COASTAL COD AND NORTH-EAST ARCTIC COD - DO THEY MINGLE AT THE SPAWNING GROUNDS IN LOFOTEN?

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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 off northern Norway. Coastal cod (CC) are relatively stationary, live and spawn along the entire Norwegian coast, including near the Lofoten Islands. In order to test if the two groups physically intermingle at the spawning grounds, cod were sampled by trawl and Danish seine at the traditionally important spawning grounds near the Lofoten Islands during the spawning season in 1995-97. Cod from 24 samples were examined for haemoglobin alleles, length, sex and stage of sexual maturity. The results indicate that: (1) NAC and CC did not mingle randomly. (2) However, specimens from both groups may stay simultaneously at the same local spawning ground within an area of less than 0.012 km^2. (3) Distribution of NAC and CC overlapped vertically, although NAC was more abundant than CC in samples from deep waters. (4) The sex ratio was skewed towards males in a majority of the samples. (5) A larger percentage of males compared to females was ready to spawn. (6) Cod shoals may be size-assorted. The results are discussed in relation to existing hypotheses about cod spawning behaviour.

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KEYWORDS: Cod; stocks; spawning; distribution.

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). The two main groups of cod in northern Norway are the north-east Arctic cod (NAC) and coastal cod (CC)(ROLLEFSEN 1934, 1954). NAC migrates from the feeding areas in the Barents Sea and near Svalbard to the spawning areas along the Norwegian coast (HYLEN 1964; BERGSTAD & al. 1987). The most important spawning area is located near the Lofoten Islands (BERGSTAD & al. 1987; BRANDER 1994). The majority of spawning of NAC occurs in March-April (SARS 1879; BERGSTAD & al. 1987), with peak spawning on 1 April (PEDERSEN 1984). CC inhabit coastal areas and fjords, migrates short distances and spawns in a large number of fjords along the Norwegian coast (ROLLEFSEN 1954; JAKOBSEN 1987), including around the Lofoten Islands (HYLEN 1964; MØLLER 1966, 1968). CC spawn over a longer time period, with peak spawning 3-4 weeks later than NAC (KJESBU 1988).

Despite that NAC and CC spawn simultaneously around the Lofoten Islands, they seem rarely to interbreed. Studies of several genetically determined characters have revealed significant differences between NAC and CC (frequency of haemoglobin-alleles: MØLLER 1966, 1968, 1969; DAHLE & JØRSTAD 1993; NORDEIDE & PETTERSEN 1998; number of vertebrae: LØKEN & al. 1994; FEVOLDEN & POGSON 1995; LØKEN & PEDERSEN 1996; NORDEIDE & PETTERSEN 1998; mitochondrial-DNA: DAHLE 1991: nuclear-DNA: FEVOLDEN & POGSON 1995, 1997). However, the genetic structure of the cod has been disputed. MORK & al. (1985) reported small differences from the cod's entire area of distribution, from studies of protein loci from muscle and liver.

There is sparse information about the cod's distribution and behaviour within the spawning grounds in Lofoten, and on which mechanisms prevent the two cod groups from interbreeding. SUND (1935) showed that spawning cod gather in shoals near the bottom at the spawning grounds. Such shoals are relatively dense during daytime compared to during the night (SÆTERSDAL & HYLEN 1959). In order to study migration after spawning, HYLEN (1964) caught NAC and CC at the spawning grounds in Lofoten and separated the two groups from otolith patterns. MØLLER (1966, 1968) sampled NAC and CC in Lofoten in order to examine genetic structure of cod off northern Norway. Møller separated the cod groups by frequency of genetically determined characters, including haemoglobin.

The aim of the present paper was to study how both sexes of NAC and CC are distributed relative to each other at the spawning grounds in Lofoten during the spawning period. I wanted to examine if:

1. NAC and CC mingle physically,
2. male and females stay apart or together,
3. percentage individuals which are ready to spawn differed between the sexes,
4. small and large cod stay apart or together.

MATERIAL AND METHODS

The cod were caught during March and April in 1995-1997 (Table 1) at the traditionally known spawning grounds in Lofoten by R/V *Oscar Sund* or a commercial fishing vessel F/V *Seibas*. Shoals of what might be spawning cod were localised by echosounder. The echosounders were 'Simrad EK 500' with 38 kHz transducer and 21.9° beam angel on R/V *Oscar Sund*, and 'Koden Chromascope Fish Finder CVS-886MK2' with 50 kHz transducer and 19° beam angle on F/V *Seibas*. In 1995 we caught the fish by trawling from R/V *Oscar Sund*, and in 1996 and 1997 by a Danish seine from F/V *Seibas*. The trawl sampled fish from approximately the lower 5 m of the water column. The speed during trawling was 2.5-3.0 kn. The Danish seine caught fish from the lower 20 m of the water column. The total swept area of both the trawl and Danish seine as estimated according to Karlsen (1989), is given in Table 1. Total time of each trawling effort was approximately ½-1 ½ hour, and effective fishing time 13-65 min (Table 1). An exception was (sample 7) outside Vesterålen, where effective fishing time was 150 min (Table 1). Total time and effective time of fishing by Danish seine were approximately 45 min and 10-15 min, respectively. Each single sample by trawl or Danish seine was kept and examined separately.

Sex, length and stage of sexual maturity of the fish were examined. Stage of sexual maturity used were 'immature', 'mature', 'spawned' and 'uncertain'. 'Spawned' means that the specimen will not spawn again before next spawning season. The stages corresponds to code 1-2, 3-5, 6 and 8, respectively in Fotland & al. (1995). The stage 'mature' also corresponds to stage 5 in Kjesbu (1991). All specimens were examined in most of the samples with less than 70-80 cod, and part of the sample was examined when the number of cod was larger.

Blood samples of cod were collected, and the haemoglobin was analysed by agar gel electrophoresis within 4 days, as described by Sick (1961) and Jørstad (1984). Haemoglobin alleles were named according to Sick (1965). Samples with frequencies of the Hbl^1-allele (1) ≤ 0.15 were grouped as 'low', (2) > 0.15 and ≤ 0.25 were grouped as 'medium', and (3) > 0.25 were grouped as 'high'. Potential discrepancy between observed

Table 1. Information about the samples where more than 30 cod were caught. 'Time' is when effective fishing started. 'Duration' is effective time of fishing. The fish were caught by bottom trawl in 1995 and by Danish seine in 1996 and 1997.

Sample no.	Date	Time	Duration (min)	Depth (m)	Catch area (km²)	Position	Name of local spawning ground	Cod in the sample N	Cod in the sample %	Footnotes
1	21 Mar 1995	1350	37	115	0.128	68°00.8'N 13°46.8'E	Urefeltet	49	98	1
2	22 Mar 1995	1310	20	155	0.069	67°51.4'N 13°26.6'E	Nappstraumen	84	42	1
3	24 Mar 1995	0950	33	55	0.115	68°08.6'N 14°07.6'E	Henningsværstraum	124	24	1
4	24 Mar 1995	1430	65	90	0.226	68°07.5'N 14°22.6'E	Moholmen	127	74	1
5	4 Apr 1995	0902	13	45	0.045	68°09.8'N 14°08.7'E	Henningsværstraum	88	52	1
6	4 Apr 1995	1500	43	115	0.149	68°02.3'N 13°46.5'E	Urefeltet	204	23	1
7	6 Apr 1995	0545	150	180	0.521	68°58.0'N 13°36.4'E	Eggakanten	>2500	90	2
8	11 Apr 1995	0845	55	80	0.191	68°10.6'N 14°08.7'E	Henningsværstraum	78	45	1
9	11 Apr 1995	1355	46	80	0.160	68°09.4'N 14°27.6'E	Moholmen	229	66	1
10	1 Apr 1996	1700	10	86	0.012	68°11.7'N 14°39.0'E	Høla	37	100	1
11	3 Apr 1996	1115	10	105	0.012	68°11.8'N 14°37.0'E	Høla			2,3
12	3 Apr 1996	1345	10	67	0.012	68°07.6'N 14°06.4'E	Henningsværstraum	6690	98	2,3
13	8 Apr 1996	1315	10	75	0.012	68°08.2'N 14°02.0'E	Henningsværstraum	>1200	96	2
14	9 Apr 1996	1215	10	82	0.012	68°11.7'N 14°39.0'E	Høla	804	76	2
15	13 Apr 1996	1100	10	98	0.012	67°55.9'N 13°18.0'E	Sund	64	59	1
16	28 Mar 1997	0745	10	98	0.012	68°11.4'N 14°37.6'E	Høla	37	100	1
17	28 Mar 1997	1145	10	98	0.012	68°11.4'N 14°37.6'E	Høla	79	63	1
18	28 Mar 1997	1400	10	112	0.012	68°08.1'N 14°29.3'E	Moholmen	461	86	1
19	28 Mar 1997	1830	10	112	0.012	68°08.1'N 14°29.3'E	Moholmen	171	74	1
20	29 Mar 1997	0815	10	112	0.012	68°08.1'N 14°29.3'E	Moholmen	106	96	1
21	3 Apr 1997	0730	10	123	0.012	68°13.0'N 14°38.7'E	Høla			2,4
22	3 Apr 1997	1400	10	110	0.012	68°06.9'N 13°58.3'E	Henningsværstraum	3939	99	2,4
23	3 Apr 1997	1745	10	100	0.012	68°07.0'N 13°58.3'E	Henningsværstraum			2,4
24	4 Apr 1997	1015	10	97	0.012	68°12.5'N 14°38.5'E	Høla	>600	100	2

Footnotes: Percentage distribution of cod in each sample is based on: (1) number of individuals, (2) weight, (3) samples 11 and 12 pooled, and (4) samples 21-23 pooled.

and expected Hardy-Weinberg number of genotypes was examined by both Chi-square test and 'Wright's fixation index' (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 homozygous genotypes, X_{12} is number of heterozygotes, and $X = X_{11} + X_{22} + X_{12}$ (CHRISTIANSEN & al. 1976). Homogeneity between samples was tested with a G-test (SOKAL & ROHLF 1981).

RESULTS

Haemoglobin allele frequencies

Frequency of the *Hbl*^{l}-allele varied from 0.077 to 0.400 (Table 2). The distribution of both genotypes and alleles were heterogeneous between the 24 samples (genotypes: $G_H = 537.9$, $p < 0.001$, d.f. = 46, G-test; alleles: $G_H = 175.9$, $p < 0.001$, d.f. = 23). Discrepancy between observed and expected Hardy-Weinberg number of genotypes was found in two (st. 5 and 12) of the 24 samples (Table 2).

Samples with 'high' *Hbl*^{l} allele-frequency (*Hbl*$^{l} > 0.25$) were abundant both in 1995 and 1996, whereas samples with 'low' *Hbl*^{l} allele-frequency (*Hbl*$^{l} \leq 0.15$) dominated in 1997 (Table 2). Of the six samples with 'medium' *Hbl*^{l} allele-frequency ($0.15 < Hbl^{l} \leq 0.25$), one (st. 6) was found in 1995, two (st. 13 and 15) in 1996, and three (st. 17, 19, and 21) were found in 1997. Cod from samples with both 'low', 'medium' and 'high' *Hbl*^{l} allele-frequencies (st. 16 - 19) were caught within few hours during the same day (28 Mar 1997). The cod in sample 16 and 17, with 'high' and 'medium' *Hbl*^{l} allele-frequencies, were caught within few hours during the same day (28 Mar 1997) and at the local spawning ground 'Høla'. Cod in samples with 'low' and 'medium' *Hbl*^{l} allele-frequencies (st. 18 and 19) were also caught within few hours during the same day and at the local spawning ground 'Moholmen'.

Mean depth of the 24 samples did not vary significantly between the years 1995-97 ($\chi^2 = 3.96$, $p = 0.13$, d.f. = 2, one-tailed Kruskal-Wallis test). Significant negative correlation was found between *Hbl*^{l} allele-frequencies and depth for the 24 samples ($r_S = -0.518$, $p < 0.05$, d.f. = 22, Spearman's correlation coefficient)(Fig. 1).

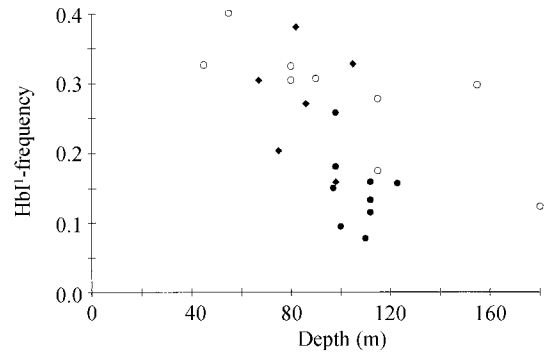

Fig. 1. *Hbl*^{l}-frequency plotted against mean depth for each of the 24 samples 1995 (○), 1996 (◆), and 1997 (●).

Table 2. Observed genotypes and frequency of *Hbl*^{l}-alleles in each sample. Chi-square test (χ^2-test) and 'Wright's fixation index' (WFI) both tests discrepancy between observed and Hardy-Weinberg number of genotypes.

Sample no.	Genotypes					Allele-* frequency	χ^2-test**	WFI
	N	*Hbl*$^{l-1}$	*Hbl*$^{l-2}$	*Hbl*$^{2-2}$	Rare	*Hbl*^{l}	χ^2	
1	48	3	20	24	1	0.277	-	–0.43
2	34	3	13	16	2	0.297	-	0.15
3	30	3	18	9	0	0.400	-	–1.39
4	93	9	39	45	0	0.307	0.02	0.13
5	46	9	12	25	0	0.326	-	2.76
6	47	2	12	32	1	0.174	-	0.63
7	162	1	38	123	0	0.124	-	–1.07
8	35	3	16	15	1	0.324	-	–0.44
9	149	13	61	69	6	0.304	0.01	–0.09
10	37	3	14	20	0	0.270	-	0.25
11	50	5	22	22	1	0.327	0.02	–0.15
12	49	8	12	26	3	0.304	-	2.60
13	64	5	16	43	0	0.203	-	1.82
14	75	10	37	28	0	0.380	0.17	–0.41
15	38	1	10	27	0	0.158	-	0.06
16	37	3	13	21	0	0.257	-	0.48
17	50	2	14	34	0	0.180	-	0.36
18	101	1	21	79	0	0.114	-	–0.31
19	80	1	22	55	2	0.154	-	–0.74
20	69	2	19	47	1	0.132	-	0.05
21	78	2	20	55	1	0.156	-	0.11
22	67	1	8	56	2	0.077	-	1.08
23	69	1	11	57	0	0.094	-	0.55
24	78	3	17	57	1	0.149	-	1.15

* χ^2-values less than 3.841 indicates no significant discrepancy from Hardy-Weinberg expected distribution of genotypes at the 95 % significance level (d.f. = 1, one-tailed). The test was carried out only when expected number of genotypes was five or larger.

** Absolute values less than approximately 2.0 indicates no discrepancy from Hardy-Weinberg expected distribution of genotypes at the 95 % significance level.

Sex ratio

Percentage males in each sample varied from 32 to 97 percent (Table 3). The sex ratio was significantly different from a 1:1 distribution in 14 (58 % of the samples) of the 24 samples (Table 3). Males dominated in 12 of the 14 sex-biased samples (Table 3).

Stage of maturity

Percentage mature males in each sample varied from 64 to 100, and percentage of mature females from 0-100 (Table 3).

More than 80 percent of the males were mature in 20 (83 % of the samples) of the 24 samples (Table 3). More than 80 percent of the females were mature in five (21 % of the samples) of the 24 samples.

Size

Mean length differed significantly between samples both for males ($F = 12.21$, $p < 0.001$, d.f. = 23, ANOVA) and females ($F = 7.45$, $p < 0.001$, d.f. = 23), when cod from all 24 samples were pooled. Mean length of males differed significantly between samples when each year was examined separately (1995: $F = 10.87$, $p < 0.001$, d.f. = 8; 1996: 9.22, $p < 0.001$, d.f. = 5; 1997: $F = 2.01$, $p = 0.045$, d.f. = 8). Mean length of females also differed significantly between samples in 1995 ($F = 6.98$, $p < 0.001$, d.f. = 8) and 1996 ($F = 5.41$, $p < 0.001$, d.f. = 5), but not in 1997 ($F = 1.55$, $p = 0.144$, d.f. = 8). Even within the same day did mean length differed between samples (sample 3 and 4, sample 8 and 9, sample 11 and 12, and sample 21 and 23, Fig. 2).

Females were significantly larger than males within 16 (67 % of the samples) of the 24 samples (Fig. 2).

DISCUSSION

Samples by trawl and Danish seine at traditionally important spawning areas near the Lofoten Islands in March and April 1995-97, indicated that: (1) NAC and CC did not mingle randomly. (2) However, specimen from both groups may stay simultaneously at the same local spawning ground within an area of less than 0.012 km^2. (3) Distribution of NAC and CC overlapped vertically, although NAC was more abundant than CC in samples from deep waters. (4) The sex ratio was skewed towards males in a majority of the samples. (5) A larger percentage of males

Table 3. Sex-distribution and stage of sexual maturity for female and male cod. χ^2-test tests the null-hypothesis that the sex-distribution is 1:1.

					Stage of maturity							
					Females				Males			
Samp. no.	Females N	Males N (%)	Unknown	χ^2-test χ^{2*}	Immature	Mature	Spawned	Uncertain	Immature	Mature	Spawned	Uncertain
1	20	24 (55)	4	0.36	50	50	0	0	4	96	0	0
2	20	14 (41)	0	1.06	100	0	0	0	36	64	0	0
3	8	22 (73)	0	6.53	25	75	0	0	18	82	0	0
4	43	47 (52)	4	0.18	86	12	0	2	28	68	0	4
5	21	24 (53)	1	0.20	48	52	0	0	8	92	0	0
6	17	30 (64)	0	3.60	18	71	12	0	0	100	0	0
7	80	74 (48)	8	0.23	38	20	40	3	10	64	23	4
8	11	24 (69)	0	4.83	36	45	18	0	4	88	8	0
9	43	104 (71)	3	25.31	53	19	28	0	2	87	12	0
10	25	12 (32)	0	4.57	20	68	8	4	17	75	0	8
11	5	44 (90)	0	31.04	40	60	0	0	0	98	0	2
12	29	21 (42)	0	1.28	21	76	0	3	0	100	0	0
13	13	50 (79)	1	21.73	8	92	0	0	0	100	0	0
14	16	59 (79)	0	24.65	31	69	0	0	3	83	7	7
15	12	26 (68)	0	5.16	8	75	17	0	0	89	4	8
16	9	28 (76)	0	9.76	0	100	0	0	0	100	0	0
17	18	32 (64)	0	3.92	28	72	0	0	6	94	0	0
18	42	59 (58)	0	2.86	38	60	2	0	2	98	0	0
19	13	17 (57)	0	0.53	31	62	8	0	0	100	0	0
20	15	53 (78)	0	21.24	27	67	7	0	0	100	0	0
21	48	30 (38)	1	4.15	10	88	0	2	3	93	0	3
22	2	65 (97)	0	59.24	0	100	0	0	0	100	0	0
23	21	48 (70)	0	10.57	0	100	0	0	0	100	0	0
24	38	40 (51)	1	0.05	18	79	3	0	0	98	3	0

* χ^2-values less than 3.841 indicates no discrepancy from a 1:1 sex-distribution (Sokal & Rohlf 1981).

compared to females were ready to spawn. (6) Cod shoals may be size-assorted.

Cod from several shoals have probably been captured in the same sample, in some of the samples. Exactly where within the spawning cycles the cod were when sampled was hard to decide. Cod has been reported to spawn during daytime (KJESBU 1989; ROSE 1993), afternoon and evening (BRAWN 1961a), and night (BRAWN 1961a; KJESBU 1989). Female cod may spawn 19 batches of eggs with from 45 to 100 hours intervals at 5-8 °C (KJESBU 1989). Each female may thus participate in the spawning during almost two months (KJESBU 1989; KJESBU & al. 1991). A large percentage of the females in our samples was mature (Table 3), which is characterised by hyaline eggs. The eggs become hyaline less than two days before spawning (KJESBU & al. 1990). This indicates that a large percentage of the females would have spawned within less than 48 hours.

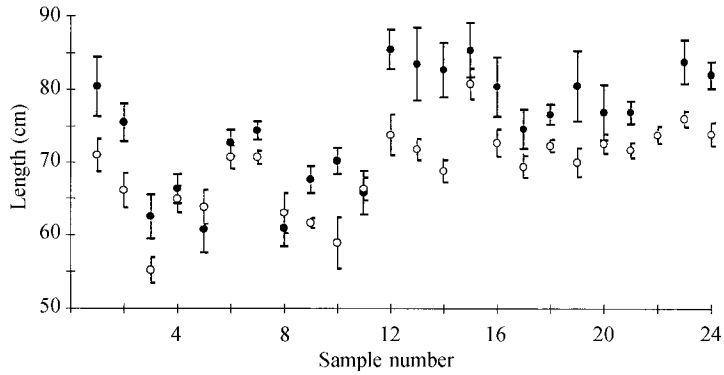

Fig. 2. Length (mean ± 95 % confidence intervals) of male (○), and female (●) cod.

Analysing population structure from studies of haemoglobin-frequencies has been disputed. Different alleles or genotypes may possess different adaptive values and they may be exposed to strong differential selection (KARPOV & NOVIKOV 1980). Thus observed allele-frequencies may result from selection (KARPOV & NOVIKOV 1980; MORK & 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 & NÆVDAL 1995).

Given that frequencies of HbI^{1} can be used as population parameters, samples with 'low' HbI^{1}-frequencies (≤ 0.15) may be grouped as NAC, and groups with 'high' frequencies (> 0.25) may be grouped as CC. Grouping of NAC is based on published frequencies of cod from the Barents Sea, which all have HbI^{1}-frequencies between 0.072 and 0.141 (FRYDENBERG & al. 1965; MØLLER 1969; DAHLE & JØRSTAD 1993). Grouping of CC is based on published frequencies of cod caught in northern Norway south of the Lofoten Islands outside the spawning season, which all show HbI^{1}-frequencies between 0.314 and 0.444 (NORDEIDE & PETTERSEN 1998). Samples with 'medium' HbI^{1}-frequencies (between 0.15 and 0.25) may be explained as consisting of either (1) a mixture of both NAC- and CC-individuals, or (2) individuals from a homogeneous population with HbI^{1}-frequencies in the actual frequency-interval. The following arguments support the first explanation: (1) Samples of cod along the coast north of the Lofoten Islands caught outside the spawning period, show HbI^{1}-frequencies in the entire interval from 0.09-0.35. Included are several samples with frequencies between 0.15 and 0.25 (MØLLER 1969; JØRSTAD & NÆVDAL 1989). Three papers conclude that cod from this northern part of the coast consist of both NAC and CC (MØLLER 1969; LØKEN & al. 1994; NORDEIDE & PETTERSEN 1998). (2) Homogeneous populations of cod with HbI^{1}-frequencies between 0.15 and 0.25 have not been found in Norwegian waters. (3) Homogeneous populations with HbI^{1}-frequencies less than 0.15 (Barents Sea: MØLLER 1969; JØRSTAD & NÆVDAL 1989), and larger than 0.25 (northern Norway south of Lofoten: FRYDENBERG & al. 1965; NORDEIDE & PETTERSEN 1998) have however been found.

To examine whether a sample consists of individuals belonging to one or more homogeneous populations of cod, discrepancy between observed and expected Hardy-Weinberg number of genotypes are usually examined with chi-squared test or 'Wright's fixation index'. The chi-squared test can only be applied when the number of expected genotypes is five or more (SOKAL & ROHLF 1981), which requires a large sample size when allele-frequencies are far from 0.5. I would have to sample 500 cod to obtain an expected number of five $HbI^{1\text{-}1}$ genotypes from a population with HbI^{1}-allele frequency of 0.10, which is typical for NAC. Five hundred cod are seldom caught in one sample at the spawning grounds, and would have required large effort to analyse. On the other hand, testing with 'Wright's fixation index' do not require large sample sizes. However, the low statistical power of the test increases the probability of making 'Type II-error'. The statistical power of the test is 0.109 in a sample (N = 100) which consists of 50 NAC (HbI^{1} = 0.10) and 50 CC (HbI^{1} = 0.30), in a 5 percent test. This means that in 89 percent of the samples from these hypothetical cod the test result would incorrectly suggest that the sample was from one homogeneous population in Hardy-Weinberg equilibrium, and not from a mixture of NAC in Hardy-Weinberg equilibrium and CC in Hardy-Weinberg equilibrium. This may explain why the discrepancy between observed and expected Hardy-

Weinberg number of genotypes was significant in only 2 of the 24 samples (Table 2).

Three papers have proposed hypotheses about the behaviour of spawning cod. From studies of spawning cod in a large tank, Brawn (1961a) suggested that a territorial male showed aggression towards a group of females and males without territories. Single ripe females left the group and swam into the male's territory. The male and female courted near the bottom and swam together to the surface where they spawned.

From studies by echosounder off Newfoundland, Rose (1993) described large numbers of spawning cod in dense shoals (> 1 cod m^{-3}) near the bottom, and pairs of cod ('spawning columns') above the main shoal. Rose suggested that the cod formed pairs within the main shoal, and swam together in pairs above the shoal to spawn.

Morgan & Trippel (1996) reported sex-biased shoals of spawning cod at and near the spawning grounds east of Canada. Male-biased shoals were common within areas where the spawning occurred, whereas female-biased shoals were common around the spawning ground. A larger percentage of both sexes was mature in male-biased shoals than in female-biased shoals. A larger percentage of females were 'spawned' in female-biased shoals than in male-biased shoals. Morgan & Trippel (1996) suggested that mature males first arrive at the spawning grounds, whereas females arrive when they are ready to spawn and return to deeper and warmer waters after spawning. The three hypotheses are not mutually exclusive.

The results from the traditionally important spawning grounds near the Lofoten Islands support the hypothesis suggested by Morgan & Trippel (1996). More than half of the samples were sex-biased in favour of males (Table 3). However, only two samples were female-biased which prevents me from concluding about percentage of females that were 'spawned' in female-biased shoals (Table 3). I did not observe any 'spawning columns' as described by Rose (1993), during more than 20 days and two nights with intense echosounder observations of spawning cod at the spawning grounds near the Lofoten Islands.

Various pre- and postmating devices that prevent interbreeding between organisms in general and between CC and NAC in particular, were discussed by Mayr (1963) and Møller (1968) respectively. Postmating isolating mechanisms are not likely, since NAC and CC have been successfully crossed and reared in laboratory (Godø & Moksness 1987). Behavioural premating mechanisms connected to courtship display (Brawn 1961a) and acoustic communication (Brawn 1961b; Hawkins & Rasmussen 1978, Hawkins 1986) seem promising, and should be examined further.

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