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THE RELATIONSHIP BETWEEN ARCTIC AND COASTAL COD IN THEIR IMMATURE STAGES ILLUSTRATED BY FREQUENCIES OF GENETIC CHARACTERS

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INTRODUCTION

The cod, *Gadus morhua* L., which inhabit the Norwegian coast and the Barents Sea, form two genetically separate populations (MØLLER 1968a). In spite of the simultaneous spawning in the same areas the two groups of cod have significant differences in frequency of the haemoglobin *HbI*[1] allele (SICK 1965) and of the blood types A and E (MØLLER 1967). The investigations did not record possible gene flow from one gene pool to another, implying that the Arctic and the coastal cod should be regarded as two sibling species (MØLLER 1968b).

The present paper describes the variation of the *HbI*[1] allele and the blood type E frequencies of samples of immature cod, which have been collected inshore and offshore at the bottom along the Norwegian coast and in the Barents Sea. Since Arctic and coastal cod are characterized by certain frequencies of these characters (MØLLER 1968a), this variation also gives expression for the relationship between immature Arctic and coastal cod.

Portions of this material have been published previously either as a part of other investigations (FRYDENBERG, MØLLER, NÆVDAL, and SICK 1965; MØLLER 1967) or as a preliminary report (MØLLER, NÆVDAL and VALEN 1967).

MATERIAL AND METHODS

The material consists of two main parts: fourteen samples of cod fry, totalling 914 specimens, from the Vestfjord, Troms, and Finnmark area (Table 1, Fig. 1); and forty-eight samples of young cod, of which the

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Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

Table 1. Date, locality and number of specimens of, and gear used for collected cod fry samples.

Sample No.	Date	Locality	Number of specimens	Gear
1	4 Oct. 63	Øksfjorden	60	Shore seine
2	4 Oct. 63	Øksfjorden	65	Shrimp-trawl
3	27 Oct. 64	Øksfjorden	60	Shrimp-trawl
4	3 Oct. 63	Gausvik, Vågsfjorden	81	Shore seine
5	28 Oct. 64	Gausvik, Vågsfjorden	73	Shore seine
6	3 Oct. 63	Rolla, Vågsfjorden	77	Shrimp-trawl
7	28 Oct. 64	Rolla, Vågsfjorden	80	Shrimp-trawl
8	5 Oct. 63	Eidsfjorden	22	Shore seine
9	5 Oct. 63	Eidsfjorden	84	Shrimp-trawl
10	9 Oct. 63	Ulsfjorden	85	Shore seine
11	9 Oct. 63	Ulsfjorden	67	Shrimp-trawl
12	8 Oct. 63	Altafjorden	68	Shore seine
13	8 Oct. 63	Altafjorden	15	Shrimp-trawl
14	1 Nov. 64	Varangerfjorden	77	Shrimp-trawl

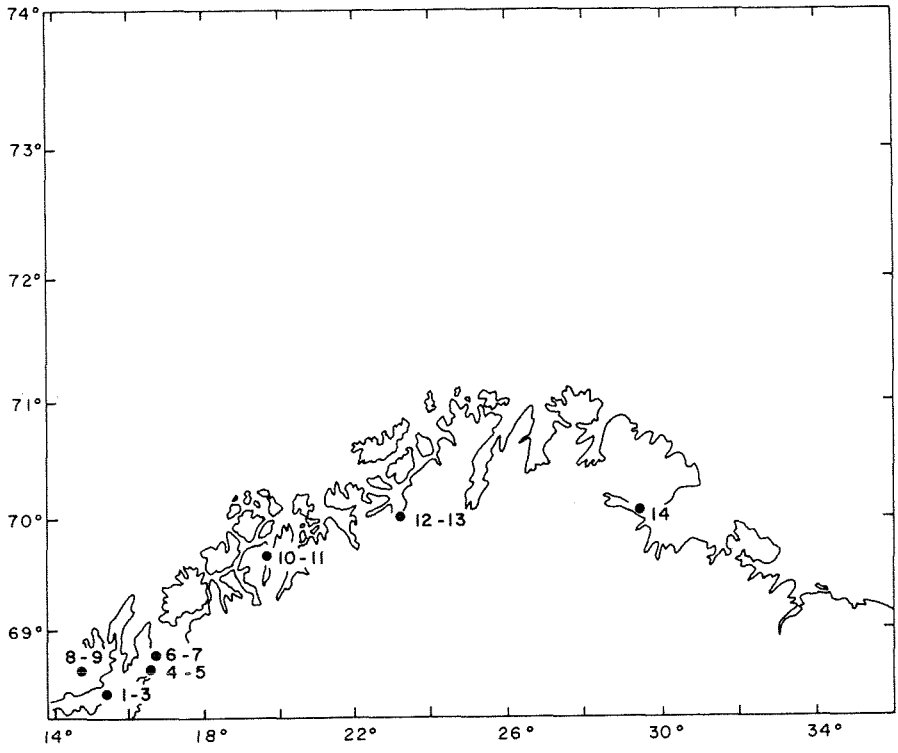

Fig. 1. The location of capture of fourteen cod fry samples.

Table 2. Date, locality and number of specimens of, and gear used for collected samples of young cod.

Sample No.	Date	Locality	Number of specimens	Gear
1	4 Oct. 63	Øksfjorden	57	Shrimp-trawl
2	27 Oct. 64	Øksfjorden	80	Shrimp-trawl
3	25 Oct. 65	Øksfjorden	109	Shrimp-trawl
4	3 Oct. 66	Øksfjorden	115	Shrimp-trawl
5	3 Oct. 63	Gausvik, Vågsfjorden	28	Shore seine
6	26 Oct. 65	Rolla, Vågsfjorden	26	Shrimp-trawl
7	28 Oct. 65	Målsnes, Malangen	85	Shrimp-trawl
8	30 Sept. 66	Målsnes, Malangen	97	Shrimp-trawl
9	10 Oct. 63	Tromsø	191	Trap-net
10	9 Oct. 63	Breivik, Ulsfjorden	20	Shore seine
11	7 Oct. 63	Breivik, Ulsfjorden	156	Shrimp-trawl
12	11 Nov. 64	Breivik, Ulsfjorden	115	Shrimp-trawl
13	16 Sept. 66	Breivik, Ulsfjorden	120	Shrimp-trawl
14	29 Oct. 65	Grøtnes, Ulsfjorden	59	Shrimp-trawl
15	28 Sept. 66	Årøy, Kvenangen	120	Shrimp-trawl
16	29 Sept. 66	Rødøy, Kvenangen	114	Shrimp-trawl
17	8 Oct. 63	Bosekop, Altafjord	156	Shrimp-trawl
18	30 Oct. 64	Bosekop, Altafjord	95	Shrimp-trawl
19	30 Oct. 65	Bosekop, Altafjord	39	Shrimp-trawl
20	19 Sept. 66	Bosekop, Altafjord	120	Shrimp-trawl
21	28 Feb. 66	Sørøya N 71° 03′, E 23° 31′	98	Trawl
22	2 Nov. 65	St. Tamsøy, Porsangerfjorden	173	Shrimp-trawl
23	16 Mar. 66	St. Tamsøy, Porsangerfjorden	119	Shrimp-trawl
24	20 Sept. 66	St. Tamsøy, Porsangerfjorden	120	Shrimp-trawl
25	27 Sept. 66	Svaerholt, Porsangerfjorden	118	Shrimp-trawl
26	6 Nov. 64	Mårøy, Laksefjord	96	Shrimp-trawl
27	5 Nov. 64	Kjeldneset, Tanafjord	120	Shrimp-trawl
28	21 Sept. 66	Kjeldneset, Tanafjord	119	Shrimp-trawl
29	26 Sept. 66	Losvik, Tanafjord	120	Shrimp-trawl
30	14 Mar. 63	Tanasnaget N 71° 06′, E 29° 00′	115	Trawl
31	20 Apr. 64	Tanasnaget N 71° 00′, E 29° 04′	40	Trawl
32	2 Mar. 66	Tanasnaget N 71° 01′, E 29° 06′	118	Trawl
33	15 Jan. 67	Tanasnaget N 70° 58′, E 28° 59′	120	Trawl
34	12 Nov. 65	Makkaur	119	Long line
35	2 Nov. 64	V. Jacobselv, Varangerfjorden	93	Shrimp-trawl
36	23 Sept. 66	Vadsø, Varangerfjorden	118	Shrimp-trawl
37	16 Jan. 67	Kiberg, Varangerfjorden	120	Trawl
38	4 Mar. 66	Malangsgrunnen N 69° 51′, E 16° 42′	97	Trawl
39	21 Nov. 64	Malangsgrunnen N 70° 00′, E 17° 10′	79	Trawl
40	19 Nov. 64	Bear Island N 73° 55′, E 18° 15′	133	Trawl
41	28 Feb. 64	Nordkapp Bank N 72° 12′, E 24° 25′	123	Trawl
42	1 Mar. 66	Nordkapp Bank N 71° 55′, E 25° 10′	120	Trawl
43	20 Apr. 64	Nordkyn N 71° 14′, E 27° 55′	90	Trawl
44	18 Jan. 67	East Bank N 70° 16′, E 32° 25′	117	Trawl
45	12 Mar. 63	East Bank N 70° 06′, E 33° 45′	138	Trawl
46	13 Mar. 63	Skolpen Bank N 70° 54′, E 34° 00′	80	Trawl
47	10 Mar. 63	Skolpen Bank N 70° 10′, E 34° 50′	150	Trawl
48	26 Jan. 67	Skolpen Bank N 71° 21′, E 35° 31′	120	Trawl

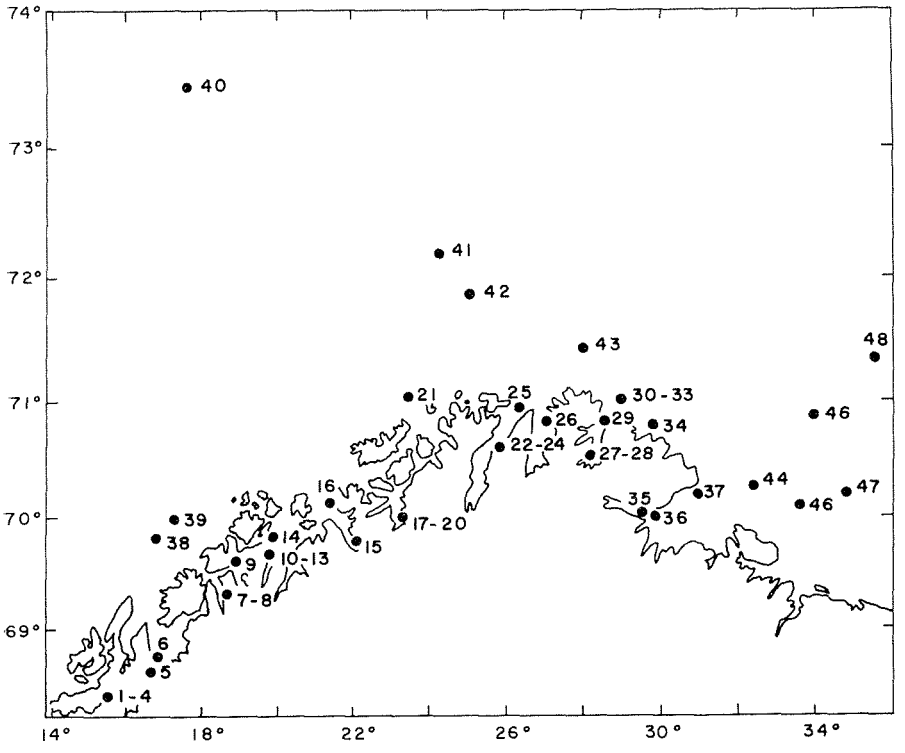

Fig. 2. The location of the forty-eight sampling stations of immature cod.

majority were from three to six years old, totalling about 5,000 specimens, from different localities in northern Norway and in the Barents Sea (Table 2, Fig. 2).

Both in Table 1 and 2 the samples are listed in geographical order from south to north and east. In Table 2 the samples from the coast are presented first and then the samples from the coastal banks and the sea. Samples taken from the same fjord are listed after locality in order from the bottom to the mouth of the fjord.

In addition to date, locality, and the total numbers of specimens in each of the samples, the tables also give information about the fishing gear used. Most of the fish were caught with the help of fishery research vessels, except for the fish caught by trap-nets and the fish in sample 34 (Table 2), which were caught by professional fishermen.

During trawling and long line fishing the depths were recorded by an echo sounder, and the approximate mean depth of the different sampling localities are given in Table 3 and 4. In the same tables the depths for the shore seine and the trap-net fishing are estimated as 2 and 15 m, respectively.

The fry blood specimens were acquired from live fish by cutting the tail, while the other blood specimens were obtained by heart puncture of live cod. The handling of the specimens, the method used in haemoglobin determinations, the blood grouping technique, and the explanation of the nomenclature used in this paper, have been described elsewhere (SICK 1965; MØLLER 1967). However, the blood type E frequency of nine samples, collected in 1963, was not determined due to lack of antisera at that time.

All specimens were analysed at the Institute of Marine Research, Bergen, except for the samples 32 to 35 which were sent to the Institute of Genetics, Copenhagen, where the electrophoresis was carried out (FRYDENBERG *et al.* 1965).

RESULTS

THE VARIATION OF THE FREQUENCY OF THE HbI¹ ALLELE IN SAMPLES OF COD FRY

Table 3 gives the distribution of the haemoglobin patterns, the frequency of the *HbI*¹ allele (q^1), and the depth of the cod fry samples. The frequencies of the samples vary between .088 (sample 7) and .432 (sample 8), and the frequencies differ significantly among samples taken in the same fjord (samples 1–3, 4–7, and 8–9) and in the same year (samples 4

Table 3. The distribution of the haemoglobin patterns, the frequency of the *HbI*¹ allele (q^1), and the depth of the cod fry samples.

Sample	*HbI*¹/*HbI*¹ homozygotes	*HbI*¹/*HbI*² heterozygotes	*HbI*²/*HbI*² homozygotes	Total of rare types	q^1	Depth of sample in meter
1	4	19	37	0	.225	2
2	4	22	39	0	.231	200
3	3	14	43	0	.167	200
4	8	19	54	0	.216	2
5	7	32	34	0	.315	2
6	0	15	62	0	.097	300
7	2	10	68	0	.088	240
8	4	11	7	0	.432	2
9	4	36	44	0	.262	250
10	6	29	50	0	.241	2
11	7	28	32	0	.313	125
12	9	25	34	0	.316	2
13	2	6	7	0	.333	70
14	3	21	52	1	.175	200

and 6, 5 and 7, and 8 and 9). The differences between these pair of samples from the same fjord are similar with high values of q^1 in shallow water and with low values in deep water.

However, the frequencies have about the same value in the samples 1 and 2, or the difference is contrary with slightly higher values in deep water in the samples 10 and 11, and 12 and 13. Regarding the difference in depth between the samples 11 and 13, and the samples 2, 3, 6, 7, and 9, the main impression is that the frequency of the *HbI*^{1} allele varies to a certain degree with the depth; the lowest values being in deeper water.

This relationship is supported further by treating the samples as grouped data. The depth versus the mean frequency of the samples belonging to the same 50 m class is plotted in Fig. 3. Only the frequencies between 51 and 150 m do not appear to fit in the diagram of correlation between depth and frequency of the *HbI*^{1} allele.

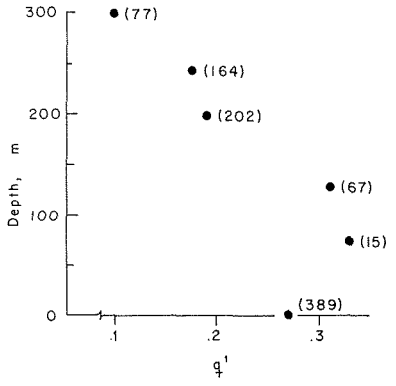

Fig. 3. Relationship between frequencies of the *HbI*^{1} allele (q^1) in in samples of cod fry and sampling depths. Figures in brackets represent the number of specimens.

THE VARIATION OF THE FREQUENCIES OF THE HbI^1 *ALLELE AND THE BLOOD TYPE E IN SAMPLES OF YOUNG COD*

The distribution of the haemoglobin patterns, the values of q^1, and of the frequency of the blood type E (p^E), together with the depth of the collected samples of young cod are listed in Table 4.

In Figs. 4 and 5 the values in samples from different localities of q^1 and p^E, respectively, are represented on a map of northern Norway and the Barents Sea. In localities which in Table 4 are shown with two or more samples, the values on the maps represent the means.

The highest values both of q^1 and p^E are found inshore (Figs. 4 and 5), whereas mostly all of the values in samples from the banks appear to be comparatively low. In most of the fjords with more than one sample the

Table 4. The distribution of the haemoglobin patterns, the frequencies of the *HbI*^{1} allele (q^1) and the blood type E (p^E), and the depth of the samples of young cod.

Sample	*HbI*^{1}/*HbI*^{1} homo-zygotes	*HbI*^{1}/*HbI*^{2} hetero-zygotes	*HbI*^{2}/*HbI*^{2} homo-zygotes	Total of rare types	q^1	p^E	Depth of sample in meter
1	4	19	34	0	.237	—	200
2	7	20	48	5	.216	.385	200
3	5	31	72	1	.188	.426	200
4	6	33	70	6	.196	.487	200
5	2	13	13	0	.304	—	2
6	1	6	18	1	.154	.269	240
7	3	20	62	0	.153	.476	200
8	5	40	52	1	.255	.674	110
9	19	83	88	1	.317	.917	15
10	2	7	11	0	.275	—	2
11	9	42	105	0	.192	—	115
12	4	38	70	3	.200	.708	110
13	1	23	96	0	.104	.458	120
14	4	17	38	0	.212	.568	175
15	6	37	76	1	.204	.508	110
16	1	18	89	6	.088	.343	295
17	9	61	86	0	.253	—	70
18	3	35	57	0	.216	.637	70
19	1	10	27	1	.154	.645	70
20	3	45	70	2	.213	.825	70
21	6	23	69	0	.179	.155	220
22	6	44	122	1	.162	.606	210
23	1	32	86	0	.143	.419	230
24	5	34	79	2	.183	.592	230
25	1	25	86	6	.114	.283	230
26	5	10	80	1	.104	.152	220
27	3	23	92	2	.121	.432	175
28	4	30	82	3	.160	.310	180
29	1	22	96	1	.100	.263	310
30	3	26	86	5	.133	—	290
31	0	9	31	0	.113	.233	220
32	3	22	89	4	.119	.164	220
33	5	28	85	2	.158	.383	100
34	2	29	87	1	.139	.187	215
35	2	31	56	4	.188	.641	200
36	1	26	91	0	.119	.244	230
37	7	39	72	2	.221	.368	110
38	1	16	80	0	.093	.208	260
39	5	19	55	0	.184	.575	220
40	3	31	90	9	.139	.101	250
41	2	23	98	0	.110	.048	265
42	1	23	96	0	.104	.112	255

Table 4 (*continued*).

Sample	*HbI*^{1}/*HbI*^{1} homo-zygotes	*HbI*^{1}/*HbI*^{2} hetero-zygotes	*HbI*^{2}/*HbI*^{2} homo-zygotes	Total of rare types	q^1	p^E	Depth of sample in meter
43	3	14	73	0	.111	.097	250
44	5	21	90	1	.132	.068	180
45	1	21	136	2	.072	—	220
46	1	14	63	2	.100	—	180
47	0	25	124	1	.083	—	230
48	1	17	102	0	.079	.100	190

sample with the lowest value of q^1 and p^E is found near the mouth of the fjord:

Vågsfjorden	q^1: .304 and .154	p^E: —
Ulsfjorden	.173 and .212	.360 and .343
Kvenangen	.204 and .088	.299 and .189
Porsangerfjorden	.163 and .114	.330 and .154
Tanafjorden	.140 and .100	.215 and .141
Varangerfjorden	.188 and .119	.401 and .130

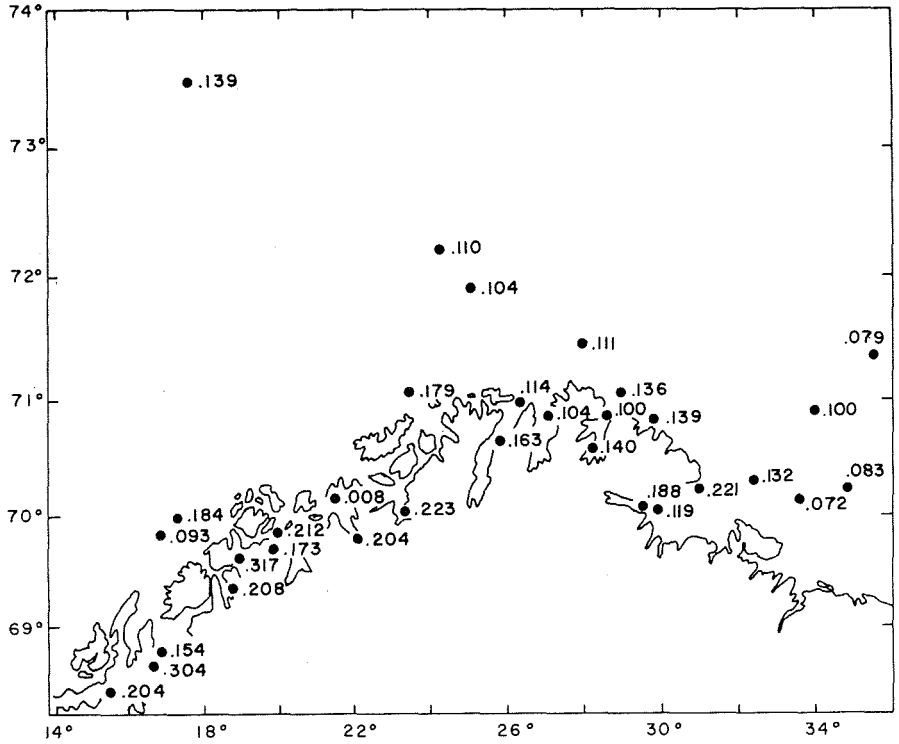

Fig. 4. The frequencies of the *HbI*^{1} allele in the different sampling localities.

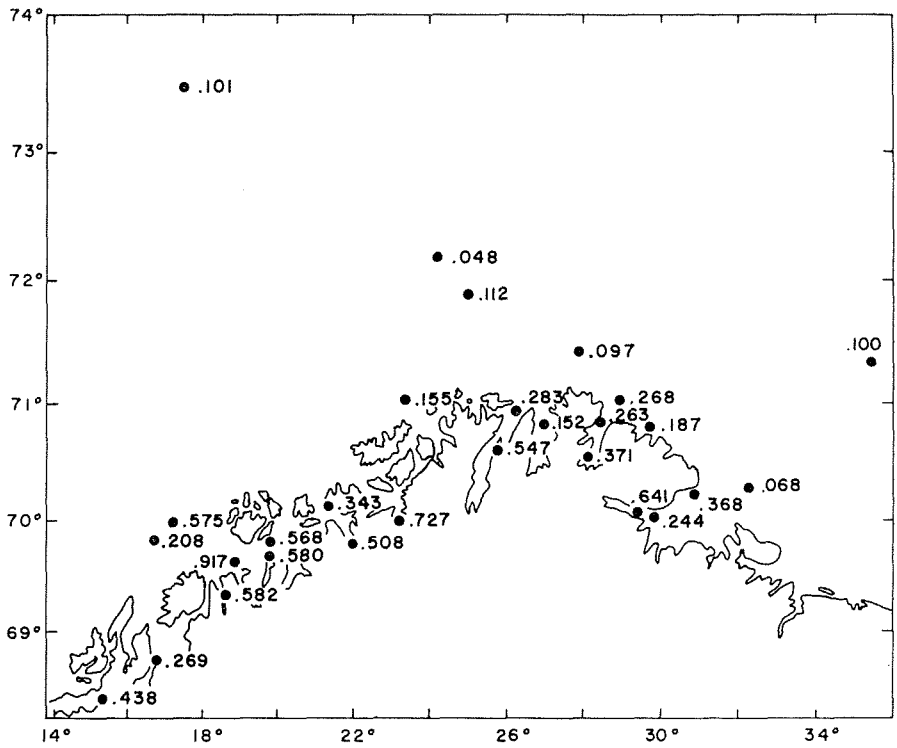

Fig. 5. The frequencies of the blood type E in the different sampling localities.

However, the figures contain more frequencies which do not fit in this general pattern, in Fig. 4 for instance, the values .212, .179, .141, and .225; and in Fig. 5 the values .917, .268, and .368. Therefore, the values of q^1 and p^E according to the depth of the sample are plotted in Figs. 6 and 7, respectively. Incidentally, the samples collected inshore and the samples within the coastal locality form four different groups as indicated on the figures.

Both in Figs. 6 and 7 the frequencies are decreasing with increasing depth. Although there are large variations from one sample to another, the values of the estimated means in each of the groups both for q^1 and p^E are decreasing continually with the values .312 and .920, respectively, near the surface to .109 and .300 at 300 m. The decline in the values of the frequencies appears greatest in the first 100 m.

The values of q^1 and p^E in samples from the sea are low (Figs. 6 and 7). Only one sample (sample 39) has intermediate values of q^1 and p^E, while the others have as low or lower values than the samples collected inshore on corresponding depth.

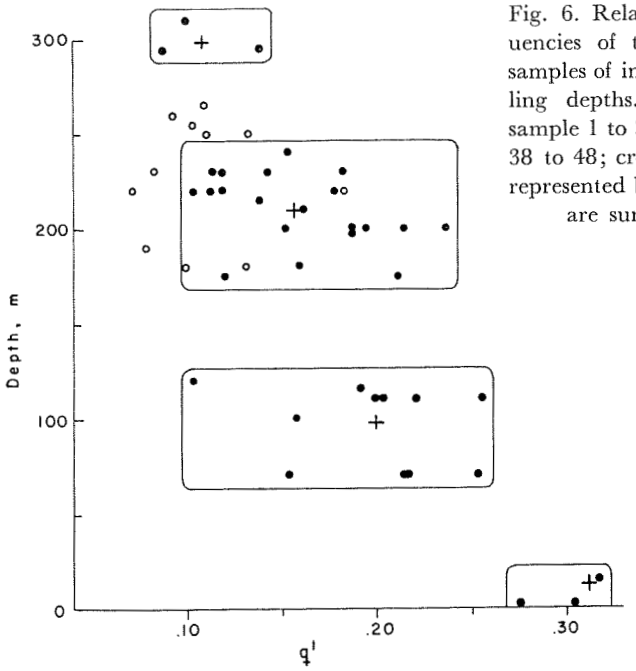

Fig. 6. Relationship between frequencies of the *HbI*^{1} allele (q^1) in samples of immature cod and sampling depths. Legend: Black dots, sample 1 to 37; open circles, samples 38 to 48; crosses, means of samples represented by black dots and which are surrounded by a line.

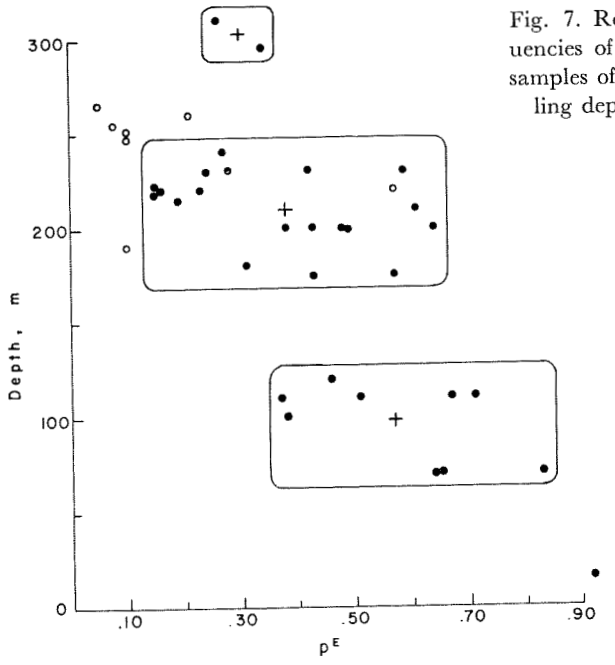

Fig. 7. Relationship between frequencies of the blood type E (p^E) in samples of immature cod and sampling depths. Legend: See Fig. 6.

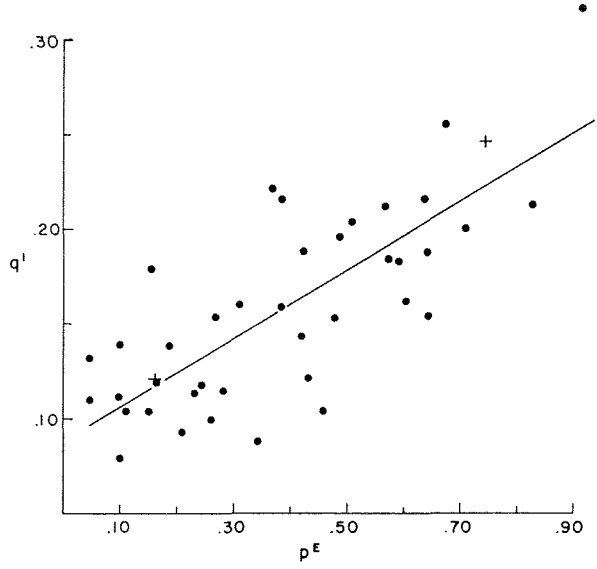

Fig. 8. Relationship between frequencies of *HbI*^{1} allele (q^1) and frequencies of the blood type E (p^E) in the samples. Legend: Black dots, values of the samples; regression line, $y = .089 + .179\ x$; crosses, mean values of the spawning groups of Arctic and coastal cod.

The value of q^1 according to the value of p^E in the same sample are plotted in Fig. 8, together with values representing spawning groups of Arctic and coastal cod in the Vestfjord and north to the Laksefjord (MØLLER 1968a).

Here too there are large variations from one sample to another. However, the values correlate (correlation coefficient .77), and the data fits a straight regression line ($y = .089 + .179x$; linear regression coefficient = .179, highly significant $P > .01$). The mean values of the Arctic cod spawning groups fit this line, while the values of the coastal spawning groups are slightly different.

THE DISTRIBUTION OF THE HAEMOGLOBIN PATTERNS

Tables 2 and 4 list the haemoglobin patterns, the homozygotes *HbI*^{1}/*HbI*^{1} and *HbI*^{2}/*HbI*^{2}; and the heterozygote *HbI*^{1}/*HbI*^{2}, in the cod fry and young cod samples, respectively. The total numbers of individuals in several of the samples are low, and the observed numbers of the different patterns of the individual samples in the tables deviate slightly from the expected numbers calculated from the Hardy-Weinberg law of genotype distributions in large random mating populations. However, by treating the samples in larger units it is possible to detect unconformity. The observed and expected distributions of the haemoglobins in cod fry is not in accordance:

	HbI^1/*HbI*^{1}	*HbI*^{1}/*HbI*^{2}	*HbI*^{2}/*HbI*^{2}
obs.	63	287	564
exp.	46.6	319.7	547.7

$\chi^2 = 9.561$; d.f. $= 1$; $P < .005$

Similarly, the samples collected inshore or on localities near the coast (samples 1 to 37) of young cod do not fit the Hardy-Weinberg law:

	HbI^1/*HbI*^{1}	*HbI*^{1}/*HbI*^{2}	*HbI*^{2}/*HbI*^{2}
obs.	150	1051	2633
exp.	118.8	1112.0	2603.2

$\chi^2 = 11.881$; d.f. $= 1$; $P < .005$

DISCUSSION

The main purpose of the present study is to investigate the relationship between Arctic and coastal cod in their immature stages by the variation of the frequencies of the *HbI*^{1} allele and of the blood type E.

Due to the sampling gear the report is restricted to cod staying near or at the bottom of the sea.

The significant differences found between the observed and the expected numbers both of samples of cod fry and of young cod, demonstrate that the samples were collected from two or more genetically separated populations.

The values of q^1 and p^E correlate (Fig. 8, page 230). The estimated values appear to represent different mixtures of individuals from two distinct populations. The mean values for Arctic cod spawning groups fit in this correlation, while the values of coastal cod spawning groups have slightly higher values of q^1 for corresponding values of p^E. Rather than sampling error the reason for this is that the two groups of samples represent genetic diversity in the coastal cod in that area. While the values of the spawning groups mostly represent samples from the Vestfjord area, the values of young cod represent samples caught in different localities all over northern Norway.

In spawning groups of Arctic and coastal cod in the Vestfjord and north to the Laksefjord the mean frequencies of the *HbI*^{1} allele were .121 and .247, respectively; and of the blood type E .162 and .722 (MØLLER 1968a). The specimens in these spawning groups were classified as Arctic and coastal cod according to the otolith type (ROLLEFSEN 1933), however, otolith types are not a well-defined character. Therefore, the actual values of the Arctic cod groups are somewhat lower than these estimated values, while those values for the coastal cod groups are higher.

The low values of q^1 and p^E in a sample signify a high percentage of Arctic cod, while relatively high values of q^1 and p^E represent a high percentage of coastal cod.

Both the values of q^1 in cod fry samples and the values of q^1 and p^E in samples of young cod were decreasing with increasing depth (Figs. 3, 6 and 7). Although there are large variations from one sample to another, these variations are probably caused by the large geographical differences in sampling localities, both in latitude and in distance from the shore. All localities in the sampling area are not given equal representation. Shallow water east of the Altafjord is poorly represented. The reason for the large drop in frequencies both of q^1 and p^E in the first hundred meters is probably due to inadequate sampling. However, the coastal cod appear to prefer the shallow waters at the coast, while the deep water are prefered by the Arctic cod; an apparent feature which is also characteristic of first year cod in late autumn.

Only one of eleven samples collected from the sea appears to contain a high percentage of coastal cod (sample 39) (Figs. 4 and 5), although the depths of these samples were not deeper than the sampling depths inshore or near the coast (Figs. 6 and 7). The frequencies of the samples show that the samples primarily consist of Arctic cod. Thus, the Arctic cod is found in the open sea, while the coastal cod strain is restricted to the coastal waters.

Despite the restricted area of sampling and the limited number of samples it is convincingly demonstrated that the relative strength of Arctic and coastal cod in northern Norway and the Barents Sea appear to depend on depth and distance from the shore.

The result confirms the results of previous studies concerning the distribution of Arctic and coastal cod, such as tagging experiments and determination of the otolith types (HYLEN 1964 and 1967; SÆTERSDAL 1956).

Differences found previously between the adult stages (MØLLER 1968a) are supported by the different environmental preferencies demonstrated here in the immature stages. There is every reason now to regard the two cod forms as two sibling species.

SUMMARY

The frequencies of the *HbI*^{1} allele and of the blood type E are recorded for samples of cod fry and of young cod at different localities in northern Norway and the Barents Sea.

Using the frequencies as an expression for the relationship between Arctic and coastal cod it is demonstrated that the relative strength of the

two cod forms appear to depend on depth and distance from the shore. The coastal cod prefer the shallow waters at the coast, while the open sea and deeper waters both offshore and inshore are prefered by the Arctic cod; thus, the two cod forms are regarded as sibling species.

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