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Evaluating Chinook salmon (*Oncorhynchus tshawytscha*) response to artificial light in support of bycatch mitigation

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Abstract: In commercial trawl fisheries in the North Pacific and US West Coast, fishermen and scientists are evaluating if artificial lights facilitate escapement of bycaught Chinook salmon (*Oncorhynchus tshawytscha*) from the trawl by attracting them to an opening provided by a bycatch reduction device. Inconsistent behaviour and escapement rates when lights were used in the trawl led us to conduct a laboratory study to evaluate the role of light properties (intensity, colour, and strobe) on marine Chinook salmon behaviour. Results from this study suggest a negative phototactic response. Light colour and strobe, and the interaction between them, differentially affected behavioural response with regard to mean swimming speed and distance from and habituation to the light. White light intensity had limited influence on response; however, the range of trialed intensities was limited. While behaviour is contextual and responses in a laboratory setting cannot be directly extrapolated to responses in fishing gear, this study highlights the significant role of light properties when trying to affect behaviour for bycatch mitigation and the importance of distinguishing between a response to light and to illuminated surroundings.

Résumé : Dans les pêches commerciales au chalut dans le Pacifique Nord et le long de la côte Ouest américaine, les pêcheurs et scientifiques tentent d'établir si des lumières artificielles facilitent l'échappement du chalut de saumons chinooks (*Oncorhynchus tshawytscha*) capturés accessoirement en les attirant vers une ouverture fournie par un dispositif de réduction des prises accessoires. Des comportements et taux d'échappement non uniformes associés à l'utilisation de lumières sur les chaluts nous ont incités à mener une étude en laboratoire visant à évaluer le rôle des propriétés de la lumière (intensité, couleur et fréquence du clignotement stroboscopique) sur le comportement de saumons chinooks marins. Les résultats de cette étude semblent révéler une réaction phototactique négative. La couleur et la fréquence de clignotement de la lumière, ainsi que leur interaction, exercent des effets comportementaux variables sur la vitesse de nage moyenne et la distance par rapport à la source lumineuse, ainsi que sur l'accoutumance à cette dernière. L'intensité de la lumière blanche n'exerce qu'une influence limitée sur le comportement, la fourchette d'intensités testées étant toutefois restreinte. Si le comportement dépend du contexte et que les réactions en laboratoire ne peuvent être directement extrapolées aux réactions des poissons dans des engins de pêche, l'étude souligne néanmoins l'important rôle des propriétés de la lumière utilisée pour modifier le comportement des poissons dans le but de réduire les prises accessoires et l'importance de départager les réactions à la source de lumière des réactions au milieu illuminé environnant. [Traduit par la Rédaction]

Introduction

Artificial lights have been an effective tool worldwide for increasing catchability and selectivity in fisheries, improving catch efficiency and mitigating bycatch (Grimaldo et al. 2018; Humborstad et al. 2018; Melli et al. 2018; Nguyen and Winger 2019; Wang et al. 2013). In the commercial trawl fisheries for walleye pollock (*Gadus chalcogrammus*; hereinafter "pollock") in the North Pacific and for hake (*Merluccius productus*) along the US West Coast, fishermen and scientists have been evaluating the potential use of artificial lights to reduce Pacific salmon (*Oncorhynchus* spp.; hereinafter "salmon") bycatch (Gauvin et al. 2013; Lomeli and Wakefield 2012, 2019). The hypothesis underlying these investigations is that salmon are positively phototactic and that artificial lights could be used to guide them to a desired location, specifically, to an area of the trawl that has been modified to allow fish to exit by way of an escapement area (a bycatch reduction device, BRD).

For Chinook salmon (*Oncorhynchus tshawytscha*), the salmonid species of most concern in the hake and pollock fisheries due to harvest-limiting catch allocations (Fissel et al. 2019; NMFS-WCR 2017), behavioural response to artificial lights in trawl gear has been inconsistent. In the hake fishery, blue lights placed near an escape portal significantly increased escapement rates, influenced where the salmon escaped, and reduced time to escape (Lomeli and Wakefield 2012, 2019). However, the addition of white light deployed with a different BRD in the pollock fishery resulted in nominally lower Chinook salmon escapement rates (Gauvin et al. 2013). Freshwater research has also found inconsistent results, reporting both positive and negative phototaxis by salmonids (Puckett and Anderson 1988). Further, for salmon, response to light appears to depend on a number of variables associated with the lights, including intensity (Anderson et al. 1988; Mazur and Beauchamp 2003; Tabor et al. 2004), colour (Migaud et al. 2007), and flicker rate (i.e., strobing; Anderson et al. 1988; Nemeth and Anderson 1992).

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Researchers and fishermen are motivated to explore the use of artificial lights based on (*i*) observations of salmon appearing to swim directly toward white-light illuminated trawl cameras; (*ii*) promising results from the hake fishery and studies reporting that highly active fish, like salmon, exhibit stronger responses to light than less mobile fish (Ryer et al. 2009); and (*iii*) studies demonstrating that lights can be used to elicit behaviour in salmonids (Brett and Groot 1963; Bui et al. 2013). To that end, we conducted a laboratory study to evaluate the influence of light intensity, colour, and strobe rate on the behaviour of hatchery-reared Chinook salmon in salt water. We aimed to provide information about Chinook salmon behaviour that can guide how artificial lights are tested in future bycatch reduction applications and to contribute to a growing body of work on sensory stimulation for fisheries selectivity and bycatch mitigation.

Materials and methods

Experimental set-up

Trial fish

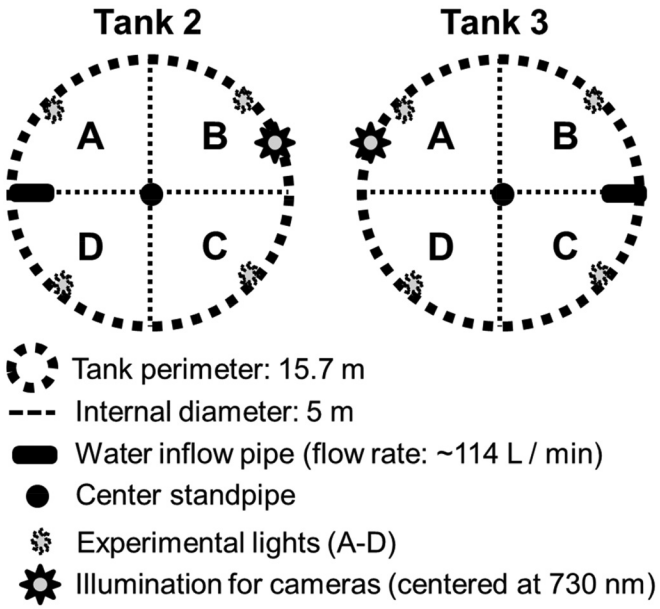
In June 2017, 258 age-0 Chinook salmon smolts from Washington Department of Fish and Wildlife (WDFW) hatcheries were transported in fresh water to NOAA's Northwest Fisheries Science Center Manchester Research Station and transitioned into sea water within a month of transfer. Ninety-eight were Green River fish, spawned and raised at the WDFW Icy Creek Hatchery; and 160 were South Fork Nooksack River fish, spawned and raised at the WDFW Kendall Creek Hatchery. Each group was held in separate 5-m diameter, 1.5-m high, flow-through (counter-clockwise) tanks, each supplied with filtered (to 20 μm) and UV-sterilized sea water. All fish were fed commercial fish feed for 5 days per week at the food manufacturer's recommended amount based on fish weight. In April 2018, the two groups of fish were combined into one holding tank in preparation for the trials and were fed for 7 days per week with a 24-hour belt feeder. Care of fish used in this study followed NOAA, NWFSC, Manchester Research Station procedures based on guidance provided by www.ccac.ca and the University of Washington's Institutional Animal Care and Use Committee.

Trial tanks

In addition to the holding tank described above, two additional tanks were used for conducting the behaviour trials, and a fourth was used to hold fish that had completed a trial (Fig. 1). The trial tanks had internal plumbing and surfaces painted dark grey or black but were otherwise identical to the holding tanks. Each of the four tanks was covered with a 6-m × 6-m × 3-m black vinyl tent, which was fabricated using heat sealing methods to prevent light seepage through seams. In addition, a TDR-MK9 archival tag (Wildlife Computers, Inc.) was used to measure light penetration through the fabric, which confirmed that the cover would block all perceptible light from entering. To prevent fish escape, the holding tanks were covered with netting and the water level was maintained at 0.75 m throughout the trials. To maintain a circadian rhythm while awaiting the trials, the cover over the holding tank was lifted up approximately 0.7 m on all four sides to let in light from the building windows. In the post-trial holding tank, a TidbiT sensor (Onset Computer Corporation) recorded water temperature every 4 hours for the duration of the study.

In both trial tanks, four light units were hung such that each marked the center of four equally sized quadrants (locations A–D, per tank; Fig. 1). The water inflow pipe was located along a shared boundary of two of the quadrants (note that this was between A and D for Tank 2, and B and C for Tank 3), and each subsequent light was spaced equidistantly around the tank's 15.7-m circumference. The lights were positioned flush against the tank wall, facing into the tank, 0.4 m from the tank bottom. The light was secured to a weight on the bottom of the tank for stability with electrical cords tethered along the tank edge.

Fig. 1. Set-up for the two trial tanks used to evaluate Chinook salmon (*Oncorhynchus tshawytscha*) behaviour in response to artificial lights. Not shown are the two cameras positioned approximately 3 m above each tank (centered and aimed directly downward), nor the tank covers. Tanks 1 and 4 (pre- and post-trial tanks, respectively) were similar, with the exception of having no experimental lights.



Light treatments

We tested behavioural responses to three light variables: (*i*) white light intensity – non-strobing; (*ii*) light colour – non-strobing; and (*iii*) light colour – strobing (Table 1). Each of these three experiments had four treatments. Four intensities were tested for non-strobing white lights: very low, low, average, and high; and the light colours tested were white, blue, green, and red. The strobe rate tested during the first set of trials was 1 s on, 1 s off (strobe rate, SR, 1) for the duration of the trial and the same for all colours. For the second set of trials, the SR was 0.25 s on, 0.5 s off (SR2). There was only one trial for SR3, a rate of 0.2 s on, 0.3 s off, which was conducted outside, but over the timeframe, of the other trials.

The light units were eight-channel PAR RGBW Digital Multiplex (DMX) lights, with the light-emitting diode (LED) boards and DMX drivers removed from their "off the shelf" housings and potted in epoxy in 3D printed housings made for this study. The spectral distribution of all the DMX LEDs was determined using a Qmini spectrometer (Pembroke Instruments, Inc.). Using the spectrometer, the wavelength of maximum absorbance (λ max) for each LED was determined (Fig. 2). For the blue, green, and red LEDs, λ max was 460, 515, and 630 nm, respectively. The white LED was bimodal with λ max at 445 nm and a secondary peak at 535 nm. The master dimmer on the DMX controller board was set at a value to prevent bleed over between colours and to ensure consistency among colours. Additionally, there was no significant spectral overlap between the blue, green, and red LED outputs from the DMX lights, and the output from the white LED overlapped the monochromatic LEDs.

Output from the LEDs was measured using a TDR-MK9 archival tag light sensor. Relative irradiance measured from the tag was converted to radiometric units and corrected to λ max for each colour according to the methods described by Britt (2009) and

Table 1. Organization of the 48 trials completed (24 trials × 2 replicate tanks) evaluating Chinook salmon (*Oncorhynchus tshawytscha*; five individuals per trial) response to artificial light.

						Treatment at each light position			
						A	B	D	C
Experiment	Trial No.		Time of day†	Trial No.	Time of day†	AM: 02:00–02:15; PM: 14:00–14:15	AM: 03:00–03:15; PM: 15:00–15:15	AM: 04:00–04:15; PM: 16:00–16:15	AM: 05:00–05:15; PM: 17:00–17:15
Intensity (white light, non-strobing)	1*		AM	13*	PM	3	4	2	1
	2		PM	14	AM	4	2	1	3
	3		AM	15	PM	2	1	3	4
	4		PM	16	AM	1	3	4	2
Colour (non-strobing)	5		AM	17	PM	Green	Blue	Red	White
	6		PM	18*	AM	Blue	Red	White	Green
	7*		AM	19	PM	Red	White	Green	Blue
	8		PM	20	AM	White	Green	Blue	Red
Colour (strobing)‡	9*	SR1	AM	21*	SR2 PM	Green	White	Blue	Red
	10		AM	22	AM	White	Blue	Red	Green
	11		PM	23	PM	Blue	Red	Green	White
	12		AM	24	AM	Red	Green	White	Blue

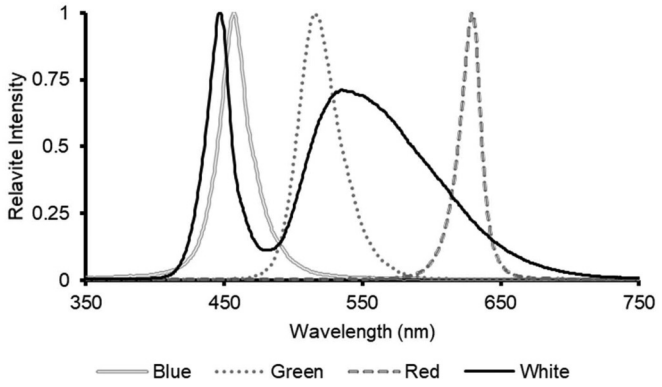
Note: Data include the three experiments and their four treatments: white light intensity (non-strobing): very low-1, low-2, average-3, and high-4; colour (strobing and non-strobing for separate experiments: white, blue, green, and red), illuminated at four light positions (A–D; see Fig. 1).

*Black boxes with white font indicate trials randomly selected for PRE and BTWN analysis.

†AM/PM: fish moved to the trial tank at 18:00 PM or 06:00 AM and the trial subsequently began at 02:00 AM or 14:00 PM, respectively.

‡Strobe rates, SRs: seconds on, seconds off; SR1: 1, 1; SR2: 0.25, 0.5; and SR3: 0.2, 0.5 (one trial only, not included in this table).

Fig. 2. Normalized spectral distribution of the LED outputs from the lights used in this study, indicating the wavelength of peak output (λ max) for the blue, green, and red LEDs was 460, 515, and 630 nm, respectively. The white LED was bimodal, with λ max at 445 nm and a secondary peak at 535 nm.



Rohan et al. (2020). The corrected radiometric units were expressed in W·m^{-2}, allowing for comparison between treatments in a unit relevant to the visual system. The four intensity levels tested with the white lights included the highest and lowest outputs capable with the DMX lighting control system and two intermediate levels (white light intensities: "very low", "low", "average", and "high"; Table 2). The intensity for the blue light was set to match the output from the "average" white light treatment as closely as was possible from the DMX control board, based on the values obtained from the TDR-MK9 archival tag. The green and red light intensities were set to the maximum output of the system to achieve values as close to the "average" white light as possible. At the highest output levels, variation in light intensity was noticed among individual DMX light units. These differences are likely attributed to minor differences in the thicknesses of the waterproofing epoxy used in the housing. Because the differences were small and did not cause overlap between treatment levels, it was deemed insignificant to the study. Regardless, the locations of the lights in the tank were randomized and each treatment was tested at each location (and therefore light unit) to account for any differences in behavioural response that may be due to the small variation in intensity between DMX light sources.

Table 2. Proportional mean light intensity for the four white light intensity treatments (high, average, low, and very low), and the colour treatments (blue, green, and red), all compared to "high" intensity white light at the light source (i.e., the tank edge; 0.68 W·m^{-2}).

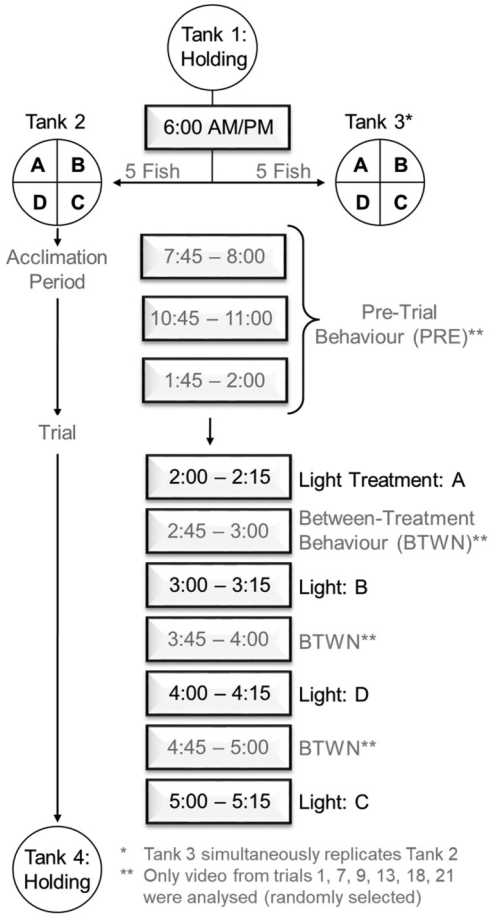
	Distance (m)					
	0 (tank edge)	0.3	0.6	1.2	2.4 (center standpipe)	Key
White						100%
High	100.0%	21.2%	5.5%	1.6%	0.3%	<50%
Average	12.4%	2.8%	0.9%	0.4%	0.3%	<25%
Low	5.3%	1.5%	0.5%	0.3%	0.3%	<10%
Very low	2.2%	0.7%	0.3%	0.2%	0.2%	<1%
Blue	42.1%	10.8%	3.1%	1.0%	0.3%	
Green	7.0%	2.4%	0.9%	0.5%	0.3%	
Red	5.3%	1.7%	0.7%	0.3%	0.2%	

Horizontal light extinction was measured from the center standpipe to the tank edge, in a straight line, creating light intensity measurements at 2.4, 1.2, 0.6, 0.3, and 0 m from the light source. When compared to the "high" white light treatment at the tank edge (i.e., at the light source; 0.68 W·m^{-2}), light levels for all treatments were over 99.7% lower at the standpipe (Table 2).

Behaviour trials

In May 2018, for each of the three experiments (i.e., white light intensity, colour – strobing, and colour – not strobing) there were sixteen trials (eight trials × replicates in two tanks; Table 1; Fig. 3). Two trials were run per day in both tanks (four total per day): one beginning at 02:00 AM and one at 14:00 PM. Each trial day, at 06:00 AM and 18:00 PM on the previous day (for the afternoon and morning trials, respectively), five fish from the holding tank, that had never experienced any light treatment, were collected and transferred to each trial tank via a water-filled, sealed black plastic container. All collections and transfers of fish were conducted in darkness. The selection of fish was randomized, as was the allocation of fish to a tank. The fish were then able to acclimate to the tank for approximately 8 hours before the trial.

Fig. 3. Workflow for the trials evaluating Chinook salmon (*Oncorhynchus tshawytscha*) response to artificial light.



Trials were conducted with five fish (opposed to individuals) to incorporate individual "personality" (Hertel et al. 2020; Stamps et al. 2012; Stamps and Groothuis 2010) and the tendency for salmon to school and use group behaviour in the marine environment (Berdahl et al. 2016). In the trawl, salmon will encounter the BRD over a range of conditions, including solitary, being surrounded by other fishes, and being among other salmon. How salmon encounter the BRD can also depend on the fishing event. For example, during turns and when the trawl is hauled back, salmon will swim forward in groups (Yochum et al. 2021).

A trial consisted of exposing the same group of fish to four different light treatments, each from one of the four physical lights (A–D) placed in the tank. Each DMX light was programmed with a colour, intensity, and strobe rate for each treatment within a trial. The order the lights were illuminated was randomly selected at the start of the study, and was maintained for all trials, in both tanks (A, B, D, C). Ordering and position of the light treatments was set such that each individual light treatment was turned on first, second, third, and fourth over the experiment, and was, therefore, turned on at each of the four physical locations over the four trials (Table 1). This was repeated such that each of these trials was conducted once both in the morning and afternoon periods. The only variation was that rather than have the strobed lights repeat in the morning and afternoon, a second strobe rate was trialed in the second round of testing. All was replicated exactly and simultaneously in the two trial tanks.

At the start of a trial (either at 02:00 AM or 14:00 PM; for all experiments and both tanks), the light at position A slowly increased to full intensity over 60 s while the other lights remained off (Fig. 3). Light-A stayed on for an additional 14 min (15 min total) and then turned off abruptly. This timing was chosen because 15 min is a reasonable amount of time that a salmon might spend in a BRD. All lights remained off for the subsequent 45 min, and then the light at position B turned on for the same duration. This pattern continued until all four lights had gone on for 15 min, with 45 min of darkness in between. The amount of time between light treatments was balanced between time needed to return to pre-trial behaviour (i.e., re-acclimate) and biological considerations (e.g., hunger state, circadian rhythm).

At the end of each trial (either 05:15 AM or 17:15 PM), the fish from each tank were anesthetized with tricaine methanesulfonate (MS-222) and measured (fork length (FL), nearest mm). The fish were subsequently put into the post-trial holding tank. During the trials, entry into the building was not allowed, and only those feeding the fish or conducting the experiment were in the building at other times. With every fish transfer, we ensured that the light placement had not been altered and that there was no debris in the water or a need for cleaning the tank. The fish were not fed while in the trial tanks.

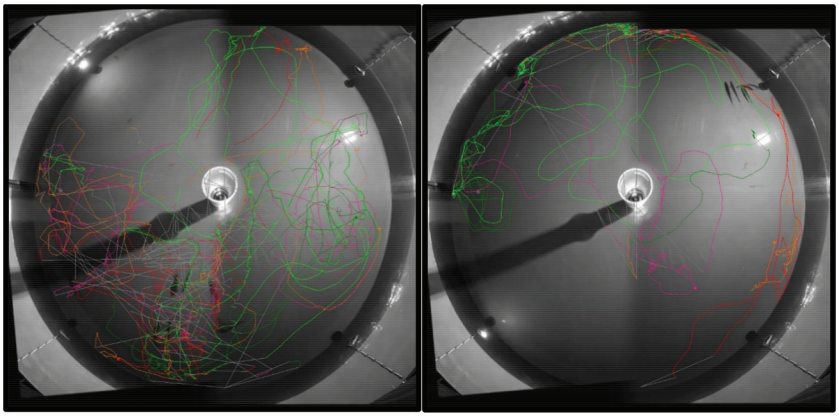
Video collection and processing

Fish behaviour was captured in both trial tanks with two 2.8-mm lens "plug and play", low light Internet Protocol (I.P.) cameras (2048 × 1536; maximum bitrate; Hikvision) with continuous recording to a Hikvision DS-7600Ns-E Series Network Video Recorder (NVR) throughout the study and downloaded daily, creating MP4 files. The cameras were secured abreast, just below the top of the tank cover, approximately 3 m above the center of the tank, each viewing approximately half of the tank. In each tank (including the holding tanks), a far red (wavelength centered at 730 nm) seed propagation and dark period grow light (100 W; at intensity setting 10; California Lightworks) was positioned approximately 0.3 m above the tank, facing toward center, with a plastic sheet covering acting as a diffuser. These lights provided some illumination for the cameras in a wavelength outside the visible spectrum for Chinook salmon (Flamarique 2005).

Segments of video footage used for analysis were trimmed from the raw video files from each camera and tank with Microsoft Movie Maker. These clips were exported as H.264 MP4 files with a resolution of 854 × 480 pixels and frame rate of 29.97 frames per second. Video clips from the two cameras, from the same period and tank, were then combined into a single video file with an Adobe Creative Cloud application (After Effects) and rendered in Adobe Media Encoder. These videos were exported as H.264 MP4 files with a resolution of 677 × 736 pixels for Tank 2 and 654 × 652 pixels for Tank 3. To overlay the video files from the two camera angles (for each tank), the files needed to be slightly rotated. This resulted in some misalignment that could not be avoided, but it did not affect the analysis.

The blended clips were used to evaluate fish during the period of acclimation to the tank (i.e., pre-trial, PRE), when the trial lights were on (LIGHT), and between treatments (BTWN; Fig. 3). For PRE behaviour, clips were analyzed near the start of — and midway through — the acclimation period and 15 min immediately prior to the trial (PRE-1–3: 19:45–20:00/07:45–08:00, 22:45–23:00/10:45–11:00, and 01:45–02:00/13:45–14:00 for AM/PM trials, respectively). For this analysis, we randomly selected one trial per each experiment and period (Trials 1, 7, 9, 13, 18, 21) for both tanks. Light treatments for all trials and both tanks were analyzed when the lights were illuminated (LIGHT-A, -B, -D, and -C: 02:00–02:15/14:00–14:15, 03:00–03:15/15:00–15:15, 04:00–04:15/16:00–16:15, and 05:00–05:15/17:00–17:15 for AM/PM trials, respectively). To evaluate BTWN behaviour, for the same trials randomly selected for PRE analysis, we analyzed fish behaviour for the 15 min prior to the second, third, and fourth lights being turned on (BTWN-1–3: 02:45–03:00/14:45–15:00, 03:45–04:00/15:45–16:00, and 04:45–05:00/16:45–17:00 for AM/PM trials, respectively).

Fig. 4. Five minutes of track lines in Tank 2 indicating the position of individual fish (by colour) during a trial with constant white light on at location A (left image) and location D (right image).



Each of the 15-min video files were processed using EthoVision XT software (Noldus), which automatically tracked Chinook salmon movement, generating *X*–*Y* locations of individual fish during the PRE, LIGHT, and BTWN periods (Fig. 4). Arena settings were specific to each tank, providing bounds for fish detection in evenly spaced zones centered on the four light units (at locations A–D). Detection settings in the software were the same for both tanks and were optimized specifically to minimize false positive detections, while maximizing the time each fish was tracked. Combined, these settings extracted areas that were very dark (e.g., shadows), had a reflection, or had evident water movement (e.g., around the standpipe), which could easily confuse the software. Each extracted area was relatively small and, combined by tank, only accounted for 1.9% and 5.3% of the total area in Tanks 2 and 3, respectively. We used the dynamic subtraction algorithm in EthoVision XT to compensate for background fluctuations and a minimum, maximum, and average number of pixels for a Chinook salmon was applied to the program to aid in tracking. Within the tracking software program, the *X*–*Y* location of each Chinook salmon was recorded at a rate of 5 times per second. A smoothing function was applied to remove any points greater than 20 cm apart between frames (i.e., swimming speed of 100 $cm \cdot s^{-1}$) as these were likely false positives. We also removed the entire track of any Chinook salmon that moved less than 1000 cm with no missed detections during the 15-min period. It was determined that these were not Chinook salmon, but instead were locations in the tanks with light contrast that the software consistently mistook for a fish. Single frame detections that did not have a detection location in the frame before or after it were also removed; these were typically false detections.

Data analysis

We performed statistical analyses in the R environment (R Core Team 2018) to evaluate behaviour during the PRE, LIGHT, and BTWN periods. The primary assessment metrics were (1) combined swimming speed (SPEED) per 15-min period, calculated as the sum of the total distance traveled by all fish in a tank divided by the sum total amount of time that all were tracked; and (2) mean distance (DISTANCE) from each light location for a given 15-min period. The second was calculated by summing, over all frames, the distances between all detected individual fish and a given light location (using the *X*–*Y* coordinates generated by Noldus at 0.2-s intervals). The sum of these values was divided by the total number of detections over the 15-min period. The sampling unit was the five fish combined. Individuals were not assessed discretely because we could not assume independence given the potential for social behaviour to influence their response (Hunter and Wisby 1964).

Evaluating pre-trial behaviour

We examined SPEED and DISTANCE for PRE-1–3 to determine if any behavioural differences were exhibited between the two trial tanks or by time of day (morning compared with afternoon). We ran mixed effect models using the R lmer function within the lme4 package to test for significant effects of our explanatory variables, trial tank, and time of day (fixed effects; Bates et al. 2015). The trial number and 15-min period (PRE-1–3) were included as random effects. An additional analysis with DISTANCE as the dependent variable included light location (A–D) as a fixed effect to determine if there were any spatial biases within a tank. For all analyses, we calculated the proportion of variance explained by the random effects in each model. *p* values were generated with the lmerTest extension for lme4 (Kuznetsova et al. 2017) and were considered significant when less than 0.05. For each test, normality of the response variable was tested with a Shapiro–Wilk test (Shapiro and Wilk 1965). In cases where the data were right-skewed, we used a log transformation.

Evaluating between-treatment behaviour

We compar*ed* SPEED and DISTANCE data between PRE and BTWN to determine whether the fish returned to their pre-trial behaviour following exposure to light or if "resting" behaviour changed after a single or multiple exposures. This informed our selection of "baseline" data to evaluate changes in behaviour when exposed to the lights. These analyses were completed using mixed effects models with the same variables as described above, with an additional independent variable describing whether the period was PRE or BTWN. A single model was created to test for differences in SPEED, and four independent models were used to test for significant differences in DISTANCE, one for each light location (A–D).

Evaluating light treatments

We used mixed-effects models to test for significant differences in SPEED in response to exposure to three light variables: intensity (1–4, lowest to highest settings; white light only), colour (white, blue, green, red), and strobe rate (no strobe and SRs 1–3). Additional explanatory variables included time of day (morning versus afternoon), trial tank, trial number, light location – order of testing (A, B, D, C). For the latter, a fifth factor was included for baseline data, which were the non-illuminated 15-min periods just prior to the lights turning on (PRE-3, and BTWN-1–3) from both tanks during the randomly selected trials.

For the spatial distribution analysis, we calculated the dependent variable as a standardized mean distance from a light location for a 15-min period ($DISTANCE_s$) to account for any spatial biases in the tanks, or any behavioural changes attributed to

multiple exposures to light. $DISTANCE_s$, calculated by light location and tank, was the difference between DISTANCE for the light treatment of interest and for the baseline value associated with that location and tank. PRE-3 data were used as the baseline for the first light illuminated (A), and BTWN-1, 2, and 3 data were used, respectively, for lights B, D, and C. If there was no difference in spatial distribution of fish between a light treatment and the corresponding non-illuminated baseline period, we would expect $DISTANCE_s$ to equal 0 (i.e., no change from baseline). A value of less than 0 would indicate a positive phototactic response to the light (i.e., they moved closer to the light than baseline), and a value greater than 0 would indicate a negative phototactic response (i.e., they moved farther away from the light than baseline). A mixed-effect model tested if the $DISTANCE_s$ during a treatment was significantly different than 0 and compared $DISTANCE_s$ values from all light treatments to see if there were any differences among them. The general linear hypothesis function (glth) in the R package multcomp was used to conduct a post-hoc Tukey's test for significant differences among colours and strobe rates (Bretz et al. 2010).

Habituation to light treatments

We evaluated potential habituation (or learning; Özbilgin and Glass 2004) to the light treatments over the 15-min exposure period and to the lights over a given trial by evaluating response to light stimulation after a single and multiple treatments. The former was evaluated by calculating SPEED and $DISTANCE_s$ in 15-s time intervals for each period, tank, and trial. This was also evaluated by intensity, colour, and strobe rate. A Spearman rank correlation test was used to determine if there was a significant linear trend. To evaluate habituation over the trial, we included the period (A, B, D, C) as a random effect in the model and calculated the amount of variance in contributed.

Results

A total of 50 trials were completed (3 experiments × 8 trials × 2 tanks; and 1 trial × 2 tanks to test SR3). While the aim was to include 5 fish per trial, of the 50, five trials had either 4 (2 trials), 6 (2 trials), or 7 fish (1 trial) in one of the tanks due to difficulties in transferring fish in the dark, resulting in 252 salmon used in this study. The number of fish per trial did not affect inclusion in the analysis. The mean (±SE) fork length of the trial fish was 263 ± 2.4 mm. Salmon were randomly selected for each tank and trial, and there was no significant difference in size between tanks or among trials (ANOVA; $p = 0.72$ and $p = 0.40$, respectively). Mean water temperature over the study period was 11.9 °C (median 12.1 °C), with patterns of increase and decrease over the course of the study, ranging from 10.98 to 12.7 °C. On average, the water temperatures for the second half of the trials (13–24; 12.4 ± 0.04 °C SE) were higher than the first half (1–12; 11.3 ± 0.07 °C SE).

The study cameras recorded consistently for 18 days, and 261 (15-min) video clips from that footage were analyzed. There were 36 video clips from the PRE periods, 31 from the BTWN periods, 64 each from the non-strobing white light intensity and colour experiments, and, from the strobing experiment, 30 from SR1, 30 from SR2, and 6 from SR3 (only white, blue, and green lights functioned for the sole SR3 trial). On average, the tracking software detected the fish in 83.7% of frames during PRE, 84.2% during BTWN, and 86.3% during LIGHT periods.

Evaluating pre-trial behaviour

There were no significant differences during the PRE periods in SPEED between tanks ($p = 0.93$; Tank 2 = 9.1 ± 1.1 $cm \cdot s^{-1}$ SE and Tank 3 = 8.6 ± 0.7 $cm \cdot s^{-1}$ SE) or between morning and afternoon ($p = 0.98$; AM = 8.9 ± 1.0 $cm \cdot s^{-1}$ SE and PM = 8.8 ± 0.9 $cm \cdot s^{-1}$ SE). Within the model, 48.8% of the variance was explained by differences among trials, while 9.7% of the variance was explained by differences in the periods (PRE-1–3) within a trial. However, for DISTANCE, there was a significant difference in the mean distance the fish were away from the light locations ($p \leq 0.001$), indicating nonrandom distribution in the tank. There was also a significant interactive effect between tank and distance from each light location ($p < 0.0001$; Fig. 5). Specifically, fish swam closer to location A in Tank 2 (237.1 ± 16.2 cm SE) than other locations in that tank (B = 299.5 ± 7.8 cm SE, C = 339.5 ± 13.8 cm SE, and D = 301.1 ± 7.9 cm SE) and swam closer to location B in Tank 3 (251.8 ± 5.0 cm SE as compared to A = 298.9 ± 9.1 cm SE, C = 303.4 ± 8.0 cm SE, and D = 355.3 ± 4.8 cm SE).

Evaluating between-treatment behaviour

During the BTWN periods 1–3, SPEED was slightly greater than during the PRE periods (10.6 ± 0.7 $cm \cdot s^{-1}$ SE compared to 8.85 ± 0.6 $cm \cdot s^{-1}$ SE), but this difference was not significant ($p = 0.051$; Fig. 5). Differences in SPEED among the trials accounted for 40.6% of the variance in the model, whereas differences between the PRE and BTWN periods (PRE-1–3 compared with BTWN-1–3) only accounted for 3% of the variance. For DISTANCE, there were significant differences between the PRE and BTWN periods in the distance that fish were away from light locations A, B, D, and C ($p < 0.05$). Salmon were further away from light locations A and B during BTWN treatments as compared to PRE periods (48.4 and 10.7 cm further on average, respectively) and were closer to light locations C and D (41.0 and 7.9 cm closer on average, respectively). Tank was a significant factor in all of the comparisons ($p < 0.01$), while time of day was not. Because there was significant random variation between tanks, and between the PRE and BTWN periods, DISTANCE for the LIGHT periods was calculated relative to the values from the proceeding non-illuminated period (baseline) by tank ($DISTANCE_s$). This reduced the effect of random variation and more directly reflected behavioural changes caused by the light treatments.

Evaluating light treatments

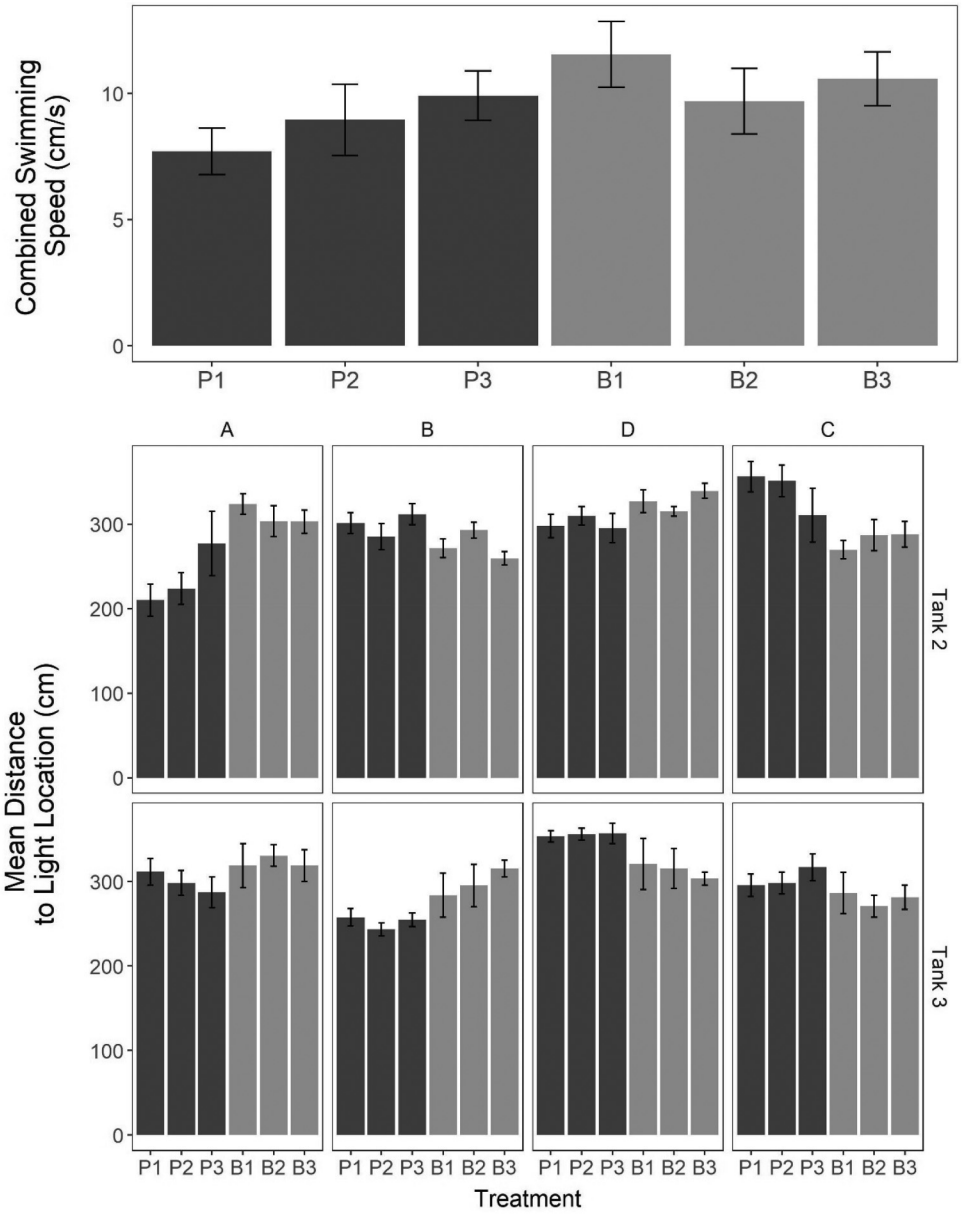
Intensity

White light intensity treatments, when evaluated over the entire 15-min period, had no significant effect on SPEED ($p = 0.45$) or $DISTANCE_s$ ($p = 0.80$); therefore, non-strobing white light trials were analysed with all intensities (very low, low, average, and high) combined. However, within the 15-min period, SPEED and $DISTANCE_s$ decreased, with the rate of decrease (slope) for SPEED similar among intensities, but variable for $DISTANCE_s$. The slope was negative and only significantly different than 0 for the very low and low intensities ($p < 0.001$ and $p = 0.002$, respectively), with the fish moving closer to the light over time than the higher intensities (Fig. 6).

Swimming speed

Swimming speed increased after exposure to all non-strobing light colours ($p \leq 0.009$ overall; white $\rho = 0.15$, $p < 0.001$; blue $\rho = 0.19$, $p < 0.001$; green $\rho = 0.14$, $p < 0.001$; and red $\rho = 0.09$, $p = 0.009$), most noticeably during the first 6 min, and swimming speed did not return to baseline levels over the course of the 15-min treatment period (Fig. 7). During the first 2 min of exposure to the light, SPEED was slightly slower (8.9 $cm \cdot s^{-1}$) compared with baseline periods (10.4 ± 0.5 $cm \cdot s^{-1}$ SE). After the first 2 min, swimming speed increased by 50% to a mean of 13.3 $cm \cdot s^{-1}$ for the remainder of the 15-min period. Overall SPEED values for the light treatments were greater when compared to baseline, but this difference was not significant. SPEED for the non-strobing white light treatments was 11.9 ± 0.5 $cm \cdot s^{-1}$ SE ($p = 0.34$), for blue light was 12.8 ± 1.4 $cm \cdot s^{-1}$ SE ($p = 0.19$), for green lights was 12.1 ± 1.0 $cm \cdot s^{-1}$ SE ($p = 0.34$), and for red lights was 12.2 ± 1.4 $cm \cdot s^{-1}$ SE ($p = 0.32$). The light location (which was also the order of illumination during the trial) only explained 2% of variance in the model.

Fig. 5. Comparison between the pre-trial (PRE; here P-1–3; dark grey) and between-treatment (BTWN; here B-1–3; light grey) periods for combined swimming speed (cm·s^{-1}) (top panel) and mean distance to each light source in the order that they were illuminated (A, B, D, C) by trial tank (bottom panels). Vertical bars represent the standard error.



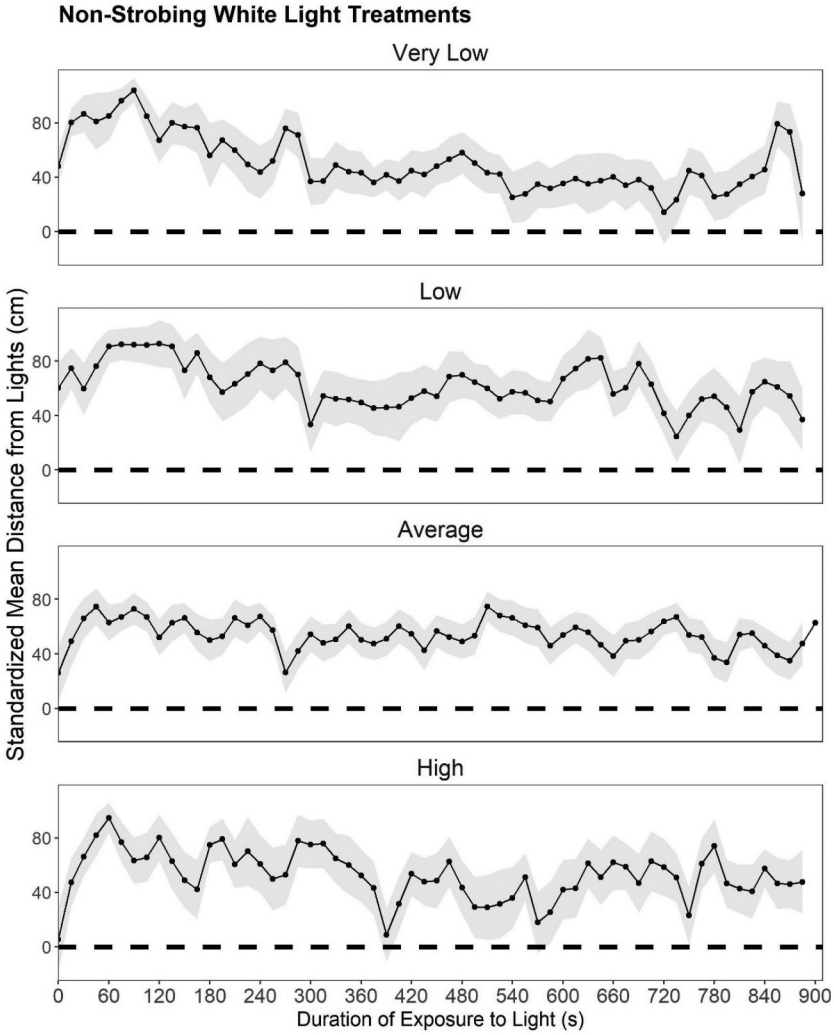
For the strobing experiment, the SPEED data were slightly right skewed so they were log-transformed for the analysis. In general, there was an increase in swimming speeds observed over the 15-min period during some of the strobe treatments; however, this was substantially more gradual and subtle when compared to the non-strobing light treatments. We found that SPEED for SR1 was significantly lower than baseline (10.4 ± 0.5 cm·s^{-1} SE) for white (5.4 ± 0.6 cm·s^{-1} SE), blue (6.98 ± 0.6 cm·s^{-1} SE), and red (7.17 ± 0.7 cm·s^{-1} SE) strobing lights ($p < 0.05$). For SRs 2 and 3, there were no significant differences in SPEED relative to baseline for all colours (Figs. 7 and 8). Compared to non-strobing light treatments, SPEED was significantly lower for SR1 ($p < 0.001$), but there was no significant difference for SR2 or SR3. For SR1, there was an increase in SPEED over the 15-min period for the blue (ρ = 0.11, p = 0.02) and red light treatments (ρ = 0.13, p = 0.003). For SR2, there was only a significant increase in swimming speed over the 15-min period for green lights (ρ = 0.21, $p < 0.001$). There was no significant trend in SPEED for SR3 treatments for white, blue, and green lights (there were no data for red lights).

Spatial distribution in the tank

The mixed-effects models indicated significant differences in DISTANCE$_s$ among colours (p = 0.006) and among strobe rates ($p < 0.001$; Fig. 9). Fish were, on average, significantly further away from the light source during white light treatments compared to blue lights (p = 0.003). For SRs 1, 2, and 3, fish were significantly further away from the light source than in the non-strobing light treatment (p = 0.007, $p < 0.001$, and p = 0.003, respectively).

For non-strobing light treatments, DISTANCE$_s$ was significantly greater than 0 (i.e., further from the light than baseline) for all light treatments: white (p = 0.003; fish were 53.24 ± 5.1 cm SE further away from the lights), blue (p = 0.04; 20.73 ± 15.2 cm SE), green (p = 0.004; 40.37 ± 11.6 cm SE), and red (p = 0.007;

Fig. 6. Standardized mean distances from non-strobing white lights, by intensity, over the 15-min treatment period in 15-s time intervals, with grey shading representing standard error. The horizontal dashed line at $y = 0$ represents no difference from the non-illuminated baseline period to which the values were compared (specific to each tank and light period).



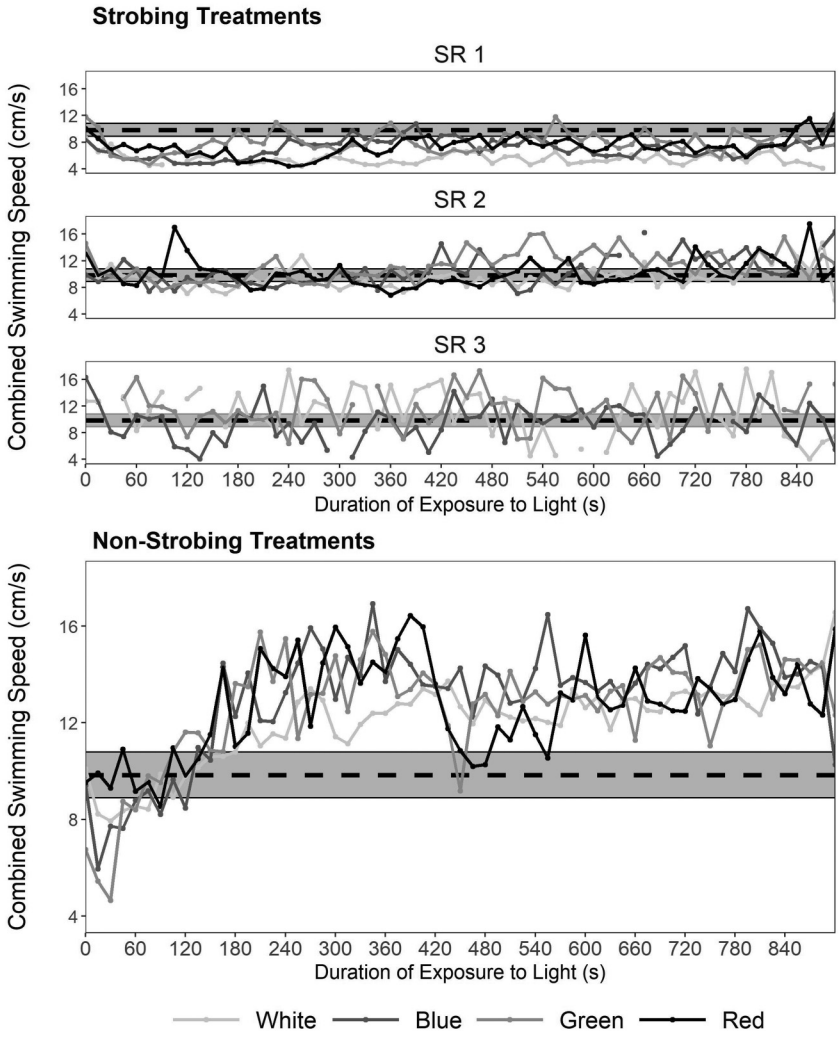
36.60 ± 8.5 cm SE; Fig. 9). For the strobing light treatments, $DISTANCE_s$ was also significantly greater than 0 for the white, blue, green, and red light treatments for SRs 1 and 2 ($DISTANCE_s$ ranged from 42.0 ± 7.5 cm SE (blue SR2) to 82.7 ± 21.1 cm SE (red SR1)). For SR3, fish were further away than during baseline (blue = 59.4 ± 9.0 cm SE; green = 71.0 ± 1.9 cm SE; and white = 88.5 ± 33.9 cm SE), but sample size precluded detecting significance.

In regard to changes over the 15-min periods, there was a significant trend of decreasing $DISTANCE_s$ for non-strobing white (ρ = –0.08, $p < 0.001$), green (ρ = –0.08, p = 0.03), and red (ρ = –0.11, p = 0.002) light treatments (Fig. 10; no significance for blue). Extrapolating regression results beyond the range of the data predicted that fish would return to baseline ($DISTANCE_s$ = 0) after 41.7 min for white light, 33.7 min for green light, and 28.5 min for red light. For the strobing treatments, there were no generalized patterns in $DISTANCE_s$ by SR or colour. For $DISTANCE_s$ over the 15-min, for SR1 there was a significant increase for blue light (ρ = 0.11, p = 0.02), a significant decrease for red light (ρ = –0.27, $p < 0.001$), and no significant trends for white or green light. For SR2, there were no trends for white, blue, green, or red light. For SR3, there were no significant trends for the three light treatments tested (white, blue, and green).

Discussion

Results from this study indicate that the colour and strobe rate of artificial lights, and interactions between them, affect behavioural response of Chinook salmon, including swimming speed, distance from the light source, and time before returning to pre-stimulus behaviour. In general, the introduction of artificial light resulted in increased swimming speeds and distance from the light location, the latter suggesting an overall negative phototactic response. With strobing, the fish were further away from the light source compared to the non-strobing lights, consistent with Anderson et al. (1988), who found that strobe lights elicited an avoidance response in Chinook salmon in fresh water, and Mueller et al. (1999), who found that salmon in fresh water do not habituate to strobe lights. By colour, fish swam the closest to the blue non-strobing light and were expected to return to baseline (habituate; based on extrapolation) the quickest for this colour. In contrast, the fish moved farthest away from the white strobing light and did not return to baseline distances over the course of the treatment. With SPEED, rates increased overall with the introduction of non-strobing light, which aligns with other studies that found fish increase swimming speed in response to a perceived threat (e.g., approaching vessel; Olsen et al. 1983). The initial reduction

Fig. 7. Combined swimming speed (cm·s^{-1}) by colour (strobing, top; non-strobing, bottom) over the 15-min exposure to artificial light in intervals of 15 s. The dashed line with grey shading represents the overall mean combined swimming speed and standard error during the baseline periods (PRE-3 and BTWN-1–3 values combined for both tanks).



in swimming speed after the initial exposure to light could be a "fright" response-reduced activity or "freezing" in response to a fear stimulus (Berejikian et al. 2003). It is important to note that, for both SPEED and DISTANCE, the size of the tank could be a limiting factor (i.e., they can only move so far away from the light).

The intensity of non-strobing white light did not differentially affect SPEED or DISTANCE$_s$, but it did influence whether the fish reduced their distance from the light over time. This suggests habituation to the lower light intensities. However, it should be noted that while the DMX lighting system did allow for testing light intensity over a three log unit range, it was unable to produce very dim light levels. This limited our ability to observe behavioural responses under both bright and dim lighting conditions. The lowest light level tested in this study was 1.04×10^{-3} W·m^{-2}. For reference, the light intensity of moonlight has been measured at 2.08×10^{-4} W·m^{-2} by Morgan and Smith (1981), and Chinook salmon have been observed to feed under moonlight and dimmer light levels (Hansen et al. 2013). Similarly, we note that light attenuation greatly reduced intensity within a short distance from the light source (Table 2). In addition, in a laboratory setting we could not account for light reflecting off the tank surfaces.

While behaviour is contextual and responses in a laboratory setting cannot be directly extrapolated to responses in fishing gear (e.g., where there are a number of other stimuli), this study provided information about the important role of light properties when trying to affect fish behaviour. Specifically, fish from this study did not exhibit a positive phototactic response to the artificial lights as we hypothesized based on anecdotal observations of salmon in trawls and the findings by Lomeli and Wakefield (2012, 2019). Instead, the negative phototactic response aligned with the results of Gauvin et al. (2013), where lights were suspected of eliciting an avoidance behaviour in salmon. Differences in findings between Lomeli and Wakefield (2012, 2019) and Gauvin et al. (2013) could be explained, in part, by the colour of the lights used in these studies (blue compared to white lights, respectively). For example, if Chinook salmon have less of a negative phototactic response and habituate to blue light, it is possible that increased escapement from the trawl reported by Lomeli and Wakefield (2012, 2019) could be linked to the light illuminating the mesh and escapement area without inducing a prolonged negative phototactic response. This could allow the netting and exit to be more visually perceptible, which could affect motivation to escape and (or) cause an interruption to the optomotor response. The contrast of the netting against the background (water) is perhaps more important than the light itself

Fig. 8. Box plots of the combined swimming speed (cm·s^{-1}) for strobing (strobe rates, SRs, 1–3) and non-strobing treatments by light colour (all intensities combined for white light), as compared to a baseline equal to 10.4 ± 0.5 cm·s^{-1} SE (overall mean combined swimming speed and standard error during the baseline periods, PRE-3 and BTWN-1–3, combined for both tanks). Values above the boxes indicate sample size (number of 15-min periods).

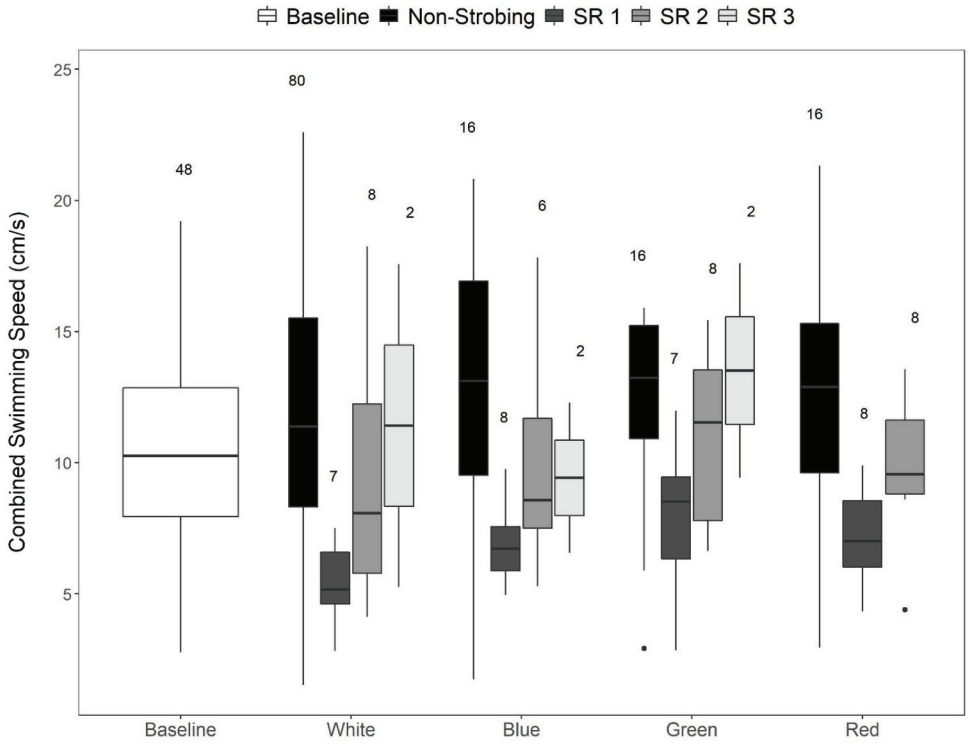


Fig. 9. Box plots of the standardized distances from a light source during the trials for non-strobing and strobing lights by colour. The dashed line at $y = 0$ represents no difference from the non-illuminated baseline period to which the values were compared (individual to each tank and light location).

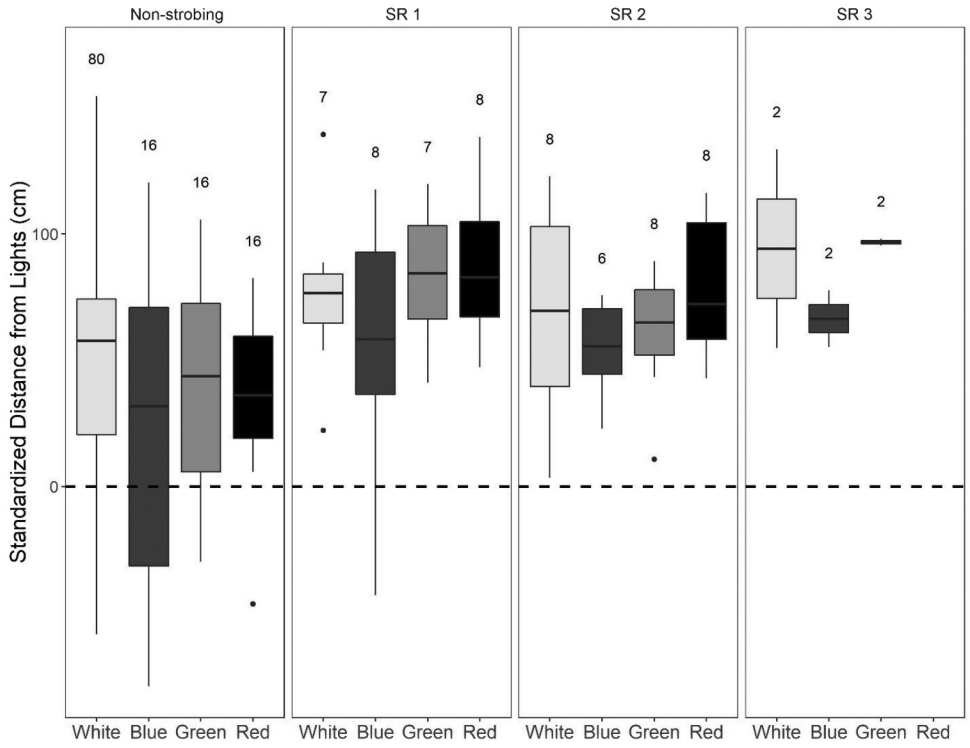
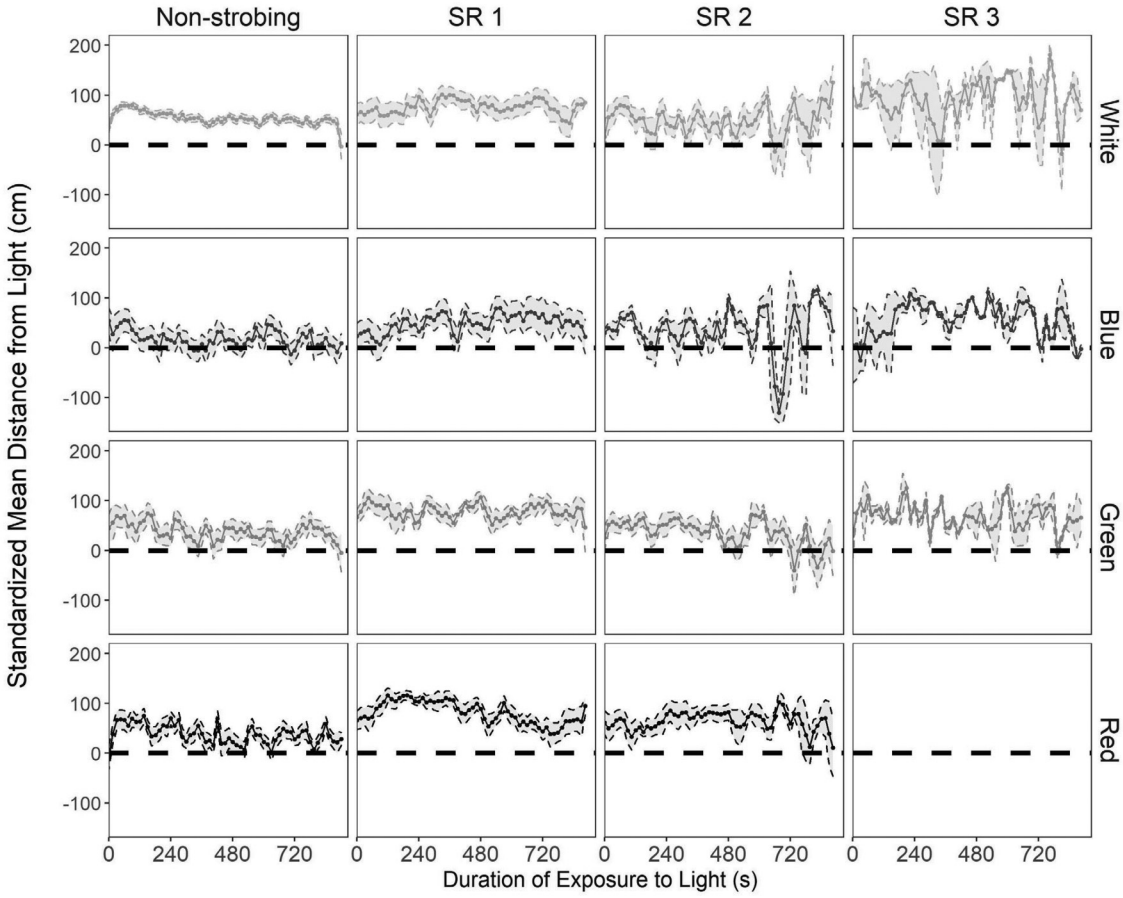


Fig. 10. Standardized mean distances from strobing and non-strobing lights, by colour, over the 15-min treatment period in 15-s time intervals, with grey shading representing standard error. The horizontal dashed line at $y = 0$ represents no difference from the non-illuminated baseline period to which the values were compared (individual to each tank and light location period).



(Kim and Wardle 1998). The light units could even create physical conditions not related to light, such as eddies that effect a rheotactic response (Arnold 1974; Brett and Groot 1963; Cech and Mussen 2010).

The results from this study can inform future efforts to reduce Pacific salmon bycatch in trawl fisheries and have applicability to research focused on salmon safety with dam passage and navigating obstacles during migration (e.g., Flamarique et al. 2006). For example, based on the observed negative phototactic response, more success could come from "repulsion" of salmon (e.g., a strobing white light aft of the BRD) rather than "attraction" using artificial light. Moreover, to increase the efficacy of a BRD, if the perception of the escapement area is a limiting factor, blue non-strobing light would likely be more successful in illuminating the area than white or strobing light. Likewise, if behavioural observations are made using cameras, this study indicates that illuminating the field of view with white light would likely influence behaviour more than using a wavelength outside of the visual spectrum or blue light.

With fisheries selectivity studies, it is important to disentangle a response to the targeted sensory stimulation from other covariates and stimuli being experienced (e.g., auditory) and to think critically about the context in which the animals are experiencing the stimulation (e.g., intrinsic and extrinsic factors, and the role of social interactions; Winger et al. 2010). For example, it is important to consider that animal behaviour in response to artificial light varies by their natural state (Grimaldo et al. 2018; Parsons et al. 2012), species (Beatty 1966; Hoar et al. 1957; Nemeth and Anderson 1992; Mazur and Beauchamp 2003; Wagner 1990), and, within species, by life stage, age, and size (Ali 1959; Lomeli et al. 2018; Mueller and Simmons 2008). Along these lines, we acknowledge that the trial fish were smaller than those that typically encounter a salmon excluder (e.g., Yochum et al. 2021) and that they were hatchery-reared. Behaviour can also vary temporally and spatially (Ben-Yami 1976; Mueller and Simmons 2008) and can be influenced by fishing variables (e.g., tow speed; Gabr et al. 2007). In behaviour trials, there is also the potential for camera illumination (Stoner et al. 2008) and placement and orientation of the lights (Hannah et al. 2015; Larsen et al. 2017; Maynard and Gaston 2010) to influence results. Moreover, behavioural responses can be influenced by the surrounding natural environment (Congleton and Wagner 1988), including ambient light conditions and time of day (Cech and Mussen 2010; Johnson et al. 2005; Protasov 1970; Puckett and Anderson 1988), light level to which the fish is adapted (Anderson et al. 1988), and water temperature and turbidity (Feist and Anderson 1991; Mueller and Simmons 2008; Vogel and Beauchamp 1999).

For future selectivity studies applying artificial light, these results highlight the importance of considering light properties when designing a study and interpreting behaviour data. Similar to context and the influence of biological, environmental, and fishing covariates, it is important to be aware of the influence light properties have on fish behaviour. A laboratory study provides an efficient mechanism to evaluate the influence of those properties before selecting lights for field trials.

Contributors' statement

Noëlle Yochum: Conceptualization, funding acquisition, project administration, supervision, methodology, investigation, formal

analysis, validation, visualization, writing — original draft. David R. Bryan: Formal analysis, validation, visualization, writing — review and editing. Lyle L. Britt: Conceptualization, methodology, investigation, formal analysis, writing — review and editing. Barry A. Berejikian: Conceptualization, resources, methodology, writing — review and editing. Rebecca Haehn: Methodology, investigation. Scott McEntire: Conceptualization, methodology. Rick Towler: Methodology, software. Jeff Atkins: Resources, methodology, investigation. Brad Gadberry: Resources, investigation. Paul Irvin: Methodology.

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References

Ali, M.A. 1959. The ocular structure, retinomotor and photo-behavioral responses of juvenile Pacific salmon. Can. J. Zool. **37**(6): 965–996. doi:10.1139/z59-092.

Anderson, J.J., Puckett, K.J., and Nemeth, R.S. 1988. Studies on the effect of behavior on fish guidance efficiency at Rocky Reach Dam: Avoidance to strobe light and other stimuli. Fisheries Research Institute, School of Fisheries, University of Washington, Seattle, WA 98195, USA. Final report to Chelan County Public Utility District No. 2.

Arnold, G.P. 1974. Rheotropism is fishes. Biol. Rev. **49**(4): 515–576. doi:10.1111/j.1469-185X.1974.tb01173.x.

Bates, D., Mächler, M., Bolker, B., and Walker, S. 2015. Fitting linear mixed-effects models using lme4. J. Stat. Soft. **67**(1): 1–48.

Beatty, D.D. 1966. A study of the succession of visual pigments in Pacific salmon (*Oncorhynchus*). Can. J. Zool. **44**(3): 429–455. doi:10.1139/z66-045.

Ben-Yami, M. 1976. Fishing with light. Food and Agriculture Organization of the United Nations. (FAO fishing manuals). Fishing News [for] the Food and Agriculture Organization of the United Nations, Farnham.

Berdahl, A., Westley, P.A.H., Levin, S.A., Couzin, I.D., and Quinn, T.P. 2016. A collective navigation hypothesis for homeward migration in anadromous salmonids. Fish Fish. **17**: 525–542. doi:10.1111/faf.12084.

Berejikian, B.A., Tezak, E.P., and LaRae, A.L. 2003. Innate and enhanced predator recognition in hatchery-reared Chinook salmon. Environ. Biol. Fishes, **67**: 241–251. doi:10.1023/A:1025887015436.

Brett, J.R., and Groot, C. 1963. Some aspects of olfactory and visual responses in Pacific salmon. J. Fish. Res. Bd. Can. **20**(2): 287–303. doi:10.1139/f63-026.

Bretz, F., Hothorn, T., and Westfall, P. 2010. Multiple comparisons using R. CRC Press. [ISBN 9781584885740.]

Britt, L.L. 2009. Ontogenetic changes in the visual ecology of northeast Pacific marine fishes. Ph.D. thesis, University of Washington, School of Aquatic and Fishery Sciences, Seattle, Wash., USA.

Bui, S., Oppedal, F., Korsøen, J., and Dempster, T. 2013. Modifying Atlantic salmon behaviour with light or feed stimuli may improve parasite control techniques. Aquacult. Environ. Interact. **3**(2): 125–133. doi:10.3354/aei00055.

Cech, J.J., and Mussen, T.D. 2010. Vibrating or flashing screens: investigating fish's ability to avoid screens and louvers using vibration and strobe lights. California Energy Commission, PIER Energy-Related Environmental Research Program CEC-500-2009-055.

Congleton, J.L., and Wagner, E.J. 1988. Effects of light intensity on plasma cortisol concentrations in migrating smolts of Chinook salmon and steelhead held in tanks or raceways and after passage through experimental flumes. Trans. Am. Fish. Soc. **117**(4): 385–393. doi:10.1577/1548-8659(1988)117<0385:EOLIOP>2.3.CO;2.

Feist, B.E., and Anderson, J.J. 1991. Review of fish behavior relevant to fish guidance systems. Fisheries Research Institute, School of Fisheries, University of Washington, Seattle, WA 98195, USA. Annual report of research to the U.S. Army Corps of Engineers.

Fissel, B., Dalton, M., Garber-Yonts, B., Haynie, A., Kasperski, S., Lee, J., et al. 2019. Stock assessment and fishery evaluation report for the groundfish fisheries of the Gulf of Alaska and Bering Sea/Aleutian Islands area: economic status of the groundfish fisheries off Alaska, 2018. Unpublished Report. National Marine Fisheries Service, Seattle, Washington. Available from https://repository.library.noaa.gov/view/noaa/23001/noaa_23001_DS1.pdf.

Flamarique, I.N. 2005. Temporal shifts in visual pigment absorbance in the retina of Pacific salmon. J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol. **191**(1): 37–49. doi:10.1007/s00359-004-0573-9. PMID:15549325.

Flamarique, I.N., Hiebert, S., and Sechrist, J. 2006. Visual performance and ocular system structure of Kokanee and sockeye salmon following strobe light exposure. N. Am. J. Fish. Manage. **26**: 453–459. doi:10.1577/M04-215.1.

Gabr, M., Fujimori, Y., Shimizu, S., and Miura, T. 2007. Trawling experiment in a circular water tank to assess the effects of towing speed, light intensity, and mesh shape on active escape of undersized fish. Fish. Sci. **73**(3): 557–564. doi:10.1111/j.1444-2906.2007.01368.x.

Gauvin, J., Gruver, J., McGauley, K., and Rose, C. 2013. Salmon excluder EFP 11-01. NOAA EFP Final Report. Available from https://scholar.google.com/scholar_lookup?journal=Salmon+Excluder+EFP+11-001+Final+Report%2E+Final+Report+Submitted+to+the+North+Pacific+Fishery+Management+Council%2C+Anchorage%2C+AK%2E&author=Gauvin+J.&author=Gruver+J.&author=McGauley+K.&author=Rose+C.&publication_year=2013.

Grimaldo, E., Sistiaga, M., Herrmann, B., Larsen, R.B., Brinkhof, J., and Tatone, I. 2018. Improving release efficiency of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in the Barents Sea demersal trawl fishery by stimulating escape behaviour. Can. J. Fish. Aquat. Sci. **75**(3): 402–416. doi:10.1139/cjfas-2017-0002.

Hannah, R.W., Lomeli, M.J.M., and Jones, S.A. 2015. Tests of artificial light for bycatch reduction in an ocean shrimp (*Pandalus jordani*) trawl: Strong but opposite effects at the footrope and near the bycatch reduction device. Fish. Res. **170**: 60–67. doi:10.1016/j.fishres.2015.05.010.

Hansen, A.G., Beauchamp, D.A., and Schoen, E.R. 2013. Visual prey detection responses of piscivorous trout and salmon: Effects of light, turbidity, and prey size. Trans. Am. Fish. Soc. **142**(3): 854–867. doi:10.1080/00028487.2013.785978.

Hertel, A.G., Niemelä, P.T., Dingemanse, N.J., and Mueller, T. 2020. A guide for studying among-individual behavioral variation from movement data in the wild. Mov. Ecol. **8**: 30. doi:10.1186/s40462-020-00216-8.

Hoar, W.S., Keenleyside, M.H.A., and Goodall, R.G. 1957. Reactions of juvenile Pacific salmon to light. J. Fish. Res. Bd. Can. **14**(6): 815–830. doi:10.1139/f57-036.

Humborstad, O.-B., Utne-Palm, A.C., Breen, M., and Løkkeborg, S. 2018. Artificial light in baited pots substantially increases the catch of cod (*Gadus morhua*) by attracting active bait, krill (*Thysanoessa inermis*). ICES J. Mar. Sci. **75**(6): 2257–2264. doi:10.1093/icesjms/fsy099.

Hunter, J.R., and Wisby, W.J. 1964. Net avoidance behavior of carp and other species of fish. J. Fish. Board Can. **21**(3): 3. doi:10.1139/f64-050.

Johnson, R.L., Simmons, M.A., McKinstry, C.A., Simmons, C.S., Cook, C.B., Brown, R.S., et al. 2005. Strobe light deterrent efficacy test and fish behavior determination at Grand Coulee Dam third powerplant forebay. Pacific Northwest National Laboratory (PNNL), Richland, Wash.

Kim, Y., and Wardle, C.S. 1998. Measuring the brightness contrast of fishing gear, the visual stimulus for fish capture. Fish. Res. **34**: 151–164. doi:10.1016/S0165-7836(97)00087-8.

Kuznetsova, A., Brockhoff, P.B., and Christensen, R.H.B. 2017. lmerTest package: tests in linear mixed effects models. J. Stat. Softw. **82**(13): 1–26. doi:10.18637/jss.v082.i13.

Larsen, R.B., Herrmann, B., Sistiaga, M., Brinkhof, J., Tatone, I., and Langård, L. 2017. Performance of the Nordmøre grid in shrimp trawling and potential effects of guiding funnel length and light stimulation. Mar. Coast. Fish. **9**(1): 479–492. doi:10.1080/19425120.2017.1360421.

Lomeli, M.J.M., and Wakefield, W.W. 2012. Efforts to reduce Chinook salmon (*Oncorhynchus tshawytscha*) and rockfish (*Sebastes* spp.) bycatch in the U.S. west coast Pacific hake (*Merluccius productus*) fishery. Fish. Res. **119–120**: 128–132. doi:10.1016/j.fishres.2011.11.003.

Lomeli, M.J.M., and Wakefield, W.W. 2019. The effect of artificial illumination on Chinook salmon behavior and their escapement out of a midwater trawl bycatch reduction device. Fish. Res. **218**: 112–119. doi:10.1016/j.fishres.2019.04.013.

Lomeli, M.J.M., Groth, S.D., Blume, M.T.O., Herrmann, B., and Wakefield, W.W. 2018. Effects on the bycatch of eulachon and juvenile groundfish by altering the level of artificial illumination along an ocean shrimp trawl fishing line. ICES J. Mar. Sci. **75**(6): 2224–2234. doi:10.1093/icesjms/fsy105.

Maynard, D., and Gaston, T.F. 2010. At-sea testing of a submerged light BRD onboard the F.V. Ocean Thief for approval in Australia's Northern Prawn Fishery. Australian Maritime College, Launceston.

Mazur, M.M., and Beauchamp, D.A. 2003. A comparison of visual prey detection among species of piscivorous salmonids: Effects of light and low turbidities. Environ. Biol. Fishes, **67**(4): 397–405. doi:10.1023/A:1025807711512.

Melli, V., Krag, L.A., Herrmann, B., and Karlsen, J.D. 2018. Investigating fish behavioural responses to LED lights in trawls and potential applications for bycatch reduction in the *Nephrops*-directed fishery. ICES J. Mar. Sci. **75**(5): 1682–1692. doi:10.1093/icesjms/fsy048.

Migaud, H., Cowan, M., Taylor, J., and Ferguson, H.W. 2007. The effect of spectral composition and light intensity on melatonin, stress and retinal damage in post-smolt Atlantic salmon, *Salmo salar*. Aquaculture, **270**(1–4): 390–404. doi:10.1016/j.aquaculture.2007.04.064.

Morgan, D.C., and Smith, H. 1981. Non-photosynthetic responses to light quality. *In* Physiological plant ecology. I. Responses to the physical

environment. *Edited by* O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler. Springer-Verlag, Berlin.

Mueller, R.P., and Simmons, M.A. 2008. Characterization of gatewell orifice lighting at the Bonneville Dam second powerhouse and compendium of research on light guidance with juvenile salmonids. Pacific Northwest National Laboratory (PNNL), Richland, WA 99352, USA.

Mueller, R.P., Neitzel, D.A., and Amidan, B.G. 1999. Evaluation of infrasound and strobe lights to elicit avoidance behavior in juvenile salmon and char. Pacific Northwest National Laboratory (PNNL), Richland, WA. Report submitted to the U.S. Department of Energy, Bonneville Power Administration, Portland, OR 97208 Project Number 86-118.

Nemeth, R.S., and Anderson, J.J. 1992. Response of juvenile coho and Chinook salmon to strobe and mercury vapor lights. N. Am. J. Fish. Manage. **12**(4): 684–692. doi:10.1577/1548-8675(1992)012<0684:ROJCAC>2.3.CO;2.

Nguyen, K.Q., and Winger, P.D. 2019. Artificial light in commercial industrialized fishing applications: A review. Rev. Fish. Sci. Aquacult. **27**(1): 106–126. doi:10.1080/23308249.2018.1496065.

NMFS-WCR. 2017. Salmon bycatch in the Pacific coast groundfish fisheries. NMFS Report 2. March 2017. National Marine Fisheries Service, Sustainable Fisheries Division, West Coast Region

Olsen, K., Angell, J., Pettersen, F., and Løvik, A. 1983. Observed fish reactions to a surveying vessel with special reference to herring, cod, capelin and polar cod. FAO Fish. Rep. **300**(1983): 131–138.

Özbilgin, H., and Glass, C.W. 2004. Role of learning in mesh penetration behaviour of haddock (*Melanogrammus aeglefinus*). ICES J. Mar. Sci. **61**: 1190–1194. doi:10.1016/j.icesjms.2004.07.001.

Parsons, G.R., Foster, D.G., and Osmond, M. 2012. Applying fish behavior to reduce trawl bycatch: Evaluation of the nested cylinder bycatch reduction device. Mar. Technol. Soc. J. **46**: 26–33. doi:10.4031/MTSJ.46.3.2.

Protasov, V.R. 1970. Vision and near orientation of fish. IPST. [Translated from Russian.]

Puckett, K.J., and Anderson, J.J. 1988. Behavioral responses of juvenile salmonids to strobe and mercury lights. Fisheries Research Institute, School of Fisheries, University of Washington, Seattle, WA 98195, USA. Final report to Stone and Webster Engineering Corporation, Boston, Mass.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/.

Rohan, S.K., Kotwicki, S., Laman, E.A., Britt, L.L., and Aydin, K. 2020. Deriving apparent optical properties from light measurements obtained using bottom-trawl-mounted archival tags. United States Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-403. doi:10.25923/42yn-1q79.

Ryer, C.H., Stoner, A.S., Iseri, P.J., and Spencer, M.L. 2009. Effects of simulated underwater vehicle lighting on fish behavior. Mar. Ecol. Prog. Ser. **391**: 97–106. doi:10.3354/meps08168.

Shapiro, S.S., and Wilk, M.B. 1965. An analysis of variance test for normality (complete samples). Biometrika, **52**(3–4): 591–611. doi:10.2307/2333709.

Stamps, J., and Groothuis, T.G.G. 2010. The development of animal personality: Relevance, concepts and perspectives. Biol. Rev. **85**: 301–325. doi:10.1111/j.1469-185X.2009.00103.x.

Stamps, J.A., Briffa, M., and Biro, P.A. 2012. Unpredictable animals: Individual differences in intraindividual variability (IIV). Anim. Behav. **83**: 1325–1334. doi:10.1016/j.anbehav.2012.02.017.

Stoner, A.W., Ryer, C.H., Parker, S.J., Auster, P.J., and Wakefield, W.W. 2008. Evaluating the role of fish behavior in surveys conducted with underwater vehicles. Can. J. Fish. Aquat. Sci. **65**(6): 1230–1243. doi:10.1139/F08-032.

Tabor, R.A., Brown, G.S., and Luiting, V.T. 2004. The effect of light intensity on sockeye salmon fry migratory behavior and predation by cottids in the Cedar River, Washington. N. Am. J. Fish. Manage. **24**: 128–145. doi:10.1577/M02-095.

Vogel, J.L., and Beauchamp, D.A. 1999. Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. Can. J. Fish. Aquat. Sci. **56**(7): 1293–1297. doi:10.1139/f99-071.

Wagner, H.-J. 1990. Retinal structure of fishes. *In* The visual system of fish. *Edited by* R. Douglas and M. Djamgoz. Springer, the Netherlands. pp. 109–157.

Wang, J., Barkan, J., Fisler, S., Godinez-Reyes, C., and Swimmer, Y. 2013. Developing ultraviolet illumination of gillnets as a method to reduce sea turtle bycatch. Biol. Lett. **9**: 20130383. doi:10.1098/rsbl.2013.0383.

Winger, P.D., Eayrs, S., and Glass, C.W. 2010. Fish behaviour near bottom trawls. *In* Behavior of marine fishes: Capture processes and conservation challenges. *Edited by* P. He. Wiley-Blackwell, Ames, Iowa. pp. 67–103.

Yochum, N., Stone, M., Breddermann, K., Berejikian, B.A., Gauvin, J.R., and Irvine, D.J. 2021. Evaluating the role of bycatch reduction device design and fish behavior on Pacific salmon (*Oncorhynchus* spp.) escapement rates from a pelagic trawl. Fish. Res. **236**: 105830. doi:10.1016/j.fishres.2020.105830.