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ARTICLE

Freshwater Ecology

Riverine fish density, predator–prey interactions, and their relationships with artificial light at night

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Abstract

Artificial light at night (ALAN) has emerged as a prevalent anthropogenic stressor in many aquatic ecosystems impacting a wide range of taxa and ecological processes. In fishes, ALAN attracts both predators and prey, potentially resulting in increased predation mortality and sublethal impacts. Increased predation mortality is especially problematic in anadromous fishes, given that many populations are diminished and out-migrating juveniles must transit illuminated waterways. Additionally, ALAN management is complex, because lighting benefits human safety, economies, and recreational pursuits. The Sundial Bridge (Redding, CA) is an iconic illuminated structure that spans a section of the little remaining spawning habitat of the endangered winter-run Chinook Salmon. It was hypothesized that bridge ALAN increased Rainbow Trout predation of winter-run fry, and a lighting management plan was implemented. However, ALAN impacts on this predator–prey interaction and species-specific responses were unknown. Therefore, we used tethered salmonid fry and ARIS sonar cameras to determine whether variable ALAN treatments (0%, 25%, 50%, and 100% intensity) altered Rainbow Trout density (RTD) and fry predation risk, while investigating the temporal relationships of RTD with ALAN. ALAN significantly increased RTD on river right when any amount of ALAN was present, potentially leading to competition and fitness consequences; RTD did not change significantly in response to ALAN on river left. Although RTD generally increased in response to ALAN, salmonid fry predation was almost nonexistent. Therefore, while ALAN may decrease out-migrant survival in other waterways, there was no evidence at our study site. Furthermore, the discrepancies between riverbanks demonstrate the complexity of ALAN and how it interacts with other environmental parameters potentially providing optimal foraging habitat. The Rainbow Trout attraction to ALAN, which occurred immediately with diminishing ambient light, indicates that complete ALAN removal may be necessary to mitigate ecological consequences of ALAN. When removal is unrealistic, ALAN should be diminished as early in the night as possible to minimize aquatic ecosystem impacts, while maintaining benefits for human populations.

KEYWORDS
ALAN, anthropogenic impacts, artificial illumination, artificial light, endangered species, fish, foraging, pollution, predator–prey interactions, Rainbow Trout, Salmon

INTRODUCTION

Aquatic pollution (e.g., nutrients, toxins, sediment) has been commonplace for centuries (Islam & Tanaka, 2004); however, since the advent of electricity, light pollution, commonly referred to as artificial light at night (ALAN), has emerged as a prevalent anthropogenic stressor in many aquatic ecosystems (Davies et al., 2014; Jechow & Hölker, 2019; Nightingale et al., 2006; Zapata et al., 2019). ALAN impacts a wide range of aquatic taxa, including zooplankton (Ludvigsen et al., 2018; Moore et al., 2000, 2006), macroinvertebrates (Moore et al., 2006; Perkin et al., 2014; Underwood et al., 2017), fishes (Becker et al., 2013; Nelson et al., 2021; Nightingale et al., 2006), shorebirds (Dwyer et al., 2013; McLaren et al., 2018; Montevecchi, 2006), sea turtles (Salmon, 2006; Salmon, Reiners, et al., 1995; Salmon, Tolbert, et al., 1995), and mammals (Yurk & Trites, 2000). Furthermore, the effects of ALAN in aquatic systems may range from individual- to ecosystem-level responses, altering foraging, migration, reproduction, predator–prey interactions, community composition, and food web dynamics (Davies et al., 2014; Nightingale et al., 2006; Zapata et al., 2019). The vast majority of human civilization is situated near coastal waters, rivers, and lakes (Kummu et al., 2011; Small & Nicholls, 2003) and human development is ever increasing, further exacerbating ALAN impacts on aquatic ecosystems (Davies et al., 2014; Jechow & Hölker, 2019; Zapata et al., 2019). Given that fishes are an essential human food source, economically valuable, and represent many trophic levels within aquatic food webs (Buchheister & Latour, 2015; FAO, 2020), determining and mitigating ALAN impacts on fishes is vital to preserve these services and the integrity of aquatic ecosystems.

Studies of ALAN on fishes have focused on attraction, foraging behaviors, and predator–prey interactions (Nightingale et al., 2006). ALAN may increase the density of both planktivorous and piscivorous fishes, prey mortality, and predation rates (Becker et al., 2013; Nelson et al., 2021; Tabor et al., 2017, 2021), likely because increased light increases foraging success across broad trophic levels (Bolton et al., 2017; Mazur & Beauchamp, 2003; Townsend & Risebrow, 1982). As such, ALAN may alter aquatic community composition (Becker et al., 2013; Bolton et al., 2017; Prinslow et al., 1980), but these impacts are not always present (Martin et al., 2021). Predation may increase under illumination while concurrently lowering predator density (Bolton et al., 2017), and foraging fish may avoid ALAN entirely (Contor & Griffith, 1995). These factors indicate that ALAN impacts vary and likely represent a trade-off between forage opportunity and predation risk (Bolton et al., 2017; Nightingale et al., 2006). Clearly, ALAN affects prey through increased risk and mortality; however, there may be corresponding sublethal effects on predators. Piscivores actively maintain position in ALAN, potentially incurring a fitness cost (Becker et al., 2013), while likely increasing their own predation risk to diurnal predators (Alexander, 1979; Harvey & Nakamoto, 2013; Nightingale et al., 2006). If prey resources or habitat space are limiting, this holding behavior coupled with attraction could result in competition, further exacerbating potential fitness consequences. Therefore, artificial illumination may have both lethal and sublethal effects that should be investigated across multiple trophic levels to get a clear understanding of how fishes may respond.

Anadromous fishes (e.g., Acipenseridae, Alosidae, Salmonidae) must navigate artificially illuminated systems during both spawning and juvenile migrations, which may contribute to population declines and the imperiled status of many species (Limburg & Waldman, 2009; Williams, 2006). Sacramento River winter-run Chinook Salmon (*Oncorhynchus tshawytscha*) are an endangered evolutionary significant unit (ESU) with a unique life history that only exists in the California Central Valley (Johnson & Lindley, 2016). Adult fish return from the ocean in the winter and mature in freshwater before they spawn in the summer (Fisher, 1994; Johnson & Lindley, 2016; Williams, 2006) in their remaining habitat, which is restricted to 30 km below Keswick Dam and impacted by the illuminated cites of Redding and Anderson, CA (California Department of Fish and Game, 2004). Juveniles then rear in freshwater and enter the ocean the following winter or spring (Fisher, 1994; Johnson & Lindley, 2016; Williams, 2006). To reduce predation risk, another likely contributor to winter-run decline (Lindley & Mohr, 2003), juvenile salmonids typically out-migrate at night (Chapman et al., 2013; Clark et al., 2016; Michel et al., 2013). However, ALAN attracts and slows out-migrating salmonids (Celedonia et al., 2011; Tabor et al., 2017, 2021; Tabor, Brown, & Luiting, 2004), delays redd emergence and dispersal (Riley et al., 2013, 2015), and increases salmonid predator density and predation risk (Nelson et al., 2021; Tabor, Brown, & Luiting, 2004). Given that ALAN could also alter spawning cues (Nightingale et al., 2006; Simons et al., 2021), the presence of ALAN within spawning, rearing, and migratory habitats could lower the survival of this endangered ESU and may have similar impacts on other anadromous fishes.

Management of ALAN presents a unique challenge, given that decreasing nighttime lighting may adversely affect economies, recreation, social interaction, and human safety, and the extent and severity of this pollutant remains unknown along many waterways (Davies et al., 2014; Davies & Smyth, 2018; Gaston et al., 2015). Although this challenge exists, many cites have adopted broad spectrum light-emitting diode (LED) lights, potentially allowing them the ability to quickly change light intensity and spectrum (Davies & Smyth, 2018). This ability and concern over light pollution has resulted in the adoption of part-time lighting (e.g., lights off after 12:00 AM) and dimming management plans (Davies & Smyth, 2018). Given that human activity remains highest during the early hours of the night (Bhattacharya & Kaski, 2019; Martín-Olalla, 2018; Monsivais et al., 2017), these types of part-time reduction and dimming plans provide a balance between economic considerations, human safety, and ecological impacts. This trade-off is particularly advantageous if ALAN impacts are most pronounced late in the night (Nelson et al., 2021). Therefore, to assess the utility of lighting management plans, it is important to understand the temporal response of fishes to ALAN presence and intensity.

The Sundial Bridge, located within the little remaining winter-run spawning habitat, is an iconic illuminated bridge in Redding, CA, that was hypothesized to increase the predation of endangered winter-run fry by resident Rainbow Trout (*Oncorhynchus mykiss*), thus decreasing out-migrant survival (Jensen, 2012). Given that a trophy Rainbow Trout fishery (≥18 in.; 45.7 cm) exists at the bridge (Plemons & Dege, 2019) and that trout consumption of salmonid fry increases with increasing light (Ginetz & Larkin, 1976), this hypothesis was not without merit, leading to new LED bridge lights and an ALAN reduction plan (Jensen, 2012). However, this hypothesis has never been empirically assessed despite the fact that any negative effects on winter-run fry could result in population-level impacts on this endangered ESU. In addition to salmon survival concerns, this bridge provides an ideal site to assess how adult Rainbow Trout respond to ALAN, elucidating impacts on a large-bodied, economically valuable species.

To assess the impacts of Sundial Bridge ALAN on fishes, our first objective was to determine whether variable ALAN intensities altered the relative Rainbow Trout density (RTD) during the night (≥90 min past sunset). To measure the temporal response of RTD to ALAN, we quantified RTD using sonar cameras during the shift from day to night and throughout the night under different ALAN treatments. During our final week of sampling, we also assessed diel patterns of RTD, further elucidating the relationships of RTD with time of day. Finally, we assessed whether Sundial Bridge ALAN impacted the relative predation risk of salmonid fry. Our study provided unique insight into how Rainbow Trout respond to artificial illumination, assessed Sundial Bridge ALAN management, provided needed empirical data on salmonid fry predation, and highlighted ALAN impacts in riverine ecosystems.

METHODS

Study site and ALAN management

Construction of the Sundial Bridge was completed in 2004 and included halogen lights, which were pointed skyward, upstream and downstream, casting ALAN on the Sacramento River (Jensen, 2012). Given repeated concerns regarding the ALAN impact on winter-run predation (Arthur, 2013; Jensen, 2012; Sandoval, 2015; Skykeepers, 2009), bridge lighting and management was revamped in 2014. Similar to other municipalities (Davies & Smyth, 2018), the halogen lights were replaced with horizontal facing broad spectrum LEDs underneath the bridge (Jensen, 2012). Beyond the perceived benefit to salmon (FISHBIO, 2018; Sandoval, 2015; Slade, 2019), switching to LEDs reduced the bridge lighting power bill and allowed for full wireless digital control over light spectrum and intensity (City of Redding, 2018; Live Design, 2015). Concurrent with the light change, the City of Redding entered into an agreement with the California Department of Fish and Wildlife (CDFW) to minimize lighting during critical out-migrating periods for winter-run fry. From 1 August to 1 February (emergence and outmigration period for winter-run fry), lights are typically operated at 25% intensity white light (roughly 3.49 lx, according to the agreement) from dusk until midnight, then reduced to 12.5% until dawn (K. Bloom, City of Redding, personal communication, 2020). Although reduced, these lux levels could still result in increased predation of salmon fry when compared with a complete absence of ALAN, given that lux <1 can increase predation success of fishes (Mazur & Beauchamp, 2003, 2006; McMahon & Holanov, 1995). As with any ALAN management, the bridge lighting issue is complex as the bridge provides an architecturally renowned landmark structure in the City of Redding, is a major tourist attraction, and is a pedestrian thoroughfare requiring a degree of lighting for safety (K. Niemer, Director of Community Services, City of Redding, personal communication, 2020).

The Sundial Bridge is also located 7 km downstream of Keswick Dam, CA, placing it in winter-run spawning and fry migratory habitat, an area with a presumably limited number of piscivorous fish species (Figure 1). This section of the Sacramento River is 0.12 km wide, had 214.76 m^3/s (±1.70 SE) mean flow, and 11.53°C (±0.01 SE) mean water temperature during our study. These flows resulted in variable velocities underneath the bridge, with river right (RR) experiencing lower flow velocities coupled with shallower waters than river left (RL; Appendix S1; Figure 2). Given sampling constraints, knowledge of the fish community in this swift flowing section of river is also limited (D. Killiam, CDFW, personal communication, 2020); however, piscivores common in the larger watershed were likely absent. Striped Bass (*Morone saxatilis*) rarely occur this far upstream, especially in the fall (M. Johnson, CDFW, personal communication, 2020), and the controlled cold-water dam releases that enable winter-run egg incubation (Johnson & Lindley, 2016; Martin et al., 2017), likely limit *Micropterus* sp. occurrence and foraging (Lawrence et al., 2012; Layher et al., 1987; Nobriga et al., 2021).

During our study, we observed three species of large-bodied fishes (≥200 mm) with opportunistic daytime video footage, spawning Chinook Salmon, Sacramento Pikeminnow (*Ptychocheilus grandis*), and Rainbow Trout. A wild resident trophy Rainbow Trout fishery exists in this section of the Sacramento River and these fish constitute the majority of angler catches (Plemons & Dege, 2019). Although hatchery Steelhead are produced in Battle Creek, a Sacramento River tributary 42 km downstream of the Sundial Bridge, this anadromous form of *O. mykiss* is rarely encountered in our study reach, because spawning adults return to the hatchery and central valley Steelhead are threatened (Plemons & Dege, 2019). Furthermore, the controlled cold-water releases from Shasta and Keswick

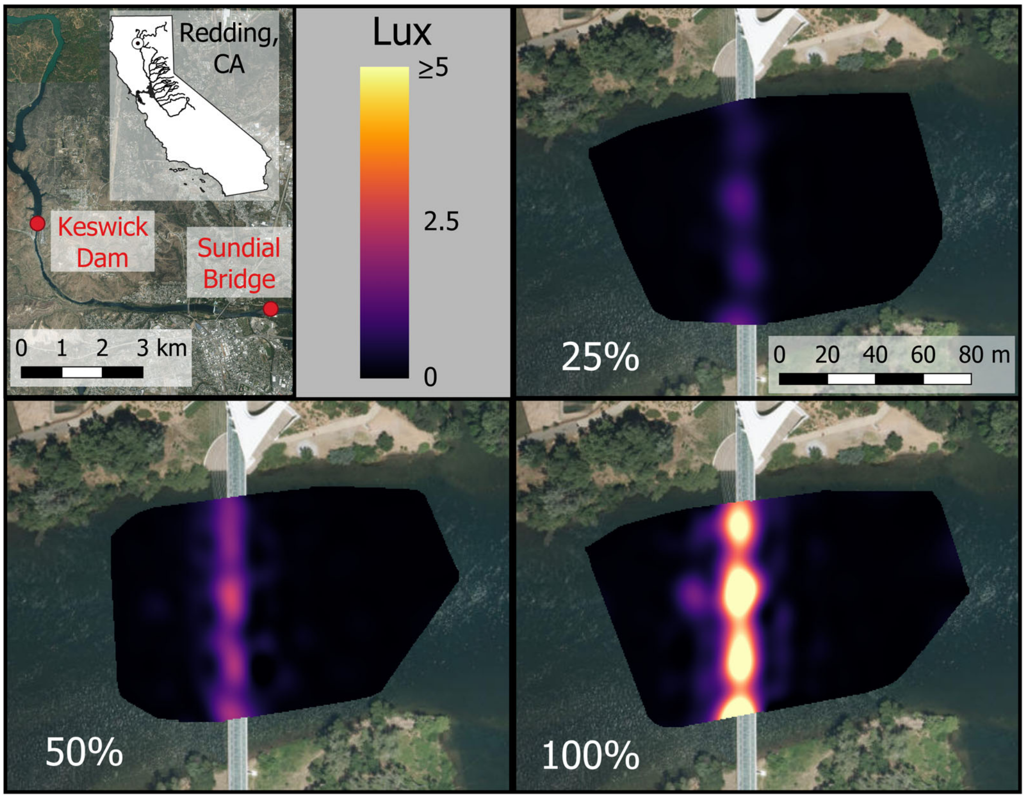

FIGURE 1 Map of Sundial Bridge and Keswick Dam (upstream barrier to anadromy), as well as survey results from 25%, 50%, and 100% light intensity treatments.

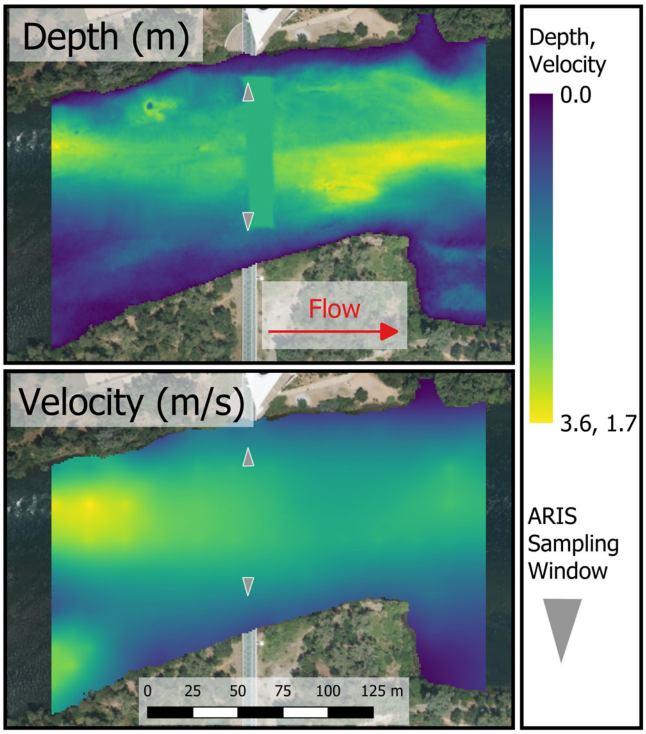

FIGURE 2 Depth (in meters) and velocity (in meters per second) of the Sacramento River at the Sundial Bridge, with a 215-m^3/s flow below Keswick Dam from our two-dimensional hydraulic model (Appendix S1). The sampling cones of the adaptive resolution imaging sonar (ARIS) cameras are denoted with gray triangles.

Dams create an ideal habitat for resident Rainbow Trout (Plemons & Dege, 2019) and previous telemetry work has confirmed a nonmigratory population (Demetras et al., 2013). Given these characteristics of this trophy fishery, our opportunistic hook and line catch of Rainbow Trout ($n = 32$, mean fork length [FL] 42.6 cm ± 0.5 SE [range = 27.9–58.4 cm]), and snorkel observation of trout underneath Sundial ALAN, we assumed that the majority of fishes we observed on sonar footage were resident Rainbow Trout.

Experimental design

We conducted our study from 31 August to 1 October 2020 to correspond with winter-run fry emergence and outmigration (Voss, 2021). To test the effects of Sundial Bridge ALAN on fishes, we established four light treatments on the bridge: no light (0%), 25%, 50%, and 100% intensity white light. The bridge lights consisted of red, green, and blue LEDs and our white light treatments used equal intensity from each color channel. Although we set equal intensity on each channel, blue and red wavelengths had higher relative peaks than green, while the green channel transmitted across a broader spectrum (Appendix S2: Figure S1). To ensure that each treatment was tested once each week, we sampled Monday through Thursday nights and randomly selected the nightly light treatments before weekly experiments began. For each experimental night, we set the bridge lighting treatment 1 h prior to sunset. We returned the bridge to its current default lighting scheme (25% blue light, in honor of COVID healthcare workers) once sampling concluded, approximately 6 h after sunset. We repeated this four-night experimental design across five consecutive weeks, with each treatment sampled once per week, resulting in five replicates of each treatment.

We surveyed ALAN intensity (in lux) of each light treatment (25%, 50%, and 100%) during a new moon after experiments concluded on 18 September 2020. To quantify the amount of lux on the river's surface, we performed light survey transects with an International Light Technologies (ILT) 2400 optometer mounted on the bow of a low-profile boat, roughly 0.3 m off the water's surface. We thoroughly covered all experimental areas of the river, including the water directly under the Sundial Bridge. To create a smooth lux profile of the experimental area and interpolate raw lux values, we used ordinary kriging implemented with the autokrig R function (Hiemstra et al., 2009). We also measured the light spectrum at each treatment with an ILT 350 Chroma Meter. Although we did not survey the 0% treatment, we used the same optometer to quantify ambient lux downstream of the bridge (outside of the influence of bridge ALAN), throughout most sampling nights.

To quantify the relative density of large (≥200 mm total length [TL]), presumably piscivorous Rainbow Trout (RTD) under the bridge and their response to ALAN on both RR and RL, we deployed paired adaptive resolution imaging sonar (ARIS; Sound Metrics Corp.) cameras each night, starting 1 h prior to sunset and ending approximately 6 h after sunset. We chose this size cutoff because most piscivorous Rainbow Trout exceed this length (Yard et al., 2011) and we have had low false-positive rates with this threshold using automated ARIS fish detection algorithms for other piscivorous fishes (Nelson et al., 2021). This sampling time frame allowed us to investigate potential nighttime (≥90 min past sunset) ALAN effects and to capture temporal trends in RTD associated with the shift from day to night. We positioned ARIS cameras on both river banks directly under the Sundial Bridge, with lens headings perpendicular to the river and aligned with the bridge. To ensure vegetation or rocks did not obstruct ARIS views, we deployed ARIS cameras in roughly 2 m of water and set viewing windows from 2 to 10 m with −2.5° pitch. During the last week of the study (28 September–1 October 2020), we deployed the RR ARIS continually for the experimental week to capture diel patterns in RTD under the Sundial Bridge, to further elucidate temporal relationships.

To determine whether a relationship between ALAN and predation risk existed at the Sundial Bridge, we recorded the time and location of predation events by tethering live prey to micro predation event recorders (mPERs). We specifically developed mPERs for this study, which were a miniaturization of the original PER design (Demetras et al., 2016) that have successfully tested the relationships of predation risk with environmental covariates (Michel et al., 2020) and ALAN (Nelson et al., 2021). We tested mPERs in the Sacramento–San Joaquin Delta, successfully recording predation events on 60 of 530 deployments (11.32%) and confirmed four of these events with ARIS footage. Given that we could not use endangered winter-run Chinook Salmon fry for tethering experiments, we used hatchery-reared Rainbow Trout fry as a surrogate. We measured the FL of 50 randomly selected surrogate individuals each week and most fish (minimum = 28 mm, mean = 43.21 mm ± 0.36 SE, and maximum = 58 mm FL) fell below the fry cutoff (<46 mm FL) similar to out-migrating winter-run in this river (Voss & Poytress, 2018, 2019, 2020). Therefore, our surrogate approach should not bias our experiment, because fry were appropriately sized and Rainbow Trout are cannibalistic (Mazur & Beauchamp, 2003; Yard et al., 2011). We tethered live fry to each mPER using 0.91 kg (2 lb) fluorocarbon fishing line looped through their mouth and operculum. We attached this tether (0.25 m in length) to 2 m of 3.63 kg (8 lb) test fluorocarbon that was attached to a magnet on the bottom of the mPER. To ensure that tethered fry were suspended 2 m below the surface upon deployment, we attached a small lead mass (3 g) at the connection of the 0.91-kg (2 lb) and 3.63-kg (8 lb) lines. We selected this depth given that anglers commonly fish for Rainbow Trout at this depth with fly fishing gear at this location. The mPERs were small enough to attach to fishing rods for deployment and retrieval. We deployed mPERs from both RR and RL by casting upstream of the Sundial Bridge (and the major influences of the associated ALAN) and letting them drift past the bridge and associated ALAN prior to retrieval. During each deployment, the mPER recorded its GPS position and time stamp every second along with whether a predation event had occurred. When tethered fry were predated upon, the attached magnet would become dislodged, thereby triggering an electronic reed switch that would register and log a predation event. Before redeployment, we ensured that tethered fry were in good condition and active, and we used fry for a maximum of three deployments before replacement. We deployed between 55 and 135 mPERs each night (mean = 83 ± 4.56 SE) from 90–330 min past sunset.

ARIS data processing

We converted raw ARIS footage to RTD prior to analysis, in such a way that this metric accounts for differences in ARIS sampling rate, removes bias associated with double counting, and incorporates both the number of fish and time spent in the ARIS sampling beam. First, to remove background interference, we processed raw ARIS footage using contiguous samples over threshold (CSOT) mode in the ARIS fish software. We then imported background subtracted CSOT files into Echoview software (version 10.2) to automatically identify and filter fish. Our workflow was similar to previous studies (Boswell et al., 2008; Helminen et al., 2020; Nelson et al., 2021) and consisted of converting multibeam data to a single-target echogram, removing targets <200 mm TL, and tracking fish pings to generate individual fish tracks. For each fish track, we exported the number of pings within 10-min time bins and summed these pings to generate total fish pings per 10 min for each ARIS throughout sampling periods. For every 10-min bin within each ARIS and sampling period, we divided the total number of fish pings by relative beam volume to generate relative fish density. Beam sample volume is a relative measure given that ARIS footage is a two-dimensional (2D) representation of a three-dimensional space, and Echoview treats it as such. Therefore, we report relative fish density as a unitless metric and use this metric for all ARIS statistical analyses. Furthermore, we assumed that the majority of these fishes were Rainbow Trout (see *Study site and ALAN management*) and will refer to relative fish density as relative RTD hereafter.

Statistical analysis

To assess whether ALAN altered RTD under the Sundial Bridge during the night, we analyzed a subset of ARIS data beginning after astronomical twilight (90–330 min past sunset). With this subset, we investigated two hypotheses: (1) did RTD differ among ALAN treatments within riverbanks and (2) did RTD differ between riverbanks within ALAN treatments. For our first hypothesis, we implemented riverbank-specific generalized linear mixed-effects models (GLMMs) with the lme4 package in R (Bates et al., 2015; R Core Team, 2021), using the gamma family and a log link, given that RTD was positive continuous proportional data. In these models, the response was RTD and we included the fixed effect of

ALAN treatment. To account for weekly variability in RTD and to protect against pseudoreplication and nonindependence, we included random effects of sampling night nested within week. To test our second hypothesis, we implemented a similar GLMM, but in this instance, we used data from both riverbanks and included the fixed effects of ALAN treatment, riverbank (RR vs. RL), and the interaction of the two. We included random effects of sampling night by riverbank interactions nested within week, to ensure that our between-riverbank comparisons were not pseudoreplicated and that assumptions of independence were met. We implemented pairwise contrasts (Tukey corrected *p* values) using the R function emmeans to test our respective hypotheses for each GLMM.

To investigate temporal patterns in RTD, we fit segmented generalized linear models (SGLMs) with the R package segmented (Muggeo, 2008). We fit separate sets of models ($n = 8$ model sets) for each light treatment at both river banks to identify treatment and riverbank-specific break points and temporal trends. Similar to nighttime density models, we fit SGLMs using the gamma family and a log link, given the characteristics of the RTD dataset. The original within-treatment generalized linear models (GLMs) that we ran with the segmented package included RTD as the dependent variable and time as the only independent variable. For each model set, we implemented four different SGLMs with zero, one, two, or three break points, and provided respective break point starting values of 0, 90, and 180 min past sunset. We chose these values because they correspond to sunset, the end of astronomical twilight, and a within-night point. The segmented.glm function iteratively fit multiple segmented glm models, updating the break point(s) until convergence was reached. The resulting model for each number of break points included both break point estimates and slope parameters (Muggeo, 2008). We selected the most parsimonious SGLM within each model set as the one with the number of break points that resulted in the lowest corrected Akaike information criterion value (AIC_c), unless the $\Delta\text{AIC}_\text{c}$ of another model with fewer break points was <2.

To observe diel patterns of RTD under the Sundial Bridge, we produced a continuous plot of RTD by time for the last week of sampling. We used density data from the first three continuous sampling nights (90–630 min past sunset) and the daytime periods between these nights (sunrise–sunset) in a gamma GLMM, to determine whether RTD differed between day and night periods, to further elucidate diel trends and relationships of density with time. Given that our continuous sampling concluded on Thursday night after ALAN experiments, we did not include the last night of sampling in this analysis (50% intensity ALAN). In this model, we included the fixed effect of time period (day vs. night) and random intercepts for each continuous day ($n = 3$) and night ($n = 3$) sampling period to protect against pseudoreplication. To investigate whether RTD responded to within-night changes in bridge lighting, we fit SGLMs in a similar manner to the above segmented analysis. For each experimental night, we tested whether zero, one, two, or three break points best fit the data and provided respective break point starting values of 360, 460, and 560 min past sunset. We chose 360 as our first starting value because that was approximately when we switched experimental light treatments to the default lighting scheme. We selected the most parsimonious SGLM within each model set as before based on $\Delta\text{AIC}_\text{c}$ values.

Predation events across all treatments were almost nonexistent; therefore, we could not perform any statistical analysis relating relative predation risk to ALAN. Summaries of our deployments are reported below along with the locations of predation events.

RESULTS

Sundial Bridge ALAN and ambient lighting

Artificial illumination on the water's surface was present underneath the Sundial Bridge and each light treatment above 0% produced measurable differences in surface lux. The maximum lux values recorded were 1.7, 3.0, and 9.2 for our 25%, 50%, and 100% illumination treatments, respectively (Figure 1). The LEDs at the Sundial Bridge produced a similar spectrum reading across all light treatments with similar intensity in both the red and blue portions of the spectrum (Appendix S2: Figure S1). Baseline ambient lux followed expected patterns, decreasing with time of day until a mean minimum value of 0.05 was reached around 60 min past sunset. Baseline lux values and temporal trends also varied among full moon (moon stage ≥90%) and dark moon nights; however, no effect on RTD was observed (Appendix S2: Figure S2).

Relative RTD

When the Sundial Bridge was illuminated, relative RTD increased at RR during night experimental periods (90–330 min past sunset). We observed some week to week variation in RTD at both riverbanks, but overall trends among treatments and riverbanks remained (Appendix S2: Figure S3). On RR, RTD was greater at illuminated treatments (25%, 50%, and 100% ALAN

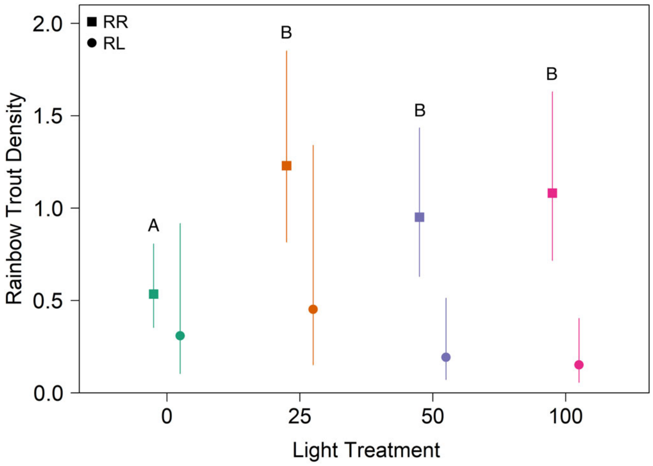

FIGURE 3 Relative Rainbow Trout density estimates and 95% CIs across artificial light at night treatments (0%, 25%, 50%, and 100% intensity) from river right (RR) and river left (RL) nighttime generalized linear mixed-effects models. Light treatments did not differ on RL and different letters above bars represent significant density differences at RR.

intensity) when compared with our dark treatment (all $p < 0.05$) and illuminated treatments did not differ from one another (Figure 3; Appendix S2: Table S1). By contrast, RTD was similar among all treatments (all $p > 0.58$) at RL. At all illuminated treatments, RTD was greater at RR than RL (all $p < 0.04$), but under no light, RTD was similar between riverbanks (Appendix S2: Table S1).

Significant break points in the relationship of RTD with time were present at both RR and RL, indicating a nonlinear response of RTD with time of day. The best fitting SGLMs included two break points for RR and one break point for RL, resulting in three slope parameters for RR and two parameters for RL models (Appendix S2: Table S2). For all RR treatments, there was no relationship of RTD with time until around sunset (Break point 1), where an exponential increase was predicted until about an hour past sunset (Break point 2). After Break point 2, the 95% CI of all treatment slopes included 0, indicating no relationship of RTD with time past this point (Figure 4; Appendix S2: Table S3). On RL, RTD was predicted to increase until about an hour past sunset (Break point 1); however, the upper end of the 50% ALAN treatment 95% CI was 54 min. After Break point 1, RTD decreased with elapsed time at the 25% and 100% ALAN treatments, had no relationship at the 50% treatment, and increased under no bridge lighting (Appendix S2: Table S4). Trends among treatments and riverbanks were similar to night GLMMs. When the bridge was illuminated, RR SGLM nighttime RTD predictions were greater than RL and 0% nights at RR (Figure 4).

Our continuous plot of RTD with time for the last week of sampling revealed similar diel patterns to the SGLM temporal relationships (Figure 5). Each night at sunset, RTD would rapidly increase until about an hour past sunset (the start of astronomical twilight). Around an hour prior to sunrise (end of astronomical dawn), RTD would rapidly decrease. Our night versus day model also demonstrated that nighttime RTD (0.705 ± 0.069 SE) was significantly greater ($p < 0.001$) than daytime density (0.026 ± 0.002 SE). We identified two break points (360 and 510 min past sunset) in the 0% treatment night, no break points in the 25% treatment night, and one break point (140 min past sunset) during the 100% treatment night (Appendix S2: Tables S5 and S6). During the 25% and 100% treatment nights, RTD continuously decreased and increased, respectively, with two different slopes on the 100% night. During the 0% treatment night, there was a rapid increase of RTD with time between Break points 1 and 2; however, there was no relationship with time prior to or after this period (Figure 5; Appendix S2: Table S6). The time between Break points 1 and 2 also corresponds to the period when we switched bridge lighting from no light to the 25% blue preset, indicating a response of RTD to our within-night light change.

Relative predation risk

Throughout our study, we completed 1471 mPER sampling drifts at the Sundial Bridge. Sampling among river banks, treatments, and weeks was balanced with approximately equal numbers of deployments for each light treatment. Sampling was also concurrent with peak winter-run fry outmigration (Voss, 2021). However, we only recorded four predation events (0.27%). Two of these events occurred upstream of the Sundial Bridge on the same 0% treatment night, and the remaining two occurred under the bridge on a 25% and 100% treatment night (Appendix S2: Figure S4).

DISCUSSION

Artificial illumination is a prevalent pollutant worldwide (Davies & Smyth, 2018; Gaston et al., 2015), and determining and mitigating ALAN impacts on fishes and aquatic ecosystems is essential given the value of these resources (FAO, 2020) and continual human development near water (Davies et al., 2014; Jechow & Hölker, 2019; Zapata et al., 2019). Similar to fish aggregation effects in other ecosystems (Becker et al., 2013; Nelson et al., 2021; Prinslow et al., 1980), Sundial Bridge

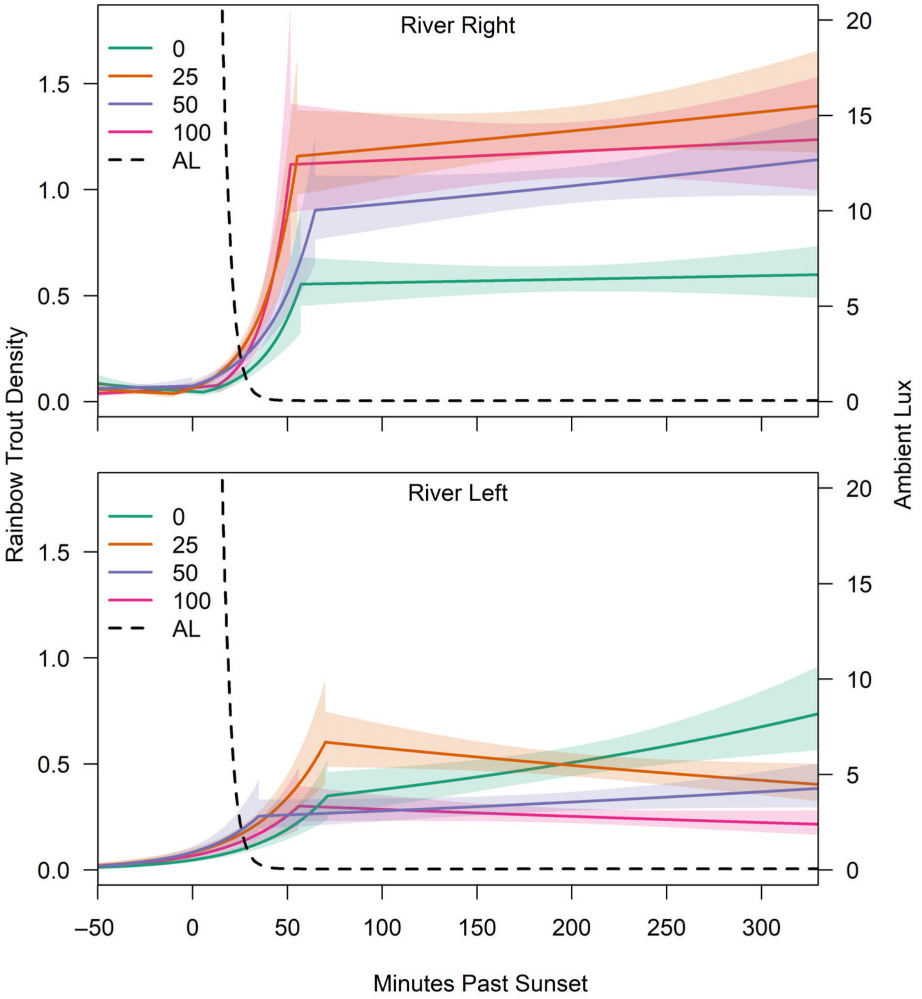

FIGURE 4 The best fitting segmented relationships of relative Rainbow Trout density (±95% CI) with minutes past sunset at river right and river left across artificial light at night treatments (0%, 25%, 50%, and 100% intensity). The dotted black line denotes the relationship of mean (across sampling nights) ambient lux (AL) with minutes past sunset. Confidence intervals for AL were too small to appear on the plot.

ALAN increased the density of large (≥200 mm) Rainbow Trout across all illuminated treatments on RR, indicating that any amount of ALAN may alter RTD. Furthermore, the temporal response of RTD to ALAN demonstrates that ALAN impacts on RR were prevalent as soon as night fell, unlike the temporal trends observed in Nelson et al. (2021). Although RTD increased, salmonid fry predation was almost nonexistent, indicating that while ALAN likely decreases out-migrant survival in other waterways (Nelson et al., 2021; Tabor et al., 2017; Tabor, Brown, & Luiting, 2004), this is probably not the case for the predators, study site, and time frame we investigated here. This mismatch between increased predators and lack of predation can be explained by a preference of Rainbow Trout for invertebrate prey (Johnson et al., 2016; Yard et al., 2011) or differences in Rainbow Trout and juvenile Chinook habitat (Tabor et al., 2014; Tabor, Celedonia, et al., 2004). The response of RTD to ALAN and time of day provides important information for ALAN management plans, sheds light on the complex foraging behavior of Rainbow Trout, and may lead to sublethal consequences on this valuable sport fish.

ALAN has been found to increase the density of predatory fishes across multiple species and ecosystems, likely due to increased foraging and predation success in illuminated areas (Becker et al., 2013; Nelson et al., 2021; Prinslow et al., 1980). Rainbow Trout primarily feed on invertebrates in lotic systems (Jenkins et al., 1970; Rundio & Lindley, 2019; Tippets & Moyle, 1978), which typically drift during the evening and night (Elliott, 1973; Rader, 1997). Since trout reaction distance and prey consumption increases with increased light (Elliott, 2011; Mazur & Beauchamp, 2003), Sundial Bridge ALAN likely allowed trout to extend drift foraging behavior late into the night. Decreased flow on RR likely increased prey capture success and lowered position maintenance energetic costs for Rainbow Trout (Johansen et al., 2020). Assuming that prey supply in the low velocity

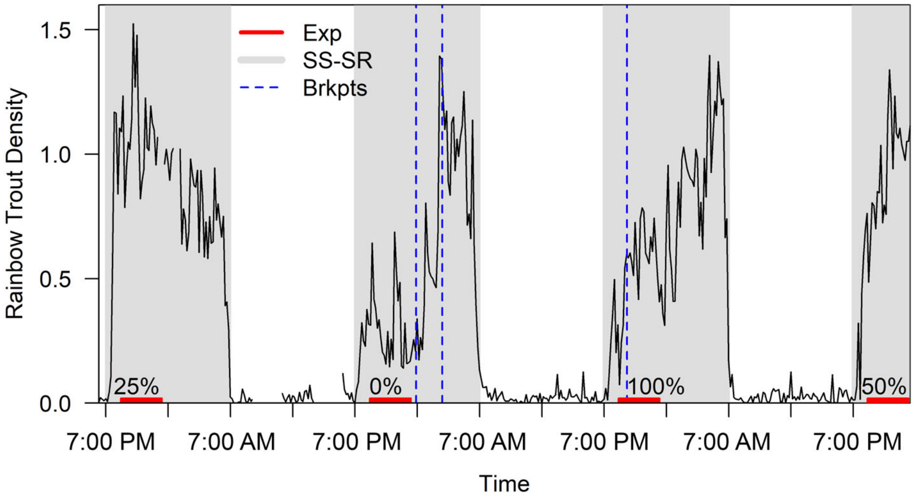

FIGURE 5 Continuous relative Rainbow Trout density during the final week of study. The gray-shaded areas are the period from sunset (SS) to sunrise (SR), the red bars on the *x*-axis indicate our nightly experimental (Exp) period (90–330 min past sunset), and each artificial light at night intensity treatment is indicated above these bars. The dashed blue lines represent significant break points (Brkpts) found in our nighttime segmented analysis.

section was not a constraint on prey intake (Johansen et al., 2020; Piccolo et al., 2014; Rosenfeld et al., 2014) the right riverbank would be an optimum foraging habitat. Therefore, higher quality foraging habitat, coupled with the foraging benefits of ALAN, likely led to greater RTD during illuminated nights on RR. The response of RTD to our ALAN treatments also demonstrates that dimmed ALAN had the same effects as 100% ALAN intensity on Rainbow Trout attraction. While ALAN dimming seems like a prudent management scheme (Davies & Smyth, 2018), removing ALAN altogether may be necessary given our results and the ability of piscivores to effectively forage in low light conditions (Mazur & Beauchamp, 2003, 2006; McMahon & Holanov, 1995).

During twilight, RTD was related to the time of day and is likely a function of invertebrate drift density and relationships of predation success with flow, depth, and light. At both river banks, RTD increased from sunset (the start of civil twilight) until about an hour past sunset (the start of astronomical twilight) and this increase occurred in the presence or absence of ALAN. However, on RR twilight density increases were greater when the bridge was illuminated, indicating a foraging response to ALAN discussed above. Densities also remained elevated above daytime levels throughout nightly experimental periods at both riverbanks. This response could indicate two potential mechanisms. First, Rainbow Trout may be conditioned to foraging benefits of Sundial Bridge ALAN, resulting in a learned behavioral response even in the dark (Dill, 1983). Second, Rainbow Trout could simply move from deep water to river margins during twilight to increase predation success concurrent with peak invertebrate drift (Brittain & Eikeland, 1988; Elliott, 1973; Jenkins et al., 1970). As ambient light decreases, the optimal foraging depth is likely constrained to shallow waters, given that light intensity rapidly attenuates with water depth (Kirk, 2011). Therefore, the swift surface waters in the river channel would be a suboptimum foraging habitat when compared with the lower flow shallower water closer to river margins (Johansen et al., 2020). We observed increased Rainbow Trout feeding and presence in river margins during twilight while hook and line sampling nearby, indicating that the second (ALAN independent) mechanism is plausible, but when ALAN is present this response is amplified. Future work deploying ARIS cameras along other riverbanks and acoustic telemetry monitoring of diurnal versus nocturnal Rainbow Trout presence at the Sundial Bridge could disentangle these mechanisms.

The diurnal versus nocturnal density pattern and the effects of ALAN on RTD at the Sundial Bridge were also apparent in the continuous ARIS sampling on RR. Each night, a large increase in fish density would occur around sunset, followed by a rapid decline around sunrise. The relationships of light, invertebrate drift, river flow velocities, and trout foraging are likely contributing to these patterns. The effects of ALAN on fish density were also present during continuous sampling within the no light treatment night. When we turned the bridge lights back on (after experiment conclusion), fish density rapidly increased from a level that was already above the diurnal baseline. Based on the above evidence, it appears that Rainbow Trout move to river margins at twilight under the Sundial Bridge, remain there until sunrise, and the addition of ALAN in favorable river habitat increases their density and probable invertebrate predation success. These trends indicate that Rainbow Trout instantaneously respond to ALAN once night falls, unlike predators in the Sacramento–San Joaquin Delta (Nelson et al., 2021), complicating the ideal early/late night ALAN trade-off for humans and fishes discussed earlier. Although this instantaneous early night ALAN impact exists, removing light late in the night will likely still provide benefits to prey fishes without adversely impacting much human activity (Bhattacharya & Kaski, 2019; Martín-Olalla, 2018; Monsivais et al., 2017).

With these proposed Rainbow Trout foraging and invertebrate prey preference mechanisms, we assumed that invertebrate prey was prevalent and that ALAN was beneficial to trout foraging; however, attraction could have sublethal effects on Rainbow Trout. Drift and nocturnal foraging by aquatic invertebrates is a strategy that provides refuge from piscine predation that is initiated by low light (Brittain & Eikeland, 1988; Moore et al., 2006). Given that ALAN lowers drift density in other lotic systems (Henn et al., 2014; Perkin et al., 2014), drift density may be diminished under Sundial Bridge illumination. If ALAN attracted Rainbow Trout, and concurrently lowered drift density, this mechanism could lead to adverse competitive interactions. If drift density remained unaffected, but ALAN altered optimal RTD above that supported by the habitat, prey resources, diel feeding patterns, and population resource partitioning, competition may also arise (Railsback et al., 2020). Elsewhere, where ALAN reduced drift density, Cutthroat Trout (*Oncorhynchus clarkii*) condition was unaffected, potentially due to increased foraging success (Perkin et al., 2014). However, Perkin et al. (2014) introduced ALAN to unilluminated streams for 30 nights and continuous exposure, which is typically present at illuminated bridges, may have greater impact. In the absence of competition, Rainbow Trout still maintained position underneath ALAN in this swift flowing river incurring a fitness cost that may not be offset by foraging success (Johansen et al., 2020). Finally, Sundial Bridge ALAN may decrease juvenile Rainbow Trout foraging (Contor & Griffith, 1995), and could potentially alter circadian rhythms and adult spawning behavior (Hernández-León, 2008; Reebs, 2002; Simons et al., 2021). Although these sublethal ALAN impacts are speculative, they have been identified elsewhere (Becker et al., 2013; Contor & Griffith, 1995; Simons et al., 2021) and provide an interesting avenue for future work, given that sublethal consequences may be subtle.

Rainbow Trout preference for invertebrate prey may explain why increased RTD with ALAN did not result in increased fry predation rates. Even when Rainbow Trout and Steelhead are piscivorous in lotic systems, the majority of their diet typically remains invertebrates (Johnson et al., 2016; Yard et al., 2011). Furthermore, much of this piscivory has been identified in hatchery-reared Steelhead (Hawkins & Tipping, 1999; Johnson et al., 2016; but see Beauchamp, 1995) and the occurrence of juvenile Chinook Salmon in the diet of either *O. mykiss* form is uncommon in lotic systems (Hawkins & Tipping, 1999; Tabor et al., 2014; Tabor, Celedonia, et al., 2004). Given that our study system consists of wild resident Rainbow Trout and winter-run Chinook fry, it is unlikely that fry predation is prevalent. This lack of Rainbow Trout piscviory in the Upper Sacramento is further supported by several additional lines of evidence. (1) Early observations from the Sacramento River found no fry in 700 trout diets (Rutter, 1902). (2) We did not find any fry in a previous Rainbow Trout diet study in Redding, CA (Demetras et al., 2013). (3) While salmon egg predation has been routinely observed during snorkel surveys by regional salmon biologists, fry predation has not (D. Killam, CDFW, personal communication, 2020). (4) Local anglers who routinely investigate trout diets, through stomach content investigation, do not encounter salmonid fry, nor do they frequently catch Rainbow Trout on fry imitation lures (A. Carruesco, AC Fly Fishing, and K. Portocarrero, SacRiverGuide, personal communication, 2020). In this river with high flow velocity, it is likely that Rainbow Trout prefer drifting invertebrates and do not need to expend energy to consume piscine prey.

Differences in winter-run fry and adult Rainbow Trout habitat may further explain the lack of piscviory and has implications for future ALAN predation work. In Washington, age 0 Coho Salmon (*Oncorhynchus kisutch*) occupy low velocity waters, while older Steelhead inhabit deeper swifter portions of the river (Bisson et al., 1988). Given that Chinook Salmon fry also inhabit shallow low velocity waters, nonoverlapping habitat use likely led to low consumption of Chinook Salmon fry by Rainbow Trout in Cedar River, WA (Tabor et al., 2014; Tabor, Celedonia, et al., 2004). While mPER drifts placed tethered fry in Rainbow Trout nocturnal habitat (2–3 m), we observed winter-run fry along riverbanks in very shallow water (<0.3 m), indicating potential differences in habitat use of these fishes. This mismatch may have led Rainbow Trout to not cue on tethered fry during nocturnal foraging, contributing to the lack of predation we recorded. In this shallow water, we also observed Scuplin (*Cottus* sp.) whose consumption rates of salmonid fry increase under ALAN (Tabor, Brown, & Luiting, 2004). Future work should test riverbank predation rates with tethering experiments to determine whether predation is impacted by ALAN in this habitat.

As with any field study, there were some important considerations and additional room for future work. While predation event recorders do not measure absolute predation in an ecosystem, they do provide a relative predation rate index and have been successfully used in several studies as an improvement over fixed tethering (Demetras et al., 2016; Michel et al., 2020; Nelson et al., 2021). The novel mPER devices we developed for this project have also proven successful with *Micropterus* species in the Sacramento–San Joaquin Delta (see *Methods*), but were untested on Rainbow Trout prior to this experiment. Although we matched common trout angling practices, further mPER testing with this species in slow moving clear waters where video and ARIS footage could be recorded is warranted. Further testing on confirmed piscivorous Rainbow Trout populations would also help decouple potential methodological and behavioral confounding. However, we do not believe that tethering strongly biased our results, because predation was almost nonexistent and predation rates are expected to be higher on tethered prey that cannot avoid capture (Peterson & Black, 1994). Although beyond the scope of our study, the Sundial Bridge provides an excellent field laboratory to investigate how fishes may respond to variable ALAN spectrums, given the available full visible spectrum color potential. While Tabor et al. (2021) found no difference among light spectrums with regards to juvenile salmon attraction, future studies at the Sundial Bridge similar to our design could build upon this work to include larger-bodied fishes and more light colors. Although Rainbow Trout piscivory is likely uncommon in this system, an in-depth Rainbow Trout diet study is needed. Extensive visual diet surveys coupled with molecular techniques will ensure that any digested or unobservable winter-run prey are identified (e.g., Michel et al., 2018). With this molecular approach, care should be taken to decouple winter-run egg and fry predation and should wait until after estimated hatch dates. Finally, we did not assess ALAN impacts on winter-run fry beyond predation risk; future studies could focus on attraction and slowed migration speed with studies aimed at determining whether more fry are present underneath the bridge on illuminated nights (e.g., Celedonia et al., 2011; Tabor et al., 2017; Tabor, Brown, & Luiting, 2004).

In conclusion, the lack of predation events at the Sundial Bridge indicates that ALAN is unlikely to have population-level impacts on winter-run fry survival at this location, given the probable lack of Rainbow Trout piscivory and potential predator–prey habitat mismatch. However, ALAN may be an important driver of predation risk during other seasons or locations where predator communities and environmental conditions are different (Nelson et al., 2021; Tabor et al., 2017; Tabor, Brown, & Luiting, 2004). For example, in the Upper Sacramento River near Red Bluff, more Striped Bass are present in the spring (M. Johnson, CDFW, personal communication, 2020). Similarly, our study does not preclude the possibility that ALAN in downstream portions of the Sacramento River may be an important driver of predation (e.g., Nelson et al., 2021) and investigations should continue. Rainbow Trout attraction to ALAN provides another example of how this anthropogenic stressor may alter the ecological functioning of aquatic systems: essential knowledge for mitigating the impacts of abundant and increasing light pollution within aquatic environments (Davies et al., 2014; Jechow & Hölker, 2019; Zapata et al., 2019). Furthermore, the discrepancies among riverbanks demonstrate that ALAN impacts are complex and intertwined with other environmental parameters, which in this case were likely river depth and flow. This attraction across all light intensities, the instantaneous response of RTD to diminishing ambient light, and the low light foraging threshold for many species (Mazur & Beauchamp, 2003, 2006; McMahon & Holanov, 1995), indicates that complete removal is necessary to alleviate ecological consequences of ALAN. When full reduction is not plausible, ALAN should be diminished to the lowest intensity necessary and turned off at the earliest time possible to minimize impacts, while maintaining safety, economic, and recreational benefits.

AUTHOR CONTRIBUTIONS

T. Reid Nelson and Cyril J. Michel designed the experiment, T. Reid Nelson and Nicholas J. Demetras designed and built the mPERs, T. Reid Nelson, Cyril J. Michel, Meagan P. Gary, Brendan M. Lehman, Nicholas J. Demetras, Jeremy J. Hammen, and Michael J. Horn completed the experiment. Michael J. Horn completed the ARIS data reduction, and Peter N. Dudley developed and implemented the 2D hydraulic model. T. Reid Nelson analyzed the data and wrote the manuscript draft, while all remaining authors contributed their comments, edits, and suggestions, which were implemented in the final manuscript.

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CONFLICT OF INTEREST

There is no conflict of interest declared in this article.

DATA AVAILABILITY STATEMENT

Data and analysis code (Nelson, 2022) are available from the Open Science Framework: https://doi.org/10.17605/OSF.IO/YFAH3.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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