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# Effects of altered photoperiod regimes during winter on growth and gonadosomatic index in Arctic charr (*Salvelinus alpinus*) reared in freshwater

Atle Foss[1] | Sten I. Siikavuopio[2] | Albert K. D. Imsland[3,4]

[1]Akvaplan niva, Bergen Office, Bergen, Norway

[2]Nofima, Tromsø, Norway

[3]Akvaplan-niva Iceland Office, Kópavogur, Iceland

[4]Department of Biological Sciences, High Technology Centre, University of Bergen, Bergen, Norway

**Correspondence**
Albert K. D. Imsland, Department of Biological Sciences, High Technology Centre, University of Bergen, 5020 Bergen, Norway.
Email: aki@akvaplan.niva.no

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## Abstract

The short- and long-term effects of altered photoperiods during winter on growth and final gonadosomatic index (GSI) were investigated in 178 individually tagged 2-year-old smolt Arctic charr from an anadromous strain. The fish were reared at ambient temperature (2.3–12.5°C) for 18 months and reared at five different photoperiods. One group was reared on constant LD16:8 (light–dark, *N* = 40) photoperiod and a second group on continuous light (LD24:0, *N* = 32) throughout the experimental period. Three groups of fish were moved from LD16:8 to LD24:0 for 44 days and subsequently back to LD16:8, that is early winter light group (Early WL: 17 November–5 January; *N* = 35), Mid WL group (5 January–23 February; *N* = 38) and Late WL group (23 February–6 April; *N* = 33). No differences in growth were found for females, whereas males reared at constant LD24:0 were larger (mean ± *SEM*, 1,780 g ± 180) compared with the Late (1,264 g ± 101) and Mid WL (1,413 g ± 120) groups towards the end the study. Exposure to continuous light during early winter significantly influenced the GSI in female Arctic charr, whereas no differences were found in the males. Female GSI (%) was lowest in the Mid WL group (1.7) and highest in the LD24:0 group (7.0). In conclusion, the present study demonstrated that application of brief continuous light treatments during January and February can possibly be used as a tool to lower subsequent female maturation in Arctic charr farming.

**KEYWORDS**

gonad development, light manipulation, salmonids, winter growth

## 1 | INTRODUCTION

As the freshwater species with the northernmost distribution in the world, the Arctic charr (*Salvelinus alpinus*) experiences large variations in day length throughout the year. Photoperiod regime is known to affect production characteristics in the species, but the relationship and interaction between photoperiod, temperature and endogenous rhythms and their effects on growth, feeding and the timing of maturation are complex (Frantzen, Arnesen, Damsgård, Tveiten, & Johnsen, 2004; Imsland & Gunnarsson, 2011; Liu & Duston, 2018, 2019). There is a general agreement that an increase in day length has a positive effect on appetite and growth in the species (Johnston, 2002; Tveiten, Johnsen, & Jobling, 1996). Mortensen and Damsgård (1993) demonstrated that the main reason for increased growth in charr during spring was the change from short to

long day, rather than just the long day length. Siikavuopio, Sæther, Skybakmoen, Uhlig, and Haugland (2009) confirmed those findings when Arctic charr, reared under continuous light conditions, were exposed to a period of short day length during winter and responded with a growth increase resulting in a 25% higher weight gain compared with that of fish reared at continuous light for the whole period. The potential effect these photoperiod regimes had on subsequent maturation of the fish was, however, not investigated.

Photoperiod manipulation has been validated as a tool that can be used to arrest or delay maturation in rearing of salmonids (Bromage, Porter, & Randall, 2001; Peterson & Harmon, 2005; Taranger et al., 1999). For Atlantic salmon (*Salmo salar*), continuous light is commonly used from December to March as part of the current production regime of Atlantic salmon in Norway to promote growth without triggering maturation (Imsland et al., 2017; Oppedal, Berg, Olsen, Taranger, & Hansen, 2006). Frantzen et al. (2004) investigated the effect of photoperiod manipulation on the timing of sexual maturation and spawning of Arctic charr and found that Arctic charr responded in a similar manner to other salmonids. Duston, Astakie, and MacIsaac (2003) found a significant increase in the proportion of higher value immature Arctic charr by applying a long photoperiod (18L:6D) for 42 days in winter followed by a short or natural photoperiod compared with fish reared on constant long day or natural photoperiod. In contrast, long-term exposure to continuous or extended light regimes has, in some cases, resulted in reduced growth and food conversion efficiency (Stefánsson, FitzGerald, & Cross, 2002), implying that the period of extended or continuous light must be harmonized with the internal rhythms of the fish in order to achieve optimal results.

The present study was set up to investigate the effect of periodic exposure to continuous light at different phases during the winter on growth and subsequent maturation in Arctic charr. Fish were reared at either constant long day (16 hr of light: 8 hr of darkness, LD16:8, continuous light; LD24:0) and transferred for a short time interval from LD16:8 to LD24:0 and back to LD16:8 again. The rationale for choosing these regimes was based on previous findings on Arctic charr (Duston et al., 2003; Imsland & Gunnarsson, 2011) and the photoperiod regime in use at the production site. The main aim was to determine whether there is a specific time during winter where a shift from LD16:8 to continuous light and back may reduce maturation without compromising growth.

## 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) in September 2007 and reared at the facilities of Kirkenes Charr, Finnmark county, Norway, until the start of the trial in April 2009. The juveniles were hatched during early spring 2007 and were 2 years old at the start of the trial period in 2009. In February 2009, all fish were tagged intraperitoneally with Trovan® Passive Transponder tags. The fish ($n$ = 178) were acclimatized for approximately 2 months and subsequently reared throughout the experiment in 4 fibreglass tanks with a volume of 1,000 L, at ambient temperature (2.3–12.5°C; Figure 1) for 18 months. Water was supplied from a freshwater lake close to the rearing site at a depth of 30 m. Water flow was set to approx. 20 L/min and was gradually increased with increasing biomass in the tanks, and oxygen levels were always kept above 80% saturation. The fish were fed a commercial dry feed (Skretting) 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. The experiment lasted from 21 April 2009 to 20 October 2010 (18 months).

### 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 design

At the beginning (21 April 2009) of the experiment and on nine subsequent occasions (2 June, 10 August, 17 November 2009, 5 January, 23 February, 6 April, 10 June, 26 August and 20 October 2010) during the experimental period, all fish were anaesthetized (benzocaine, 50 µl/L) and individual weight recorded to the nearest 0.5 g.

The fish with the initial mean weight of (*SEM*) 261 (7) were stocked in four tanks with two tanks reared at continuous light and two tanks reared at a photoperiod of LD16:8. Both groups were, therefore, replicated. Initial density in the rearing tanks was between 8.3 and 10.4 kg/

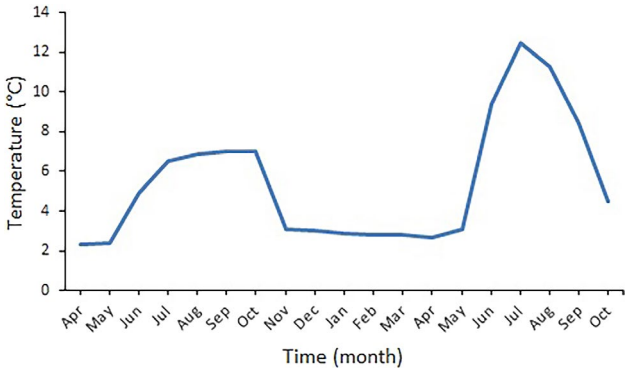


**FIGURE 1** Mean monthly temperature at the rearing facility (Kirkenes Charr) during the trial period (April 2009–October 2010)

$m^3$. As the experiment progressed, the groups being exposed to continuous light for a limited period during winter were transferred from the LD16:8 tanks to the LD24:0 tanks for the given period and back again to their original tank when the exposure period had ended. The experimental groups included one group that was held at a constant long day (LD16:8, $N$ = 40) photoperiod for the whole period; three tagged subgroups from this group were transferred to continuous light for a period of approx. 44 days for three consecutive periods during winter (Early, Mid and Late WL (winter light)) ($N$ = 35, 38 and 33 for Early WL, Mid WL and Late WL, respectively) followed by a long day photoperiod until slaughtering (Table 1). In each case, the three transfer groups were moved from the two LD16:8 tanks to the two LD24:0 tanks so that these three groups were also replicated. The last group was held at a continuous light regime, as commonly used in the production of Arctic charr, for the whole period (LD24:0, $N$ = 30) in two replicate tanks. The fish were slaughtered in a nearby commercial fish processing plant in October 2010, the gonad weighed and the sex of all individuals determined. The fish were killed with a blow to the head followed by a gill cut and exsanguination. The proportion of males and females (%) was similar in all groups (58:42–53:47). Final density in the rearing tanks varied between 32.3 and 36.5 kg/$m^3$.

Specific growth rate (SGR) was calculated according to the formula of Houde and Schekter (1981):

$$\mathrm{SGR} = (e^g - 1) \times 100.$$

where $g = (\ln W_2 - \ln W_1)(t_2 - t_1)^{-1}$ and $W_2$ and $W_1$ are weights (g) at days $t_2$ and $t_1$, respectively.

Gonadosomatic index (GSI) was calculated as.

$$\mathrm{GSI} = (\text{Gonad weight}/\text{Body weight}) \times 100.$$

## 2.4 | Statistical analysis

All statistical analyses were performed using STATISTICA™ 13.0. To assess normality of distributions, a Kolmogorov–Smirnov test (Zar, 1984) was used and homogeneity of variances was tested using Levene's $F$ test (Brown & Forsythe, 1974).

Mean individual growth trajectories were analysed using a growth curve analysis (GCM) multivariate analysis of variance (MANOVA) model (Chambers & Miller, 1995; Timm, 1980). The model equation of the GCM had the form:

$$\mathbf{Y}(n \times p) = \mathbf{X}(n \times q)\,\mathbf{B}(q \times p) + \mathbf{B}(n \times p) \quad (1)$$

where $\mathbf{Y}$ (n × p) are the growth-at-age vectors.

$$y = (y_1, y_2, \ldots y_p) \quad (2)$$

for each p (age) measurements on n individual fish; $\mathbf{X}$ (n × q) is the design matrix or the set of extraneous variables measured for each individual; that is, q = $\mathrm{age}_p$+photoperiod $\mathrm{regime}_i$ (i = LD8:16, LD24:0, Early WL, Mid WL, Late WL + $\mathrm{replicate}_j$); $\mathbf{B}$ (q × p) is the matrix of parameters estimated by the model; $\mathbf{E}$ (n × p) is the matrix of deviations for each individual from the expected value of $\mathbf{Y}$ = $\mathbf{XB}$. Separate analyses were done for each sex. As the GCM analyses included both fixed (photoperiod group) and random (replicate) factors, statistical testing was performed using the VEPAC (Variance Estimation and Precision) program in STATISTICA™. In this module of the programme, the variance components for both the random and fixed effects are estimated with a restricted maximum-likelihood estimate (REML) procedure (Demidenko, 2004).

Individual size ranking (initial size rank (21.04.09) versus. final size rank (20.10.10)) and individual growth rate ranking (initial growth rate (21.04.09–03.06.09) versus. final growth rate (26.08.10–20.10.10)) were tested using Spearman's rank correlation ($r_{Sp}$) (Zar, 1984). Possible differences in mean weight and GSI were analysed using a two-way model III nested ANOVA, where the replicates were nested within treatments. Significant ANOVA's were followed by a Student–Newman–Keuls (SNK) multiple comparison test to identify differences among treatments. A significance level ($\alpha$) of 0.05 was used if not stated otherwise.

# 3 | RESULTS

## 3.1 | Growth

For the whole experimental period, the fish reared under the different photoperiod regimes did not differ in their growth patterns (MANOVA ($_{\mathrm{TREATMENT}}$), Wilk's $\Lambda_{7,\,28}$ = 0.50, $p$ > .1). But periodic differences were seen in the growth of the males as the individual growth trajectories for the males differed from February 2010 onwards (MANOVA ($_{\mathrm{TREATMENT}}$), Wilk's $\Lambda_{4,\,16}$ = 0.75, $p$ < .05), whereas no differences were seen in female growth at any time. Significant differences were also found in growth-at-age trajectories of male

**TABLE 1** Schematic overview over the experimental groups and treatments

| Groups | $N$ (♂/♀) | Spring–autumn | Early winter | Mid winter | Late winter | Spring–autumn |
|---|---|---|---|---|---|---|
| LD16:8 | 40 (22/18) | LD16:8 | LD16:8 | LD16:8 | LD16:8 | LD16:8 |
| Early WL | 35 (19/16) | LD16:8 | LD24:0 | LD16:8 | LD16:8 | LD16:8 |
| Mid WL | 38 (22/16) | LD16:8 | LD16:8 | LD24:0 | LD16:8 | LD16:8 |
| Late WL | 33 (18/15) | LD16:8 | LD16:8 | LD16:8 | LD24:0 | LD16:8 |
| LD24:0 | 32 (17/15) | LD24:0 | LD24:0 | LD24:0 | LD24:0 | LD24:0 |

*Note:* Early winter: 17 November–5 January; Mid winter: 5 January–23 February; Late winter: 23 February–6 April.

experimental groups ($MANOVA_{TREATMENT \times AGE}$, Wilk's $\Lambda_{3, 12} = 0.77$, $p < .05$) from February onwards.

The initial mean weight (*SEM*) was 261 (7) g and did not differ significantly between tanks or groups (two-way nested ANOVA, $p > .45$). The overall final mean weight did not differ significantly when data from both sexes were combined and were as follows: 1.50 kg (LD24:0 group), 1.49 kg (Early WL group), 1.40 kg (Mid WL group), 1.32 kg (LD16:8 group) and 1.20 (Late WL group). When analysed for each sex, no differences in mean weights between experimental groups were found for the females (two-way nested ANOVA, $p > .20$; Figure 2b). For the males, the group reared on constant LD24:0 was larger (Student–Newman–Keuls (SNK) post hoc test, $p < .05$; Figure 2a) than the Late WL group in August and October in the second year of the study. Final weight of the LD24:0 was also significantly larger compared with the Mid WL group (SNK post hoc test, $p < .05$).

## 3.2 | Size and growth ranking

Apart from males in the Mid WL group ($r_{Sp} = 0.61$, $p < .01$), no significant size rank correlation (initial weight vs. final weight) was found in any experimental group of either sex ($r_{Sp} < 0.13$, $p > .10$). Positive correlations between initial and final growth rates were not found in any experimental group of either sex ($r_{Sp} < 0.28$, $p > .09$).

## 3.3 | Final GSI

Exposure to continuous light during early winter significantly influenced the final GSI in female Arctic charr (two-way nested ANOVA, $p < .05$), whereas no differences were found between males. Female GSI (%) was lowest (SNK post hoc test, $p < .05$; Figure 3b) in the Mid WL group (1.7) and highest in the LD24:0 group (7.0).

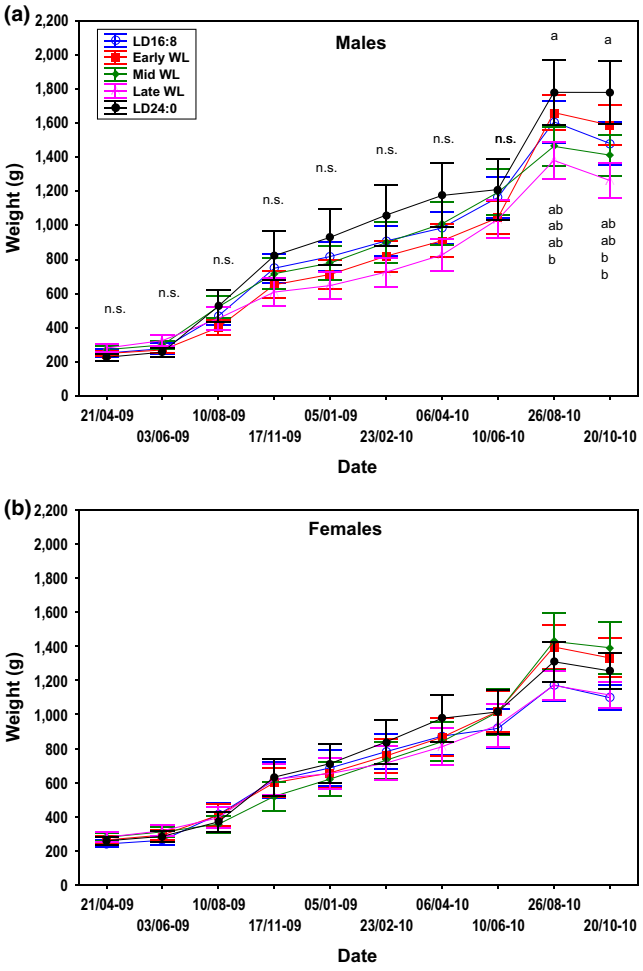


**FIGURE 2** Mean body weight of tagged juvenile Arctic charr reared at five different photoperiod treatments. The vertical lines show the standard error of mean (*SEM*). Different letters indicate a statistical difference (Student–Newman–Keuls test, $p < .05$) with a as the highest value, ns = not significant. Each data point represents combined values for replicate groups. No significant differences were found for females

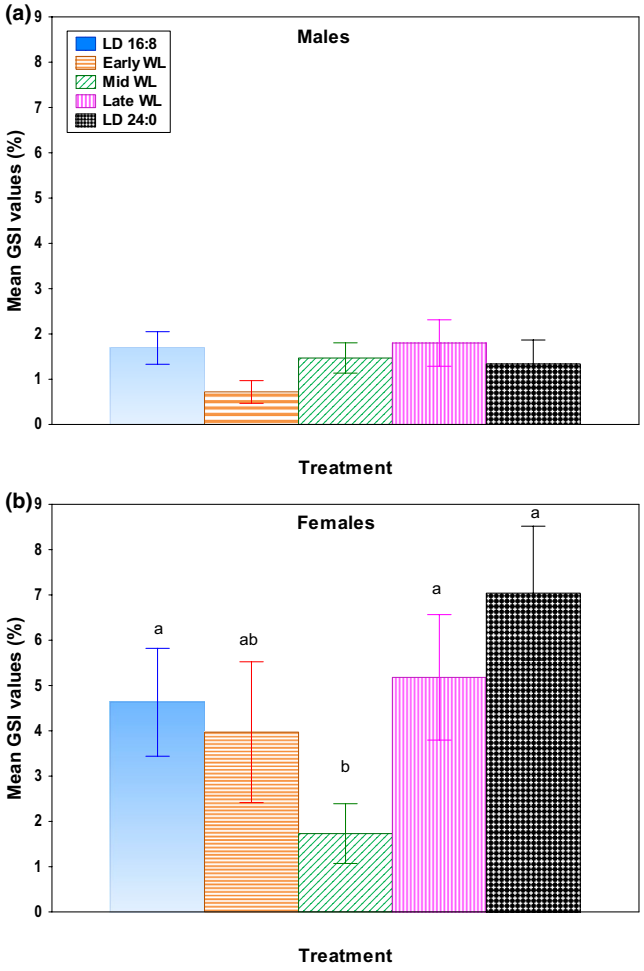


**FIGURE 3** The mean gonadosomatic index (GSI) of male (a) and female (b) juvenile Arctic charr reared at five different photoperiod treatments. The vertical lines show the standard error of mean (*SEM*). Different letters indicate a statistical difference (Student–Newman–Keuls test, $p < .05$) with a as the highest value. Each data point represents combined values for replicate groups. No statistical differences were found for males

## 4 | DISCUSSION

### 4.1 | Growth and size dispersal

Altered photoperiods affected the growth pattern of male Arctic charr, whereas no changes in growth were found for females. Growth of Arctic charr is often stimulated following changes in day length, and the growth of fish reared under a changing photoperiod may be better than in fish kept on constant photoperiod. Mortensen and Damsgård (1993) reported that Arctic charr (4–50 g) reared at constant short or long days grew equally well but a group of fish reared for a period on a short photoperiod followed by long photoperiod showed a significant increase in growth. In a long-term study, Siikavuopio et al. (2009) reported a 25%–30% higher growth rate of wild Arctic charr held under culture condition and exposed to intervals of short day length in between periods of continuous light compared with a group reared at continuous light. Gunnarsson et al. (2012) reported that Arctic charr reared using a 6-week short photoperiod between periods of continuous light showed improved long-term growth compared with fish kept in continuous light. However, a change from short days to long days does not necessarily result in increased growth, as demonstrated by Bottengård and Jørgensen (2008) who found no immediate increase in growth in Arctic charr after transfer from short days to continuous light in late winter. This is similar to the current findings where a 44-day increase in photoperiod from LD16:8 to continuous light did not lead to improved growth in any group. Hence, it might appear as if the growth of Arctic charr is less sensitive to acute photostimulation than other salmonids (Imsland et al., 2017).

Possible formation of size hierarchies was performed by comparing individual size ranking at the start and termination of the trial. It should be noted that no behaviour observation was performed during the experimental period, but according to staff at rearing facility, aggressive behaviour was rarely seen during the trial. The present size ranking data show that, with the exception of one group (male Mid WL group), no size rank correlations were seen in any experimental group of either sex indicating low, or no, formation of size hierarchies within the experimental tanks. Such size hierarchies are common under culture conditions (Brännäs, 2009; Imsland, Nilsen, & Folkvord, 1998; Jobling & Baardvik, 1994; Petursdottir, 2002) and can lead to higher growth size heterogeneity with negative effect on growth as growth can be suppressed by competition under such conditions (Brännäs, 2009; Imsland et al., 1998). For Arctic charr, it is possible to reduce aggression leading to formation of size hierarchies by applying forced exercise (high current in tanks) (Brännäs, 2009) or by avoiding to rear too size similar fish together (Baardvik & Jobling, 1990; Wallace & Kolbeinshavn, 1988). Under conditions promoting hierarchy formation, the largest fish at the beginning is expected to get the largest share of the feed, grow the fastest and have the highest weight at the end (Brännäs, 2009; Petursdottir, 2002) and the fact that almost no stable size ranking was found in the present study indicates that dominance hierarchies did not develop within the experimental groups. A possible explanation can be related to the experimental layout of this study. The experimental fish was divided into five experimental groups in four experimental tanks where fish were transferred from LD16:8 to LD24:0 for 44 days and then back to LD16:8. This frequent transfer of fish between tanks may have counteracted formation of stable size and growth rankings thereby suppressing the formation of size hierarchies within the experimental tanks.

The ambient rearing temperature in the trial varied between 2.3 and 12.5°C. For most of the study period, the growth was uniform, whereas the growth of the fish increased in the second summer of the experimental period when temperature was between 10 and 12.5°C. Arctic charr will grow at temperatures as low as 0.3°C (size range 200–300 g, Brännäs & Linnér, 2000; size range 2–25 g, Borgstrøm, Isdahl, & Svenning, 2015), and the upper limits for growth are near 20°C (size range 1–5 g, Lyytikäinen, Koskela, & Rissanen, 1997; size range 15–26 g, Thyrel, Berglund, Larsson, & Naslund, 1999). Accordingly, the rearing temperatures in this trial are well within the temperature tolerance range of the species. Rearing temperature was between 2.7 and 3.1°C in the period when fish were moved from LD16:8 to LD24:0 so it is unlikely that a possible interaction effect between temperature and photoperiod may have occurred as all transfer groups experienced very similar temperatures in the photoperiod transfer period. For Atlantic salmon, the findings of Døskeland et al. (2016) suggest that the magnitude of the effect of continuous light on growth is inversely related with temperature which results in significant interaction between temperature and photoperiod. Clarke, Shelbourn, and Brett (1978) suggested that the rate-controlling effect of temperature might be the reason for the short duration of the growth-enhancing effect of long photoperiod at higher temperature in sockeye, *Oncorhynchus nerka*, and coho, *O. kisutch*, salmon.

### 4.2 | Final GSI

For salmonids, it is well established that photoperiod can be used to either advance or delay the time of maturation (Bromage et al., 2001) and photoperiod is also used in commercial fish farming to postpone or suppress maturation. Duston et al. (2003) reported lower maturation rate and increased proportion of high-value fish (>1 kg) in Arctic charr exposed to long photoperiod (LD18:6) for 42 days during winter followed by a short (LD8:16) or natural photoperiod compared with Arctic charr reared under constant long days. Recently, Liu and Duston (2019) fed yearling (30 g) Arctic charr at different feeding regimes during fall and winter and exposed each group to three different photoperiods (LD24:0, LD18:6 or simulated natural day length, LDN) during a 15-week period (October–February). Maturation in October the following year was significantly reduced in the LD24:0 and LD18:6 (<6%, sexes pooled) compared with the LDN group (43%, sexes pooled), whereas food deprivation was only effective in reducing maturation during winter and it was concluded that a long photoperiod during winter from October to February could reliably suppress early sexual maturation among age 2 Arctic charr.

The findings of Liu and Duston (2019) are in line with findings in the present study where a 44-day period of continuous light in January and February (Mid WL group) resulted in lower female maturation in the following autumn. In the present study, fish were moved from LD16:8 to continuous light, resulting in lower maturation if applied in January–February whereas Liu and Duston (2019) transferred fish from LDN to LD24:0 or LD18:6 from October to February leading to reduced maturation in the following autumn. This may indicate that both timing and directional change are important in altering the sexual maturation cycle in Arctic charr in line with the suggestions of Liu and Duston (2018).

Restricted feeding reduces growth and adiposity (Shearer, Silverstein, & Plisetskaya, 1997), but if applied for a short time during the window of 'critical decision point' for maturation, it can lead to delayed maturation with little effects on the final weight due to compensatory growth during the following full feeding period (Taranger et al., 2010). Imsland and Gunnarsson (2011) subjected groups of Arctic charr to two different ration levels, 100% (full ration) and 50% (half ration) in two 6-week periods during autumn (September–November) and winter (December–February). In between the restricted ration periods and from February onwards, all fish were fed full ration. In the following summer and autumn, signs of lower maturation were seen for females in the feed-restricted group. The latter period of that study is in line with the Mid WL group of current study where changes in photoperiod regime resulted in lower maturation. Thus, it may be hypothesized that this period is the critical period for maturation in the subsequent year. Periods of food restrictions can affect the maturation rate of Arctic charr although results are contrasting (e.g. Liu & Duston, 2019). Similar results have been presented for Atlantic salmon (Thorpe, Talbot, Miles, & Keay, 1990), Chinook salmon, *Oncorhynchus tshawytscha* (Shearer, Parkins, Gadberry, Beckman, & Swanson, 2006) and Atlantic halibut (Foss et al., 2009).

## 5 | CONCLUSION

At present, Arctic charr is commonly reared under continuous light throughout both during the juvenile stage and during the on-growing phase, whereas present data indicate that a 44-day rearing period on continuous light in January and February (Mid WL group) resulted in lower female GSI but no changes in female growth. Male growth was highest in the group reared at continuous light throughout the study period. Accordingly, we recommend the application of brief continuous light treatments during the juvenile phase (January to February) as a tool to lower female maturation in Arctic charr farming.

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## DATA AVAILABILITY STATEMENT

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

## ORCID

*Sten I. Siikavuopio* https://orcid.org/0000-0003-2481-8870
*Albert K. D. Imsland* https://orcid.org/0000-0003-0077-8077

## REFERENCES

Baardvik, B. M., & Jobling, M. (1990). Effect of size-sorting on biomass gain and individual growth rates in Arctic charr, *Salvelinus alpinus* L. *Aquaculture*, *90*, 11–16. https://doi.org/10.1016/0044-8486(90)90278-U

Borgstrøm, R., Isdahl, T., & Svenning, M. A. (2015). Population structure, biomass, and diet of landlocked Arctic charr (*Salvelinus alpinus*) in a small, shallow High Arctic lake. *Polar Biology*, *38*, 309–317. https://doi.org/10.1007/s00300-014-1587-6

Bottengård, L., & Jørgensen, E. H. (2008). Elevated spring temperature stimulates growth, but not smolt development, in anadromous Arctic charr. *Comparative Biochemistry and Physiology*, *151*, 596–601. https://doi.org/10.1016/j.cbpa.2008.07.019

Brännäs, E. (2009). The effect of moderate exercise on growth and aggression depending on social rank in groups of Arctic charr (*Salvelinus alpinus* L.). *Applied Animal Behaviour Science*, *119*, 115–119. https://doi.org/10.1016/j.applanim.2009.03.003

Brännäs, E., & Linnér, J. (2000). Growth effects in Arctic charr reared in cold water: Feed frequency, access to bottom feeding and stocking density. *Aquaculture International*, *8*, 381–389.

Bromage, N., Porter, M., & Randall, C. (2001). The environmental regulation of maturation in farmed finfish with special reference to the role of photoperiod and melatonin. *Aquaculture*, *197*, 63–98. https://doi.org/10.1016/S0044-8486(01)00583-X

Brown, M. B., & Forsythe, A. B. (1974). Robust tests for the equality of variances. *Journal of the American Statistical Association*, *69*, 364–367. https://doi.org/10.1080/01621459.1974.10482955

Chambers, R. C., & Miller, T. J. (1995). Evaluating fish growth by means of otolith increment analysis: Special properties of individual-level longitudinal data. In D. H. Secor, J. M. Dean, & S. E. Campana (Eds.), *Recent developments in fish otolith research* (pp. 155–175). Columbia: University of South Carolina Press.

Clarke, W. C., Shelbourn, J. E., & Brett, J. R. (1978). Growth and adaptation to sea water in 'underyearling' sockeye (*Oncorhynchus nerka*) and coho (O. *kisutch*) salmon subjected to regimes of constant or changing temperature and day length. *Canadian Journal of Zoology*, *56*, 2413–2421.

Demidenko, E. (2004). *Mixed models – theory and applications*. New York, NY: Wiley.

Døskeland, I., Imsland, A. K. D., Fjelldal, P. G., Stefansson, S. O., Roth, B., Eriksen, K. E., … Handeland, S. (2016). The effect of low temperatures and photoperiods on growth and vertebra morphometry in Atlantic salmon. *Aquaculture International*, *24*, 1421–1434. https://doi.org/10.1007/s10499-016-9999-7

Duston, J., Astakie, T., & MacIsaac, P. F. (2003). Long-to-short photoperiod in winter halves the incidence of sexual maturity among Arctic charr. *Aquaculture*, *221*, 567–580. https://doi.org/10.1016/S0044-8486(03)00029-2

Foss, A., Imsland, A. K., Vikingstad, E., Stefansson, S. O., Norberg, B., Pedersen, S., … Roth, B. (2009). Compensatory growth in Atlantic halibut: Effect of starvation and subsequent feeding on growth, maturation, feed utilization and flesh quality. *Aquaculture*, *290*, 304–310. https://doi.org/10.1016/j.aquaculture.2009.02.021

Frantzen, M., Arnesen, A. M., Damsgård, B., Tveiten, H., & Johnsen, H. K. (2004). Effects of photoperiod on sex steroids and gonad maturation

in Arctic charr. *Aquaculture*, *240*, 561–574. https://doi.org/10.1016/j.aquaculture.2004.07.013

Gunnarsson, S., Imsland, A. K., Arnarson, I., Siikavuopio, S. I., Gústavsson, A., & Thorarensen, H. (2012). Enhanced growth of farmed Arctic charr (*Salvelinus alpinus*) following a temporal treatment of short day photoperiod. *Aquaculture*, *350–353*, 75–81.

Houde, E. D., & Schekter, R. C. (1981). Growth rates, rations and cohort consumption of marine fish larvae in relation to prey concentrations. *Rapports et Proces-verbaux des Réunions. Conseil International Pour L'éxploration De La Mer*, *178*, 441–453.

Imsland, A. K., & Gunnarsson, S. (2011). Growth and maturation in Arctic charr (*Salvelinus alpinus*) in response to different feed rations. *Aquaculture*, *318*, 407–411. https://doi.org/10.1016/j.aquaculture.2011.05.049

Imsland, A. K., Nilsen, T., & Folkvord, A. (1998). Stochastic simulation of size-variation in turbot: Possible causes analysed with an individual based model. *Journal of Fish Biology*, *53*, 237–258. https://doi.org/10.1111/j.1095-8649.1998.tb00978.x

Imsland, A. K. D., Roth, B., Fjelldal, P. G., Stefansson, S. O., Handeland, S., & Miklasen, B. (2017). The effect of continuous light at low temperatures on growth in Atlantic salmon reared in commercial size sea pens. *Aquaculture*, *479*, 645–651. https://doi.org/10.1016/j.aquaculture.2017.07.014

Jobling, M., & Baardvik, B. M. (1994). The influence of environmental manipulations on inter- and intra- individual variation in food acquisition and growth performance of Arctic charr, *Salvelinus alpinus*. *Journal of Fish Biology*, *44*, 1069–1087. https://doi.org/10.1111/j.1095-8649.1994.tb01277.x

Johnston, G. (2002). *Arctic charr aquaculture*. Hoboken, NJ: Blackwell Publishing.

Liu, Q., & Duston, J. (2018). Efficacy of 24 h light to reduce maturation in Arctic charr (*Salvelinus alpinus*) is dependent on both the start date and duration. *Aquaculture*, *484*, 44–50. https://doi.org/10.1016/j.aquaculture.2017.10.039

Liu, Q., & Duston, J. (2019). Long photoperiod in winter is more effective than food deprivation in stopping unwanted sexual maturation in Arctic charr. *Aquaculture*, *501*, 213–218. https://doi.org/10.1016/j.aquaculture.2018.11.007

Lyytikäinen, T., Koskela, J., & Rissanen, I. (1997). The influence of temperature on growth and proximate body composition of underyearling Lake Inari arctic char *(Salvelinus alpinus* (L.)). *Journal of Applied Ichthyology*, *13*, 191–194. https://doi.org/10.1111/j.1439-0426.1997.tb00120.x

Mortensen, A., & Damsgård, B. (1993). Compensatory growth and weight segregation following light and temperature manipulation of juvenile Atlantic salmon (*Salmon salar* L.) and Arctic charr (*Salvelinus alpinus* L.). *Aquaculture*, *114*, 261–272.

Oppedal, F., Berg, A., Olsen, R. E., Taranger, G. L., & Hansen, T. (2006). Photoperiod in seawater influence seasonal growth and chemical composition in autumn sea-transferred Atlantic salmon (*Salmo salar* L.) given two vaccines. *Aquaculture*, *254*, 396–410. https://doi.org/10.1016/j.aquaculture.2005.10.026

Peterson, R. H., & Harmon, P. R. (2005). Changes in condition factor and gonadosomatic index in maturing and non-maturing Atlantic salmon (*Salmo salar* L.) in Bay of Fundy sea cages, and the effectiveness of photoperiod manipulation in reducing early maturation. *Aquaculture Research*, *36*, 882–889. https://doi.org/10.1111/j.1365-2109.2005.01297.x

Petursdottir, T. E. (2002). Influence of feeding frequency on growth and size dispersion in Arctic charr *Salvelinus alpinus* (L.). *Aquaculture Research*, *33*, 543–546. https://doi.org/10.1046/j.1365-2109.2002.00739.x

Shearer, K., Parkins, P., Gadberry, G., Beckman, B., & Swanson, P. (2006). Effects of growth rate/body size and a low lipid diet on the incidence of early sexual maturation in juvenile male spring Chinook salmon (*Oncorhynchus tshawytscha*). *Aquaculture*, *252*, 545–556. https://doi.org/10.1016/j.aquaculture.2005.06.027

Shearer, K. D., Silverstein, J. T., & Plisetskaya, E. M. (1997). Role of adiposity in food intake control of juvenile chinook salmon (*Oncorhynchus tshawytscha*). *Comparative Biochemistry and Physiology A*, *118*, 1209–1215. https://doi.org/10.1016/S0300-9629(97)86801-6

Siikavuopio, S. I., Sæther, B. S., Skybakmoen, S., Uhlig, C., & Haugland, E. (2009). Effects of a simulated short winter period on growth in wild caught Arctic charr (*Salvelinus alpinus* L.) held in culture. *Aquaculture*, *287*, 431–434. https://doi.org/10.1016/j.aquaculture.2008.10.060

Stefánsson, M. Ö., FitzGerald, R. D., & Cross, T. F. (2002). Growth, feed utilization and growth heterogeneity in juvenile turbot *Scophthalmus maximus* (Rafinesque) reared under different photoperiod regimes. *Aquaculture Research*, *33*, 177–187.

Taranger, G. L., Carrillo, M., Schulz, R. W., Fontaine, P., Zanuy, S., Felip, A., … Hansen, T. (2010). Control of puberty in farmed fish. *General and Comparative Endocrinology*, *165*, 483–515. https://doi.org/10.1016/j.ygcen.2009.05.004

Taranger, G. L., Haux, C., Hansen, T., Stefansson, S. O., Bjornsson, B. T., Walther, B. T., & Kryvi, H. (1999). Mechanisms underlying photoperiodic effects on age at sexual maturity in Atlantic salmon, *Salmon salar*. *Aquaculture*, *177*, 47–60.

Thorpe, J. E., Talbot, C., Miles, M. S., & Keay, D. S. (1990). Control of maturation in cultured Atlantic salmon, *Salmo salar*, in pumped seawater tanks, by restricted food intake. *Aquaculture*, *86*, 315–327.

Thyrel, M., Berglund, I., Larsson, S., & Naslund, I. (1999). Upper thermal limits for feeding and growth of 0+ Arctic charr. *Journal of Fish Biology*, *55*, 199–210. https://doi.org/10.1111/j.1095-8649.1999.tb00669.x

Timm, N. H. (1980). Multivariate analysis of variance of repeated measurements. In: P. R. Krishnaiah (Ed.), *Handbook of Statistics Vol. 1, Analysis of Variance* (pp. 41–87). Amsterdam, the Netherlands: North-Holland Publishing Company.

Tveiten, H., Johnsen, H. K., & Jobling, M. (1996). Influence of maturity status on the annual cycles of feeding and growth in Atlantic charr reared at constant temperature. *Journal of Fish Biology*, *48*, 910–924.

Wallace, J. C., & Kolbeinshavn, A. G. (1988). The effect of size grading on subsequent growth in fingerling Arctic charr, *Salvelinus alpinus* (L.). *Aquaculture*, *73*, 101–110.

Zar, J. H. (1984). *Biostatistical analysis*, (2nd ed.). Englewood Cliffs, N.J: Prentice-Hall Inc.

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