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Photoperiod regulation of growth of juvenile Atlantic halibut (*Hippoglossus hippoglossus* L.)

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Abstract

Juvenile Atlantic halibut (*Hippoglossus hippoglossus* L., initial weight (SD) 31.1 g (±5.8 g)) were reared for 147 days at a constant temperature of 11°C and subjected to four different light regimes from February 10: continuous light (LD 24:0), simulated natural photoperiod of Bergen (60°25′N, LDN), constant 8 h light:16 h dark (LD 8:16) and LD 8:16 switched to continuous light on May 4 (LD 8:16–24:0). Fish exposed to LD 24:0 had a significantly higher specific growth rate (1.05% day^{-1}) than those on LDN (0.98% day^{-1}). Fish exposed to LD 8:16 had the poorest growth (0.80% day^{-1}). The group on LD 8:16–24:0 (overall growth rate 0.94% day^{-1}) grew poorly at first but subsequently increased growth rate after having been exposed to continuous light. This response was delayed by at least 21 days, suggesting that the fish needed some time to adapt to the change in photoperiod. Sensitivity to continuous light became less pronounced under summer photoperiods (above approximately 18 h daylength), which suggested that continuous light could be used to improve growth in juvenile halibut when the natural daylength is less than approximately 18 h. Overall mortality was 11.9%, with significantly higher mortality being observed in the LDN (17.4%) and LD 8:16–24:0 (17.1%) groups than in the LD 24:0 (6.2%) and LD 8:16 (6.8%) groups. Size-dependent mortality was seen in LD 8:16–24:0 in all periods from

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May 4 to July 6, with mortality being higher amongst small fish.

Keywords: Growth; Mortality; Photoperiod; Juvenile halibut

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1. Introduction

Growth in fish is influenced by several biotic and abiotic factors: Photoperiod is classified as a directive factor (Brett, 1979), controlling growth as a ''zeitgeber'' through its influence on endogenous rhythms (Eriksson and Lundqvist, 1982; Stefansson et al., 1991; Imsland et al., 1995; Porter et al., 1998) and photoperiod is known to influence circulating levels of growth hormone (Björnsson, 1997). The manipulation of environmental factors such as temperature, salinity and photoperiod currently is used to modulate fish growth in culture (Jobling, 1994). When photoperiod is increased, fish may adjust to the new photoperiod by displaying higher feeding activity, growth and food utilization (Boehlert, 1981; Woiwode and Adelman, 1991). The sensitivity to photoperiod stimulation has also been found to change with season (Clarke et al., 1989) and a directional effect of photoperiod has been demonstrated in some species (Clarke et al., 1978).

Previous findings on the effects of photoperiod on growth in flatfish are contradictory. Fuchs (1978) found no significant effect of photoperiod manipulation on growth of sole, *Solea solea*. However, it was subsequently found that extended photoperiod may have growth-enhancing effects on plaice, *Pleuronectes platessa*, and sole (Fonds, 1979), greenback flounder, *Rhombosolea tapirina* (Hart et al., 1996) and turbot, *Scophthalmus maximus* (Imsland et al., 1995, 1997).

Similarly, previous research on photoperiod effects on growth in halibut also is contradictory. Hallaråker et al. (1995) found no significant differences between natural photoperiod and a continuous light regime, whereas Jonassen et al. (2000) did. Therefore, the photoperiod effect on growth in juvenile halibut needs to be verified. Moreover, the seasonal change in sensitivity to photoperiod and the directional effect of photoperiod on growth has not been investigated in juvenile halibut. This should be clarified in order to establish the light regime that will allow optimal growth in aquaculture. The aim of the present study was to further clarify the effect of photoperiod on growth of juvenile Atlantic halibut (*Hippoglossus hippoglossus* L.) and to investigate the sensitivity to changing photoperiod.

2. Material and methods

2.1. Fish material and rearing conditions

The experimental stock were juvenile halibut of mixed parental background (wild brood-stock), produced by Stolt Sea Farm Bømlo, Norway. After hatching in January/February, the larvae were stored in 6.5 m^3 silos at 6°C for 45 days, before being transferred to plastic bags in a seawater pond (Haa-pollen) with natural light conditions and water temperature of 7.5°C. The larvae were fed live natural zooplankton. At a size of approximately 0.2 g, the fish were weaned to formulate feed indoors in tanks with a diameter of 3 m in conditions of simulated natural photoperiod. On December 12, 1995, at a mean weight of 10 g, the fish were transferred to indoor tanks at Stolt Sea Farm Øye, Norway, and held at 9–10°C under continuous light and feeding. On January 19, 1996, a total of 580 juveniles (mean weight 18 g) were transported to laboratory facilities in Bergen and randomly distributed among eight square 1 m^2 grey fibreglass tanks, each with a rearing volume of 500 l. Tanks were supplied with aerated sea water (33.3 ± 0.6‰) at 11 ± 0.3°C. The water flow was initially 4 l min^{-1} and was increased gradually to keep oxygen saturation above 80%. Photoperiod was kept at continuous light conditions until the start of the experiment. Light was provided by a Luma standard 35 W fluorescent daylight tube installed in the cover of each tank. Light intensity measured at the tank bottom was approximately 73 lux. With the exception of the days on which they were sampled, the fish were fed commercial dry feed (Skretting marine fish feed, pellet sizes 4 and 6 mm) for 30 min twice daily (10^{45}–11^{15} and 15^{45}–16^{15}) using automatic feeders. Of the 72–73 fish (initial mean weight (SD) 31.1 g (±5.8 g)) in each tank, 30–32 fish were individually tagged intraperitoneally on February 10, with a passive integrated transponder (Fisheagle® PIT). No fish died during tagging, but six missing or malfunctioning tags were later replaced.

2.2. Experimental design

At the start of the experiment on February 10, four different light regimes were established with two replicates for each treatment (Fig. 1): continuous light (LD 24:0), simulated natural photoperiod of Bergen (60°25′N, LDN), constant 8 h light:16 h dark

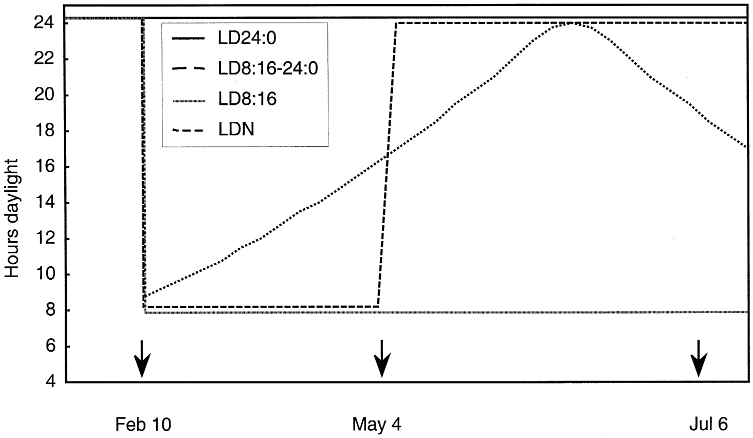

Fig. 1. Light regimes established for the four experimental groups: continuous light (LD 24:0), simulated natural photoperiod of Bergen (60°25′N, LDN), constant 8 h light:16 h dark (light from 09:00–17:00 h, LD 8:16) and LD 8:16 switched to continuous light on May 4 (LD 8:16–24:0). Prior to the start of the experiment on February 10, all fish had been held on continuous light.

(light from 09:00–17:00 h, LD 8:16) and LD 8:16 switched to continuous light on May 4 (LD 8:16–24:0). A computer programme (Lysstyr 2.00; Hansen, 1990) generated the light regimes, including a few minutes of twilight. Only tagged fish (30–32 in each tank) were used in the growth analyses. Mortality was recorded for both tagged fish and untagged fish. On February 26, the fish were treated with formaldehyde (1:4000) due to infection with the parasitic ciliate *Trichodina hippoglossi*. Mortality was observed from late April to late May. Viral encephalopathy and retinopathy (VER) was identified in three fish, by immunohistochemistry, using the anti-Striped Jack Nervous Necrosis Virus (SJNNV) rabbit serum, according to the methods described in Grotmol et al. (1997).

2.3. Studied parameters

The fish were weighed individually to the nearest 0.1 g every 3 weeks throughout the experiment. Specific growth rate (SGR) was calculated as:

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

where $g = (\ln W_2 - \ln W_1)\,(t_2 - t_1)^{-1}$ and W_2 and W_1 are weights (g) on days t_2 and t_1, respectively (Houde and Schekter, 1981). Group means of SGR were calculated by combining individual SGRs within replicates. SGR for a given interval was regressed against geometric mean (GM) weight in the same interval. GM was calculated as: $\mathrm{GM} = (W_1 \times W_2)^{1/2}$ (Croxton, 1967). To avoid pseudoreplication in the regression, the individual SGR data for each tank were combined ($n = 22$–29).

2.4. Statistical methods

All statistical analyses were conducted using Statistica 5.0 and 7.0 (StatSoft, 1995). A Kolmogorov Smirnov test (Zar, 1996) was used to assess the normality of distributions, and the Levene's F-test (Brown and Forsythe, 1974) was used to assess the homogeneity of variances. Mortality between groups was tested using a χ^2 test (Zar, 1996). A t-test was used to test for size-dependent mortality within groups (Zar, 1996), with the GM weight of surviving fish being tested against the mean weight of dead fish. Analyses of weight and SGR were conducted using a two-way nested Model III ANOVA (Zar, 1996), where the replicates (random) were nested within light regimes (fixed). For data involving repeated measurements of SGR of PIT tagged fish, a multivariate analysis of variance (MANOVA, Johnson and Wichern, 1992) was used. Significant ANOVAs were followed by a Newman–Keuls multiple comparison test (Zar, 1996) to identify differences among treatments. A significance level (α) of 0.05 was used, if not otherwise stated.

3. Results

3.1. Mortality

Overall mortality was 11.9% (69 fish), significantly higher mortality being observed in the LDN and LD 8:16–24:0 groups than in the LD 24:0 and LD 8:16 groups from

Table 1
Mortality of juvenile halibut (tagged and untagged fish together) reared under four different photoperiods Replicates ($n = 2$) are pooled. Different letters indicate significant differences in mortality between experimental groups in the same period (χ^2-test, $P < 0.05$).

Date	LD 24:0		LD 8:16		LD 8:16–24:0		LDN	
	n	Mortality	*n*	Mortality	*n*	Mortality	*n*	Mortality
Feb 10–Mar 2	145	0	146	1	146	1	144	2
Mar 2–Mar 23	145	1	145	0	145	0	142	0
Mar 23–Apr 13	144	0	145	0	145	0	142	2
Apr 13–May 4	144	4	145	1	145	0	140	1
May 4–May 25	140	2^{a}	144	3^{a}	145	10^{b}	139	9^{b}
May 25–June 15	138	1	141	2	135	7	130	6
June 15–July 6	137	1	139	3	128	7	124	5
Total mortality		9^{a}		10^{a}		25^{b}		25^{b}

May 4 to May 25 ($\chi^2 = 13.58$, $P < 0.05$, Table 1). Size-dependent mortality was seen in LD 8:16–24:0 in all periods from May 4 to July 6 and in LDN from May 25 to June 15 ($t = 2.88$, $P < 0.05$), with mortality being higher amongst small fish.

3.2. Size and growth

Only tagged fish were used in the growth analysis. There were significant differences in mean weight between treatments (two-way nested Model III ANOVA, $P < 0.001$, Fig. 2), with LD 24:0 fish having the highest mean weight from March 2 onwards, and LD 8:16 fish having the lowest mean weight from June 15 onwards. No significant differences in mean weight were observed between the LDN and LD 8:16–24:0 groups.

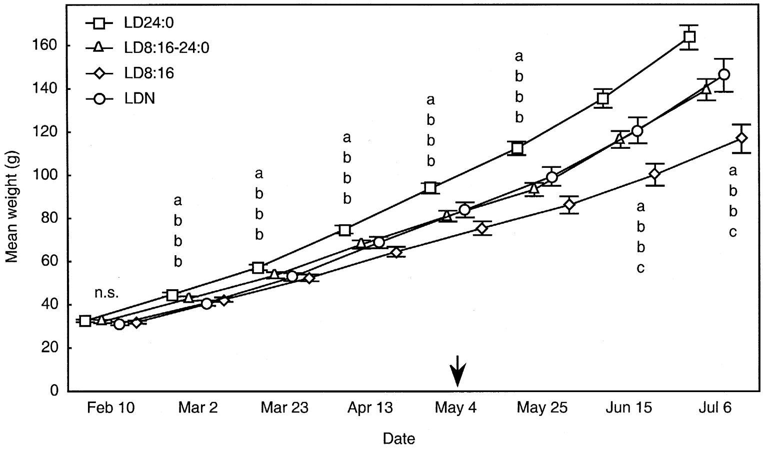

Fig. 2. Mean weights (standard error of mean) of juvenile Atlantic halibut on four different photoperiods. Arrow indicates time of change in photoperiod from LD 8:16–24:0. Different letters indicate statistical difference within each date (two-way nested ANOVA, $P < 0.05$). n.s. = Not significant.

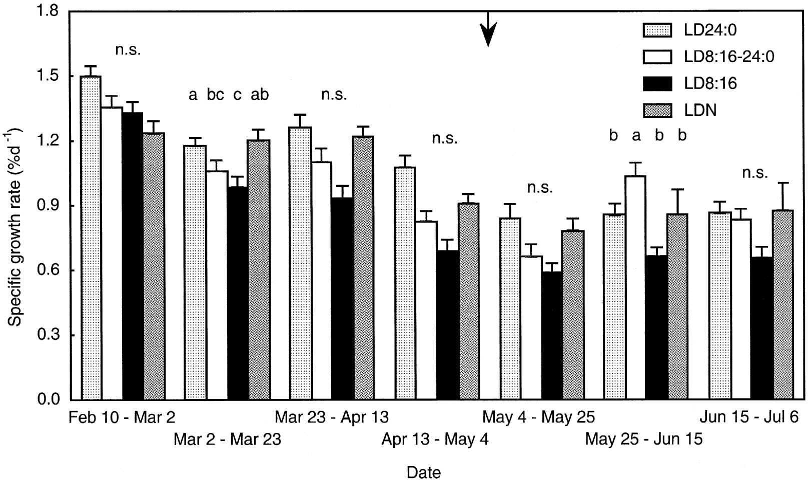

Fig. 3. Specific growth rates (standard error of mean) of juvenile Atlantic halibut on four different photoperiods. Arrow indicates change in photoperiod for LD 8:16–24:0. Different letters indicate statistical difference within each date (two-way nested ANOVA, $P < 0.05$). n.s. = Not significant.

SGRs from February 10 to July 6 were 1.05, 0.94, 0.80 and 0.98% day^{-1} for LD 24:0, LD 8:16–24:0, LD 8:16 and LDN groups, respectively, there being significant

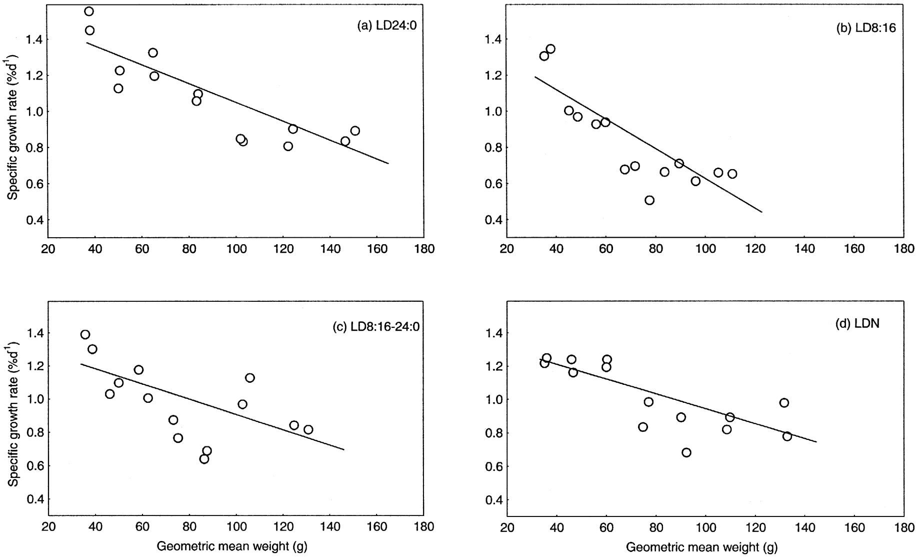

Fig. 4. Growth rate (SGR)−geometric mean (GM) regression of juvenile Atlantic halibut on four different photoperiods: (a) $\mathrm{SGR} = 1.5685 - 0.0056\mathrm{GM}$, $r^2 = 0.77$, $P < 0.001$; (b) $\mathrm{SGR} = 1.4516 - 0.0088\mathrm{GM}$, $r^2 = 0.70$, $P < 0.001$; (c) $\mathrm{SGR} = 1.3249 - 0.0045\mathrm{GM}$, $r^2 = 0.38$, $P < 0.05$; (d) $\mathrm{SGR} = 1.3820 - 0.0047\mathrm{GM}$, $r^2 = 0.61$, $P < 0.001$. Each point represents the mean of 22–29 fish from each replicate.

differences; highest in LD 24:0 and lowest in LD 8:16 (two-way nested Model III ANOVA, $P < 0.001$). From February 10 to May 25, the growth rate declined in all groups (Fig. 3). When the growth periods for this time interval were combined, the SGR was significantly higher in LD 24:0 than in other treatments, whereas it was the lowest in the LD 8:16 treatment (two-way nested Model III ANOVA, $P < 0.01$). Despite a generally faster growth in LD 24:0, a significantly higher SGR compared to the LD 8:16 and LD 8:16–24:0 groups was only observed during the second 3-week growth period. Growth from May 25 to June 15 was significantly faster in LD 8:16–24:0 compared to the other treatments (two-way nested Model III ANOVA, $P < 0.05$, Fig. 3), but the increase in SGR following the sudden increase in photoperiod of the LD 8:16–24:0 group on May 4 was delayed by one 3-week growth period. The gradual increase in photoperiod experienced by the LDN group only promoted a slight increase in growth rate (Fig. 3). An inverse relationship between SGR and weight was noticed in all groups (linear regression, $P < 0.05$, Fig. 4), but the relationships differed between treatment groups. The most rapid decline was observed in the LD 8:16 fish and LD 8:16–24:0 fish showed the weakest correlation between growth and weight ($r^2 = 0.38$, Fig. 4).

4. Discussion

Mortality during the period from May 4 to May 25, probably due to the VER virus, accounted for most of the mortality (11.9%). The groups that were exposed to an increase in photoperiod (LD 8:16–24:0 and LDN) had the highest mortality, the increase in mortality in LD 8:16–24:0 coinciding with the period following the switch to continuous light. Mortality in LD 8:16–24:0 was highest amongst small fish. This may have contributed to underestimation of the growth rate, because smaller fish have an inherently faster growth than bigger fish.

In nature, photoperiod is an important environmental signal in the control of a variety of seasonally changing processes, including growth rate (Müller, 1978; Ricker, 1979; Gwinner, 1986). Hallaråker et al. (1995) found that juvenile halibut transferred from natural photoperiod in the middle of January (60°25′N, approximately 8 h light) to continuous light did not grow faster than fish kept on natural photoperiod. This contrasts with the present experiment where a marked growth-enhancing effect of continuous light (LD 24:0) was observed from the beginning of the experiment and after LD 8:16–24:0 group was switched from 8 h light to continuous light on May 4. The latter observations are in agreement with those of Jonassen et al. (2000), who found that Atlantic halibut exposed to continuous light grew better than fish exposed to simulated natural photoperiod from midwinter to early spring. Other studies on flatfish species such as plaice and sole (Fonds, 1979) and turbot (Imsland et al., 1995) have revealed a similar growth-enhancing effect of continuous light. The observed response to a sudden increase in photoperiod (LD 8:16–24:0 group in our study), where the increase in growth is delayed by at least 21 days after the exposure of the fish to continuous light, has not previously been shown for juvenile Atlantic halibut. Such a delayed response has previously been seen in Atlantic salmon held in sea cages and subjected to continuous additional light superimposed on natural photoperiod (Kråkenes et al., 1991; Hansen et al., 1992; Endal et al., in press), suggesting that the fish required time to adapt to the change in photoperiod.

The inverse relationship between fish size and growth rate found for all groups is in accordance with the general size-dependent growth of fish (Brett, 1979; Jobling, 1983; Dabrowski, 1986), also previously reported for halibut (Hallaråker et al., 1995; Björnsson and Tryggvadóttir, 1996; Jonassen et al., 1999). However, the steeper slope of the regression for fish exposed to the LD 8:16 ($\beta = -0{,}0088$, Fig. 4) suggests that growth rate decreased faster on short photoperiods and the weak correlation between growth and weight for the LD 8:16–24:0 group probably was due to the enhanced growth seen following the switch to continuous light. Hallaråker et al. (1995) reported a gradual increase in growth of halibut as the daylength of the LDN regime increased. A similar seasonal effect on growth was indicated in LDN fish towards the end of the present experiment, despite the confounding effect of a reduction in growth rate with increasing size. The same confounding effect of size could explain the apparently transient effect of the increase in the photoperiod in the LD 8:16–24:0 group.

Salmonid fish appear to be more sensitive to changing photoperiods than to constant long daylengths (Endal et al., in press), with an increasing photoperiod giving the greatest growth-enhancing effect (Gross et al., 1965; Jobling, 1994; Endal et al., in press). In the present experiment, the LD 24:0 fish showed the overall highest growth rate, and even under natural summer photoperiod, LDN did not have faster growth than their LD 24:0 counterparts. This suggests that daylength per se is more important than the gradual directional changes in photoperiod for growth in juvenile halibut. However, because the halibut used for this study were subjected to continuous light for approximately 2 months prior to the start of the experiment, all except the LD 24:0 group experienced a sudden reduction in daylength on February 10. Previous photoperiod exposure may have an important influence on growth response to light regimes Hoar, 1988; Clarke et al., 1989), a decrease in photoperiod having a growth-depressing effect in several species (Brett, 1979; Skilbrei et al., 1997). Thus, photoperiod history and the initial reduction in daylength may in part account for the differences in growth rate observed during the first weeks of the present experiment.

Sensitivity to photoperiod stimulation has been found to change with season (Clarke et al., 1989; Endal et al., in press) and temperature (Solbakken et al., 1994; Jonassen et al., 2000). Imsland et al. (1995) found continuous light to be stimulatory for juvenile turbot in early spring (60°25′N), while in late spring, growth was faster in fish exposed to natural photoperiod. However, in the present experiment, continuous light resulted in faster growth than natural winter and spring photoperiod, while LDN and LD 24:0 showed similar growth rates from May 25 to July 6. This can be explained by the reduced difference in daylength between LD 24:0 and LDN (approximately 18 h daylight on May 25) as natural daylength increases, suggesting that the sensitivity to continuous light became less pronounced under summer photoperiods. Therefore, it is proposed that continuous light should be used to improve growth in juvenile halibut when the natural daylength is less than approximately 18 h. However, in order to establish the light regime that gives optimal fish growth for a complete production cycle, the effect of photoperiod should be investigated in different age groups and at different times of the year. The effect of photoperiod on sex-dependent growth and age of first maturity should also be investigated.

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