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Light intensity affects growth and sexual maturation of Atlantic salmon (*Salmo salar*) postsmolts in sea cages

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Abstract

The aim of the present study is to test the extent to which different intensities of continuous additional light affect somatic growth and sexual maturation in Atlantic salmon postsmolts in sea cages. Postsmolts (9 200 individuals) were randomly distributed among four commercial sized sea cages and exposed to either natural light or natural light + continuous additional light of low, medium or high intensity from January to June. In May the high light intensity group had a significantly higher mean live body weight than the other groups, and at the end of the experiment in June, all groups differed in mean gutted weight. There was a positive logarithmic regression between level of light intensity exposure during night and mean gutted weight. A small proportion of fish matured sexually (after 1.5 years in seawater) in the natural light group, whereas no maturation was detected in the light groups. These results suggests that to affect growth and proportion of maturation in Atlantic salmon by additional light, there might be different threshold values of light intensity.

Keywords: *Salmo salar*, postsmolt, growth, sexual maturation, light intensity, photoperiod.

L'intensité de la lumière affecte la croissance et la maturation sexuelle au stade "post-smolt" du saumon atlantique (Salmo salar) *élevé en cages.*

Résumé

L'objectif de cette étude est de tester dans quelle mesure l'intensité lumineuse d'éclairage continu additionnel affecte la croissance somatique et la maturation sexuelle des post-smolts du saumon atlantique élevé en cages en mer. Des posts-smolts (9 200 individus) ont été répartis de façon aléatoire dans 4 cages de taille commerciale, et exposés à la lumière naturelle avec ou sans source lumineuse supplémentaire, de basse, moyenne ou de forte intensité, de janvier à juin. En mai, le groupe éclairé par de fortes intensités lumineuses avait atteint un poids vif moyen supérieur à celui des autres groupes, et à la fin de l'expérience en juin, tous les groupes présentaient des poids éviscérés moyens différents. Il y a une régression logarithmique positive entre le niveau d'exposition à la lumière durant la nuit et le poids éviscéré. Une faible proportion de poissons appartenant au groupe exposé à la lumière naturelle atteignaient leur maturité sexuelle après 1,5 ans en eau de mer, tandis qu'aucune maturation n'était détectée dans les groupes éclairés. Ces résultats suggèrent que les seuils d'intensité lumineuse nécessaires pour affecter la croissance ou la maturation sexuelle sont différents.

Mots-clés : *Salmo salar*, post-smolts, croissance, maturité sexuelle, intensité lumineuse, photopériode.

INTRODUCTION

Atlantic salmon reared in sea water under natural photoperiod show seasonal variations in appetite and growth rate (*e.g.* Smith *et al.*, 1993; Taranger, 1993; Forsberg, 1995; Kadri *et al.*, 1997). This phenomenon appears to be strongly influenced by changes in photoperiod (Eriksson and Lundquist, 1982; Smith *et al.*, 1993; Taranger, 1993; Forsberg, 1995). Continuous light or extended photoperiods have been shown to enhance the growth rate of Atlantic salmon in fresh water (Saunders *et al.*, 1985; Villarreal *et al.*, 1988; Saunders *et al.*, 1989; Saunders and Harmon, 1990; Stefansson *et al.*, 1991; Solbakken *et al.*, 1994) and in sea water (Saunders and Harmon, 1988; Kråkenes *et al.*, 1991; Endal *et al.*, 1991; Taranger *et al.*, 1991; Hansen *et al.*, 1992; Taranger *et al.*, 1995). It has been shown however, that Atlantic salmon reared in sea water experience a decrease in growth rate during the first 6-12 weeks after onset of continuous light in winter (*e.g.* Endal *et al.*, 1991), whereas an immediate increase in growth rate is shown in fresh water (*e.g.* Saunders *et al.*, 1989; Solbakken *et al.*, 1994). The incidence of sexual maturation has shown a reduction at the 1-sea-winter stage (Taranger *et al.*, 1995) and 2-sea-winter stage (Taranger *et al.*, 1991; Hansen *et al.*, 1992) after subjecting the fish to an abrupt change to continuous additional light during the first or second winter at sea, respectively. The effects of an abrupt change from short to long photoperiod on growth and sexual maturation may be due to advancements of postulated endogenous circannual rhythms controlling a seasonal growth pattern and onset of puberty in Atlantic salmon (Hansen *et al.*, 1992; Taranger, 1993). Continuous additional light on sea cages is superimposed onto natural light. Hence, during the hours of normal daylight, ambient light will normally have a higher intensity than the artificial light, while the latter will be the main light source at night. Salmon in sea cages, exposed to continuous additional light with different intensities, experience a different day/night light intensity ratio, dependent upon the ambient level at daytime and the constant level at night. Light intensities experienced by fish in sea cages also depend upon other factors such as water turbidity and swimming depth of the fish. No previous experimental work has investigated the potential effects of different light intensities of continuous additional light on growth rates and sexual maturation in sea cages. It is possible that threshold values of light intensities must be exceeded before growth rate and sexual maturation are affected. Higher light intensities may give earlier and stronger responses in seawater, similar to those responses already indicated on growth and smolting in freshwater (Stefansson *et al.*, 1991).

The aim of the present study is to test whether Atlantic salmon postsmolts in sea cages exposed to continuous light of different light intensities during winter and spring influence growth and incidence of sexual maturation at the 1-sea-winter stage.

MATERIALS AND METHODS

The experiment was carried out at Matre Aquaculture Research Station, Norway (61° N). Previously immature Atlantic salmon (1.83 kg, SEM ± 0.04 kg, aged 24 months from hatching), were transferred from fresh water as 1 + smolts in May 1995 and reared in sea cages under a natural photoperiod until 10 January 1996. Then they were randomly distributed among four 12m × 12m × 12m cages each with a population of approximately 2 300 fish. One group was exposed to natural light (NL) and three groups to continuous additional light (LL) of low (LL-LOW), medium (LL-MED) and high (LL-HIGH) intensity until harvest on 24 June 1996. Each LL-cage was illuminated 24 hours per day by 4 metal halogen lights (Norselight, N-1760 Berg, Norway. Bulbs: Philips HPI-T) mounted 4 m apart, in a square around the centre of the cage, approximately 1 m above the surface. The different light intensities were created by combining bulbs with different power ratings, and filters mounted in front of them (Table 1). Spectral irradiance was measured

Table 1. – Light intensities given Atlantic salmon postsmolts reared in sea cages and exposed to natural light (NL) or continuous additional light of different intensities; low intensity (LL-LOW), medium intensity (LL-MED) and high intensity (LL-HIGH). Light measurements are given for the centre of the cage and where taken at midnight and midday on the 29 November 1995 with a Secchi depth of 18 m. It was no moon and it was cloudy throughout the samplings. The measurements at 10 m depth at night are measured as some fish are swimming above the spectroradiometer.

	LL-HIGH	LL-MED	LL-LOW	NL	Daylight
Bulb effect (W)	3200	600	280		
Filter reduction (%)	0	55-0*	88		
Estimated bulb effect (W)	3200	270-600*	35		
Estimated $W.m^{-2}$ cage surface	22,2	1.9-4.1*	0.24		
Irradiance, 5 m depth ($W.m^{-2}$)	0.749	0.144	0.060	0.000	2.3
Irradiance, 10 m depth ($W.m^{-2}$)	0.120	0.037	0.012	0.003	1.6
Illuminance, 5 m depth (lux)	340	60	27	0.0	749
Illuminance, 10 m depth (lux)	56	17	5	0.1	594

(*) indicates destroyed filters which were replaced after unequal time periods dependent upon weather conditions. The measurements were taken at approximately half burnt filters.

using a LI-1800UW spectroradiometer (LI-COR inc., Lincoln, U.S.A.) in each cage around midnight, and outside the cages at midday. The values were integrated and given as irradiance in $W.m^{-2}$ and as illuminance in lux calculated by CIE standard correction (Table 1). The spectral composition of the artificial lights showed a narrower distribution with increasing depth and at 5 m ranged from 400 to 700 nm with two peaks, at 535 and 592 nm. Daylight, at 5 m depth, had a wider distribution than artificial light, ranging between 365 and 710 nm and was more normally distributed, without specific peaks. The ambient day/night light intensity ratio was lowest in the LL-HIGH group and highest in the NL group, with the actual ratio following changes in daytime intensity.

Temperature and salinity were measured 5 days per week from 0.1 m to 18 m depth at 1 m intervals. Water turbidity was quantified using a Secchi disc (Ø = 33 cm). Vertical distribution of the fish was measured continuously by an echosounder system (Bjordal *et al.*, 1993). Fish were fed commercial dry feed (9 and 12 mm, Royal AB redline, T. Skretting AS, Norway) in excess (10-15 % waste feed) and given three meals per day, lasting 30 minutes each (0900 - 0930, 1130 - 1200 and 1400 - 1430). Each experimental group was starved for 10 days prior to harvest (last sample). During the experiment the fish were treated for sea lice (*Lepeoptheirus salmonis*) with azamethiphos (Salmosan vet., Ciba-Geigy) on 28 March and 9 May.

Data sampling and analysis

Fork length (to the nearest cm) and live body weight (to the nearest 10 g) were measured on random samples taken from each group every sixth week (n = 98 - 116 from each group). The fish were anaesthetized with metomidate hydrochloride (Wild-life Pharmaceuticals, CO, USA) according to Olsen *et al.* (1995). Mean individual gutted weight at harvest was calculated by dividing the total gutted weight harvested by the total number of fish harvested in each experimental group (corrections were made on 1.8-3.5 % of fish in each group for 10 % loss of head). In addition, a random sample was taken at the harvest plant (n = 86 - 100 from each group) for estimations of live body weight (all fish corrected for 5 % blood loss), length and K. Fultons condition factor (K) was calculated using: $K = (W \times L^{-3}) \times 100$, where W is the live body weight (g) and L is the fork length (cm) of each fish (Busacker *et al.*, 1990). Specific growth rate (SGR, % per day) was calculated from the formula: $SGR = (e^{q}-1)100$ (Houde and Scheckter 1981), where $q = (\ln(W_2)-\ln(W_1)) / (t_2-t_1)$ (Bagenal and Tesch, 1978) and where W_2 and W_1 are the average live body weights at day t_2 and t_1, respectively. The SGR for the last growth period was calculated by using only the days of feeding, not including 10 days of starvation (no growth) before harvest, while length growth was assumed to continue during the starvation period (Misund, 1996). Sexual maturity was assessed at harvest by internal examination; gonads were taken from a subsample of each group (n = 86 - 266) and weighed. Gonadosomatic index (GSI) was calculated using the following equation; GSI = gonad weight × 100 / live body weight. Males with a GSI < 0.18 % and a gonad weight < 10 g were considered immature. Females with a GSI < 0.30 % and gonad weight < 14 g were also considered immature. These assumptions were made from GSI *vs.* gonad weight plots showing distinct bimodal distributions, where the upper and lower mode were assumed to represent maturing and immature fish, respectively.

Data were analyzed for normality by probability plots and Kolmogorov-Smirnov test (Sokal and Rohlf, 1995), and for homogeneity of variances by Levenes' test (Brown and Forsythe, 1974). Parametric statistics were used on the data which conformed to a normal distribution and exhibited homogeneity of variances. One way analysis of variance (ANOVA; Zar, 1996) was used for comparison of fish weight, length and K, except on the gutted fish weights recorded from the total number of fish at the harvesting plant. Where ANOVA tests showed significant differences among the groups, a Student-Newman-Keules multiple comparison test was applied (Zar, 1996). Comparison of gutted weights at harvest was based on number of fish in each weight class (1 - 8 kg, 1 kg intervals, 10 g accuracy) and compared using a Kruskal-Wallis test followed by a nonparametric multiple comparison with unequal sample sizes and tied ranks (Dunns test; Zar, 1996). Incidence of sexual maturation in the LL groups were compared with the NL group using a Chi-square test (Sokal and Rohlf, 1995).

RESULTS

The weekly mean temperature at the swimming depth of the fish decreased from 9.5°C in January to 7.0°C in early May, and thereafter increased to 10°C in June. Salinity ranged from 2.3 to 21.7 in the surface layer, and from 28 to 34 below 4 m depth during the entire experimental period. Secchi depth varied from 15 - 20 m from January to mid-March and decreased subsequently to 5 - 11 m until the final reading was taken in June. Mortality in all groups was negligible (<1.0 %) during the experimental period.

Growth

There were no significant differences in body weight between groups 11 weeks after onset of continuous light (Fig. 1). The pattern of SGR and length growth did not show any consistent differences between the groups during the first 11 weeks (Table 2). However, after 17 weeks (in May), fish in the LL-HIGH group had higher live body weights compared to fish in all other groups ($F = 5.11$, $p = 0.002$). SGR from week 11 to 17 (March to May) was highest in the LL-HIGH group followed by the LL-LOW and LL-MED groups

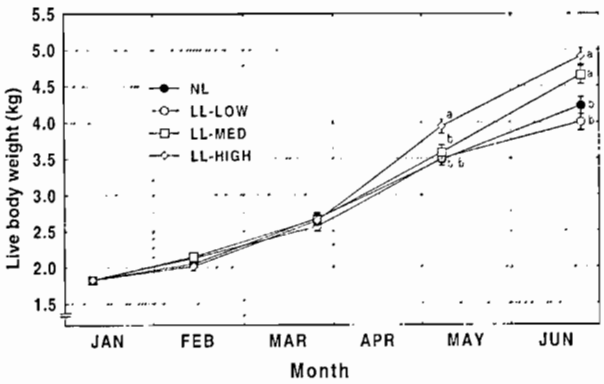

Figure 1. – Mean fish weight of Atlantic salmon postsmolts reared in sea cages and exposed to natural light (NL) or continuous additional light of different intensities; low intensity (LL-LOW), medium intensity (LL-MED) and high intensity (LL-HIGH). Vertical bars denote SEM. Different letters indicates significant differences ($p \leq 0.05$). Number of fish sampled in each group is 86-209.

with the lowest SGR in the NL group. After 23 weeks (in June), the random sample at harvest showed that live body weights of the LL-HIGH and LL-MED groups were higher than the LL-LOW and NL groups ($F = 12.07$, $p<0.001$). The mean gutted weights in the total sample in June varied significantly among all groups (NL = 3.48 kg, LL-LOW = 3.66 kg, LL-MED = 3.85 kg, LL-HIGH = 4.07 kg; $p<0.001$) and showed a positive relationship with light intensity measured at night at 10 m depth ($W = 161 \times \ln(i) + 4\,393$, $R^2 = 0.99$, i = irradiance, W = weight). From week 17 to 23 (May-June), the SGR was highest in LL-MED and LL-HIGH groups followed by NL and lowest in LL-LOW group, when based on the random sample at harvest. However SGR based on the total gutted weights, calculated back to live body weights, showed that all LL groups had a higher SGR compared to the NL group. Mean fork length (all group mean) increased from 51 cm at start to 68 cm at the end of the experimental period, and did not show any significant differences between groups.

Condition factor

Condition factor (K) in the NL group showed an increase ($F = 12.69$, $p<0.001$) from week 5 to 11 (Feb. to March) and was higher than all LL groups ($F = 6.27$, $p<0.001$) in March (Fig. 2). However, during the next 6

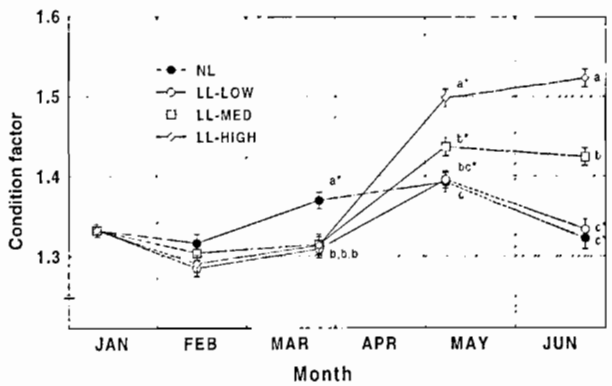

Figure 2. Condition factor of Atlantic salmon postsmolts reared in sea cages and exposed to natural light (NL) or continuous additional light of different intensities; low intensity (LL-LOW), medium intensity (LL-MED) and high intensity (LL-HIGH). Vertical bars denote SEM. Significant differences ($p \leq 0.05$) between groups are indicated by different letters within sample date and by (*) within the same group compared to the previous sample date. Number of fish sampled in each group is 86-209.

weeks from March to May, the K of all LL groups increased (LL-LOW: $F = 60.67$, $p<0.001$; LL-MED: $F = 50.59$, $p<0.001$; LL-HIGH: $F = 142.90$, $p<0.001$). The increase was most pronounced in the LL-HIGH group, which had a significantly higher K value than all other groups, while the LL-MED group had a significantly higher K value than the NL group ($F = 18.55$, $p<0.001$). K decreased in the NL ($F = 15.87$, $p<0.001$) and LL-LOW groups ($F = 14.17$, $p<0.001$) from week 17 to 23 (May-June). At harvest, the K value was highest in the LL-HIGH group followed by LL-MED, LL-LOW and NL. All groups were significantly different from each other ($F = 60.13$, $p<0.001$)

Table 2. – Specific growth rate (SGR in % of body weight per day) and growth in length (mm.day^{-1}) of Atlantic salmon postsmolts reared in sea cages and exposed to natural light (NL) or continuous additional light of different intensities; low intensity (LL-LOW), medium intensity (LL-MED) and high intensity (LL-HIGH), n=86-209. SGR in brackets is based on the total weight of gutted fish in June back-calculated to mean live body weight.

Group	Period							
	10 Jan. -13 Feb.		13 Feb. - 26 Mar.		26 Mar. - 08 May		08 May - 24 June	
	SGR	mm/day	SGR	mm/day	SGR	mm/day	SGR	mm/day
NL	0.33	0.66	0.64	0.97	0.59	1.18	0.49 (0.41)	1.12
LL-LOW	0.44	0.97	0.45	0.74	0.73	1.16	0.34 (0.52)	0.84
LL-MED	0.47	0.97	0.52	0.89	0.69	0.97	0.65 (0.59)	1.28
LL-HIGH	0.28	0.62	0.65	1.17	0.94	1.27	0.55 (0.49)	0.98

Table 3. – Sexual maturation of Atlantic salmon at the 1-sea-winter stage reared in sea cages and exposed to natural light (NL) or continuous additional light of different intensities; low intensity (LL-LOW), medium intensity (LL-MED) and high intensity (LL-HIGH).

	Group			
	NL	LL-LOW	LL-MED	LL-HIGH
No. of mature fish	12	0	0	0
No. of immature fish	187	86	266	99
% maturation	6	0	0	0
p-level (χ^2-test)		0.018	< 0.001	0.012

apart from the LL-LOW group which was not significantly different from the NL group.

Sexual maturation

The proportion of sexually maturing fish at the sea-winter stage was 6 % in the NL group, whereas no maturation was detected in the LL groups (Table 3). All LL groups differed from the NL group ($p<0.02$) and all maturing fish were male.

DISCUSSION

The higher growth during the experiment found in all LL groups compared to the NL group is in agreement with previous studies on salmonids in fresh water (Saunders *et al.*, 1985; Villarreal *et al.*, 1988; Stefansson *et al.*, 1991; Solbakken *et al.*, 1994) and in sea water (Kråkenes *et al.*, 1991; Endal *et al.*, 1991; Taranger *et al.*, 1991; Hansen *et al.*, 1992; Taranger *et al.*, 1995) where exposure to LL or long photoperiods during winter and spring resulted in an increased growth rate. The growth enhancement effect demonstrated in this experiment can possibly be explained by an adjustment of an endogenous rhythm controlling seasonal growth patterns in the salmon and/or by direct photostimulation of growth (Saunders and Harmon, 1988; Kråkenes *et al.*, 1991; Endal *et al.*, 1991; Taranger *et al.*, 1991; Hansen *et al.*, 1992; Taranger, 1993).

In the present study, four different day/night light intensity ratios were operating as a result of continuous additional light being superimposed over natural daylight (the light intensity difference between groups at night remaining constant). The four day/night light intensity ratios gave a graded response in growth, with the lowest ratio (LL-HIGH) giving the most rapid and pronounced increase in growth rate. The earlier increase and better growth with higher light intensity at night was observed in earlier work carried out on juvenile salmon in fresh water. Stefansson *et al.*, (1991) showed that the ratio between day/night intensity is important with respect to timing and increase in growth rate. Earlier growth responses and advanced smolting were demonstrated in one group of fish reared under a day/night light intensity ratio of 1 400lux/1 400lux, successively followed by a group of day/night light intensity ratio 1 400 lux/27 lux, and finally followed by a simulated natural photoperiod group with a day/night light intensity ratio of 1 400 lux/darkness. By contrast, freshwater juvenile salmon reared under simulated natural photoperiod of 27, 335 or 715 lux at daytime (day/night light intensity ratio equal to infinity in all groups) showed no differences in growth rate (Stefansson *et al.*, 1993), indicating that different light intensities *per se* had no effects on growth. Taken together our study and the two of Stefansson *et al.* (1991, 1993), indicate that growth rate is influenced by the relative difference between day and night light intensity rather than the absolute intensity.

In contrast to the previous studies in sea water, no consistent initial reduction in SGR or length growth was recorded in any of the LL groups following onset of continuous light, compared with the NL group. However, K was lower in all LL groups than in the NL group 11 weeks after onset of continuous light (in March). This may indicate a lower initial feed intake in the LL groups compared to the NL group during this period, as previous studies have shown a direct positive correlation between feed intake and K (Storebakken and Austreng, 1987; Kindschi, 1988; Wotton, 1990; Klontz *et al.*, 1991; Juell *et al.*, 1994; Misund, 1996). Thus the K in the LL groups may indicate an initial growth depression during the first 11 weeks which we were unable to detect on mean body weight with the present sampling strategy.

The reduced incidence of maturation in the LL groups compared to the NL group is in accordance with the findings of Taranger *et al.* (1991), Hansen *et al.* (1992), Taranger (1993) and Taranger *et al.* (1995). Reduced sexual maturation in the LL groups may be due to a photoperiodic advancement of a postulated 'decision period' during winter and early spring as previously suggested in salmonids (Duston and Bromage, 1988; Taranger, 1993; Thorpe, 1994*a, b*). Failure to build up sufficient energy stores or reach a critical gonadal development before or during the advanced 'decision period' may have prevented the fish from maturing in the present year (Taranger, 1993; Thorpe, 1994*a, b*). By contrast, Kråkenes *et al.* (1991) and Endal *et al.* (1991) noted a higher incidence of maturation at the 1-sea-winter stage following an abrupt change to continuous light during winter/spring. Their findings can be explained by a very different experi-

mental setup with small cages which might have led to higher maturation.

In contrast to the graded growth response to different light intensities, no gradation was found in sexual maturation response in the LL groups. The threshold value of light intensity on sexual maturation may therefore be lower than that which affects growth rate.

The authors are aware of some weaknesses in the study, such as lack of replications and difficulties of random sampling in large populations. However, we preferred to do the study under commercial conditions so that growth, behaviour and physiology were kept at a realistic level.

CONCLUSION

The results of this study suggest that light intensity is of importance to the effect of continuous additional light on growth in Atlantic salmon, whereas all intensities employed of continuous additional light were equally effective in reducing the proportion of sexually maturing fish groups. This study gives further evidence to support the use of continuous additional light during winter and spring as a simple and effective method to enhance growth and reduce the incidence of maturation in farmed salmon.

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