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Haemoglobin polymorphism in *Gadus morhua*: Genotypic differences in maturing age and within-season gonad maturation*

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ABSTRACT: 276 specimens of Atlantic cod (*Gadus morhua* L.) were caught during spawning in a restricted area of the Trondheimsfjord, Norway, in April and May 1979. Genotypes at the polymorphic haemoglobin locus *Hbl* differed significantly with respect to mean age at maturation (in males) and mean gonadic development stage (in females). There was no indication of population mixing in the genotypic composition at *Hbl* or at any of the 4 polymorphic tissue enzyme loci investigated (*LDH-3, IDH-1, PGM,* and *PGI-1*. The findings obtained were considered with regard to temperature-related differences in the functional properties of Hbl molecules, and genotypic differences in growth, age at maturation, and fishing mortality. At the present stage of investigation, the natural selection pattern seems directional and strong. However, the *Hbl* allele frequencies observed in cod from the examined areas reveal no detectable changes over a period of two decades (~ 4 generations). The current pattern of commercial exploitation causes, through size selection, a modification of the rate of erosion of the inferior allele, but additional factors must be in force, which play a role in its current abundance in an evolutionary perspective. The observed *Hbl* genotypic differences in the exact within-season time for spawning might be one such factor. A potential sexual difference in genotypic fitness might be another, but this has yet to be confirmed. The apparent existence of considerable natural and artificial selection forces acting upon cod haemoglobin genotypes makes *Hbl* allele frequencies unreliable for use in population structure analyses.

INTRODUCTION

Previous studies on population genetics of the Atlantic cod (*Gadus morhua* L.) by means of electrophoretically detectable protein polymorphisms were concerned with haemoglobins (locus *Hbl*; Sick, 1961). Later on they included serum esterase (Nyman, 1965), serum transferrin (Möller, 1966), as well as a wide range of tissue enzymes (Lush, 1969; Odense et al., 1969; Dando, 1974; Jamieson, 1975; Cross & Payne, 1978; Mork et al., 1982).

However, the genetic population structure concept of cod in the eastern Atlantic is still largely based on results from *Hbl* analyses performed in the 1960s (e.g. Frydenberg et al., 1965; Sick, 1965a, b; Möller, 1968; Jamieson & Jonsson, 1971). In these early reports the possibility that selection forces of moderate magnitude could have acted on the genotypic composition of samples was often considered (see e.g. Frydenberg et al., 1965, 1967, 1969), and a possible fitness superiority of heterozygotes was discussed by

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Sick (1965a). However, the reliability of *Hbl*^{1} allele frequencies for use in population delineation studies was never really doubted.

Evidence which has accumulated from more recent reports indicates that the genotypic composition at *Hbl* in populations can be very sensitive to temperature regimes: Karpov & Novikov (1980) demonstrated experimentally that cod haemoglobin molecules differ in their functional properties at different temperatures; the Hbl$^{2-2}$ type was, as expected from its geographical distribution in populations, better adapted to low temperatures, while the Hbl$^{1-1}$ showed advantages at higher (> 13 °C) temperatures. The heterozygote was consistently intermediate in performance. The observations by Mork et al. (1983a), in a Norwegian coastal population, were in agreement with these findings: among immature specimens the genotypic size rank (pooled sexes) was *Hbl*$^{2-2}$ >*Hbl*$^{1-2}$ >*Hbl*$^{1-1}$ in each out of 4 succeeding age groups. Subsequent analyses of more extensive material from the same areas confirmed the existence of *Hbl* genotypic size differences (Mork et al., 1983b), but indicated that the size rank of genotypes differed between sexes: in males the rank was as reported previously (*Hbl*$^{2-2}$ >*Hbl*$^{1-2}$ >*Hbl*$^{1-1}$), while in females the heterozygote was superior (the rank was *Hbl*$^{1-2}$ >*Hbl*$^{2-2}$ >*Hbl*$^{1-1}$). However, a common trend in both sexes was the consistently inferior size of the *Hbl*$^{1-1}$ genotypes. The observations could not be adequately explained by population mixture in the samples (Mork et al., 1983a). Thus the haemoglobin polymorhpism of Atlantic cod seemed to offer a clear-cut case of natural selection acting phenotypically detectably upon genotypes at a single locus. The inferior growth of *Hbl*$^{1-1}$ genotypes in both sexes is expected to reduce the proportion of the *Hbl*^{1} allele in each new generation through a reduced gamete production. Interestingly, indications of such a change have not been observed during almost 20 years of sampling (~ 4 generations) in the Trondheimsfjord, where the two common *Hbl* alleles occur in approximately equal proportions (Frydenberg et al., 1965; Mork et al., 1983a). Thus, there must be factors which counteract such a development. Mork et al. (1983a) pointed out that the genotypic selection by fishing gear is one such factor, and showed, by a genetic tagging experiment carried out for four years after release, that the fishing mortality in fast-growing *Hbl*^{2}-possessing genotypes was in fact higher than that in *Hbl*^{1}-possessing genotypes.

However, exploitation by selective gear is of relatively recent origin, and there must presumably be some other advantages of *Hbl*^{1}-possessing specimens which have prevented the extinction of this allele in evolutionary frames. Since the Hbl$^{1-1}$ molecule is a superior respiratory pigment at high temperatures (Karpov & Novikov, 1980), milieu regimes which favour *Hbl*^{1}-possessing genotypes (survival rates) may, potentially, occur during summer in the actual areas.

The egg number of female cod is a linear function of body weight (Daan, 1975). Presumably, a difference in the egg production in genotypes influences allele frequencies in each new generation more efficiently than genotypic differences in male gamete production. Besides the *Hbl* genotypic size differences, there are also significant differences in the age at first spawning (maturing age; A_m) for cod *Hbl* genotypes in the Trondheimsfjord: otolith studies in 118 male spawners showed a significantly lower A_m for the *Hbl*$^{2-2}$ genotype (Mork et al., 1983b). The A_m of heterozygotes was intermediate but not significantly lower than that of *Hbl*$^{1-1}$. A_m may be as important as the general growth rates for the total number of offspring from a specimen. Here the genotypic ranks in males (cf above) are of greater relative importance, but information on the potential

genotypic rank in females is still crucial for understanding the dynamics of this polymorphism. Such information was lacking in these previous studies, and additional sampling was required.

A third way (besides growth rates and A_m) by which genotypic differences among spawners may influence allelic success or failure in each new generation is the exact within-season timing of spawning in relation to environmental factors (temperature, presence or absence of prey organisms and predators). It was therefore of interest to investigate potential differences in the distribution of gonadic stages in *Hbl* genotypes of samples taken in the spawning season.

The aim of the present study was to check the previous observations of *Hbl* genotypic differences with respect to A_m in males, to obtain information on this aspect in females, and to investigate potential within-season *Hbl* genotypic differences in the annual ripening process. In addition, information from other polymorphic loci was desired in order to have a *Hbl*-independent check on the genetic homogeneity of the investigated sample.

MATERIALS AND METHODS

A total of 276 specimens of cod *(Gadus morhua)* were taken during spawning with gill nets and shrimp trawl in the Trondheimsfjord, Norway, in April and May 1979. Blood samples for haemoglobin genotyping were drawn from the heart post mortem, stored at 0 °C, and analysed (agar gel electrophoresis) within 12 hours. Tissue samples cut out from heart, liver, and white skeletal muscle were stored at −30 °C for up to one year before being analysed (starch gel electrophoresis) for the enzymes LDH (lactate dehydrogenase, E.C. No. 1.1.1.27), IDH (isocitrate dehydrogenase, E.C. No. 1.1.1.42), PGM (phosphoglucomutase, E.C. No. 2.7.5.1), and PGI (phosphoglucoisomerase, E.C. No. 5.3.1.9). Analytical procedures and nomenclature for haemoglobins followed Sick (1961, 1965 a): agar gel electrophoresis (1 % agar; phosphate buffer pH = 7.3) revealed distinct, red bands which could be scored directly on the gels; double-banded patterns in heterozygotes (Hbl^{1-2}, which produce both the Hbl^{1-1} and the Hbl^{2-2} molecular form) and single bands in homozygotes (Hbl^{1-1} and Hbl^{2-2}: Fig. 1). Starch gel electrophoresis of

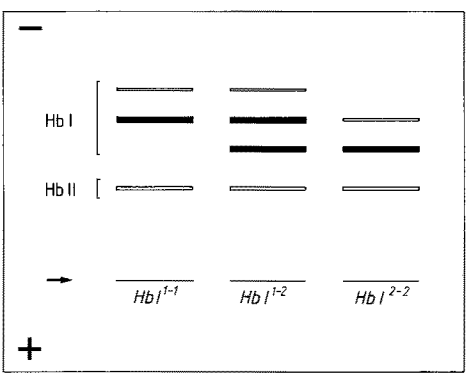

Fig. 1. Cod haemoglobins. Schematic electropherogram showing the three most common genotypes at HbI as revealed by agar gel electrophoresis at pH = 7.3. Site of sample application indicated by arrow

tissue extracts and specific enzyme staining followed Mork et al. (1982): LDH and IDH were analysed using the continuous buffer system described by Clayton and Tretiak (1972), while the discontinuous buffer system of Ridgway et al. (1970) was used for PGI and PGM. The system of nomenclature applied for tissue enzymes follows Allendorf & Utter (1979): the abbreviations LDH, PGI etc. denote the proteins. When in italics, the same abbreviations denote the loci coding for these proteins. If more than one locus codes for a specific enzyme, they are numbered *1, 2,* etc. in order of increasing anodic mobility of their gene products. The most common allele at polymorphic loci is designated *100,* while variant alleles are denoted in terms of electrophoretic mobility of their products relative to the most common band. The enzyme loci and alleles referred to in this report were described by Mork et al. (1982).

Otoliths were collected for the determination of individual age, and age at maturation (A_m) according to Rollefsen (1933). All except 27 individuals were sexed. The gonadic development stage was recorded according to Sivertsen (1935): I = immature, II = ripening, III = ripe, and IV = spent.

RESULTS

The observed genotypic distribution at *Hbl,* as shown in Table 1, did not deviate from expectations under genetic equilibrium. Nor did the genotypic proportions deviate from Hardy-Weinberg distribution at any of the polymorphic enzyme loci scored. The calculated allele frequencies at these loci are shown in Table 2. Further, there were no

Table 1. *Gadus morhua.* Genotypic composition at *Hbl* in spawners from the Trondheimsfjord 1979. Expected numbers under genetic equilibrium in parenthesis. Goodness of fit of observed to expected values: $\chi^2_1 = 0.928$, P = 0.335

Genotypes		
Hbl^{2-2}	Hbl^{1-2}	Hbl^{1-1}
74 (70.0)	130 (138.0)	72 (68.0)

Table 2. *Gadus morhua.* Allele frequencies at enzyme loci in 276 spawners from the Trondheimsfjord 1979

Locus	Allele	Allele frequency
LDH-3	*100*	0.61
	70	0.39
LDH-1	*100*	0.83
	140	0.17
PGM	*100*	0.95
	80	0.04
	70	0.01
PGI-1	*100*	0.71
	135	0.26
	65	0.03

indications of linkage disequilibrium (Hill, 1974) between any pair of loci (sum of χ^2_1 from 10 pairwise comparisons were 15.135, P = 0.127).

Maturing age in *Hbl* genotypes

Otolith data on the maturing age (A_m) were obtained in 129 males and 117 females. The A_m varied from 3 to 8 years in both sexes. The mean A_m was calculated for each *Hbl* genotype group in males and females, and the differences were tested by single factor analyses of variance in each sex (Table 3). The significant heterogeneity of A_m in males

Table 3. *Gadus morhua.* Mean age at first spawning (± standard deviation) for *Hbl* genotypes. N = numbers of genotypes. An analyses of variance revealed significant heterogeneity of means in males, but not in females [F-values were 4.20 (P = 0.017) and 1.01 (P = 0.367), respectively]

Sex	Hbl^{2-2}	N	Hbl^{1-2}	N	Hbl^{1-1}	N
Males	5.19 (± 0.75)	36	5.22 (± 0.97)	63	5.80 (± 1.20)	30
Females	5.09 (± 1.04)	31	5.31 (± 0.94)	55	5.42 (± 0.72)	31

was further analysed by a Newmann-Keul test which allowed the overall conclusion that $Hbl^{2-2} = Hbl^{1-2} \neq Hbl^{1-1}$. Thus, while the observed rank of *Hbl* genotypic A_m was identical in the two sexes, the A_m heterogeneity was significant only in males, where the Hbl^2-possessing genotypes recruit to the spawning stock at a significantly lower age than the Hbl^{1-1} genotype.

Within-season gonadic development in *Hbl* genotypes

Data on the gonadic development stage were available for a total of 249 specimens. In both sexes, only stages II, III, and IV were observed. The actual distribution within sexes and *Hbl* genotypes is shown in Table 4. From these values, the mean gonadic

Table 4. *Gadus morhua.* Number of specimens at different gonadic development stages; grouped according to sex and *Hbl* genotype. Data from 249 specimens caught during spawning in the Trondheimsfjord in 1979

Genotype	Gonadic development stage					
	II		III		IV	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Hbl^{2-2}		3	34	23	2	5
Hbl^{1-2}	2	16	60	36	3	3
Hbl^{1-1}	4	10	25	20	1	1

development stage of *Hbl* genotypes within each sex was calculated (Table 5). Analyses of variance of these genotypic means revealed significant heterogeneity in females, but not in males (Table 5). The heterogeneity in females was analyzed by Newmann-Keul

Table 5. *Gadus morhua.* Mean gonadic stage (± standard deviation) of *Hbl* genotypes in sexes. Data from Table 4. An analysis of variance revealed significant heterogeneity of genotypic means in females (F = 4.29, P = 0.016), but not in males (F = 2.44, P = 0.090)

Sex	Hbl^{2-2}	Hbl^{1-2}	Hbl^{1-1}
Males	3.05 (± 0.23)	3.02 (± 0.28)	2.90 (± 0.40)
Females	3.07 (± 0.51)	2.76 (± 0.54)	2.71 (± 0.53)

test procedures which led to the overall conclusion that $Hbl^{2-2} \neq Hbl^{1-2} = Hbl^{1-1}$. Thus, the same nominal rank with respect to mean gonadic stage in *Hbl* genotypes was observed in both sexes, but the genotypic heterogeneity was statistically significant only in females, where the Hbl^{2-2} specimens had significantly more developed gonads than the two other genotypes at the time of sampling.

Genetic homogeneity of the investigated *Hbl* groups

The 6 *Hbl* genotypic groups (3 in each sex) considered in the analyses above were compared with respect to allele frequencies at the other polymorphic loci. In each sex the three possible comparisons: Hbl^{2-2} vs Hbl^{1-2}, Hbl^{2-2} vs Hbl^{1-1}, and Hbl^{1-2} vs Hbl^{1-1} were performed for allelic proportions (2×2 χ^2-contingency tables, variant alleles pooled) at *LDH-3, IDH-1, PGM,* and *PGI-1.* No signs of genetic heterogeneity were observed. Pooled χ^2 from 24 pairwise comparisons were 30.005, P = 0.185. Thus there are no indications that the various observations in the *Hbl* genotype groups could have been caused by the unproportional occurrence of specimens from different populations (with different biological characteristics) in these groups.

DISCUSSION

The present results are in accordance with previous observations on the apparent selection at cod *Hbl,* but add some important new traits to the picture (Table 6). Thus,

Table 6. *Gadus morhua.* Summary of observations of *Hbl* genotypic ranks with respect to some properties of relevance to fitness. Imm. = immatures, mat. = matures

Characteristic	Sex	Rank of genotypes	Reference
Growth	Males (imm.)	$Hbl^{2-2} > Hbl^{1-2} > Hbl^{1-1}$	Mork et al. (1983a)
	Females (imm.)	$Hbl^{1-2} > Hbl^{2-2} > Hbl^{1-1}$	Mork et al. (1983b)
Maturing age	Males (mat.)	$Hbl^{2-2} > Hbl^{1-2} = Hbl^{1-1}$	Mork et al. (1983b)
		$Hbl^{2-2} = Hbl^{1-2} > Hbl^{1-1}$	This report
	Females (mat.)	$Hbl^{2-2} = Hbl^{1-2} = Hbl^{1-1}$	This report
Within-season gonadic development	Males (mat.)	$Hbl^{2-2} = Hbl^{1-2} = Hbl^{1-1}$	This report
	Females (mat.)	$Hbl^{2-2} > Hbl^{1-2} = Hbl^{1-1}$	This report

cod *HbI* genotypes differ not only in growth rates (Mork et al, 1983a), and in age at maturation (Mork et al., 1983b), but even in the within-season time for spawning (as indicated by gonad development). Potentially, the two latter points are secondary effects of growth rate differences. Previous observations, too, like *HbI* genotypic differences in fishing mortality (Mork et al., 1983a), and sexual differences in *HbI* allele frequencies in individual trawl catches (Mork et al., 1982), may probably be explained as effects of such genotypic size differences.

Most, if not all, natural cod populations are exposed to a continuous exploitation by size-selecting fishing gear. Where genotypic differences (e. g. growth, maturing age) exist, such exploitation may have a considerable effect on the genotypic composition of populations. Under such circumstances it is not at all certain that *HbI* allele frequencies can be regarded as valid population parameters. Moreover, if samples for genetic studies are taken with size-selecting gear, too, the bias will be increased. These facts seriously affect the reliability of characteristics at *HbI* for use in population structure analyses, and may well have caused erroneous conclusions in previous applications. Such effects have, presumably, also affected the *HbI*-related characteristics studied in this investigation. However, a continuous selection by commercial exploitation will, expectedly, act to level out existing genotypic differences and make the remaining part of the stock more homogeneous with respect to the actual characteristics. Against this background the present values for some of the *HbI* genotypic differences may be regarded as conservative estimates. There may, however, be other pitfalls which may cause sampling artifacts in studies of cod *HbI*. These are implicit in the suggestion of Karpov & Novikov (1980) that cod specimens are able to choose habitats with temperatures suitable for their *HbI* genotype. Although not experimentally confirmed, such an ability may well exist; after all, the cod as a species is known to avoid extremely cold and warm waters. However, the effects of such genotypic maneuvres would be unpredictable and cannot be meaningfully discussed at present. Moreover, the *HbI* genotypic composition in the present sample did not seem to have been influenced by such phenomena.

In males, the HbI^2-possessing genotypes show superior growth (immatures) as well as lower mean age at maturation (Table 6). If fast-growing specimens mature at lower age, one might expect the female *HbI* heterozygotes (Table 6) to display a somewhat lower mean age at maturation. We were, however, not able to detect statistically significant maturation age differences between female *HbI* genotypes in the present material.

Since, in males, the HbI^2-possessing genotypes seem to be consistently more effective producers of gametes, the seemingly stable *HbI* allele frequencies in the Trondheimsfjord indicate the action of one or more factors which counteracts this male effect. Immigration could be such a factor; the frequency of the HbI^1 allele increases southwards among Norwegian coastal cod (Frydenberg et al., 1965), and a gene flow may take place from more southern populations, for instance by transport with the Norwegian Coastal Current (cod eggs and larvae are pelagic), or by active migrations of more developed specimens. Alternatively, the *HbI* allele frequencies may be stabilized by some form of frequency-dependent selection of presently unknown nature, or by a heterozygote fitness superiority in females which was indicated by genotypic growth rates in immatures (Table 6). The possibility that the genotypic patterns of growth, maturing age, within-season gonad development, or mortality differ between sexes will

be evaluated through further studies of *HbI* genotypes in females, in which the rank of genotypes with respect to the various characteristics has been less consistent in the materials processed so far (Table 6).

A very consistent trait in the hitherto investigated materials is the generally inferior performance of the HbI^{1-1} genotype compared to the others, which applies to both growth, maturing age, and within-season gonadic development rates (the latter is not necessarily a drawback; cf. below). All these characteristics may be components of total fitness. The significance of growth rates (egg production) and maturing age (length of reproductive period) is obvious. The effect on fitness of differences in within-season gonadic development (exact spawning time) may be more subtle. In an estuarine system like the Trondheimsfjord the aquatic environment may undergo dramatic changes during the period in which cod spawning occurs (approximately March to June). The changing milieu factors include water temperature, surface-layer salinity, brackish water run-off, plankton blooms, and abundance of predators on eggs and larvae. Relatively modest differences in ripening time for *HbI* genotypes may result in radically different environments for their offspring and thus contribute significantly to e. g. survival rates. It is thus possible that a somewhat delayed spawning (on average) of HbI^{1}-possessing genotypes may be an advantage which counteracts the effect of the better growth and lower maturation age for HbI^{2}-possessing genotypes. However, milieu factors show annual variation, and such effects are probably not efficient in maintining allele frequencies at a stable level.

The exact way in which individual haemoglobins influence e. g. growth rates is not known. Presumably they act through general effects on individual vigour and stamina (hunting/competition). In this context, the observed sexual differences with respect to the intrinsic rank of genotypes (Table 6) are interesting and indicate substantial differences in the general biology or behaviour between sexes. Sexual behavioural differences among spawning cod are well-known and often manifested, for instance in the proportion of males and females in gill net catches (e. g. passive gear): among approximately 1000 spawners caught with gill nets in the Trondheimsfjord in 1977, some 980 were males (unpublished materials). This phenomenon is believed to be caused by a generally higher level of activity in males on the spawning grounds. Patterns of activity and behaviour in sexes among immatures are largely unknown, but might prove to be an interesting field for studies.

At any rate, the very existence of different *HbI* genotypic growth patterns may indicate that the growth process in fishes involves intense hunting and competition for food in which inherited advantages are readily expressed in growth rates, and it appears that growth rates may be a more sensitive indicator of the action of selection forces than, e. g., differential mortality as detected from observed and expected (Hardy-Weinberg) genotypic distributions. In the present case, we would not expect to find such substantial *HbI* genotypic growth differences among captive cod which are fed in excess in the laboratory. An experiment which aims at the clarification of this aspect is currently in progress.

If, as seems probable, environmental temperature is the factor responsible for the observed *HbI* genotypic growth differences, one might expect the effects to vary geographically. The relative proportions of alleles at *HbI* in cod from different climatic regions (cf. "Introduction") may be interpreted as indications of such selection regimes,

but their existence remains to be confirmed by detailed analyses. In search for general principles in the dynamics of this polymorphism, it might be rewarding to investigate patterns of *HbI* genotypic performances, with respect to the characteristics listed in Table 6, in cod stocks inhabiting areas of low and high temperature extremes for this species.

The above interpretations of present and previous observations are all based on the assumption that the samples were drawn from single reproduction units. The validity of our conclusions could be seriously affected by the presence of individuals from more than one population in the various samples. However, the present material consisted exclusively of ripe cod caught in a very restricted area during spawning. Further, there were no signs of genetic heterogeneity at any one of four independent enzyme loci. Thus, lacking any sign of population heterogeneity, it seems justified to regard the observations as representative for occurrences in one Mendelian population.

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