

A laboratory experiment to determine the dispersal response of Atlantic salmon (*Salmo salar*) fry to street light intensity

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SUMMARY

1. The effect of a range of ecologically relevant broader spectrum street light intensities on the dispersal timing of Atlantic salmon (*Salmo salar*) fry was investigated to assess the efficacy of a proposed management tool, the dimming of lamp brightness, for reducing the ecological consequences of artificial night light on aquatic ecosystems. Dispersal timing under treatment street light intensities of 8, 4, 2 and 1 lux was compared to that under a control night light intensity of 0.1 lux, representative of approximately half that experienced from a full moon.
2. Dispersal timing was significantly delayed (by 1.4 to 2.2 days), and its diel pattern significantly disrupted under the treatment street light intensities. However, the dose–response for both delay and disruption effects was not linear, with a strong effect apparent at 1 lux, and little or no additional impact seen when the light intensity was increased further. Under control conditions, the mean time of dispersal was 3:58 h after dusk, with very few fry (<4%) dispersing during daylight hours. For the treatment street light intensities, the mean time of dispersal of fry was significantly later (5:31 h after dusk at 1 lux) at night, and a much wider distribution of fry dispersal times was apparent with many more fry (19% at 1 lux) dispersing during daylight hours.
3. Survival to dispersal in aquarium conditions was high ($\geq 97.8\%$) and comparable in the control and treatment street light intensities. However, in the wild, the period between fry dispersal and the establishment of feeding territories is considered to be of critical importance in the dynamics of salmonid populations and any disruption may significantly increase predation and reduce fitness.
4. The findings of this aquarium-based investigation suggest that the dimming of lamp brightness has little potential as a successful management strategy to reduce the disruptive impact of street lighting surrounding freshwater ecosystems. We therefore recommend that the best course of action is to maintain and increase natural unlit areas.

Keywords: artificial night light, freshwater fish, fry dispersal, salmon, urban environments

Introduction

Artificial night light has increased dramatically during the last century raising concern regarding the potential impact on populations and ecosystems throughout the biosphere (Longcore & Rich, 2004; Rich & Longcore, 2006; Sutherland *et al.*, 2006; Royal Commission on Environmental Pollution, 2009; Hölker *et al.*, 2010a). Globally, the use of artificial night light is continuing to increase

(estimated at 6% per annum; Hölker *et al.*, 2010a) both in previously unlit regions of the developing world and in heavily developed countries (estimated at 3% per annum in the U.K.; Royal Commission on Environmental Pollution, 2009). Different types of street lights have varying spectral compositions. The most common type of street light in the U.K. (low-pressure sodium vapour lamps) emits light that is narrowly concentrated in the longer wavelengths of the visible spectrum, appearing

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yellow or orange to the human eye. Replacement lights, for example metal halide, compact fluorescent light (CFL) and light-emitting diode (LED) lamps, emit considerably more light across the visible spectrum especially at shorter wavelengths, providing superior colour rendering for human vision (Royal Commission on Environmental Pollution, 2009). However, these more naturalistic whiter lights could lead to significant changes in the impact of artificial light on natural systems (Rich & Longcore, 2006; Royal Commission on Environmental Pollution, 2009), particularly in aquatic ecosystems where penetration through water will increase (Becker *et al.*, 2013). Moreover, there is growing concern regarding how anthropogenic freshwater stressors might interact with each other (Ormerod *et al.*, 2010) and that the effects of artificial night light may be confounded with other urban stressors making it difficult to determine the role it has played in declines in freshwater biodiversity and ecosystem functioning (Perkin *et al.*, 2011). Freshwater ecosystems are often the most significantly impacted (Revenge *et al.*, 2005), and those tasked with their preservation are becoming increasingly concerned with the way artificial light at night is altering these ecosystems (Perkin *et al.*, 2011). This change to the nocturnal environment and the behaviour of nocturnal species has potentially far reaching consequences and is a major threat to species biodiversity (Hölker *et al.*, 2010a; Perkin *et al.*, 2011). The issue becomes more pertinent when considering the impact that artificial light will have on species that are already a conservation concern (Mora *et al.*, 2007), such as Atlantic salmon (*Salmo salar*) (Riley *et al.*, 2013).

For fish, light is a directive factor, as natural light patterns will influence their behaviour (Fry, 1971) and recent evidence suggests that the diel behaviour of fish can be modified in response to artificial night light (see review in Nightingale, Longcore & Simenstad, 2006). In salmonids, the emergence and dispersal of fry from spawning redds occurs principally at night (see review in Riley *et al.*, 2013). The period between fry emergence and the establishment of feeding territories is a time when mortality can be very high and appears to be of critical importance in the dynamics of salmonid populations (Armstrong *et al.*, 2003). Synchronous nocturnal salmonid fry emergence and dispersal is a predator avoidance tactic (Peterman & Gatto, 1978; Godin, 1982; Fraser, Huntingford & Thorpe, 1994; Riley & Moore, 2000; Tabor, Brown & Luiting, 2004). However, a recent investigation demonstrated that the dispersal of Atlantic salmon fry is both delayed and disrupted by broader wavelength street lamps at a light intensity level of 12

lux (Riley *et al.*, 2013), suggesting that recruitment under such conditions may be reduced. Riley *et al.* (2013) used a light intensity of 12 lux to reproduce the maximum artificial night light intensities they measured at river level at significant urban Atlantic salmon spawning sites in chalk streams across southern England: River Frome at Dorchester, up to 22.7 lux; River Avon at Salisbury, up to 11.3 lux; River Test at Romsey, up to 6.1 lux; River Itchen at Bishopstoke and Winchester, up to 20.0 and 12.9 lux, respectively (Riley *et al.*, 2013). Although 12 lux is ecologically relevant, and below some national guidelines for minimum horizontal illuminance values for street lighting levels (an average of 15 lux in Great Britain; British Standards Institute, 2003, 2008: and an average of 20 lux in North America; Illuminating Engineering Society of North America, 2000), it is towards the upper end of night light intensities likely to be encountered at river level at urban salmon spawning locations. More typical levels of urban street lighting will fall between the intensities measured from direct street lighting by Riley *et al.* (2013) and indirect urban sky glow that can be as high as 0.5 lux (Kurtze, 1974). Indeed, a recent study reported that common moderate to high ambient intensities of artificial light at night in urban stream reaches were between 0.6 and 4.0 lux (Meyer & Sullivan, 2013).

Recent studies have reviewed management options and developments for reducing the ecological consequences of artificial night light (Royal Commission on Environmental Pollution, 2009; Gaston *et al.*, 2012, 2014b). These have included: (i) preventing areas from being artificially lit, (ii) reducing the trespass of lighting, (iii) changing the spectrum of lighting, (iv) limiting the duration of lighting and (v) changing the intensity of lighting (from Gaston *et al.*, 2012, 2014b). Along riparian corridors, the first three of these are likely to conflict with other social, economic or ecological objectives and will therefore be very difficult to achieve because: (i) riparian corridors are often preferred sites for human habitation/activities so the complete or partial removal of artificial night light may be neither practical nor desirable; (ii) luminaire developments are generally aimed at directing artificial night light downwards (i.e. to illuminate either the road surface or objects below the light source) thereby reducing the ecological impact of trespass in an upward or horizontal direction; and (iii) there is a drive towards more energy efficient whiter light sources providing superior colour rendering for human vision, often perceived to improve public safety through crime and road accident reduction (Royal Commission on Environmental Pollution, 2009; Gaston *et al.*,

2012, 2014a). The fourth proposed management option is likely to be ineffective at alleviating many impacts on nocturnal or crepuscular animals, including salmonid fry dispersal and smolt migratory behaviour, because peak demand for lighting (the hours immediately after dusk and before dawn) often coincides with peak activity (Riley & Moore, 2000; Gaston *et al.*, 2012; Riley *et al.*, 2012, 2013). Therefore, this study targeted the remaining management option: (v) reducing the intensity of broader wavelength street lamps, and aimed to determine whether this will significantly reduce the impact on Atlantic salmon fry dispersal. Specifically, we compared the dispersal timing of fry from artificial redds housed in an aquarium under a range of ecologically relevant street light intensities. The results will provide evidence-based information that can be used as a management tool to identify sites where potential impacts may currently exist and help guide mitigation strategies along riparian corridors, aiding the protection of freshwater fish species in urban environments.

Methods

Experiments were conducted in 10 75-L black plastic, deep substratum incubators (Edmonds, Riley & Maxwell, 2011; Riley *et al.*, 2013) at the Cefas Laboratory aquarium, Lowestoft, U.K. (52°27'33'N, 1°44'22'E). The incubators were positioned in the aquarium to produce pairs of replicates (in mirror image away from the artificial night light source) exposed to artificial night light intensities at *c.* 8, 4, 2, 1 and 0.1 lux, while maintaining all 10 incubators at similar light intensities during the day. The 0.1 lux artificial night light intensity is representative of approximately half that experienced from a full moon (0.2 lux, Austin, Phillips & Webb, 1976; 0.1 to 0.3 lux, Rich & Longcore, 2006) and as such is considered to be the control.

Artificial night lighting was provided using a lamp (Philips Master Cosmo White; CPO-T White 45W/628PGZ12) (Royal Philips Electronics Inc., Amsterdam, the Netherlands) fitted in a luminaire (Philips 'iridium series' opti-C street lighting unit) installed at a height of 1.7 m. This equipment is typical of the energy efficient ceramic metal halide street lamps currently used to illuminate city centres, residential areas, minor roads and pathways and is typically installed at a height of 4 to 6 m. To compensate for a lower installation height in the aquarium, 10 neutral density filter sheets (E-Colour+ #298 0.15, transmission = 69.3%; Rosco Laboratories Inc., Stamford, Connecticut, U.S.A.) were fitted over the luminaire (plus an additional filter over only one half of the

luminaire) to reduce the lights intensity without changing its spectral distribution. Daytime lighting in the aquarium was provided by eight, daylight mimicking, low-pressure mercury discharge fluorescent lamps (Philips Master TL-D 58W/865; 1.5 m in length) fitted into four luminaires (Philips Pacific 2× TL-D 58W 220–240 V HFR). Each lamp was dimmable through a 0–10 V signal on the electronic ballast fitted in each luminaire. A mechanical timer switch (Grasslin, St. Georgen, Germany) was used to trigger a bespoke electronic timer (EFI Ltd, Lowestoft, U.K.) that both switched the daytime and night lighting on or off at the correct time and also increased or decreased the 0–10 V signal to the electronic ballast within each daylight luminaire to provide a 5-min mimicked dawn and dusk period each day. Day length was calculated for the study location using the method of Hohenkerk & Yallop (2004) and adjusted accordingly each week. However, once hourly sampling commenced, day length was maintained at a constant duration of 14 h.

Light intensity readings (measured using a digital light meter, Tenmars TM-201, minimum resolution = 0.1 lux, accuracy ±8%; Tenmars Electronic Co Ltd, Taipei, Taiwan) were taken (at the start and end of the experiment) at the water surface in the centre of each incubator during daytime lighting, and at night once the street lamp had fully warmed up. In addition, minimum and maximum day and night light intensity readings were determined by scanning the entire water surface of each incubator (Table 1). For daytime lighting, the range of light intensities overlapped across all incubators. However, there was some evidence of the 1.0 lux incubators having slightly lower intensities than the 0.1 lux incubators, relative to the variation between replicates (centre: 1.0 lux coefficient = −155.5, $P = 0.02$; maximum: 1.0 lux coefficient = −129.0, $P = 0.03$; minimum: 1.0 lux coefficient = −141.5, $P = 0.05$; each based on an ANOVA with d.f. = 4,5). For night lighting, the intensity at the centre was the same for each replicate pair of incubators. The maximum levels were clearly separated ($P < 0.001$) between treatment, as were the minimum levels ($P < 0.001$), although at ≥ 1 lux there was some overlap between the maximum at one intensity and the minimum at the next intensity level.

De-chlorinated mains water inflow (ambient temperature: mean 9.7°C; max 11.3°C; min 7.7°C) was gravity-fed (mean 252.8 L h⁻¹; max 300 L h⁻¹; min 220 L h⁻¹) to each incubator from a large outdoor header tank through a perforated pressure plate, lined with 20 to 30 mm of pea gravel, fitted into each incubator base. Outflow was via standing overflow pipes discharging

Table 1 Light intensity readings (lux) measured at the water surface of each incubator during daytime and artificial night lighting (light meter minimum resolution = 0.1 lux)

Incubator	Light intensity (lux)					
	Daytime lighting			Night lighting		
	Centre	Max	Min	Centre	Max	Min
0.1 A	1062	1120	849	0.1	0.1	0.1
0.1 B	1072	1157	893	0.1	0.1	0.1
1.0 A	902	1004	731	1.0	1.5	0.7
1.0 B	921	1015	728	1.0	1.3	0.7
2.0 A	1045	1117	813	2.0	3.0	1.1
2.0 B	927	1001	667	2.0	2.8	1.2
4.0 A	1012	1083	854	4.0	5.9	2.9
4.0 B	1089	1102	904	4.0	5.5	2.6
8.0 A	1109	1135	921	8.0	11.4	4.0
8.0 B	1169	1177	864	8.0	12.1	4.1

into perforated stainless steel counting boxes placed within fry troughs. The mirror image replicates for each artificial night light intensity treatment discharged into different fry troughs. Water temperature measurements were collected from within these troughs using Tinytags (Gemini Data Loggers UK Ltd.). These programmable data loggers underwent a three-point calibration (at 0, 15 and 30°C) by Gemini before deployment and were programmed to record temperature once every hour. Subsequent analysis of the temperature data showed no significant differences (Student's *t*-test; $n = 1438$, $P = 0.49$) between the mean temperatures (both 9.7°C) recorded in each trough.

On 22 February 2012, 500 eyed Atlantic salmon eggs (development *c.* 260 degree-days) were randomly assigned to each incubator. To replicate reported burial depths (Crisp & Carling, 1989; Bardonnnet & Baglinière, 2000; Armstrong *et al.*, 2003) and the substratum exploited by spawning salmonids in the chalk streams of southern England (Crisp & Carling, 1989; W. D. Riley, unpublished data), the eggs were buried 150 to 180 mm deep within washed 15- to 40-mm gravel. The water depth between the gravel surface and the outflow was measured at 100 mm in all incubators.

The perforated stainless steel counting boxes into which the water from each incubator discharged were checked each day for any dispersing fry. As soon as one fry had dispersed, the number and total wet mass (nearest 0.01 g) of fry dispersing from each incubator was recorded at dawn and dusk each day. Hourly sampling commenced when developmental degree-days suggested that initial dispersal was imminent (Edwards, 1978). Prior to hourly sampling a total of six fry were recorded

(across all incubators), and these fish were included in the analysis of overall survival, but excluded from all other analysis. Hourly sampling continued post-peak dispersal until <20 fry had dispersed (across all incubators) over a 24-h period. The substratum from each incubator was then carefully removed and the number of fry that had not dispersed was recorded; a total of 35 fry were removed (across all incubators) during this process; again these were included in the analysis of overall survival but excluded from all other analysis.

To transform the hourly sampling periods into a numerical variable, a decimal 'sampling day' was assigned to each fry dispersal as sampling day + sampling hour/24. Hourly sampling commenced following dusk on 31 March (day 1) and continued until dusk on 21 April (day 22). The mean time of fry dispersal was calculated for each incubator. For these mean values, analysis of variance with Tukey's honest significant difference (HSD) method for pairwise comparison (with 5% family-wise error rate) was used to compare the dispersal times for the different treatments, with each other, and with the controls. Analysis was carried out in R v3.0.1 (R Development Core Team, 2013).

The mean mass of dispersing fry per incubator per hour was calculated from the hourly totals for each incubator. An exploratory analysis was carried out on trends in mean mass with days since the start of hourly sampling by fitting a generalised additive model (Wood, 2006) to the data from each incubator by day and night separately. These models used a thin plate regression spline with shrinkage and basis dimension (*k*) of 10. For further analysis, a mixed effects model (Pinheiro & Bates, 2000) was fitted to mean mass with fixed effects being factors for day or night and night light level (0.1, 1, 2, 4 or 8 lux), a linear trend for time since the start of hourly sampling, and all interactions of the three variables, and random effects being the mean and linear trend for each incubator. This allowed any additional variation between incubators to be included in analysing the effect of light level. All the statistical models used the number of fry that each mean mass was derived from as statistical weight; this was to account for the fact that the mean mass calculated when more fry dispersed will be more precise. Model selection was then carried out on the fixed effects, using likelihood ratio tests and a 5% significance level, to produce a simplified final model which was refitted using restricted maximum likelihood.

Hourly patterns of dispersal were investigated using circular statistics (Batschelet, 1981). For each night light intensity, the mean vector (μ) (mean time of dispersal

± 95 th percentile confidence limits) and the mean vector length (r , expressed as a value between 0 and 1, with higher values indicating that observations are clustered more closely around the mean) were calculated. Rayleigh's uniformity tests were performed for each treatment to calculate the probability (P) of the observations under the null hypothesis that dispersal was uniformly distributed throughout the diel cycle. Differences between the treatments were investigated by a circular version of the chi-square test and by comparing the data from the incubators exposed to the street-lit conditions with the mean vector of the control data (V -test). All circular statistics were carried out in Oriana (www.kovcomp.com/oriana/).

The percentage of fry surviving during the whole experimental period was calculated for each incubator, and survival under street-lit (1 to 8 lux) and control (0.1 lux) conditions were compared using a randomisation test based on all 45 possible combinations of the 10 incubators to the two groups (Manly, 2001).

Results

Dispersal day

Figure 1 shows the number of fry dispersing from each of two incubators by sampling day at the five levels of night light intensity during the night (Fig. 1a) and during daylight hours (Fig. 1b). The dispersal data (Table 2, Fig. 2a) show a wide range of dispersal dates in all incubators. However, between the control (0.1 lux) and the treatment artificial night light intensities, there was an increase in dispersal day for the central section of the distribution and the differences in mean dispersal day were statistically significant relative to the variation between incubators (ANOVA, d.f. = 4,5, $F = 18.7$, $P = 0.003$). Mean dispersal day was between 1.4 and 2.2 days later under the treatment artificial night light intensities (Table 3, Fig. 2b), and all pairwise comparisons against the control were statistically significant (Tukey's HSD, adjusted $P < 0.05$). The latest mean dispersal corresponded to the highest artificial night light level (8.0 lux), but the 95% confidence intervals for the different treatment intensities of street lighting all overlapped (Table 3, Fig. 2b) and all pairwise comparisons between treatment artificial night light intensities were non-significant (Tukey's HSD, adjusted $P > 0.05$).

Including daytime light intensities did not significantly (d.f. = 1,4; $F = 0.84$; $P = 0.41$) improve the model fit after accounting for differences in night light intensities.

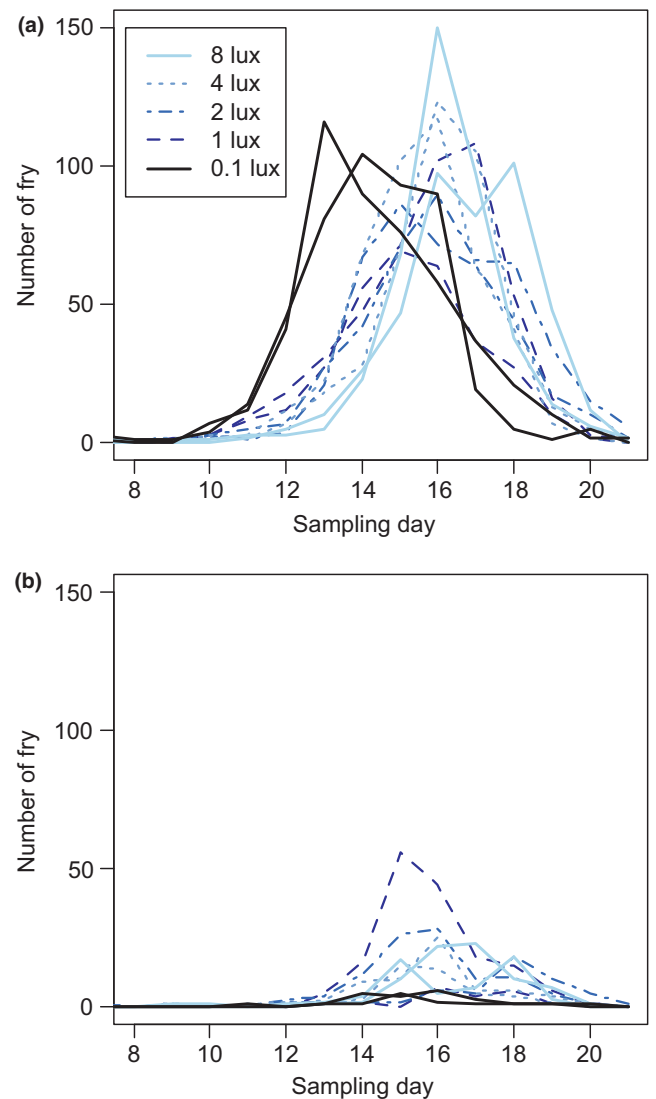


Fig. 1 Number of fry dispersing from each of two incubators by sampling day at five levels of night light intensity: (a) during night hours and (b) during day hours. X-axis truncated at sampling day 8, during night hours a total of 19 fry emerged earlier than day 8, during day hours a total of three fry emerged earlier.

Diel dispersal pattern

Summary statistics for the analysis of the diel dispersal pattern for each night light intensity are presented in Table 4. For all night light intensities, the null hypothesis was rejected in favour of directedness (Rayleigh test, $P < 0.001$), that is the dispersal times were directed around particular periods of time following the onset of dusk. Under control conditions, the mean time of dispersal was 3:58 h after dusk ($r = 0.74$), with very few fry (<4%) dispersing during daylight hours (Fig. 1b). For the 1.0, 2.0, 4.0 and 8.0 lux artificial night light treatments, the mean time of dispersal of fry was significantly

Table 2 Summary of survival and dispersal for each incubator. All incubators had 500 eggs at the start of the experiment. Hourly sampling commenced following dusk on 31 March (day 1) and continued until dusk on 21 April (day 22)

Incubator	Total no. surviving	Total % surviving	No. fry emerging during 24 h sampling	Dispersal day mean	Dispersal day SD
0.1 A	489	97.8	484	14.4	2.14
0.1 B	500	100.0	498	14.6	2.14
1.0 A	492	98.4	483	15.7	1.99
1.0 B	489	97.8	487	16.0	1.94
2.0 A	497	99.4	492	16.1	1.84
2.0 B	492	98.4	488	16.5	2.22
4.0 A	490	98.0	489	16.3	1.71
4.0 B	493	98.6	491	15.8	1.69
8.0 A	494	98.8	489	16.5	1.55
8.0 B	496	99.2	490	16.9	1.90

($P < 0.001$) later in the night: mean times of 5:31, 4:47, 5:45 and 5:31 h after dusk, respectively (Table 4). Compared to the controls, significantly more fry (Student's *t*-test; d.f. = 8; $P < 0.003$) dispersed during the hours of daylight in the four treatment groups (12–19%), with the highest number in the 1.0 lux artificial night light treatment (Table 4; Fig. 1b).

Circular plots of the data revealed that the diel patterns of dispersal between the control conditions and the street-lit treatments were very different (Fig. 3). This is due to both the later, but also much wider distribution of fry dispersal times under street-lit treatments. These differences were found to be significant ($P < 0.001$) when comparing the mean vectors ($\pm 95\%$ CL's) by performing a chi-square test on the sample distributions and when comparing the dispersal times of the fry exposed to street-lit conditions against the mean vector of the control group (*V*-test for combined data) (see Table 4).

Fry mass

Examining the mean mass of fry dispersing from each incubator each hour (Fig. 4) and fitting GAM curves (not shown) to each incubator day/night combination showed a mixture of constant trends, linear trends and fluctuations in mean mass across time, for example for 0.1 lux at night. Overall, there were no consistent nonlinear trends so linear trends were used in further modelling.

The selected linear mixed effects (lme) model (Table 5, Fig. 4) indicated there was a marginally larger mean mass at day relative to night after accounting for sampling day and hour ($+0.004$ g, $P = 0.0007$) and different slopes by light level ($P = 0.014$), with an almost constant trend for the control incubators at 0.1 lux (-0.00006 g d⁻¹) and small decreases in mean fry mass with time for

the treatment street-lit incubators (between -0.0011 and -0.0023 g d⁻¹).

The variation between incubators (SD = 0.010) was small in relation to the variation between individual fry (within-group SE = 0.025) indicating that mean masses were not strongly correlated within incubators or between treatments, while Fig. 4 illustrates the relatively large amount of individual variation around the fitted means. Data and model checking showed outlying masses in the day 1 lux and night 8 lux data and one fry dispersing early (day 2.5) in the day 8 lux data (see Fig. 4). These values were checked and confirmed as valid. Trials removing them and then refitting the selected model did not change the conclusions drawn.

Survival

Survival was high ($\geq 97.8\%$) in all incubators (Table 2) and comparable in the control and street-lit treatments (control mean 98.9%, street-lit mean 98.6%; randomisation test $P = 0.71$).

Discussion

The dispersal of Atlantic salmon fry in an aquarium was significantly delayed and disrupted by broader spectrum street light intensity levels of 1 to 8 lux. The dose-response for both delay and disruption effect is not linear, with a strong effect apparent at 1 lux and little additional impact seen when the light intensity is increased further to 2, 4 and 8 lux. The current investigation has therefore identified the intensity at which artificial light has a disruptive impact on natural Atlantic salmon fry dispersal behaviour, somewhere between natural full moonlit conditions of 0.2 lux (Austin *et al.*, 1976) and artificially lit conditions of 1.0 lux, with little additive

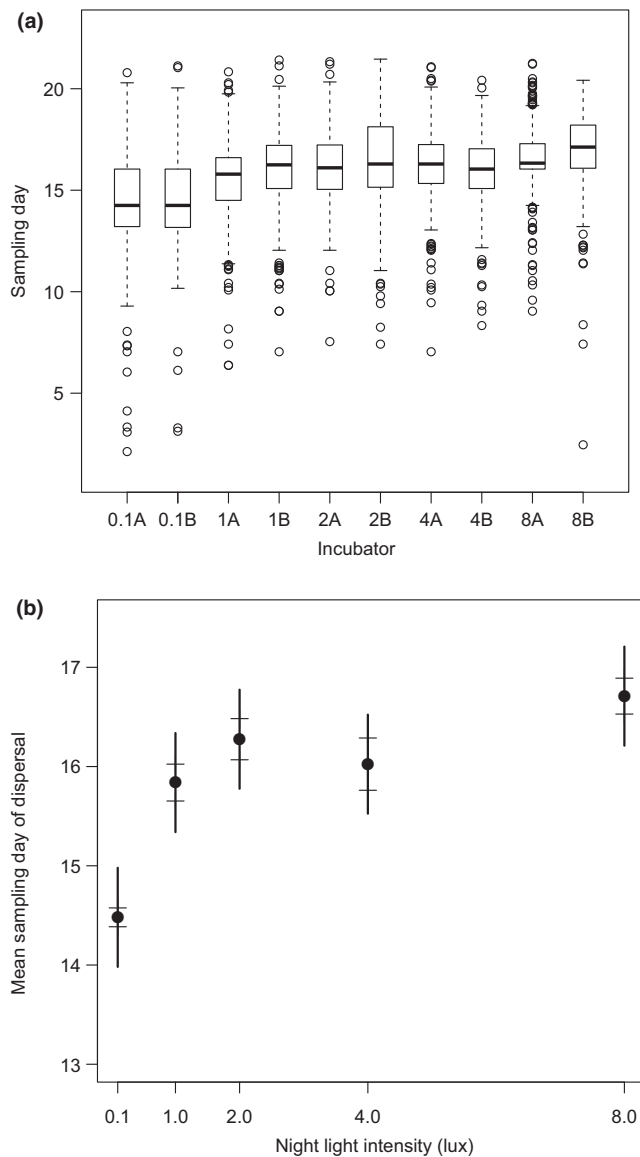


Fig. 2 (a) Box plot showing the distribution of dispersal day for fry from each of two incubators by sampling day at five levels of night light intensity. Horizontal lines show the medians, the boxes indicate the central 50% of the values, dashed vertical lines extend to cover the majority of the data, and circles show outlying values. (b) Mean dispersal day (filled circles) for fry at each night light intensity with 95% confidence intervals for mean (vertical lines) from analysis of variance and observed means by incubator (horizontal lines). Night light intensity 0.1 lux is considered to be the control. Note that the *y*-axis does not start at day 1.

effect of changing behaviour with increasing light intensity once this low threshold intensity was breached.

The period between fry dispersal and the establishment of defended feeding territories is a critical period in the life cycle of the Atlantic salmon, and populations experience high mortality during this time (Armstrong *et al.*, 2003). Any disruption to the timing of important

Table 3 Analysis of variance coefficients for effect of light intensity on mean dispersal day. Intercept is estimated at 0.1 lux and other coefficients show difference from intercept, SE is standard error, CI is 95% confidence interval

	Coefficient	SE (95% CI)	<i>t</i> value	<i>P</i>
Intercept	14.48	0.194 (14.0, 15.0)	74.57	<0.001
1 lux	1.36	0.275 (0.7, 2.1)	4.95	0.004
2 lux	1.80	0.275 (1.1, 2.5)	6.54	0.001
4 lux	1.54	0.275 (0.8, 2.2)	5.62	0.002
8 lux	2.23	0.275 (1.5, 2.9)	8.12	<0.001

life history events will have fitness consequences for organisms (Bradshaw & Holzapfel, 2010). In the wild, the delay and disruption to fry dispersal reported in this investigation would most likely impact fitness initially by diminishing the protectoral role afforded by natural synchronous nocturnal fry dispersal as a predator avoidance tactic (Peterman & Gatto, 1978; Godin, 1982; Fraser *et al.*, 1994; Riley & Moore, 2000; Tabor *et al.*, 2004). In addition, the small decrease in mean fry mass, with time, observed in those dispersing under the artificial light treatments (despite the relatively crude method used to weigh each of the batches of dispersing fry) is suggestive that these fry, having delayed their dispersal, have reduced their available energy reserves. Fry that delay dispersal are likely to be physically weaker and may find it harder to compete for a feeding territory. The energy reserves with which fry would ordinarily leave the natal redd give them a degree of flexibility in the timing of their first feeding (Miller *et al.*, 1988) in order to allow them to compete with other fry for a prime feeding territory. As such, those fry dispersing without this are at a competitive disadvantage. This reduction in fitness at the individual level can have population level consequences, through increased mortality rates (Armstrong *et al.*, 2003; Milner *et al.*, 2003), although in the controlled aquarium environment used in this investigation, survival to dispersal was unaffected by the artificial light treatments.

The light intensity at which Atlantic salmon fry dispersal is shown to be impacted in this investigation is much lower than that previously reported (Riley *et al.*, 2013). This finding is of particular importance, as light pollution is often associated with urban sky glow and light escape from large urban conurbations, yet a light intensity of between 0.2 lux and 1 lux will commonly be found in suburban, periurban and rural areas (Perkin *et al.*, 2011). Although the majority of adult Atlantic salmon spawn in upland reaches of river systems (Riley *et al.*, 2013), away from urban areas subjected to the effects of artificial night light, the results of this investigation

Table 4 Summary of circular statistics and dispersal data by night light intensity during the period of hourly sampling: n = number of fry that dispersed, μ = the mean time after dusk (hrs) and associated confidence limits (CL), r = mean vector length, significance (P) of the Rayleigh test for randomness, significance (P) of the chi-square (χ^2) test, significance (P) of the V -test for directedness and the number of fry dispersing during daylight hours (percentage in parenthesis)

	Night light intensity (lux)				
	0.1	1	2	4	8
N	982	970	980	980	979
μ	03:58	05:31	04:47	05:45	05:31
95% CL (\pm)	00:11	00:17	00:16	00:14	00:15
r	0.736	0.541	0.559	0.639	0.605
P (Rayleigh test)	<0.001	<0.001	<0.001	<0.001	<0.001
P (chi square test)*		<0.001	<0.001	<0.001	<0.001
P (V -test) [†]		<0.001	<0.001	<0.001	<0.001
Daylight n (%)	35 (4)	184 (19)	155 (16)	113 (12)	136 (14)

*Chi-square test only performed to test combined data for each treatment.

[†] V -tests performed (incubators exposed to >1 lux only) using the mean vector for the 0.1 incubators (control data) combined (03:58).

suggest that even a few streetlights used to light villages and footpaths could have an impact on the dispersal behaviour of wild salmon fry in these areas. In addition, with clear small streams more susceptible to the penetration of light (Perkin *et al.*, 2014a), there is an increased potential for an impact of artificial light in these headwater reaches.

Given the rate at which the level of artificial light at night is increasing, both in the U.K. and globally, there is likely to be much discord between the need to protect our freshwater ecosystems from this stressor and the trend of lighting our nocturnal environment. With this in mind, this investigation sought to systematically determine the threshold intensity of artificial light at which broader spectrum street lamps no longer impacted the dispersal behaviour of Atlantic salmon fry. This was conducted to assess the efficacy of a proposed management tool, the dimming of lamp brightness, selected as being the most universally applicable management strategy for mitigating the negative impacts of light pollution around freshwater ecosystems, as previously outlined in the introduction. The results of the investigation, however, suggest that this method has little potential as a successful management strategy, due to the triggering threshold of light disrupted behaviour being somewhere between 0.2 lux and 1 lux. Given that a reduction in street lighting below 1 lux is unlikely to be accepted, we recommend that the best course of action is to maintain and increase natural unlit areas as the most effective measure in reducing the disruptive impact of street lighting. However, any reduction in light intensity at a purposefully lit source will ultimately reduce the area affected by that light source. Either of these approaches will have social and economic

conflicts, as many people associate the presence of nocturnal street lighting with feeling safe and secure in their environment, thus are resistant to any perceived reduction in lighting numbers, intensity or duration (Hölker *et al.*, 2010b). Nevertheless, a number of schemes have been piloted across the U.K. to reduce the amount of light pollution, with counties across England and Wales taking part in projects to determine public response to measures reducing artificial lighting at night (Lockwood, Selwyn & Morgan-Taylor, 2011). It was found that residents would not accept a complete turn off of street lights at a certain time; however, many found dimming an acceptable compromise (Royal Commission on Environmental Pollution, 2009; Lockwood *et al.*, 2011).

An alternative solution that may provide the required compromise is the use of flexible control systems; including on-demand street lighting along riparian footpaths. These may be useful tools for mitigating impacts by providing street lighting when required for human use, but also ensuring there are sufficient dark periods for normal nocturnal behaviour. There is a current drive towards ensuring street lighting is more energy efficient, whether necessitated by environmental concern or the need to adhere to budget cuts; this movement is replacing yellow low-pressure sodium vapour lamps with white light metal halide or LED lamps. While this shift in lighting colour has the potential to increase the amount of light penetrating water (Becker *et al.*, 2013), these new lamps, unlike their sodium vapour predecessors, are better able to operate using flexible on-demand lighting systems (Royal Commission on Environmental Pollution, 2009). In addition, the use of red lights, which have limited penetration through water, along riparian corridors could also be considered (Becker *et al.*, 2013).

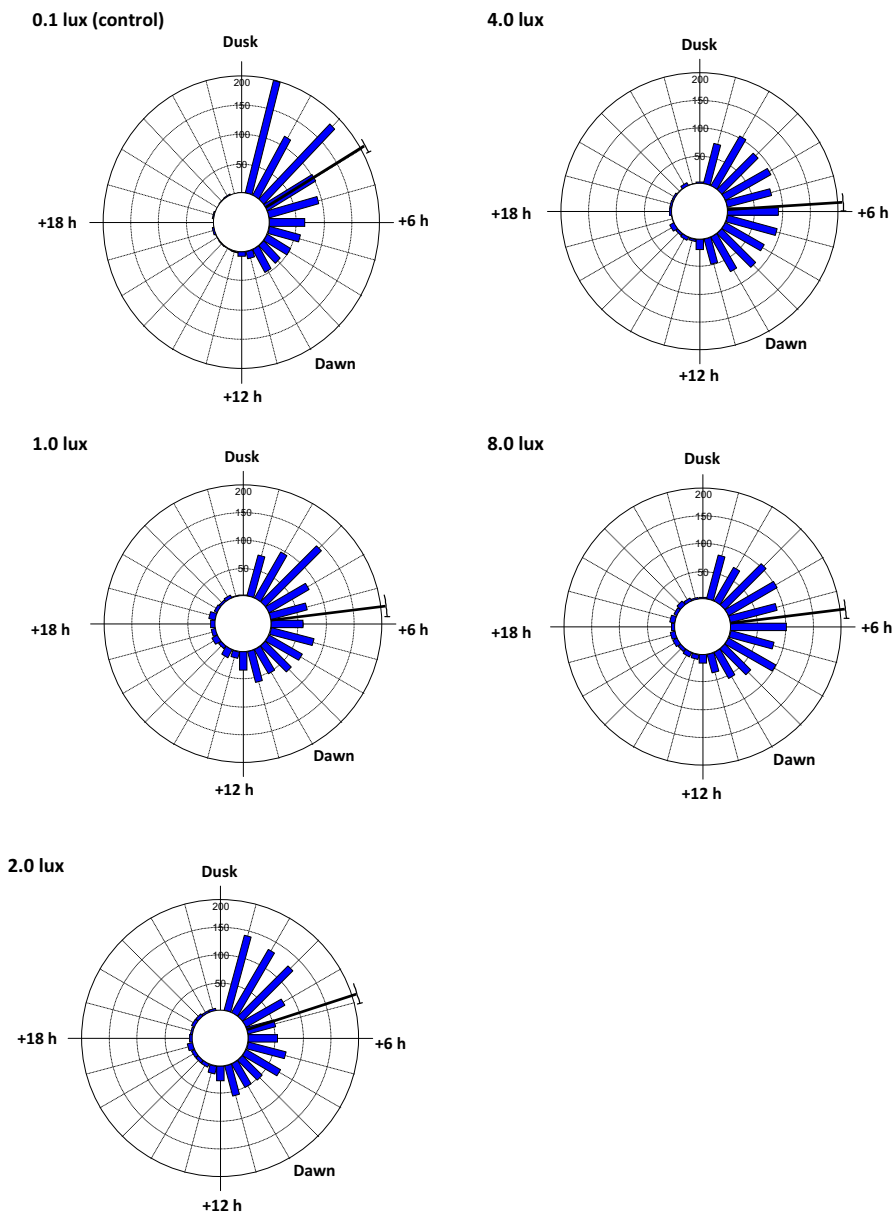


Fig. 3 Circular plots of the diel patterns of fry dispersal in relation to hours following the onset of dusk. Data are presented for the control conditions (0.1 lux) and each artificial night light intensity treatment. Also indicated are the mean dispersal times (95% confidence limits) for each treatment and the onset of dawn.

However, neither one of these measures has been tested in a field setting to ascertain their environmental impact, and as such warrant further investigation. It has also been suggested that the unpredictable periods of light produced by on-demand lighting will be more disruptive and disorientating to nocturnal animals than the constant light of full night illumination (Royal Commission on Environmental Pollution, 2009).

A final area that warrants further investigation is the role of multiple stressors and the interaction between them in impacting species behaviour and population viability. In the U.K., no pristine freshwater ecosystems remain; almost all have been impacted by diverse anthropogenic activity (including habitat alteration,

addition of pollutants and changes in land use and drainage) (Revenge *et al.*, 2005) and most are now managed to a lesser or greater extent (UK National Ecosystem Assessment, 2011). There are concerns that multiple interacting stressors in freshwater ecosystems (Ormerod *et al.*, 2010) may confound the role of artificial light in urban systems (Perkin *et al.*, 2011) and form part of the complex drivers behind the widely observed effect of urbanisation on freshwater ecosystems, often termed 'urban stream syndrome' (Walsh *et al.*, 2005). Atlantic salmon are known to have some key spawning areas in rivers around towns and villages (Riley *et al.*, 2013) where there are likely to be multiple anthropogenic stressors acting, such as water pollution and increased

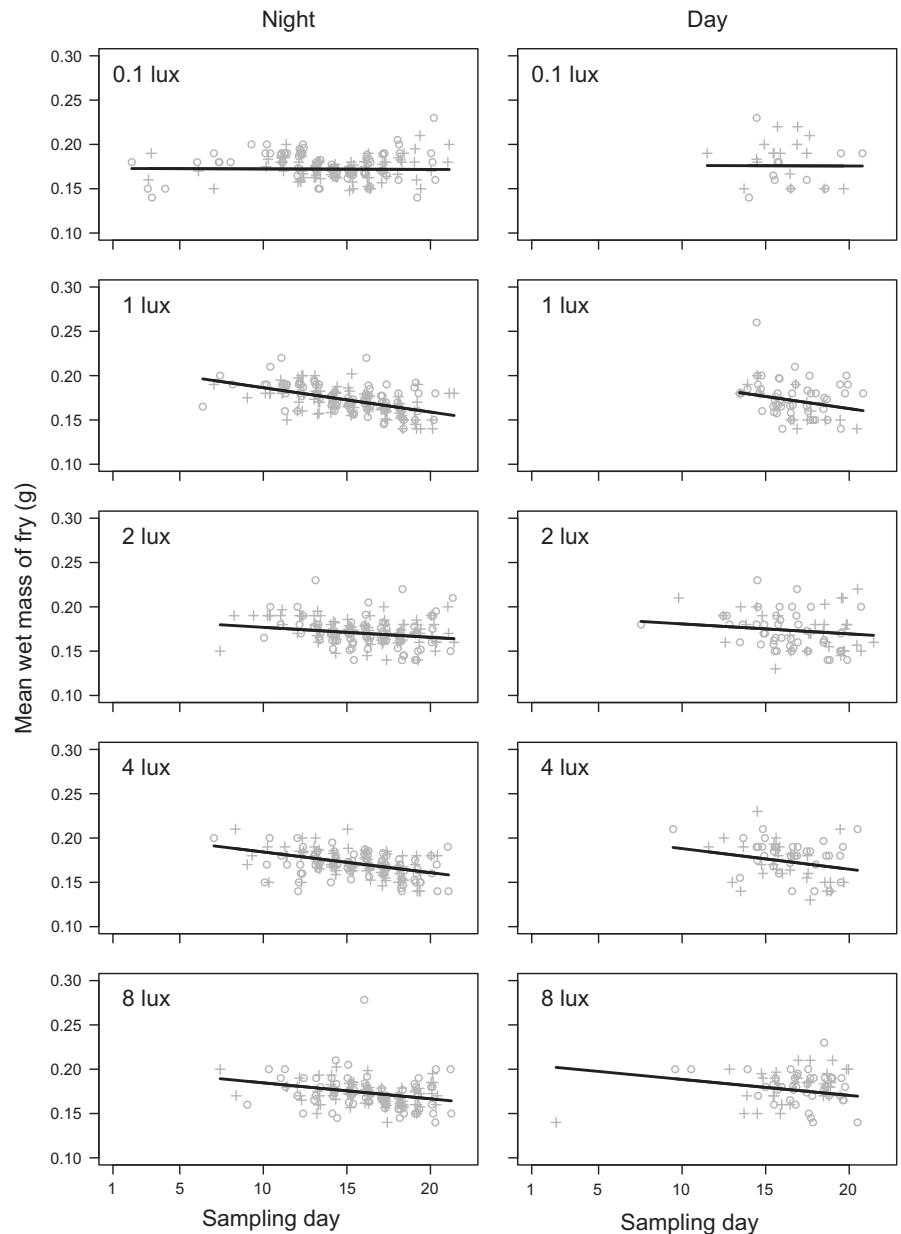


Fig. 4 Mean wet mass of dispersing fry per hour per incubator against sampling day; cross and circle symbols denote the two incubators at each light level; and solid line is the model fit from a weighted lme model (see text for details and Table 5 for model coefficients).

sedimentation from urban run-off. In addition, climate change is a further stressor that is of great concern for freshwater ecosystems. Rivers are most sensitive to climate change as they are directly affected by both changes in temperature and changes in rainfall (Ormerod, 2009). It has been suggested that population declines seen in Atlantic salmon are a result of warmer, dryer summers (Clews *et al.*, 2010). The way in which climate change will impact freshwater species over the next decade is difficult to predict (Joint Nature Conservation Committee, 2007); however, some studies suggest that a rise in temperature may have already impacted Atlantic salmon (Clews *et al.*, 2010).

It is thought that some animal populations will be unable to cope with multiple stressors that occur simultaneously (Novacek & Cleland, 2001; Folke *et al.*, 2004; Mora *et al.*, 2007). Multiple disturbances can act together and strengthen the impact of the others, resulting in a much quicker rate of biodiversity losses (Mora *et al.*, 2007; Solomon *et al.*, 2007; Darling & Côté, 2008). For example, declines in rotifer populations have been reported to be up to fifty times faster, when multiple stressors are acting, compared to control populations at constant temperatures (Mora *et al.*, 2007). It is therefore imperative that we attempt to understand the way artificial light at night interacts

Table 5 Linear mixed effects model for mean dispersal mass.

Dayhr is sampling day and hour (as decimal days), lux is night light intensity, night defined as the 10 h after dusk, and nfry is the number of fry in the hourly dispersal data for each mean mass

Fixed effects	numDF	denDF	F-value	P-value
(Intercept)	1	1120	42661.84	<0.0001
dayhr	1	1120	28.19	<0.0001
lux	4	5	0.68	0.637
day/night	1	1120	11.51	0.0007
dayhr: lux	4	1120	3.12	0.0144

Fixed effects	Estimate	c. 95% CI	
		Lower	Upper
Intercept	0.173	0.155	0.191
dayhr	-0.00006	-0.00120	0.00109
1 lux	0.041	0.007	0.075
2 lux	0.015	-0.019	0.049
4 lux	0.035	-0.001	0.070
8 lux	0.030	-0.006	0.065
day/night = day	0.00387	0.00167	0.00606
dayhr: 1 lux	-0.00269	-0.00434	-0.00103
dayhr: 2 lux	-0.00107	-0.00271	0.00057
dayhr: 4 lux	-0.00227	-0.00398	-0.00056
dayhr: 8 lux	-0.00174	-0.00345	-0.00003

Random effects: Formula: ~dayhr Incubator			
	Estimate	Lower	Upper
SD (Intercept), i.e. Incubator	0.01011	0.00328	0.03121
SD (dayhr)	0.00063	0.00020	0.00200
cor (intercept, dayhr)	-0.973	-0.998	-0.643
Within-group SE	0.0250	0.0240	0.0261

Variance function:	Power of variance covariate
Formula: ~nfry	Power -0.5

with other anthropogenic stressors on endangered species, populations and ecosystems; it is only with a clear and comprehensive understanding of these issues that we can successfully develop effective management strategies (Didham *et al.*, 2007; Mora *et al.*, 2007; Perkin *et al.*, 2014b).

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