Hydrobiologia (2019) 841:191–203
https://doi.org/10.1007/s10750-019-04022-1

PRIMARY RESEARCH PAPER

Experimental evaluation of the effect of a light-emitting diode device on Chinook salmon smolt entrainment in a simulated river

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Received: 27 February 2019 / Revised: 4 July 2019 / Accepted: 9 July 2019 / Published online: 23 July 2019
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Abstract The entrainment and impingement of fish into water diversion infrastructure is one of the several factors contributing to their decline. Here, controlled experiments assessed the potential for a behavioral guidance device [a light-emitting diode (LED) light array] strobing at various spectra to reduce the entrainment of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) into a water diversion pipe. Fish were tested during the day and night, and under control conditions (light off) and red, blue, and white spectra strobing at 2 Hz. Fish entrainment into the diversion pipe was evaluated. Results indicated greater entrainment at night compared to day. All trials at night with the LED light strobing had higher entrainment than the control, with blue and white spectra corresponding to greater entrainment than red spectra. During the day, the white spectra treatment was different from the red treatment, with lower entrainment. LED lights employed to repel migratory juvenile salmon away from water intake structures may be ineffectual but there is potential for the light to be used as an attractant to guide fish towards desirable features such as "safe" areas (bypass channels or fishways).

Keywords Behavioral guidance · *Oncorhynchus tshawytscha* · Visual ecology · Water diversion

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Handling editor: Eric Larson

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10750-019-04022-1) contains supplementary material, which is available to authorized users.

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Introduction

Hydropower infrastructure, such as dams and water diversions for irrigation, fragment freshwater river systems with detrimental effects to biodiversity and ecosystem functioning (Fahrig, 2003; Dudgeon et al., 2006; Vörösmarty et al., 2010). In California, agricultural development and the subsequent construction of levees has resulted in the installation of over 3700 water diversion structures on the Sacramento and San Joaquin rivers. These divert, in an average year, more than 40% of the rivers' flow to supply 80% of the agricultural and urban water uses (Hanak et al., 2011; CDWR, 2014). These diversions pose a significant entrainment threat to fish species, including out-migrating Chinook salmon [(*Oncorhynchus tshawytscha,* (Walbaum, 1792)] smolts, as fish can either get impinged or inadvertently drawn with the water and transferred into machinery and irrigation ditches (Coutant & Whitney, 2000; Herren & Kawasaki, 2001; Kimmerer, 2008; Mussen et al., 2013, 2014a, b, 2015). These processes are one of the several contributing factors to the decline of Chinook salmon in California's central valley, USA (Moyle et al., 2011). The Sacramento River winter-run Chinook salmon was classified as Endangered under the state and the federal Endangered Species Act (ESA) in 1989 and 1994, respectively, and the Central Valley spring-run Chinook salmon was listed as Threatened under both the state and federal ESA's in 1999 (CDFW, 2014). There is a continued need to create affordable and effective solutions to reduce fish entrainment at water intake structures without reducing the volume of water extracted.

Fish screens are generally effective at minimizing juvenile salmonid entrainment into water diversion infrastructure (Swanson et al., 2004; Gale et al., 2008; Walters et al., 2012; Mussen et al., 2015); however, they are costly to install and maintain. Fish screens have been installed at many large water diversion projects in California and are required by law to be installed on new or renovated water diversion structures; however, 95% remain unscreened (CDFW, 1996; Calfish, 2012). Exploiting a fish's innate behavioral response to visual, auditory, or tactile environmental stimuli is a promising method to distance fish from harmful infrastructure, either by repelling fish from a dangerous path or directing them to a favorable path such as a bypass channel (Coutant, 1999; Noatch & Suski, 2012). For example, Mussen et al., (2014a) and (2014b) showed that a vibrating ring reduced entrainment into a water diversion pipe during the night (see also Knudsen et al., 1997). Lighting is an appealing alternative or addition to screens as it may be less costly to maintain (as it does not accumulate as much debris) and it does not decrease water extraction rates.

The use of white strobe lighting or mercury vapor bulbs has had mixed results in guiding juvenile Chinook. In large low-velocity water bodies they have been shown to repel juvenile Chinook (Nemeth & Andersen, 1992; Brown, 2000; Mueller et al., 2001; Johnson et al., 2005; Richards et al., 2007); however, in hydraulic conditions that more accurately simulate rivers, juvenile Chinook salmon were initially repelled but then attracted to white strobe lights (4 × 200 lumens flashing white light-emitting diode) (Mussen et al., 2014a) which increased entrainment. Kock et al. (2009) similarly found increased entrainment of juvenile salmonids when using white strobe lighting [(*Oncorhynchus mykiss* (Walbaum, 1792)]. Additionally, differences in light intensity can change the stimulus from being repulsive to attractive (Nemeth & Andersen, 1992) and the required power for this type of lighting is a major implementation cost (Patrick et al., 1985; Brown, 2000; Richards et al., 2007). More recently, therefore, work has begun exploring a range of light frequencies and strobe frequencies of light-emitting diodes (LEDs) for improved performance (Elvidge et al., 2018; Hansen et al., 2018; Ford et al., 2017, 2018).

Using different light spectra is a promising tool for behavioral guidance of fishes as spectral sensitivity varies among species (Lythgoe, 1980). Proximately, the wavelengths fish are sensitive to are determined by the types of photoreceptors in their retina (and the ratios of visual pigments within these photoreceptors). But ultimately, spectral sensitivity is determined by the species' evolutionary history, notably the influence of environmental light on predator–prey interactions (Lythgoe, 1979, 1980; Munz & McFarland, 1977; Levine & MacNichol, 1979; Douglas and Hawyshyn, 1990). While sensitivity to certain wavelengths is a good indication that these wavelengths are useful for

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detecting objects in the water column (Levine & MacNichol, 1982; Novales-Flamarique & Hawryshyn, 1993, 1994, 1997), the attractiveness or repulsiveness of different spectra will be strongly affected by environmental context and can only be determined behaviorally.

Strobing different colored LED's has proven to be effective at behaviorally repelling or attracting a variety of fish species (e.g., Ford et al., 2017, 2018; Elvidge et al., 2018). Pacific salmon (*Oncorhynchus* sp.) have broad-spectrum color vision (Niwa & Tamura, 1969; Nakano et al., 2006), although spectral sensitivity varies throughout their life cycle and with changing environmental conditions (Beatty, 1966; Tsin & Beatty, 1977; Cheng & Novales-Flamarique, 2004; Novales-Flamarique, 2005). Out-migrating Chinook salmon smolts are at the greatest risk of entrainment relative to other periods of their lifecycle, and at this time [100–140 days post-hatch (dph)] spectral sensitivity shifts to 600 nm (redder) in the L-wavelength cones (Novales-Flamarique, 2005). Recent work exposing Chinook salmon smolts to different spectra emitted from an LED behavioral guidance device in the lab found that red light (L-wavelength) had a repulsive effect during the day, but not at night (Hansen et al., 2018). There was also some evidence of a potentially attractive response of fish to blue (S-wave) and green (M-wave) light during the day (Hansen et al., 2018). These experiments were conducted on small shoals of four fish in a 4000-l indoor flume (250×92 cm^2) at a water depth of 30 cm and velocity of 0.15 m/s. While the results were informative, from a fisheries management perspective, it is necessary to conduct tests in a larger flume (to more realistically emulate hydropower or irrigation facilities), at greater shoal sizes. It is also important to conduct trials outdoors to mimic natural lighting. Responses of fish to water flow can dominate their behavioral decisions, constraining or reducing their response to other behavioral stimuli (Patrick et al., 1985; Carlson, 1994; Popper & Carlson, 1998; Enders et al., 2009). Therefore, it is important to test fish in more realistic environmental (including hydraulic) conditions as these more accurately represent conditions near water diversion infrastructure in natural waterways.

The goal of this experiment was to assess the effectiveness of different light spectra (red, blue, white, off-control) at reducing entrainment of out-migrating Chinook salmon smolts into an unscreened water diversion pipe within a simulated river. To assess the potential of different light spectra to behaviorally guide Chinook salmon smolts, we monitored the movement and entrainment of groups of fifty fish (as this species shoals in nature) in a 501,000-l flume simulating river conditions (see "Methods"). Entrainment was defined as the total number of fish that were pulled into (i.e., entrained) the water diversion pipe during the experiment (see "Methods"). We hypothesized that red would be the most repulsive spectra (Hansen et al., 2018) with this treatment having the lowest amount of entrainment, and that if any spectra were to be attractive and therefore potentially increase entrainment, it would be blue (Hansen et al., 2018). Fish were tested during the day and during the night as juvenile salmon often migrate during the night (Ingram & Wilder, 2006; Chapman et al., 2013) and we hypothesized that there may be different effects of light spectra on entrainment depending on time of day (Simmons et al., 2004; Hansen et al., 2018).

Materials and methods

Experimental animals

The majority of fall-run Chinook salmon in the Sacramento River system are of hatchery origin (Barnett-Johnson et al., 2007), therefore experiments were conducted with age-0 Chinook salmon acquired from US Fish and Wildlife Service's Coleman National Fish Hatchery (Anderson, California), hatched in March of 2018. Approximately 3000 fish were split equally between two 455L flow though circular tanks supplied with air-equilibrated groundwater from a dedicated well at UC Davis' Center for Aquatic Biology and Aquaculture (CABA). Tanks were held outside in natural light conditions, with fine black mesh lids. Fish were held at 11°C for 2 months before being raised to 15.5°C to increase growth rate. Temperature in the holding tanks was raised to 18.5°C 1 month before being assayed in the experiment to match the ambient temperature of the well water used to supply the flume. Fish were fed ad libitum commercial salmonid diet. Experiments were conducted in July 2018 when fish were $\sim$ 120–150 days post-hatch (dph). The mean $\pm$ SE fork length was

9.0 ± 0.04 cm and the mean ± SE mass was 10.9 ± 0.13 g. This size is comfortably within the range of Fall-Run out-migrants (6.0–12.0 cm), as documented by rotary screw trap monitoring (SacPAS).

Experimental flume

Experiments were conducted at UC Davis' J. Amorocho Hydraulics Laboratory in a 501,000-l outdoor flume (18.29 × 3.05 × 3.2 m^3) with a simulated riverbank (ramp) located down the entire length of the flume at a 26.6° slope from one wall of the flume to the base. A 0.46-m diameter unscreened diversion pipe was built near the flume's center, above the angled ramp with its base attached to the side of the flume 0.3 m above the ramp to simulate a typical irrigation pipe found along the levees of the Sacramento or San Joaquin river (Figs. 1a, b; 2). The behavioral guidance device was placed on the top of the diversion pipe, facing across the flume (see Fig. 2). The device was developed by ATET-Tech, Inc. (Thornhill, ON) as a behavioral guidance device for migratory fishes, designed for use in a field setting. The device (35 × 12 × 9 cm^3) consists of 162 LED modules that can each produce red, green, and blue light and strobe rates up to 40 Hz for all color combinations.

Fish were constrained to swimming within the main channel of the flume by stainless steel screens (0.6 cm mesh) placed upstream and downstream. Water depth was maintained at 2.2 m. Water source was the same used for fish housing. A 0.15-m/s sweeping velocity was generated to simulate a river current, and a water withdrawal rate through the pipe of 0.57 m^3/s. This set-up simulated ecologically and hydraulically relevant conditions common to the Sacramento river and near-identical set-ups have been utilized in several experiments investigating Chinook salmon smolt and green sturgeon *Acipenser medirostris* (Ayres, 1854) behavior and entrainment (Mussen et al., 2013, 2014a, b, 2015; Poletto et al., 2014, 2015; Ercan et al., 2017). A detailed description of the flume and its operational methods can be found in Mussen et al. (2013).

Experimental protocol

Fish (n = 50 ± 1) were transported (approximately 1.8 km) from their housing at CABA to the experimental flume in a cooler with an air stone, then transferred into a submerged release cage (0.91 × 1.22 × 0.41 m^3 covered in 0.6 cm steel mesh) using a 2.1-m-long, 15.2-cm-diameter PVC tube. The release cage was 9.3 m upstream of the diversion pipe, which provided the fish with the maximum possible distance to orientate themselves to

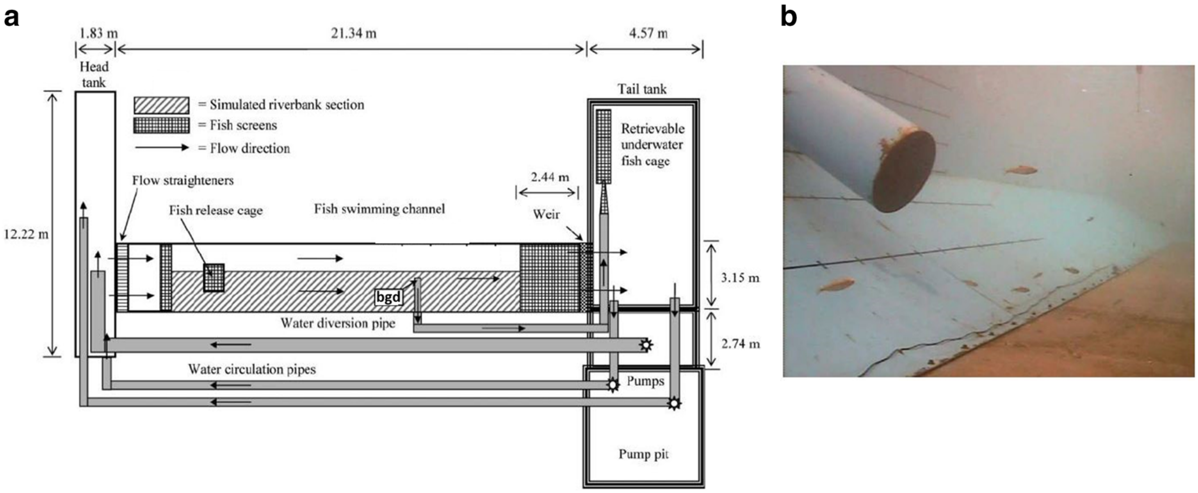

Fig. 1 **a** Flume diagram (top view) used in experiments, showing dimensions, water circulation, and location of the behavioural guidance device (bgd), and **b** underwater picture of water diversion pipe inlet and swimming Chinook salmon smolts Modified from Mussen et al. (2013)

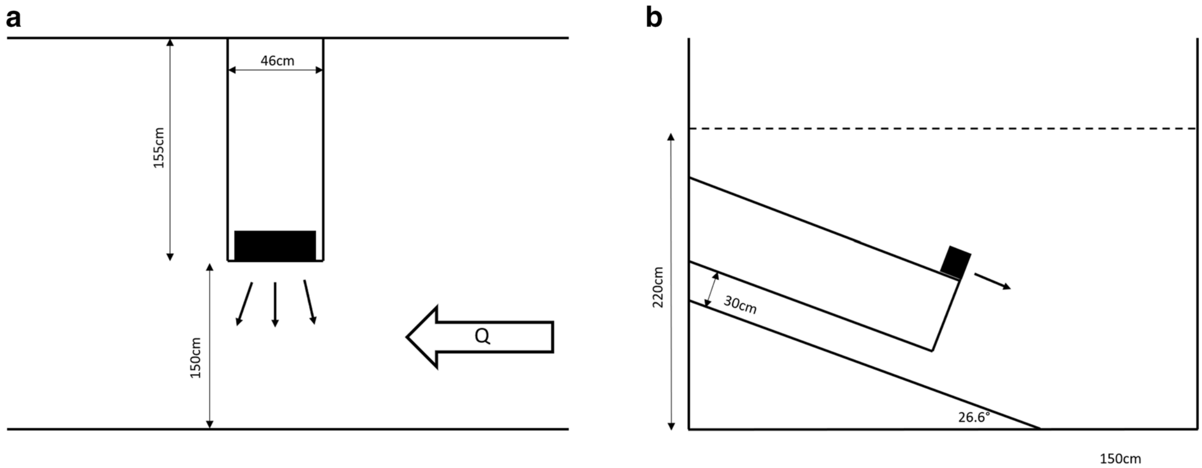

Fig. 2 LED behavioral guidance device placement diagram (**a** top view, **b** downstream view) used in experiments, showing dimensions, light direction (small black arrows), and flow direction (large white arrow, Q)

the current before encountering the diversion pipe. Prior to fish transfer to the release cage, hydraulic engineers started the flume so that fish acclimatized at the experimental water velocity (0.15 m/s). After a 30-min acclimation period the behavioral guidance device was activated to project the specified treatment color and strobing frequency (2 Hz). A strobing frequency of 2 Hz was used as it is predicted to increase the repulsive effects of light (Brown, 2000; Sager et al., 2000; Noatch & Suski, 2012; Ford et al., 2018) although it had a non-significant effect compared to constant light on Chinook salmon smolt behavior in work by Hansen et al. (2018). The treatment colors (red, blue, white, and off-control) were chosen based on Chinook salmon smolt spectral sensitivities (Parker & Hawryshyn, 2000; Novales-Flamarique, 2005) and previous results utilizing the behavioral guidance device on Chinook salmon smolts (Hansen et al., 2018) and white sturgeon (*Acipenser transmontanus* Richardson, 1836), which has similar spectral sensitivities (Ford et al., 2018). After acclimation and activation of the guidance device, fish were released via a remote pulley system and the cage was slowly winched out of the water column. Experimental fish were free to explore the flume, swimming upstream and downstream past the water diversion pipe for 60 min. The number of upstream and downstream passages of a cross section aligned with the pipe diversion were recorded by an observer from behind a Perspex viewing window. At the end of the experiment, fish were re-captured from the main body of the flume using a seine net. Fish that were entrained were transported along with the water (via gravity) into an extractable underwater cage with a removable mesh bag located in the tail tank. Non-entrained and entrained fish were placed into separate recovery tanks and were counted, weighed, and measured for FL. Water temperature and turbidity (NTU) were recorded at the beginning and the end of the experiment based on measurements by sensors incorporated into the behavioral guidance device. Water temperature was 21.5°C ± 0.1 (Mean ± SE) and turbidity levels were 301 ± 3.3 NTU (Mean ± SE). Test temperatures were within the bounds of what occurs in nature (CFDG, 2007). Light readings (μmol/m^2/s) within the water column surrounding the water diversion pipe were measured during the day and during the night for each spectra treatment using a quantum flux meter (LI-COR LI-1400). Readings were taken 60 cm downstream of the pipe, directly in line with the pipe and 60 cm upstream of the pipe at 30 cm intervals from the pipe's mouth across to the opposite wall (see Table S1). One to three trials during the day (09:00–16:30 h) and one to three trials during the night (21:00–04:00 h) were run every 24 h. Each trial was 60 min long.

The experimental design was a 2 × 4-fully crossed factorial, with time of day (day or night) and spectra (off-control, red, blue, or white—all strobing at 2 Hz) as the two factors. Experimenters recorded three dependent variables: (1) Entrainment (E), defined as the total number of fish entrained into the diversion pipe in each trial; (2) number of pipe passages (PP), defined as the number of fish that passed the diversion pipe in each trial; and (3) entrainments per pipe passage (EPP), calculated by dividing entrainment by the number of pipe passages. The number of pipe passages (PP) and entrainments per pipe passage (EPP) were only able to be calculated for the day trials as fish were not visible at night. Number of pipe passages (PP) is a coarse-scale proxy for activity but more importantly also allows for the calculation of entrainments per pipe passage, a metric which allows evaluation of entrainment as a function of the interaction of fish with the water diversion pipe.

Data analysis

All data analysis was conducted in the R computing environment (R Core Team, 2018) using RStudio (v1.1.383) and were done using packages *car* (Fox & Weisberg, 2011), *lme4* (Bates et al., 2015), *multcomp* (Hothorn et al., 2016), and *ggplot2* (Wickham, 2016). P-values were considered significant at the $\alpha = 0.05$ level, and significance of all categorical variables in generalized linear models was tested using the Wald χ^2 Test. To ensure model assumptions were met, model residuals were graphically evaluated for normality, outliers, and homoscedasticity as appropriate. All post hoc tests used single-step P value adjustments to account for multiple comparisons.

Fish size [fork length (FL) and mass] was compared among treatments and among end points (entrained into diversion pipe or remaining in flume) using generalized linear models with a Gaussian error distribution and identity link function for FL, and a Gamma error distribution and an inverse link function for mass.

To explore how treatments affected the likelihood of entrainment, we performed a generalized linear mixed model (GLM, binomial error distribution, and logit link function). We set time of day and spectra as interacting categorical predictor variables to see if they predicted entrainment (E). Mean fish size (FL) per trial and water temperature at the end of each trial were centered and included as additive predictors to control for potential differences in experimental conditions between trials. We ran post hoc comparisons on the interaction treatment to give 16 pairwise comparisons of interest for time of day and spectra out of a possible 28 comparisons.

For trials conducted during the day, we explored whether spectra had an effect on the number of pipe passages (PP) or the entrainment per pipe passage (EPP). Analysis was conducted with GLMs (Poisson error distribution and log link function and binomial error distribution with a logit link function, respectively). Models also included centered variables of mean fish size (FL) in each trial, and water temperature at the end of each trial to account for potential differences in experimental conditions between trials. Post hoc tests of all possible pairwise combinations of spectra ($n = 6$) were conducted for each model.

All data generated or analyzed during this study are included in this published article (and its supplementary information files).

Results

Generalized linear models indicated that fish size (FL and Mass) were not significantly related to spectra ($P = 0.11$, $P = 0.38$, respectively), nor to experimental endpoint (entrained into diversion pipe or remaining in flume; $P = 0.06$, $P = 0.11$, respectively). Nor were there significant interactions between spectra and time of day ($P = 0.11$, $P = 0.11$ respectively). However, there were significant differences in both size metrics between day and night (Mass: $\chi^2 = 14.63$, $df = 1$, $P = 0.0001$; FL: $\chi^2 = 5.804$, $df = 1$, $P = 0.016$), with night experiments having significantly larger fish (Table 1).

The probability of entrainment was significantly related to the interaction between time of day and spectra ($\chi^2 = 41.16$, $df = 3$, $P < 0.0001$), with entrainment generally greater during the night than during the day (Fig. 3, Table 1). Post hoc analysis showed significantly greater entrainment during the night than the day under the blue spectra (Estimate = 2.79, SE = 0.295, $z = 9.43$, $P < 0.001$), white spectra (Estimate = 4.26, SE = 0.59, $z = 7.16$, $P < 0.001$), and red spectra (Estimate = 1.46, SE = 0.30, $z = 4.92$, $P < 0.001$) but no significant difference between night and day under the control (off) treatment (Estimate = 0.81, SE = 0.43, $z = 1.87$, $P = 0.47$). During the night, entrainment was significantly greater under blue and white spectra compared to red spectra (Estimate = 1.27, SE = 0.19, $z = 6.65$, $P < 0.0001$, Estimate = 0.99, SE = 0.18, $z = 5.25$, $P < 0.0001$, respectively) and the control treatment

Table 1 Summary data of each spectra treatment [control (light off), and red, blue, and white light strobing at 2 Hz] during the day and night

Treatment	Fish FL (cm)	Fish mass (g)	Pipe passes (PP) (Mean ± SE)	Entrainment (E) (Median ± SE)	Entrainments per pipe passage (EPP) (Median ± SE)
Day					
Off	9.0 ± 0.1	10.2 ± 0.4	40.29 ± 12.02	0 ± 0.1	0.0 ± 2.9
Red	9.2 ± 0.1	11.3 ± 0.4	35.57 ± 9.27	2 ± 1.3	5.8 ± 4.1
Blue	8.9 ± 0.1	10.3 ± 0.4	40.14 ± 10.76	1 ± 1.1	5.7 ± 4.3
White	8.8 ± 0.1	10.3 ± 0.4	70.00 ± 15.45	0 ± 0.2	0.0 ± 0.6
Night					
Off	9.3 ± 0.1	11.9 ± 0.3	NA	2 ± 0.1	NA
Red	9.1 ± 0.1	11.3 ± 0.3	NA	7 ± 1.3	NA
Blue	9.0 ± 0.1	11.0 ± 0.3	NA	17 ± 2.4	NA
White	9.2 ± 0.1	11.7 ± 0.3	NA	15 ± 2.9	NA

All trials were conducted with 50 juvenile Chinook salmon, and each treatment was replicated in seven trials

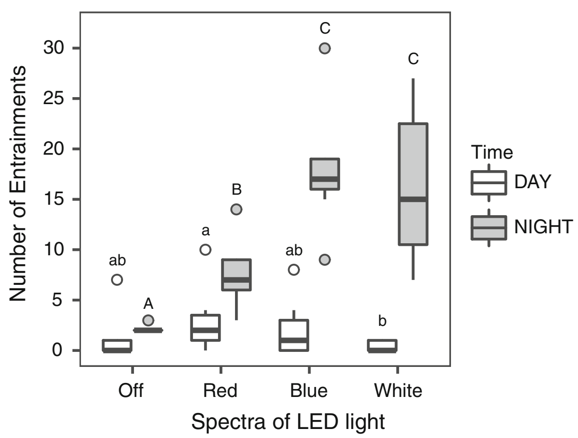

Fig. 3 Number of Chinook salmon entrained by treatment (time of day and spectra) out of 50 individuals entering each experimental trial ($N = 7$). Uppercase letters indicate significant differences between night time trials, while lowercase letters indicate significance of day time trials. Only the control (off) treatment had no significant difference in entrainment between day and night trials. Heavy line within box indicates median, boxes span from 25 to 75 percentile (the interquartile range; IQR), and whiskers extend 1.5*IQR. No whisker appears if the minimum or maximum value is within the IQR. When points occur beyond whiskers, they are shown. Open diamonds indicate mean values

(Estimate = 2.69, SE = 0.29, $z = 9.15$, $P < 0.0001$, Estimate = 2.40, SE = 0.29, $z = 8.3$, $P < 0.0001$, respectively). However, blue and white were not significantly different from one another ($P = 0.59$). During the day, the only significant difference between entrainment was between the red and white spectra, with lower entrainment in the white light (Estimate = − 1.81, SE = 0.63, $z = 2.89$, $P = 0.047$). Additionally, the generalized linear model indicated that there was significantly greater entrainment at lower water temperatures (Estimate = − 0.48, SE = 0.12, $z = -3.92$, $P < 0.0001$) but there was no significant effect of FL ($P = 0.52$).

During daytime control trials (LED off) juvenile salmon passed the diversion pipe on average 40.3 times (SE = 12.0) during the 60 min trial period, and had a 0.039 (SE = 0.028) entrainment per pipe passage score. There was a significant effect of spectra on pipe passes (PP; $\chi^2 = 47.1$, $df = 3$, $P < 0.0001$) and on entrainment per pipe passage (EPP; $\chi^2 = 31.3$, $df = 3$, $P < 0.0001$). Pairwise post hoc tests among the four spectra ($n = 6$ comparisons) indicated that there were significantly more pipe passes under the white light treatment, and significantly lower entrainment per pipe passage for the white light treatment than all other spectra (Table 1). Additionally, the generalized linear models indicated that there were significantly more pipe passes in trials with a smaller mean fish size (Estimate = − 0.37, SE = 0.06, $z = -6.49$, $P < 0.0001$), and a higher entrainment per pipe passage for trials with a smaller mean fish size (Estimate = − 1.50, SE = 0.43, $x = -3.49$, $P < 0.001$). There were no significant effects of water temperature on number of pipe passages or entrainment per pipe passage ($P = 0.30$, $P = 0.19$, respectively).

Discussion

The entrainment of juvenile Chinook salmon smolts was influenced by both time of day and the spectra emitted from an LED behavioral guidance device. Entrainment was significantly higher during the night than during the day. This may have been because fish moved passed the water diversion pipe more at night; however, as fish were not visible at night, this was not quantifiable. When the light was off (control treatment) entrainment was similar during the day and night—which concurs with previous experiments using this flume and species (Mussen et al., 2013). However, entrainment in the wild is higher for other fish species at night (Nobriga et al., 2004) and juvenile salmon are known to migrate down the Sacramento River at night (Ingram & Wilder, 2006; Chapman et al., 2013). Thus, further work at water diversion pipes in natural settings should assess whether there is differential entrainment for Chinook salmon smolts depending on time of day, where aspects such as predation risk (that were absent in the flume) may be relevant.

In contrast to a previous experiment that used the LED behavioral guidance device with Chinook salmon smolts (Hansen et al., 2018), the effect of the various spectra treatments was significant during the night. During the night, all wavelengths of light emitted from the behavioral guidance device increased entrainment compared to the control (LED off) treatment. Therefore, rather than repelling the fish away from the behavioral guidance device and therefore the water diversion pipe, light emitted from the device at night seemingly had an attractive effect. This was particularly true for blue and white light which had significantly greater entrainment than red light. This result contrasts to the work with another Pacific salmon species *Oncorhynchus masou masou* (Brevoort, 1856), where differences in spectra were not found to have any influence in attempts to behaviorally guide the fish (Terazono, 1998). If blue and white light did indeed attract more fish into the vicinity of the water diversion pipe, it is likely that the inflow velocity was too great for the fish to escape. Portz (2007) determined the burst swimming velocity of similar sized Chinook salmon smolts to be 0.6 m/s, whereas the intake velocity at the water diversion pipe could exceed 2.2 m/s (Ercan et al., 2017). It is also possible that at close vicinity the bright lights induced a "torpor-like" state or a sensory distraction that led to a reduced escape response and thus a further increase in entrainment (Novales-Flamarique et al., 2006). Chinook salmon smolt entrainment similarly increased under white strobe lighting in Mussen et al. (2014b), and Kock et al. (2009) also found that strobe light illumination increased juvenile steelhead entrainment at turbine induction slot inlets. Considering (i) the statistically significant increase in entrainments at night under blue and white light, and (ii) the need to improve the effectiveness of existing fish bypasses for downstream migrants and fishways for upstream migrants, future work should explore optimal light intensities for attraction. In this study, white and blue light emitting at an intensity of ~ 1–6 µmol/m^2/s (dependent on the distance from the light source, Table S1) was attractive to Chinook salmon smolts and should be used as a guide for future experimental designs using Chinook salmon smolts and other salmonids.

Overall entrainment was comparable to that found in a previous study (Mussen et al., 2013), which used the same flume at the same water diversion rate (0.57 m^3/s) and sweeping velocity (0.15 m/s). However, the Chinook salmon tested in that study were larger [~ 13.0 ± 0.15 cm FL (Mean ± SE)] than in the current study (9.0 ± 0.04 cm FL (Mean ± SE)). Entrainment in the current study was much lower than in Mussen et al. (2014b) which had comparable fish sizes; however, those trials ran for twice as long (120 compared to 60 min) and had a greater density of fish in the flume (37.5% greater). If one compares the entrainment per pipe passage between the sets of experiments, the results are more similar: ~ 2% (Mussen et al., 2013), and ~ 4% (Spring), ~ 1% (Summer) (Mussen et al., 2014a) compared to ~ 0% in the current study in control conditions and ~ 6% with the blue light on (median values). Mussen et al. (2015) had higher entrainment per pipe passage, up towards 15%; however, fish in these experiments were particularly small at 6.6 ± 0.6 cm FL (Mean ± SE). Entrainment of juvenile Chinook salmon in natural waterways passing similarly sized water diversion pipes is unknown. A study at Princeton Pumping Plant calculated a 0.05% entrainment risk for juvenile Chinook salmon (Hanson, 2001) but extrapolating these findings along with ours to estimate wild fish entrainment risk is very difficult given the limited information regarding the locations and operation schedule for unscreened diversions and the paucity of information about space use of Chinook salmon around these pipes.

The low percentages of fish entrainment per pipe passage across experiments generally suggests that the fish can sense the water diversion pipe and move past it at a safe distance (> 44 cm, Mussen et al., 2013) and avoid becoming entrained. Chinook salmon smolts avoid moving into novel, darkened structures and also avoid areas of increased water velocity (Kemp et al., 2005; Enders et al., 2009). During the day, fish likely could see the pipe and may have been visually deterred by it. At night, however, despite reduced or even absent visual cues in the control (LED off) treatment, fish were still able to largely avoid being entrained. It is likely that they used their lateral line to sense the change in flow direction and velocity and avoid the area. Water velocity increases dramatically as fish approach the diversion pipe intake, by a factor of 17 compared to the main channel sweeping velocity, and it may be that the fish that did get entrained were simply unable to react fast enough to the velocity gradient (Mussen et al., 2013). Critically, even if entrainment per pipe passage is low, management agencies must be mindful that smolts may encounter hundreds of these unscreened pipes during their out migration.

Chinook salmon have evolved a visual system that ensures they can function effectively in different environmental light conditions (Munz & McFarland, 1977; Levine & MacNichol, 1979, 1982) and have photoreceptors which are sensitive to all the spectral wavelengths tested (Novales-Flamarique, 2005). Maximum spectral sensitivity in Chinook salmon smolts (in their rods) is in the lower-middle wavelengths (500 nm, greener light) (Novales-Flamarique, 2005), but it was hypothesized red would be the most repulsive spectra due to results in previous experiments (Hansen et al., 2018) and because in natural conditions of the Pacific coastal and river systems it contrasts best with background light (Novales-Flamarique & Hawryshyn, 1993). Indeed, red light was less attractive than blue or white light, having significantly fewer entrainment events at night; however, it was still attractive compared to the off treatment (control). Blue light is closer to the maximal spectral sensitivity in the rods of Chinook salmon smolts than red light is; however, it is not conclusive how exactly these sensitivities translate to the movement behavior of Chinook salmon smolts navigating past an LED behavioral guidance device. While spectral sensitivity was a good predictor of behavioral response in other species, with peak spectral sensitivities resulting in repulsion in *Plecoglossus altivelis* (Temminck & Schlegel, 1846) (Hino, 1979; Furuse, 1999) and attraction in *Acipenser transmontanus* (Ford et al., 2018), previous experiments emitting light at the maximal spectral sensitivity of Chinook salmon smolts did not translate to effective repulsion or attraction (Hansen et al., 2018). Precisely how these results extend beyond juvenile Chinook salmon to other salmonids is an area that needs further research. Comparative work has shown that salmonids generally have a non-specific visual system that is predominately dominated by middle wavelength sensitivity (Niwa & Tamura, 1969; Parker & Hawryshyn, 2000; Nakano et al., 2006). Therefore, results from this study could help inform research on other species of salmonids. However, considering our work did not establish a correlative link between spectral sensitivity and effective repulsion and attraction of juvenile Chinook salmon, and that spectral sensitivity changes according to environmental stimuli and state of maturation (Beatty, 1966; Tsin & Beatty, 1977; Cheng & Novales-Flamarique, 2004; Novales-Flamarique, 2005), we would be hesitant to extrapolate these results too far.

The null effect of spectra treatment during the day [as opposed to previous experiments where it had a significant effect (Hansen et al., 2018)] may be partially explained by differences in the ambient light environment. In Hansen et al. (2018), there was up to an eightfold increase in the quantum flux light readings (μmol/m^2/s) when the behavioral guidance device was on compared to when it was off. The exact difference was dependent on the wavelength emitted and the distance to the behavioral guidance device at which the reading was taken (Hansen et al., 2018). Hansen et al. (2018) was conducted indoors in a much smaller flume than the current experiment, which was conducted outside (under a large canopy) in a large flume more closely mimicking environmental conditions found near water diversion pipes on the Sacramento River. Here there was a maximum 2.5-fold increase in the quantum flux light readings (μmol/m^2/s) when the behavioral guidance was on compared to when it was off (see Table S1). In addition, this twofold increase was only when the light reading was taken 1 ft from the behavioral guidance device. The difference in light was reduced to almost nothing at further distances (see Table S1). When this is taken into consideration it is perhaps not surprising that there was no effect of spectra treatment during the day. The result instead reflects the importance of ambient light conditions and environmental context for the effectiveness of using a light source for behavioral guidance. Therefore, while overall light intensity is known to be important for determining the effect of a light source on Chinook salmon movement behavior (Nemeth & Andersen, 1992), it is very likely that the difference in intensity between the light source and the background light is similarly critical (Levine & MacNichol, 1982; Novales-Flamarique & Hawryshyn, 1993, 1994, 1997), which will be of practical concern when placing the behavioral guidance device in the natural environment where ambient light levels will fluctuate dramatically on an hourly and seasonal timescale.

Future experiments should consider varying other environmental variables that will likely affect movement and visual stimulation in Chinook salmon smolts. Although difficult to manipulate at large scales, temperature will be important considering its effect on social interactions, exploration, and activity rates (Peck et al., 2009; Bartolini et al., 2015). In our study, entrainment was less at higher temperatures, and it is possible that an increase in swimming performance may partially explain this (Poletto et al., 2017); however, much more research needs to be conducted. It is also vital to consider turbidity, as increased particulate matter ('gelbstoff': short-wave absorbing compounds) will cause changes in both light intensity and spectral frequency, shifting background light to longer wavelengths (Levine & MacNichol, 1979; Utne Palm, 2002), and has also been shown to change fish migratory behaviors (Lloyd et al., 1987; Newcombe & MacDonald, 1991). As well as a systematic assessment of the response of fish to combinations of environmental factors, due to the complexity of environmental factors that may affect the attraction or repulsion of fish to the underwater behavioral guidance device, pilot studies should be undertaken in natural waterways at water diversion sites of special concern. Tracking of fish movement near water diversions in natural waterways and in laboratory flumes (for example, with DIDSON technology (Boswell et al., 2008)) will help determine encounter rates and more precise movement characteristics, which will greatly assist management decisions as well as the design of future manipulative experiments.

Conclusions

The results of this experiment suggest that using the ATET-tech behavioral guidance device to repel Chinook salmon smolts from water diversion pipes on the Sacramento and San Joaquin rivers may be ineffectual and likely increase entrainment during the night. However, the potential attractive qualities of the blue and white light are promising from a management perspective and future studies should explore whether these spectra can be utilized as an attractant system to guide fish towards a bypass near water diversion infrastructure or improve the effectiveness of fishways. There is also the need to determine the optimal light intensity for attraction for blue and white light. This has been a successful area of research with age-0 white sturgeon (*Acipenser transmontanus*), where incorporating the guidance device emitting green light at 20 Hz with a louver has been effective at increasing bypass ratios (Ford et al., 2017, 2018).

Acknowledgements This work was supported by the University of California, Davis Agricultural Experiment Station [Grant # 2098-H], and the Woodland Davis Clean Water Agency [Agreement #A29651]. The authors thank the Fangue Laboratory and J. Amorocho Hydraulics Laboratory members for all their assistance with fish rearing and flume operation. The authors also thank two anonymous reviewers for constructive comments towards improving this manuscript.

Compliance with ethical standards

Conflicts of interest PHP and MS are principals of ATET-Tech, the manufacturer of the LED device tested here. None of the other authors have a financial stake in ATET-Tech. Although PHP and MS were involved in study design and interpretation, all data were collected by the academic research team.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the University California, Davis.

References

Barnett-Johnson, R., C. B. Grimes, C. F. Royer & C. J. Donohoe, 2007. Identifying the contribution of wild and hatchery Chinook salmon (*Oncorhynchus tshawytscha*) to the ocean fishery using otolith microstructure as natural tags. Canadian Journal of Fisheries and Aquatic Sciences 64: 1683–1692.

Bartolini, T., S. Butail & M. Porfiri, 2015. Temperature influences sociality and activity of freshwater fish. Environmental Biology of Fishes 98: 825–832.

Bates, D., M. Maechler, B. Bolker & S. Walker, 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1–48.

Beatty, D. D., 1966. A study of the succession of visual pigments in Pacific salmon (*Oncorhynchus*). Canadian Journal of Zoology 44: 429–455.

Boswell, K. M., M. P. Wilson & J. Cowan Jr., 2008. A semi-automated approach to estimating fish size, abundance, and behavior from dual-frequency identification sonar (DIDSON) data. North American Journal of Fisheries Management 28: 799–807.

Brown, R., 2000. The potential of strobe lighting as a cost effective means for reducing impingement and entrainment. Environmental Science and Policy 3: 405–416.

CalFish, 2012. California fish passage assessment database. CalFish, California Cooperative Anadromous Fish and Habitat Data Program [available on internet at www.calfish.org].

Carlson, T. J., 1994. Use of Sound for Fish Protection at Power Production Facilities: a Historical Perspective of the State of the Art. Battelle Pacific Northwest Laboratories, Portland.

CDFW (California Department of Fish and Wildlife), 1996. Statewide fish screening policy [available on internet at http://www.dfg.ca.gov/fish/Resources/Projects/Engin/Engin_ScreenPolicy.asp].

CDFG (California Department of Fish and Game), 2007. Timing, composition and abundance of juvenile salmonid emigration in the Sacramento River near Knight's Landing, October 2001–July 2002 [available on internet at https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=45739].

CDFW (California Department of Fish and Wildlife), 2014. State and federally listed endangered and threatened animals of California [available on internet at http://www.dfg.ca.gov/biogeodata/cnddb/pdfs/TEAnimals.pdf].

CDWR (California Department of Water Resources), 2014. Draft California water plan, update 2013 [available on internet at http://www.Waterplan.water.ca.gov/cwpu2013/prd/index.cfm].

Chapman, E. D., A. R. Hearn, C. J. Michel, A. J. Amman, S. T. Lindley, M. J. Thomas, P. T. Sandstrom, P. T. Singer, M. L. Peterson, R. B. MacFarlane & A. P. Klimley, 2013. Diel movements of out-migrating Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*) smolts in the Sacramento/San Joaquin watershed. Environmental Biology of Fishes 96: 273–286.

Cheng, C. L. & I. Novales-Flamarique, 2004. Opsin expression: new mechanism for modulating colour vision. Nature 428(6980): 279.

Coutant, C. C., 1999. Think like a fish! Emphasising the 'behaviour' in behavioural guidance systems. Hydrology Review 17: 18–24.

Coutant, C. C. & R. R. Whitney, 2000. Fish behaviour in relation to passage through hydropower turbines: a review. Transactions of the American Fisheries Society 129: 351–380.

Dudgeon, D., A. H. Arthingtom, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Leveque, R. J. Naiman, A. H. Prieur-Richard, D. Soto, M. L. Stiassney & C. A. Sullivan, 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81: 163–182.

Elvidge, C. K., M. I. Ford, T. C. Pratt, K. E. Smokorowski, M. Sills, P. H. Patrick & S. J. Cooke, 2018. Behavioural guidance of yellow-stage American eel *Anguilla rostrate* with a light-emitting diode device. Endangered Species Research 35: 159–168.

Enders, E. C., M. H. Gessel & J. G. Williams, 2009. Development of successful fish passage structures for downstream migrants requires knowledge of their behavioural response to accelerating flow. Canadian Journal of Fish & Aquatic Sciences 66: 2109–2117.

Ercan, A., M. L. Kavvas, K. Carr, Z. Hockett, H. Bandeh, T. D. Mussen, D. E. Cocherell, J. B. Poletto, J. J. Cech Jr. & N. A. Fangue, 2017. Hydraulics near unscreened diversion pipes in open channels: large flume experiments. JAWRA Journal of the American Water Resources Association 53: 431–441.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecological and Evolutionary Systems 34: 487–515.

Ford, M. I., C. K. Elvidge, D. Baker, T. C. Pratt, K. E. Smokorowski, P. Patrick, M. Sills & S. J. Cooke, 2017. Evaluating a light-louver system for behavioural guidance of age-0 white sturgeon. River Research & Applications 33: 1286–1294.

Ford, M. I., C. K. Elvidge, D. Baker, T. C. Pratt, K. E. Smokorowski, P. Patrick, M. Sills & S. J. Cooke, 2018. Preferences of age-0 white sturgeon for different colours and strobe rates of LED lights may inform behavioural guidance strategies. Environmental Biology of Fishes 101: 667–674.

Fox, J. & S. Weisberg, 2011. An {R} Companion to Applied Regression, 2nd ed. Sage, Thousand Oaks CA.

Furuse, M., 1999. Spectral response properties of S-potentials in the retina of the ayu, *Plecoglossus altivelis*. Nippon Suisan Gakkaishi 65: 903–904.

Gale, S. B., A. V. Zale & C. G. Clancy, 2008. Effectiveness of fish screens to prevent entrainment of Westslope Cutthroat Trout into irrigation canals. North American Journal of Fisheries Management 28: 1541–1553.

Hanak, E., J. Lund, A. Dinar, B. Gray, R. Howitt, J. Mount, P. Moyle, & B. Thompson, 2011. Managing California's water: from conflict to reconciliation [online]. A report by the Public Policy Institute of California. [available on internet at http://www.ppic.org/main/publication.asp?i=944].

Hansen, M. J., D. E. Cocherell, S. J. Cooke, P. H. Patrick, M. Sills & N. A. Fangue, 2018. Behavioural guidance of Chinook salmon smolts: the variable effects of LED spectral wavelength and strobing frequency. Conservation Physiology 6: coy032.

Hanson, H., 2001. Are juvenile Chinook salmon entrained at unscreened diversions in direct proportion to the volume of water diverted. Contributions to the Biology of Central Valley Salmonids 2: 331–342.

Herren, J. A. & S. S. Kawasaki, 2001. Inventory of water diversions in four geographic areas in California's Central Valley. Fish Bulletin 179: 343–355.

Hino, S., 1979. Avoidance reaction to the light stimulation in ayu, *Plecoglossus altivelis*. Jogyouhoukokusyo 4: 42–45.

Hothorn, T., F. Bretz & P. Westfall, 2016. Simultaneous inference in general parametric models. Project for Statistical Computing, Vienna, Austria.

Ingram, J. F. & R. M. Wilder, 2006. Seasonal variation in diel activity patterns of Chinook Salmon in the Sacramento-San Joaquin River delta. Poster presented at Interagency Ecological Program 2006 Annual Workshop, Pacific Grove, California [available on internet at www.fws.gov/stockton/jfmp/datareports.asp].

Johnson, P. N., K. Bouchard & F. A. Goetz, 2005. Effectiveness of strobe lights for reducing juvenile salmonid entrainment into a navigation lock. North American Journal of Fisheries Management 25: 491–501.

Kemp, P. S., M. H. Gessel & J. G. Williams, 2005. Fine-scale behavioral responses of Pacific salmonid smolts as they encounter divergence and acceleration of flow. Transactions of the American Fisheries Society 134: 390–398.

Kimmerer, W. J., 2008. Losses of Sacramento River Chinook salmon and delta smelt to entrainment in water diversions in the Sacramento-San Joaquin delta. San Francisco Estuary and Watershed Science 6: 2.

Knudsen, F. R., C. B. Schreck, S. M. Knapp, P. S. Enger & O. Sand, 1997. Infrasound produces flight and avoidance responses in Pacific juvenile salmonids. Journal of Fish Biology 51: 824–829.

Kock, T. J., S. D. Evans, T. L. Liedtke, D. W. Rondorf & M. Kohn, 2009. Evaluation of strobe lights to reduce turbine entrainment of juvenile steelhead (*Oncorhynchus mykiss*) at Cowlitz Falls Dam, Washington. Northwest Science 83: 308–314.

Levine, J. S. & E. F. MacNichol, 1979. Visual pigments in teleost fishes: effect of habitat, microhabitat, and behaviour on visual system evolution. Sensory Processes 2: 95–131.

Levine, J. S. & E. F. MacNichol, 1982. Colour vision in fishes. Scientific American 246: 140–149.

Lloyd, D. S., J. P. Koenings & J. D. LaPerriere, 1987. Effects of turbidity in fresh waters of Alaska. North American Journal of Fisheries Management 7: 18–33.

Lythgoe, J. N., 1979. Ecology of Vision. Clarendon Press, Oxford.

Lythgoe, J. N., 1980. Vision in fish: ecological adaptations. In Ali, M. A. (ed), Environmental Physiology of Fishes. Plenum Press, New York: 431–446.

Moyle, P. B., J. V. Katz & R. M. Quinones, 2011. Rapid decline of California's native inland fishes: a status assessment. Biological Conservation 144: 2414–2423.

Mueller, R. P., D. A. Neitzel & B. G. Amidan, 2001. Evaluation of infra-sound and strobe lights for eliciting avoidance behaviour in juvenile salmon and char. In Coutant, C.C. (ed), Behavioural Technologies for Fish Guidance. American Fisheries Society, Symposium 26, Bethesda, Maryland: 79–89.

Munz, F. W. & W. N. McFarland, 1977. Evolutionary adaptation of fishes to the photic environment. In Crescitelli, F. (ed), The Visual System in Vertebrates. Springer, Berlon: 193–274.

Mussen, T. D., D. E. Cocherell, Z. Hockett, A. Ercan, H. Bandeh, M. L. Kavvas, J. J. Cech Jr. & N. A. Fangue, 2013. Assessing juvenile Chinook Salmon behavior and entrainment risk near unscreened water diversions: large flume simulations. Transactions of the American Fisheries Society 142: 130–142.

Mussen, T. D., D. Cocherell, J. B. Poletto, J. S. Reardon, Z. Hockett, A. Ercan, H. Bandeh, M. L. Kavvas, J. J. Cech Jr. & N. A. Fangue, 2014a. Unscreened water diversion pipes pose an entrainment risk to the threatened Green Sturgeon, *Acipenser medirostris*. PLoSONE 9: e86321.

Mussen, T. D., O. Patton, D. Cocherell, A. Ercan, H. Bandeh, M. L. Kavvas, J. J. Cech Jr. & N. A. Fangue, 2014b. Can behavioral fish-guidance devices protect juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) from entrainment into unscreened water diversion pipes? Canadian Journal of Fisheries and Aquatic Sciences 71: 1209–1219.

Mussen, T. D., D. E. Cocherell, O. Patton, D. Jauregui, A. Ercan, H. Bandeh, D. Meier, S. Thomas, M. L. Kavvas, J. J. Cech Jr. & N. A. Fangue, 2015. Modified water diversion structures can behaviorally deter juvenile Chinook salmon from entrainment. Transactions of the American Fisheries Society 144: 1070–1080.

Nakano, N., R. Kawabe, N. Yamashita, T. Hiraishi, K. Yamamoto & K. Nashimoto, 2006. Colour vision, spectral sensitivity, accommodation, and visual acuity in juvenile masu salmon *Oncorhynchus masou*. Fisheries Science 72: 239–249.

Nemeth, R. S. & J. J. Andersen, 1992. Response of juvenile Coho and Chinook salmon to strobe and mercury vapour lights. North American Journal of Fisheries Management 12: 684–692.

Newcombe, C. P. & D. D. MacDonald, 1991. Effects of suspended sediments on aquatic ecosystems. North American Journal of Fisheries Management 11: 72–82.

Niwa, H. & T. Tamura, 1969. Investigation of fish vision by means of S-potential. II. Spectral sensitivity and colour vision. Revue canadienne de biologie/editee par l'Universite de Montreal 28: 79–88.

Noatch, M. R. & C. D. Suski, 2012. Non-physical barriers to deter fish movements. Environmental Reviews 20: 71–82.

Nobriga, M. L., Z. Matica & Z. P. Hyamanson, 2004. Evaluating entrainment vulnerability to agricultural irrigation diversions: a comparison among openwater fishes. In Feyrer, F., L. R. Brown, R. L. Brown & J. J. Orsi (eds), Early Life History of Fishes in the San Francisco Estuary and Watershed. American Fisheries Society, Symposium 39, Bethesda, Maryland: 281–295.

Novales-Flamarique, I., 2005. Temporal shifts in visual pigment absorbance in the retina of Pacific salmon. Journal of Comparative Physiology A 191: 37–49.

Novales-Flamarique, I. & C. W. Hawryshyn, 1993. Spectral characteristics of salmonid migratory routes from southern Vancouver Island (British Columbia). Canadian Journal of Fisheries and Aquacultural Sciences 50: 1706–1716.

Novales-Flamarique, I. & C. W. Hawryshyn, 1994. Ultraviolet photoreception contributes to prey search behaviour in two

species of zooplanktivorous fishes. Journal of Experimental Biology 186: 187–198.
Novales-Flamarique, I. & C. W. Hawryshyn, 1997. Is the use of underwater polarized light by fish restricted to crepuscular time periods? Vision Research 37: 975–989.
Novales-Flamarique, I., S. Hiebert & J. Sechrist, 2006. Visual performance and ocular system structure of Kokanee and Sockeye salmon following strobe light exposure. North American Journal of Fisheries Management 26: 453–459.
Parker, D. C. & C. W. Hawryshyn, 2000. Spectral and ultraviolet-polarisation sensitivity in juvenile salmonids: a comparative analysis using electrophysiology. The Journal of Experimental Biology 203: 1173–1191.
Patrick, P. H., A. E. Christie, D. Sager, C. Hocutt & J. Stauffer Jr., 1985. Responses of fish to a strobe light/air-bubble barrier. Fisheries Research 3: 157–172.
Peck, L. S., M. S. Clark, S. A. Morley, A. Massey & H. Rossetti, 2009. Animal temperature limits and ecological relevance: effects of size, activity and rates of change. Functional Ecology 2: 248–256.
Poletto, J. B., D. E. Cocherell, T. D. Mussen, A. Ercan, H. Bandeh, M. L. Kavvas, J. J. Cech Jr. & N. A. Fangue, 2014. Efficacy of a sensory deterrent and pipe modifications in decreasing entrainment of juvenile green sturgeon (*Acipenser medirostris)* at unscreened water diversions. Conservation Physiology 2(cou056): 2015.
Poletto, J. B., D. E. Cocherell, T. D. Mussen, A. Ercan, H. Bandeh, M. L. Kavvas, J. J. Cech Jr. & N. A. Fangue, 2015. Fish-protection devices at unscreened water diversions can reduce entrainment: evidence from behavioural laboratory investigations. Conservation Physiology 3: cov040.
Poletto, J. B., D. E. Cocherell, S. E. Baird, T. X. Nguyen, V. Cabrera-Stagno, A. P. Farrell & N. A. Fangue, 2017. Unusual aerobic performance at high temperatures in juvenile Chinook salmon, *Oncorhynchus tshawytscha*. Conservation Physiology 5: cow067.
Popper, A. N. & T. J. Carlson, 1998. Application of sound and other stimuli to control fish behaviour. Transactions of the American Fisheries Society 127: 673–707.
Portz, D. E., 2007. Fish-holding-associated stress in Sacramento River Chinook Salmon (*Oncorhynchus tshawytscha*) at south delta fish salvage operations: effects on plasma constituents, swimming performance, and predator avoidance. Doctoral dissertation. University of California, Davis.
R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [available on internet at https://www.R-project.org/].
Richards, N. S., S. R. Chips & M. L. Brown, 2007. Stress response and avoidance behaviour of fishes as influenced by high frequency strobe lights. North American Journal of Fisheries Management 27: 1310–1315.
SacPAS: Central Valley Prediction & Assessment of Salmon. UW Columbia Basin Research. [available on internet at http://www.cbr.washington.edu/sacramento/].
Sager, D. R., C. H. Hocutt & J. R. Stauffer Jr, 2000. Avoidance behaviour of *Morone americana*, *Leiostomus xanthurus* and Brevoortia tyrannus to strobe light as a method of impingement mitigation. Environmental Science & Policy 3: 393–403.
Simmons, M. A., R. L. Johnstone, C. A. McKinstry, C. S. Simmons, C. B. Cook, R. S. Brown, D. K. Tano, S. L. Thorsten, D. M. Faber, R. Lecaire & S. Francis, 2004. Strobe light deterrent efficacy test and fish behaviour determination at Grand Coulee Dam Third Powerplant Forebay. Pacific Northwest National Laboratory PNNL-14512. Department of Energy USA.
Swanson, C., P. S. Young & J. J. Cech Jr., 2004. Swimming in two-vector flows: performance and behavior of juvenile Chinook salmon near a simulated screened water diversion. Transactions of the American Fisheries Society 133: 265–278.
Terazono, K., 1998. The use of light to guidance system of masu salmon in dam pool (part 1). Dam Engineering 129: 50–58.
Tsin, A. T. C. & D. D. Beatty, 1977. Visual pigment changes in rainbow trout in response to temperature. Science 195: 1358–1360.
Utne Palm, A. C., 2002. Visual feeding of fish in a turbid environment: physical and behavioural aspects. Marine and Freshwater Behaviour and Physiology 32: 111–128.
Vörösmarty, C. J., P. B. McIntyre, M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. A. Sullivan, C. R. Liermann & P. M. Davies, 2010. Global threats to human water security and river biodiversity. Nature 467: 555–561.
Walters, A. W., D. M. Holzer, J. R. Faulkner, C. D. Warren, P. D. Murphy & M. M. McClure, 2012. Quantifying cumulative entrainment effects for chinook salmon in a heavily irrigated watershed. Transactions of the American Fisheries Society 141: 1180–1190.
Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer, New York.

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