Research Square

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Ontogenetic variation in phototactic responses of juvenile chum salmon (Oncorhynchus keta) under different light intensities

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Research Article

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Abstract

Phototactic behavior plays an important role in habitat selection, predator avoidance, and migration in juvenile fishes, yet ontogenetic variation in responses to light intensity remains poorly understood. I examined the phototactic responses of chum salmon (*Oncorhynchus keta*) fry to white LED illumination under controlled laboratory conditions and compared the results with previously published data for smolts obtained using an identical experimental protocol. Fry (mean standard length 40.8 mm) were exposed to six light treatments ranging from 7 to 4,217 lx in an indoor raceway tank. Phototactic response was quantified as the cumulative number of fish observed near the light source and analyzed using generalized linear mixed models with a negative binomial distribution. A model including a quadratic effect of light intensity provided a substantially better fit than a linear model (ΔAIC = 22.3). Phototactic response increased with increasing light intensity at low irradiances but declined under high-intensity illumination, indicating a significant nonlinear relationship. Both the linear and quadratic effects of light intensity were significant, whereas life stage was not retained as a significant predictor in the final model. Nevertheless, fry tended to exhibit lower response values than smolts across most light conditions. At illuminances exceeding approximately 1,000 lx, both fry and smolts showed reduced occurrence near the light source, suggesting avoidance of strongly illuminated environments. The similar response patterns observed before and after smoltification suggest behavioral continuity during early ontogeny in *O. keta*. These findings indicate that strong illumination may be avoided by juvenile chum salmon and provide new insights into the ecological significance of phototactic behavior during their freshwater life stage.

INTRODUCTION

Structures such as dams and weirs, built for purposes including irrigation, hydropower production, and flood control, commonly act as barriers to fish migration within river systems. By interrupting longitudinal connectivity, these installations can disrupt fish movement and have adverse effects on aquatic biodiversity and ecosystem processes (Dudgeon et al. 2006; Endou et al. 2006; Fukushima et al. 2007; Vörösmarty et al. 2010). To mitigate these impacts, fishways are often constructed to divert part of the flow around such obstacles, enabling migratory species to move upstream when appropriately designed (Hayashida et al. 2015; Shimoda et al. 2019; Masumoto et al. 2022).

In contrast, downstream passage remains problematic because intake structures typically withdraw much larger volumes of water than fishways, making them more likely to attract fish. As a result, many individuals are entrained into hydropower turbines, where they may suffer injury or mortality. This cumulative loss can be particularly severe for migratory species such as salmon fry (Coutant and Whitney 2000).

In recent years, techniques have been developed to guide juvenile salmonids at night using LED lights (Hansen et al. 2018, 2019; Matsuda 2024). In previous behavioral experiments that included chum salmon *Oncorhynchus keta* (Walbaum, 1792) (Matsuda 2024), an important fisheries species in Japan,

smolts of ~ 100 mm standard length (SL) exhibited negative phototaxis to a white LED light source greater than 1,000 lux (lx) at the water surface, but did not show positive phototaxis to any of the light intensities tested. However, *O. keta* fry are generally released at a size of ~ 45 mm fork length (FL), which is before smoltification (Hasegawa 2019). Subyearling salmonids have been reported to exhibit positive phototactic behavior (Tabor et al. 2017). Tanizawa et al. (2024) found that positive phototaxis weakened significantly during a relatively short period of juvenile growth (~ 10–50 mm total length) in centrarchid fishes. Although *Oncorhynchus keta* smolts (mean size 101 mm SL) appeared to congregate near a white LED light source with a weak intensity (Matsuda 2024), the result was not statistically significant (see Matsuda 2024: Fig. 2a,d). Therefore, to understand the phototactic behavior of fry at the stocking size, their behavioral response to a spectrum of light intensities would need to be understood. This study aimed to understand how varying light intensities could be used as a guidance mechanism at downstream bypass structures. This study used an indoor tank experiment to evaluate the phototactic response of *O. keta* fry under varying intensities of white LED light at the water surface. In addition, to assess the effects of life stage on phototactic behavior, I integrated the dataset of *O. keta* smolts reported by Matsuda (2024) and analyzed it using the same analytical framework.

MATERIALS AND METHODS

The experimental procedures were carried out at the Nikko Field Station (NFS) of the Fisheries Technology Institute, which belongs to the National Research and Development Agency, Japan Fisheries Research and Education Agency (FRA). In the autumn season, eggs of *O. keta* originating from a wild strain in the Ishikari River, Hokkaido, were provided by the FRA's Salmon Research Department, Fisheries Stock Assessment Center, and subsequently incubated at approximately 10°C. The hatched fry were maintained under a natural light–dark cycle, supplemented during the daytime by fluorescent lighting (1.58–556 lx at the water surface) for routine tank maintenance. At the time of the experiment, the fry were 64 to 80 days post-hatch (hatching dates: 8–24 January 2025), with an average standard length (SL) of 40.8 ± 2.4 mm (n = 100). Because smoltification in *O. keta* begins 2 months after hatching (Kaeriyama 1986), the fry used were in a state where smoltification was about to begin. Upon completion of the experimental trials, fish were euthanised using an overdose of 0.5% phenoxyethanol, followed by measurements of SL and body weight.

Experimental trials were conducted in an indoor raceway-style tank (major axis: 5 m; minor axis: 1.6 m; depth: 0.7 m; water level: 0.13 m) (Fig. 1). Two submersible pumps were placed in the raceway to produce a gentle flow and simulate rheophilic conditions. Within the tank, water velocity was highest in front of the submersible pumps and lowest behind them. The tank perimeter was shielded with opaque plastic sheets to block external light sources.

To provide controlled lighting, four white LED units (LRF-80/60W500G-USB; NS Lighting Co., Ltd, Japan) were mounted on a transparent acrylic panel (300 × 200 × 3 mm) using a clamp at one end of the tank. These lights were positioned 0.7 m above the tank bottom. A USB LED controller (NSUBP4; NS Lighting Co., Ltd) enabled remote adjustment of illumination intensity from outside the enclosed area. Without

the LEDs, light levels at the tank bottom remained at 0 lx. The designated observation area was defined as the region within 1 m from the LED units. A camera (WAT-910HX/RC; Watec Co., Ltd, Japan) with infrared floodlights of wavelength 850 nm (S20D-IR; Scene Electronics (HK) Co. Ltd, China) was installed above the tank to record fish behavior continuously throughout the trials. Water from a natural spring at NFS flowed into the tank at a constant rate (~ 0.6 l s^{-1}), with temperatures ranging from 9.0°C to 9.8°C. Experiments were conducted between 07:00 and 10:30.

Each trial included 10 individuals, with 10 replicated trials in total (100 individuals overall). To acclimate, fish were introduced into the tank by 11:00 a.m. on the day prior. Shortly after placement, overhead fluorescent lighting (~ 200 lx at surface) was turned off and the fish remained in darkness until 07:30 the following morning. Chen et al. (2021) demonstrated that larval zebrafish (*Danio rerio*) adjust their phototactic behavior according to a luminance set point determined by previous light exposure, indicating that responses to a given light intensity depend on recent light history rather than absolute luminance alone. Therefore, lighting stimuli were applied in six 30-min stages: starting from complete darkness (control), followed by incremental exposure to LED intensity grades:

Grade 1 (11.83 log photons cm^{-2} s^{-1} = 7.05 lx),

Grade 2 (12.48 log photons cm^{-2} s^{-1} = 31.7 lx),

Grade 3 (13.98 log photons cm^{-2} s^{-1} = 101 lx),

Grade 4 (14.59 log photons cm^{-2} s^{-1} = 418 lx),

Grade 5 (15.01 log photons cm^{-2} s^{-1} = 1,077 lx),

Grade 6 (15.60 log photons cm^{-2} s^{-1} = 4,217 lx).

Measurements of light intensity were taken beneath the LED units using a fiber-optic spectrometer (USB4000; Ocean Optics, USA), calibrated with a standard light source (DH2000-CAL; Ocean Optics, USA). Because the lowest intensity (Grade 1) fell below the spectrometer's detection threshold, its lux value was measured using a lux meter (LX-1108; Mother Tool Co., Ltd, Japan), and the corresponding photon flux was extrapolated based on its relationship with Grade 2 values (Thimijan and Heins 1983). To maintain a 0.7-m distance between the bottom of the tank and the white LED devices, the position of the lights was adjusted at the time the measurement was taken with the USB4000 sensor.

The initial 10 min of each grade was designated for acclimation, and behavioral analysis was based on fish location during the final 20 min. The number of fish that were within the arena (i.e., within 1-m distance from the white LED devices) was counted at 30-s intervals by freezing the video images. The number of fish exhibiting phototactic responses was counted in each of the 40 still images obtained from each trial, and the counts were then summed to obtain a total value for each light treatment.

Statistical analyses

To enable comparison with *O. keta* fry used in the present study (64–80 days post-hatch, mean standard length 40.8 mm), we reanalyzed a dataset of *O. keta* smolts (~ 7 months post-hatch, mean standard length 101 mm) previously reported by Matsuda (2024). The experimental procedures used for both datasets were identical.

To evaluate the effects of light intensity and life stage on phototactic response, I employed a generalized linear mixed model (GLMM). The response variable was the cumulative count of fish observed within the arena during each trial (count). Light intensity (log photons cm^{-2} s^{-1}) and life stage (fry or smolt) were included as fixed effects, and trial was included as a random effect. I initially fitted a GLMM assuming a Poisson distribution. However, residual diagnostics revealed significant overdispersion (dispersion ratio = 5.21, $p < 0.001$). Therefore, subsequent analyses were conducted using a GLMM with a negative binomial distribution (nbinom2) to account for the observed variance structure.

To evaluate the response pattern to light intensity, light intensity was treated as a continuous variable, and the following two models were fitted and compared using Akaike's Information Criterion (AIC).

Linear model:

count~light+lifestage+(1|trial)

Quadratic model:

count~light+light2 + lifestage+(1|trial)

All statistical analyses were conducted using R version 4.5.1 (R Core Team, 2025). GLMMs were fitted using the glmmTMB package, and statistical significance was determined at $p < 0.05$.

Ethical Statement

The care and use of experimental animals complied with the animal welfare laws, guidelines, and policies of the Fisheries Research and Education Agency (FRA). The experimental procedures were reviewed and approved by the FRA. FRA does not assign specific permit or approval reference numbers to studies of this type; therefore, as the procedures were not expected to cause pain or significant distress to the experimental fish, no permit number is available for this study.

RESULTS

The total number of fry that were observed close to the white LED devices (i.e., within the arena) in each trial under each light intensity are presented by box-and-whisker plots in Fig. 2. The median values of the box-and-whisker plots for fry and smolts (see Fig. 2 and Matsuda 2024: Fig. 2a) at each irradiance level (log photons cm^{-2} s^{-1}) were 96.5 and 101.0 in darkness (control), 84.5 and 158.5 at 11.83 (= 7.05 lx), 152.5 and 159.0 at 12.48 (= 31.7 lx), 127.0 and 107.5 at 13.98 (= 101 lx), 96.5 and 68.5 at 14.59 (= 418 lx), 12.0 and 54.0 at 15.01 (= 1,077 lx), and 8.5 and 40.0 at 15.60 (= 4,217 lx), respectively.

The results of the statistical analyses are presented in Table. 1. When light intensity was treated as a continuous predictor, the linear model including light intensity and life stage as fixed effects did not detect significant effects of either light intensity ($\beta = -0.025$, SE = 0.020, $z = -1.26$, $p = 0.206$) or life stage ($\beta = 0.253$, SE = 0.180, $z = 1.41$, $p = 0.160$). However, inspection of residual diagnostics suggested an inadequate fit of the linear model. The quadratic model provided a substantially better fit than the linear model (AIC = 1553.0 vs. 1575.3; ΔAIC = 22.3). In the quadratic model, both the linear term of light intensity ($\beta = 0.381$, SE = 0.083, $z = 4.57$, $p < 0.001$) and the quadratic term ($\beta = -0.028$, SE = 0.006, $z = -4.99$, $p < 0.001$) were significant. These results indicate a significant non-linear relationship between light intensity and phototactic response (defined as the total number of fish observed within the arena). Specifically, phototactic response increased with increasing light intensity at lower irradiances in both fry and smolts, but declined under the highest light conditions (see Fig. 2 and Matsuda 2024: Fig. 2a).

Life stage was not retained as a significant predictor in the final model ($\beta = 0.301$, SE = 0.166, $z = 1.81$, $p = 0.070$), although smolts tended to exhibit higher phototactic responses than fry across light conditions.

DISCUSSION

In the present study, the phototactic behavior of *Oncorhynchus keta* fry at a size corresponding to that used for stocking was evaluated under different light intensities. The results demonstrated that phototactic response did not change monotonically with increasing light intensity. Instead, the response exhibited a nonlinear pattern, peaking at intermediate light intensities and declining under stronger illumination. This pattern was supported by the significant quadratic term in the negative binomial GLMM, suggesting that the phototactic response of *O. keta* fry reaches an optimum at intermediate light levels.

Interestingly, the main effect of life stage (fry versus smolt) did not reach statistical significance ($p = 0.070$). Therefore, within the range of light intensities examined in this study, fry and smolts appear to exhibit broadly similar phototactic responses. Nevertheless, fry consistently tended to show lower response values than smolts under many light conditions. Consequently, the possibility that developmental changes influence sensitivity to light cannot be excluded. Given the available sample size, statistical power may have been insufficient to detect subtle differences between life stages, and further investigation is warranted. In contrast to the findings of Tanizawa et al. (2024), who reported a rapid decline in positive phototaxis during early growth stages in centrarchid fishes, the present results suggest an opposite tendency in salmonids.

Previous studies demonstrated that *O. keta* smolts exhibited negative phototaxis to white LED light intensities exceeding 15.01 log photons cm^{-2} s^{-1} (equivalent to 1,077 lx), whereas no statistically significant positive phototaxis was observed under weaker illumination conditions (Matsuda 2024). The present study showed that fry generally exhibited lower phototactic responses than smolts, suggesting that fry, like smolts, do not display positive phototaxis toward white LED illumination. However, fry also showed reduced occurrence near the light source under illuminances exceeding 1,077 lx, indicating that

high-intensity white LED illumination may induce negative phototaxis in this life stage as well. The decline in phototactic response under high light intensities is likely attributable to avoidance behavior elicited by intense illumination.

Oncorhynchus masou (Brevoort, 1856) typically remains in freshwater for approximately 18 months after hatching before undergoing smoltification and downstream migration (Hosoya 2015). Pre-smolt *O. masou* exhibit positive phototaxis only under relatively dim illumination, whereas post-smolt individuals display positive phototaxis across a wider range of light intensities (Matsuda 2024). Furthermore, neither life stage shows negative phototaxis to high-intensity white LED illumination (1,077–4,217 lx) (Matsuda 2024). Previous studies have suggested that juvenile salmonids inhabiting rivers generally prefer darker environments (Shirvell 1990), and the ecological differences associated with smoltification may explain the contrasting phototactic characteristics observed between these developmental stages. In contrast, *O. keta* begins smoltification approximately two months after hatching and subsequently migrates downstream (Kaeriyama 1986; Hosoya 2015). Consequently, the relatively short freshwater residence period of this species may result in a greater degree of behavioral continuity before and after smoltification. This may explain why fry and smolts exhibited similar responses to light in the present study. The results suggest that *O. keta* juveniles may avoid potential predation risk in river environments by avoiding strongly illuminated conditions during the juvenile stage.

At the same time, the increased occurrence observed under intermediate light conditions suggests that weak illumination may serve as an orientation cue. Positive phototaxis has previously been reported in juvenile salmonids (Tabor et al. 2017), and the present findings are broadly consistent with this observation.

The primary objective of this study was to provide fundamental information for the development of behavioral control techniques using white LED illumination immediately after the release of *O. keta* fry. Because fry did not exhibit a clear tendency toward positive phototaxis, the effectiveness of using white LED illumination to attract fry in rivers at night is likely limited. In contrast, white LED light sources producing surface illuminance greater than approximately 1,000 lx may be useful for deterring both fry and smolts from intake structures associated with weirs and dams.

Several limitations should be acknowledged. First, the experiment was conducted in an indoor tank environment and therefore did not incorporate the complex hydraulic conditions, ambient light regimes, schooling behavior, or predator presence characteristic of natural rivers. Second, only white LED illumination was examined, and the influence of wavelength-specific responses was not evaluated. Future studies should assess guidance efficiency under field conditions and examine how light color, light-source arrangement, and hydraulic conditions interact to influence fish behavior.

Declarations

I can confirm that this manuscript has not been published elsewhere and is not under consideration in whole or in part by any other journal. The author has no conflicts of interest to declare.

This work was supported by the National Research and Development Agency, Japan Fisheries Research and Education Agency. Keishi Matsuda conceived and designed the study, analysed the data and drafted the manuscript. The author confirms that the data supporting the findings of this study are available within the article or its supplementary materials.

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The author received no funding for this study.

Author Contribution

Keishi Matsuda conceived and designed the study, analysed the data and drafted the manuscript.

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Data Availability

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

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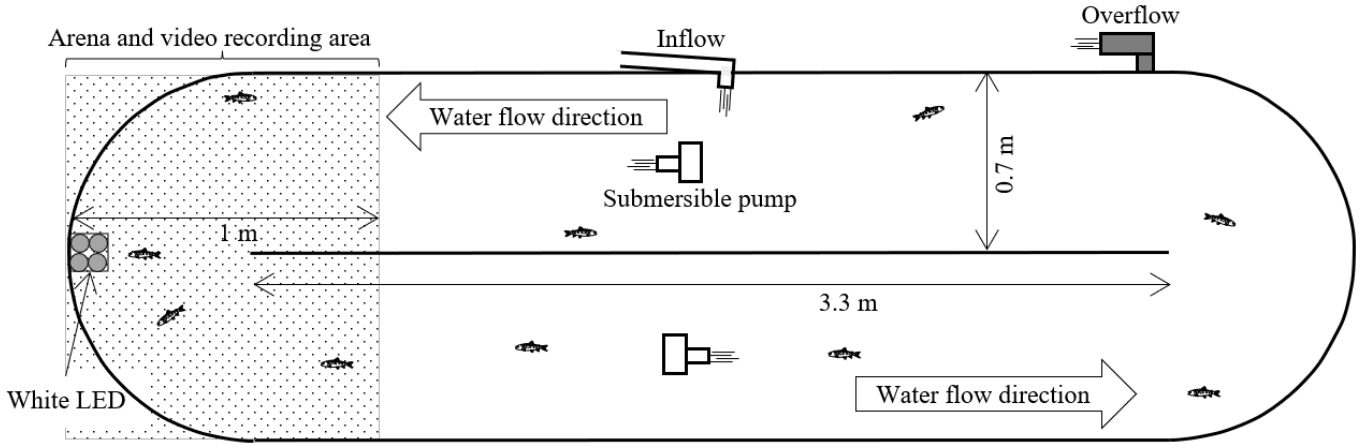
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Tables

Table 1
Results of the selected quadratic negative binomial GLMM

Predictor	Estimate	SE	z	p
Intercept	4.469	0.235	18.99	< 0.001
Light intensity	0.381	0.083	4.57	< 0.001
Light intensity²	-0.028	0.006	-4.99	< 0.001
Life stage (smolt)	0.301	0.166	1.81	0.070
Random effect (trial): variance = 0.064, SD = 0.253. AIC = 1553.0.				

Figures



Raceway tank (major axis: 5 m; minor axis: 1.6 m; depth: 0.7 m; water depth: 0.13 m)

Figure 1

Diagram of the raceway tank for testing the phototactic response of juvenile salmon to white LED lights, highlighting the observation arena and video recording area.

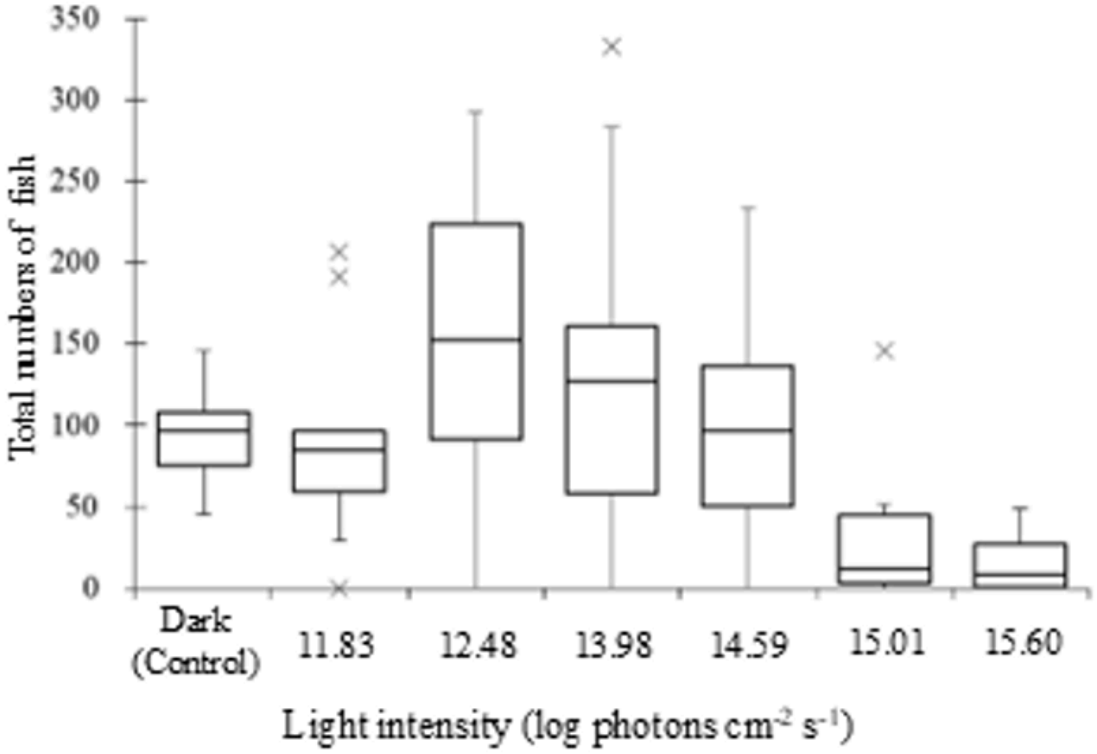


Figure 2

Total numbers of *Oncorhynchus keta* fry that were observed close to the white LED devices under each light intensity or under darkness (control) in each trial; trials were run by increasing the light intensity of the white LED devices, by six grades of 30-min duration each.