



NOTE

Atlantic salmon *Salmo salar* instantaneously follow vertical light movements in sea cages

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ABSTRACT: Atlantic salmon in marine farming environments are exposed to potentially detrimental conditions through space and time. For instance, the vertical distribution of parasitic salmon lice larvae shifts in response to changing salinity conditions. We examined whether stock can be moved away from harmful depths using constant-rate vertical movements of lights at night over short periods. Salmon held in research-scale sea cages were exposed to light movements between depths of 0–12 m and at 5 different speeds (1, 2, 4, 8 and 16 m min⁻¹) on 3 nights. Fish were acclimated to lights fixed at 8 m depth in a temperature- and salinity-stratified cage environment, partitioning salmon into surface-positioned (47%) and light-positioned subgroups (53% of the population). A high proportion (50–65%) of the light-positioned group followed lights between upper and lower cage sections when moved up to a critical speed of 4 m min⁻¹. However, the surface-positioned group always persisted. Following decreased when lights were moved at higher speeds, equivalent to or faster than fish swimming speeds measured under fixed lighting. Instantaneous vertical light movements at night may effectively move salmon away from fluctuating unsuitable depths (e.g. lice-rich depths), into temporary favourable depths (e.g. surface brackish waters to treat against stenohaline parasites), and throughout cages to avoid crowding in narrow depth ranges.

KEY WORDS: *Salmo salar* · Moving light · Swimming depth · Management · Fish behaviour

INTRODUCTION

Atlantic salmon *Salmo salar* distribute variably and unevenly in sea cage environments, selecting preferred depths in response to gradients in environmental and internal drivers (Oppedal et al. 2011). Paradoxically, their position can be at odds with that which optimises their welfare. Harmful depth-specific conditions occur in salmon sea cages (e.g. Dempster et al. 2009), which can fluctuate spatio-temporally. For instance, free-living infective stages of the parasitic salmon louse *Lepeophtheirus salmo-*

nis concentrate at different depths depending on vertical salinity gradients (Jones & Beamish 2011). Also, salmon periodically aggregating in a narrow depth range at extreme densities (Oppedal et al. 2011) can lower dissolved oxygen levels as they respire (Johansson et al. 2006). These adverse conditions may be mitigated by manipulating salmon depth in sea cages over short time scales.

Artificial light effectively modifies salmon swimming depth in sea cages at night (Juell & Fosseidengen 2004, Oppedal et al. 2007). Sudden vertical light adjustments reposition salmon (Juell & Fossei-

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dengen 2004), and moving lights in the horizontal plane induce a sustained swimming response in tank-held salmon (Herbert et al. 2011). If salmon also follow constant-rate light movements in vertical trajectories, they could be used by farmers to control salmon depth instantaneously to avoid harmful conditions.

A major concern with using artificial lighting is that other environmental variables affect salmon swimming depth and override light attraction under some circumstances (Oppedal et al. 2011). For instance, light attractiveness fades in temperature-stratified environments when optimal temperatures for salmon thermoregulation ($\sim 17^{\circ}\text{C}$; Johansson et al. 2006) occur outside illuminated depths (Oppedal et al. 2007). Attraction also diminishes if lights are of lower intensity (Stien et al. 2014). Therefore, salmon may not be drawn to moving artificial light when overriding motivational factors are present.

To guide stock away from adverse depth-specific conditions, we investigated (1) whether constant-rate vertical light movements induce mass-following of salmon in research-scale sea cages, and (2) what light movement speeds are followed. The experiment was conducted using low-intensity lights in a highly stratified marine environment together reducing the motivational strength of light.

MATERIALS AND METHODS

Experimental setup. In autumn 2013 at the Institute of Marine Research farm facility at Smørdalen, Masfjorden, Norway (60°N , 5°E), 2 adjacent square research-scale sea cages ($12 \times 12 \times 12$ m, 1728 m³) containing 11 000 Atlantic salmon (mean \pm SE; density = 5.74 kg m⁻³, fork length = 39.1 ± 4.1 cm, mass = 902 ± 268 g) were exposed to light movement treatments of 5 speeds: 1, 2, 4, 8 and 16 m min⁻¹ repeated over 3 consecutive nights (11–12, 12–13 and 13–14 November 2013) (see Fig. 1). These were equivalent to fish swimming speeds of 0.04, 0.09, 0.17, 0.34, and 0.68 body lengths (BL) s⁻¹ based on mean fish size.

Prior to the trial, fish were adapted to a single low-intensity LED lamp (custom-made lamps, AKVA Group ASA) centrally positioned at 8 m depth in both cages for 2 mo. Lamp colours were 375–425 nm and total irradiance was adjusted to achieve 0.1 μE at 1 m distance from the light source (see details in Stien et al. 2014). Fish were fed a commercial diet (9 mm, Optiline + pellets, Skretting) using farm practices to satiation, though hunger status on experimental nights was unknown.

On an experimental night, light movement treatments were conducted simultaneously in both cages and in random order (see Fig. 1). Lights remained fixed at 8 m depth for 15 min before and after each movement (see Fig. 1). Light vertical movement was provided by hauling lights using an automatic motorised winch (Belitronics HF 5000, Lunde, Sweden) between the surface and cage bottom (starting from a fixed position at 8 m depth, then down to 12 m, up to 0 m and back down to 8 m) for 3 cycles. Treatments were performed between 19:30 and 00:30 h (local time) after a mean (\pm SE) sunset time of 16:12 h ± 1 min and during a waxing gibbous moon phase.

Fish and light depths. Fish depth was quantified using an echo-integration system (Lindem Data AcquisitionOslo, Norway) cabled to upward facing transducers (42° beam, 50 KHz, 0.001 s pulse, 1 s echo listening, 6 s pulse interval) 7 m below each cage (Bjordal et al. 1993). Echo intensity was captured at 0.07 m depth intervals between 0.25 and 12 m and later converted to relative echo intensity as a measure of fish percentages per depth. Light depth was monitored in time-stamped video recordings from underwater cameras (360° pan/tilt Orbit Subsea camera) secured to the same winch as lights. The number of echo sounder data-points was standardized across treatment replicates by randomly selecting how many data-points were recorded during the fastest light speed treatment (16 m min⁻¹, 52 data-points).

Fish swimming speed. Swimming speeds of salmon were measured before and after each treatment via underwater cameras. The video system only recorded from one camera at a time, so the recording was swapped between cameras in random order so both cages were viewed before and after treatments. For each period, swim speeds of 15 fish in both north and south directions (1080 measurements in total) were calculated in body lengths (BL) s⁻¹ from the time required for a fish's snout until tail to pass a vertical reference line (Dempster et al. 2009).

Environmental variables. Water temperature, salinity, and dissolved oxygen were measured via a CTD (SD204, SAIV AS) profiling between 0 and 12 m at 0.6 m min⁻¹ on a Belitronics winch. Mean values at 0.5 m depth intervals were calculated for each experimental night.

Statistical analysis. Differences in mean fish percentages in the upper 6 m of cages between light depths at 3 m increments were examined by one-way ANOVA for each light movement treatment. This measure of fish distribution captured changes in the proportion of fish in surface (above 6 m depth) and light-associated subgroups that were present. Signif-

icant ANOVA results were followed by Tukey post-hoc comparisons to determine statistical groupings. Residual plots and Levene's tests assessed normality and homogeneity of variance, respectively, and data were transformed where appropriate. Levels of significance are $p < 0.05$ and values are presented as mean \pm SE.

RESULTS

Cage environments were stratified, with a cooler and less saline surface layer, and constant conditions below 6 m depth. Temperatures and salinities were slightly higher on Night 1 (9–13°C and 19–32 ppt, respectively) compared to Night 2 (8–13°C and 12–32 ppt) and 3 (8–13°C and 12–31 ppt), due to rainfall after the first night. Dissolved oxygen remained $>70\%$ saturation and was elevated in surface waters (72–90% saturation).

When lights were fixed at 8 m, fish displayed a bimodal vertical distribution, with a surface-positioned subgroup in the upper 6 m of cages (mean \pm SE: $46.9 \pm 0.5\%$), and another around the light source in the bottom 6 m (mean \pm SE: $53.1 \pm 0.5\%$) (Fig. 1). In these instances, fish at lights swam in school formations at a mean speed of $0.36 \pm 0.01 \text{ BL s}^{-1}$.

Light movements generally caused the light-positioned subgroup to follow the light, while the

surface-positioned subgroup persisted, and the 2 groups merged when the light entered surface waters (Fig. 1). Shifts in the percentage of fish between the upper and lower cage sections were detected as lights moved between depths at $1\text{--}4 \text{ m min}^{-1}$ ($F_{3,100} = 18.17\text{--}36.17$, $p < 0.0001$), but not at the higher speeds (8 m min^{-1} : $F_{3,100} = 0.75$, $p = 0.524$; 16 m min^{-1} : $F_{3,100} = 1.57$, $p = 0.202$) (Fig. 2). At these lower speeds of $1\text{--}4 \text{ m min}^{-1}$, lights moving through the bottom 3 m of cages (9–12 m) resulted in 47.5–48.6% of fish positioning in the upper 6 m (Fig. 2), and this shifted to 75.1–82.9% in the upper 6 m when lights entered the top 3 m of cages. The magnitude of this shift increased with decreasing light movement speeds, with 34.4, 29.2, 26.7, 7.1 and 1.2% of the population moving between upper and lower cage sections at 1, 2, 4, 8 and 16 m min^{-1} , respectively (Fig. 2). From slowest to fastest movement speeds, the light-followers represented 64.7, 55.0, 50.3, 13.4 and 2.3% of the light-associated subgroup that was present under fixed lighting.

DISCUSSION

We demonstrate that Atlantic salmon *Salmo salar* in sea cages follow constant-rate vertical light movements at speeds up to 4 m min^{-1} . However, in this study a surface subgroup was not attracted by either deep-stationary or moving lights, indicating the pres-

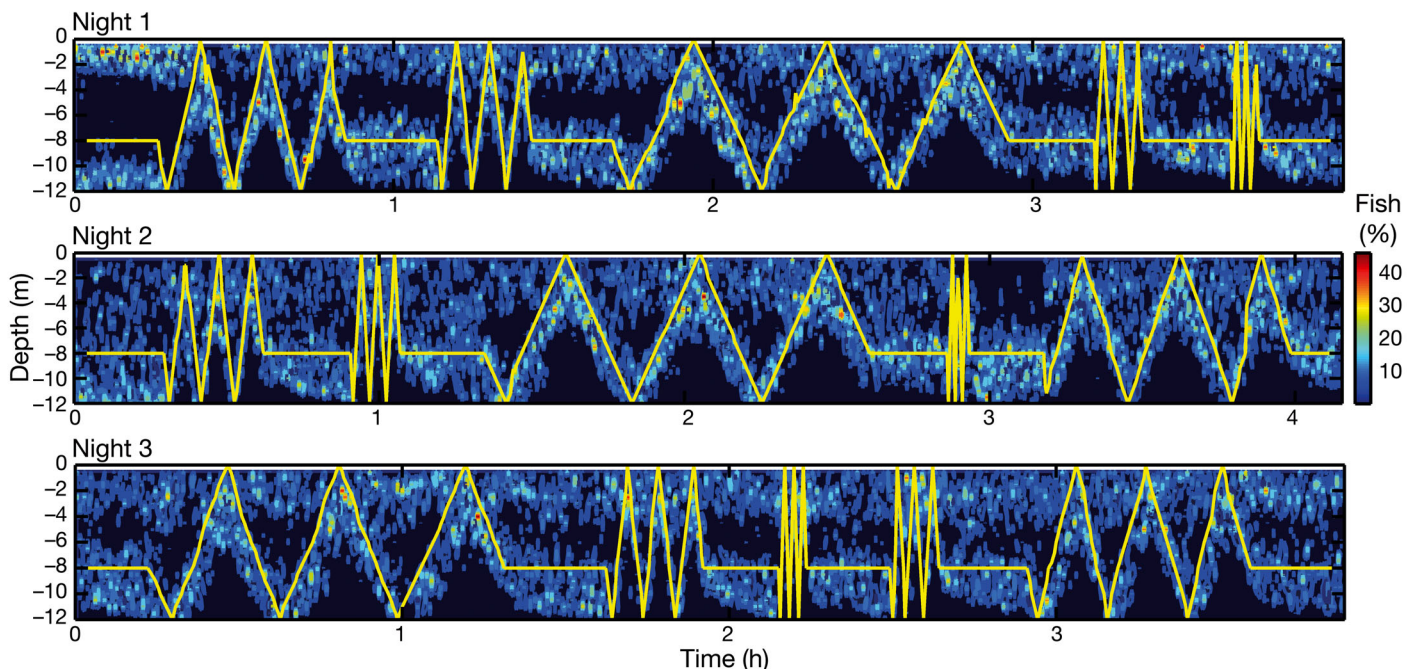


Fig. 1. Depth distribution (colour-coded percentages of fish at 0.5 m depth increments using data from a single cage) of Atlantic salmon *Salmo salar* during the 3-night study where fixed submerged lights positioned at 8 m were moved at a constant rate between 0–12 m for 3 cycles at 5 different speeds (yellow line indicates light depth)

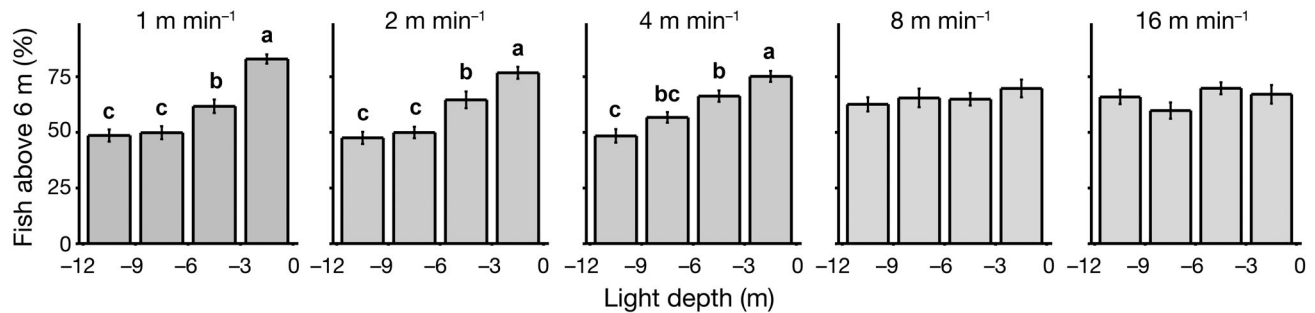


Fig. 2. Mean percentages of Atlantic salmon *Salmo salar* in the upper 6 m of cages when lights were within 3 m depth increments during movements at 1, 2, 4, 8 and 16 m min⁻¹. Letters indicate significantly ($p < 0.05$) different groups from post-hoc (Tukey HSD) comparisons following significant ANOVA results

ence of other overriding motivating factors. Short-term guidance of fish with lights throughout cage depths has wide-ranging potential applications in salmon farm management.

This is the first report of salmon in sea cages following constant-rate vertical light movements. Juell & Fosseidengen (2004) found similar salmon depth adjustments when lights were abruptly switched between 5 cage depths over 48 h. The decision to follow lights is likely to preserve visual acuity for schooling behaviour, which requires vision and lateral line senses (Partridge & Pitcher 1980). Fish may be evolutionarily driven to school to reduce energy expenditure, increase hunting potential, lower predation, and improve tracking of favourable conditions (Handegard et al. 2012, Berdahl et al. 2013, Hemelrijk et al. 2014). The fact that salmon eyes respond slowly to changes in light levels (Guthrie & Muntz 1993) from daylight to darkness, may also account for the attractiveness of artificial night lighting and the following of moving light sources.

Salmon were not guided by the fastest vertical light movements (8 and 16 m min⁻¹ equal to 0.34, and 0.68 BL s⁻¹ of experimental fish, respectively) which matched or out-paced swimming speeds measured at fixed lighting (0.36 BL s⁻¹). Atlantic salmon are capable of critical swimming speeds up to 3.0 BL s⁻¹ in flow tanks (Lijalad & Powell 2009); however, fast speeds may not be used by fish groups attempting to occupy moving environmental conditions (patches) they prefer. Berdahl et al. (2013) found fish groups seek out preferred patches by swimming faster as conditions worsen and navigating toward slower swimmers. Reduced swim speeds in optimal spaces also shortens inter-individual distances and increases densities (Berdahl et al. 2013). Moving lights too quickly may not attract large salmon groups because faster individuals tend not to gather followers and are spaced further apart.

A surface-positioned subgroup was not affected by light movements, suggesting the lack of pre-existing motivational strength for artificial light is not changed by these movements. In this study, weakened light attraction may have been attributable to overriding internal factors such as hunger, which motivated fish to reside at the surface (e.g. Frenzl et al. 2014), or environmental conditions. Temperature is known to override light attraction in Atlantic salmon (Oppedal et al. 2007), but it may not have been the driver for the behaviour of the surface-positioned subgroup in this study as warmer depths optimising salmon thermoregulation (Johansson et al. 2006) were in the lower cage sections. It is possible that the surface fish were infected by salmon lice (0.85 lice fish⁻¹ detected before the start of our study) and selected shallow low-salinity areas to self-treat against these freshwater-susceptible parasites (Gjelland et al. 2014). The surface fish were also potentially excluded from restricted lit areas under low-intensity lighting (Stien et al. 2014) and exhibiting shallow swimming, typical of salmon in cages during the night under natural light (Oppedal et al. 2011). Further research is needed to further define lighting arrangements and movement types that gather more followers. For example, moving commercial anti-maturation lamps (8–100 μ E, Stien et al. 2014) rather than low-intensity lights (0.1 μ E) may considerably strengthen following.

CONCLUSION

Instantaneously moving salmon to new depths with underwater artificial light at night has diverse commercial applications. For best results, our study suggests moving lights at ≤ 4 m min⁻¹ and in the absence of overriding factors. Potential applications include steering salmon away from the depth of salmon lice infective stages (cf. Frenzl et al. 2014), which varies

depending on salinity depth profiles (Jones & Beamish 2011). Using lights to attract salmon into temporary areas of low salinity (e.g. 12 ppt surface waters in this study) may also cause the removal of attached lice and other ecto-parasites sensitive to low salinities (Bricknell et al. 2006, Parsons et al. 2001). Additionally, moving salmon constantly throughout cage depths may prevent extreme schooling densities in narrow depth ranges (Oppedal et al. 2011), which can cause hypoxic conditions (Johansson et al. 2006). Manipulating salmon swimming behaviour with vertical light movements could therefore improve parasite control, fish welfare and production for the salmon aquaculture industry.

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