Effects of short-term starvation periods on flesh quality in Arctic charr (Salvelinus alpinus) in different seasons

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Abstract
Possible effects of short-term starvation on flesh quality in Arctic charr were studied in spring (March) and summer (August). Groups of juvenile Arctic charr (mean weight March 536 g ± 24; August 461 g ± 15 SEM) were starved for 1, 2 and 4 weeks (March) and 1, 2 and 3 (August). After each starvation period, the fish were slaughtered, and flesh samples collected in order to investigate quality and textural properties in the different experimental groups. Starvation had a positive effect on flesh quality giving firmer texture and lower gaping scores. Starved fish had lower cathepsin activity at slaughter, and a similar difference was seen one-week post mortem. The results showed that the effect of starvation period was seasonally dependent. Starvation had a larger effect in summer, where a three-week starvation resulted in firmer texture, whereas this was not seen during spring.

KEYWORDS
Arctic charr, flesh quality, food deprivation, season

INTRODUCTION

As part of the slaughter process, it is normal to starve fish 3–20 days before slaughter to empty the stomach and intestines of its contents (Einen & Thomassen, 1998) and to improve freshness quality. This is to ensure the hygiene of the fish product which applies to all food production. Starvation prior to slaughter is used to a greater extent to reduce metabolism before handling and transport (Lines & Spence, 2012), which increases the fish’s ability to cope with demanding situations. The same metabolic forces that ensure the fish’s ability to cope with stress are also important for the quality of the fish flesh (Lines & Spence, 2012; Mørkøre, Mazo, Tahrinovic, & Einen, 2008). Previous studies have shown that starving of fish prior to slaughter will have a quality improving effect on the fish flesh in salmon (Einen, Mørkøre, Rørå, & Thomassen, 1999; Mørkøre et al., 2008). The mechanisms behind it are a reduction in glycogen and proteolytic enzymes, while at the same time, muscle proteins such as connective tissue strengthen the bonds (Swatland, 1990; Torgersen et al., 2014). However, the effect of prolonged starvation and the time this is carried out has not been investigated previously in Arctic charr, although positive effects from reduced feeding have been noted (Imsland & Gunnarsson, 2011). Previous studies on farmed Atlantic halibut (Hippoglossus hippoglossus, Foss et al., 2008) demonstrated that 5 weeks of starvation had a positive effect on the quality during periods of high growth (summer), whereas throughout the winter, when growth was low, this has little to no effect. This means that the effects of starvation can differ in different parts of the year. The influence of temperature on muscle texture hardness has been studied in Atlantic salmon (Salmo salar) and is known to decrease during summer months (Espe et al., 2004; Roth et al., 2005), and the effect of season may overshadow endogenous
rhythms and affect flesh quality (Roth et al., 2005). Further, activity of proteases, such as cathepsins, is widely described in the literature to be an important contributor to protein degradation and muscle softening (Bahuaud et al., 2009; Lerfall et al., 2015; Lysenko et al., 2015) whereas cathepsin activity in Arctic charr muscle has not been studied before.

Arctic charr (*Salvelinus alpinus*) has several features that make it an attractive species for farming in colder climates (Imsland, Gunnarsson, & Thorarensen, 2020). It has a relatively high growth rate at low temperatures (Le François, Lemieux, & Blier, 2002; Gunnarsson et al., 2011; Sillavuopio, Foss, Saether, Gunnarsson, & Imsland, 2013), it can be reared at high densities (Jørgensen, Christiansen, & Jobling, 1993) and the flesh is perceived to be of high quality (Gines, Valdimarsdóttir, Sveinsdóttir, & Thorarensen, 2004; Gunnarsson et al., 2012). Few studies have investigated variations in fillet quality in Arctic charr related to commercial production conditions. Gines et al. (2004) investigated the effect of rearing temperature and strain (two Icelandic strains) on fillet texture and found that raw fillets from fish reared at 15°C received higher values for hardness and fracture ability than those reared at 10°C, regardless of strain. Gunnarsson et al. (2012) investigated several flesh quality parameters (fillet pH, fillet gaping and fillet colour) in Arctic charr reared under different photoperiods and found no differences in relation to different photoperiod. Possible effects of short-term starvation on flesh quality parameters in Arctic charr are at present not known although findings on Atlantic salmon indicate that starvation will influence the flesh quality.

The aim of this study was to study the effect of different short-term starving periods in spring (March) and summer (August) on flesh quality and textural properties in juvenile Arctic charr.

2 | MATERIALS AND METHODS

2.1 | Experimental fish and conditions

The fish used in the experiment were from a multiple generation farmed Arctic charr strain, commonly denoted the Hammerfest Strain, originating from Lake Storvatn (70°N, 24°E), Northern Norway. Juvenile Arctic charr with mean weight (±SEM) 3.5 ± 0.5 g were achieved from commercial farmer (Sjøblink Blokken AS, Nordland county, Norway) in September 2012 and reared at the facilities of Kirkenes Charr, Finnmark county, Norway, until the start of the trial in March 2014. The juveniles were hatched during early spring 2012 and were two-year old at start of the trial period in 2014. The fish (*N* = 40 in March and *N* = 79 in August) were acclimatized for approximately two months and subsequently reared throughout the experiment in two fibre glass tanks with a volume of 1,000 L, at ambient temperature (Min 2.3°C in April, Max 12.5°C in July, mean 6.8°C, Figure 1) and at continuous light (LD24:0). Water was supplied from a freshwater lake close to the rearing site at a depth of 30 m. The fish were fed a commercial dry feed (Skretting, Stavanger, Norway) in excess, using automatic feeders and additional handfeeding to control appetite. A 36 W fluorescent daylight tube integrated in each tank cover provided light, and the respective photoperiods were maintained using electronic timers.

2.2 | Ethics statement

The experiment described has been approved by the local responsible laboratory animal science specialist under the surveillance of the Norwegian Animal Research Authority (NARA) and registered by the Authority and thereby conforming to Directive 2010/63/EU.

2.3 | Experimental set-up

In March (spring, *N* = 40) and August (summer, *N* = 79) of 2014, a group of 119 Arctic charr were moved to two replicate tanks and starved for 0, 1, 2 and 4 weeks in the spring (March, *N* = 10 in each group) and for 0, 1, 2 and 3 weeks (*N* = 19–20 in each group in August, Figure 1). These fish were in both cases taken from a larger production group in larger production tanks and moved to the 1,000 L experimental tanks. Care was taken to reach similar experimental weights in both cases. At each

![Figure 1](image-url) Mean monthly temperature at the rearing facility (Kirkenes Charr) during the trial period (March–August 2014). The horizontal bars indicate the starving regimes in March (0, 1, 2 and 4 weeks) and August (0, 1, 2 and 3 weeks) [Colour figure can be viewed at wileyonlinelibrary.com]
sampling, the fish were killed with a blow to the head. Immediately after slaughtering, the fish were exsanguinated by a gill cut, placed into ice water for 30–40 min, gutted, filleted and stored on ice in a cooled storage room for 7 days. The fillets were used for chemical analysis 7 days post mortem as some time is expected to elapse prior to consumption of the product (Jittinandana et al., 2005), so investigation of quality aspects shortly after slaughtering may not reflect changes seen in the final product from a consumptive perspective.

2.4 | Fish quality and texture measurements

The left fillet of the sampled fish was divided into two parts. One part of the fillet was weighed and dried at 105°C from 16 to 24 hr (NMIKL 123,1991), for estimating the dry content of the muscle and hence the water content (WC) of the muscle. The other part was weighed and centrifuged (Sorvall® RC5Cplus, Thermo Fisher Scientific Inc, USA) for 15 min at 4°C using 1,500 rpm with an SLA 1500™ rotor. Water holding capacity (WHC) was calculated according to the formula of Skjønsbø, Ore, and Hendriksen (2007).

Muscle pH was measured, by a Mettler Toledo Seven Go pro™ with an Inlab 489 pH probe (Mettler Toledo INC).

Information on hardness, breaking strength and profile was obtained using a Texture Analyzer (TA-XT®-plus Texture Analyzer, Stable Micro Systems) with a load cell of 25 kg. A flat-ended cylinder (10 mm) was used as test probe. Seven days after collection, the puncture test was assessed in two locations on the Norwegian Quality Cut (NQC, NS 1975) directly on the fillets (skin on) transverse to the muscle fibre orientation. The probe was programmed to penetrate 80% into the initial fillet height, and max forces were recorded in addition to forces at 40%, 60% and 80% compression (Roth et al., 2010; Roth, Oines, Rotabakk, & Birkeland, 2008). The speed of the probe was set to 1 mm/s. The breaking force was defined as the force required to penetrate the cylinder through the fillet surface and hardness (N) as the highest force recorded during the first compression cycle (Bourne, 1977).

2.5 | Cathepsin B and L activities

Samples for cathepsin activity were measured in the muscle at day 0 and day 6 post mortem. Analyses were prepared, using a modified method described by Bahuaud et al. (2010). Muscle samples were taken from the dorsal part of the Norwegian Quality Cut (NQC) from six fish in the 0- and 3-week starving group in August 2014 and immediately frozen at ~80°C prior to further analyses. Cathepsin B + L, cathepsin B and cathepsin L total activities were measured on muscle homogenates, prepared by homogenizing 100 mg of muscle tissue in 300 µl of extraction buffer (100 mM Na-acetate in 0.2% Triton X-100, pH 5.5) in Precellys tubes CK 28 (2 ml) and homogenized using Ultra Turrax (IKA, USA) at 525 g. Obtained homogenates were centrifuged at 16,016 g (4°C, 30 min), and the supernatants were used to measure enzyme activities.

Cathepsin B + L and cathepsin B activities were measured fluorometrically, according to a modified method described by Kirschke, Wood, Roisen, and Bird (1983). To estimate cathepsin L activity, the activity of cathepsin B was subtracted from cathepsin B + L activity (Bahuaud et al., 2009). All samples were analysed in triplicate, and the mean was calculated. The activity was expressed in µU/g muscle where 1 U was defined as 1 µmol product produced per minute at 40°C.

2.6 | Statistical analysis

To assess normality of distributions, a Kolmogorov–Smirnov test (Zar, 1996) was used and homogeneity of variances was tested using Levene’s F test (Brown & Forsythe, 1974). One-way ANOVA (Zar, 1996) was used to test for possible effect of starvation period on body weight, muscle pH, flesh quality and protease activity. For comparing breaking force and hardness at a given compression of the different starvation groups in each season, the sample height was as covariate into the factorial ANOVA (ANOVA). Student–Newman–Keuls (SNK) multiple comparison post hoc test (Zar, 1996) was used to identify differences among treatments. A significance level (α) of 0.05 was used if not stated otherwise.

3 | RESULTS

3.1 | Body weight and muscle pH

An effect of starving on growth was seen during summer as body weight was successively lower with length of the starving period (SNK post hoc test, p < .05, Table 1), whereas no significant weight loss was found in the spring sampling. However, starving only had minor effect on the fish glycogen reserves as muscle pH was stable in relation to both starving period and season (Table 1) with the exception of higher pH in the 2-week starving group in spring (SNK post hoc test, p < .05, Table 1).

3.2 | Flesh quality and texture

The water holding capacity (WHC) increased with increased length of the starving period for both the spring and summer sampling (SNK post hoc test, p < .05, Table 1). A starvation of two weeks increased the WHC with approximately 1% in both seasons. Apart from 4 week starving in spring, muscle gaping declined in both seasons with the starving period (SNK post hoc test, p < .05, Table 1) whereas this trend was more pronounced during summer (Table 1). The textural properties of the fillets were softer in the summer groups (SNK post hoc test, p < .01, Table 2). Hardness increased with increasing starvation time in summer (SNK post hoc test, p < .05, Table 2), whereas this was not seen in the spring.
3.3 | Protease activity

Starved fish had lower cathepsin activity (SNK post hoc test, \( p < .05 \), Figure 2) at slaughter, and this difference was also seen after one-week storage (Figure 2).

4 | DISCUSSION

Flesh quality of the Arctic charr in the present study was influenced by season as has also been seen in previous studies on salmonids (Espe et al., 2004; Hagen, Solberg, Sirnes, & Johnston, 2007) and is therefore an obvious and relevant parameter in commercial aquaculture. The analysis of fillet quality indicated a reduced fillet hardness with season which may be linked to higher growth during summer. This is in accordance with the findings of Johnston (1999) and Rasmussen (2001). The fish were reared under ambient temperature, which was substantially lower in March (around 3°C) than in August (around 11°C) in which the latter is considered being near the optimal temperature for growth for Arctic charr of this size (Imsland et al., 2020; Pétursdóttir & Eybórsdóttir, 1993; Síikavuopio, Saether, Johnson, Evensen, & Knudsen, 2014). Seasonal variations in growth and feeding are known to occur both for anadromous and for landlocked populations of Arctic charr, with lower growth rates in winter (Arnesen, Jørgensen, & Jobling, 1993; Jobling, 1987; Sæther, Johnson, & Jobling, 1996). In line with present findings, Markøre and Rørvik (2001) investigated the product quality of farmed Atlantic salmon defined by fillet hardness and found the highest values during the winter period. Imsland et al. (2009) found a seasonal effect on flesh quality in Atlantic halibut with a tendency towards lower hardness in summertime compared with winter.

The starved fish displayed lower mean weight during summer already after two weeks, probably related to higher metabolic turnover and better growth in optimal temperature conditions (Imsland et al., 2020) during the summer period at the fish farm. Arctic charr ability to tolerate starvation during several months in their natural habitat is well documented (Hawley, Rosten, Haugen, Christensen, & Lucas, 2017; Klemetsen, Knudsen, Staldvik, & Amundsen, 2003) as Arctic charr experience large seasonal fluctuations in environmental conditions and food availability (Jørgensen & Johnsen, 2014).

### TABLE 1

<table>
<thead>
<tr>
<th>Season</th>
<th>Starvation (weeks)</th>
<th>Mean weight (g)</th>
<th>Condition factor</th>
<th>pH</th>
<th>WHC (%)</th>
<th>Gaping</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>0</td>
<td>564 (30)</td>
<td>1.37 (0.06)</td>
<td>6.39 (0.03)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>94.5 (0.2)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.6 (0.3)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>519 (17)</td>
<td>1.35 (0.07)</td>
<td>6.41 (0.01)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>95.6 (0.3)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.8 (0.3)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>547 (30)</td>
<td>1.31 (0.05)</td>
<td>6.53 (0.04)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>95.3 (0.2)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.4 (0.3)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>516 (19)</td>
<td>1.33 (0.09)</td>
<td>6.43 (0.01)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>95.4 (0.3)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.0 (0.4)&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>10</td>
</tr>
<tr>
<td>Summer</td>
<td>0</td>
<td>502 (18)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.29 (0.08)</td>
<td>6.43 (0.02)</td>
<td>94.7 (0.2)&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1.4 (0.2)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>480 (14)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.28 (0.05)</td>
<td>6.40 (0.01)</td>
<td>94.5 (0.2)&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.8 (0.2)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>443 (13)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.29 (0.04)</td>
<td>6.40 (0.02)</td>
<td>95.5 (0.1)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.7 (0.2)&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>420 (14)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.26 (0.11)</td>
<td>6.45 (0.01)</td>
<td>95.8 (0.1)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.4 (0.1)&lt;sup&gt;c&lt;/sup&gt;</td>
<td>20</td>
</tr>
</tbody>
</table>

Significant differences between treatment groups are indicated with superscripted letters (Student–Newman–Keuls test, \( p < .05 \)). Separate analyses were done each season.

**Abbreviation:** \( N \), number of samples.

### TABLE 2

<table>
<thead>
<tr>
<th>Season</th>
<th>Starvation (weeks)</th>
<th>Breaking force (Nm)</th>
<th>Hardness 40%</th>
<th>Hardness 60%</th>
<th>Hardness 80%</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>0</td>
<td>4.7 (0.3)</td>
<td>4.0 (0.2)&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>4.5 (0.2)&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>10.4 (0.5)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>4.4 (0.3)</td>
<td>3.9 (0.2)&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>4.4 (0.2)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>10.8 (0.5)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>4.4 (0.2)</td>
<td>3.6 (0.2)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.6 (0.1)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>8.8 (0.3)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>4.6 (0.1)</td>
<td>4.2 (0.1)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>4.5 (0.1)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>9.5 (0.4)&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>10</td>
</tr>
<tr>
<td>Summer</td>
<td>0</td>
<td>3.8 (0.3)</td>
<td>2.5 (0.1)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.6 (0.1)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>10.4 (0.3)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>3.8 (0.2)</td>
<td>2.9 (0.1)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.4 (0.1)&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>20</td>
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<tr>
<td></td>
<td>2</td>
<td>4.1 (0.3)</td>
<td>2.7 (0.1)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.6 (0.1)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>10.0 (0.3)&lt;sup&gt;b&lt;/sup&gt;</td>
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<tr>
<td></td>
<td>3</td>
<td>4.9 (0.3)</td>
<td>3.5 (0.2)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>4.2 (0.1)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>11.8 (0.3)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>20</td>
</tr>
</tbody>
</table>

Significant differences between treatment groups are indicated with superscripted letters (Student–Newman–Keuls test, \( p < .05 \)). Separate analyses were done each season.

**Abbreviation:** \( N \), number of samples.
Anadromous Arctic charr show rapid growth and can double their body weight and increase their body lipids during only a few weeks in seawater in the summer (Jobling, Tveiten, & Hatlen, 1998; Jørgensen, Johansen, & Jobling, 1997). In general, fish can tolerate long periods without food, and some do not lose weight even during periods of prolonged starvation (Cassidy, Saulnier, & Lamarre, 2016; McCue, 2010). In addition, water accumulation in the tissues and organs can mask the loss of lipids and proteins during food deprivation when measuring the mass of live animals (Cassidy et al., 2016; McCue, 2010). For example, after eight and twelve weeks of food deprivation, there is a proportional increase in organ water content as lipid content decreases in Arctic charr (Miglavs & Jobling, 1989) whereas short periods of feed deprivation do not lead to changes in fat and water content of the Arctic charr fillet (Imsland & Gunnarsson, 2011). In the present study, short-term starvation leads to reduced body weight during summer. This is in line with previous findings that starvation leads to down regulation in both growth hormone (GH) and insulin like growth factor I (IGF-I) during spring in Arctic charr (Frantzen et al., 2004), thereby effecting the growth pattern of the fish.

Although the results of fillet quality measurement (fillet hardness) were based on a relatively simple experiment set-up at one sampling point from each starving group, the results show that the quality in terms of hardness is lower for summer groups whereas fillet hardness increases with length of starving period in the summer sampling. Some studies on other fish species have also shown that starvation has a significant effect for improving the flesh quality of the starved fish, for example less gaping and harder texture (Foss et al., 2009), increased WHC, hardness, springiness (Lv, Hu, Xiong, You, & Fan, 2018), whereas other studies have not found similar effects on flesh quality (Bjørnevåg et al., 2017; Young, Morris, Huntingford, & Sinnott, 2005). In fish, flesh texture is shown to be influenced by a number of different factors, such as light regime (Hagen & Johnsen, 2016; Hemre et al., 2004), temperature (Roth et al., 2005), feeding (Einen et al., 1999), slaughter and filleting method (Kiessling, Espe, Ruohon, & Mørkøre, 2004; Kristoffersen, Vang, Larsen, & Olsen, 2007) and season (Espe et al., 2004; Imsland et al., 2017). Fast growth has been found to promote softness of Atlantic salmon fillets (Mørkøre & Rorvik, 2001), but there is limited knowledge on underlying causes of the correlation between fast growth and softness (Lysenko et al., 2015; Moreno et al., 2016). In the current study, a lower protease activity was seen in the Starved group compared with un-starved fish which is probably linked to higher growth in the un-starved fish. In contrast, Cassidy et al. (2016) found no observable effects of 36 days food deprivation on the protease activities in red and white muscle, heart or gills, but an effect was seen in the liver, where the ubiquitin proteasome pathway seemed to be activated during fasting conditions. The authors speculated if Arctic charr regulate protein metabolism during food deprivation to conserve proteins. Cathepsins are involved in fast muscle protein breakdown and turnover (Hagen, Solberg, & Johnston, 2008) and may reflect softening of the muscle tissue which may explain the softer tissue seen in the un-starved fish during the high growth period (summer) in present study. The findings of Imsland et al. (2017) indicate that harvesting Atlantic salmon during periods of high growth can negative effect on flesh quality in the form of softer muscle tissue. Although the fish in the current study were not of harvesting size, a similar relationship between fast growth and tissue softness was found as seen in the study of Imsland et al. (2017).

5 | CONCLUSION

Starvation had a positive effect on flesh quality in Arctic charr, resulting in a firmer texture and lower gaping score. The effect was dependant on season, as starvation had a pronounced effect in summer, where a three-week starvation resulted in firmer texture, whereas this was not seen during spring.
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CONFLICT OF INTEREST
There is no conflict of interest related the findings presented in this manuscript.

AUTHOR CONTRIBUTIONS
B.R. designed the study and carried out texture analyses. A.K.D.I. analysed the data and wrote the paper. L.B.C. carried out cathepsin and texture analyses. S.I.S. and A.F. designed and carried out the study and coordinated the project. All co-authors drafted the manuscript.

DATA AVAILABILITY STATEMENT
Data sharing is not applicable to this article due to commercial restrictions.

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