ICES Journal of Marine Science, 63: 235–245 (2006)
doi:10.1016/j.icesjms.2005.11.005

Comparison of growth rate among different protein genotypes in Atlantic cod, *Gadus morhua*, under farmed conditions

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Jørstad, K. E., Karlsen, Ø., Svåsand, T., and Otterå, H. 2006. Comparison of growth rate among different protein genotypes in Atlantic cod, *Gadus morhua*, under farmed conditions. – ICES Journal of Marine Science, 63: 235–245.

A major aim of the aquaculture industry in Norway is to develop sustainable farming of Atlantic cod, *Gadus morhua* L. A great deal of research, including farming trials and stock enhancement, has been performed on this species in Norway during the past two decades. The success of domestication of a new species depends on the genetic variability of the wild broodstock and the selection of appropriate genotypes for the farming environment. Growth experiments under farmed conditions, including genetic analyses, were started as early as 1983 after the breakthrough of cod juvenile production in mesocosm systems. At later stages (1988 and 1992 year classes), more detailed studies were conducted under farmed conditions. Based on individual tagging and genotyping (blood and white muscle biopsy sampling), estimates of growth performance (specific growth rate, SGR) of the various genotypes within six polymorphic protein loci were obtained. In general, the SGR in the two experiments varied through the year as a function of temperature and body size. In the 1988 year-class experiment, only a few statistically significant differences (ANOVA) were detected among genotypes, measured as mean weight and SGR. The 1992 year-class experiment included two different cod stocks, Northeast Arctic (NE) and Norwegian coastal (NC) cod, which were reared for about two years in the same net pen. Further, during this experiment, only a few genotypes exhibited significantly different growth within the NE group. No consistency was found in the variation with regard to protein loci investigated, growth periods studied, and relationship with temperature variation.

Keywords: Atlantic cod farming, protein electrophoresis, specific growth rates of protein genotypes, temperature variation.

Received 1 October 2004; accepted 3 November 2005.

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Introduction

The Atlantic cod, *Gadus morhua* L., is found on both sides of the North Atlantic and is one of the most important commercial species in this geographic area. In the northeast region, the early genetic studies (Møller, 1966, 1968) provided evidence for a complex population structure – a large oceanic cod stock (Northeast Arctic, NE cod) and a number of more or less genetically differentiated Norwegian coastal (NC) cod stocks. Unlike migrating oceanic cod (Bergstad *et al.*, 1987), the coastal cod is stationary (Jakobsen, 1987; Svåsand, 1990), and a large number of distinct spawning sites are found in fjords and coastal areas along the Norwegian coast (Jakobsen, 1987). In population genetic studies based on protein markers (allozymes), only minor frequency differences were found (Jørstad, 1984; Mork *et al.*, 1985; Jørstad and Nævdal, 1989), which was confirmed by Mork and Giæver (1999), who suggested that the differences were caused by environmental influence. Recent studies based on various DNA techniques, however, confirm the existence of genetic differences among cod stocks (Fevolden and Pogson, 1995, 1997; Nielsen *et al.*, 2001; Knutsen *et al.*, 2003; Sarvas, 2005).

The breakthrough of mass production of juvenile cod in marine ponds, as described by Øiestad *et al.* (1985), opened up the possibility of large-scale cod stock enhancement (Svåsand *et al.*, 2000) as well as the possibility of developing intensive cod farming (Svåsand *et al.*, 2004). Several experiments have also been carried out comparing performance (survival and growth) of juvenile cod belonging to

1054-3139/$30.00

different genotypic groups (Jørstad and Nævdal, 1989; Nævdal *et al.*, 1992), but the overall results are difficult to interpret. The recent review of Imsland and Jonsdottir (2003) also considered genotype studies in samples of wild cod (Mork *et al.*, 1984; Gjøsæter *et al.*, 1992), and they recommended more detailed studies of genotypic performance under identical laboratory conditions.

Interest in farming Atlantic cod has increased in recent years. In contrast with the use of ponds or sea enclosures (Kvenseth and Øiestad, 1984; Øiestad *et al.*, 1985), most juvenile cod are now produced in intensive systems (Svåsand *et al.*, 2004). Domestication to farming conditions is likely to result in genetic changes in the captive population (e.g. Allendorf and Utter, 1979). In terms of developing a viable cod farming industry in Norway, the initial selection of cod strains and genotypes from the wild stocks may be essential to economic success. The potential for developing a large-scale breeding programme for cold-water fish species has been evaluated by Gjedrem (2000), and the first studies on estimating heritabilities for economically important traits have already been performed (Gjerde *et al.*, 2004).

Better growth in some genotypes has been reported, and these should be of particular interest in cod farming. In samples of juvenile coastal cod, Mork *et al.* (1984) found that some *HbI** genotypes displayed superior growth under certain conditions and suggested that these would be of great value for cod farmers. This could be because of differences in the oxygen-binding capacities of the respective molecules in relation to temperature (Karpov and Novikov, 1980; Brix *et al.*, 1998). Recently, behavioural studies of various *HbI** genotypes under hatchery conditions suggested that one genotype (*HbI* 2/2*) showed a more active feeding response (Salvanes and Hart, 2000), which could be associated with increased feed uptake and growth performance. More attention in recent years, however, has been paid to identifying quantitative trait loci (QTL), which could be directly involved in performance under farmed conditions (e.g. Danzmann *et al.*, 1999; Sakamoto *et al.*, 1999; Cnaani *et al.*, 2003). Proteins such as allozymes and haemoglobin are essential in biochemical and metabolic processes, which may be linked to overall performance (survival and growth) in the farming environment. In another example, the screening for QTLs in rainbow trout (see discussion in Ferguson and Danzmann, 1998) included both allozyme and microsatellite markers (Jackson *et al.*, 1998).

During a successful cod juvenile production in Hyltropollen in 1983 (Kvenseth and Øiestad, 1984), Jørstad (1986a) performed allozyme screening of farmed cod (Kvenseth *et al.*, 1985). In the first cod farming experiment, no differences in mean length among different protein genotypes were detected (Jørstad, 1986b). However, more detailed comparisons of genotypic growth have been conducted subsequently at the Institute of Marine Research in Bergen. In this contribution, we have selected two farming experiments in which allozyme and haemoglobin screening were conducted on individual tagged cod. By combining the genotypic information and measurements at different ages, genotypic performance in the various experiments was measured, and comparisons among different genotypes were made at six different protein loci.

Material and methods

Description of cod stocks and experiments

Experiment I — 1988 year class

Broodstock was selected from mature cod of the 1983 year class (see above), and the fish were allowed to spawn naturally in a large spawning pen. Eggs were collected and incubated in a hatchery. Two to three days after hatching, the yolk-sac larvae were released into a large saltwater pond at Parisvatnet Field Station (60°38′N 4°49′E) in Øygarden, near Bergen, where the offspring were raised on natural plankton. Juveniles were harvested and kept in net pens at Parisvatnet, before they were transported to Austevoll Aquaculture Station, where the outgrowing experiment was performed.

All fish were individually tagged (Floy Anchor tags) in January 1989 and raised in net pens at the station. The overall aim of the experiment was to study the performance of cod under various feeding regimes (Lehmann *et al.*, 1991; Kjesbu and Holm, 1994). In this comparison, however, only groups with large numbers of fish that were raised under standard feeding conditions were included. All fish were measured at regular intervals from February 1989, and the blood and the white tissue of the tagged fish were sampled in September 1991, with final measurements taken in November 1991. The number of fish identified to the various genotypes within the six protein loci is summarized in Table 1.

Experiment II — 1992 year class

This experiment was performed at the Parisvatnet Field Station (see above). The fish consisted of a mixture of offspring from two different stocks: (i) genetically marked (GM) coastal cod from the Austevoll region and (ii) wild Northeast Arctic (NE) cod from the Lofoten area (68°N 14°E). The GM cod strain was developed from the 1983 year class in Hyltropollen and has been described elsewhere (Jørstad *et al.*, 1991). This stock was used to compare early strain performance with NE cod under identical conditions carried out in spring 1992 at the Austevoll Aquaculture Station (van der Meeren *et al.*, 1994; van der Meeren and Jørstad, 2001). The individual groups from this experiment were pooled and transported to Parisvatnet in July 1992. The fish were kept in net pens in the sea, fed commercial dry pellets, and individually tagged (Floy Anchor tags) in December 1992. The fish were measured at regular intervals and were sampled for blood and white muscle tissue in March 1993. Comparisons of growth performance of

Table 1. Experiment I: 1988 year class. The number of cod identified to different genotypic groups at six loci, for each sampling period.

Loci/genotypes	Feb 1989	Jul 1989	Dec 1989	Jun 1990	Dec 1990	Apr 1991	Jun 1991	Nov 1991
LDH-3 70/70*	26	25	26	24	24	24	21	26
LDH-3 70/100*	129	127	124	121	121	122	117	127
LDH-3 100/100*	83	83	81	76	82	82	78	83
GPI-1 30/100*	6	6	6	6	6	6	6	6
GPI-1 100/100*	146	144	143	137	140	140	132	145
GPI-1 100/150*	83	82	79	74	78	78	74	82
GPI-1 100/100*	8	8	8	8	8	8	7	8
PGM 30/100*	3	3	3	3	3	3	3	2
PGM 70/100*	9	9	9	9	9	9	9	9
PGM 100/100*	236	233	229	218	225	225	213	235
mIDHP-2 70/100*	3	3	3	3	3	3	3	3
mIDHP-2 100/100*	245	242	238	227	234	234	221	243
GPD 90/100*	4	4	4	4	4	4	4	4
GPD 100/100*	231	228	225	215	221	222	209	229
GPD 100/130*	11	11	10	10	10	10	10	11
HbI 1/1*	95	93	93	87	90	90	82	94
HbI 1/2*	113	112	109	106	109	109	105	112
HbI 2/2*	40	40	39	37	38	38	37	40

the two different cod stocks were reported by Svåsand *et al.* (1996). The information on growth performance for individual tagged fish enabled us to compare the growth of various genotypes for two protein loci (haemoglobin, *HbI**, and glucose phosphate isomerase, *GPI-1**).

Collection of samples and genotyping

The same sampling procedures were followed in the two experiments. The individually tagged fish were carefully anaesthetized, and using a sterile syringe, blood samples (about 100 µl) were drawn from the large blood vessel in the gill from each fish. The samples were mixed with one drop of heparin and kept on ice until analysis in the laboratory in Bergen, usually one to three days after collection. They were analysed using agar gel electrophoresis (Jørstad, 1984, modified from Sick, 1961) to identify the different haemoglobin *HbI** genotypes. Description of banding patterns corresponding to the three different genotypes is given elsewhere (Sick, 1961; Dahle and Jørstad, 1993; Husebø *et al.*, 2004).

Small samples of white tissues were taken by biopsy from each fish, kept on ice during sampling, and later frozen at −80°C. These samples were analysed as soon as possible (within two weeks) by starch gel electrophoresis, as described elsewhere (Jørstad, 1984). Five different enzymes, all detected in white muscle tissue, were analysed: lactate dehydrogenase (LDH), isocitrate dehydrogenase (IDH), glycerophosphate dehydrogenase (GPD), phosphoglucomutase (PGM), and phosphoglucose isomerase (GPI). All enzymes have been described as polymorphic in cod (Jørstad, 1984; Mork *et al.*, 1985). Sea temperatures were recorded throughout both experiment periods.

Estimates of genotypic growth and statistical comparisons

After genotyping, the fish in each experiment were grouped according to the genotypic class for the protein loci in question, and their lengths and weights at the various ages were determined from the individual tagging information. This combination allowed for the calculation of mean length and weight, as well as specific growth rate (length and weight increments in the various periods investigated) of each genotype at various ages for all genetic loci investigated. The data presented here include mean weight and SGR (weight increments). The following equation was used: SGR (specific growth as percentage daily increment in weight) $= (e^{g} - 1)\ 100\ g = [\ln$ (body weight on day $b) - \ln$ (body weight at day $a)]/(b - a)$. In both experiments, comparisons of mean weight and SGR of the different genotypes were carried out using ANOVA. In cases where the Brown−Forsythe test rejected the hypothesis of homogeneity, a Welch's ANOVA was used.

Results

Identification of genotypes

Based on the description by Sick (1961), a strong red banding zone can be identified on agar electrophoresis, corresponding to loci designated *HbI**. In a collection of samples, the three main banding patterns can be identified

Table 2. Experiment II: 1992 year class. The number of cod identified to different genotype groups at two polymorphic loci. Numbers are given for each sampling period.

Locus/genotypes	Dec 1992	Jan 1993	Feb 1993	Mar 1993	Apr 1993	Jun 1993	Jul 1993	Sep 1993	Jan 1994	Nov 1994
NE Arctic cod										
GPI-1 30/100*	4	4	4	4	3	4	4	4	4	3
GPI-1 100/100*	56	57	57	57	57	52	51	50	50	35
GPI-1 100/150*	249	254	253	256	257	232	228	229	220	150
GPI-1 150/150*	49	48	48	48	49	43	43	43	40	30
HbI 1/1*	2	2	2	2	2	2	2	2	2	1
HbI 1/2*	61	61	61	61	63	56	55	56	55	37
HbI 2/2*	199	202	201	204	204	183	180	179	170	121
Coastal cod										
HbI 1/1*	27	27	27	27	27	25	25	24	24	14
HbI 1/2*	26	26	25	26	26	25	25	24	22	12
HbI 2/2*	9	9	9	9	9	8	8	8	8	3

that correspond to three different genotypes − *HbI* 1/1*, *HbI* 1/2*, and *HbI* 2/2*. In the experiments described here, all three genotypes were present at the frequencies expected for coastal cod from the region in question (Frydenberg *et al.*, 1965; Svåsand *et al.*, 1990; Jørstad *et al.*, 1994).

For the polymorphic enzymes analysed, the most informative loci were *LDH-3** and *GPI-2**. Three different genotypes (*LDH-3* 70/70*, *LDH-3* 70/100*, and *LDH-3* 100/100*) were found in the *LDH** locus, which was as expected for the fish used in the experiments. In the *GPI-2** locus, four different genotypes, designated *GPI-2* 30/100*, *GPI-2* 100/100*, *GPI-2* 100/150*, and *GPI-2* 150/150*, were detected in the two experiments. For the low polymorphic enzyme loci (*PGM**, *IDH-2**, and *GPD**), only a few rare genotypes were found, and the number of fish identified to the different genotype groups within each locus is summarized in Table 1 (Experiment I) and Table 2 (Experiment II), respectively.

Growth performance in different experiments

Experiment I

The initial mean weight of the fish in this experiment was 249.9 g (s.d. = 31.6 g) in December 1989, rising to 3631 g (s.d. = 1085 g) when the fish were harvested in November 1991. During this period, the temperature varied seasonally (Figure 1), with the lowest values (4−6 °C) during winter and the highest (14−16 °C) in summer.

The number of fish with the various protein genotypes is given in Table 1, which shows that only a few genotypes were found for some of the protein loci investigated, especially *GPD**, *mIDHP**, and *PGM**. The mean body weights at different times for the genotypes at six loci are given in Figure 2, demonstrating only minor differences in nominal values for different genotypes at all the loci investigated. Statistical testing (ANOVA) revealed only two significant differences (ANOVA): *GPD** − November 1991 ($F = 3.38$; $p = 0.048$) and *PGM** − November 1991 ($F = 26.5$; $p = 0.005$). Both of these loci had only a few specimens in some of the genotype classes (Table 1). All other comparisons were not significantly different.

Similar analyses were carried out for SGR, based on weight increments (Figure 3), and as expected, there was large seasonal variation. All fish, irrespective of sex, matured and spawned in spring 1991, i.e. at about two years after hatching. This accounts for the negative values in SGR (Figure 3). The statistical tests revealed four significantly different cases, including *GPI-1** − December 1989 ($F = 3.78$; $p = 0.0133$) − and for the *LDH-3** locus at three different times: June 1990 ($F = 4.21$; $p = 0.016$), April 1991 ($F = 3.94$; $p = 0.019$), and November 1991

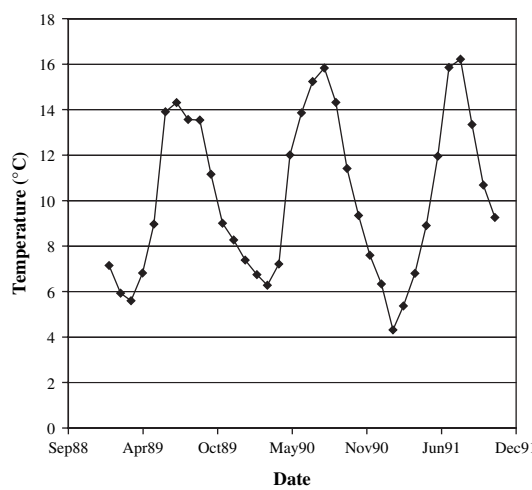

Figure 1. Temperature variation (monthly average, °C) in seawater (2-m depth) during Experiment I (1988 year class) conducted at the Institute of Marine Research, Austevoll.

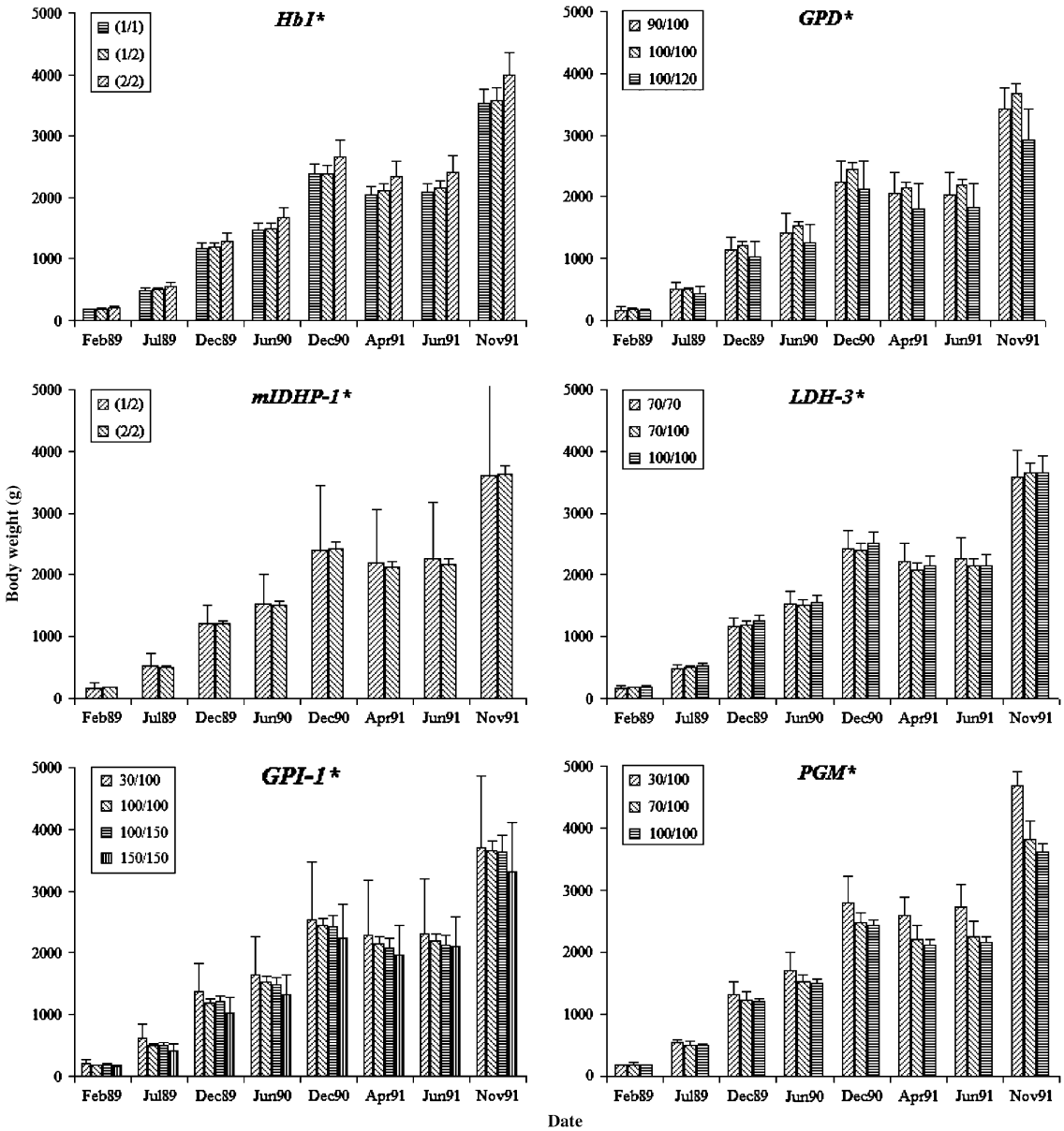

Figure 2. Experiment I: 1988 year class. Mean body weight ± 2 s.e. of different genotypes for six protein loci at different times during on-growing (1988–1991) at the Institute of Marine Research, Austevoll.

($F = 4.61$; $p = 0.013$). There was no consistency with respect to superior growth over the three periods, as each different genotype had the highest SGR at one time. There was no consistency or trend in the observations of the traits examined in relation to genotype over the seven sampling periods or in relation to temperature variation.

Experiment II

This experiment was carried out during a period of nearly two years, and the mean weight of the fish increased from an initial weight of 109 g (s.d. = 29.0 g) to 1470 g (s.d. = 324 g) at the end of the experiment. During the period, the sea temperature varied from 4°C to 14°C (Figure 4), which is almost the same as in the experiment in the Austevoll region (Experiment I). In January/February 1994, all of the NC were either maturing or spawning, while seven (two males and five females) of the NE group were classified as immature (Svåsand *et al.*, 1996).

As described earlier the experiment consisted of a mixture of two different cod stocks, NE Arctic and NC cod (van der Meeren *et al.*, 1994; Svåsand *et al.*, 1996). The

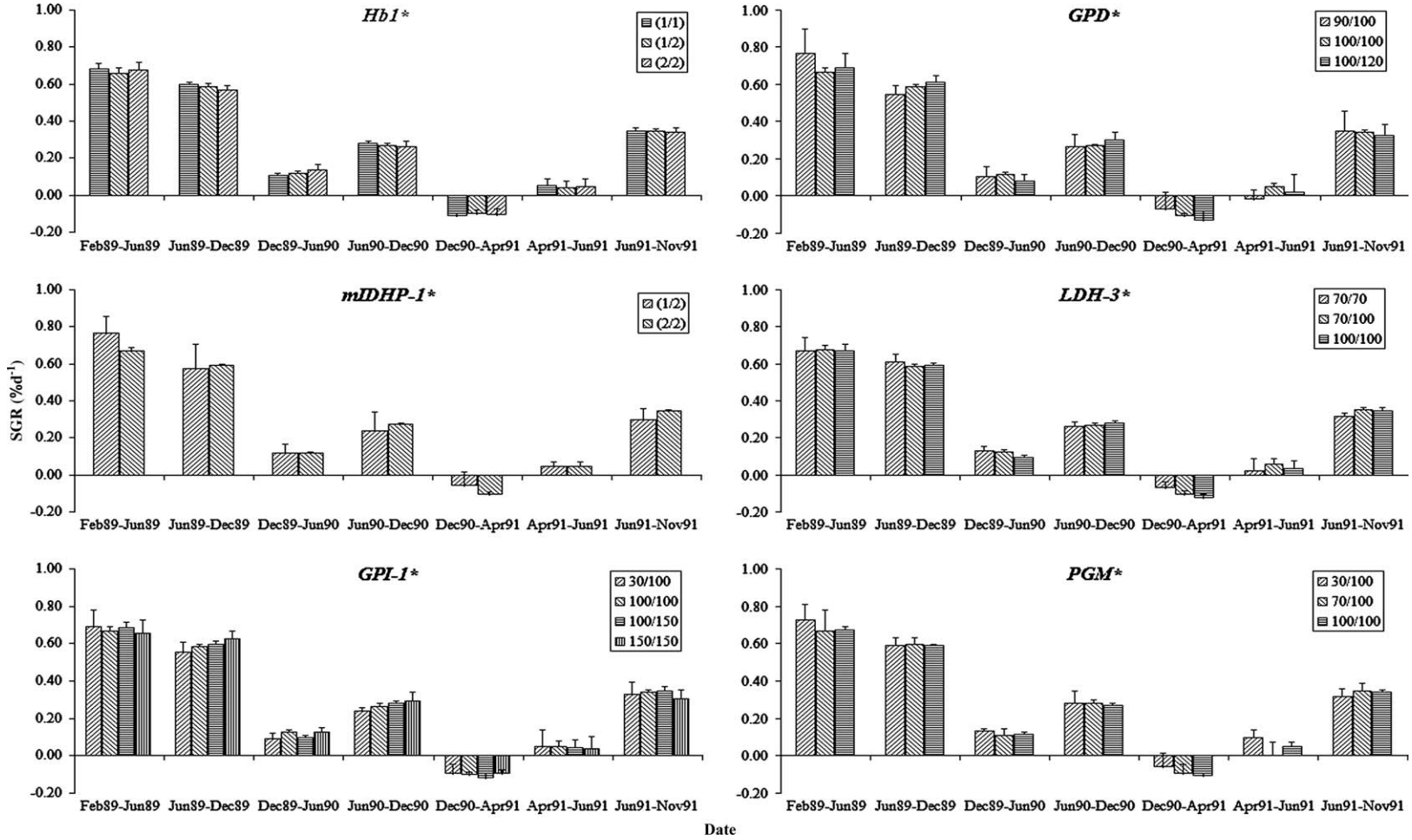

Figure 3. Experiment I: 1988 year class. Specific growth rate, SGR (weight increment) ± 2 s.e. of genotypes for six protein loci at different times during on-growing (1988−1991) at the Institute of Marine Research, Austevoll.

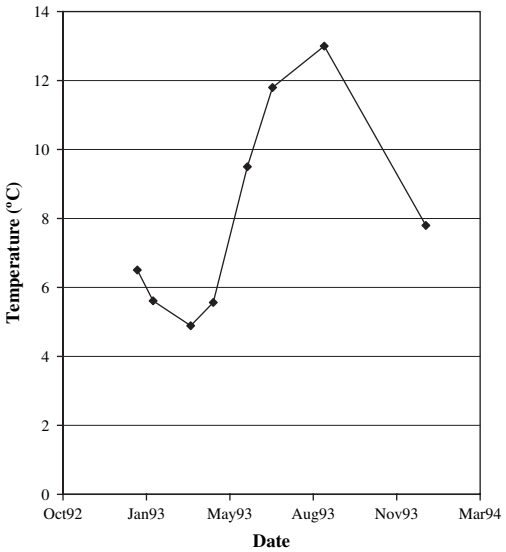

Figure 4. Temperature variation (monthly average, °C) in seawater (2-m depth) during Experiment II (1992 year class) conducted at the Institute of Marine Research, Parisvatnet, Øygarden.

coastal cod group, however, was the offspring of a genetically marked strain (Jørstad *et al.*, 1994), of which all the offspring were homozygous for a rare allele (*GPI-1* 30*). For this reason, only different genotypes at the *HbI** locus could be estimated for the NC group. On the other hand, reasonable numbers of the various genotypes for this locus were identified, as shown in Table 2. The mean weights for the different genotypes at different times are given in Figure 5, and in two cases, April 1993 ($F = 3.21$; $p = 0.047$) and July 1993 ($F = 3.46$; $p = 0.039$), significant differences were detected. In the SGR comparisons, only one significantly different value (February 1993; $F = 3.36$; $p = 0.042$) was found (Figure 6).

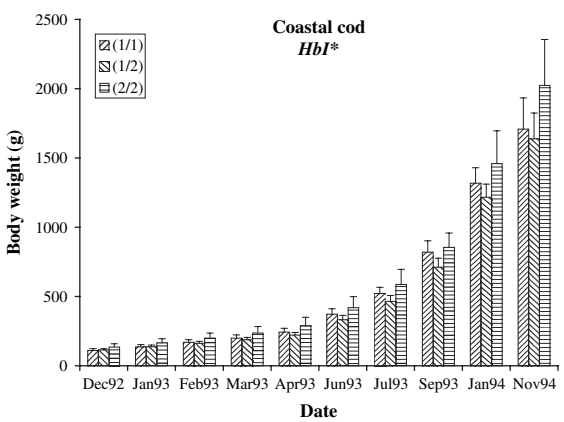

Figure 5. Experiment II: 1992 year class/NC coastal cod. Mean body weight ± 2 s.e. of different *HbI** genotype groups at different times during on-growing (1992–1994) at the Institute of Marine Research, Parisvatnet.

For the NE group, genotypic information for both *HbI** and *GPI-1** loci was obtained for the Northeast Arctic cod (NE) group. As shown, only two fish were of genotype *HbI* 1/1*. Based on the number of fish identified to genotypic group shown in Table 2, the corresponding mean weights are summarized in Figure 7. No significant differences were found in the *HbI** locus, and three comparisons were significant in the *GPI-1** locus, including March 1993 ($F = 2.936$; $p = 0.033$), January 1994 ($F = 3.81$; $p = 0.011$), and November 1994 ($F = 2.79$; $p = 0.042$).

The data obtained for SGR for the NE Arctic group genotypes are shown in Figure 8. Significantly different values were obtained for the *HbI** locus, April 1993 ($F = 4.55$; $p = 0.032$), July 1993 ($F = 3.22$; $p = 0.041$), and September, 1994 ($F = 3.66$; $p = 0.027$). For the *GPI-1** locus, four significant comparisons were detected including January 1993 ($F = 4.04$; $p = 0.026$), April 1993 ($F = 6.62$; $p = 0.0002$), July 1993 ($F = 4.22$; $p = 0.026$), and September 1993 ($F = 4.30$; $p = 0.004$). For both loci, no particular genotype possessed consistent superior growth over several periods. In contrast, as seen in Figure 8, the genotype with the highest SGR was different for each period. Further, no trends were noted regarding temperature variation throughout the investigation period. Considering the whole experiment, a similar situation was obtained when a comparison was made of mean length and specific growth rate (measured as length increments; data not shown). A few significant values were also found in these comparisons, but there seemed to be no consistency over time or with regard to variations associated with temperature.

Discussion

The first cod-farming experiment in Norway was based on the 1983 year class of cod juveniles produced in Hyltropollen in Austevoll (Kvenseth and Øiestad, 1984). This year class consisted of offspring from wild mature coastal cod collected in the Austevoll region (Jørstad, 1986a; Svåsand *et al.*, 1990). Based on individual tagging and protein genotyping (six polymorphic protein loci), the mean lengths of various genotypes within each of the protein loci were compared over an on-growing period of 34 months (Jørstad, 1986b). Only a few cases of significant differences between genotypes were detected, with no consistency over time or the protein loci investigated. Thus, the data obtained from that experiment provide no evidence for the existence of any genotypic superiority with regard to growth under the farming conditions used.

In the present study, based on two different year classes (1988 and 1992), more detailed investigations were conducted, including SGR estimates in different periods and temperatures. In general, the results obtained in Experiments I and II were similar to those obtained in the first

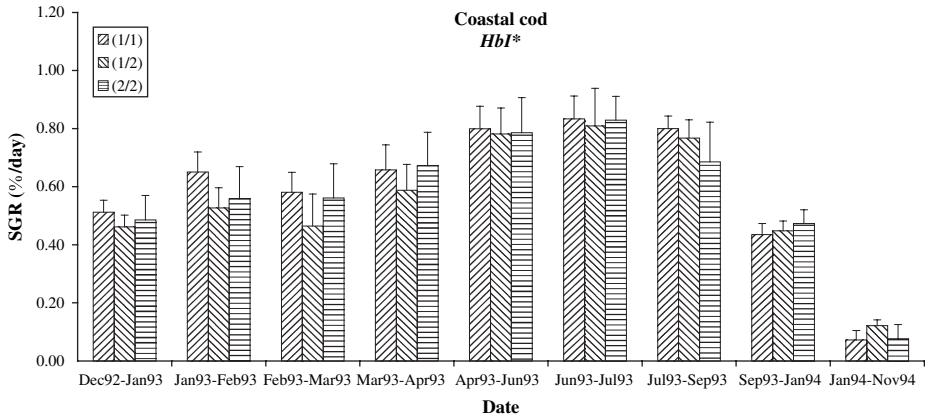

Figure 6. Experiment II: 1992 year class/NC coastal cod. Specific growth rate, SGR (weight increment) ± 2 s.e. of *HbI** genotype groups at different times during on-growing (1992−1994) at the Institute of Marine Research, Parisvatnet.

1983 year-class study (Jørstad, 1986b). As shown (Tables 1 and 2), the genotypic distributions at three of the loci (*HbI**, *LDH-2**, and *GPI-1**) analysed here provide sufficiently large sample sizes for reliable genotypic comparisons. For the other loci investigated (*PGM**, *GPD**, and *mIDHP**), the sample sizes of the rare genotypes were small, limiting the power of detecting possible differences among genotypic groups. Overall, only a few significant differences among protein genotypes were found in the two experiments, but no one genotype showed consistently high growth over the course of the experiments. The data presented here were focused on mean weight of genotypes at different times during the experiments and SGR (weight increment) during each of the growing periods. Similar results were obtained for mean length and length increment estimates (data not shown). Our comparisons of the SGR estimates, with temperature variation through the seasons, also revealed no indications or trends of superior growth.

Although not consistent over the study period, some significant differences were detected at the *GPI-1** and *HbI** loci in Experiment II, mainly when SGRs were compared. As this experiment consisted of a mixture of genetically marked coastal cod and offspring of NE cod (van der Meeren *et al.*, 1994), we cannot exclude stock differences between the two main groups. In the same experiment, as described by Svåsand *et al.* (1996), seasonal differences in SGR between the two groups were detected, suggesting that NE cod have a relatively fast growth rate at low temperatures.

As discussed by Imsland and Jonsdottir (2003), there are a number of genotypic studies of cod, especially for the *HbI** locus, with contrasting results and conclusions. Karpov and Novikov (1980) found differences (depending on temperature) in oxygen-binding capacities between the different genotypes. At 15 °C and below, the genotype *HbI* 2/2* had the highest affinity for oxygen, while *HbI* 1/1* was more efficient at high temperatures (15−20 °C and above). These findings were confirmed in later studies (Brix *et al.*, 1998), and these observations are believed to be the explanation (Karpov and Novikov, 1980) for the large variation in *HbI** genotypes along the Norwegian coast demonstrated in earlier studies (Frydenberg *et al.*, 1965; Møller, 1968). Attempts to reveal genotypic differences in growth based on wild cod samples have provided inconsistent results from genotypic analyses based on immature coastal

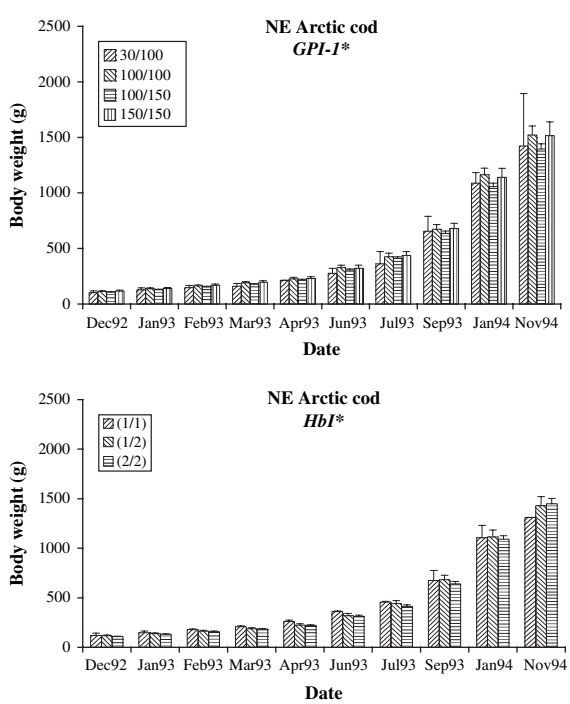

Figure 7. Experiment II: 1992 year class/NE Arctic cod. Mean body weight ± 2 s.e. for genotypes at two protein loci (*HbI**; *GPI-1**) at different times during on-growing (1992−1994) at the Institute of Marine Research, Parisvatnet.

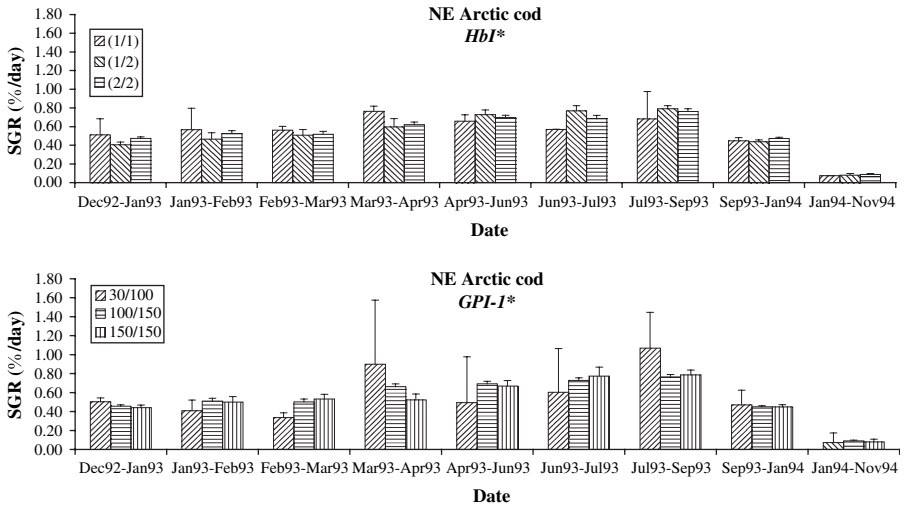

Figure 8. Experiment II: 1992 year class/NC Arctic cod. Specific growth rate, SGR (weight increment) ± 2 s.e. of *HbI** and *GPI-1** genotypes at different times during on-growing (1992−1994) at the Institute of Marine Research, Parisvatnet.

cod samples from Trondheimsfjorden. Mork *et al.* (1984) found evidence for faster growth rates of the genotype *HbI* 2/2*. On the other hand, similar studies of wild cod on the Skagerrak coast (Gjøsæter *et al.*, 1992) and on mesocosm-produced juvenile cod (Jørstad and Nævdal, 1994) did not confirm consistent growth differences between *HbI** genotypes.

These observations led to behavioural studies that tested the feeding behaviour and success of juveniles of known *HbI** genotypes (Salvanes and Hart, 2000). These studies found a better prey-capture success for the genotype *HbI* 2/2*, and the authors suggested that this was associated with feeding motivation, hence better growth. It would be quite attractive for the cod farming industry, at least in its early stages of development, if there existed a clear relationship between growth performance and the genotype *HbI* 2/2*.

The data obtained in this study provide no evidence of growth differences (SGR) between the three *HbI** genotypes under controlled farming conditions, even within periods of relatively large temperature differences. The two experiments reported are quite comparable with the farming conditions used by the industry, and unfortunately, we were unable to find any consistent evidence for the superiority of any genotype of any of the six protein loci investigated, including the *HbI** locus. Unlike most of the other studies cited above, the results obtained in the two comprehensive experiments presented here describe growth performance over a long period, from the juvenile stage to after maturity.

Some of the inconsistency in genotypic results discussed above could be the result of differences among the stocks investigated, sample sizes, and the hatchery conditions used. In all studies based on wild samples, as well as the various experiments performed including this contribution, the actual number of offspring families in the test material is unknown. This actually makes it impossible to distinguish between differences resulting from family and genotype group performance. New experiments are needed, however, to clarify some of the confusing results described in the literature. Such experiments should be based on well-defined family groups with known genotypes at the *HbI** locus, and preferably families in which the two broodstock fish were heterozygotes for the locus in question. If this is carried out at the *HbI** locus, all three genotypes will be present within the same family and can be compared directly for growth performance.

The results obtained involved two cod-farming experiments covering the full farming period until post-maturation. We found no indication of superior growth associated with any of the protein genotypes tested. The potential for genetic improvement of marine farming of species such as cod is dependent on the correct estimation of heritability of economically important traits such as growth, disease resistance, late maturation, and meat quality. The first heritability estimates for cod were provided for early growth and survival (Gjerde *et al.*, 2004). Those authors investigated the period from tagging of the juveniles (200 days after hatching) to 70 days later, and found significant heritability estimates for growth. The most important period is, however, the outgrowing period to market size. Based on the current interest in cod farming, a cod selective breeding programme is now being established in Tromsø, Norway, including large-scale facilities and selective broodstocks. Therefore, more comprehensive heritability estimates of various traits, including disease resistance (Kettunen *et al.*, pers. comm.) will be available, possibly in the near future. In addition, Atlantic cod are also included in the planned national consortium in Norway, which will focus more in detail on genomics of marine species (Frank Nilsen, pers. comm.).

Acknowledgements

We are indebted to the staff of the Institute of Marine Research, Austevoll and Parisvatnet, for participating in the sampling and handling of a large number of fish. Ole Ingar Paulsen assisted in the different electrophoretic analyses and Eva Farestveit with data processing.

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