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Genetic heterogeneity and growth properties of different genotypes of Atlantic cod (*Gadus morhua* L.) at two spawning sites off south Iceland

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Abstract

To investigate possible differences in life history traits of Atlantic cod in Icelandic waters, cod were collected at two spawning areas off Southwest Iceland (Loftstaðahraun and Kantur) in two surveys during the spawning season. The sampled fish were measured and age and sex determined. In addition they were analysed for allelic variation at the synaptophysin (*Syp* I) locus. Significant differences in growth performance and *Syp* I genotype distributions were found between the sampling localities. The cod sampled at Loftstaðahraun displayed higher mean weight and length compared to the cod from Kantur and this was mainly related to higher age. Significant differences in genotype (*Syp* I) were also observed between cod collected at the two sampling sites. The results indicate that the cod spawning in south Icelandic waters do not belong to one panmictic population and these populations seem to display different life histories.

Keywords: Atlantic cod; *Gadus morhua*; Growth performance; Genetic differentiation

1. Introduction

Studies on many fish species, including Atlantic cod, have clearly demonstrated that life history traits, e.g. growth performance and age at first maturity, may vary within and between different populations (Gjedrem et al., 1987; Conover and Present, 1990; Van der Meeren et al., 1994; Fjallstein and Magnussen, 1996; Svåsand et al., 1996; Conover et al., 1997). Van der Meeren et al. (1994) reported lower growth for Arcto-Norwegian (AN) larvae compared to Norwegian coastal (NC) larvae and Svåsand et al. (1996) reported higher growth in juvenile NC cod than AN cod. The AN cod also had lower hepatosomatic and gonadosomatic indices, and were thinner than the NC cod. These results indicate population specific differences in growth performance in Atlantic cod and conform to the results of many workers who have concluded that there exists differentiation between AN and NC cod populations both in polymorphic (Dahle and Jørstad, 1993; Dahle, 1995; Fevolden and Pogson, 1997), and morphometric and meristic traits (e.g. vertebrae number, Løken et al., 1994; otolith structure, Jakobsen, 1987). Also, Nordeide (1998) found that the AN and

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NC cod do not mingle randomly at the spawning grounds off northern Norway although specimens from both groups may stay simultaneously at the same local spawning ground.

Considerable effort has been made in the past to study the possible subdivision of cod populations in the northern Atlantic, including the application of a variety of stock identification techniques (Schmidt, 1930; Rollefsen, 1933; Sick, 1965; Jamieson and Jónsson, 1971; Cross and Payne, 1978; Mork et al., 1985; Galvin et al., 1995; Pogson et al., 1995; Ruzzante et al., 1996; Fevolden and Pogson, 1997) but without a clear conclusion. Studies of cod populations at Iceland have produced contradictory results. The work of Jamieson and Jónsson (1971) and Jónsson (1996) indicates the presence of different units of cod in Icelandic waters, whereas Árnason et al. (1992, 2000) found no evidence of such differentiation. Recently, the work of Jónsdóttir et al. (1999, 2001) indicated considerable population sub-structuring of cod in Icelandic waters. The discrepancy of the studies of Jamieson and Jónsson (1971), Jónsson (1996) and Jónsdóttir et al. (1999, 2001) on one hand, and the studies of Árnason et al. (1992, 2000) on the other hand, shows that we still have limited knowledge of the population structuring of Atlantic cod in Icelandic waters.

In this paper, we have focused on the genetic structure and growth performance of cod at two different spawning sites (Loftstaðahraun and Kantur) located on the south coast of Iceland. The genetic structure was examined in samples from two subsequent months during the spawning season, using the synaptophysin (*Syp* I) locus as a genetic marker. Growth performance of Atlantic cod from the two spawning sites was compared in relation to the *Syp* I genotypes. The data were used to test the null hypothesis that cod in the sampled areas represent the same gene pool displaying similar life history traits.

2. Materials and methods

2.1. Sample collection

Samples were collected during surveys by the Marine Research Institute, Reykjavik, during the spawning season in 1997. A total of 351 specimens of Atlantic cod were collected at two known spawning localities (Jónsson, 1982, 1996; Marteinsdóttir et al., 2000), Loftstaðahraun and Kantur (Table 1). These localities are ca. 50 nautical miles apart. Loftstaðahraun (Fig. 1) midpoint 63°44′N, 20°52′W, is a submarine rocky mount, depth range 50–70 m, and Kantur (Fig. 1) midpoint 63°17′N, 19°12′W, is a very steep continental slope, with depth ranging from 130 to 430 m. Two samples were obtained at each location with a time-interval of 2–3 weeks. At Loftstaðahraun, the samples were collected at 3–4 and 18–20 of April (Loftst.-April-1 and Loftst.-April-2) and on the 25–26 of March and 15–16 of April at Kantur (Kantur-March and Kantur-April). The fish were caught using bottom-trawl (Loftstaðahraun) and gill nets (Kantur). At the Kantur location the sampling sites were ca. 13 nautical miles apart (Fig. 1), thus, the cod samples were tested for intra-area relation. No intra-area genetic differences were observed (Fishers exact test, $P > 0.65$), and so the Kantur subsamples were pooled for inter-area comparisons.

2.2. Growth measurements

Total length (cm) and body weight (g) were recorded. All fish were sex determined and otoliths

Table 1
Locations, number of specimens (*N*), positions (mid-position), date of collection, depth (m), and sex ratio of sampled Atlantic cod in Icelandic waters used in this study

Sampling sites	*N*	Position	Date	Depth (m)	Sex ratio (% females)
Loftstaðahraun-April-1	83	63°46′N, 20°50′W	3–4 April 1997	43	35
Loftstaðahraun-April-2	79	63°44′N, 20°53′W	18–20 April 1997	55	13
Kantur-March	92	63°17′N, 19°13′W	25–26 March 1997	284	46
Kantur-April	97	63°17′N, 19°12′W	15–16 April 1997	284	64

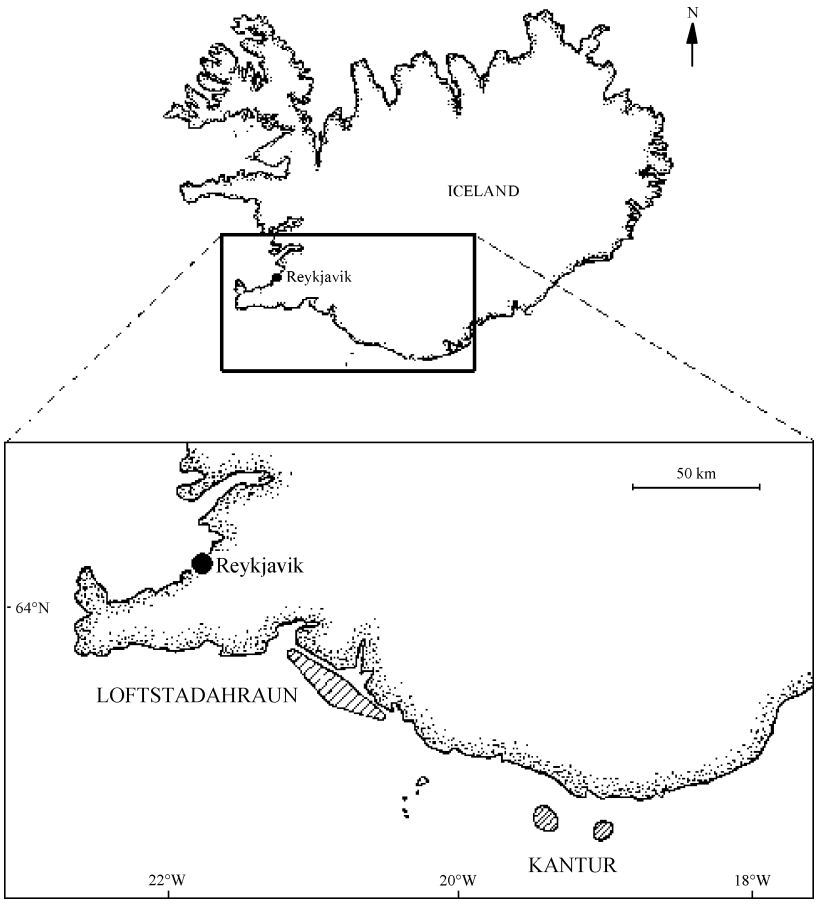

Fig. 1. Sampling sites of Atlantic cod off south Iceland (see Table 1 for details).

were taken for age determination. The condition factor (Fulton's K) was calculated as: $K = (\text{whole body weight}/(\text{total length})^3) \times 100$. Absolute growth rate ($G$) for each year class was calculated as: $G = \frac{1}{365}(\text{mean weight year}_{n+1} - \text{mean weight year}_n)$. Genotype related differences in size, length, K and growth rate were tested based on the genotype classification criteria of the *Syp* I locus (see below).

2.3. Genetic analysis

Gill arches were dissected from adult fish and stored in 96% ethanol. Approximately 200 mg of gill tissue were then used to extract DNA by phenol-extraction (Taggart et al., 1992). The nucleotide sequence data of Fevolden and Pogson (1997) were used to construct primers that amplify a region of the synaptophysin (*Syp* I) gene by the polymerase chain reaction (PCR) that contain the polymorphic *Dra* I site. All samples were screened for variation at the *Syp* I locus using the reaction conditions described by Jónsdóttir et al. (1999) modified from Fevolden and Pogson (1997). Digested PCR products were visualized in 2% agarose gels stained with ethidium bromide.

2.4. Statistical methods

All statistical analyses on growth variables were performed with STATISTICA^{TM} 5.0 (StatSoft, 1994). To assess normality of distributions a Kolmogorov–Smirnov test (Zar, 1996) was used, and homogeneity of variances was tested using the Levene's F test. One-way MANOVA (Johnson and Wichern, 1992) was applied to test for significant differences in weight,

length and condition factor, between the four samples (i.e., Loftst.-April-1, Loftst.-April-2, Kantur-March, Kantur-April). Separate MANOVAs were performed for each sex. The MANOVAs were followed by one-way ANOVA (Zar, 1996) between the samples, where each variable was tested separately. Significant ANOVAs were followed by a Student–Newman–Keuls multiple comparison test to locate differences among the samples (Zar, 1996). Analysis of covariance (ANCOVA) with age as covariate was used to test for genotype related differences in weight, length and *K*-factor for each sample. Weight at age and growth rates (i.e. weight increment between year classes) of the different genotypes were tested with a one-way ANOVA.

As the cod at Loftstaðahraun and Kantur were caught using different types of gear it is important to compare specimens at similar size and age when performing spatial comparison. To test for overall differences in body size, a three way mixed model ANCOVA was used to analyse which of the factors, sex (fixed), genotype (fixed), sample (random), and age (covariate) influenced body size. The ANCOVA allows for a gear independent test of spatial differences as we are comparing similar aged fish. The model equation of the ANCOVA had the form

$$y_{ijkl} = \mu + \alpha_i + \delta_j + \gamma_k + \alpha\delta_{ij} + \alpha\gamma_{ik} + \delta\gamma_{jk} + \alpha\delta\gamma_{ijk} + \beta x_{ijk} + \varepsilon_{ijkl}$$

where μ is the overall mean, α_i, δ_j and γ_k, are the effects of sex, genotype and sample site, respectively, $\alpha\delta_{ij}$ is the interaction of sex and genotype, $\alpha\gamma_{ik}$ the interaction of sex and samples, $\delta\gamma_{jk}$ the interaction of genotype and samples, $\alpha\delta\gamma_{ijk}$ the interaction of sex, genotype and samples, βx_{ijk} the coefficient of the covariate (age), ε_{ijklm} the error term.

In cases with non-significant statistical tests, power $(1-\beta)$ analysis for those tests were performed using the PASS program package (Hintze, 1996) using $\alpha = 0.05$.

Allele and genotype frequencies and F_{ST} values (Wright, 1978; Reynolds et al., 1983) were calculated using the ARLEQUIN 1.1 computer package (Schneider et al., 1997). The genetic structure of the sampling populations was studied using an analysis of molecular variance (AMOVA) framework (Weir and Cockerham, 1984). The samples were separated into two groups: Loftstaðahraun group (Loftst.-April-1 and Loftst.-April-2), and Kantur group (Kantur-March and Kantur-April), and the significance of the variance components was tested using non-parametric permutation procedures (Excoffier et al., 1992). Departure from Hardy–Weinberg equilibrium was tested in the AMOVA test by taking into account the differences between genotypes found within individuals (Schneider et al., 1997). The average heterozygosity was calculated using direct counts, and the estimates based on Hardy–Weinberg expectations. Sex-specific frequencies of the *Syp* I locus were tested in a contingency χ^2-test (Zar, 1996) (Table 2). A Bonferroni correction (Johnson and Field, 1993) of the significance level $(\alpha = 0.05)$ was applied when testing for significant differences in allele frequencies and for significant departures from Hardy–Weinberg expectations.

3. Results

3.1. Genetic differentiation

No significant differences in the frequency of the *Syp* I locus were found within areas ($F_{ST} < 0.02$,

Table 2
Frequencies of *Syp* I^A and *Syp* I^B alleles and heterozygote frequencies of cod from two locations in south Icelandic waters in March and April 1997

Locus	Allele	Loftstaðahraun-April-1	Loftstaðahraun-April-2	Kantur-March	Kantur-April
Syp I	*N*[a]	83	79	92	97
	Syp I^A	0.876	0.791	0.288	0.283
	Syp I^B	0.124	0.209	0.712	0.717
	H[b]	0.186 (0.220)	0.291 (0.333)	0.423 (0.412)	0.505 (0.408)

[a] Number of specimens analysed at each site.
[b] Frequencies of heterozygotes, observed (expected).

$P > 0.10$), or between sexes ($\chi^2_1 < 2.6$, $P > 0.10$). Although every sampling location was in Hardy–Weinberg equilibrium ($P > 0.15$), the total material (all samples compiled) was not in Hardy–Weinberg equilibrium ($P < 0.05$). The compiled allele frequencies in the two sample groups (i.e. Loftstaðahraun vs. Kantur) were significantly different at the *Syp* I locus when tested by conventional *F*-statistics ($F_{ST} > 0.40$, $P < 0.001$) and by AMOVA testing ($P < 0.05$, Table 3). The AMOVA test also indicated that 47% of the total allelic variance was due to differences between the two sample groups (Table 3).

3.2. Sex ratio

Percentage females in the samples collected at each sampling site varied from 13 to 64% (Table 1). The sex ratio of the samples was significantly different from a 1:1 distribution in both Loftstaðahraun samplings ($\chi^2_1 > 10.5$, $P < 0.01$) and at Kantur in April ($\chi^2_1 = 7.2$, $P < 0.01$). In the Kantur samples the proportion of females increased from March to April whereas in the Loftstaðahraun samples the female proportion decreased from early April to late April.

3.3. Growth indices

Mean age of the Loftstaðahraun cod was significantly higher (Kruskal–Wallis ANOVA, $H = 20.9$, $P < 0.001$) than the Kantur cod. The mean ages (S.D.) of the four samples were: Loftst.-April-1, 8.3 (2.0); Loftst.-April-2, 8.2 (2.0); Kantur-March, 7.2 (0.9) and Kantur-April, 7.1 (1.0). The difference in age composition of the different sampling localities was reflected in size differences between the sampling stations as the Loftstaðahraun cod were significantly heavier, longer and had higher condition factors (Table 4) than the cod from Kantur (one way MANOVA, Wilk's lambda $(\Lambda)_{9,842} = 0.31$, $P < 0.001$). Using age as a covariate, condition factor (K) varied between the sampling sites (two way ANCOVA, $F > 7.3$, $P < 0.01$) with higher K in the Loftstaðahraun group compared to the Kantur group.

Within area comparison of age specific growth properties of the different *Syp* I genotypes was possible (due to few samples in most categories) only for males at Loftstaðahraun. Significant differences in age specific size and length were found (one way ANCOVA, $F_{2,157} = 9.1$, $P < 0.01$) as the *Syp* I^{AA} had the highest weight and length at age. As no further testing was possible, we pooled the samples to compare growth properties of the different genotypes. Overall, significant differences were found also in the age specific size of the different genotypes (one way ANCOVA, $F_{2,348} = 10.4$ $P < 0.001$, Fig. 2). In all cases when significant differences were found between genotypes, the *Syp* I^{AA} displayed the highest weight at age and the *Syp* I^{BB} the lowest (one way ANOVA, $F > 12.5$, $P < 0.05$, Fig. 2). No differences in weight between genotypes were found for the

Table 3
Analysis of molecular variance (AMOVA) and hierarchical *F*-statistics (fixation indices) for the cod groups analysed in the present study. The genetic structure is analysed at the individual level so that the within individual variance is a test for global departure from Hardy–Weinberg equilibrium. Groups: Loftstaðahraun group (Loftst.-April-1, Loftst.-April-2), Kantur group (Kantur-March, Kantur-April)

Source of variation	d.f.[a]	Sum of squares	Variance component	Variance explained by AMOVA model	F_{XY}
Among groups	1	55.60	*0.1516*[*]	46.9	0.468
Among sampling sites within groups	2	0.63	0.0008	0.3	0.004
Among individuals within sampling sites	347	59.80	−0.0055[b]	−1.8[b]	−0.032[b]
Within individuals	351	64.50	*0.1776*[**]	54.6	0.454
Total	701	180.52	0.3236	100	

[a] Degrees of freedom. For calculation of d.f., see Schneider et al. (1997).

[b] Note that the *F*-statistic estimators in the AMOVA model are random variables and can take either positive or negative values (Long, 1986) negative values indicating excess of heterozygotes (Long, 1986; Excoffier et al., 1992). Such negative estimates should be interpreted as zero (Long, 1986) in the AMOVA model, i.e. the variance explained by among individuals within sampling sites is zero in the present study.

[*] $P < 0.05$.

[**] $P < 0.01$.

Table 4
Comparison of weight (kg), length (cm) and condition factor (K) of three different *Syp* I genotypes of male and female Atlantic cod at Loftstaðahraun and Kantur in March and April 1997[a]

Sampling site	*Syp* I genotype	Sex	N	Weight (kg)	Length (cm)	K
Loftstaðahraun-April-1	AA	M	43	15.0 (5.0)	106.2 (10.1)	1.21a (0.15)
	AB	M	8	15.0 (4.4)	105.8 (9.3)	1.24a (0.08)
	BB	M	3	14.9 (7.3)	109.3 (14.2)	1.06b (0.24)
	AA	F	22	19.3 (7.5)	109.3 (9.9)	1.41 (0.20)
	AB	F	7	17.4 (5.4)	111.4 (11.4)	1.23 (0.17)
	BB	F	0	NA	NA	NA
Loftstaðahraun-April-2	AA	M	46	12.3 (4.5)	102.5 (10.1)	1.09a (0.12)
	AB	M	19	10.5 (4.6)	99.4 (10.4)	1.01b (0.15)
	BB	M	4	13.2 (6.0)	107.0 (14.0)	1.01b (0.13)
	AA	F	5	19.9 (6.4)	114.6 (9.0)	1.28 (0.22)
	AB	F	4	17.5 (7.2)	115.2 (15.1)	1.11 (0.27)
	BB	F	1	8.4	93	1.05
Kantur-March	AA	M	2	7.6 (0.9)	89.0 (4.2)	1.08a (0.02)
	AB	M	16	6.6 (0.7)	86.3 (3.9)	1.02ab (0.07)
	BB	M	32	6.4 (1.5)	86.3 (6.4)	0.98b (0.06)
	AA	F	5	6.3 (1.1)	82.4 (5.3)	1.11a (0.15)
	AB	F	23	6.3 (1.2)	84.6 (5.4)	1.04ab (0.06)
	BB	F	14	6.0 (1.2)	84.1 (5.6)	1.00b (0.09)
Kantur-April	AA	M	1	4.2	74	1.04
	AB	M	18	6.3 (1.2)	85.2 (5.4)	1.01 (0.11)
	BB	M	16	5.1 (1.6)	81.1 (6.7)	0.94 (0.09)
	AA	F	2	4.1 (0.5)	71.0 (4.2)	1.12a (0.06)
	AB	F	31	6.2 (1.7)	84.8 (7.7)	1.00b (0.09)
	BB	F	29	6.1 (1.6)	84.0 (7.1)	1.01b (0.08)

[a] Results are given as mean value (S.D.). Letters (a and b) indicate statistical differences in mean K between genotypes (AA, AB, BB) (one way ANOVA) at each sampling site. Separate tests were performed for each sex.

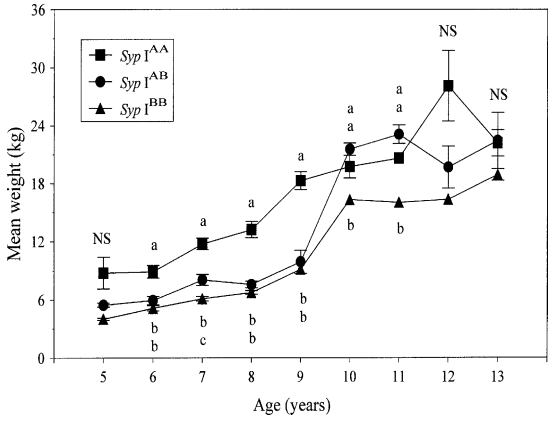

Fig. 2. Mean weight at the age of three *Syp* I genotypes of Atlantic cod at different ages. Data from the different sampling sites are compiled. Vertical lines indicate standard errors (S.E.). Different letters indicate significant differences (one way ANOVA followed by Student–Newman–Keuls multiple comparison test) within each age group; NS: not significant.

youngest and the oldest age groups (Fig. 2, power $(1-\beta) > 0.70$). Genotypic differences in condition factor were found for males at Loftst.-April-1, Loftst.-April-2 and Kantur-March, and for females at Kantur-March and Kantur-April (Table 4). In all cases the *Syp* I^{AA} genotype had the highest K (Student–Newman–Keuls test, $P < 0.05$) and the *Syp* I^{BB} the lowest K. Large variations in year-to-year absolute growth rates were found for all genotypes (Fig. 3). When growth data for the 5–9 year old cod and for the 9–13 year old cod were compiled, no significant differences in absolute growth rates were found (power > 0.35) but the *Syp* I^{AA} displayed higher growth for the younger fish compared to the other genotypes (Fig. 3).

As we found differences in allele frequency between Loftstaðahraun and Kantur, we tested for overall differences in body size using a three way ANCOVA with sex, genotype and sampling sites as main factors and age as a covariate (Table 5). Based on

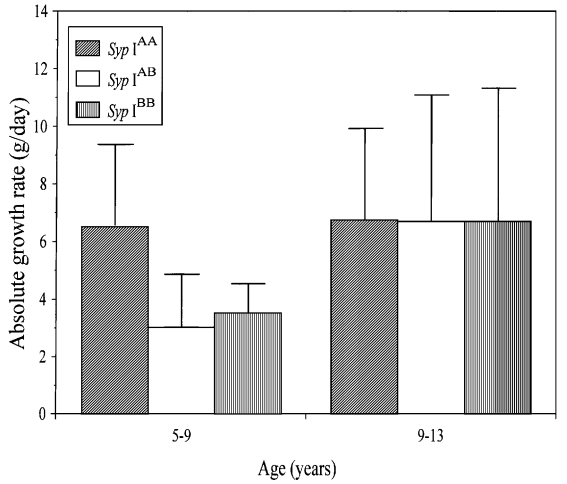

Fig. 3. Absolute growth (g/day) of year classes 5–9 and 9–13 of the three *Syp* I genotypes. Data from the different sampling sites are compiled. Vertical lines indicate S.E.

the ANCOVA, body size was related to genotype, sampling site, and age. There were no significant interaction effects between sex, genotype and sampling site, whereas the regression lines for the genotypes and samples were non-parallel (Table 5).

Table 5
Analysis of covariance (ANCOVA) of body size (y) in female and male cod, of different *Syp* I genotypes at different sampling sites as a function of age (A) and the main factors sex (S), genotypes (G) and sampling sites (LK); d.f.: degrees of freedom

Source of variation	d.f.	F-ratio	P
Main effects			
Sex (S)	1	1.53	0.301
Genotypes (G)	2	6.73	<0.01
Sampling sites (LK)	3	24.00	<0.001
Interaction, main effects			
$S \times G$	2	1.52	0.219
$S \times$ LK	3	2.69	0.088
$G \times$ LK	6	1.19	0.138
$S \times G \times$ LK	6	0.54	0.775
Covariate			
Age (A)	1	265.07	<0.001
Parallelism of covariate			
$S \times A$	1	1.20	0.274
$G \times A$	2	11.80	<0.001
LK $\times A$	3	12.62	<0.001
Error	325		

4. Discussion

4.1. Growth performance of cod at Loftstaðahraun and Kantur

In the present study, large size differences between cod from the different sampling sites were observed, and these differences were related to both age and genotype composition. These findings are consistent with previous reports on size and age variation of cod in this area (Marteinsdóttir et al., 2000). Further, overall genotype related differences in weight and length were observed, and condition factors varied between the genotypes as the *Syp* I^{AA} exhibited significantly higher K than did *Syp* I^{BB} (Table 4). As there was a clear difference in the genetic composition of cod from Loftstaðahraun and Kantur, with significantly lower *Syp* I^{A} allele frequencies in Kantur samples, these differences in weight at age and condition factor could reflect differences in growth performance of the sampling groups. This is further strengthening by the non-significant interactions between samples and genotype and sex in the overall ANCOVA model indicating a consistent trend between *Syp* I genotype and body size (Table 5). The difference in the condition of the *Syp* I genotypes might influence the viability characteristics of cod larvae. Marteinsdóttir and Steinarsson (1998) investigated maternal influence on egg size and viability of Icelandic cod eggs and larvae and found significant correlations between condition factors of female cod and mean egg size and larval feeding success. Accordingly, the genotypic differences in condition seen in the present study might be reflected in different quality and viability of larvae produced by the different *Syp* I genotypes.

There are at least three interrelated explanations of the differences in weight at age and condition found between genotypes and sampling sites: (i) differences in mean growth performance, (ii) differences in environmental conditions, (iii) individual genotypic growth differences. First, recent studies of cod at the Faeroes and in Norway have demonstrated differences in mean growth performance of different populations (Van der Meeren et al., 1994; Fjallstein and Magnussen, 1996; Svåsand et al., 1996). Svåsand et al. (1996) studied growth performance of individually tagged Arcto-Norwegian (AN) and Norwegian coastal cod (NC)

which were reared together for 1 year. NC cod displayed significantly higher mean growth and condition compared with AN cod, and the authors suggested that there might exist inter-population differences in body growth and allocation of energy. Such inter-population differences in growth performance has also been reported for several teleost species including American shad, *Alosa sapidissima* (Leggett and Carscadden, 1978), splitnose rockfish, *Sebastes diploproa* (Boehlert and Kappenman, 1980), weakfish, *Cynoscion regalis* (Shepherd and Grimes, 1983), Atlantic silversides, *Menida menida* (Conover and Present, 1990), striped bass, *Morone saxatilis* (Conover et al., 1997), and Atlantic halibut, *Hippoglossus hippoglossus* (Jonassen et al., 2000; Imsland et al., 2000). These findings indicate that inter-population variation in life history traits may be widespread in temperate fishes.

Second, it is also possible that the differences in weight at age and condition factor may reflect differences in environmental temperatures in the feeding areas of the two groups. Earlier studies have shown that there is a general tendency towards lower condition in fish inhabiting waters having lower temperatures (Haug et al., 1989; Solbakken et al., 1994; Imsland et al., 1995). Cod spawning at Kantur tend to migrate towards feeding areas off the east coast of Iceland whereas cod spawning at Loftstaðahraun tend to migrate towards the west coast (Jónsson, 1996; Jónsdóttir et al., 1999). Sea temperatures off east Iceland are generally lower than off the southwest and west-coast (Stefánsson and Jónsdóttir, 1974). Hence, the genotype related differences in weight at age and condition factor seen in the present study could be related to differences in migratory patterns of the cod at Kantur and Loftstaðahraun. Further studies are needed to explore this possibility.

Third, individual differences in growth performance might explain the observed difference in growth indices. Every individual in a group of fish can be assigned an individual growth factor X_i that indicates the relative growth rate of individual i in relation to average growth rate in the population. Few studies have tried to assess this underlying individual genetic growth factor (Forsberg, 1995; Imsland et al., 1998) although it is axiomatic that individuals vary in growth. Modelling efforts with turbot, *Scophthalmus maximus* (Imsland et al., 1998) suggest that the inherent individual genetical variability in growth and its autoregressive behaviour have large impact on growth variability in fish. Such growth variability can have a large effect on the dynamics of a cohort (Chambers and Leggett, 1992; DeAngelis et al., 1993; Rice et al., 1993). Fevolden and Pogson (1995) reported genotypic differences in growth of *Syp* I genotypes. Using length/age ratio as an index of growth they found that the *Syp* I^{AA} genotype displayed the highest mean growth and *Syp* I^{BB} the lowest growth. Further, they found significant differences in *Syp* I allele frequencies between two samples of Arctic and Norwegian coastal cod populations. This difference in allelic frequencies was confirmed in a later study (Fevolden and Pogson, 1997). In both studies the *Syp* I^{AA} genotype is much more common in coastal cod samples indicating higher growth of Norwegian coastal cod compared with Arctic cod which conforms to the findings of Svåsand et al. (1996). In the present study, we found indications of lower growth performance in the sampled populations in which the genotype *Syp* I^{BB} is most common (i.e. Kantur-March and April) in line with Fevolden and Pogson (1995) and Svåsand et al. (1996). However, to test whether differences in growth performance between genotypes and sampling groups are genetically or environmentally based would require fish to be reared under controlled and equal conditions in the laboratory.

4.2. Genetic divergence at Loftstaðahraun and Kantur

In line with previous results (Jónsdóttir et al., 1999, 2001) the present study indicates genetic differentiation between cod populations in Icelandic waters. The distinction in the *Syp* I allele frequencies between Loftstaðahraun group and Kantur group is in line with the findings of Fevolden and Pogson (1995, 1997) in Norwegian waters. Our findings contrast sharply with those obtained by Árnason et al. (1992), using a restriction analysis of mitochondrial DNA (mtDNA). The fact that subpopulation structure can be detected with cDNA-based nuclear random fragment length polymorphisms (RFLP) in Icelandic (Jónsdóttir et al., 1999, 2001), Canadian (Pogson et al., 1995), and Norwegian waters (Pogson et al., 1995; Fevolden and Pogson, 1995, 1997), but not with restriction analysis of mtDNA (Smith et al., 1989; Árnason et al., 1992) (with a notable exception, see Dahle, 1991) or

with mitochondrial cytochrome *b* DNA sequence variation (Pepin and Carr, 1993; Carr et al., 1995; Árnason and Pálsson, 1996; Árnason et al., 2000), implies that the mtDNA techniques might be less appropriate to detect differences in cod stock structure than the cDNA RFLP technique, at least at local scales.

Further, our data show that the differences in *Syp* I allelic frequencies between Loftstaðahraun group and Kantur group are relatively unchanged within the same spawning season (Tables 2 and 3). This issue of temporal stability in *Syp* I frequencies between these samples has been discussed in detail in another publication (Jónsdóttir et al., 2001), and the results further confirm the distinct differentiation between the two investigated cod populations (Loftstaðahraun and Kantur) on a temporal scale of 1 year. The stability of the allele frequencies indicates that the cod at the two spawning sites studied here, Loftstaðahraun and Kantur, do not intermingle at the spawning grounds. Tagging experiments have indicated that spawners from these two sites display different patterns of migration when leaving the spawning areas (Jónsson, 1996). There are also indications that the spawning time of cod in these two areas may differ to some extend. Marteinsdóttir and Pétursdóttir (1995) and Marteinsdóttir and Björnsson (1999) have shown that spawning starts earlier among the larger cod spawning close to the shore (Loftstaðahraun and other areas) compared to smaller cod spawning out on the bank and on the continental edge southwest and west of the country. Similarly, spawning in the area of Kantur appears to start later in the season although the time of peak spawning is similar in both areas (Marteinsdóttir, unpublished data). Accordingly, it is possible that the distinct location of the two spawning sites, as well as the partial differences in spawning time or migration pattern act as an isolating mechanism reducing the possibility of interbreeding between the cod from the two sampling sites studied here.

The pronounced difference in the *Syp* I allele frequencies detected between the cod populations at Loftstaðahraun and Kantur, together with the genotype related differences observed in weight and length and condition factor, might raise the question if this locus is valid as a genetic stock marker due to possible influence of evolutionary forces. Pogson et al. (1995) argued that with the exceptional high differentiation seen between cod populations at the *Syp* I locus both in Norwegian and Icelandic waters (Fevolden and Pogson, 1995, 1997; Jónsdóttir et al., 1999, 2001) the selection coefficient would have to be extremely strong to be the only causative agent of this heterogeneity. Thus, they concluded that breeding structure is a more likely contributor to the observed genetic differences (Fevolden and Pogson, 1995) than only genetic selection.

5. Conclusions

Our findings indicate growth performance, age and genetic differentiation between cod populations off south Iceland. The results indicate that the cod spawning in south Icelandic waters do not belong to one panmictic population and these populations may display different life histories. Growth experiments under identical environmental conditions would be required to test the hypothesis if populations differ in growth performance.

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References

Árnason, E., Pálsson, S., 1996. Mitochondrial cytochrome *b* DNA sequence variation of Atlantic cod *Gadus morhua* from Norway. Mol. Ecol. 5, 715–724.

Árnason, E., Pálsson, S., Arason, A., 1992. Gene flow and lack of population differentiation in Atlantic cod, *Gadus morhua* L., from Iceland, and comparison of cod from Norway and Newfoundland. J. Fish Biol. 40, 751–770.

Árnason, E., Petersen, P.H., Kristinsson, K., Sigurgíslason, H., Pálsson, S., 2000. Mitochondrial cytochrome *b* DNA sequence

variation of Atlantic cod from Iceland and Greenland. J. Fish Biol. 56, 409–430.

Boehlert, B.W., Kappenman, R.F., 1980. Variation of growth with latitude in two species of rockfish (*Sebastes pinniger* and *S. diploproa*) from the Northeast Pacific Ocean. Mar. Ecol. Prog. Ser. 3, 1–10.

Carr, S.M., Snellen, A.J., Howse, K.A., Wroblewski, J.S., 1995. Mitochondrial DNA sequence variation and genetic stock structure of Atlantic cod (*Gadus morhua*) from bay and offshore locations on the Newfoundland continental shelf. Mol. Ecol. 4, 79–88.

Chambers, R.C., Leggett, W.C., 1992. Possible causes and consequences of variation in age and size at metamorphosis in flatfishes (Pleuronectiformes): an analysis at the individual, population and species levels. Neth. J. Sea Res. 29, 7–24.

Conover, D.O., Present, T.M.C., 1990. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides form different latitudes. Oecologia 83, 316–324.

Conover, D.O., Brown, J.J., Ehtisham, A., 1997. Countergradient variation in growth of young striped bass (*Morone saxatilis*) from different latitudes. Can. J. Fish. Aquat. Sci. 54, 2401–2409.

Cross, T.F., Payne, R.H., 1978. Geographic variation in Atlantic cod, *Gadus morhua*, off eastern North America: a biochemical systematics approach. Can. J. Fish. Aquat. Sci. 35, 117–123.

Dahle, G., 1991. Cod, *Gadus morhua* L., population identified by mitochondrial DNA. J. Fish Biol. 38, 295–303.

Dahle, G., 1995. Genetic structure of the north-east Atlantic cod (*Gadus morhua* L.), an appraisal of different molecular techniques. Ph.D. Thesis. University of Bergen, Norway.

Dahle, G., Jørstad, K.E., 1993. Haemoglobin variation in cod—a reliable marker for Arctic cod (*Gadus morhua* L.). Fish. Res. 16, 301–311.

DeAngelis, D.L., Rose, K.A., Crowder, L.B., Marschall, E.A., Lika, D., 1993. Fish cohort dynamics: application of complementary modelling approaches. Am. Nat. 142, 604–622.

Excoffier, L., Smouse, P.E., Quattro, J.M., 1992. Analysis of molecular variance inferred form metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics 131, 479–491.

Fevolden, S.E., Pogson, G.H., 1995. Differences in nuclear DNA RFLPs between the Norwegian coastal and the north-east Arctic population of Atlantic cod. In: Skjoldal, H.R., Hopkins, C., Erikstad, K.E., Leinaas, H.P. (Eds.), Ecology of Fjords and Coastal Waters. Elsevier, Amsterdam, pp. 403–415.

Fevolden, S.E., Pogson, G.H., 1997. Genetic divergence at the synaptophysin (*Syp* I) locus among Norwegian coastal and north-east Arctic populations of Atlantic cod. J. Fish Biol. 51, 895–908.

Fjallstein, I., Magnussen, E., 1996. Growth of Atlantic cod (*Gadus morhua* L.) of Faroe Bank strain and Faroe Plateau strain in captivity. ICES, C.M. 1996/F:12.

Forsberg, O.I., 1995. Empirical investigations on growth of post-smolt Atlantic salmon (*Salmo salar* L.) in land-based farms. Evidence of a photoperiodic influence. Aquaculture 133, 235–248.

Galvin, P., Sadusky, T., McGregor, D., Cross, T., 1995. Population genetics of Atlantic cod using amplified single locus minisatellite VNTR analysis. J. Fish Biol. 47, 200–208.

Gjedrem, T., Gjerde, B., Refstie, T., 1987. A review of quantitative genetic research in salmonides at AKVAFORSK. In: Weir, B.S., Eisen, J.E., Goodman, M.M., Namkoono, G. (Eds.), Proceedings of the Second International Conference on Quantitative Genetics, pp. 527–535.

Haug, T., Huse, I., Kjørsvik, E., Rabben, H., 1989. Observations on the growth of juvenile Atlantic halibut (*Hippoglossus hippoglossus* L.) in captivity. Aquaculture 80, 79–86.

Hintze, J.L., 1996. PASS 6.0—Power Analysis and Sample Size for Windows. NCSS, Kaysville, Utah.

Imsland, A.K., Folkvord, A., Stefansson, S.O., 1995. Growth, oxygen consumption and activity of juvenile turbot (*Scophthalmus maximus*) reared under different temperatures and photoperiods. Neth. J. Sea Res. 34, 149–159.

Imsland, A.K., Folkvord, A., Nilsen, T., 1998. Stochastic simulation of size-variation in turbot: possible causes analysed with an individual based model. J. Fish Biol. 53, 237–258.

Imsland, A.K., Jonassen, T.M., Kadowaki, S., Berntssen, M., Stefansson, S.O., 2000. Intraspecific differences in physiological efficiency of juvenile Atlantic halibut (*Hippoglossus hippoglossus* L.). J. World Aquat. Soc. 31, 285–296.

Jakobsen, T., 1987. Coastal cod in northern Norway. Fish. Res. 5, 223–234.

Jamieson, A., Jónsson, J., 1971. The Greenland component of spawning cod at Iceland. J. Conc. Int. Explor. Mer. 161, 65–72.

Johnson, C.R., Field, C.R., 1993. Using fixed-effects model multivariate analysis of variance in marine biology and ecology. Mar. Biol. Ann. Rev. 31, 177–221.

Johnson, R.A., Wichern, D.W., 1992. Applied Multivariate Statistical Analysis. Prentice-Hall, Englewood Cliffs, NJ, p. 642.

Jonassen, T.M., Imsland, A.K., FitzGerald, R., Bonga, S.W., van Ham, E., Nævdal, G., Stefánsson, M.Ö., Stefansson, S.O., 2000. Geographic variation in growth and food conversion efficiency of juvenile Atlantic halibut related to latitude. J. Fish Biol. 56, 279–294.

Jónsdóttir, Ó.D.B., Imsland, A.K., Daníelsdóttir, A.K., Thorsteinsson, V., Nævdal, G., 1999. Genetic differentiation among Atlantic cod in Icelandic waters: synaptophysin (*Syp* I) and haemoglobin variation. J. Fish Biol. 54, 1259–1274.

Jónsdóttir, Ó.D.B., Daníelsdóttir, A.K., Nævdal, G., 2001. Genetic differentiation among Atlantic cod (*Gadus morhua* L.) in Icelandic waters: temporal stability. ICES J. Mar. Sci. 58, 00–00.

Jónsson, E., 1982. A survey of spawning and reproduction of the Icelandic cod. Rit Fiskideildar 6 (2), 1–45.

Jónsson, J., 1996. Tagging of cod (*Gadus morhua*) in Icelandic waters 1948–1986. Rit Fiskideildar 14, 7–82.

Leggett, W.C., Carscadden, J.E., 1978. Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): evidence for population specific life history strategies in fish. J. Fish. Res. Bd. Can. 35, 1469–1478.

Løken, S., Pedersen, T., Berg, E., 1994. Vertebrae numbers as an indicator for the recruitment mechanisms of coastal cod of northern Norway. ICES Mar. Sci. Symp. 198, 510–519.

Long, J.C., 1986. The allelic correlation structure of gainj- and kalam-speaking people. I. The estimation and interpretation of Wright's *F*-statistics. Genetics 112, 629–647.

Marteinsdóttir, G., Björnsson, H., 1999. Time and duration of spawning among cod in Icelandic waters. ICES, CM 1999/Y:34.

Marteinsdóttir, G., Pétursdóttir, G., 1995. Spatial and temporal variation in reproduction of Icelandic cod at Selvogsbanki and nearby coastal areas. ICES, C.M. 1995/G:15.

Marteinsdóttir, G., Steinarsson, A., 1998. Maternal influence on the size and viability of Iceland cod *Gadus morhua* eggs and larvae. J. Fish Biol. 52, 1241–1258.

Marteinsdóttir, G., Guðmundsdóttir, Á., Thorsteinsson, V., Stefánsson, G., 2000. Spatial variation in abundance, size composition and viable egg production of spawning cod (*Gadus morhua* L.) in Icelandic waters. ICES J. Mar. Sci. 57, 824–830.

Mork, J., Ryman, N., Ståhl, G., Utter, F., Sundnes, G., 1985. Genetic variation in Atlantic cod (*Gadus morhua*) throughout its range. Can. J. Fish. Aquat. Sci. 42, 1580–1587.

Nordeide, J.T., 1998. Coastal cod and north-east Arctic cod—do they mingle at the spawning grounds in Lofoten? Sarsia 83, 373–379.

Pepin, P., Carr, S.M., 1993. Morphological, meristic, and genetic analysis of stock structure in juvenile Atlantic cod (*Gadus morhua*) from the Newfoundland shelf. Can. J. Fish. Aquat. Sci. 50, 1924–1933.

Pogson, G.H., Mesa, K.A., Boutilier, R.G., 1995. Genetics population structure and gene flow in the Atlantic cod *Gadus morhua*: a comparison of allozyme and nuclear RFLP loci. Genetics 139, 375–385.

Reynolds, J., Weir, B.S., Cockerham, C.C., 1983. Estimation for the coancestry coefficient: basis for a short-term genetic distance. Genetics 105, 769–779.

Rice, J.A., Miller, T.J., Rose, K.A., Crowder, L.B., Marschall, E.A., Trebitz, A.S., DeAngelis, D.L., 1993. Growth rate variation and larval survival: inferences from an individual-based size-dependent predation model. Can. J. Fish. Aquat. Sci. 50, 133–142.

Rollefsen, G., 1933. The otoliths of cod. Fiskeridir. Skrift. Ser. Havunder. 5, 23–32.

Ruzzante, D.E., Taggart, C.T., Cook, D., Goddard, S., 1996. Genetic differentiation between inshore and offshore Atlantic cod (*Gadus morhua*) off Newfoundland: microsatellite DNA variation and antifreeze level. Can. J. Fish. Aquat. Sci. 53, 634–645.

Schmidt, J., 1930. The Atlantic Cod (*Gadus callarias* L.) and Local Races of the Same, Vol. 18. C.R. Lab., Carlsberg, pp. 1–72.

Schneider, S., Kueffer, J.M., Roessli, D., Excoffier, L., 1997. Arlequin, Version 1.1: A Software for Population Genetic Data Analysis. Genetics and Biometry Laboratory, University of Geneva, Switzerland.

Shepherd, G., Grimes, C.B., 1983. Geographic and historic variations in growth of weakfish, *Cynoscion regalis*, in the Middle Atlantic Bight. Fish. Bull. 81, 803–813.

Sick, K., 1965. Haemoglobin polymorphism of cod in the North Sea and the North Atlantic ocean. Hereditas 54, 49–69.

Smith, P.J., Birley, A.J., Jamieson, A., Bishop, C.A., 1989. Mitochondrial DNA in the Atlantic cod, *Gadus morhua*: lack of genetic divergence between eastern and western populations. J. Fish Biol. 24, 369–373.

Solbakken, V., Hansen, T., Stefansson, S.O., 1994. Effects of photoperiod and temperature on growth and parr–smolt transformation in Atlantic salmon (*Salmo salar* L.) and subsequent performance in seawater. Aquaculture 121, 13–27.

StatSoft, 1994. STATISTICA, Version 5.0. StatSoft, Inc., Tulsa, OK.

Stefánsson, U., Jónsdóttir, S., 1974. Near-bottom temperature around Iceland. Rit Fiskideildar 5 (2), 1–73.

Svåsand, T., Jørstad, K.E., Otterå, H., Kjesbu, O.S., 1996. Differences in growth performance between Arcto-Norwegian and Norwegian coastal cod reared under identical conditions. J. Fish Biol. 49, 108–119.

Taggart, J.B., Hynes, R.A., Prodöhl, P.A., Ferguson, A., 1992. A simplified protocol for routine total DNA isolation from salmonid fishes. J. Fish Biol. 40, 963–965.

Van der Meeren, T., Jørstad, K.E., Solemdal, P., Kjesbu, O.S., 1994. Growth and survival of cod larvae (*Gadus morhua* L.): comparative enclosure studies of Northeast Arctic cod and coastal cod from western Norway. ICES Mar. Sci. Symp. 198, 633–645.

Weir, B.S., Cockerham, C.C., 1984. Estimating *F*-statistics for the analysis of population structure. Evolution 38, 1358–1370.

Wright, S., 1978. Evolution and the Genetics of Populations: Variability Within and Among Natural Populations. University of Chicago Press, Chicago, IL.

Zar, J.H., 1996. Biostatistical Analysis, 3rd Edition. Prentice-Hall, Englewood Cliffs, NJ, p. 662.