.1)	(0.8)	(1.9)	(0.1)	(2.6)	(12.2)	(0.8)	(14.5)	(1.9)	(0.1)					

The heterogeneity test was not significant: $X^2_{17} = 16.362$; $0.5 > P > 0.3$. The allele *GPI-A*^{108} was uncommon and was combined with *GPI-A*^{79} for the contingency test. The X^2 value was not significant: $X^2_{36} = 47.671$; $0.5 > P > 0.3$. These results are shown in Tables 25 and 26.

3.4.3 Discussion

The samples of whiting analysed for *PGM* and *GPI* appear to represent a single population. There is no evidence to suggest that there are differences between whiting from the northern and southern regions. The differences in parasitic infestation observed by Kabata (1967) may apply to adult fish which may have a restricted distribution. In parallel with the distribution of cod larvae, it is not unreasonable to suggest that the larval phase distribution by wind-driven currents may allow sufficient mixing to maintain a panmictic population.

3.5 Saithe populations

Samples of saithe were collected from 13 sites in the North Sea, Hebrides, west coast of Ireland and Rockall Bank. They were analysed at the *GPI-A* and *LDH-A* loci.

3.5.1 Glucose phosphate isomerase (GPI-A: EC 5.3.1.9) analysis

The isozymes observed at this locus were assumed to be controlled by three alleles, *GPI-A*^{104}, *GPI-A*^{100} and *GPI-A*^{90}. Observed and expected phenotype numbers and gene frequencies are shown in Table 27.

Heterozygotes at this locus were uncommon, *GPI-A*$^{100/104}$ occurring once and *GPI-A*$^{100/90}$ only thirteen times in 317 individuals. As a consequence, there were low expected numbers in both the heterogeneity test and the contingency test and these have been omitted.

3.5.2 Lactate dehydrogenase (LDH-A: EC 1.1.1.27) analysis

The isozymes observed at this locus were assumed to be controlled by two alleles: *LDH-A*^{128} and *LDH-A*^{100}. Observed and expected phenotype numbers and gene frequencies are shown in Table 28. Neither the heterogeneity test ($X^2_{11} = 4.021$; $0.98 > P > 0.95$) nor the contingency test ($X^2_{12} = 16.673$; $0.2 > P > 0.1$) were significant (Tables 29 and 30).

Table 25 Heterogeneity X^2 test for whiting at the *GPI-A* locus. (Expected numbers are shown in parentheses.)

Sampling site (ICES rectangle)	Homozygotes	Heterozygotes	N	X^2	Sampling site (ICES rectangle)	Homozygotes	Heterozygotes	N	X^2
47E8	17 (19.137)	23 (20.863)	40	0.458	38F6	23 (20.050)	17 (19.950)	40	0.870
45E7	21 (21.787)	19 (18.213)	40	0.063	37F1	20 (22.765)	29 (26.235)	49	0.627
43E9	22 (21.762)	18 (18.238)	40	0.006	35F0	20 (25.723)	36 (30.277)	56	2.355
41E9	9 (7.219)	7 (8.781)	16	0.801	35F1	8 (7.136)	3 (3.864)	11	0.298
41F5	35 (40.289)	55 (49.711)	90	1.257	35F2	18 (20.050)	22 (19.950)	40	0.420
40E8	13 (10.771)	11 (13.229)	24	0.837	34F0	20 (21.500)	29 (27.500)	49	0.186
40F1	18 (21.400)	27 (23.600)	45	1.030	34F0	19 (19.088)	21 (20.912)	40	0.001
39F0	17 (22.031)	31 (25.969)	48	2.124	33F1	28 (25.730)	22 (24.270)	50	0.413
39F6	23 (17.488)	17 (22.512)	40	3.087	33F1	13 (17.300)	22 (17.700)	35	2.113
38F5	29 (29.389)	34 (33.611)	63	0.010					
					Total	373 (384.0)	443 (432.0)		

Sum of X^2 values = 16.956
Total X^2 value = 0.594
Heterogeneity X^2_{17} = 16.362 $0.5 > P > 0.3$

Table 26 Contingency test of allele distribution at the *GPI-A* locus in whiting. (Expected numbers in parentheses are calculated from row and column totals.)

Sampling site (ICES rectangle)	Alleles 104	100	79¹	N	X^2	Sampling site (ICES rectangle)	Alleles 104	100	79¹	N	X^2
47E8	25 (27.843)	49 (47.010)	6 (5.147)	80	0.516	38F6	30 (27.843)	48 (47.010)	2 (5.147)	80	2.112
45E7	26 (27.843)	53 (47.010)	1 (5.147)	80	4.227	37F1	39 (34.108)	54 (57.587)	5 (6.305)	98	1.195
43E9	21 (27.843)	55 (47.010)	4 (5.147)	80	3.296	35E0	51 (38.980)	56 (65.814)	5 (7.206)	112	5.845
41E9	13 (11.137)	17 (18.804)	2 (2.059)	32	0.486	35F1	5 (7.657)	17 (12.928)	0 (1.415)	22	3.620
41F5	58 (62.647)	104 (105.77)	18 (11.581)	180	3.932	35F2	30 (27.843)	48 (47.010)	2 (5.147)	80	2.112
40E8	17 (16.706)	27 (28.206)	4 (3.088)	48	0.326	34F0	42 (34.108)	49 (57.587)	7 (6.305)	98	3.183
40F1	30 (31.324)	54 (52.886)	6 (5.790)	90	0.087	34F0	37 (27.843)	41 (47.010)	2 (5.147)	80	5.704
39F0	30 (33.412)	57 (56.412)	9 (6.176)	96	1.645	33F1	24 (34.804)	67 (58.762)	9 (6.434)	100	5.532
39F6	30 (27.843)	43 (47.010)	7 (5.147)	80	1.176	33F1	19 (24.363)	45 (41.134)	6 (4.504)	70	2.041
38F5	41 (93.853)	75 (74.040)	10 (8.107)	126	0.640						
						Total	568	959	105	1632	

Contingency X^2_{36} = 47.671 $05 > P > 0.3$

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¹*GPI-A*^{108} pooled with *GPI-A*^{79}

Table 27 Phenotype numbers and allele frequencies at the *GPI-A* locus in saithe. (Expected numbers are shown in parentheses.)

Sampling site (ICES rectangle)	Observed phenotypes			N	Allele frequencies		
	104/100	100/100	100/90		104	100	90
38E0		39 (39.00)		39		1.000	
42E2		13 (13.00)		13		1.000	
42E2	1 (0.95)	8 (8.02)		9	0.056		
43E0		24 (24.00)		24		1.000	
43D5		30 (30.00)		30		1.000	
51E8*		49 (49.00)		49		1.000	
51F0*	1 (0.96)	31 (31.05)	1 (0.96)	33	0.015	0.970	0.015
49E8*		9 (9.00)		9		1.000	
49F0*	1 (0.96)	15 (15.02)		16	0.031	0.969	
47E8*		8 (8.00)		8		1.000	
47F0*	1 (0.99)	21 (21.00)		22	0.023	0.977	
47F2	3 (2.91)	40 (40.04)		43	0.035	0.965	
45F4	1 (0.99)	21 (21.00)		22	0.023	0.977	

Table 28 Phenotype numbers and allele frequencies at the *LDH-A* locus in saithe. (Expected numbers are shown in parentheses.)

Sampling site (ICES rectangle)	Observed phenotypes			N	Allele frequencies	
	128/128	128/100	100/100		128	100
38E0	1 (0.1)	2 (3.8)	36 (35.1)	39	0.051	0.949
42E2	0 (0.5)	5 (4.0)	8 (8.5)	13	0.192	0.808
42E2	1 (0.1)	0 (1.8)	8 (7.1)	9	0.111	0.889
43E0	0 (0.0)	1 (1.0)	23 (23.0)	24	0.021	0.979
43D5	0 (0.0)	1 (1.0)	29 (29.0)	30	0.017	0.983
51E8*	0 (0.4)	9 (8.2)	40 (40.4)	49	0.092	0.908
51F0*	0 (0.1)	4 (3.8)	29 (29.1)	33	0.061	0.939
49E8*	0 (0.0)	1 (0.9)	8 (8.1)	9	0.056	0.944
49F0*	0 (0.1)	3 (2.7)	13 (13.1)	16	0.094	0.906
47E8*	0 (0.0)	0 (0.0)	8 (8.0)	8	0.000	1.000
47F0*	0 (0.2)	4 (3.6)	18 (18.2)	22	0.091	0.909
47F2	1 (0.1)	3 (4.7)	39 (38.1)	43	0.058	0.942
45F4	0 (0.0)	1 (1.0)	21 (21.0)	22	0.023	0.977

Table 29 Heterogeneity X^2 test for saithe at the *LDH-A* locus. (Expected numbers are shown in parentheses.)

Sampling site (ICES rectangle)	Homozygotes	Heterozygotes	N	X^2
38E0	37 (35.205)	2 (3.795)	39	0.940
42E2	8 (8.962)	5 (4.038)	13	0.332
42E2	9 (7.222)	0 (1.778)	9	2.216
43E0	23 (23.021)	1 (0.979)	24	0.0005
43D5	29 (29.017)	1 (0.983)	30	0.0003
51E8*	40 (40.827)	9 (8.173)	49	0.100
51F0*	29 (29.242)	4 (3.758)	33	0.018
49E8*	8 (8.056)	1 (0.944)	9	0.004
49F0*	13 (13.281)	3 (2.719)	16	0.035
47E8*	8 (8.000)	0 (0.000)	8	0.000
47F0*	18 (18.364)	4 (3.636)	22	0.044
47F2	40 (38.291)	3 (4.709)	43	0.697
45F4	21 (21.023)	1 (0.977)	22	0.001
Total	283 (279.5)	34 (37.5)		

Sum of X^2 values = 4.387
Total X^2 value = 0.366
Heterogeneity X^2_{11} = 4.021 $0.98 > P > 0.95$

Table 30 Contingency test of allele distribution at the *LDH-A* locus in saithe. (Expected numbers in parentheses are calculated from row and column totals.)

Sampling site (ICES rectangle)	Alleles		N	X^2
	128	100		
38E0	4 (4.921)	74 (73.079)	78	0.184
42E2	5 (1.640)	21 (24.360)	26	7.344
42E2	2 (1.136)	16 (16.864)	18	0.702
43E0	1 (3.028)	47 (44.972)	48	1.450
43D5	1 (3.785)	59 (56.215)	60	2.188
51E8*	9 (6.183)	89 (91.817)	98	1.370
51F0*	4 (4.164)	62 (61.836)	66	0.007
49E8*	1 (1.136)	17 (16.864)	18	0.017
49F0*	3 (2.019)	29 (29.981)	32	0.509
47E8*	0 (1.009)	16 (14.991)	16	1.077
47F0*	4 (2.776)	40 (41.224)	44	0.576
47F2	5 (5.426)	81 (80.574)	86	0.036
45F4	1 (2.776)	43 (41.224)	44	1.213
Total	40	594	634	

Contingency X^2_{12} = 16.673 $0.2 > P > 0.1$

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* Sample from four ICES rectangles. Code refers to the upper left-hand rectangle.

3.5.3 Discussion

It appears from the results of the genetic analysis of saithe that this species is homogeneous. The motivation for this study originated in a request to discover if there was any genetic method which would separate the saithe caught in EC and Norwegian territorial waters. Fish do not respect political boundaries and the major North Sea spawning area (Damas, 1909) appears to enclose the international limit of EC and Norwegian waters. Saithe are known to undergo considerable migrations and the lack of variation between saithe from Rockall Bank and the North Sea may reflect this behaviour.

4. Conclusions

The results obtained for these four gadoid species suggest that, with the exception of those cod of the Irish Sea, the populations are homogeneous. Whilst statistically-significant genetic differences can represent stock differentiation, similarities are more difficult to explain. In the North Sea, there may be sufficient mixing of the larval phase to result in overall stock unity, while Irish Sea cod results provide some evidence to suggest that isolation of stocks can be maintained by a specific current system. It is also possible that stock similarities may result from selection of a stable, balanced polymorphism in similar environmental conditions. The *LDH* in cod is found with virtually identical gene frequencies at the *LDH-B* locus across its range, whereas other loci such as *GPI-B* and transferrin have revealed considerable differences.

These findings stress the need to identify and investigate as many loci as possible when attempting to study the population genetics of a species.

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