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Haemoglobin frequencies and vertebral numbers of cod (*Gadus morhua* L.) off northern Norway – test of a population structure hypothesis

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Cod (*Gadus morhua* L.) off northern Norway are divided into two main groups. The north-east Arctic cod (NAC) migrate southwards from the Barents Sea to the main spawning area near the Lofoten Islands on the coast of northern Norway. Eggs and larvae are carried northwards along the coast into the Barents Sea by the Norwegian Coastal Current. Coastal cod (CC) are present along the entire Norwegian coast and are relatively stationary. Cod were sampled in deep and shallow waters at 11 localities in northern Norway south of Lofoten. The results show haemoglobin-allele frequencies and vertebral numbers that are typical for coastal cod. The variation in haemoglobin-allele frequencies between samples was relatively small in this study, compared with similar studies from north of Lofoten. These results indicate a less heterogeneous cod population structure to the south compared with the north of the Lofoten Islands. This conforms to the hypothesis that some NAC settle along the coast and in the fjords of northern Norway north of Lofoten.

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Introduction

The Atlantic cod (*Gadus morhua* L.) is distributed over a large geographic area with different stocks having different life-history characteristics and migration patterns (Brander, 1994). In northern Norway, the north-east Arctic cod (NAC), migrates from the feeding areas in the Barents Sea and near Svalbard to the spawning areas along the Norwegian coast (Hylen, 1964; Bergstad *et al.*, 1987; Brander, 1994). The most important spawning area, where 65–75% of the NAC eggs are spawned, is located near the Lofoten Islands between 67°30′N and 68°30′N (Fig. 1) (Brander, 1994). Another major spawning area is off Møre. Minor spawning areas and areas with occasional spawning are located along the coast from Finnmark to south of Møre (Fig. 1). The eggs, larvae and juveniles of the NAC cod drift in the Norwegian Coastal Current from the spawning areas in the south, along the coast and into the Barents Sea in the north (Bergstad *et al.*, 1987; Sundby *et al.*, 1989; Brander, 1994). The coastal cod (CC) inhabit coastal areas and fjords, migrate short distances and spawn in a large number of fjords along the coast (Rollefsen, 1954; Jakobsen, 1987), including around the Lofoten Islands (Møller, 1966; Sundby, 1994; Nordeide, unpublished data). Little is known about drift of their eggs and larvae.

NAC have been distinguished from CC by several characteristics. The average number of vertebrae in NAC is between 53 and 54, which is higher than for CC (ca. 52–53 vertebrae) (Schmidt, 1930; Løken *et al.*, 1994; Fevolden and Pogson, 1995). The frequency of one of the two common haemoglobin alleles (HbI^1) is near 0.10 for NAC and from about 0.25 to 0.50 for CC in northern Norway (Frydenberg *et al.*, 1965; Møller, 1966). The NAC and CC also differ in otolith structure (Rollefsen, 1933; Møller, 1968; Jakobsen, 1987), mitochondrial DNA (Dahle, 1991), and probably also nuclear DNA (Fevolden and Pogson, 1995).

Several studies have supported the hypothesis that both NAC and CC are present along the coast and in some fjords in northern Norway. From studies of

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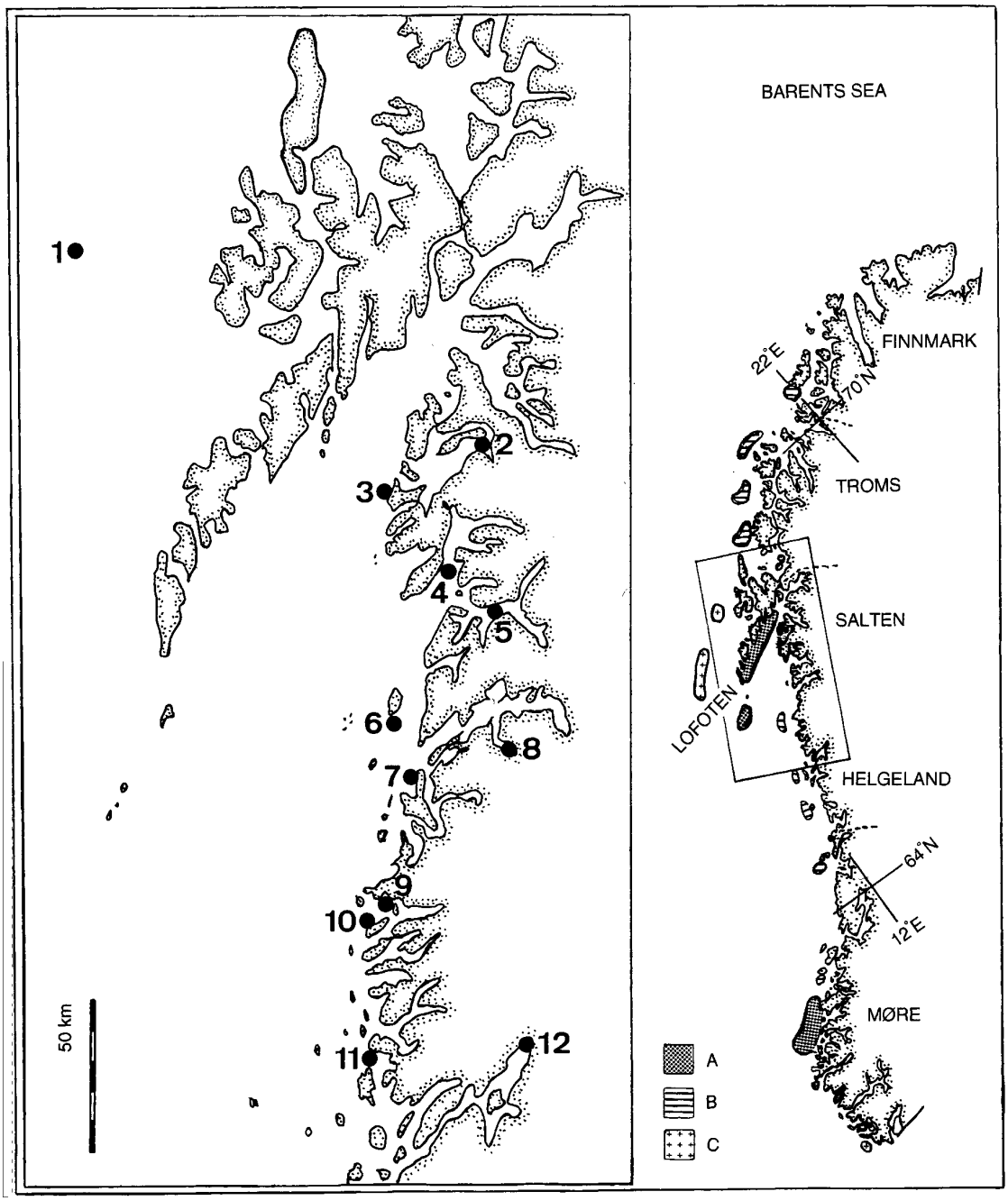

Figure 1. *Left*: the study area including stations 1–12 (●) where cod were caught in the present study. *Right*: distribution of spawning areas of the north-east Arctic cod, redrawn from Brander (1994). (A) major spawning areas; (B) minor spawning areas; and (C) areas of occasional spawning.

polymorphism in blood proteins (including haemoglobin) of cod fry and 3–6-year-old cod, Møller (1969) concluded that CC were present in shallow water and NAC in deeper water. Løken *et al.* (1994) came to similar conclusions from studies of average numbers of vertebrae of cod.

The stock structure of cod in northern Norway south of Lofoten has received little attention. The influence from NAC should be less to the south compared with the north of the most important spawning area of NAC, since the eggs, larvae and juveniles are carried northwards by the Norwegian Coastal Current. According to

Møller (1969) and Løken *et al.* (1994), we may predict that *HbI*^{1}-allele frequencies, and average vertebral counts of cod sampled south of Lofoten, are less heterogeneous compared to north of Lofoten since there will be less mixing. The aim of this study was to test this prediction. We studied *HbI*^{1}-allele frequencies and vertebral numbers of cod from 11 stations at deep and shallow waters south of Lofoten, and compared them with previously published samples from north of Lofoten.

Materials and methods

The cod were collected from October 1994 to September 1996 at 11 localities in fjords and on the coast of northern Norway south of Lofoten, from Sagfjord in the north to Mo i Rana in the south (Fig. 1, Table 1). An additional sample (station 1, Fig. 1) was collected during the spawning period along the known migration route of the NAC from the Barents Sea to Lofoten. The data from station 2 and 3 (Table 1) are from pooled samples from three and two time periods, respectively. The rest of the samples were caught during 1–9 subsequent days. Gillnets, lines and trawls were used to catch the fish.

Studies of growth zones in otoliths suggested that the median age of the cod (station 1 excluded) was 3–4 years, and more than 80% were 2–6 years old. Total length of the cod was measured to the nearest cm. Vertebral numbers including the urostylar half-vertebrae were counted. Sampling of blood was described by Møller (1968). The haemoglobin was analysed by agar gel electrophoresis within 4 d as described by Sick (1961) with modifications by Jørstad (1984). The haemoglobin alleles were named according to Sick (1965).

Published *HbI*^{1}-allele frequencies of cod caught in fjords and along the coast of northern Norway north of Lofoten and in the Barents Sea (Frydenberg *et al.*, 1965; Møller, 1969; Jørstad, 1984; Jørstad and Nævdal, 1989; Dahle and Jørstad, 1993), were compared to *HbI*^{1}-allele frequencies from samples in northern Norway south of Lofoten. The latter frequencies are those presented in the present study (Table 1, stations 2–12) in addition to frequencies from four published samples (Frydenberg *et al.*, 1965). We excluded published *HbI*^{1}-allele frequencies of potential mature cod caught during the spawning period from January to May, and frequencies calculated from samples of less than 30 cod. The data are available from the authors. In order to compare the *HbI*^{1}-allele frequencies between different regions in northern Norway, we grouped the samples into four regions: Barents Sea, Finnmark, Troms–Lofoten, and Salten–Helgeland (Fig. 1). We sometimes refer to the region Salten–Helgeland as "northern Norway south of Lofoten".

The discrepancy between observed and expected frequencies of genotypes was tested both with chi-squared test (Sokal and Rohlf, 1981) and a test based on Wright's fixation index of subpopulations (WFI):

$$WFI=[(4X_{11}X_{22}-X_{12}^2)/((2X_{11}+X_{12})\ (X_{12}+2X_{22}))]\sqrt{X}$$

where X_{11} and X_{22} are number of homozygote genotypes, X_{12} are number of heterozygotes and $X=X_{11}+X_{22}+X_{12}$ (Christiansen *et al.*, 1976). Homogeneity between samples was tested with a G-test (Sokal and Rohlf, 1981). ANOVA-tests were carried out using SYSTAT software version 5. The F-test was performed on ln-transformed data with EXCEL software version 4.0.

Results

Frequencies of *HbI*^{1}-allele

Frequencies of the *HbI*^{1}-allele in the stations south of Lofoten varied from 0.314 to 0.444 (Table 1, station numbers 2–12). No significant deviation between observed and expected Hardy–Weinberg distribution of genotypes was observed (Table 1). Wright's fixation index was positive, but not significant, for 9 of the 12 stations (Table 1). Positive indexes indicate a deficit of heterozygotes, which may be caused (1) by a mixture of two populations with different allele frequencies, or (2) by selection (Christiansen *et al.*, 1976).

Allele frequencies as well as genotype distribution were not found to be heterogeneous between the 11 stations south of Lofoten (alleles: $G_H=16.04$, $p>0.05$, d.f.$=10$, G-test; genotypes: $G_H=19.51$, $p>0.1$, d.f.$=20$). The *HbI*^{1}-allele frequency of cod collected along the known migration route of the NAC north of Lofoten was 0.124 (Table 1, station 1). Including all stations and testing again, the frequencies of both alleles and genotypes were heterogeneous between the stations (alleles: $G_H=104.03$, $p<0.001$, d.f.$=11$; genotypes: $G_H=102.78$, $p<0.001$, d.f.$=22$).

The coefficient of variation between stations of *HbI*^{1}-allele frequencies of cod in Salten–Helgeland, was less than half that of (1) Troms–Lofoten, (2) Finnmark, and (3) the Barents Sea (Table 2). The differences were significant when stations from all depths were pooled, and even when only stations from depths less than approximately 150 m were taken together (Table 3).

Rare haemoglobin alleles

Rare haemoglobin genotypes were found in four out of 12 stations (Table 1). The 12 rare haemoglobin genotypes are numbered according to Frydenberg *et al.* (1965, Fig. 3). We found two number 9 genotypes at station 6, one number 4 genotype at station 7, two

Table 1. Genotypes and allele frequencies of *Hbl*^{1} of cod sampled in northern Norway. Individuals with rare haemoglobin alleles were excluded before the allele frequencies were calculated. Chi-squared test (χ^2-test) and a test based on Wright's fixation index (WFI), both tests for deviations between observed and Hardy–Weinberg distributions of genotypes. Gear: A=bottom trawl, B=prawn trawl, C=gillnets, D=lines.

Station no.	Area	Date	Position	Depth (m)	Gear	n	Genotypes				Allele freq. *Hbl*^{1}	χ^2-test χ^{2*}	WFI†	Vertebral numbers		
							11	12	22	Rare				n	Mean	S.D.
1	Eggakant	Apr 95	68°58′N 13°36′E	160–200	A	162	1	38	123	0	0.124	0.28‡	−1.07	25	53.20	0.764
2	Sagfjord	Jun–Nov 95	67°58′N 15°50′E	5–50	C	74	10	27	37	0	0.318	1.85	1.36	36	52.39	0.964
3	Engeløya	Dec 95–Jul 96	67°57′N 14°55′E	5–50	C	34	7	12	15	0	0.382	2.17	1.47	21	52.33	0.577
4	Nordfolla	Jun 96	67°40′N 15°11′E	235–290	A, B	118	13	48	57	0	0.314	0.36	0.60	55	53.00	0.903
5	Sørfolla	Nov 95	67°33′N 15°04′E	20–120	A	58	6	27	25	0	0.336	0.11	−0.33	58	52.55	0.940
6	Landego	Sep 96	67°19′N 14°16′E	245–265	A	94	12	37	43	2	0.332	0.79	0.89	31	52.48	0.677
7	Bodø	Oct 94	67°10′N 14°13′E	15–25	B	137	31	56	49	1	0.434	3.56	1.89	52	52.04	0.791
8	Misvær	Jul 96	67°08′N 14°54′E	0–50	D	54	13	22	19	0	0.444	1.66	1.29	30	52.43	0.774
9	Ørnes	Jun 96	66°53′N 13°53′E	20–40	A	58	10	28	20	0	0.414	0.00	0.04	24	52.04	0.859
10	Meløy	Jun 96	66°47′N 13°22′E	140–205	A	80	14	31	35	0	0.369	2.25	1.50	26	52.69	0.679
11	Lurøy	Jun 96	66°29′N 13°05′E	50–100	A	76	10	35	29	2	0.372	0.01	−0.11	25	51.76	0.831
12	Mo i Rana	Jul 96	66°19′N 14°07′E	0–50	D	81	14	33	27	7	0.412	0.47	0.69	42	52.26	0.767

*χ^2-values less than 3.841 indicate no deviation from Hardy–Weinberg distribution of genotypes at the 95% significance level (d.f.=1, one-tailed) (Sokal & Rohlf, 1981).
†Absolute values less than approximately 2.0 indicate no deviation from Hardy–Weinberg distribution at the 95% significance level (Christiansen *et al.*, 1976).
‡Tested after pooling all homozygotes, since expected numbers of *Hbl*^{1} were less than 5 (Lessios, 1992).

Table 2. Statistics of published *Hbl*^{1}-allele frequencies of cod within each region of northern Norway (Frydenberg *et al.*, 1965; Møller, 1969; Jørstad, 1984; Jørstad & Nævdal, 1989; Dahle & Jørstad, 1993). *Hbl*^{1}-allele frequencies from the present study are included in region Salten–Helgeland. Statistics were carried out on non-transformed data. N is number of *Hbl*^{1}-allele frequencies included in the analysis.

Region	Depth (m)	n	Mean	Standard deviation	Coefficient of variation
	<150	0	—	—	—
Barents Sea	All	14	0.103	0.024	23.2
	<150	5	0.231	0.061	26.4
Finnmark	All	16	0.170	0.059	34.8
	<150	17	0.259	0.065	25.0
Troms–Lofoten	All	35	0.229	0.071	31.0
	<150	8	0.389	0.045	11.7
Salten–Helgeland	All	15	0.378	0.041	10.9

Table 3. F- and p-values from the F-test when comparing inter-sample differences in mean *Hbl*^{1}-allele frequencies of cod between different regions in northern Norway. Included in the analysis are published *Hbl*^{1}-allele frequencies (Frydenberg *et al.*, 1965; Møller, 1969; Jørstad, 1984; Jørstad & Nævdal, 1989; Dahle & Jørstad, 1993), and *Hbl*^{1}-allele frequencies from the present study. The latter frequencies are included in region Salten–Helgeland. Tests were carried out on ln-transformed data. p-values are two-tailed.

Region	Depth (m)	Barents Sea	Finnmark	Troms–Lofoten	Salten–Helgeland
	<150		—	—	—
Barents Sea	All		1.94^{NS}	2.45*	4.62†
	<150	—		1.24^{NS}	4.97*
Finnmark	All	1.94^{NS}		1.27^{NS}	8.94‡
	<150	—	1.24^{NS}		6.18*
Troms–Lofoten	All	2.45*	1.27^{NS}		11.33‡

*Shows $p<0.05$; †shows $p<0.01$; ‡shows $p<0.001$; NS shows $p\geq0.05$.

number 4 genotypes at station 11, and of the seven rare genotypes at station 12 one was number 4, two number 5 and four number 6. The frequency of rare genotypes was 0.021, 0.007, 0.026 and 0.086 in each of stations 6, 7, 11 and 12, respectively, and 0.005 when stations 1–11 were taken together.

Vertebral numbers

Mean number of vertebrae in the stations south of Lofoten varied from 52.04 to 53.00 (Table 1, station numbers 2–12). The mean vertebral number of the cod collected north-west of Lofoten was 53.20 (Table 1, station 1). Significant heterogeneity in the number of vertebrae was revealed between the stations, regardless of whether or not the station north-west of Lofoten was included (stations 1–12: $F=7.98$, $p<0.001$, d.f.$=11$, ANOVA; stations 2–12: $F=6.513$, $p<0.001$, d.f.$=10$). Significant heterogeneity was also revealed when only stations at depths less than 150 m were taken together (station 2, 3, 5, 7, 8, 9, 11 and 12: $F=3.357$, $p=0.002$, d.f.$=7$).

Discussion

The results indicate no detectable influence from NAC on the cod stock structure in northern Norway south of Lofoten, during the study period. The *Hbl*^{1}-allele frequencies of cod sampled off northern Norway south of Lofoten turned out to be typical for CC in northern Norway (Frydenberg *et al.*, 1965; Møller, 1966). They were also different from the sample collected north-west of Lofoten along the known migration route of the NAC during the spawning period. No discrepancy between observed and Hardy–Weinberg expected genotypes was observed, and no significant intersample variation was found. The average number of vertebrae was between 52 and 53, which is within the typical interval of CC (Schmidt, 1930; Løken *et al.*, 1994; Fevolden and Pogson, 1995).

The cod population structure of the Atlantic cod along the coast of northern Norway, seems to be less heterogeneous to the south compared with the north of the main spawning area of the NAC in Lofoten. This applies when our results are compared with similar studies of *HbI*^{1}-allele frequencies (Table 2 and 3), and average number of vertebrae (Løken *et al.*, 1994) from north of Lofoten. A heterogeneous cod population structure north of the Lofoten Islands is further suggested from studies of otolith growth zones of cod in Finnmark (Jakobsen, 1987).

Analysing population structure from studies on haemoglobin frequencies has been disputed. Different alleles or genotypes may possess different adaptive values and they may be exposed to strong differential selection (Karpov and Novikov, 1980). Thus observed allele frequencies may result from selection (Karpov and Novikov, 1980; Mork *et al.*, 1984a,b). However, recent reviews concluded that such frequencies are stable enough to be used as population parameters at least within a few decades (Ferguson, 1995; Johansen and Nævdal, 1995). The present paper shows very similar *HbI*^{1}-allele frequencies to the four samples from northern Norway south of Lofoten presented more than 30 years ago (Frydenberg *et al.*, 1965). This stability conforms to the conclusions of recent reviews.

NAC and CC have been artificially crossed and the offspring reared under different temperature regimes by Løken and Pedersen (1996). The results suggest that vertebral number is in part genetically determined. Vertebral numbers may therefore be valuable for determining the structure of cod stocks.

Studies of *HbI*^{1}-allele frequencies seem to be a useful method to separate NAC from CC (discussed above). However, it is probably not a powerful method to detect potential local populations of cod. The frequency of rare genotypes (0.086) at station 12 was very high. The frequency in each of stations 6, 7 and 11 was slightly above published frequencies, whereas when station 1–11 were taken together the frequency was about equal to published frequencies (Frydenberg *et al.*, 1965; Dahle and Jørstad, 1993). The high number of rare alleles in station 12, and the significant differences between samples in mean vertebral numbers, may both be interpreted as indications of local populations. However, before conclusions can be drawn, potential local populations of cod must be studied by other methods in addition to those applied in the present study.

We conclude that the results from our analyses of frequencies of *HbI*^{1}-alleles and average number of vertebrae, indicate that cod along the coast and in fjords off northern Norway south of Lofoten, are less heterogeneous compared with cod north of Lofoten. The results conform to the hypothesis that some NAC settle along the coast and in the fjords of northern Norway north of Lofoten (Møller, 1969; Løken *et al.*, 1994).

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