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Full compensatory growth before harvest and no impact on fish welfare in Atlantic salmon after an 8-week fasting period

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A R T I C L E I N F O

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A B S T R A C T

Individually tagged Atlantic salmon postsmolts (≈1200 g, 46 cm) reared in triplicate indoor holding tanks were fasted for 8 weeks at 12 °C and subsequently refed for 5 weeks, whereafter they were transferred to triplicate sea cages in a common garden setup together with a continuously fed control group until harvest size of ≈6100 g and 73 cm. At the end of the fasting period fish had lost 7.3% mass and the condition factor had decreased from 1.23 to 1.06. Furthermore, fasted fish were 544 g lighter and 3.8 cm shorter than fed controls, corresponding to a size difference of 50%. Following refeeding, feed intake gradually increased and surpassed the feed intake of controls. As such, fasted fish eventually showed compensatory growth and at harvest weight and length were similar to controls. At harvest, males were larger than females, and immature fish were larger than maturing fish in both treatment groups. The proportion of maturing fish was 25% higher in the fed control group. During the fasting period fish behaviours were video monitored, but no aggressions were observed. After the 8-week fasting period, fish welfare was scored based on the salmon welfare index model. Only minor deviations were found and at similar regularities between fasted and control fish. To assess potential long-term impacts on welfare status, vertebral deformities were quantified with radiology at harvest. Occurrence of vertebral deformities were low and similar between treatments. In conclusion, this study shows that Atlantic salmon are highly flexible with regards to growth patterns in response to food availability, and that a prolonged fasting period neither cause signs of reduced welfare in the short or in the long term.

1. Introduction

In Atlantic salmon (*Salmo salar*) aquaculture, great efforts are made to ensure high growth rates and fish are fed to satiation every day to maximize production performance. Meanwhile, periods of varying length of voluntary or involuntary fasting occur owing to several factors. For instance, to avoid poor water quality, feed withdrawal is used as a tool to empty the gut of the fish before major farming operations that involve crowding, pumping, delousing, transportation, and slaughter (Ashley, 2007; Waagbø et al., 2017; Noble et al., 2018). When fish are suffering from diseases, appetite is often reduced. Most notably is the salmon alphavirus that causes pancreas disease, where affected fish may get anorectic for weeks or months (McVicar, 1987; McLoughlin and Graham, 2007; Føre et al., 2016). Suboptimal environmental conditions, particularly hypoxia and high temperatures during summer heatwaves reduce appetite and may also cause long periods of voluntary fasting (Dempster et al., 2016; Remen et al., 2016; Stehfest et al., 2017; Wade et al., 2019). Furthermore, the industry-wide trend with moving production to more exposed locations may result in periods of stormy weather conditions where feeding regimes practically become impossible (Hvas et al., 2017a, 2021a).

Regardless of the underlying cause, any occurrences where farmed Atlantic salmon cannot be fed or are reluctant to eat is a major concern from a production perspective owing to the perceived economic loss from forgone growth (Aunsmo et al., 2014). From an animal welfare perspective, prolonged fasting periods may also lead to concerns as ethical and legal obligations to farm animals arguably are violated (Webster, 2001; Branson, 2008; Norwegian Ministry of Agriculture and Food, 2009). The RSPCA welfare standards for farmed Atlantic salmon states a maximum allowable fasting time of 40 h before transport and 72 h before harvest (RSPCA, 2021). However, this standard does not provide any reference to scientific literature but is based on expert opinion

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from two technical advisory groups.

When animals are fasting, they will undergo three successive metabolic phases broadly characterized by the main source of fuel involved. Stored glucose in the form of glycogen is first used, then fat stores are mobilized, and ultimately muscle proteins are catabolized which implies severe starvation (Wang et al., 2006; McCue, 2010). Since fish are ectothermic animals with low metabolic rates, they are capable of enduring long fasting periods by primarily relying on their fat reserves and without suffering irreversible detrimental consequences. For instance, Atlantic salmon fasted for 11 to 12 weeks during winter only lost 11% of their body weight and weight loss was mainly caused by a reduction in visceral and fillet fat (Lie and Huse, 1992; Einen et al., 1998). However, it must be noted that these studies were made on larger fish (2 and 5 kg, respectively) and at low water temperatures, which are factors that will improve resilience to fasting as larger Atlantic salmon have lower mass specific metabolic rates and higher fat reserves while lower temperatures further decrease metabolic rates (Hvas et al., 2017b; Oldham et al., 2019). Fasting time will therefore have a greater impact on smaller Atlantic salmon and at higher water temperatures (e.g., Hevrøy et al., 2011).

Following prolonged periods of feed withdrawal or restricted feeding, several species of fish are able to compensate weight loss by accelerating growth to rates above those of continuously fed counterparts once favorable conditions are restored (reviewed by Ali et al., 2003). Studies on compensatory growth in farmed Atlantic salmon most often report partial compensation, but this can be ascribed to growth trajectories only being followed for a limited time after periods of fasting or restricted feeding (Reimers et al., 1993; Johansen et al., 2002; Remen et al., 2014). From an aquaculture production point of view, whether compensatory growth is partial or full is first relevant to evaluate when the fish are harvested. Whether Atlantic salmon are capable of fully compensating growth loss will depend on the length of the fasting period, remaining time until harvest, and other confounding farm management, environmental, and health related factors that may impact appetite and growth performance.

While farmed Atlantic salmon are able to withstand long periods of fasting and to some extent can compensate loss of growth afterwards when conditions are better, less is known about associated impacts on fish welfare. Physiologically, Atlantic salmon post-smolts maintain their metabolic scope for activity, swimming capacity, and ability to respond and recover adequately from acute stress during up to 4 weeks of fasting (Hvas et al., 2020, 2021b). Key functions associated with good fish welfare therefore appear to be preserved when fasting for extended periods. However, a more direct evaluation of welfare status as provided by the salmon welfare index model would be useful as well (Stien et al., 2013). For instance, fasting periods could lead to aggressive behaviours among conspecifics, nutrient deficiency, and a repressed immune system which then may translate into visible impacts on welfare status such as increased occurrences of fin, skin, eye and snout injuries, together with increased risks of infections and disease. Furthermore, fish welfare status may be negatively affected both on the short and on the long-term following extended fasting periods, where particularly nutrient deficiency and repressed immune functions may cause longer term impacts such as poor bone health or inability to properly reattain healthy growth trajectories (Fjelldal et al., 2009, 2012).

The purpose of this study was to evaluate impacts on fish welfare in Atlantic salmon post smolts following an 8-week fasting period and to compare growth trajectories during fasting and subsequent refeeding with a continuously fed control group until harvest. Furthermore, in addition to assessing the capacity for compensatory growth, potential long-term fish welfare impacts following an extended fasting period was also assessed from occurrences of vertebrae deformities. A final objective was to quantify maturation rates at harvest between fasted and continuously fed Atlantic salmon, as lower maturation rates in fasted Atlantic salmon previously have been observed (Thorpe et al., 1990; Reimers et al., 1993).

2. Materials and methods

2.1. Animal husbandry and sampling schedule

This study was made between January and November 2020 and was approved by the Norwegian Food Safety Authority under permit number 21448 in accordance with national legislations with regards to animal use in scientific research.

Atlantic salmon post smolts (Aquagen) were maintained at the Institute of Marine Research, Matre Research Station, Norway in six large indoor holding tanks (⌀ = 3 m) at 12 °C and 25 ppt under a natural simulated photoperiod. An open flow-through of 150 l min^{-1} of aeriated, filtered and UVC treated water into each tank ensured a constant adequate water quality by keeping oxygen levels above 80% saturation in outlet water and removing waste products. Each tank contained approximately 130 fish that were fed commercial pellets (Optiline 4.5–9 mm pellets according to fish size, Skretting, Norway) in excess via automated feeding devices every day. Three tanks were used as controls and three tanks were subjected to the fasting protocol. Prior to initiating the fasting protocol, fish had been acclimating in these conditions for 1.5 months.

An overview of sampling events are summarized in Table 1. On January 28 feeding was stopped in the fasting treatment tanks. Two days later all fish were PIT tagged (12 mm standard ISO tag) using a pistol grip injector, and their weight and length were recorded. In all sampling events fish were anaesthetized in 100 mg l^{-1} ms-222 (Finquel Vet) for a maximum of 5 min.

On February 25 and March 10, corresponding to 4 and 6 weeks of fasting, respectively, a subsample of 30 fish per tank were measured for size parameters. On March 24, corresponding to 8 weeks of fasting, size parameters were recorded in all fish and welfare status was assessed using the salmon welfare index model (Stien et al., 2013). Following this sampling event normal feeding was reinitiated in the fasting treatment tanks.

On April 29, 5 weeks after feeding was resumed, size parameters were recorded again, and all fish were transferred from the indoor holding tanks to the outdoor experimental sea cage facilities at the Matre Research Station in Smørdalen (60.87°N, 5.55°E). Here, fish were randomly allocated into three sea cages (5 m × 5 m and 7 m deep) in a common garden setup and subjected to standard salmon production protocols. The sea cage environment was continuously monitored with a CTD-profiler (SAIV AS, Bergen, Norway) to measure water temperature, salinity and oxygen levels throughout the water column. Typical for fjord environments, a vertical salinity gradient was present with a brackish surface layer of 14–18 ppt and an increasing salinity with depth to 25–30 ppt. Oxygen levels remained within the normoxic range (above 75% O_2 saturation). Seasonal and depth-based variation in water temperature during this phase of the experiment are summarized in Fig. 1. Since Atlantic salmon behaviorally choose to occupy the water depth with the highest temperature up to about 16 °C (Oppedal et al., 2011), it

Table 1
Time overview of the experiment.

Date	Sampling event	Measurements
January 30	2 days fasting, start sampling	Size parameters, pit tagging
February 25	4 weeks fasting	Size parameters (subsample)
March 10	6 weeks fasting	Size parameters (subsample)
March 24	8 weeks fasting ends	Size parameters, welfare scoring
April 29	5 weeks refeeding, sea cage transfer	Size parameters
July 1	2 months at sea	Size parameters
November 9	Harvest, 6 months at sea	Size parameters, maturation, sex, x-rays

This study was made in 2020 at Matre Research station, Norway. Fish were first kept in indoor holding tanks and later transferred to sea cages at Smørdalen in Masfjorden.

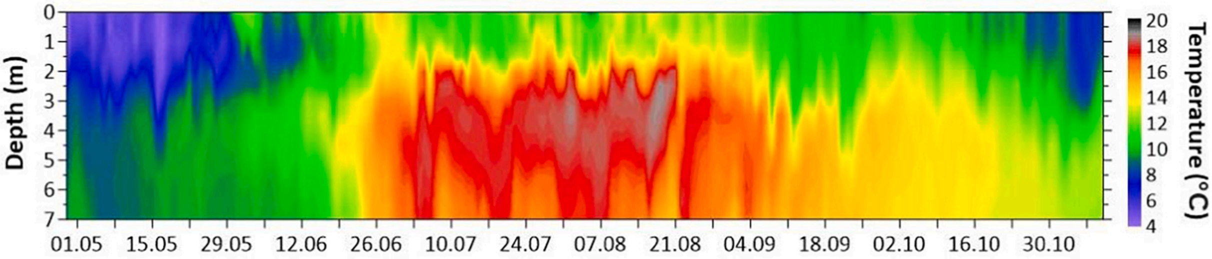

Fig. 1. Contour plot of water temperatures in the sea cage environment between April 29 and November 9 in 2020. Farmed Atlantic salmon tend to occupy depths where water temperature is highest.

can be inferred that this is the temperature the fish experienced for most of the time. As such, experienced water temperatures first ranged from 10 to 14 °C in May and June, up to 16 °C in July, August and September, and down to 12–14 °C in October and November (Fig. 1).

On July 1, two months after sea cage transfer, size parameters were recorded again in all fish. On November 9, the fish were harvested after having been in the sea cages for six months. Final size parameters were recorded, and fish were opened to determine sex and maturation status. At this stage mature fish were fully mature with running milt and ovulated eggs while immature fish had gonads with a clear immature phenotype. Hence, maturity status was assessed by dissection followed by visual inspection. A subsample of 95 fish were taken for subsequent radiological analyses of the spinal column.

2.2. Behavioural observation of aggressive interactions

Each tank was surveilled by a camera mounted 3 m above the tank center that covered the water surface and enabled monitoring of fish swimming behaviour and social interactions. Video was recorded for 0.5 h per day, and a ten min sequence for each week during the 8-week fasting period was scrutinized for potential aggressive interactions between fish in all tanks. Categories of aggression included biting and burst directed towards other fish.

2.3. Welfare scoring

When assessing fish welfare status at the end of the 8-week fasting period, an adjusted scoring system based on Noble et al. (2018), Stien et al. (2013) and Pettersen et al. (2014) was used. In the original scoring system in Noble et al. (2018), the welfare indicator scores ranges from 0 to 3, where 0 indicate no deviation from normal, 1 is a minor deviation, 2 is a clear deviation, and 3 a severe deviation. As a large number of fish (N = 739) were scored in the present study, detailed examination was not possible due to time constraints. Therefore, only the frequencies of clear or severe (score 2 and 3) were analyzed. The indicators scored were scale loss, skin hemorrhages, wounds, fin damage, cataract, eye injury, and snout damage.

2.4. Feed intake during refeeding

To record the trajectory of feed intake over the 5-week period of refeeding in the holding tanks prior to sea cage transfer, waste feed was collected and weighed 25 min after all meals except on refeeding days 14, 15, 17, 18, 23, 30, 31, and 34. The method described by Helland et al. (1996) was used to calculate the dry weight of feed eaten (hereafter called feed intake). The feed intake was calculated relative to the current estimated total biomass in each tank and expressed as percentage of biomass.

2.5. Radiology

After harvest, a subsample of 95 fish were radiographed as whole fish with a direct radiology system (Canon CXDI-410C Wireless, CANON, INC, Japan) and a portably x-ray unit (Hiray Plus, Model Porta 100 HF, JOB Corporation, Japan) using 88 cm with 40 kV and 10 mAs. Each fish was evaluated for occurrences of vertebra deformities along the vertebral column (Witten et al., 2009).

2.6. Calculations and statistics

The condition factor of the fish was calculated as 100 · weight · $(\text{length}^3)^{-1}$ (Fulton, 1904; Nash et al., 2006).

The specific growth rate (SGR) in percentage growth per day was calculated as (LnW2 – LnW1) · 100 · $(\text{T2-T1})^{-1}$, where W2 and W1 are the weight at day T2 and T1, respectively (Stefansson et al., 2009).

For the sake of simplicity owing to nearly all welfare scores being either 1's or 0's in all of the morphological traits assessed, the percentage of total fish with a deviation for a particular trait was calculated for each treatment group along with a mean score of fish with an observed deviation.

The number of vertebral deformities per fish was expressed as frequencies for each treatment group.

A two-way ANOVA along with Tukey's test was used to assess differences in size parameters between treatment groups at various sampling times and used to assess differences in size parameters at harvest between fish of different sex and maturation status. Pearson's chi squared test was used to test for difference in sexual maturation rates between treatments at harvest. A *P*-value below 0.05 was considered significant and data are presented as mean ± s.e.m. unless specified otherwise.

3. Results

3.1. Feeding and growth

Eight weeks of fasting in Atlantic salmon decreased their weight from 1179 ± 11 g to 1091 ± 11 g which corresponded to a weight loss of 7.4% and an SGR of −0.14 (Fig. 2, Table 2). Meanwhile the length increased from 45.6 ± 0.1 cm to 46.8 ± 0.2 cm, resulting in a decrease in condition factor from 1.231 ± 0.003 to 1.056 ± 0.0.002. At the end of the 8-week fasting period, fed control fish were on average 544 g heavier, 3.8 cm longer, and 0.18 higher in condition factor compared to the fasting group. Expressed as a percentage, control fish were here 50% larger than the fasted fish.

Following periods of refeeding, the fasting group showed a gradual increase from an initial daily feed intake of ≈0.2% at the start to ≈1.1% at refeeding day 32, while the control group had a stable feed intake of ≈0.7% during this period (Fig. 3).

After 5 weeks of refeeding size differences remained similar, where fed fish were 596 g heavier and 4.2 cm longer than fasted fish (Fig. 2). At this sampling point, all fish were transferred from the indoor holding tanks to sea cages. The day after sea transfer, 8 dead fish were registered with equal distribution between treatments, while no further mortalities were registered by the farm technicians during the remaining growth

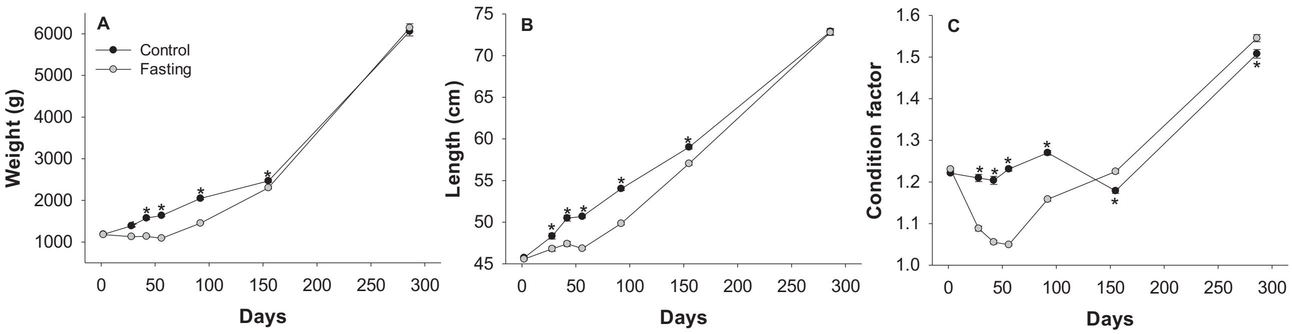

Fig. 2. Size parameters and compensatory growth.

Fish fasted from day 0 to 56 (8 weeks) and then fed normally until harvest (grey circles), and control fish with no fasting periods (black circles). Statistical differences between treatment groups at specific sampling points are indicated with asterisks (Two-way ANOVA, $P < 0.05$). Data are mean ± s.e.m.

Table 2

Specific growth rates (SGR; % growth per day).

Period	Control	Fasting
0–8 weeks (fasting)	0.58	−0.14
8–13 weeks (refeeding)	0.62	0.79
0–2 months at sea cages	0.19	0.84
2–6 months at sea cages	0.75	0.69
0–6 months at sea cages	0.57	0.74
Start to harvest	0.58	0.57

The mean SGR at different time intervals in the two treatments.

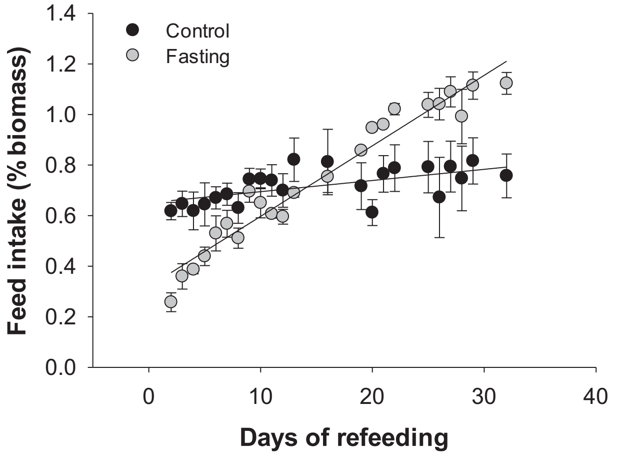

Fig. 3. Feed intake over 5-weeks of refeeding after an 8-week fasting period compared to a continuously fed control group.

Data are mean ± s.e.m. of the treatment holding tanks (N = 3) with corresponding linear regressions; $y = 0.004\times + 0.651$, $R^2 = 0.36$ for controls, and $y = 0.028\times + 0.319$, $R^2 = 0.95$ for the fasting group.

phase prior to harvest. Two months of growth in sea cages decreased the size gap between the two treatment groups to 168 g, and moreover, the fasting group had now attained a significantly higher condition factor than the control group (Two-way ANOVA and Tukey test, $P < 0.001$; Fig. 2). During the first two months at sea, the fasting treatment had an SGR of 0.84 while it was 0.19 in the control group (Table 2).

At harvest following 6 months of growth in sea cages the weight and length of the two treatments were similar (Two-way ANOVA and Tukey test, $P = 0.21$ and $P = 0.86$, respectively), while the fasting treatment maintained a significantly higher condition factor than the control group (Two-way ANOVA and Tukey test, $P < 0.001$; Fig. 2). The overall SGR during the entire experimental period was similar between the two treatments at 0.58 and 0.57 in control and fasted fish, respectively (Table 2). The mean harvest size across treatments was 6101 g, 72.8 cm, and 1.53 in condition factor which corresponded to a 5.2-fold increase in size over the course of the experimental trial that lasted 285 days. At harvest the number of fish identified from PIT tags were 292 and 294, with a male/female ratio of 43/57 and 45/55 in the control and fasting groups, respectively. Signs of sexual maturation was observed in 26.4% of the control fish and in 19.7% of the fasted fish and with a higher occurrence of maturing males (N = 54 in controls and N = 42 in fasted fish) than maturing females (N = 23 in controls and N = 16 in fasted fish; Pearson's chi-squared test, $P < 0.001$). Significant differences in size parameters were found at harvest based on sex and maturation status (Fig. 4). Specifically, immature males were larger than immature females, and mature fish were smaller than immature fish regardless of sex. Furthermore, immature fish had higher condition factors while mature males were longer and had lower condition factors than mature females (Fig. 4). The fasting treatment did not significantly affect size parameters at harvest based on sex and maturation status except for mature males being longer in the control group (Fig. 4).

3.2. *Fish welfare*

No aggressive interactions between individuals in any of the tanks were observed in the video analyses of the 8-week fasting period.

No clear or severe deviations from normal were observed in any fish (N = 739) in either the fasted or fed group after the fasting period, with the exception of fin damage score 2 and 3, respectively, on two individuals in the fasted group. Minor deviations of snout damage, skin hemorrhage, and fin damage, which is commonly observed in farmed salmon (Folkedal et al., 2016), were observed on several fish in both groups, but could not be reliably quantified.

At harvest x-rays were made on a subsample of fish to determine prevalence of skeletal deformities in the vertebral column. In 58% of the control fish and in 68.9% of the fasting fish, no deformities were found. As such, occurrences of vertebral deformities were slightly more common in the control group, although bone health overall was considered good (Fig. 5).

4. Discussion

4.1. *Weight loss*

In the present study, Atlantic salmon lost 7.4% of their mass over an 8-week fasting period at 12 °C which corresponded to an SGR of −0.14. This result is generally in agreement with earlier work on prolonged fasting effects in larger farmed Atlantic salmon when considering variation in fasting times and water temperature between studies. For instance, two months of fasting in winter resulted in an SGR of −0.10 and 6% loss of body mass (Reimers et al., 1993). Similarly, a longer fasting period of 11–12 weeks reduced body mass by 10–11% (Lie and Huse, 1992; Misund, 1996; Einen et al., 1998), corresponding to similar

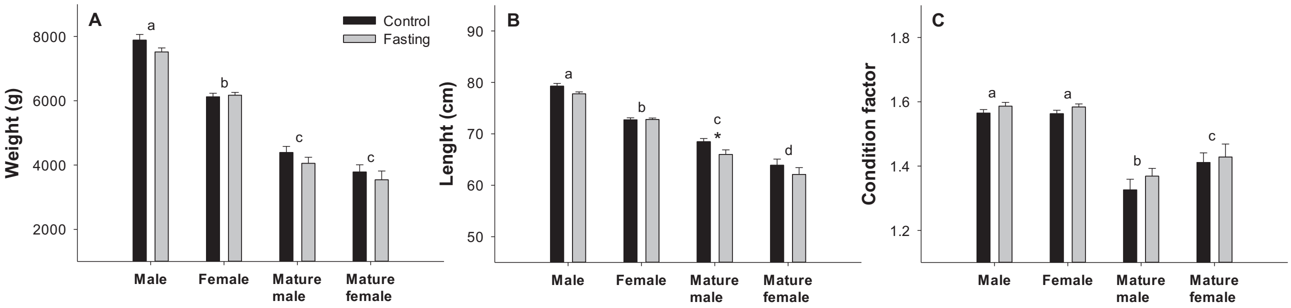

Fig. 4. Effects of sexual maturation and sex on size parameters at harvest.
Statistical differences between sex and maturation status are indicated with different letters, and significant differences between treatment (control or fasting) within sex and maturation status are indicated with asterisks (Two-way ANOVA and Tukey test, $P < 0.05$). Data are mean ± s.e.m.

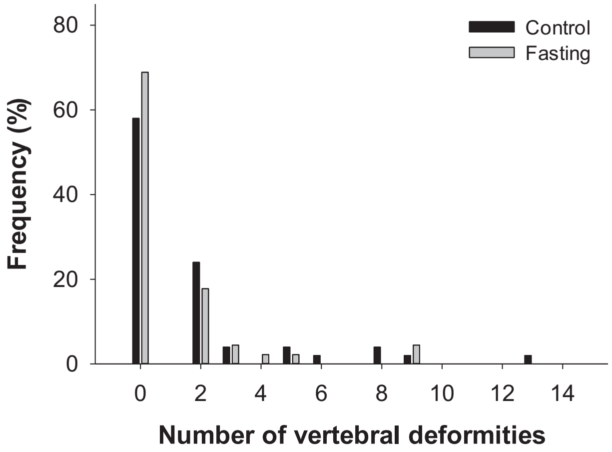

Fig. 5. Vertebral deformities.
After harvest 45 fish from the fasting treatment and 50 control fish were x-rayed to assess prevalence of vertebral deformities in the spinal column. The figure shows percentages of x-rayed fish with a specific number of deformed vertebrae.

negative SGR's as in the present study. The magnitude of weight loss in Atlantic salmon therefore appear to be consistent over time and presumably reflects similar routine metabolic rate requirements to maintain homeostasis in the absence of food. However, it should be noted that weight loss as a function of time is not a linear process, as the rate of weight loss is highest initially whereafter it slows down in later weeks (Lie and Huse, 1992). This can be ascribed to a range of time-dependent adaptive physiological and biochemical responses to fasting in Atlantic salmon which results in a stepwise reduction in metabolic rates (Hvas et al., 2020). Some of the mechanisms involved to reduce energy expenditure in fish when food supplies are limited or unavailable includes changes in gene expressions, decreasing enzyme activity in muscles, reduced protein synthesis, and increased efficiency of mitochondria (Méndez and Wieser, 1993; Bermejo-Nogales et al., 2015; Cassidy et al., 2016; Salin et al., 2018). As such, owing to these time-dependent changes in physiological functions, it will be difficult to make accurate extrapolations of how long Atlantic salmon can cope without food solely based on the current available studies. Nonetheless, the 8–12-week fasting periods that have been explored so far does not appear to cause a stage of severe starvation as signified by depletion of fat reserves and the onset of muscle protein catabolization (e.g., Wang et al., 2006). Considering that the condition factor only dropped from 1.2 to 1.0 in the present study further suggest that Atlantic salmon theoretically could endure substantially longer fasting periods. For instance, in a study on Atlantic cod (*G. morhua*), a fasting regime was used to reduce condition factors from 1.0 to 0.5, which the fish were able to endure although at a cost of a reduced swimming capacity (Martínez et al., 2004).

During the 8 weeks of fasting while losing mass, the length increased by 1.2 cm. Continued length growth in the absence of food has been documented previously in Atlantic salmon, and shows that growth of the vertebrae and muscle development can work independently of each other during fasting or restricted feeding (Einen et al., 1998; Hvas et al., 2021b). Moreover, continued length growth while fasting may prepare the fish for rapid muscle growth once feed becomes available again. As such, observations of continued length increase can be used as an additional indicator for that a given fasting regime not yet has become too severe.

4.2. Growth performance

At harvest the fasting group had attained similar weights and lengths as the control group and thereby demonstrated full compensatory growth following an 8-week fasting period. Considering that control fish were 50% larger at the end of the fasting period (1636 g vs 1091 g) makes this catch-up growth performance a remarkable achievement. Furthermore, the mean harvest size attained of 6.1 kg was larger than what is typically reported in farmed Atlantic salmon maintained under similar conditions and production periods. For instance, in previous studies from the same research facility as in the present one, mean harvest sizes were 4.3, 3.2, and 5.8 kg, respectively (Oppedal et al., 1999, 2006; Thorland et al., 2020). As such, the growth performance reported here was generally high irrespective of treatments, and the observed compensatory growth in the fasting treatment can therefore not be ascribed to unexplained stunted growth in the control group.

Immature male fish being larger than immature female fish, as well as maturing fish being smaller regardless of sex was to be expected based on previous studies on farmed Atlantic salmon at harvest (Rye and Refstie, 1995; Thorland et al., 2020). Nevertheless, the rather substantial size disparities between immature and maturing fish highlight why the onset of sexual maturation is regarded as such a major issue from a production cost perspective. Hence, apart from increased growth rate, one of the main traits that have been consistently selectively bred for in successive generations of farmed Atlantic salmon is delayed maturity (Gjedrem et al., 1991; Gjøen and Bentsen, 1997).

Interestingly, the proportion of maturing fish was reduced from 26.3% in controls to 19.7% in the fasting treatment which corresponds to 25% fewer mature fish at harvest. Similarly, a reduction in mature fish following two months of fasting was previously reported, although the effect here was larger with a 48% and 32% reduction among females and males, respectively (Reimers et al., 1993). In line with this, by fasting Atlantic salmon every second week for two months, maturation rates were reduced by 35% (Thorpe et al., 1990). While it is unclear why prolonged fasting periods or intermittent fasting may reduce or delay maturation, it is anyhow an interesting observation from a production cost perspective. Perhaps cyclical periods of fasting followed by excessive feeding could provide better production results than daily ad libitum feeding regimes that presently are used in the aquaculture industry.

The fact that fasted Atlantic salmon had fully compensated growth loss before harvest questions the strict emphasis on daily ad libitum feeding regimes currently practiced in Atlantic salmon aquaculture. The perceived worry of economic loss from reduced production performance is evidently unwarranted owing to the highly flexible nature of growth trajectories in Atlantic salmon. Hence, as stated by others, accelerated growth in response to previous food restriction provides evidence that growth rates are regulated, and moreover, reduces variance in sizes by causing growth trajectories to converge over time (Ali et al., 2003). Farmed Atlantic salmon may therefore inevitably reach the same size in the same amount of time regardless of day-to-day feeding regimes as long as they can feed until satiation periodically. For instance, not feeding the fish in the weekends will likely not make much of a difference with regards to final harvest size, provided they are presented with compensatory feed amounts during weekdays.

Obviously, there is a limit for compensatory growth capacity in Atlantic salmon. This limit will ultimately depend on the magnitude of growth loss during periods of fasting or restricted feeding and the subsequent available time for catch-up growth before harvest time. In the present study, complete compensatory growth following 8-weeks of fasting was not observed until the final harvest sample, although size differences compared to controls were already minor after two months at sea corresponding to roughly 3 months of refeeding. Furthermore, other factors known to reduce appetite such as health issues or suboptimal environmental conditions would extend the required time for full compensatory growth. Therefore, while Atlantic salmon and other species of fish are able to accelerate growth rates beyond those of unrestrictedly fed counterparts once favorable conditions returns, to fully catch-up in size may still require several months, as shown in the present study.

4.3. Fish welfare

After an 8-week fasting period, fish welfare status was similar to the control group and only minor deviations were observed generally. Thus, we found no evidence that a prolonged fasting period by itself reduces fish welfare in Atlantic salmon on the short term. Similarly, important physiological functions such as swimming abilities, aerobic scope, and stress responses were preserved over a 4-week fasting periods in Atlantic salmon postsmolts (Hvas et al., 2020, 2021b). As such, Atlantic salmon are evidently well able to endure long fasting periods without suffering detrimental health or performance related consequences. Moreover, zero observed occurrences of aggression in either treatment during the fasting period in the present study suggest that fasting does not agitate Atlantic salmon postsmolts kept at commercially relevant densities.

Provided a long fasting period causes a state of significant nutrient deficiency and repressed functionality of the immune system, negative impacts on fish welfare may first manifest themselves at a later point in time. For instance, by increasing the risks of disease development, poor bone health, or the inability to reattain healthy appetite and growth. However, the display of increasing feed intake rates during refeeding and eventual compensatory growth suggest that the fasted fish remained in excellent health throughout the experiment. Furthermore, less vertebral deformities were observed in the fasting treatment at harvest compared to the control group, although incidences of deformities were low overall. Hence, we also did not find any evidence that fish welfare was negatively affected on the long term.

The welfare of fish in aquaculture is currently receiving increased attention from both NGO's, consumers, producers, and researchers (Noble et al., 2018; Kristiansen et al., 2020). Animal ethics originally developed for endothermic agricultural animals, such as the five freedoms (Brambell, 1965; Webster, 2001), are here often sought applied to the situation of farmed fish with mixed results. For instance, one of the five freedoms is the freedom from hunger and thirst, which has raised concern with regards to allowable fasting periods in Atlantic salmon aquaculture. However, since Atlantic salmon and other species of fish naturally are adapted to persevere for long periods without eating, and have indeterminate growth as well as highly flexible growth trajectories, the concept of hunger as a welfare concern arguably makes less sense than in the case of land-based endothermic farm animals. The present study corroborates this notion by being unable to document any negative impact on fish health or growth following prolonged fasting. Welfare guidelines (e.g., RSPCA, 2021) that seek to define allowable fasting times for farmed Atlantic salmon may therefore ultimately be meaningless, at least from a practical point of view owing to that the fasting periods investigated so far with a focus on fish welfare (4–8 weeks) are substantially longer than any fasting period realistically encountered in most commercial settings. Furthermore, periods of several weeks where fish are not eating will mainly be associated with either poor environmental conditions such as temperature extremes and hypoxia (Dempster et al., 2016; Wade et al., 2019), or health issues such as pancreas disease (Føre et al., 2016). In those situations, the welfare concerns are first and foremost poor rearing environments and poor fish health, and not the fact that these factors induce voluntary fasting.

5. Conclusion

In this study, we have shown that farmed Atlantic salmon were able to fully compensate growth loss following an 8-week fasting period by accelerating feed intake and growth rates above those of continuously fed counterparts. However, catch-up growth still took several months to achieve which emphasizes the need for longer studies to fully discern compensatory growth capacities in fish. The 8-week fasting period did not reduce fish welfare status neither in the short or in the long term as documented via scoring of external morphology traits, bone health, and by monitoring social behaviour. Formulating welfare guidelines for allowable fasting periods may therefore ultimately be redundant since the required time to initiate severe starvation takes much longer than any realistically encountered fasting period in Atlantic salmon aquaculture. Finally, the fasting treatment had a lower incidence of maturing fish, indicating that daily ad libitum feeding may accelerate sexual maturation, or alternatively, reduced nutrient availability may reduce the ability to enter sexual maturation. As such, exploring the effect of periodic fasting on maturation frequency would be an interesting area for future study since Atlantic salmon clearly are flexible with regards to growth patterns in response to food availability.

Authors' contribution

This work was conceived and performed by all authors. M.H. wrote the manuscript while all co-authors provided critical feedback before approving the final version.

Declaration of Competing Interest

The authors declare no competing or financial interests.

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