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Gender-specific responses of mature Atlantic cod (*Gadus morhua* L.) to feed deprivation

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ABSTRACT

Atlantic cod (*Gadus morhua* L.) is one of the most important commercial fish species in Norway and the peak fishing season coincides with spawning from January to April. Live-storage of cod may extend the marketing season for fresh cod products. Cod can be held for up to 12 weeks after capture, and current regulations allow the fish to be held without feeding for four weeks. We investigated whether the response to long-term feed deprivation differed between mature males and females. The fish, caught off Andenes (Norway) in March 2015 using Danish seine, were held without feeding for 82 days, and samples were taken 2, 26, 54 and 82 days after capture. At each sampling, the weights of whole and gutted fish (head on), liver and gonads were measured. Additionally, fillet protein concentrations were analysed. Females lost total weight, gutted weight and liver mass more rapidly than males, but the reduction in gonad mass was significantly higher in males than in females. At termination, after 82 days, fillet protein concentration in males was higher (16.3% ± 0.4) than in females (14.9% ± 0.4). With regard to loss of gutted weight and reduction in muscle protein concentration, the tolerable fasting period of mature spawning Atlantic cod of good biological condition is 54 days, but this can vary depending on upon the initial condition of the fish

1. Introduction

Atlantic cod (*Gadus morhua* L.) is one of the most important commercial species in Norway with seasonal supplies being linked to the annual spawning cycle. Northeast Atlantic cod migrate from feeding areas in the Barents Sea to the Norwegian coast to spawn, and spawning occurs from the end of January to April/May (Nordeide and Båmstedt, 1998; Brander, 2005). Most cod are caught during the first five months of the year and the supply of fresh cod is limited for the remainder of the year. Extending the season through live-storage could create new possibilities for marketing fresh cod products.

Atlantic cod display natural seasonal variations in weight and condition related to fish size, seasonal feeding patterns and spawning (Fordham and Trippel, 1999; Schwalme and Chouinard, 1999; Mello and Rose, 2005), with somatic weight and condition usually decreasing during maturation and spawning. Cod is a lean fish and the liver is the main organ for energy storage in the form of lipids (Love, 1988). Variations in liver weight can be linked to food supply (Black and Love, 1986; Jobling et al., 1991), and if the fish are deprived of food, liver lipids are mobilized and used as an energy source. Muscle tissue, primarily muscle protein, is also mobilised (Black and Love, 1986).

Most Atlantic cod taken in the Norwegian coastal fisheries are caught in spring during the spawning season. Norwegian regulations (FOR-2004-12-22-1878, 2004) allow wild-caught fish to be held in sea cages for up to 12 weeks, with an initial four weeks without feeding. It is currently unknown what implications these regulations have for the welfare of the live fish and fillet quality after slaughter. Consequently, it is of interest to investigate changes that occur when mature cod are held without food for several weeks, and to examine whether there are gender-specific differences. At present, little is known about how the nutritional status of females and males affects mobilization and utilization of energy reserves during feed deprivation.

The objective of the present study was to investigate whether mature female and male Atlantic cod differ in their responses to feed deprivation during the spawning and post-spawning periods.

2. Materials and methods

2.1. Capture and handling procedures

The work was carried out in compliance with Norwegian laws and regulations relating to animal welfare, and was approved by veterinary authorities (Code number: 7327).

Atlantic cod were caught on 18 March 2015 on the Røra fishing ground (69.3° N, 15.6° W) off the coast of Andenes, Norway, using Danish seine. The captured fish (ca 10 t) were hauled from a depth of 100–130 m at an initial speed of 1.6 ms^{-1} followed by 0.7 ms^{-1}. They were transferred to a sea cage (70 m diameter Polar circle pen) at Bjarkøy (Troms) within a day of capture. Following seven days of recovery, the fish were transported by well-boat to the Aquaculture Re-

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search station (Skulgambukt, Tromsø). On 26 March 400 cod were transferred to the onshore facility at Kraknes, Tromsø. The next day the fish were tagged with external T-Bar Anchor Tags (FD-68B, Floy Tag & Manufacturing Inc., Seattle, WA, USA) under anaesthesia (MS 222, 0.1 mg L^{-1}), weighed and length measured. Then, the fish were distributed equally between two indoor tanks (4 m diameter, total volume 20 000 L) with flow-through seawater at 4.0–5.6 °C and 81–100% oxygen saturation. The fish were then held without feeding for the remaining 73 days of the trial. A natural photoperiod regime was used throughout the trial.

2.2. Sampling procedures

Twenty five fish were sampled from the sea cage at Bjarkøy 2 days after capture. The fish were killed, weighed, measured and dissected. Then, the sex and weights of gutted fish (head-on) liver and gonads were recorded, and the gastro-intestinal tract of each fish was examined for the presence of food remains. After transfer to the onshore site at Kraknes, 60 fish were sampled on days 26, 54 and 82 after capture (Table 1). At slaughter, 30 fish were taken at random from each tank and stunned by a blow to the head. Next, total weight and length were measured and individuals were identified by reading their tag number. The fish were then exsanguinated by cutting the ventral and dorsal aorta followed by bleeding for 30 min in a container (600 L) with running seawater (~ 5 °C). Following gutting, the sex, weight of liver, gonads and gutted fish (head-on) were recorded, and the gastro-intestinal tract was checked for the presence of remnants of prey. The weights of gonads and liver were used to calculate the gonadosomatic index (GSI) and hepatosomatic index (HSI) as a percentage of total body weight (Table 1).

The fish were then packed in plastic boxes containing ice (8–10 kg ice per 16–18 kg fish), transported to Nofima, Tromsø (approx. 35 min by road), filleted and skinned. The loin from each fillet (~500 g) was put in a zipper bag (300 × 400 mm) and frozen at −30 °C until analysed for protein concentration.

2.3. Protein content in fillet

Fillet samples were analysed for females and males subjected to food deprivation for 2 (♀ = 5; ♂ = 5), 56 (♀ = 10; ♂ = 10) and 82 days (♀ = 10; ♂ = 10). Protein concentration was determined from nitrogen (N × 6.25) using the AOAC Official Method 981.10 (AOAC, 1983) with minor modifications. Prior to analysis, approximately 200 g from each frozen loin was thawed (1 °C, 18 h) and minced (3 × 1 min) using a handheld mixer BRAUN Multimix (Type 4642, Spain). Then three technical replicates of each mince were mixed with 15 mL 95–97% sulphuric acid and copper catalyst added. The samples were then analysed using a Tecator Digestor model 2020 and distilling unit 2300 (Foss Analytical, Hillerød, Denmark).

2.4. Calculations and statistical analysis

Relative weight (RW) and relative length (RL) were determined to explore the changes in fish length and weight during feed deprivation (Table 2). The values were calculated by dividing an individual's length and weight at the time of sampling by values obtained for the same individual at the time it was tagged. A two-sample *t*-test was used to examine for differences in RW and RL between females and males at each time of sampling and one-way ANOVA was used to investigate whether there were differences within a sex over time (Appendix A, Table A.1 in Supplementary material). RL did not change with time so calculation relating to changes in fish and organ weight were based on a standardized body length 90 cm; this represents the average body length of females and males used in the experiment (Table 1). Calculations were carried out using regression analysis with data being log-transformed prior to analysis.

In studies with an allometric scaling component, as was the case here, analyses are often carried out using linear regression following logarithmic transformation of the data (Peters, 1983; Schmidt-Nielsen, 1984; Reiss, 1989). Ordinary Least Square (OLS) regression was used to analyze data collected for females and males at different times after the onset of feed deprivation (Appendix A, Tables A.2–A.5 in Supplementary material). The regression line is ln Weight metric = ln a + b * ln Length, where the weight metric refers to total body weight, gutted weight, liver weight or gonad weight. The OLS estimates of ln a (intercept) and b (slope) minimize the sum of squared deviations (SS) between observed and predicted values (Quinn and Keough, 2002), and once the estimates are known, predictions can be made for a fish of a standardized length (90 cm).

Analysis of covariance (ANCOVA) was used to compare regressions for weight metrics for the sexes at each sampling time; sex was used as the categorical predictor variable (factor) and length as the covariate. ANCOVA was also used to examine changes in the metrics for each sex over time; in these analyses the categorical predictor variable was days since capture. The Tukey post-hoc test was used to identify where there were significant changes in the response variables.

Table 1
Biological data of experimental fish sampled at different times during feed deprivation.

Sampling	Food deprivation							
	2 days		26 days		54 days		82 days	
Sex	♀	♂	♀	♂	♀	♂	♀	♂
N	10	15	21	39	20	40	20	40
Body weight (g)	6730 ± 471	6881 ± 641	6543 ± 340	6048 ± 284	5827 ± 309	5506 ± 218	4772 ± 311	4914 ± 256
range	4780–9400	3140–11340	3452–10106	2708–9640	2902–8024	2738–8626	2474–7342	2168–8094
Body length (cm)	91.3 ± 2.2	90.1 ± 2.6	91.9 ± 1.6	89.2 ± 1.3	92.7 ± 1.9	89.4 ± 1.2	89.1 ± 1.9	87.3 ± 1.4
range	79–102	74–103	75–104	72–104	75–104	66–99	70–104	67–104
HSI[a]	5.4 ± 0.6	4.7 ± 0.5	6.1 ± 0.4	4.3 ± 0.3	5.6 ± 0.5	4.1 ± 0.3	2.8 ± 0.3	3.1 ± 0.3
range	1.3–8.4	1.3–7.3	1.5–8.9	0.9–8.9	1.6–10.9	1.2–11.6	0.8–5.0	0.8–7.6
GSI[b]	13.8 ± 2.1	12.7 ± 0.9	7.7 ± 1.0	5.6 ± 0.6	2.0 ± 0.1	1.8 ± 0.4	1.8 ± 0.1	1.1 ± 0.2
range	1.8–24.6	7.9–18.7	1.9–18.2	0.9–13.9	1.4–2.7	0.5–11.1	0.5–2.8	0.2–5.8

(Mean ± SE of mean).

[a] HSI (Hepatosomatic index) = (liver weight/body weight) × 100.

[b] GSI (Gonadosomatic index) = (gonad weight/body weight) × 100.

Table 2
Relative weight (RW) and relative length (RL) of fish used in the trial, from the tagging day to the time of sampling.

	Number	Days since tagging	RW	RL
Males	38	17	0.896 ± 0.008	1.001 ± 0.005
	40	45	0.787 ± 0.013	0.992 ± 0.004
	40	73	0.753 ± 0.006	1.001 ± 0.004
Females	21	17	0.812 ± 0.002	0.997 ± 0.002
	20	45	0.728 ± 0.006	1.001 ± 0.006
	20	73	0.702 ± 0.003	0.993 ± 0.003

A two-sample *t*-test was used to examine for differences in protein concentration between females and males within the sampling times and one-way ANOVA was used to explore for differences within a sex over time (Appendix A, Table A.7 in Supplementary material).

3. Results

There was a wide range of fish sizes in each sample (Table 1) since the fish were not size-sorted prior to the trial. On the tagging day, the body weights of sampled fish varied from 2818 g to 11378 g, and length varied from 70 to 104 cm. The numbers of sampled males exceeded that of females, but it is not known whether this is representative for the population as a whole. None of the fish that were examined during the course of the trial had food remains in the gastro-intestinal tract.

At the first sampling, 2 days after capture, there were no significant differences in the total weight-length relationships between the sexes ($F(1, 22) = 0.4$; $p = 0.510$) (Fig. 1A), but relationships for gutted weights were significantly different ($F(1, 22) = 15.81$; $p = 0.001$) (Fig. 1B). For any given body length the gutted weight of a male was greater than that of a female. When fish were sampled at the end of the trial, 82 days after capture, males had higher total weights ($F(1, 57) = 5.7$; $p = 0.02$) and gutted weights ($F(1, 57) = 6.92$; $p = 0.016$) than females of the same length (Fig. 1C, D).

Relative weight (RW) decreased over time and the decrease was significantly greater for females than males (Table 2, Appendix A, Table A.1 in Supplementary material). On the other hand, there was no evidence that relative length (RL) changed over time. The results indicate that, during the experiment, each individual decreased in body mass while the body length was stable. This confirms the validity of reference to a fish of standardized length (90 cm) for presentation and comparison of weight metrics of mature male and female cod.

The changes in the weights of liver, gonads, total and gutted weights over time are presented for fish of standardized length (90 cm) (Fig. 2). In the initial sample (March 20), the estimated total weight of 90 cm females (6397 g) appeared to be slightly lower than that of males (6551 g), and the weights of gonads and livers seemed to be higher in females (950 g and 358 g) than in males (812 g and 281 g). There were, however, no significant differences between the sexes for any of these weight metrics at the start of the trial, but the gutted weight of females (4568 g) was significantly lower than that of males (4981 g) (Appendix A, Tables A.2–A.6 in Supplementary material; Figs. 1 and 2).

During feed deprivation, both females and males decreased in total weight and on the last day of sampling the body weight of 90 cm females (4776 g) was significantly lower than that of males (5159 g) of the same length (Figs. 1C and 2). Body weight loss during the first 54 days was linked to a substantial reduction in the size of the gonads of both sexes (Fig. 2) with gonad depletion being significantly higher in males than in females ($F(1, 53) = 63.904$; $p = 0.000$). Significant differences between the sexes for gonad weight were also detected in fish that had been deprived of food for 82 days ($F(1, 55) = 11.397$; $p = 0.001$).

A slight decline in liver weight was evident during the first 54 days of feed deprivation but was more pronounced during the last 28 days of the trial (Fig. 2). Weight of gutted fish (head-on) decreased with prolonged feed deprivation (Fig. 2) with the gutted weight of females being significantly lower than that of males at the end of the trial ($F(1, 57) = 6.917$; $p = 0.016$).

Muscle protein concentrations were similar at the start of the trial (females: 17.4% ± 0.2; males: 17.4% ± 0.5) (Fig. 3). In males, protein concentration was stable for 54 days of food deprivation, but protein concentration in females decreased, leading to significantly lower protein concentrations in females (16.5% ± 0.3) than in males

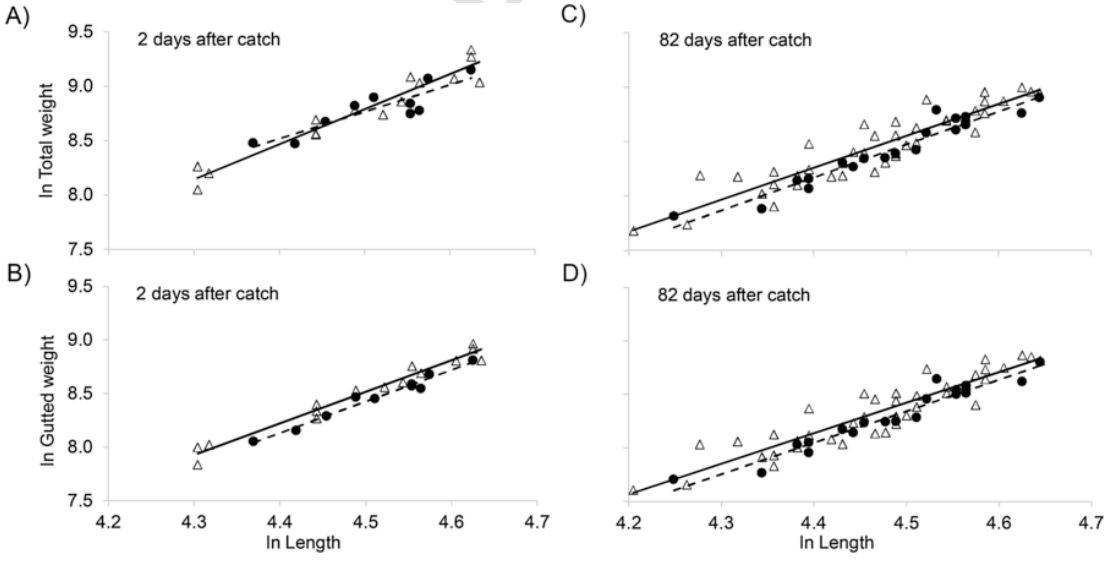

Fig. 1. The relationships between log-transformed total (ln Total weight) and gutted (ln Gutted weight) weights and body length (ln Length) for females (●) and males (Δ) on days 2 and 82 after capture. The ln Length of 4.5 is equivalent to fish with body length 90 cm. Information about regression and statistical comparisons is given in Supplementary data (Appendix A, Tables A.2 and A.3).

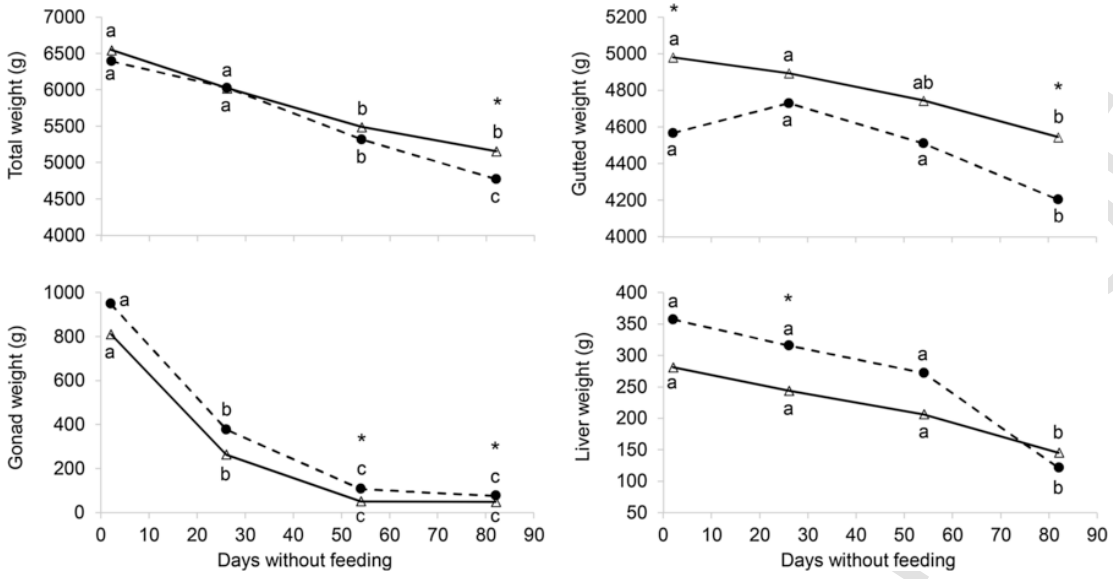

Fig. 2. Changes in predicted total and gutted weights, the weights of gonads and livers in mature female (●) and male (Δ) Atlantic cod of standardised length 90 cm during 82 days of feed deprivation. Lower case letters indicate significant differences ($p < 0.05$) between sample days within sexes, and asterisks (* = $p < 0.05$) show the significant differences between sexes on a given sampling date.

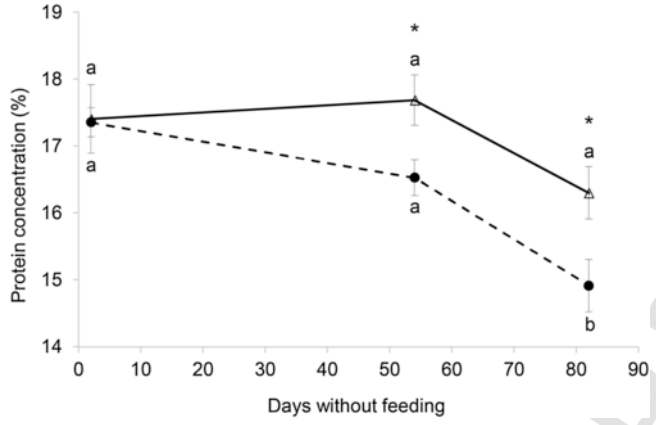

Fig. 3. Changes in muscle protein concentration of mature female (●) and male (Δ) Atlantic cod during live-storage for 82 days without feeding. Lower case letters indicate differences ($p < 0.05$) between sample days within sexes, and asterisks (* = $p < 0.05$) show the significant differences between sexes on a given day of sampling.

(17.7% ± 0.4) ($F(1, 18) = 6.306$; $p = 0.022$). The differences between the sexes increased thereafter and on the final day of sampling the protein concentration in females was 14.9% ± 0.4 and 16.3% ± 0.4 in males.

4. Discussion

The fish used in the trial were sexually mature and in good condition, based on assessment of GSI and HSI (Table 1). HSI can be used to assess the nutritional status of fish species that store energy in the liver (Jobling, 1988; Hemre et al., 1993). RW decreased in the absence of the food but RL was stable (Table 2), and this formed the basis for comparisons based on fish of standardized length (90 cm) (Fig. 2). A lack of change in body length in spawning cod was also registered by Rakitin et al. (2001) and Fordham and Trippel (1999).

There were no significant differences between male and female cod regarding size of gonads and livers at the start of the trial even though the livers and gonads of females tended to be larger (Fig. 2). Given the knowledge about the differences between the sexes in growth and maturation (Love, 1988; Karlsen et al., 1995), the mature female cod would have been expected to have larger livers and gonads than the males.

Although individual organ sizes did not differ significantly between the males and the females, the tendency for the liver and gonads of the females to be larger had an overall effect on gutted weights. At the start of the trial, the gutted weights of the males were larger than those of females of the same body length (Figs. 1B and 2).

Females responded differently to feed deprivation than males. Females lost more body weight and much of the weight loss occurred during the first 54 days of the trial (Fig. 2). During this period, the weight loss was linked mainly to a reduction in the size of the gonads in both sexes (Fig. 2). Mating behavior was observed during the sampling carried out after 26 days of feed deprivation, with some males and females swimming with their urogenital openings closely aligned (Brawn, 1961; Hutchings et al., 1999). The fish used in the trial were caught in March, partway through the spawning season (Nordeide and Båmstedt, 1998; Brander, 2005), so the fish were probably spawning actively during the first few weeks of the trial.

Gonad size varied considerable both over time and within a given sample (Table 1). A possible explanation for this could be related to a combination of the Atlantic cod being a multiple batch spawner (Kjesbu, 1989; Jobling and Pedersen, 1995; Rakitin et al., 2001) and that individual fish were in different phases of spawning at the time of capture and sampling. As a result of being batch spawners females can exhibit different stages of egg ripening during the spawning season. Males tend to be in spawning condition for a longer period than females (Hutchings and Myers, 1993).

During extended periods of feed deprivation, the nutritional reserves of fish become depleted. The liver is a major organ for energy storage in cod and liver size is related to feed intake and HSI can, therefore, provide an indication of the nutritional status of the fish (Black and Love, 1986; Jobling et al., 1991). During feed deprivation there is mobilization of liver reserves (Table 1; Fig. 2) along with white muscle glycogen, and these gradually become depleted (Black and Love, 1986). Thereafter, muscle proteins become increasing uti-

lized to supply energy needs. Our findings indicate that energy was taken from both the liver and muscle in both sexes. The latter is demonstrated in the form of both a reduction in gutted body weight (Figs. 1B, D and 2) and muscle protein concentration (Fig. 3). Reliance on protein as an energy source increased as time progressed. In addition, sexual dimorphism became obvious after 54 days of feed deprivation when females had lower muscle protein concentrations than males, and differences increased towards the end of the trial (Fig. 3). These results concur with those of Hagen and Solberg (2010) who reported decreased protein concentration in the muscle of farmed cod that had been deprived of food for 11 weeks.

Patterns of feeding, growth, metabolism and energy storage in cod vary during the course of a year (Eliassen and Vahl, 1982a; Eliassen and Vahl, 1982b; Love, 1988; Fordham and Trippel, 1999; Schwalme and Chouinard, 1999; Solberg and Willumsen, 2008). For example, Solberg and Willumsen (2008) reported that farmed cod of both sexes decreased in body weight between February and April despite being fed to satiation. Female cod exhibited a reduction in gutted weight, and females lost more muscle protein than males. According to Fordham and Trippel (1999) both sexes show little interest in food at the start of the spawning season, but towards the end of spawning, the fish begin to feed, with males consuming less than females. On the other hand, there is evidence that wild cod do feed whilst on the spawning grounds (Michalsen et al., 2008; Krumsick and Rose, 2012) although there is uncertainty about whether it is males or females that are most prone to feed. Michalsen et al. (2008) reported fewer empty stomachs, and greater levels of stomach fullness, in females than males, whereas Krumsick and Rose (2012) concluded that females ate less than males. In our study, none of the fish examined 2 days after capture had food remains in their gastro-intestinal tract, and the fish were deprived of food thereafter. This may provide an explanation for the reduction in gutted weight seen during spawning in both sexes and the greater reduction in muscle protein concentration seen in the feed-deprived females towards the end of our study.

When summarizing our results, it appears that feed deprivation affects mature female cod to a greater degree than males. When viewed from the perspective of reductions in gutted weight and muscle protein concentration, the tolerable fasting period for Atlantic cod during spawning and post-spawning is approximately 54 days. However, the length of time over which feed deprivation can be tolerated is likely to vary depending on upon the initial nutritional condition and size of the energy reserves of individual fish.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2016.12.010.

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