Variation in fecundity among different genotypes of cod (Gadus morhua L.)

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Líf- og umhverfisvísindadeild
Háskóli Íslands
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12 eininga ritgerð sem er hluti af
Baccalaureus Scientiarum gráðu í líffræði

Leiðbeinendur
Prof. Guðrún Marteinsdóttir
Dr. Timothy B. Grabowski

Líf- og umhverfisvísindadeild
Verkfræði- og náttúruvísindasvið
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Sími: 525 4000

Skráningarupplýsingar:
Lovísa Ólöf Guðmundsdóttir, 2010, Variation in fecundity among different genotypes of cod (Gadus morhua L.). BS ritgerð, Líf- og umhverfisvísindadeild, Háskóli Íslands, 23 bls.

ABSTRACT

The cod stock around Iceland consists of separate components characterized by different migration behavior, phenotype and genotype. Two kinds of behavior types, deep water behavior and shallow water behavior, have been observed and a significant difference in otoliths indicates an elongated separation between the two groups. These behavior types are connected to the *Pan*-I locus as *Pan*-I^{AA} fish mostly exhibits shallow water behavior, *Pan*-I^{BB} fish mostly exhibits deep water behavior but *Pan*-I^{AB} fish both behavior types. Ovary and oocyte samples from Icelandic cod *Gadus morhua* were collected from eight locations south of Iceland in spring 2009. We used the auto-diametric fecundity method to evaluate the potential fecundity of cod, determined the genotype at the *Pan*-I locus and compared fecundity for different genotypes. We did not find a significant difference between genotypes but our results still suggest a possible variance in fecundity that needs further investigation.

ACKNOWLEGMENTS

I first and foremost would like to thank my instructors, Prof. Guðrún Marteinsdóttir and Dr. Timothy B. Grabowski, for their endless assistance during sampling, data processing and writing of this report. I also want to thank the captain and crew of Ljósafell and Reginn for providing us with fish, Kjartan Árni Albertsson for his assistance with image analyzing, Thor Aspelund and Bruce McAdam for their help with the statistics work and Lísa Anne Libungan and Jónas Páll Jónasson for their help during sampling and writing of this report.

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INTRODUCTION

One of the fundamental aspects of life is reproduction and thus also fecundity. Fecundity refers to an organism's potential reproductive output and is usually defined as the number of offspring per individual (Krebs 2001). Reproductive strategies of fishes have great diversity and environmental adaptations are numerous (Bone & Moore 2007). Most fishes have high potential fecundity but only a small fraction of spawned eggs survive to adulthood due to starvation or predation (Kaiser et al. 2005). In Atlantic cod, as in other marine species, fecundity is highly influenced by numerous factors. Potential fecundity has been shown to be positively correlated to length and weight (Marteinsdóttir et al. 2000; Marteinsdóttir & Begg 2002) and condition has a significant positive effect on both maturation and fecundity as fish in better condition invests more in reproduction than fish in poor condition (Marteinsdóttir & Begg 2002; Kjesbu et al. 1998). These factors also affect the initiation of spawning in cod (Marteinsdóttir & Björnsson 1999; Kjesbu 1994)

Separate components within the cod stock around Iceland have been identified in several studies. The presence of two major groups of north and south have been established on more than one occasion (Jónsdóttir et al. 2006a; Jónsdóttir et al. 2006b, Pampoulie et al. 2006) and a difference between depths has been observed (Pálsson & Þorsteinsson 2003; Jónsdóttir et al. 2006a; Jónsdóttir et al. 2006b; Pampoulie et al. 2006; Pampoulie et al. 2008). The fish seem to differentiate both structurally and behaviorally. Pálsson and Þorsteinsson (2003) observed two main feeding migrations south of Iceland of shallow-water fish that mostly stay above 200 m and deep-water fish that spend much of their time deeper than 200 m. Jónsdóttir et al. (2006) examined otoliths of fish from shallow water (> 125 m) and deep water (< 125 m) south of Iceland and detected a significant difference between the two, indicating a elongated separation between the groups. These two behavior types have now been shown to be connected to the *Pan*-I locus but in a research done by Pampoulie et al. (2008) most of the *Pan*-I^{AA} fish displayed shallow water feeding behavior, *Pan*-I^{BB} fish showed deep water feeding behavior and *Pan*-I^{AB} displayed both behavior types. New research indicates that there is also a significant morphologic difference between genotypess where for example fish carrying the BB allele has greater gaps between their fins than fish carrying the AA allele (McAdam et al. *in prep*). The *Pan* I locus seems to have a complicated relationship with growth and condition. A recent study showed that length-at-age was negatively correlated with genotype frequency which is possibly the effect of size selective fishing (Jónsdóttir et al. 2008). There has also been observed a significant difference in the

condition between different behavior types and genotypes. Cod in deep water (> 200 m) generally has higher hepatosomatic index than shallow water fish (< 200 m) (Pardoe et al. 2008) which is in agreement with another new study where the index was highest for fish carrying the *Pan*-I^{BB} and lowest for the *Pan*-I^{AA} genotype (Jónsdóttir er al. 2008). However, for Fulton´s condition factor the trend was opposite as it was highest for fish carrying the *Pan*-I^{AA} and lowest for the *Pan*-I^{BB} (Jónsdóttir et al. 2008).

In this study our objective was to see if potential fecundity of the Icelandic cod stock is uniform for fish with different *Pan*-I genotype. We focused on fish from different depths south of Iceland. To evaluate potential fecundity we used a combination of the common method of gravimetric counting (Kjesbu & Holm 1994) and a relatively new method which involves photographing the oocytes and measuring their diameter using an image analyzing program (Thorsen & Kjesbu 2001). As condition has been shown to affect fecundity in Atlantic cod (Marteinsdóttir & Begg 2002) and that condition varies with genotype (Jónsdóttir et al. 2008) some difference in fecundity was expected but the effect of the genotype unknown.

MATERIALS AND METHODS

SAMPLE COLLECTION

Ovary samples were taken from Atlantic cod captured at eight locations south of Iceland in spring 2009 by two commercial vessels using trawls and gill nets (Fig. 1). The cod were captured on 9, 10 and 23 March, stored on ice, and worked up within 48 hours of capture.

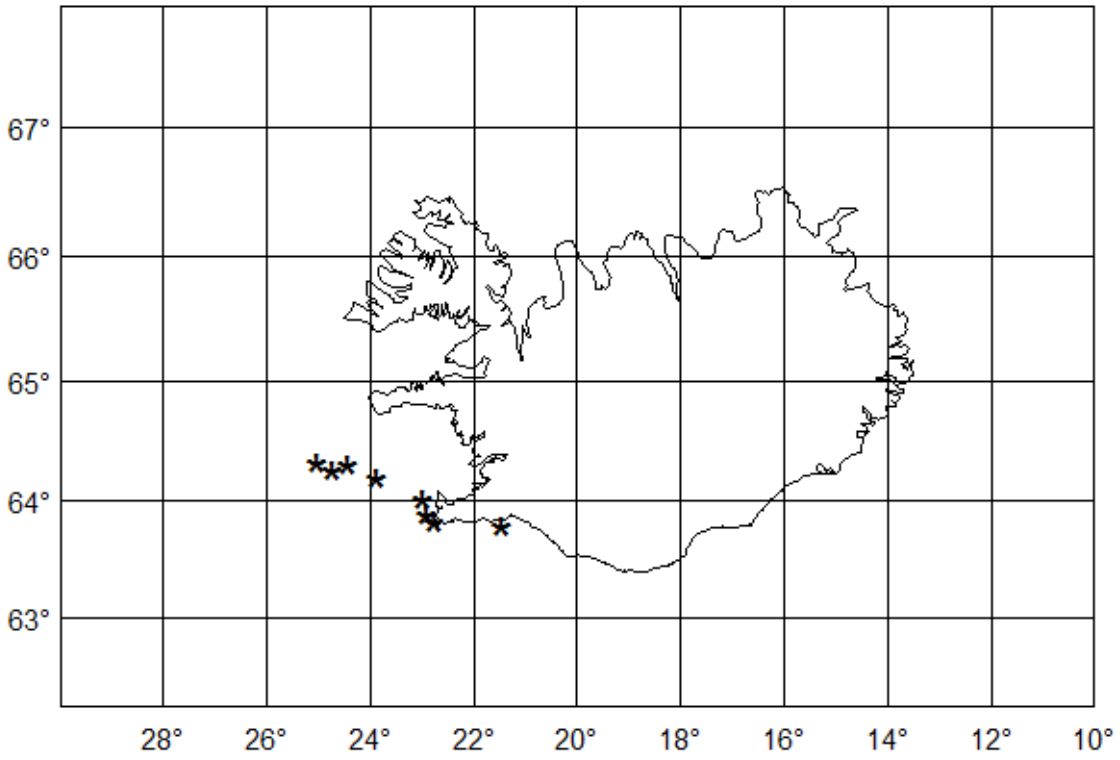

Figure 1. Sampling locations south of Iceland.

Each individual was measured to the nearest cm in total length (TL) and total weight (W), gutted weight (W_{gutted}), liver weight (W_{liver}), and ovary weight (OW) were measured to the nearest gram. Additionally we calculated Fulton's condition factor (K) and the hepatosomatic index (HIS) for each fish.

$$K = \frac{W}{L^3} \times 100 \quad (1)$$

$$HSI = \frac{LW}{W} \quad (2)$$

W is total weight in grams, L is total length in cm and LW is liver weight in grams.

A small ovary sample, approximately 10 g, was taken and fixed in a 3.6% buffered formaldehyde solution. Cod oocytes swell when placed in formaldehyde, but their original diameter could be determined using the following relationship (Svåsand et al. 1996):

$$Fresh\ diameter\ (\mu m) = 19 + 0.947 \times fixed\ diameter\ (\mu m) \quad (3)$$

Additional oocyte subsamples were taken from ten randomly-selected females, weighed to the nearest 0.001g and potential fecundity estimated using the gravimetric method. We counted the oocytes in each of these samples to establish a predictive model of oocyte density (NG) based on oocyte diameter (OD) by combining the NG with the appropriate OD for each female that was found with image analyzing. NG is defined as the number of oocytes in a sample divided by the total weight of that sample. Potential fecundity (PF) was estimated for every individual using NG and OW as described by Thorsen & Kjesbu (2001):

$$F_P = OW(g) \times NG(no./g) \quad (4)$$

A small gill sample was preserved in 95% ethanol and used to determine the genotype at the *Pan* I locus. Genotyping was conducted by Matís (Reykjavik, Iceland) following the protocol described by Pampoulie et al. (2006) but using the primers as described by Nielsen et al. (2007).

MEASURING OOCYTE SIZES

We followed the method described by Thorsen and Kjesbu (2001) to measure oocytes, the auto-diametric fecundity method. Briefly, the oocytes were photographed with an Evolution LC color camera (Media Cybernetics, Bethesda, Maryland, USA) connected to a Leica MZ9.5 binocular microscope (Leica Microsystems, Wetzlar, Germany) under 10x magnification using the image analyzing program, Optimas 6.5 (Media Cybernetics, Bethesda, Maryland, USA). Oocytes were shaken by hand for a few seconds to break them apart, then drawn from the container with a pipette and placed in a petri dish. Special care was taken in spreading the oocytes to avoid clumping so the image analyzing program could identify and measure individual cells. One drop of dishwasher detergent was added to the petri dish to prevent the oocytes from sticking to the water surface. The photos were analyzed with ImageJ (National Institutes of Health, USA, available at http://rsb.info.nih.gov/ij/), a free image processing program. A macro was used to process all photos that measured the area of each oocyte, and exported the results to a spreadsheet. A minimum of 100 oocytes were measured for each

female. Oocyte diameter was then calculated from the oocyte area (OA) using the circle area formula, solved for diameter:

$$OD = 2 \times \sqrt{OA/\pi} \quad (5)$$

DATA ANALYSIS

All data was natural log transformed to meet parametric assumptions. Linear regression was used to evaluate the relationship between OD and NG. This relationship was used to calculate NG for each individual based on OD as determined with image analysis. Remaining statistical analyses were performed with the statistical package R (R Development Core Team 2009), with a critical level of significance set at $\alpha = 0.05$. We used a general linear model to examine the relationship between variability in fecundity and total length, gutted weight, ovary weight, hepatosomatic index and Fulton's conditions factor. The difference in potential fecundity between genotypes was assessed with analysis of covariance (ANCOVA). The fecundity data were assessed as to the minimum number of fish needed to detect any variance in potential fecundity with a specified statistical power. Power (1-β) is the probability of rejecting a null hypothesis when it is false and the alternative hypothesis is correct, where β, the type II error, is the probability of accepting a false null hypothesis (Sokal and Rolf 1995). Determination was made at power of 90% probability of detecting a difference in fecundity.

RESULTS

A total of 80 fish were sampled from the eight locations. Only a single female carried the *Pan*-I^{AA} genotype, 22 carried the *Pan*-I^{AB} genotype, 55 carried the *Pan*-I^{BB} genotype and one could not be decoded. One fish from each genotype had immature oocytes that could not be analyzed. These two fish were therefore not included in the fecundity analysis along with the *Pan*-I^{AA} genotype female and the female that could not be decoded.

Mean potential fecundity did not differ significantly between the *Pan*-I^{AB} (4,418,379 ± 435,890 oocytes per female) and the *Pan*-I^{BB} genotype (4,018,283 ± 242,387 oocytes per female) according to W_{gutted} - HSI model ($F_{3,71} = 1.92$; $P = 0.17$) and TL - HSI model ($F_{3,71} = 55.36$; $P = 0.08$). Due to low sample size and inequality in the relative proportion of the *Pan*-I genotypes, a power test analysis was conducted and suggested that a sample size of 353 fish was needed to detect a difference of approximately 500,000 oocytes between the *Pan*-I^{AB} and

Pan-I^{BB} genotypes with 90% confidence. HSI (μ_{AB} = 0.08, μ_{BB} = 0.09, p=0.231) and K (μ_{AB} = 1.08, μ_{BB} = 1.06, p=0.560) did not differ significantly between the two genotypes.

The oocyte subsamples used for establishing the relationship between oocyte density (NG) and oocyte diameter (OD) ranged from 0.034 grams to 0.160 grams in size and contained 118-694 oocytes per sample. NG showed a strong inverse relationship with OD (Fig. 2; $F_{1,8}$ = 47.8 ; p < 0.001; R^2 = 0.86). A regression formula was used to calculate NG:

$$NG = 2.139 \times 10^{11} \times OD^{-2.638} \quad (6)$$

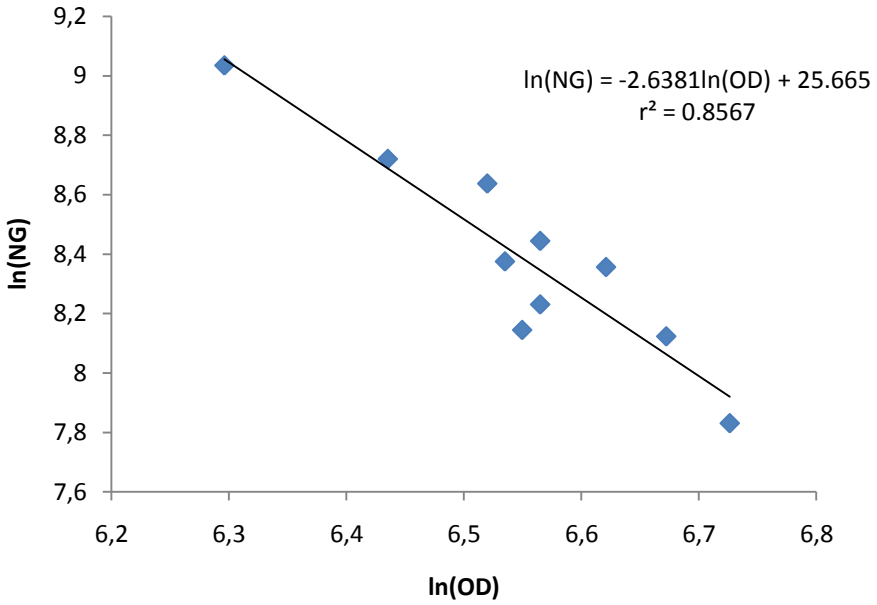

Figure 2. Log transformed oocyte diameter (OD) versus the number of oocytes per gram of ovary (NG).

Number of measured oocytes ranged from 100-475 between females, with an average of 194 ± 8 measured per sample. There was great variance in oocyte size between females with the smallest area measured being 0.057 mm^2 while the biggest was 1.463 mm^2 or a difference of 96.1% total. Oocyte size was also highly varied within females and in the most extreme case ranged from 0.067 mm^2 to 1.463 mm^2. The proportion of connective tissue and immature oocytes in total ovary weight had to be taken into consideration before fecundity could be calculated. This ratio was set to 5% based on previous investigations (Kjesbu & Holm, 1994). Potential fecundity (PF) was calculated for each female once fresh OD and NG was established by combining equations (4) and (6).

$$PF = OW(g) \times NG(no./g) \quad (4)$$

$$NG = 2.139 \times 10^{11} \times OD^{-2.638} \quad (6)$$

$$PF = OW(g) \times 2.139 \times 10^{11} \times OD^{-2.638} \quad (7)$$

Fecundity estimations using the gravimetric method were in good agreement with potential fecundity estimated with the auto-diametric fecundity method. Potential fecundity found with the auto-diametric fecundity was consistently higher than the estimated using the gravimetric method (table 1) but the correlation between the two was still very high (r^2=0,891) (figure 3).

Table 1. Potential fecundity estimated with gravimetric method and auto-diametric fecundity method. OW is ovary weight in grams, NG is number of oocytes per gram of ovary and OD is oocyte diameter in micrometers.

	Potential fecundity (PF) no. of oocytes	
	Gravimetric method	*Auto-diametric fecundity method*
Fish nr.	$PF = OW(g) \times NG(no./g)$	$PF = OW(g) \times 2.139 \times 10^{11} \times OD^{-2.638}$
1	*5,619,455*	*7,230,066*
2	*4,410,274*	*7,565,663*
3	*3,587,529*	*4,970,802*
4	*7,146,513*	*9,324,615*
5	*2,566,111*	*4,995,461*
6	*7,530,596*	*11,753,195*
7	*3,747,158*	*5,549,135*
8	*2,809,241*	*4,694,163*
9	*5,394,286*	*7,761,650*
10	*4,476,300*	*7,192,116*

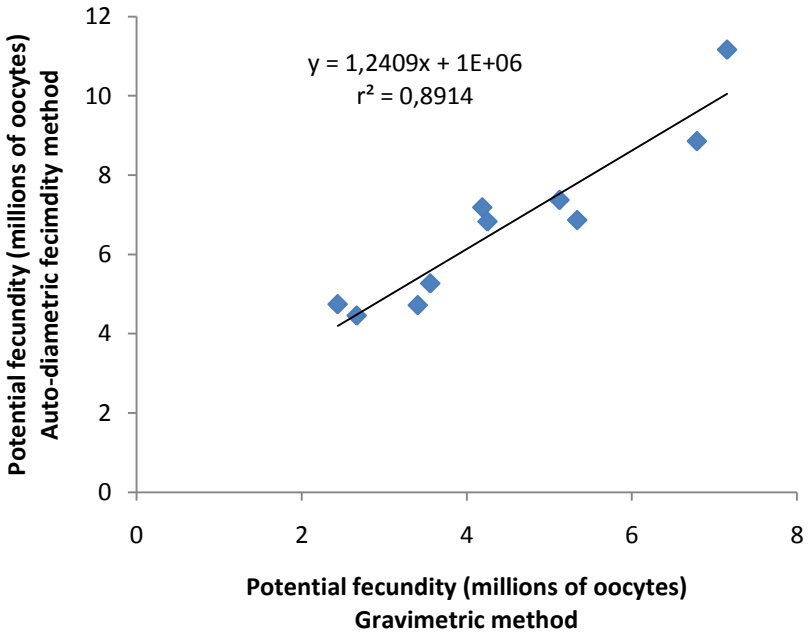

Figure 3. The relationship between fecundity using the gravimetric method and the auto-diametric fecundity method.

Potential fecundity ranged from 0.44 to 8.53 million oocytes with an average of 4,130,310 ± 212,394, for all females combined. Gutted weight was the best predictor of PF, explaining 82% of the total variation in fecundity for the *Pan*-I^{AB} genotype fish and 80% for the *Pan*-I^{BB} genotype fish. Total length was also a strong predictor, explaining 44% of the variation in fecundity for the *Pan*-I^{AB} genotype and 65% of the variation for the *Pan*-I^{BB} genotype. HSI did not have as strong relationship with fecundity with the coefficient of determination only 0.08 for the combined groups of AB and BB. A few different models were used to analyze the fecundity and the difference between genotypes. A linear model with two variables, W_{gutted} and *Pan* genotype, explained 81% of the total variation in fecundity but failed to find a significant difference in fecundity between the two genotypes ($p = 0.43$). Including HSI in the model resulted in an improvement of the model, increasing the explained variation of PF relationship by 3.69%. This improvement turned out to be significant with ($p < 0.001$) but the difference in fecundity between the genotypes was still not significant ($p = 0.17$). A model with TL and the *Pan* genotype explained 61% of the variability in fecundity but difference in fecundity between genotypes was not significant ($p = 0.27$). Adding HSI to the model resulted in a significant improvement of 8.56 % ($p < 0.001$) but still did not show a significant difference in fecundity between genotypes ($p = 0.08$).

Table 2. Regression equations for potential fecundity (PF) on weight (W), gutted weight (W_{gutted}), hepatosomatic index (HSI) and Fulton's condition factor (K).

	Regression equation	**n**	**r^2**	**P**
Weight (g)				
AB	PF = 42.17*W^1.29	21	0.81	< 0.001
BB	PF = 14.10*W^1.40	54	0.80	< 0.001
AB & BB	PF = 17.99*W^1.37	75	0.80	< 0.001
Gutted weight				
AB	PF = 17.48*W_{gutted}^1.43	21	0.82	< 0.001
BB	PF = 8.89*W_{gutted}^1.50	54	0.80	< 0.001
AB & BB	PF = 10.11*W_{gutted}^1.49	75	0.80	< 0.001
Total length				
AB	PF = 0.19*TL^3.77	21	0.74	< 0.001
BB	PF = 0.03*TL^4.16	54	0.58	< 0.001
AB & BB	PF = 0.05*TL^4.05	75	0.61	< 0.001
Hepatosomatic index				
AB	PF = 4.11*10^6*HSI^0.01	21	5.28*10^-5	0.975
BB	PF = 2.5*10^7*HSI^0.80	54	0.15	< 0.01
AB & BB	PF=1,56*10^7*HSI^0.590	75	0.08	< 0.05
Fulton's condition factor				
AB	PF = 3.90*10^6*K^0.27	21	0.01	0.638
BB	PF = 3.25*10^6*K^1.83	54	0.27	< 0.001
AB & BB	PF = 3.42*10^6*K^1.29	75	0.16	< 0.001

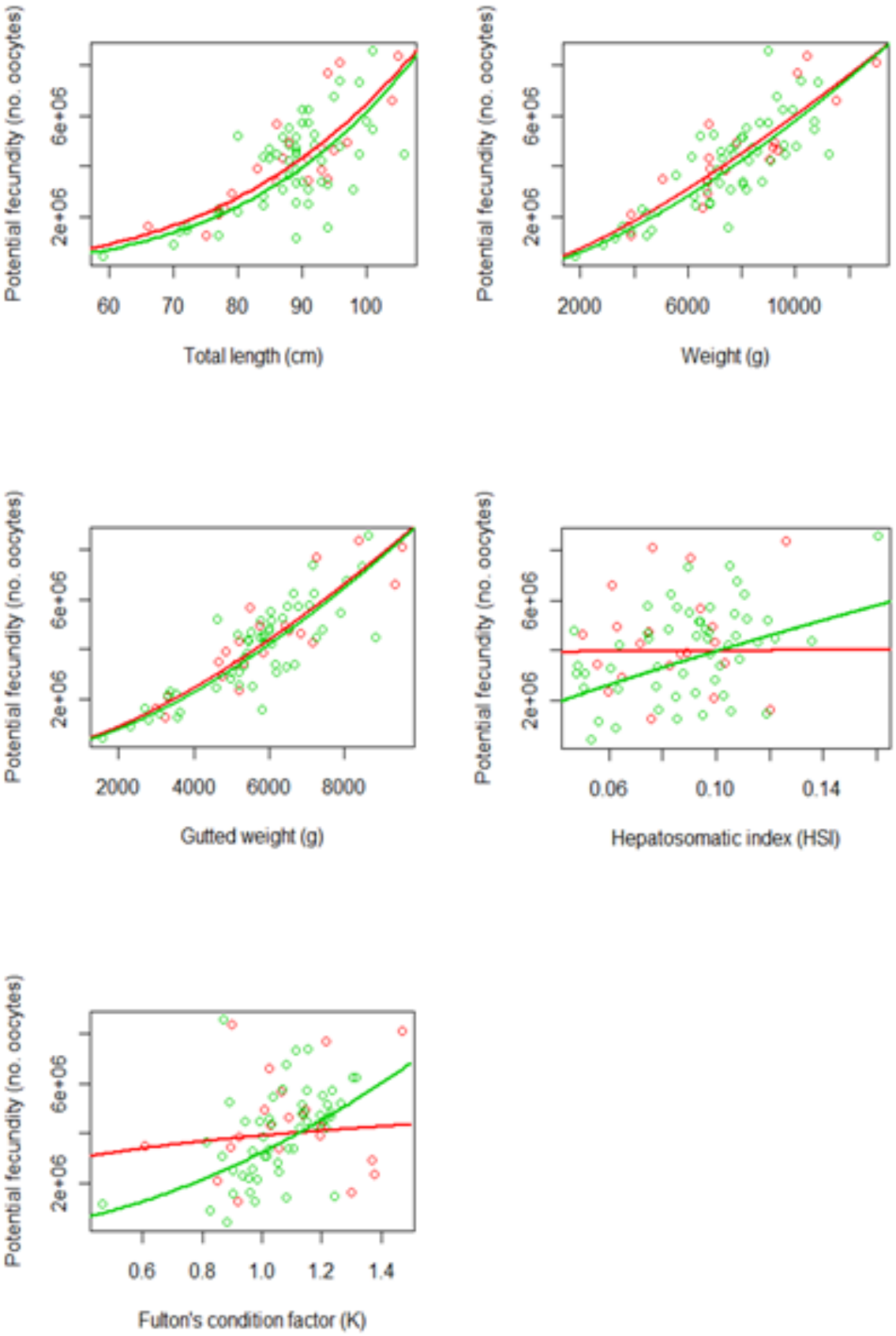

Figure 4. Potential fecundity's correlation with weight, gutted weight, length, hepatosomatic index and Fulton's condition factor. The Pan-I^{AB} fish is red but the Pan-I^{BB} fish green.

DISCUSSION

Potential fecundity did not differ significantly for the two genotypes acquired and we did not find a significant difference in condition. This may have been partially because of the small sample size. The TL-HSI model was marginally significant with a p-value of 0.08 while the W_{gutted}-HSI model had a p-value of 0.17 but instead had a higher explanatory value. We found regression equations for fecundity and various factors amidst length. When the slopes of the fecundity-length equations for the two different genotypes were compared there was an obvious difference. This difference did not turn out to be significant ($F_{3,71} = 37.98$, $p = 0.64$) but might nonetheless be an indicator of variability in fecundity between the two genotypes. When compared to Marteinsdottir and Beggs (2002) results we see a similar trend for relative fecundity and total length (fig. 5). The AB genotype had slightly higher relative fecundity-at-length than the BB genotype but both genotypes had a significant relationship with length ($p_{AB} = 0.01$, $p_{BB} = 0.02$). Nonetheless we did not see as a highly significant relationship as Marteinsdottir and Begg did.

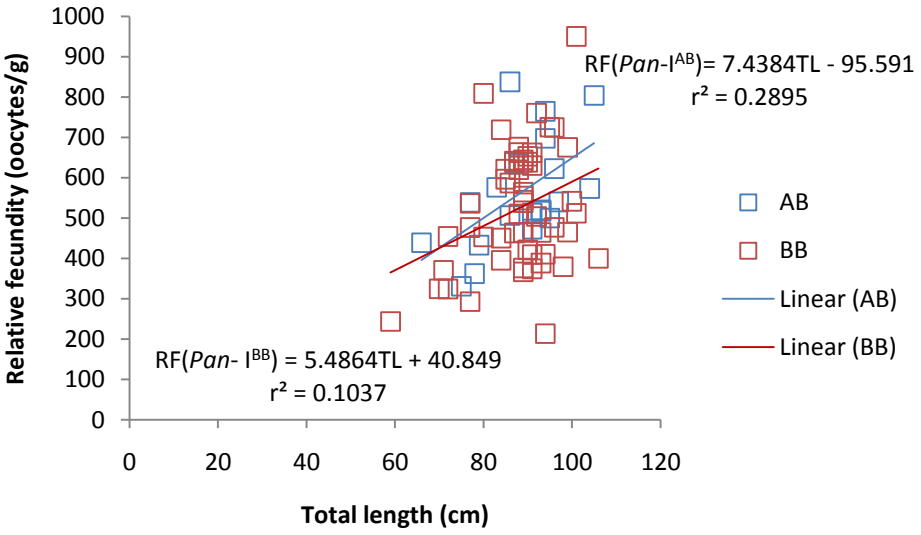

Figure 5. Relative fecundity (RF) of cod.

Estimated relative fecundity (RF) for fish of standard size (70, 90 and 120 cm) for the two genotypes in 2009 is similar to the results of Marteinsdóttir and Begg (2002) from 1995-2000. The estimated RF for a 70 cm fish is slightly lower in 2009 than the average of the years 1995-2000, about the same for a 90 cm fish and a bit higher for a 120 cm fish.

Table 3. Regression equations for relative fecundity (RF) on female length (L) for Pan-I^{AB} and Pan-I^{BB} genotypes from 2009 and regression equations from Marteinsdóttir and Begg (2002). Estimated relative fecundity for a standard fish, 70, 90 and 120 cm long.

Genotype	***Regression***	***r^2***	***P***	***RF-70***	***RF-90***	***RF-120***
Pan-I^{AB}	*RF = 7.4 x TL – 95.6*	*0.29*	*0.01*	*425*	*574*	*796*
Pan-I^{BB}	*RF = 5.5 x TL + 40.8*	*0.10*	*0.02*	*425*	*534*	*699*
1995	*RF = 4.8 x TL + 91.2*	*0.20*	*< 0.001*	*427*	*523*	*667*
1996	*RF = 4.6 x TL + 184.7*	*0.23*	*< 0.001*	*507*	*599*	*737*
1997	*RF = 5.5 x TL – 8.4*	*0.14*	*< 0.001*	*377*	*486*	*652*
1998	*RF = 8.3 x TL – 200.2*	*0.38*	*< 0.001*	*381*	*547*	*796*
1999	*RF = 4.5 x TL + 258.6*	*0.19*	*< 0.001*	*574*	*664*	*799*
2000	*RF = 5.1 x TL + 1.68.6*	*0.21*	*< 0.001*	*525*	*628*	*781*

Numbers of studies have explored the structure of the cod populations around Iceland. These studies have identified local populations with different life history (Pálsson & Þorsteinsson 2003; Jónsdóttir et al. 2006a; Jónsdóttir et al. 2006b) and a genetic variance that can be used as an indicator of different behavior types (Pampoulie et al. 2006; Pampoulie et al. 2008). In our study the fish was caught at different depths in hope of getting different behavior types and genotypes but frequency of the B allele at the *Pan*-I locus has been shown to increase with depth (Pampoulie et al. 2006). Unfortunately, we only got one fish with the *Pan*-I^{AA} genotype so this group could not be included in the fecundity analysis. The two remaining groups of *Pan*-I^{AB} genotype and *Pan*-I^{BB} genotype did not turn out to have a significant difference in potential fecundity (P = 0.17). As the AB genotype has been known to show both types of feeding behavior it is possible that our fish was all from same behavior type, presumably the deep water behavior. This might explain why we failed to find significant difference in fecundity. If the fish were however from different behavior groups the results of our study indicate that in spite of potentially different life histories it does not seem to influence fecundity.

In our study we used the relatively newly described auto-diametric fecundity method (Thorsen & Kjesbu 2001). It is a rapid way to estimate fecundity for a high number of samples and does not rely on accurate subsample weighing like the widely used gravimetric method. It also has the advantage over the gravimetric method that sampling can be done at sea where accurate measuring would not be possible and the accuracy of pre-weighed bottles would be jeopardized by the smallest leakage or evaporation (Thorsen & Kjesbu 2001). The biggest disadvantage is the standardization it requires. The oocyte diameter is negatively correlated with the light density of the background light and fixation can affect roundness (Thorsen & Kjesbu, 2001). These factors should not have affected our main results as fixation and light settings were identical for all samples. The Atlantic cod is multiple batch-spawner with oocytes of different growth phases present at each time (Tomkiewicz et al. 2003). As expected we did observe high variance in size or up to 95% difference. Earlier research had suggested that oocyte size distribution is homogeneous in cod ovaries (Kjesbu & Holm, 1994) justifying photographing of only a small random sample for each fish like we did.

The strong relationship between oocyte density (NG) and oocyte diameter (OD) has been established for Atlantic cod on several occasions (Thorsen & Kjesbu 2001; Klibansky & Juanes 2008; Alanso-Fernández et al. 2009). The observed correlation was therefore as expected. This relationship is the key regression in the use of the auto-diametric fecundity method. Weight, length and condition were positively correlated with fecundity. These results are in agreement with previous studies on the effect of these factors on fecundity (Marteinsdóttir & Begg 2002).

Recently there has been some research done on the function of the *Pan* I locus and the way the environment affects it. It´s role is not fully understood but we do know that the *Pan* I^A and the *Pan* I^B alleles differ on a nucleotide level and protein level (Pogson 2001). How environmental factors affect the selection of the *Pan* I locus is not known but it is clear that it is under a strong Darwinian selection (Pogson 2001; Pogson & Mesa, 2004). People have speculated how this selection may affect the stock structure. In a recent paper Jónsdóttir et al. (2008) reports higher growth rates for the least frequent genotype in both north and south and a significant difference in condition between the genotypes. She conjectures that this is possibly due to size-selective fishing as the fish that has the highest length-at-age is removed first. Árnason et al. (2009) state that selective pressure is most certainly due to habitat-specific fishing mortality and it will lead to a collapse of the population and fishery. Maturation at a smaller size and higher fecundity-at-length than before has no also been observed (Yoneda &

Wright 2004). They found that the slope of the fecundity-length relationship had increased from the 1970' to recent years and that there was negative relationship between the intercept and the slope. Our fecundity-length relationship was consistent with their results but our slope of 4.05 and intercept of 4.89×10^{-2} is similar their recent year regressions. This change in fecundity-length relationships is possibly due to size selective fishing (Yoneda & Wright 2004).

Although this study failed to find a significant difference in fecundity between the obtained genotypes our results strongly suggest that further research is necessary. Bigger sample size from deep and shallow water is needed and ideally also samples from north and south. Fecundity is plainly an important factor of stock recruitment. If the separate populations of cod do in fact have significantly different potential fecundity it can be a crucial factor in management but now the cod stock is managed as a single unit. Speculations like these can only be answered with extended research combined with the knowledge already at hand.

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