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Effects of light source and intensity on sexual maturation, growth and swimming behaviour of Atlantic salmon in sea cages

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ABSTRACT: We investigated how highly efficient LED light sources may be used in Atlantic salmon cage farming. Specifically, we tested the incidence of sexual maturation and growth patterns in autumn sea-transferred Atlantic salmon *Salmo salar* L. during their second sea winter given continuous artificial light (LL) (between 13 January and 18 June) of 5 different intensities using LED sources, compared to a single intensity provided by a metal halide (MH) source or a control treatment of natural light (NL). Growth effects were independent of light source, but increased with irradiance. We propose a model wherein sufficiently high irradiance from the artificial light source will give a long day signal throughout late winter and spring, an intermediate irradiation will give a long day signal until it is outcompeted by the seasonal increase in natural light, and an irradiance that is always below the threshold will not be perceived as different from natural light. Sexual maturation in males (6.1% under NL) was evenly arrested at all intensities, and swimming activity at night increased during winter in lit groups. We conclude that LED lamps may replace MH sources at similar intensity. Reducing the light irradiance of the superimposed light reduced the growth-stimulating effect, but all irradiances reduced the incidence of sexual maturation.

KEY WORDS: *Salmo salar* · Photoperiod · Salmonid aquaculture · Cage environment

INTRODUCTION

In the late 1980s and early 1990s, experimental studies demonstrated the potential of using artificial light as a method for reducing the incidence of unwanted sexual maturation (Taranger et al. 1995, Oppedal et al. 1997) and increasing growth rate (Saunders & Harmon 1988, Kråkenes et al. 1991, Hansen et al. 1992) in cage-farmed Atlantic salmon *Salmo salar*. The commonly adopted protocol has been to use continuous artificial light between early January and June (Leclercq et al. 2011). This protocol reduces the incidence of sexual maturation (see review by Taranger et al. 2010) and stimulates somatic growth (e.g. Hansen et al. 1992, Oppedal et al. 1997, 2006). The continuous light treatment between January and June is an advancing photoperiod (e.g. Taranger et al. 2010), which phase-advances endogenous rhythms (Duston & Bromage 1988, Bromage et al. 2001) and reduces the incidence of sexual maturation by advancing and shortening a critical time window (gate) during which puberty commences (Duston & Bromage 1988, Taranger et al. 2010). It can also advance a seasonal growth pattern (Oppedal et al. 1999, 2006, Endal et al. 2000, Nordgarden et al. 2003) and/or affect growth by direct photo-stimulation (Saunders & Harmon 1988, Komourdjian et al. 1989, Björnsson et al. 1997). Light also affects both vertical distribution and swimming behaviour (Oppedal et al. 2001).

In most of the studies cited above, relatively high intensity, wide spectrum, metal halide lamps were

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used, but these powerful lamps have a high running cost (Leclercq et al. 2011) and potential welfare impacts (Migaud et al. 2007). In earlier studies on Atlantic salmon (Oppedal et al. 1997, 1999) and rainbow trout *Oncorhynchus mykiss* (Taylor et al. 2006), where continuous light was superimposed on the natural light in cages or tanks, the growth response was dependent on the light intensity/irradiance of the superimposed light. Vice versa, Leclercq et al. (2011) found a linear relationship between maturation rate and mean light-irradiance (from light sources giving different light spectra) in the rearing volume, but their study could not characterize the effect of light intensity on growth.

Following the success of cage illumination, specially designed underwater lighting systems have been developed. Some of these are built from light-emitting diodes (LEDs), and have a long lifespan without a weakened output effect, high electrical efficiency, come to full brightness without the need for a warm-up time, can be built to emit specific light distributions and can be dimmed down to a desired irradiance.

The aim of the present study was to compare the growth, incidence of sexual maturation and swimming speed of 2-sea winter (2SW) autumn-transferred Atlantic salmon reared under continuous light (LL) of 5 different intensities using a specially designed LED lamp compared to 1 intensity using a metal halide (MH) source and a control treatment of natural light (NL).

MATERIALS AND METHODS

The experiment was carried out at the Institute of Marine Research sea cage facilities at Matre in Masfjorden, Norway (60.8° N), from 13 January to 18 June 2012. About 40 000 Atlantic salmon (mean ± SD: 3.3 ± 0.9 kg) were pumped into a well-boat and randomly re-distributed into 13 experimental cages. We used 2SW fish to increase the potential for sexual maturation. Each cage was 12 m long × 12 m wide × 12 m deep (1728 m^3) and was stocked with approximately 3077 individuals. These fish were produced from eyed eggs (Aqua Gen AS, Trondheim, Norway) incubated on 13 January 2010, first fed under continuous light from 16 March 2010 and reared under a 6 wk light:dark 12:12 h photoperiod followed by 6 wk under continuous light before being transferred to seawater as underyearling smolts (84 ± 12 g) on 22 October 2010. The fish were reared in 4 cages under natural photoperiod until the start of the experiment on 13 January 2012.

Experimental design

An overview of the experimental farm with placement of the treatment groups is shown in Fig. 1. Three cages were exposed to NL and 10 cages to continuous additional light (LL). The lamps were positioned centrally within the cage, at 7 m depth from January and moved to 5 m depth in early April. These depths were chosen to match the preferred temperature and swimming depth of the fish (Oppedal et al. 2007), which were confirmed using echo-sounders continuously displaying vertical distribution (Oppedal et al. 2011). Three of the LL cages were illuminated by 1 submersed MH lamp of 400 W (Sublite 400W Integra, Akvagroup), and 7 cages were illuminated by custom-made dimmable LED lamps (modified SubLED400W, Akvagroup) with maximum power rating of 400 W. The LED lamps were built from selected individual LEDs (neutral

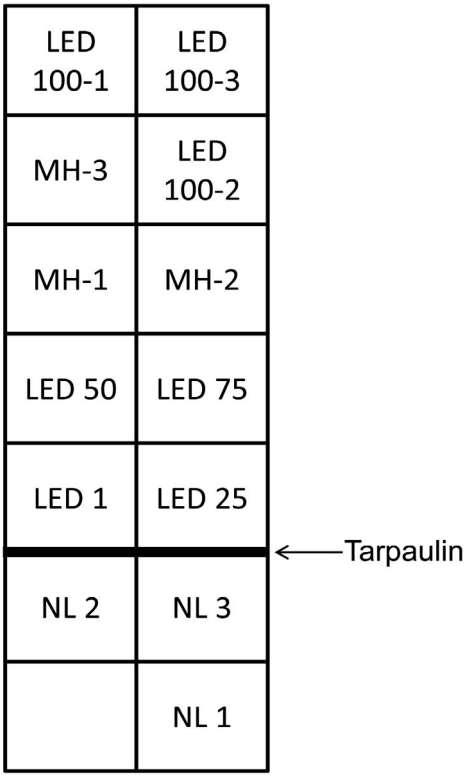

Fig. 1. Overview of the experimental farm with the placement of the different experimental cages. Three cages were illuminated by natural light (NL), 3 by submersed 400 W metal halide (MH) lamps and 7 by light-emitting diode (LED) lamps. Three of the LED-lit cages were illuminated with the LED sources at their maximum output (100%), with the remaining 4 LED lamps dimmed down to 75, 50, 25 and 1% (minimum setting possible). See 'Materials and methods' for more details

white, royal blue, blue and cyan) to generate a normal light distribution with slightly more energy in the blue-green colour spectrum (Fig. 2). Three of the LED-lit cages were illuminated with the LED sources at their maximum output (100%), with the remaining 4 LED lamps dimmed down to 75, 50, 25 and 1% (minimum setting possible). Measured light irradiances 0.5 m from light sources at the start of the trial in decreasing order were: 3.8, 3.3, 2.3, 1.13 and 0.06 µmol s^{-1} m^{-2} for LED lamps and 4.5 µmol s^{-1} m^{-2} for MH lamps. Six tarpaulins (5 m wide × 10 m deep) were mounted between control cages and lit cages to minimize stray lighting. Each tarpaulin overlapped the neighbouring tarpaulin by 1 m. Group placement in cages was chosen to keep the highest intensities away from low intensity and control groups (Fig. 1). The 3 replicates of both LED and metal halide treatment were randomly allocated. The fish were fed commercial dry feed (Optiline 2500-9, Skretting) in excess twice daily (between 08:00 and 10:00 h and between 13:00 and 15:00 h). Due to technical problems with the light and feeding system, 1 replicate LED cage (LED 100-3) was removed from all analysis.

Dead fish were removed from the cages every day. Mortality was low (<0.7%) during the study and was not related to treatment.

Sampling

On 16 January, 13 April and 18 June, approximately 100 fish from each cage were sampled. Consequently the study involved 3 samples and 2 periods (first period between 16 January and 13 April and last period between 13 April and 18 June). Fish were sampled with a casting net (5 × 5 × 7 m) which was deployed at the cage bottom for 15 to 25 min, after which it was rapidly pulled to the surface. From this sample (300–1000 individuals), subsamples of 10 to 50 fish were netted out using a crane-operated, 1 m diameter circular net. In January and April, the fish were anaesthetised (Finquel®, 100 mg l^{-1}), weighed to the nearest 10 g, fork length measured to the nearest cm and returned to the cage. In June, the fish were killed with a blow to the head followed by bleeding, measurements were taken, and the fish were opened, sex determined and the gonads weighed. Males with a gonadosomatic index (GSI) > 0.4% (e.g. Endal et al. 2000) and females with a GSI > 0.5% were considered to have started their sexual maturation.

Swimming speed

Cameras were positioned at the depth of the main school to describe representative swimming speed by observing NL, MH and LED at 100% output (LED100) cages on 1 random day/night within each period (17/21 February, 27/29 March and 31 May). Instantaneous swimming speeds were calculated in body lengths (BL) s^{-1} by recording the time taken between the snout and the tail of a fish passing a vertical reference. Perpendicular to the main current direction, a random sample of 10 fish was observed in both directions to account for potential effects of water current speed. Observations within the dark cages at night were aided by use of an infra-red light source (see Korsøen at al. 2009).

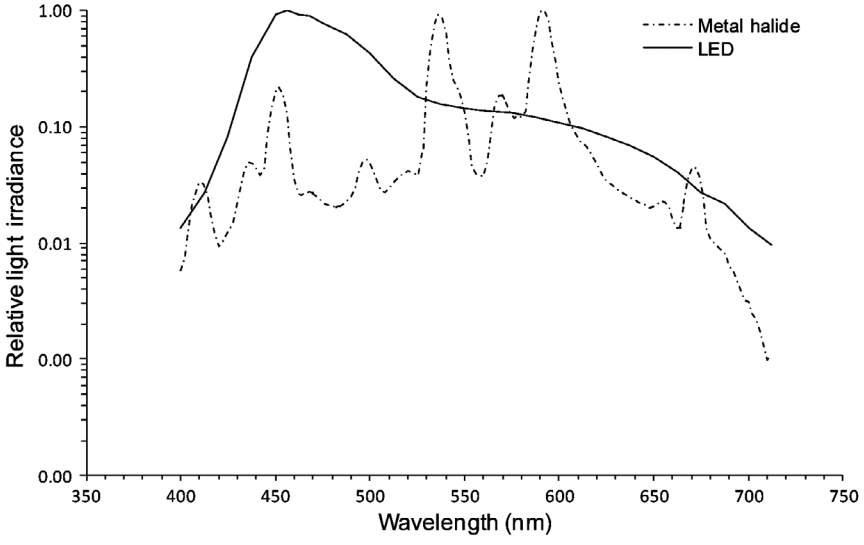

Fig. 2. Spectral distribution of the light emitted by the LED and metal halide lamps. The LED lamps were built from selected individual LEDs (neutral white, royal blue, blue and cyan) to generate a normal light distribution with slightly more energy in the blue-green colour spectrum

Light spectral composition and intensity

The spectral irradiance of the 2 lamps over the visible spectrum (λ 400–740 nm; Fig. 2) was measured 0.5 m from the light source within a tank of saltwater using a spectrophotometer (RAMSES-ACC.VIS hyperspectral UV-VIS, TriOS) in a dark room. At their full output, both the MH and LED lamps gave measureable irradiance between 400 and 715 nm. However, a broad peak of the LED lamp was evident between 425 and 525 nm (blue and green area). The MH lamp had several narrow-banded peaks, at 592 nm (orange), 536 (green/yellow), 452 (violet/blue) and 570 nm (yellow).

At the farm, measurements were carried out using a LI-193SA spherical quantum sensor (LI-COR) with a sensitivity down to 0.01 µmol s^{-1} m^{-2} and a LI1400 logger unit. NL daytime measurements were done on 21 February at 13:00 h with no cloud cover, with snow on the mountains, but with no direct sunlight at the farm. Measurements started at 0.1 m depth and were done for every meter depth down to 13 m. Night measurements (no moon) were done at horizontal distances between 0.5 and 15.5 m from the lamp (0.5 m intervals) with the light sensor head pointing towards the light source. Light irradiance decreased quickly with distance from the surface (Fig. 3, NL-day) and the different light sources (Fig. 3). Already at 4 m distance, the irradiance was down to 1% of the value measured 0.5 m from both the MH and LED lamp at full power. Both night and daytime measurements were done outside the experimental cages to avoid interference from the fish. No measureable irradiance was found in the NL cages during the night. The Secchi depth during measurements was 10 m.

During the night of 7 March, the irradiances within a cage holding fish were measured. The measurements were done with 3 m distance between the lamp and the sensor, at 2 m depth (with few fish present between lamp and sensor), and at 5 m depth (depth of highest biomass estimated from the on-line echo sounder. The measurements were done every 15 s between 21:00 and 22:00 h (2 m, few fish) and 23:00 and 00:00 h (5 m, maximum density). During the measurements, the fish positioned themselves evenly from the cage wall towards the cage centre, but avoided the nearest 2 m around the lamp. Based on the average light irradiance measured over 1 h (Fig. 4), and an approximately 1 m broad school of fish between lamp and sensor, at a relevant density for caged farmed salmon, the attenuation of light irradiance by the fish was approximately 50%.

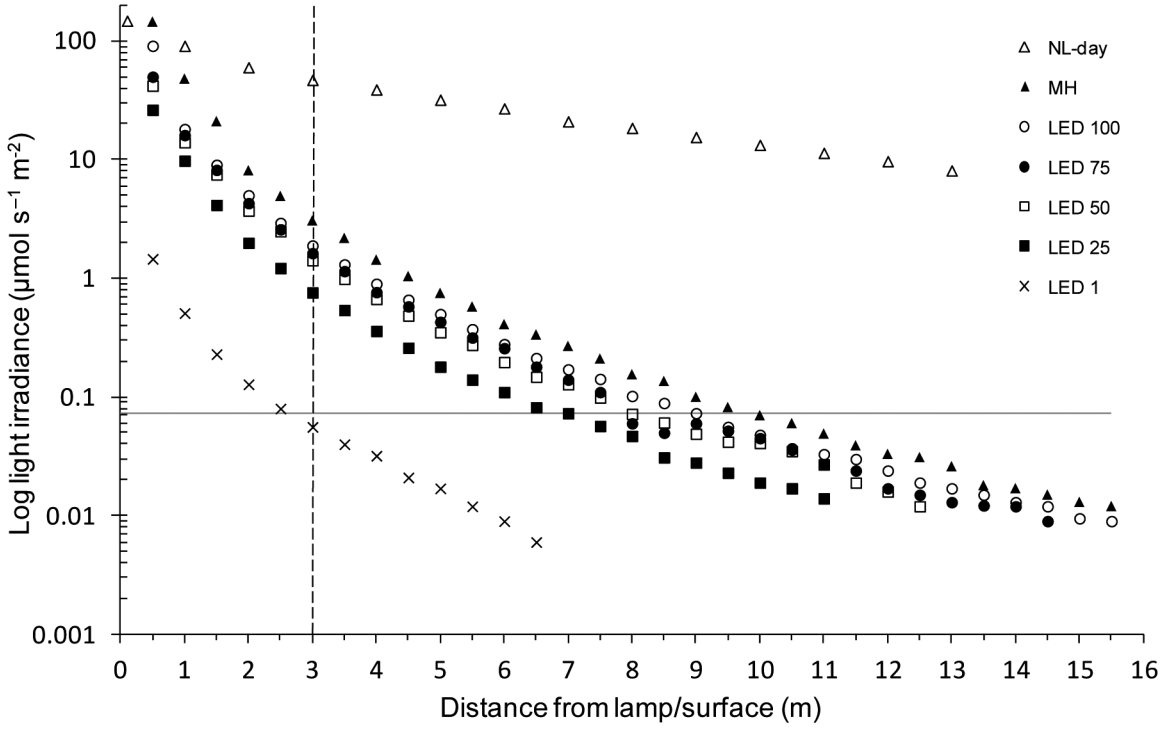

Fig. 3. Horizontal profile of light-attenuation generated by the LED and metal halide (MH) lamps measured on a night with no moon. The light intensity at different depths on a clear day, but with no direct sunlight, is included for comparison (NL-day). The horizontal line is the irradiation necessary to reduce plasma melatonin to daytime levels (see Migaud et al. 2006); the vertical line shows the irradiance values used in the correlation analysis (Fig. 6)

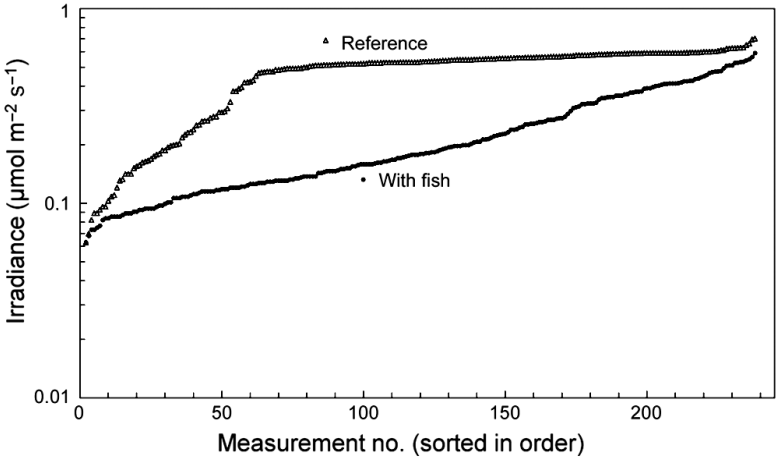

Fig. 4. Light irradiance measured 3 m from a metal halide lamp at a reference depth in cages (2 m depth with few Atlantic salmon present between lamp and sensor), compared to measurements at the depth of the highest biomass (5 m) with fish between the lamp and the measurement probe. Data were stored every 15 s, sorted and plotted in increasing order. The reference data were collected between 21:00 and 22:00 h (mean ± SD; 0.47 ± 0.16 µmol s^{-1} m^{-2}) and data with fish present between 23:00 and 00:00 h (0.23 ± 0.13 µmol s^{-1} m^{-2})

Temperature and salinity

The fish farm where the experiment was done is located 1500 m from the outlet of a hydroelectric powerplant and has a brackish (<25 ppt) layer between 0 and 2–5 m (Fig. 5A). The temperature at 5 m (below the brackish layer) varied between 6 and 8°C until March, between 7 and 10°C during April and May and between 9 and 12°C in June (Fig. 5B).

Calculations and statistics

Fulton's condition factor (K) was calculated as $100W/L^3$, where W is body weight (g) and L is fork length (cm) (Busacker et al. 1990). The change in K (ΔK) was calculated as $K_2 - K_1$ (K at $t_2 - K$ at t_1). Specific growth rate (SGR,% d^{-1}) was calculated as (exp(q) – 1)100 (Houde & Scheckter 1981), where $q = [\ln(W_2) - \ln(W_1)]/(t_2 - t_1)$ (Bagenal & Tesch 1978) and W_2 and W_1 are average body weight at times t_2 and t_1, respectively. The GSI was calculated using: GSI = {[gonadal weight (g)100]/body weight (g)}.

Statistica version 12 (Dell Statistica) was used for statistical analysis and the preparation of graphs. Within sampling points (dates), nested ANOVAs were used to test for significant effects of: (1) treatment (NL, MH and LED100) on weight and SGR with replicate (sea-cage) nested as a random factor in treatment groups; (2) treatment and time of day (day/night) on swimming speed, with replicate nested as a random factor in treatment group and time point. Significant nested ANOVAs were followed by factorial ANOVAs and Newman-Keuls post hoc tests. To reveal possible significant correlations between irradiance and body weight, K, SGR and ΔK, Pearson product moment correlations were computed within sampling points. The analysis was done on the LED-illuminated groups to find the effect of LED irradiation and later on all illuminated groups (LED and MH) to find the effect of irradiance independent of illumination technique; $p < 0.05$ was regarded as significant. The irradiances 3 m from the light source (Fig. 3) were used in the correlation analysis, and for the replicated groups (LED100 and MH) the mean value was used. χ^2 tests were used to test group differences (NL, MH, LED100) in the incidence of sexually mature males (level of significance Bonferroni adjusted to $p < 0.017$).

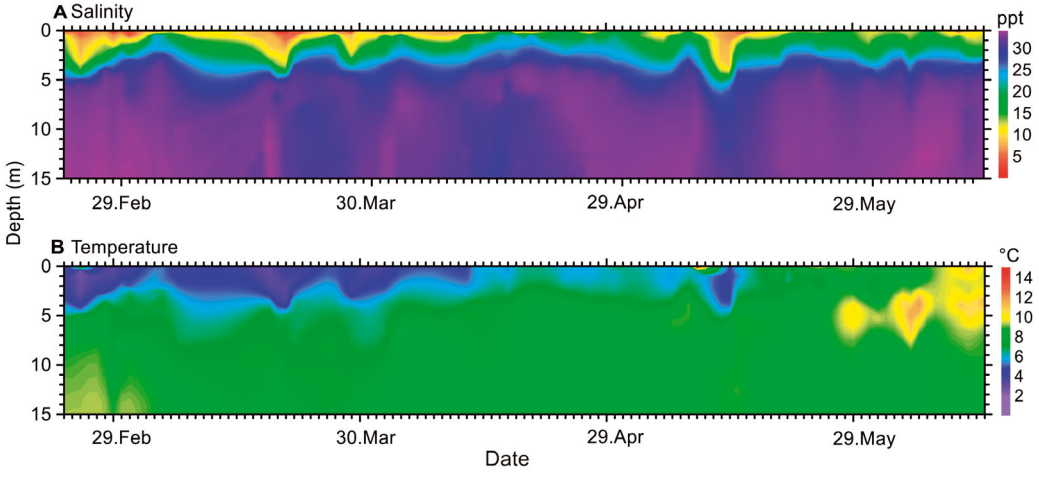

Fig. 5. (A) Salinity (ppt) and (B) temperature (°C) between 0 and 15 m depth during the experiment

RESULTS

The Atlantic salmon reared under continuous light for 5 mo from January were heavier and had a higher condition factor than salmon reared under natural light. The growth effect was independent of lighting technology (LED or MH) but was dependent on light irradiance; growth rate between April and June was positively correlated with LED irradiance.

Growth and sexual maturation

Neither photoperiod, lighting technology nor irradiance gave significant effects on weight, SGR, K or ΔK in the first period (until 13 April) (Table 1, Fig. 6). In the last period, the MH and LED100 groups grew faster than the NL group and were significantly larger and had a significantly higher condition factor in June (Table 1).

In the last period there was a significant correlation between LED irradiance and SGR ($p = 0.02$, $r^2 = 0.89$, Fig. 6B) and a close to significant correlation ($p = 0.07$, $r^2 = 0.73$, Fig. 6D) between LED irradiation and ΔK. In June there was a close to significant correlation between LED irradiance and weight ($p = 0.10$, $r^2 = 0.65$, Fig. 6A) and K ($p = 0.08$, $r^2 = 0.69$, Fig. 6C). If the MH data were included in the correlation analysis (MH irradiance = 3.06 µmol s^{-1} m^{-2}), the correlations (irrespective of illumination technique) were all significant (weight: $p = 0.03$, $r^2 = 0.72$; K: $p = 0.03$, $r^2 = 0.75$; SGR: $p = 0.01$, $r^2 = 0.93$; ΔK: $p = 0.04$, $r^2 = 0.71$), and SGR and ΔK increased with irradiance in the last period and weight and K in June increased with irradiance.

The incidence of sexually mature males was significantly higher in the NL group than in the MH or LED100 groups (Table 1). A generally low incidence of maturation did not allow for testing the effects of LED irradiance. In females, sexual maturation was only found in 1 of the NL cages (Table 1).

Swimming speed

Swimming speed (V_{day} and V_{night}) was only significantly affected by treatment in February (NL, MH and LED100), but with significant effects of time of day (day/night) and with significant interaction between treatment and time of day in all 3 sampled periods. V_{day} of the NL fish averaged 0.8, 0.65 and 0.63 BL s^{-1} in February, March and May, respectively, and V_{night} values were significantly reduced to 25 and 26% of their respective V_{day} values in February and March and with a smaller, but significant reduction to 84% in May (Fig. 7). The V_{day} of the MH and LED100 groups was significantly lower than that of the NL group in March, and MH was significantly

Table 1. Mean ± SD weight and condition factor (K) of Atlantic salmon *Salmo salar* given for each cage and treatment group in January, April and June, and incidence of sexual maturation (%) for males (M; mature fish gonadosomatic index, GSI > 0.4%) and females (F; mature fish GSI > 0.5%) for each cage registered at the June sampling. Significant differences within sample dates are noted by different superscript letters. The number of sampled fish per cage varied between 93 and 148. NL: natural light; LED 1, 25, 50, 100: light-emitting diode lamp dimmed down to a percentage (1, 25, 50 or 100%) of its maximum output; MH: metal halide lamp

Sample date	16 January		13 April		18 June			
Group	Weight (kg)	K	Weight (kg)	K	Weight (kg)	K	Mature M (%)	Mature F (%)
NL 1	3.02 ± 0.86	1.14 ± 0.12	5.44 ± 1.50	1.31 ± 0.14	6.64 ± 1.47	1.29 ± 0.14	13.7	9.8
NL 2	3.21 ± 0.92	1.18 ± 0.13	5.44 ± 1.32	1.28 ± 0.14	6.27 ± 1.62	1.25 ± 0.11	2.5	0.0
NL 3	3.20 ± 0.90	1.15 ± 0.10	5.13 ± 1.17	1.26 ± 0.13	6.05 ± 1.30	1.22 ± 0.11	5.6	0.0
LED 1	3.10 ± 0.90	1.15 ± 0.11	4.98 ± 1.25	1.27 ± 0.11	5.99 ± 1.39	1.24 ± 0.11	0.0	0.0
LED 25	3.25 ± 0.81	1.15 ± 0.09	5.33 ± 1.34	1.23 ± 0.14	6.58 ± 1.41	1.29 ± 0.11	6.3	0.0
LED 50	3.27 ± 0.91	1.16 ± 0.13	5.12 ± 1.46	1.25 ± 0.11	6.49 ± 1.74	1.33 ± 0.14	0.0	0.0
LED 75	3.23 ± 0.75	1.16 ± 0.10	5.00 ± 1.10	1.22 ± 0.12	6.47 ± 1.60	1.28 ± 0.13	0.0	0.0
MH 1	3.30 ± 0.98	1.17 ± 0.13	4.97 ± 1.38	1.26 ± 0.12	6.86 ± 1.71	1.36 ± 0.13	0.0	0.0
MH 2	3.26 ± 0.92	1.17 ± 0.14	5.11 ± 1.39	1.23 ± 0.12	7.18 ± 1.40	1.33 ± 0.09	3.6	0.0
MH 3	3.28 ± 0.88	1.17 ± 0.13	5.33 ± 1.38	1.26 ± 0.13	7.33 ± 1.57	1.35 ± 0.11	0.0	0.0
LED 100 1	3.29 ± 0.86	1.19 ± 0.10	5.36 ± 1.32	1.28 ± 0.16	7.07 ± 1.64	1.33 ± 0.10	0.0	0.0
LED 100 2	3.44 ± 0.81	1.20 ± 0.11	5.23 ± 1.43	1.26 ± 0.13	7.27 ± 1.52	1.33 ± 0.14	0.0	0.0
NL	3.14^a ± 0.89	1.16^a ± 0.01	5.34^a ± 1.34	1.28^a ± 0.18	6.32^a ± 1.51	1.25^a ± 0.12	6.1^a	3.3
MH	3.28^a ± 0.92	1.17^a ± 0.01	5.14^a ± 1.39	1.25^a ± 0.12	7.12^b ± 1.57	1.35^b ± 0.11	1.3^b	0.0
LED100	3.37^a ± 0.83	1.19^a ± 0.01	5.30^a ± 1.37	1.27^a ± 0.14	7.16^b ± 1.58	1.33^b ± 0.12	0.0^b	0.0

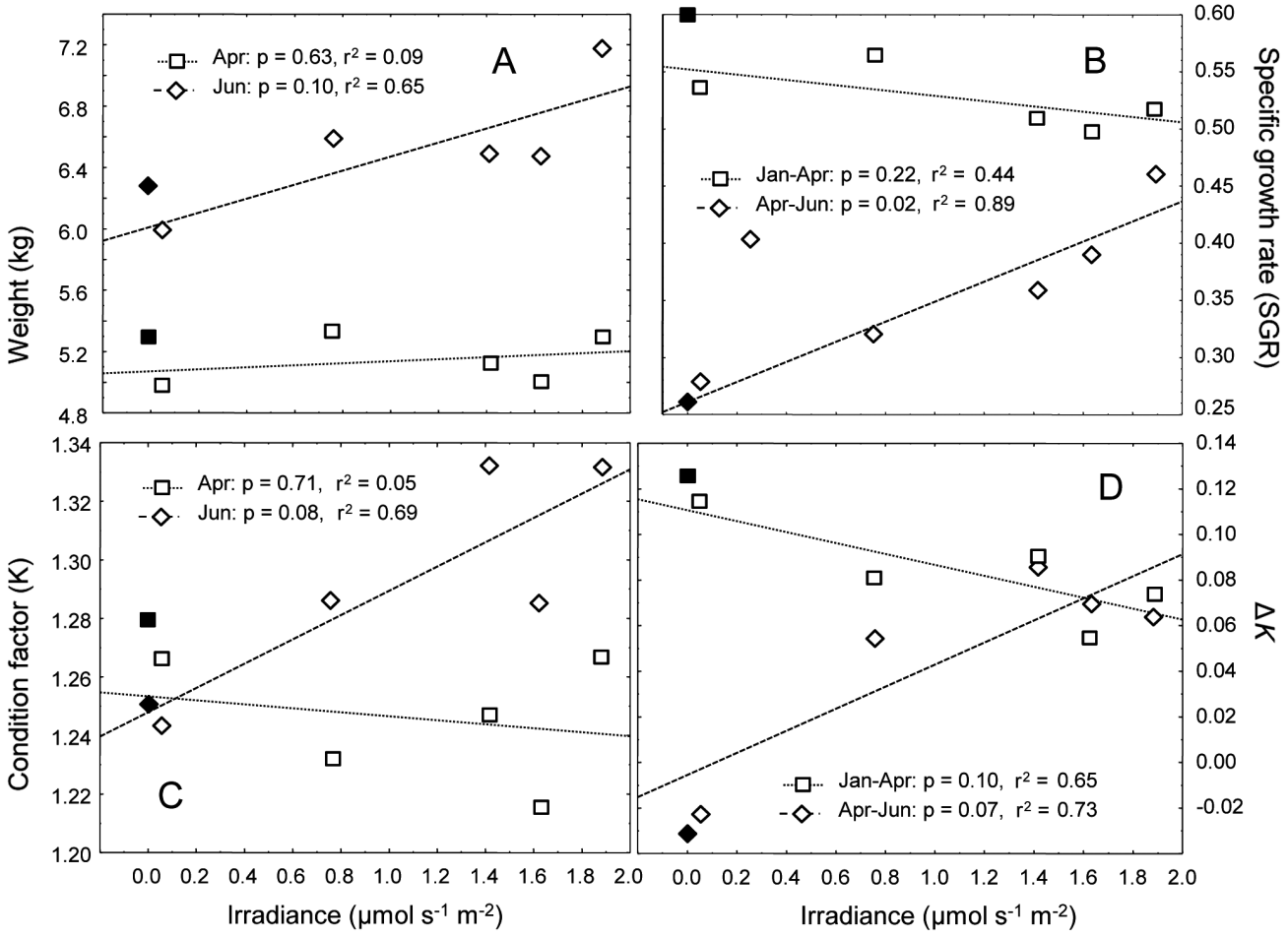

Fig. 6. Correlation between irradiance 3 m from the LED light sources (vertical line in Fig. 3) and (A) weight, (B) specific growth rate, (C) condition factor *K* and (D) change in condition factor (Δ*K*) of Atlantic salmon *Salmo salar*. The corresponding values of the natural light (NL) group (black symbols) are included for illustrational purposes, but were not included in the correlation analysis

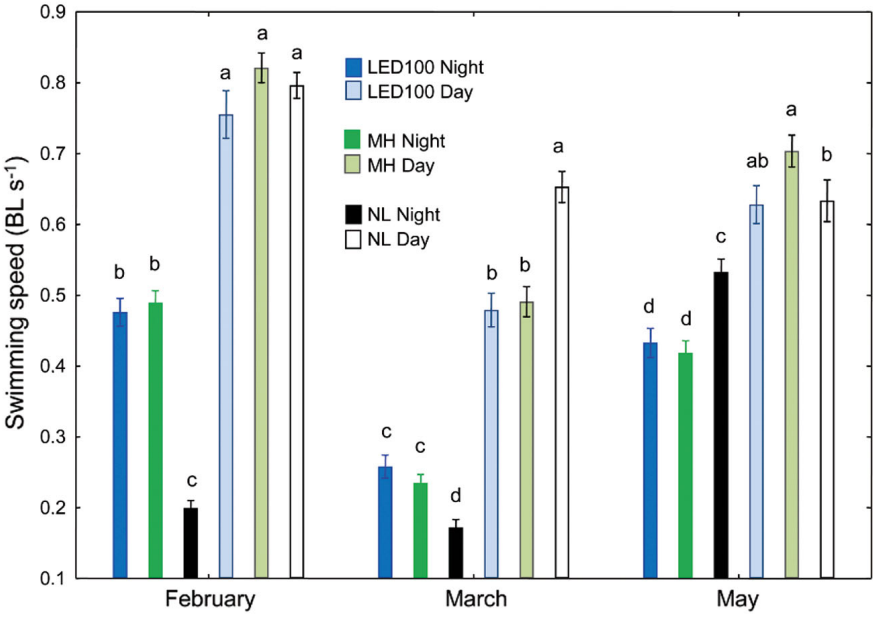

Fig. 7. Nighttime and daytime average swimming speed (body lengths [BL] s^{-1}) of Atlantic salmon *Salmo salar* in the natural light (NL), metal halide (MH) and maximum-output LED (LED100) groups in February, March and May

higher than the NL group in May. Also in the MH and LED100 groups, V_{night} was significantly lower than V_{day} at all times. However, V_{night} of MH and LED100 was significantly higher than NL in February and March and lower in May, and the reduction was only between 48 and 69% of their V_{day} values.

DISCUSSION

This study confirms that highly efficient LED light sources may replace the traditionally used MH lamps at the same irradiation. Altogether our results are in line with earlier studies showing that continuous artificial light superimposed on the natural light cycle from about winter solstice has a growth-stimulating effect on Atlantic salmon in sea-cages (Kråkenes et al. 1991, Hansen et al. 1992, Oppedal et al. 1997, 2006, Duncan et al. 1999, Endal et al. 2000, Johnston et al. 2003). This growth stimulation is related to the light/extended photoperiod itself, and not to a longer feeding period (Kråkenes et al. 1991, Taylor et al. 2006). Published data indicate that fish growth follows a seasonal pattern influenced by variations in day length (reviewed by Boeuf & Falcón 2001). Further, the fact that Endal et al. (2000) and Oppedal et al. (2006) found a continuation of faster growth than under natural light, also after artificial lighting ceased, supports the theory of an adjusted circannual growth rhythm. Along the same lines, Oppedal et al. (1997, 1999, 2003, 2006), Nordgarden et al. (2003) and Johnston et al. (2003) found distinct shifts in the seasonal patterns of SGR and condition factor following the onset or switching off of artificial light. In the present study, no differences were found after 3 mo, but the groups that were reared under continuous light were significantly heavier and had a higher condition factor 5 mo after the onset of light, harmonizing with the studies above.

It has also been suggested that growth enhancement under long photoperiods is caused by a direct photo-stimulation of growth (Saunders & Harmon 1988, Komourdjian et al. 1989). Johnston et al. (2003) compared the muscle growth of salmon reared under continuous and natural light from the start of the first sea winter, and found that continuous light increased muscle fibre recruitment, possibly by overcoming a short day inhibition of myogenic progenitor cell proliferation. These fish had 28.5% higher fibre number than fish reared under natural light 40 d after the onset of continuous light. As the rate of hypertrophy was unaffected by the light treatment, fish under continuous light subsequently grew better and reached 30% higher body weight after mid-summer. A significantly higher condition factor paralleled the growth increase (Johnston et al. 2003). The development of condition factor in the study of Johnston et al. (2003) is very similar to the results of Nordgarden et al. (2003) and Oppedal et al. (2003, 2006), but in the latter studies, the fish were followed for an additional 6 mo, an extension that revealed a seasonal pattern.

In the studies above, relatively high-intensity light sources were used, but as shown in the present study, where SGR between April and June increased with increasing LED light irradiance, and in earlier studies on Atlantic salmon (Oppedal et al. 1997) and rainbow trout (Taylor et al. 2006), the growth response to the continuous light can be dependent on the light intensity/irradiance. However, in studies using Atlantic salmon juveniles reared under a simulated natural photoperiod (SNP) (winter and spring), combining darkness with a photophase with different light intensities, Stefansson et al. (1993) found no effect of light intensity (27 to 715 lux) on growth, and Handeland et al. (2013) concluded that a light intensity above 20–40 lux was needed to achieve optimal growth. Similarly, growth was insignificant between salmon fry reared at continuous 1400 lux, continuous 27 lux or a photoregime where a 1400 lux SNP photophase was superimposed on a continuous 27 lux background illumination (Stefansson et al. 1990). In rainbow trout reared under a 16 h light:8 h dark photoperiod (Kwain 1975), growth was reduced under 0.2 lux, but not under 2 or 20 lux. Taken together, these studies indicate that unless the light intensity is so low that it affects the feeding ability (0.03–0.04 lux, see Elliott 2011), growth in salmonids is little affected by light intensity. However, studies wherein continuous light was superimposed on the natural light in cages or tanks found a positive correlation between growth and the irradiance of the superimposed light in Atlantic salmon (Oppedal et al. 1997) and rainbow trout (Taylor et al. 2006).

In vertebrates, the pineal gland produces melatonin (described as a biological time-keeping hormone) at night, resulting in high levels in the plasma and cerebrospinal fluid during the night and low levels during the day (reviewed by Mayer et al. 1997, Falcón et al. 2010, Migaud et al. 2010). Moreover, differential results between *ex vivo* pineal production and *in vivo* melatonin studies in salmon indicate that retinal and deep brain photoreception may also contribute to the control of melatonin production by the pineal gland (Migaud et al. 2006). In some species, this rhythm is under endogenous control, but in salmonids, melatonin production seems to be under

photoperiod control only (Falcón et al. 2007), and the circulating melatonin levels reflect the light–dark regime accurately (Alvariño et al. 1993, Randall et al. 1995).

The ability of the light environment to suppress this rhythmic melatonin production is often used as an indication of its success, and Porter et al. (2000) proposed a model where the 'dark' phase melatonin must be reduced below a threshold level to alter growth and sexual maturation. Later, Migaud et al. (2006) indicated 0.016 W m^{-2} (0.074 µmol s^{-1} m^{-2}) as a threshold, where higher irradiances give melatonin levels comparable to daytime levels, and Leclercq et al. (2011) found a maximum suppression of sexual maturation when nighttime mean irradiance was kept above 0.012 W m^{-2} (0.056 µmol s^{-1} m^{-2}). However, in a study on Atlantic cod *Gadus morhua* pineal gland, Vera et al. (2010) found that the intensity threshold was dependent on the light intensity in the previously experienced 'day', an idea that also has been suggested for Atlantic salmon (Oppedal et al. (1997) and rainbow trout (Taylor et al. 2006). In a cage farm like in our study, artificial light is superimposed on the natural light, which increases in period and irradiance during late winter and spring (Fig. 8). If the irradiance from the artificial light source is high enough, it will give a long day signal throughout late winter and spring, and an irradiance that is below the threshold at all times will not be perceived as different from the natural light. Indeed, seen from the present correlation between changes in condition factor and SGR, the fish receiving the lowest LED irradiation developed equally and had a comparable swimming speed (see below) as the fish under natural light. A light source giving an intermediate irradiation will, however, give a long day signal until it is outcompeted by the natural light. It is therefore possible that an intermediate light irradiance will give a long day signal for a shorter period of time and be more comparable to Endal et al. (2000) where continuous light for shorter periods in between November and July gave an intermediate growth stimulation compared to continuous light throughout, and natural light.

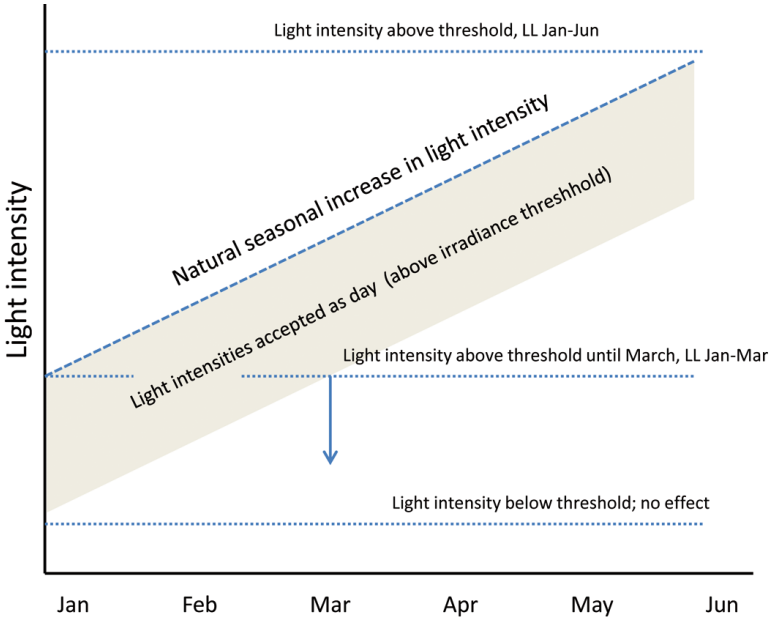

Fig. 8. Possible model for how artificial light of different intensities can translate into a periodic continuous light effect. Natural light increases in period and irradiance during late winter and spring. If the irradiance from the artificial light source is high enough, it will give a long day signal throughout late winter and spring, while irradiances that remain below the threshold will not be experienced as different from the natural light. A light source at intermediate irradiation will give a long day signal until it is outcompeted by the natural light. LL: continuous artificial light

Swimming activity

The main effect of the continuous light was to increase the nighttime swimming activity (V_{night}) during the winter and early spring in accordance with Oppedal et al. (2001) and in contrast to the high V_{day} and low V_{night} of the NL fish (earlier described by Juell & Westerberg (1993), Juell (1995) and Oppedal et al. (2001). This diel rhythm in swimming speed under natural light has been related to light level and might reflect a natural activity rhythm or a loss of ability to school below a critical light level (Juell 1995). Also the increase in V_{night} in the NL group during late spring and early summer has been observed by Oppedal et al. (2001).

It is generally assumed that exercise training up to speeds of 1.5 BL s^{-1} improves growth rates and food conversions in many species of fish (see review by Davison 1997). Thus, it is possible that the increased V_{night} of the illuminated groups could be a factor contributing to their increased growth rate. However, Kiessling et al. (1994) found no difference in growth between Chinook salmon *Oncorhynchus tshawytscha* reared at water currents of 0.5 and 1.0 BL s^{-1}, and Solstorm et al. (2015) found no difference in growth between Atlantic salmon reared at 0.2 or 0.8 BL s^{-1}. Thus, no differences in growth were found between salmonids

swimming at speeds comparable to those observed in the present study (0.2–0.9 BL s^{-1}). Moreover, similar growth differences are found between salmon that are reared under continuous light and natural photoperiod (Nordgarden et al. 2003, Oppedal et al. 2003) when the fish are swimming against the current in tanks. This indicates that the difference in swimming activity is of minor importance for the growth effects seen in the present study.

It is more important that the swimming activity will increase the light exposure of each individual. Light irradiance decreased quickly with distance from the different light sources and was attenuated by at least 50% by the other fish when measured at a fixed point. However, when the fading natural light is weaker than the artificial light, the salmon will move towards the light to retain schooling behavior (Juell et al. 2003). This photic attraction (see Juell et al. 2003, Oppedal et al. 2007, Stien et al. 2014, Wright et al. 2015) and swimming activity (Oppedal et al. 2001, present study) will level out the light exposure between individuals and increase the average irradiance compared with the levels measured at a fixed point.

Sexual maturation

The reduced incidence of sexual maturation in the LL groups in the present study concur with an earlier study on 2SW salmon (Taranger et al. 1998), and studies on grilse maturation (1SW) in spring-transferred (Taranger et al. 1995, Oppedal et al. 1997, Porter et al. 1999, Leclercq et al. 2011), and autumn-transferred (Oppedal et al. 2006) salmon. The reduction in the incidence of sexual maturation was also independent of lighting technology, in line with Leclercq et al. (2011), who suggested that light irradiance rather than light technology or light spectral composition was the prime parameter reducing the incidence of sexual maturation. However, in the present study, the overall incidence of sexual maturation was very low and the data did not allow for testing of the effect of light intensity on incidence of sexual maturation. However, if we compare our measured irradiances with the threshold value of Migaud et al. (2006), this was reached 9.5 m and 9.0 m from the MH and LED100 light sources and corresponding values for the dimmed LED lamps were 8 m (LED75), 7.8 m (LED50), 7 m (LED25) and 2.5 m (LED1). This means that the full volume of all LL cages except LED1 had irradiations above the theoretical threshold level. This effective volume is reduced by the attenuation of the fish, but this is again counteracted by their swimming activity, which brings them close enough to the lamps often enough to make the irradiation in all LL cages high enough to reduce the incidence of sexual maturation.

CONCLUSIONS

The present study confirms that high intensity light superimposed on natural light from January to June in salmon cage farming increases growth, reduces the incidence of sexual maturation and allows the salmon to swim during the night. LED lamps may replace MH at similar intensity, as light irradiance was more important than the lamp type. Reducing the light irradiance of the superimposed light reduced the growth-stimulating effect, but all irradiances reduced the incidence of sexual maturation. We suggest that the salmon interpret a light regime composed of artificial light superimposed on a natural light environment as a long day until the artificial light is outcompeted by the natural light. The consequence of this hypothesis would be that the natural light, which increases in period and irradiance during late winter and spring, will turn off a long day signal and that intermediate irradiances will have the same effect as a shorter period of higher intensity continuous light.

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