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SIGNIFICANCE OF POPULATION GENETICS ON MANAGEMENT OF HERRING STOCKS

By

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ABSTRACT

A large number of herring samples from Norwegian waters were analysed for polymorphism in a number of enzyme loci by using starch gel electrophoresis. Significant differencies in phenotype distribution and allele frequencies were observed in samples from fjords and different area. Very clear frequency variations in the two loci of lactate dehydrogenase, show the existence of geneticially differentiated stocks of herring in different area.

The significance of using the present methods of population genetics for revealing the population structure of herring is discussed.

INTRODUCTION

One of the most important problems in fish biology and management of the resources, is concerned with the identification of different stocks within a fish species. The present classifica-

tion of fish stocks is mainly based on analysis of meristic characters (number of vertebrae, keeled scales, fin rays, gill rakers), time of spawning, growth characters and migration behaviour. The genetic control of the variation observed for these biological parameters are obscure. However, stock classification should be based on genetic properties which are transferred from one generation of fish to the other.

Application of population genetic methods to study population structure of herring in Norwegian seawater was initiated in 1965 by Nævdal (1969, 1970). Genetic variation in blood proteins and some enzymes was observed, and some heterogeneities among inshore populations of herring were found. The genetic variation, however, was limited as compared to the variation in meristic characters (Panish and Saville 1965).

In 1978 the work on herring populations was continued, and the method of enzyme electrophoresis (Harris and Hopkinson 1976) using different tissue enzymes was applied. As described below, the sampling area was also increased. In this paper we present some of the data obtained from genetic analysis of two polymorphic enzyme loci in herring samples from different areas and different years. The data are tentatively treated and homogeneity tests are used to test whether different samples are drawn from different populations. Management and surveillance of identified herring stocks, conservation of locally adapted stocks, and further genetic and biological classification of such stocks are discussed.

MATERIALS AND METHODS

Samples of white muscle of herring were collected on research vessels during the years 1978-80. The sampling area are shown in Fig. 1 and Fig. 2. Sampling date, locality and other characteristics are found in Table 1 and Table 5.

A few of the samples were frozen and transported to the laboratory for analysis of polymorphic enzymes. The main part of the samples, however, were analysed onboard the research vessels

during the cruises by using a new electrophoretic apparatus designed for running the genetic analysis at sea (Jørstad, in preparation).

All samples were analyses by starch gel electrophoresis (Gordon 1975), and the sliced gels were selectively stained for a number of enzymes (Harris and Hopkinson 1976, Siciliano and Shaw 1976). Initially, we stained for the following polymorphic enzymes: lactate dehydrogenase (LOH), malate dehydrogenase (MDH), malic enzyme (ME), isocitrate dehydrogenase (IDH), phosphoglucose isomerase (PGI), phosphoglucomutase (PGM) and aspartate aminotransferase (AAT). Malic enzyme and aspartate aminotransferase showed little variation between different samples, and for this reason, these two enzymes were not analysed in the major part of the samples.

After staining of the enzymes, the starch gels were dryed for permanent storage.

At present we are only able to report on the data obtained from the analysis of LDH-1 and LDH-2.

The nomenclature used for designing of enzyme loci and alleles, followed the suggestions of Allendorf and Utter (1979). Initially, we obtained the best resolution of LDH isozymes by using starch gels made from Poulik buffer, pH 8.7 (Ward and Beardmore, 1976). The numbering of different alleles for the LDH-1 and LDH-2 loci were made according to the anodic mobility at this pH. In this report, we still use the original numbering of alleles also when the rutine gels were run in histidine buffer, pH 7.0.

The statistical methods used are described in Sokal and Rohlf (1969).

RESULTS

Lactate dehydrogenase isozymes in herring tissue have earlier been described (Odense, Allen and Leung 1966), and Nævdal

(1970) studied herring population from Norwegian waters. Because of different nomenclature, direct comparisons of alleles are difficult, but we assume that the earlier designations B', B and B'' (B gene) correspond to the LDH-2 (70, 100 and 110) alleles used in the present paper. Possibly due to different electrophoretic methods and extention of sampling area, three different alleles were found for the LDH-1 locus (earlier named A gene).

Pictures of starch gels stained for LDH are shown in Fig. 3 where different phenotypes for the two LDH loci are demonstrated. All possible phenotypes within each locus were found.

The phenotype distributions and allele frequencies observed in each sample within the main areas are summerized in Table 1.

A homogeneity test based on the pooled samples from each area are shown in Table 2. Pairwise comparisons of phenotype distributions (homogeneity test) and gene frequencies (Student t-test) from all areas are shown in Table 3 and 4 respectively. Very clear heterogeneity exists within the total material, and evidently the herring samples in the fjords are different from the samples from coastal areas and also from one another.

The samples from northern Norway are more closely compared in Table 6 (data in Table 5). These samples consist of mature herring in February, larvae in July and 0-group in December, all representing the same year of spawning. Except for the sample from Balsfjord, no significant differences exist between these samples. The sample from Balsfjord, however, showed very high frequencies of LDH-1 (160), LDH-1 (200) and LDH-2 (110), and thus differed from all other samples analysed. The distribution of phenotypes also showed an excess of homozygotes compared to expected values from Hardy-Weinberg's equation, indicating mixing of individuals from two (or more) population units (Wahlungs effect).

In conclusion all statistical tests have revealed heterogenety and highly significant differencies between samples from dif-

ferent areas and localities. Especially some fjord populations seem to differ considerably from the more oceanic stock(s) and from one another.

DISCUSSION

a. Genetic analysis of herring populations in Norwegian waters.

For a long time, it has been known that the herring species consist of a great number of subunits which differ in several biological characteristics (Heincke 1898, Parrish and Saville 1965). Earlier studies on genetic characters (Ridway, Sherburne and Lewis 1970; Simonarsson and Watts 1969; Odense and Allen 1971; Nævdal 1970) have only revealed small differencies in gene frequencies in spite of a high degree of polymorphism present in herring (Ligny 1969; Utter, Hodgins and Allendorf 1974; Anderson pers. comm.). The results described in this study, however, show a high amount of variation in phenotype distribution and allele frequencies. The data obtained from genetic analysis of two polymorphic enzyme loci of herring, clearly demonstrate the existance of genetic differentiated populations with their own gene pool. Compared to the earlier investigations in Norwegian waters (Nævdal 1969, 1970), this is possible due to new electrophoretic methods and extending of the sampling area.

Most clearly demonstrated by the data from northern Norway, highly significant differencies exist between samples within a relative small area.

The distribution of phenotypes in the major part of the material analysed (Table 2), do not differ from the expected values calculated from Hardy-Weinberg distribution. In the sample from Balsfjord, however, a low number of heterocygotes for both loci were observed, and mixing of population units with different genetic compositions (Wahlungs effect) is indicated. The observed distribution of phenotypes are possibly due to transportation of herring larvae from spawning grounds on the coast and partly mixing with offspring from locally spawned herring in the Balsfjord area.

The heterogeneity observed in the present study, gives valuable information about the stock structure og herring in the area investigated. On the basis of distribution of LDH phenotypes, one large oceanic population (Atlanto-scandian herring) and a number of fjord populations seem to exist, all with their own gene pool.

Tentative results from analysis of other polymorphic enzymes seem to confirm the results described above (Jørstad, unpublished).

However, more careful tests of homogeneity (data not shown) indicate presence of heterogeneity within some of the fjord populations and also within the oceanic stock. Before extending this point further, we want to include the data obtained for the other enzymes in the statistical tests. Most samples from the oceanic stock are drawn from mature fish, and we also want to compare the genetic data with general biological data (year classes, growth rate, scale characters etc.) before drawing any conclusions.

b. Genetics in management of fish resources.

During the last decade genetic research have revealed a high level of genetic diversity in all kind of living organisms (Powell 1975). Today, it is generally recognized that each species consists of a number of genetic differentiated populations which also differ in meristic characters, environmental preference and population behaviour. Locally adapted population are thought to be the results of long time evolution, and have developed valuable properties for survival under specified conditions.

The problems of concervation of such genetic resources have recently been discussed by several workers (Frankel 1974; Harlan 1975; Soulé and Wilcox 1980). The survival of different species and genetic differentiated populations seem to be connected to the evolutionary potential and the adaptation to a changing environment (Soulé 1980). Existing evidence suggest that the genetic diversity present in natural populations, both

on the species and the population level, are one of the most important factors concerned with future evolution and survival (Frankel and Soulé 1981). Within a population, correlation seems to exist between genetic variability and biological properties like growth, fecundity and fitness.

The existence of genetic differentiated population within economically important fish species have also been reported. As discussed by others (Smith, Hillestad, Manlove and Marchinton 1976) management of fish resources are dependent of knowledge of the population structure for each fish species. However, in spite of earlier attempts to use genetic methods in definitions of marine fish stocks (de Ligny 1969; Jamieson 1974), the present population models for marine fish stocks and surveillance of these are exclusively based on biological data. This is possibly due to the lack of basic knowledge of the genetic structure of important fish species.

With reference to the general genetic results discussed above, the present situation demand for an increased effort to identify fish stocks and mapping of genetic resources (Anon. 1980a).

Increasing fishing effort as well as other human offshore activities suggest a heavy pressure on all kinds of fish resources in the future. Unless precautions are taken in the management programs, the number of differentiated fish stocks and the genetic variation within them are likely to be reduced.

At present time the method used in population genetic research offer a well developed technique for revealing the genetic structure of populations. These methods can easily be incorporated in the ongoing biological sampling programs of important fish species. Tissue samples of fish on which biological data are recorded, can be analysed for a number of genetic characters and thus permitting direct comparisons between biological and genetic data. Compared to the expensive surveillance programs based on biological information, the cost of genetic analysis are almost negligable.

For the reasons discussed, we believe that future management of fish resources must be based on stock models which summerize biological, genetic and ecological information. In addition to the currently used requirement of proper management, precautions should be included in the management programs in order to preserve as much of the genetic variation within fish species and fish stocks as possible.

By concerving the genetic diversity in natural fish stocks, the evolutionary potential for these resources are maintained, and this kind of management offer the possibility for future use of these resources in aquaculture (Anon. 1980b).

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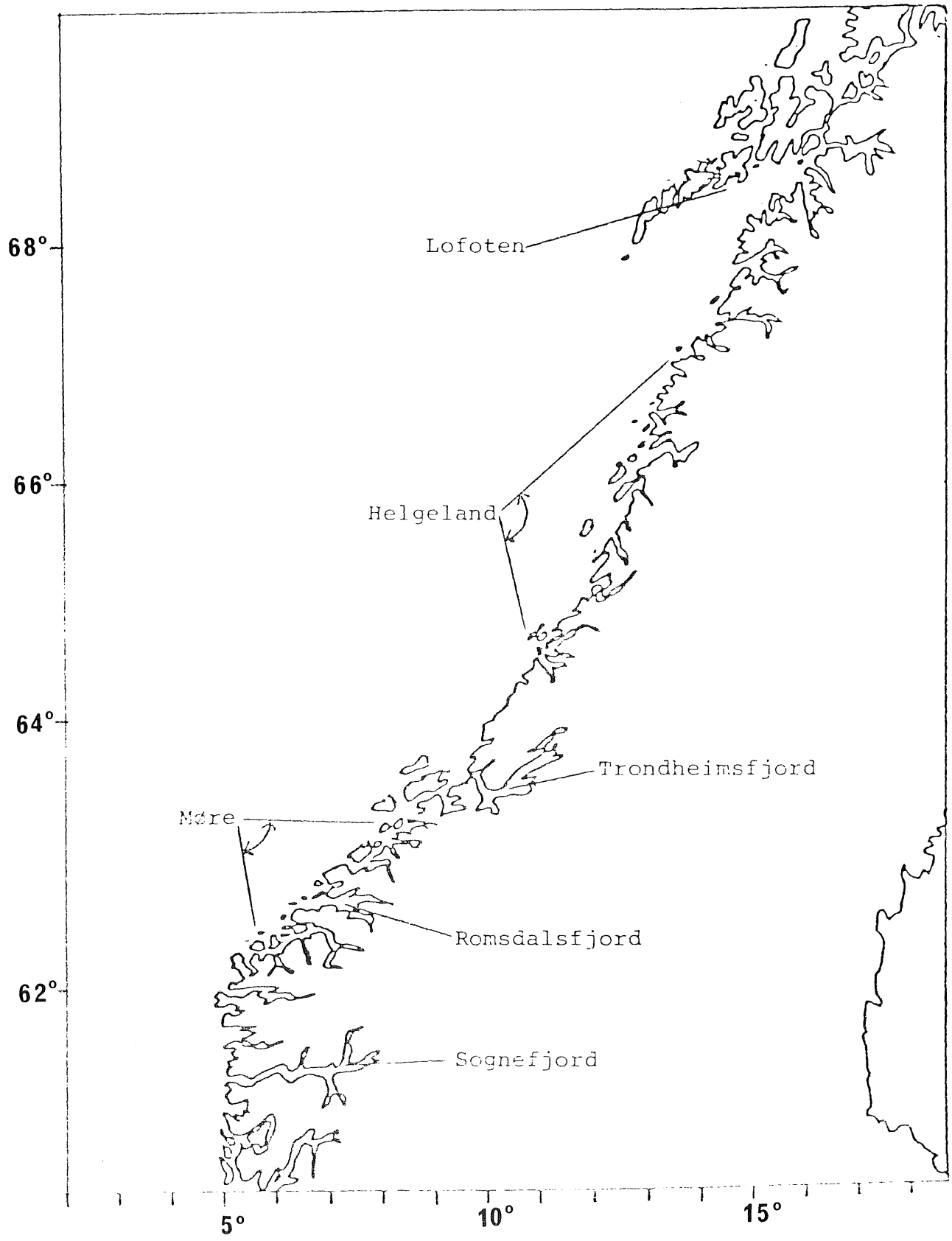

Fig. 1. Sampling area of herring 1978-1980.

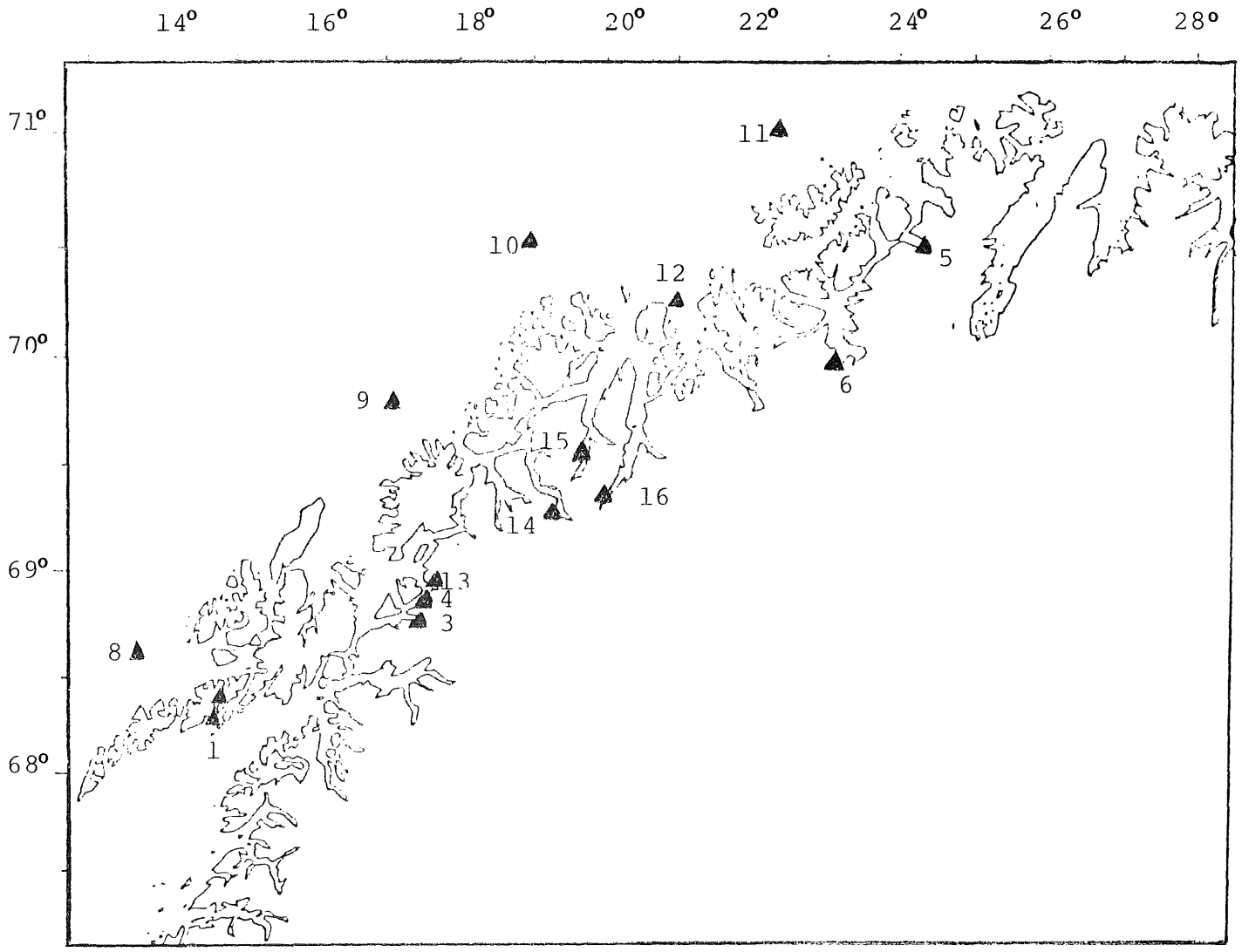

Fig. 2. Sampling localities in northern part of Norway.

1. Hølla v/Svolvær
2. Austnesfjorden
3. Gratangen
4. Lavangen
5. Repparsfjord
6. Kafjord i Altafjord
7. Austnesfjorden
8. Gimsøy
9. Hekkingen
10. Sørfugløya N
11. Sørøya N
12. Kvænangen
13. Sagfjorden
14. Balsfjorden
15. Ullsfjorden
16. Storfjord i Lyngen

Table 1. Distribution of LDH phenotypes and allele frequencies in different area during the years 1978-80. m = mature fish.

			LDH-1									LDH-2								
			phenotypes						allele frequencies			phenotypes						allele frequencies		
Area	Year	age group	100/100	100/160	100/200	160/160	160/200	200/200	100	160	200	70/70	70/100	70/110	100/100	100/110	110/110	70	100	110
Sogne	nov.78	0-1	91	8	0	1	0	0	0.95	0.05	-	0	3	0	95	2	0	0.02	0.97	0.01
fjorden	nov.79	0-1	41	8	0	1	0	0	0.90	0.10	-	0	2	0	39	2	0	0.02	0.96	0.02
	nov.80	0	83	4	0	0	0	0	0.98	0.02	-	0	6	0	77	4	0	0.03	0.95	0.02
Møre	nov.78	m	464	28	0	2	0	0	0.97	0.03	-	0	49	0	436	1	0	0.05	0.949	0.001
	febr.79	m	571	32	0	0	0	0	0.97	0.03	-	2	58	0	535	1	0	0.05	0.948	0.002
	nov.79	m	167	7	0	0	0	0	0.98	0.02	-	0	11	1	153	1	0	0.03	0.97	0.003
	febr.80	m	1451	49	0	0	0	0	0.98	0.02	-	1	149	0	1447	2	0	0.05	0.95	0.0006
	nov.80	1	184	14	2	0	0	0	0.95	0.04	0.01	0	26	0	274	0	0	0.04	0.96	-
	nov.80	m	182	8	2	0	0	0	0.97	0.02	0.01	1	20	0	169	0	1	0.06	0.94	0.003
Romsdals-	nov.78	0	91	8	0	0	0	0	0.96	0.04	-	0	6	0	84	8	1	0.03	0.92	0.05
fjorden	nov.79	0	350	34	0	0	0	0	0.96	0.04	-	0	37	0	328	19	1	0.05	0.92	0.03
	nov.80	m	148	8	2	1	0	0	0.96	0.03	0.01	0	3	0	136	19	1	0.01	0.92	0.07
	nov.80	1	156	6	0	0	0	0	0.98	0.02	-	0	11	0	145	13	0	0.03	0.93	0.04
Trondheims-	nov.78	m	176	20	0	1	0	0	0.94	0.06	-	1	11	0	140	42	3	0.03	0.85	0.12
fjorden	nov.79	m	166	18	0	1	0	0	0.95	0.05	-	1	8	0	134	37	4	0.03	0.85	0.12
	nov.79	0	251	34	0	3	0	0	0.93	0.07	-	1	14	1	199	68	4	0.03	0.84	0.13
	nov.80	m	288	45	14	2	0	1	0.91	0.07	0.02	0	13	2	150	80	7	0.03	0.78	0.19
	nov.80	1	154	15	14	4	0	0	0.90	0.06	0.04	0	12	0	127	50	1	0.03	0.83	0.14
	nov.80	0	77	16	3	0	0	0	0.90	0.08	0.02	0	9	0	68	17	2	0.05	0.84	0.11
Helgeland	febr.79	m	95	6	0	0	0	0	0.97	0.03	-	0	4	0	94	0	0	0.02	0.98	-
	nov.79	0	1138	6	0	0	0	0	1.0	-	-	4	122	2	1074	8	0	0.05	0.947	0.003
	febr.80	m	184	14	0	0	0	0	0.96	0.04	-	0	13	0	189	0	0	0.03	0.97	-
	nov.80	1-2	181	10	1	0	0	0	0.97	0.03	-	0	20	0	172	0	0	0.05	0.95	-
	nov.80	0	169	13	1	0	0	0	0.96	0.04	-	0	24	0	157	2	0	0.07	0.92	0.01
Lofoten	nov.78	m	90	9	0	0	0	0	0.95	0.05	-	1	7	0	91	0	0	0.05	0.95	-
	febr.79	m	187	11	0	0	0	0	0.97	0.03	-	0	21	0	177	0	0	0.05	0.95	-
	nov.79	m	91	5	0	0	0	0	0.97	0.03	-	0	8	0	88	0	0	0.04	0.96	-
	febr.80	m	183	8	0	0	0	0	0.98	0.02	-	0	14	0	178	0	0	0.04	0.96	-
	nov.80	m	70	1	0	0	0	0	0.99	0.01	-	0	5	0	64	0	0	0.04	0.96	-

Table 2. Test of homogeneity base on phenotype distributions in different sampling area. Observed number of phenotypes and expected HW distribution of genotypes are shown.

Area	LDH-1 no. fish	100 100	100 160	100 200	160 160	160 200	200 200	G/df	p	LDH-2 no. fish	70 70	70 100	70 110	100 100	100 110	110 110	G/df	p
Sogne-fjord	230	215	14	0	1	0	0	0.58/1	0.45	230	0	11	0	211	8	0	5.02/1	0.025
	exp.	214	15	–	–	–	–			exp.	–	10	–	211	7	–		
Møre	3163	3019	138	4	2	0	0	55.2/1	∿0	3334	4	313	0	3012	4	1	3.6/1	0.058
	exp.	3018	139	3.9	2	–	–			exp.	8	305	–	3015	6	–		
Romsdals-fjord	889	745	138	4	2	0	0	67.4/1	∿0	812	0	57	0	693	59	3	2.74/1	0.098
	exp.	749	130	3	6	–	–			exp.	1	53	2	695	60	1		
Trondheims-fjord	1302	1112	148	34	8	0	0	66.9/1	∿0	1206	3	67	3	818	294	21	13.4/1	∿0
	exp.	1111	151	31	5	2	–			exp.	1	63	11	827	281	24		
Helgeland	1875	1766	102	6	0	0	0	11.8/1	∿0	1883	4	183	2	1684	10	0	4.0/1	0.46
	exp.	1767	100	6	2	–	–			exp.	5	182	1	1683	11	–		
Lofoten	655	621	34	0	0	0	0	7.6/1	0.007	654	1	55	0	598	0	0	0.02/1	0.99
	exp.	622	33	–	–	–	–			exp.	1	54	–	598	–	–		

Total heterogeneity G=209.0, df=5, p∿0 G=28.78, df=5, p∿0

Table 3. Homogeneity test between different area based on phenotype distribution in LDH-1 and LDH-2 loci.

	Sogne-fjord	Møre	Romsdals-fjord	Trondheims-fjord	Helgeland	Lofoten
Sogne-fjord		G=35.3 df=3 p∿0	G=23.98 df=3 p∿0	G=91.62 df=3 p∿0	G=20.4 df=3 p∿0	G=4.38 df=2 p=0.112
Møre			G=294.9 df=5 p∿0	G=1005.0 df=6 p∿0	G=11.2 df=5 p∿0	G=1.34 df=2 p=0.52
Romsdals-fjord				G=146.8 df=6 p∿0	G=177.8 df=4 p∿0	G=50.02 df=2 p∿0
Trondheims-fjord					G=656.2 df=6 p∿0	G=47.8 df=2 p∿0
Helgeland						G=1.5 df=2 p=0.472

Table 4. Student's t-test of observed frequencies of LDH-2(110) between different area.

	Sogne-fjord	Møre	Romsdals-fjord	Trondheims-fjord	Helgeland	Lofoten
no. of fish	230	3334	812	1206	1883	654
freq. of LDH-2(110)	0.017	0.001	0.040	0.141	0.003	≈0.0008
Sogne-fjord		t=2.91 p<0.01	t=1.89 p>0.05	t=7.06 p<0.001	t=2.17 p>0.02	t≈2.67 p<0.01
Møre			t=8.68 p<0.001	t=21.03 p<0.001	t=1.61 p>0.05	t≈0.156 p>0.1
Romsdals-fjord				t=8.09 p<0.001	t=6.98 p<0.001	t≈6.58 p<0.001
Trondheims-fjord					t=17.9 p<0.001	t≈14.9 p< 0.001
Helgeland						t≈1.17 p>0.1

Table 6. Student's t-test of observed frequencies of LDH-2(110) between different sampling localities in northern part of Norway.

	Austnes-fjord	Sørfugl-øya	Sørøya	Kvænangen	Sagfjord	Balsfjord	Ullsfjord	Stor-fjord
Austnes-fjord		t≈0.89 p>0.1	t≈0.49 p>0.1	t≈0.41 p>0.1	t≈0.41 p>0.1	t≈19.9 p<0.001	t≈0.61 p>0.1	t≈0.89 p>0.1
Sørfugl-øya			t≈0.30 p>0.1	t≈0.41 p>0.1	t≈0.39 p>0.1	t=15.2 p<0.001	t≈0.31 p>0.1	t≈0
Sørøya				t≈0.09 p>0.1	t≈0.08 p>0.1	t≈14.9 p<0.001	t≈0	t≈0.30 p>0.1
Kvænangen					t≈0	t≈15.7 p<0.001	t≈0.09 p>0.1	t≈0.41 p>0.1
Sagfjord						t≈15.6 p<0.001	t≈0.09 p>0.1	t≈0.41 p>0.1
Balsfjord							t≈15.3 p<0.001	t=15.2 p<0.001
Ullsfjord								t≈0.31 p>0.1

Table 5. Distribution of LDH phenotypes and allele frequencies in herring samples from northern Norway. m = mature fish, L = larvae sample.

Sample no.	Year	Locality	age group	LDH-1 phenotypes						LDH-1 allele frequencies			LDH-2 phenotypes						LDH-2 allele frequencies		
				100/100	100/160	100/200	160/160	160/200	200/200	100	160	200	70/70	70/100	70/110	100/100	100/110	110/110	70	100	110
1	Feb.79	Hølla v/Svolvær	m	95	4	0	0	0	0	0.98	0.02	-	0	13	0	86	0	0	0.07	0.93	-
2	Feb.79	Austnesfjorden	m	92	7	0	0	0	0	0.96	0.04	-	0	8	0	91	0	0	0.04	0.96	-
3	Des.79	Gratangen	0	92	4	0	0	0	0	0.96	0.04	-	1	9	0	86	0	0	0.06	0.94	-
4	Des.79	Lavangen	0	84	8	0	0	0	0	0.96	0.04	-	0	8	0	82	2	0	0.04	0.95	0.01
5	Des.79	Repparsfjord	0	47	1	0	0	0	0	0.99	0.01	-	0	6	0	42	0	0	0.06	0.94	-
6	Des.79	Kåfjord i Altafjord	0	47	1	0	0	0	0	0.99	0.01	-	0	4	0	42	1	0	0.04	0.95	0.01
7	Feb.80	Austnesfjorden	m	183	8	0	0	0	0	0.98	0.02	-	0	14	0	178	0	0	0.04	0.96	-
8	July 80	Gimsøy	L	36	2	0	0	0	0	0.97	0.03	-	0	5	0	33	0	0	0.07	0.93	-
9	July 80	Hekkingen	L	-	-	-	-	-	-	-	-	-	0	4	0	33	0	0	0.05	0.95	-
10	July 80	Sørfugløy N	L	93	3	0	0	0	0	0.98	0.02	-	1	11	0	83	1	0	0.07	0.92	0.01
11	July 80	Sørøya N	L	74	6	0	0	0	0	0.96	0.04	-	0	11	0	69	0	0	0.07	0.93	-
12	July 80	Kvænangen	L	92	4	0	0	0	0	0.98	0.02	-	0	10	0	86	0	0	0.05	0.95	-
13	Des.80	Sagfjorden	0	88	7	0	0	0	0	0.96	0.04	-	2	10	0	83	0	0	0.07	0.93	-
14	Des.80	Balsfjorden	0	37	7	15	17	70	63	0.23	0.27	0.50	0	1	0	33	43	137	0.002	0.258	0.74
15	Des.80	Ullsfjorden	0	87	4	0	0	0	0	0.98	0.02	-	1	10	0	80	0	0	0.07	0.93	-
16	Des.80	Storfjord i Lyngen	0	94	2	0	0	0	0	0.99	0.01	-	3	7	0	85	1	0	0.07	0.93	0.01

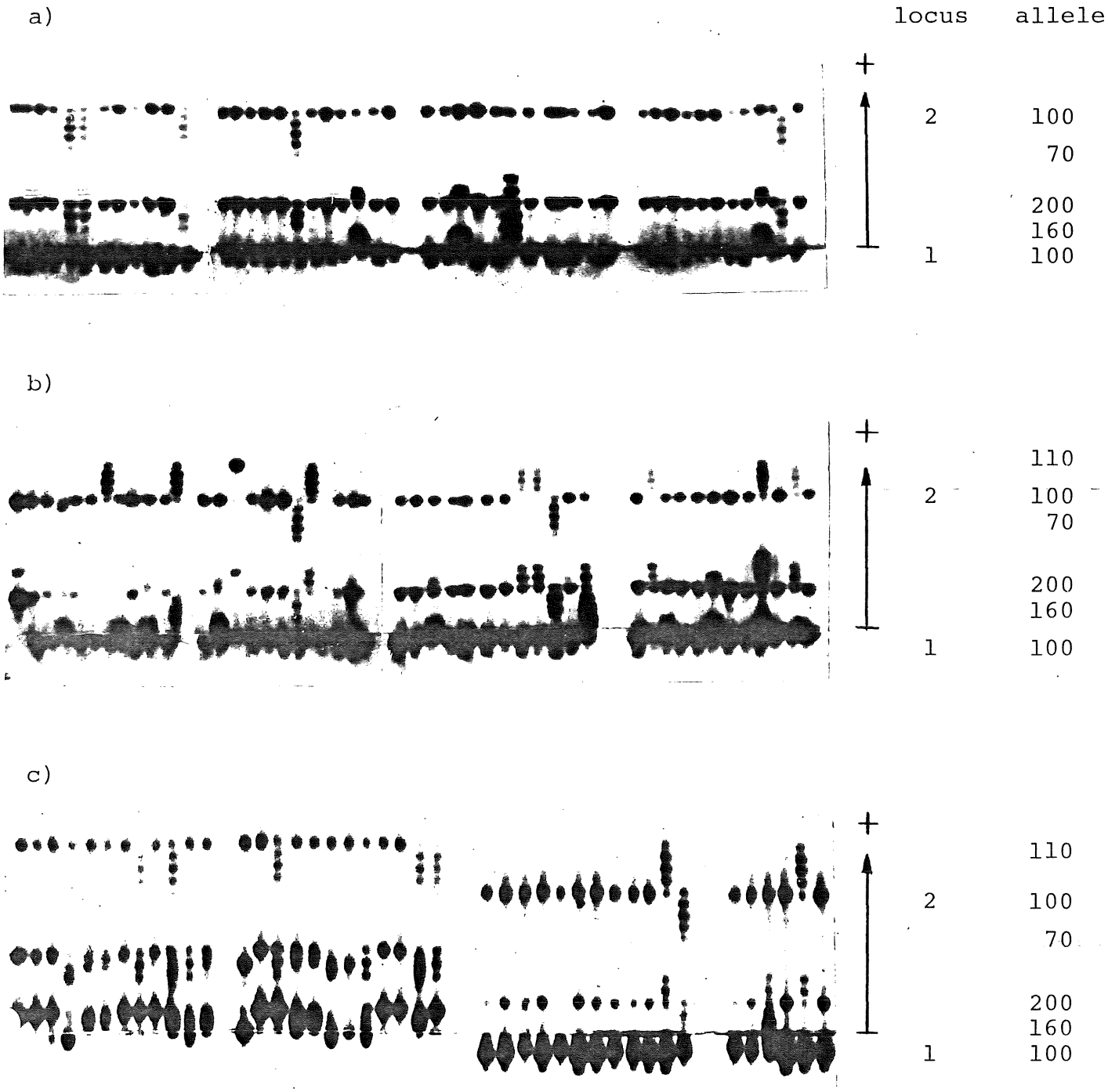

Fig.3 Part of starch gels stained for lactate dehydrogenase(LDH).

a) Sample from the Møre area(Sundalsøra).

b) Sample from Trondheimsfjorden(Åsenfjord).

c) Sample from Balsfjord and a control sample from Trondheimsfjord in the right part of the gel.