DR. THOMAS REID NELSON (Orcid ID : 0000-0002-7960-2084)

DR. JEREMY HAMMEN (Orcid ID : 0000-0002-9000-6283)

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Effects of artificial lighting at night (ALAN) on predator density and salmonid predation

T. Reid Nelson[1*], Cyril J. Michel[1], Meagan P. Gary[1], Brendan M. Lehman[1], Nicholas J. Demetras[1], Jeremy J. Hammen[2], Michael J. Horn[2]

University of California Santa Cruz, Institute of Marine Sciences, affiliated with the National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Science Center, 110 McAllister Way, Santa Cruz, California 95060, USA[1]

Fisheries and Wildlife Resources Group, United States Bureau of Reclamation, USBR 86-68290, Denver, CO 80225-0007.[2]

*Corresponding author:** thomas.nelson@noaa.gov, ORCID: 0000-0002-7960-2084, (336) 817 - 8846

Running head: ALAN impacts predator density and salmon predation

[A]Abstract

Predation of juvenile salmonids within California's Sacramento – San Joaquin Delta (the Delta) has been identified as a contributing factor to low survival during outmigration through the system. Artificial lighting at night (ALAN) may contribute to increased levels of salmonid predation by attracting predators and prey, increasing predator reaction distance, and foraging success. To assess ALAN effects on predator (piscivorous fishes) density and the relative predation risk of Chinook Salmon *Oncorhynchus tshawytscha* smolts in the Delta, we preformed field based experiments with introduced ALAN. We used ARIS (Adaptive Resolution Imaging Sonar) cameras to generate predator density estimates in light and dark treatments throughout nightly experiments at 30 minute intervals. We simultaneously deployed predation event recorders (PERs) to estimate the impact of ALAN intensity (lux) on relative predation risk of Chinook Salmon smolts. Early in the night (1-3 hours past sunset), predator density and relative predation risk of smolts was unrelated to ALAN. However, late in the night (3-5 hours past sunset) ALAN presence increased predator density and the relative predation risk of juvenile salmonids increased with increasing lux. Predation risk was also positively related to predator density, and increased late-night predator density under ALAN, coupled with late-night foraging benefits of ALAN, likely contributed to the lux risk relationship. The exact mechanism behind this discrepancy between early and late-night trends is unknown and could be a result of our experimental design or the predator community sampled here. However, if these temporal trends prove robust to future investigations, late-night lighting reduction campaigns during outmigration, could maximize the human benefits of ALAN, while minimizing the negative impacts on salmonids. Overall, our findings align

with others and suggest that ALAN increases juvenile salmonid predation. Although many questions remain unanswered, it appears that reducing artificial illumination is a practical management strategy to reduce predation.

[A]Introduction

The diel light cycle is a driving force of animal behavior and ecological interactions (Navara and Nelson 2007; Hölker et al. 2010a; Hölker et al. 2010b). However, the abundance and projected increase of artificial lighting at night (ALAN) disrupts ecological processes across a wide range of taxa (Gaston et al. 2013; Gaston et al. 2014a; Zapata et al. 2019). ALAN affects animal migration and orientation, foraging and predation, reproduction, and even human health (Navara and Nelson 2007). Although ALAN impacts in terrestrial ecosystems are apparent, ALAN also affects aquatic environments, given that many urban areas are near coastlines, estuaries, and freshwater shorelines (Davies et al. 2014; Jechow and Hölker 2019; Zapata et al. 2019). The presence of ALAN in aquatic environments attracts prey species and piscivorous fishes (Becker et al. 2013; Lehman et al. 2019), increases the foraging efficiency and predatory behavior of fishes (Bolton et al. 2017), and increases the reaction distance and prey consumption rate of fishes (Vogel and Beauchamp 1999; Mazur and Beauchamp 2003; Mazur and Beauchamp 2006). Therefore, ALAN in the aquatic environment may increase piscivorous fish predation rates and negatively impact prey survival.

Juvenile salmonids face a gauntlet of potential predators as they migrate from freshwater to marine environments (Poe et al. 1991; Rieman et al. 1991; Osterback et al. 2013). Predation risk is exacerbated in clear waters (Gregory and Levings 1998) and out migrating salmonids employ nocturnal migrations as one strategy to minimize this risk (Chapman et al. 2013; Clark et al. 2016; Furey et al. 2016). However, in many ecosystems, salmonid outmigration traverses anthropogenically altered habitat and urban centers (Michel et al. 2013; Michel et al. 2015; Schroeder et al. 2015), likely leading to increased ALAN exposure (Jechow and Hölker 2019; Zapata et al. 2019). Given that ALAN aggregates and slows out migrating salmon, attracts predators (including fishes, birds, and mammals), and increases piscivore consumption of salmonids (Yurk and Trites 2000; Tabor et al. 2004; Celedonia et al. 2011; Tabor et al. 2017), increased migratory ALAN exposure likely increases juvenile salmonid predation risk and mortality.

The Sacramento-San Joaquin River Delta (the Delta) is a heavily modified tidal freshwater system consisting of large interconnected waterways that drain the Central Valley of California (Monsen et al. 2007;

Lehman et al. 2019). The Delta provides water for irrigation and municipalities across a large portion of the state and habitat for threatened and endangered fish species (Ingebritsen et al. 2000; Mount and Twiss 2005; Williams 2006). Four runs of Chinook Salmon *Oncorhynchus tshawytscha* (winter, spring, fall, and late-fall) and steelhead *Oncorhynchus mykiss* must pass through the Delta during both juvenile and spawning migrations (Williams 2006). Populations of these salmonids have drastically declined over the past century and poor juvenile survival is a contributing factor (Yoshiyama et al. 1998; Williams 2006; Lindley et al. 2009). Current survival estimates of out migrating juvenile Chinook Salmon, or smolts, through the Delta are as low as 5% (Buchanan et al. 2018; Buchanan et al. 2013) and are likely affected by predation from non-native fishes (Buchanan et al. 2018; Grossman 2016; Michel et al. 2018).

Management strategies that minimize out migrant mortality are needed to rebuild salmonid populations. Decreasing the interaction of juvenile salmonids and their predators may be a way to lower predation induced mortality. Removing anthropogenic contact and aggregation points between predators and prey is likely one way to decrease these interactions (Lehman et al. 2019). Major metropolitan areas located throughout the Delta (e.g., Sacramento, Stockton, and Antioch, CA), and elsewhere along rivers of the California Central Valley, likely produce an abundance of ALAN, and ALAN has been identified as a prevalent predator-prey contact point (Lehman et al. 2019). Therefore, we investigated whether ALAN affected piscivorous fish (predator) density and the relative predation risk of Chinook Salmon smolts in the Delta. This study was an important first step in determining if ALAN removal or intensity reduction may be a viable management strategy to help lower predation mortality in the Delta and other waterways.

[A]Methods

[C]*Study System*. — Prior to ocean entry, all out migrating Central Valley Chinook Salmon pass through the heavily modified Delta and San Francisco estuary (Nichols et al. 1986), typically in the spring (Williams 2006). During outmigration, nocturnal movements are preferred in all river reaches except the estuary (Chapman et al. 2013) and migration speed is slowest in the Delta (Michel et al. 2013). Salmon released in the Sacramento River take on average 12.4 days to reach the Delta and 13.2 days to migrate from the Delta to the ocean (Michel et al. 2013). Most Delta land is below water level, waterways are channelized and leveed, and riprap covers 73% of mainstream shorelines (Ingebritsen et al. 2000; Mount and Twiss 2005; Lehman et al. 2019). Invasive fishes and vegetation are prevalent in the Delta (Underwood et al. 2006; Brown

et al. 2007) and may contribute to poor survival of out migrating salmonids (Grossman 2016; Michel et al. 2018; Zeug et al. 2020).

Delta piscivores consist of fishes, birds, and mammals. Piscivorous fishes that may consume juvenile salmonids are dominated by invasive species, including Striped Bass *Morone saxatilis*, Largemouth Bass *Micropterus salmoides*, other black basses (*Micropterus* spp.), sunfish (*Lepomis* and *Pomoxis* spp.), and catfish (Ictaluridae) (Grossman 2016; Michel et al. 2018). The Sacramento Pikeminnow *Ptychocheilus grandis* is the only significant native piscivorous fish in this system (Brown and Moyle 1981). Avian and mammalian piscivory within the Delta is poorly studied (Grossman 2016). However, avian salmonid predation occurs in San Francisco Bay (Evans et al. 2011; Adrean et al. 2012; Riensche et al. 2012), and piscivorous aves that occur in the Delta (e.g. terns, gulls, cormorants, and herons), depredate salmonids elsewhere (Osterback et al. 2013; Evans et al. 2016; Sherker 2020). Mammalian (e.g. river otters, harbor seals, and sea lions) depredation of juvenile salmonids also occurs in other ecosystems (Dolloff 1993; Yurk and Trites 2000; Chasco et al. 2017) and is possible in the Delta.

[C]*Experimental design*.— We conducted our study during spring 2019 (April 22, 2019 - June 7, 2019) at five sites in the Western Sacramento-San Joaquin River Delta (Figure 1). For each of the first two study weeks, predation experiments occurred on four consecutive nights within a single site (L3, L4, Figure 1). We randomly chose the light location within experimental reaches (upstream or downstream) without replacement to ensure that both locations were equally represented each week. After the first two weeks, we found an insignificant effect of light location on relative predation risk with a Cox proportional hazards model (p = 0.69, Cox 1972). Therefore, we only visited new experimental sites on two consecutive nights and we randomly selected the single light location before experiments began. Experiments occurred at three more sites (L6, L7, L8, Figure 1) using this design; however, predation at these sites was almost nonexistent (mean 2% predation). Therefore, we revisited the second site (L4) over two more weeks, and employed the two night experiment once each week.

We delineated our experimental reaches within each site with floating lines, measuring 200m in length (along-shore), and 25-50m in width (perpendicular to shore). All reaches had riprapped shorelines, and we defined within reach treatments as the 100m upstream and downstream sections of the reach. We mounted the artificial light source on a 4m pole and placed it at the waterline halfway within the upstream (50m into reach) or downstream (150m into reach) portion of the reach, depending on the experimental

treatment. The light source was two LED floodlights, which emitted 20,000 lux, and was oriented parallel with the waterline (Figure 2).

To assess the relationship of ALAN intensity with the relative predation risk of juvenile salmon, we used predation event recorders (PERs, Demetras et al. 2016). Each PER was an independent drifting GPS enabled platform baited with a tethered hatchery-origin live Chinook Salmon smolt (87mm ± 0.01 SE mean Total Length [TL]) at 1 m depth. To tether each smolt, we looped fluorocarbon fishing line through their mouth and operculum. We attached this tether to a magnet that initiated a timer when it was pulled by a predation event (event time). To determine the exact location and time of predation events, we subtracted event time from deployment end time. On average, we had 82 (± 3.6 SE) PER deployments each night that typically began one hour after sunset and continued for four hours. To ensure that PERs traversed both light and dark treatments, we deployed PERs at the reach end where tidal flow carried them through the entire reach and spread them along the width of this end. When PERS reached the opposite end of the 200 m reach, they were collected and returned to the starting point. Before redeployment, we ensured that each PER had an active tethered smolt in good condition and used smolts 2-3 times, when no predation occurred.

Predation event recorders do not provide an estimation of absolute predation rates as tethered prey are less able to evade capture. However, PERs provide a cost-effective method to investigate drivers of predation and predator response that would be difficult to detect otherwise (Demetras et al. 2016; Michel et al. 2020a; Michel et al. 2020b). Our PERs were slightly modified versions of those described in detail in Demetras et al. (2016). Specifically, we constructed PERs with 5.08 cm diameter clear PVC pipe with the majority of components (GPS, timer, reed switch) contained within the PVC housing and sealed with a rubber end cap. Given the PERs' ability to capture precise predation locations and times, we were able to associate ALAN intensity (lux) with each observed predation event.

To compare predator density among light and dark treatments, we deployed ARIS (Adaptive Resolution Imaging Sonar, Sound Metrics Corp.) cameras in experimental reaches at 50 and 150m (Figure 2). We positioned ARIS cameras at approximately 2 m depth, with one ARIS located directly offshore of the light source (light treatment) and the other 100m distant (dark treatment). Cameras continuously recorded from the start of PER deployments to the end, with a viewing window of 2 to 10 m, a -1° pitch, and a lens heading perpendicular to the reach length. In addition to among treatment comparisons, ARIS cameras provided predator density data that we incorporated into our predation risk models.

[C]*Light surveys.*—After all PERs were retrieved, we surveyed surface light intensity (lux) within experimental reaches from a motorized vessel using an ILT2400 optometer. We performed survey transects at the inside floating line, the middle of the reach, and the outside line. We measured light attenuation with depth directly parallel to the light source at the nearshore and offshore limits of the study site. Starting at the surface, we lowered the optometer at 0.5 meter intervals until the bottom or 4 meters was reached and held it for 1 minute at each unique depth to record a mean lux value. To account for variation with distance from the light source and inherent variability among nights, we standardized lux at depth by dividing the value at each depth by the surface value from each cast. This value was light attenuation (*At*) and we fit the following exponential decay equation

$$At = e^{[\,-(kd \,*\, depth \,+\, kt \,*\, turb)]},$$

where *kd* (attenuation with depth) and *kt* (attenuation with turbidity [*turb*]) were fit with both coefficients or only *kd*. The model of best fit had a corrected Akaike Information Criterion (AICc, -467.772) within 2 units of the model with the lowest AICc (-469.411) and included the fewest parameters, *kd* (1.279) and depth.

We interpolated lux across experimental reaches using the R function autoKrige (Hiemstra et al. 2008) and assigned each PER GPS position a lux value at the water surface and at depth. This function generated an exponential variogram (we fixed this model type within the function) from each survey and used weighted least squares to select the best fitting values of nugget, range, and sill. Using this model, we interpolated water surface lux over a 500,000 cell grid, which resulted in smooth, fine-scale lux values across experimental reaches for each night (Figure 3). We assigned interpolated surface lux values to each PER GPS position and used the above attenuation model to predict lux at 1 m depth; the approximate depth where tethered smolts drifted. If any PERs drifted outside of the survey bounds, we assigned the lux value from the nearest grid cell. Our lux meter malfunctioned during the second night of sampling at L7, so this night was removed from PER predation risk analysis.

[C]*ARIS data reduction and processing.*—To post-process ARIS footage, we used Echoview version 10.2. This software removed background data and excess noise, and identified all fish or fish-like objects (targets) ≥ 200 mm in the ARIS footage (Boswell et al. 2008). We then manually reviewed each fish-like object and removed all non-fish before analysis. Although both ARIS cameras were deployed with similar settings each night, frame rate differed between and within cameras, given inherent processing speed differences between computers throughout sampling nights. To account for differing frame rate and instances of Echoview assigning multiple unique identifiers to the same fish (double counting), we used fish density

instead of fish counts for analysis. To calculate fish density, we exported total beam sampling volume and the total number of fish pings in 30 minute increments from each ARIS (light, dark ALAN treatments) on each experimental night. We then divided the number of fish pings by beam volume within the corresponding 30 minute time frame, to obtain fish per m^3 for each 30 minutes of sampling within each treatment on a given night. The number of fish pings and beam volume within a given time frame are inherently tied to frame rate. For example, ARIS A has a frame rate of 4 frames/second and ARIS B has a frame rate of 8 frames/second and each ARIS samples 4 m^3 each frame. Assuming that one fish is continually present on both ARIS A and B for an entire 30 minute window, ARIS A would sample 28,800 m^3 and have 7,200 fish pings in 30 minutes, and ARIS B would sample 57,600 m^3 with 14,400 fish pings. The resulting 30 minute fish density for both hypothetical ARIS cameras would be 0.25 fish m^{-3} 30min^{-1}. The ARIS in the light treatment malfunctioned during the sixth night of sampling at L4 and density data was not recorded for this night, therefore it was censored from all statistical analyses. Although we do not know large fish species, it is likely that these fishes are mainly piscivores (see Discussion), and fish density will be referred to hereafter as predator density.

[C]*Statistical analysis*.—To determine if ALAN altered predator density and if predator density was related to time of night, we analyzed ARIS data with a generalized linear mixed-effects model (GLMM) using the lme4 package in R (Bates et al. 2015; R Core Team 2019). We fit the GLMM using the Gamma family and a log link, given that the data distribution of 30 min predator density was non-normal and non-negative. To remove the few zeros in the dataset (n = 13, 5.75% of data) and allow the Gamma model to run, we added 1 x 10^{-9} to all density measurements before GLM analysis. We included ALAN treatment, minutes past sunset (30 minute bin increments 1-8), and the interaction of ALAN and minutes past sunset as independent variables in the GLMM. To account for potential differences in baseline predator density among sampling nights and the fact that each ALAN treatment was resampled throughout each night, we included a random effect of sampling night in the GLMM. To investigate the interaction of minutes past sunset and ALAN on predator density, we split the data into early (1-3 hours past sunset) and late-night (3-5 hours past sunset) subsets and ran GLMMs without the interaction term.

To assess whether the relative predation risk of Chinook Salmon smolts was related to lux, time of night, and predator density, we evaluated Cox proportional hazards models with the R function coxph (Cox 1972; Therneau 2015). We included lux, minutes past sunset, mean 30 minute predator density among light and dark treatments throughout experimental nights, and the interaction of lux and minutes past sunset as independent variables. To investigate the interaction of minutes past sunset and lux, we split the data into

early (1-3 hours past sunset) and late-night (3-5 hours past sunset) subsets and ran Cox models without the interaction term. We checked proportional hazards assumptions of Cox models using the cox.zph function in R (Therneau 2015). Although lux at depth was predicted from surface lux, we evaluated another set of Cox models using this variable instead of surface lux to demonstrate how predation risk responded to changes in lux at depth. To investigate the relative effect on predation risk of each variable, we also ran the Cox models using scaled (independent) variables. Neither of these approaches changed overall model fits or significance; however, they provided further insight that we might have missed in original model output.

[A]Results

We found that predator density was positively related to ALAN presence late in the night. When we analyzed all density data, the effects of minutes past sunset and ALAN presence on predator density were non-significant; however, a significant interaction between these two variables was present (Table 1). In the early-night model (1-3 hours past sunset), neither minutes past sunset or ALAN presence had a significant relationship with predator density. While in the late-night model (3-5 hours past sunset), predator density was predicted to increase by a factor of 3.96 in the presence of ALAN (Figure 4A) and no relationship of minutes past sunset was detected (Table 1). This difference in the ALAN effect between early and late-night models demonstrates why the interaction of ALAN and minutes past sunset was significant in the overall model.

Relative predation risk of Chinook Salmon smolts increased with artificial illumination intensity (lux) late in the night and was positively related to predator density in all models (Figures 3, 4B, and 5). In the full night model, relative predation risk had a positive relationship with predator density, a negative relationship with minutes past sunset, and a positive relationship with the interaction of minutes past sunset and lux. However, no overall relationship of relative predation risk with lux was detected (Table 2). Neither minutes past sunset or lux was significantly related to predation risk in the early-night model (1-3 hours past sunset), but the positive relationship with predator density remained. In the late-night model (3-5 hours past sunset), relative predation risk was predicted to increase by factors of 1.030 (scaled factor = 1.217) and 1.502×10^{19} (scaled factor = 1.987) for each unit increase in lux and predator density, respectively, and no significant effect of minutes past sunset was detected (Table 2, Figure 5). For each unit increase of lux at 1m depth in the late-night model, the raw factor change was greater (1.111). However, this increase was because lux at depth only varied from 0 - 20, while lux at the surface varied from 0 - 72 (Table 2). Similar to the predator density

models, the significant interaction of lux and minutes past sunset in the overall model was the result of a significant effect of lux late in the night with no effect early in the night on relative predation risk.

[A]Discussion

With continuing human development along rivers, estuaries and coastlines, it will be increasingly important to consider the impacts of artificial lighting at night (ALAN) on aquatic organisms and ecosystems (Davies et al. 2014; Jechow and Hölker 2019; Zapata et al. 2019). Elsewhere, ALAN has attracted young salmonids and their predators, resulting in elevated predation rates (Tabor et. al 2004; Tabor et. al 2017). Similarly, introduced ALAN in the Delta increased predator density and relative predation risk of Chinook salmon smolts; however, these effects were only detected three hours past sunset and later. These results indicate that ALAN reduction may decrease predation rates and mortality of out migrating salmonids in the Delta and are an important first step in assessing ALAN impacts along outmigration routes in the California Central Valley and elsewhere.

As with any field experiment, there were notable environmental limitations and assumptions associated with our study. First and foremost, our metric of relative predation risk focused only on predators and does not take into account any prey effects, given that we used tethered smolts. Nonetheless, the PER technique has been used to investigate environmental drivers of predation (Demetras et al. 2016; Michel et al. 2020a; Michel et al. 2020b) and the drifting PER tether likely mimics natural prey behavior better than traditional fixed tethering experiments. Given this tethering limitation and the focus on predators, future research should determine how ALAN affects free swimming out migrating smolts. Detailed analysis of past, current, and future smolt telemetry data comparing migration speed, timing, and mortality in illuminated and dark-river reaches (e.g. Celedonia et. al. 2011), is one way to elucidate these ALAN effects. Field experiments where free swimming acoustically tagged smolts are released under artificially illuminated and dark conditions coupled with a high resolution telemetry array, could also be used to determine if ALAN affects smolt movement and migration. Artificial illumination may reduce migration speed and survival, because Salmon outmigration is predominately nocturnal (Chapman et al. 2013; Clark et al. 2016; Furey et al. 2016) and ALAN attracts and slows juvenile Salmon (Tabor et al. 2004; Celedonia et al. 2011; Riley et al. 2013; Tabor et al. 2017). This attraction may bring salmonids closer to shore exposing them to mammalian (e.g. river otters, Dolloff 1993) and avian piscivores (e.g. herons, Sherker 2000), as well as benthic (e.g. Sculpin and Catfish) and vegetation associated (e.g. Largemouth Bass) piscivorous fishes (Michel et al. 2018; Michel et al.

2020a). If ALAN sufficiently slows outmigration, increased water temperatures, low river flows, and prolonged exposure to predators along the outmigration corridor could also reduce salmonid survival (Henderson et al. 2019; Michel et al. 2020a). Although our study found a response of predators to ALAN, future investigations focused on prey responses will help elucidate if ALAN reduction is a viable restoration strategy.

While we were not able to identify the large fishes used for predator density calculations to species, it is likely that many were piscivores, given the positive relationship between density and relative predation risk. Furthermore, we conducted opportunistic hook and line sampling on a few occasions prior to nightly experiments, and both Largemouth Bass *Micropterus salmoides* and Striped Bass *Morone saxatilis* were caught and released at site L4. These species are common predators of salmonid smolts in the Delta (Sabal et al. 2016; Michel et al. 2018) and were likely a major component of the predator community in this study. Because this study was conducted at night, we could not use traditional video recordings to identify PER predators. Coupling underwater infrared light sources with traditional video (Mazur and Beauchamp 2003) may aid in nighttime predator community identification without introducing additional light in the visible spectrum (Jordan and Howe 2007; Horodysky et al. 2010; Mitchem et al. 2018). However, sampling area of traditional video would likely be less than our ARIS cameras and would be problematic in turbid waters. Combining ARIS with this infrared assisted video analysis could be advantageous for low light predator density and community analysis. Our predator density metric also did not differentiate between individual fish remaining under the light source or new individuals being attracted to the light, distinctions that are potentially important, but are pooled in our analysis. Future work should investigate differences in fish behavior in dark and illuminated treatments to determine how ALAN may change the behavioral response of fishes.

Predator density was greater in ALAN treatments and relative predation risk of Chinook Salmon smolts increased with increasing ALAN intensity (lux) three hours past sunset and later. However, no ALAN impacts on density or predation risk were detected early in the night. These discrepancies may be driven by ambient light levels and the relationship of predation success with light. Foraging efficiency and predation success of piscivorous fishes increases with increasing light levels, but fish can also successfully forage in low light (McMahon and Holanov 1995; Mazur and Beauchamp 2003; Mazur and Beauchamp 2006). Mazur and Beauchamp (2003) suggested that salmonids have a foraging threshold around 1 lux, with success continually increasing until it asymptotes around 20 lux. However, for Largemouth Bass this threshold could be as low as ambient moon light (0.003 lux, McMahon and Holanov 1995). Early in experimental nights, ambient light

levels may have been sufficient for successful foraging and depredation throughout experimental reaches, resulting in similar predator densities and predation risk throughout the reach. After three hours past sunset, an ambient light foraging threshold may have been reached where predation success was diminished in unilluminated reach sections. The additional light provided by ALAN likely allowed for continued unimpeded predation success in illuminated portions of the reach. This increased success likely led to greater predator density in ALAN treatments and increased predation risk with increasing lux late in the night. Therefore, the overall decrease in predation risk with elapsed minutes past sunset may be explained by decreasing successful foraging area with time.

The late-night relationship of elevated predation risk with increasing lux was also likely driven by increased predator density in ALAN treatments, given that predation risk was positively correlated with predator density in all models. The increased foraging success of predators in ALAN would have also contributed to the elevated predation risk with lux. However, decoupling these two drivers was not possible in our experiment. To elucidate foraging thresholds and quantify the effects of ambient illumination on predation risk, future studies should deploy a light meter throughout the night to monitor background illumination.

The lack of ALAN effects on predation early in the night could also be a result of the predator community we sampled and our experimental lights. As mentioned above, predation risk in our study was higher earlier in the night, but ALAN did not affect density or predation risk during this time. Assuming that the majority of our predators were roving channel associated fishes (e.g. Striped Bass), it may have taken time for them to cue into the light, which we established each night. If our light was a permanent fixture, perhaps fishes and other piscivores would have established nocturnal feeding habits under this fixture early in the night. For example, harbor seals that fed on out migrating salmonids under an illuminated bridge, were most abundant 1 - 1.5 h after nightfall and decreased as the night progressed (Yurk and Trites 2000). It is also possible that our experimental ALAN attracted prey fishes, which in turn attracted predators (Becker et al. 2013), but this mechanism took time to establish. Future studies could replicate our experiment at existing artificial illumination sources to see if the delayed ALAN effect exists at established light sources across variable predator communities. ARIS footage could also be recorded continuously at illuminated and unilluminated sites to determine how light impacts prey and predator density on a 24 hour cycle (e.g. Becker et al. 2011).

Another pertinent direction for future research that would benefit ALAN management is to determine a minimum lux value that does not impact fishes. Our experiment did not empirically test variable lux intensity; however, we did sample a large range of lux values that may provide insight into predator response. If we fit a penalized spline to the lux predictor in our late-night Cox model, predation risk does not increase until after 8 lux is reached. A similar trend can be seen in the top right panel of Figure 2, with greater increases in predation percentage after 10 lux. However, we did not use this spline in our final model, given that the linear fit was much better (ΔAIC_c = 12.33), so this value should be interpreted with caution. Additionally, this minimum value may only be relevant to the system and predator community studied here. Previous work has suggested ALAN intensities should remain as low as possible (< 0.1 lux) to mitigate impacts on salmonids during outmigration (Tabor et al. 2004; Tabor et al. 2017). To determine a minimum lux management goal, future experimental tests of ALAN intensity with variable treatments among experimental nights are needed.

The discrepancies between early and late-night ALAN effects on predator density and predation risk could prove useful for ALAN management. For humans, artificial illumination is one of the building blocks of modern society and many social, recreational, and economic benefits result from ALAN (Doll et al. 2006; Hölker et al. 2010a; Gaston et al. 2014b). However, human activity is still highest during the day and early hours of the night, decreasing as the night progresses (Monsivais et al. 2017; Martín-Olalla 2018; Bhattacharya and Kaski 2019). Our results suggest that ALAN effects on predator density and predation may be minimal early in the night, but this trend could be driven by our experimental light design and predator community. If these temporal trends prove robust to future investigations, late-night lighting reduction campaigns during outmigration could maximize the human benefits of artificial illumination, while minimizing the negative impacts on out migrating salmonids. Overall, our findings align with others and suggest that ALAN increases juvenile salmonid predation (Tabor et al. 2004; Tabor et al. 2017). Although many questions remain unanswered, it appears that reducing artificial illumination is a practical management strategy to reduce predation on out migrating salmonids.

[A]Acknowledgements

[A]References

Adrean, L. J., D. D. Roby, D. E. Lyons, K. Collis, and A. F. Evans. 2012. Potential Effects of Management on Caspian Tern Hydroprogne caspia Predation on Juvenile Salmonids at a Colony in San Francisco Bay, California. Transactions of the American Fisheries Society 141(6):1682-1696.

Bates, D., M. Maechler, B. Bolker, S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Becker, A., A. K. Whitfield, P. D. Cowley, J. Järnegren, T. F. Naesje, and E. Crispo. 2013. Potential effects of artificial light associated with anthropogenic infrastructure on the abundance and foraging behaviour of estuary-associated fishes. Journal of Applied Ecology 50(1):43-50.

Bhattacharya, K., and K. Kaski. 2019. Social physics: uncovering human behaviour from communication. Advances in Physics: X 4(1):1527723.

Bolton, D., M. Mayer-Pinto, G. F. Clark, K. A. Dafforn, W. A. Brassil, A. Becker, and E. L. Johnston. 2017. Coastal urban lighting has ecological consequences for multiple trophic levels under the sea. Science of The Total Environment 576:1-9.

Boswell, K. M., M. P. Wilson, and J. H. Cowan Jr. 2008. A Semiautomated Approach to Estimating Fish Size, Abundance, and Behavior from Dual-Frequency Identification Sonar (DIDSON) Data. North American Journal of Fisheries Management 28(3):799-807.

Brown, L. R., and P. B. Moyle. 1981. The Impact of Squawfish on Salmonid Populations: A Review. North American Journal of Fisheries Management 1(2):104-111.

Brown, L. R., J. K. Thompson, K. Higgins, and L. V. Lucas. 2007. Population density, biomass, and age-class structure of the invasive clam Corbicula fluminea in rivers of the lowers San Joaquin River watershed, California. Western North American Naturalist 67(4):572-586, 15.

Celedonia, M. T., R. A. Tabor, S. Damm, D. W. Lantz, T. M. Lee, Z. Li, B. E. Price, W. Gale, and K. Ostrand. 2011. Movement and Habitat Use of Chinook Salmon Smolts, Northern Pikeminnow, and Smallmouth Bass Near the SR 520 Bridge 2008 Acoustic Tracking Study. U.S. Fish and Wildlife Service.

Chapman, E. D., A. R. Hearn, C. J. Michel, A. J. Ammann, S. T. Lindley, M. J. Thomas, P. T. Sandstrom, G. P. Singer, M. L. Peterson, R. B. MacFarlane, and A. P. Klimley. 2013. Diel movements of out-migrating Chinook salmon (Oncorhynchus tshawytscha) and steelhead trout (Oncorhynchus mykiss) smolts in the Sacramento/San Joaquin watershed. Environmental biology of fishes 96(2):273-286.

Chasco, B., I. C. Kaplan, A. Thomas, A. Acevedo-Gutiérrez, D. Noren, M. J. Ford, M. B. Hanson, J. Scordino, S. Jeffries, S. Pearson, K. N. Marshall, and E. J. Ward. 2017. Estimates of Chinook salmon consumption in Washington State inland waters by four marine mammal predators from 1970 to 2015. Canadian Journal of Fisheries and Aquatic Sciences 74(8):1173-1194.

Clark, T. D., N. B. Furey, E. L. Rechisky, M. K. Gale, K. M. Jeffries, A. D. Porter, M. T. Casselman, A. G. Lotto, D. A. Patterson, S. J. Cooke, A. P. Farrell, D. W. Welch, and S. G. Hinch. 2016. Tracking wild sockeye salmon smolts to the ocean reveals distinct regions of nocturnal movement and high mortality. Ecological Applications 26(4):959-978.

Cox, D. R. 1972. Regression Models and Life-Tables. Journal of the Royal Statistical Society: Series B (Methodological) 34(2):187-202.

Davies, T. W., J. P. Duffy, J. Bennie, and K. J. Gaston. 2014. The nature, extent, and ecological implications of marine light pollution. Frontiers in Ecology and the Environment 12(6):347-355.

Demetras, N. J., D. D. Huff, C. J. Michel, J. M. Smith, G. R. Cutter, S. A. Hayes, and S. T. Lindley. 2016. Development of underwater recorders to quantify predation of juvenile Chinook salmon (Oncorhynchus tshawytscha) in a river environment. Fishery Bulletin 114(2):179-185.

Doll, C. N. H., J.-P. Muller, and J. G. Morley. 2006. Mapping regional economic activity from night-time light satellite imagery. Ecological Economics 57(1):75-92.

Dolloff, C. A. 1993. Predation by River Otters (Lutra canadensis) on Juvenile Coho Salmon (Oncorhynchus kisutch) and Dolly Varden (Salvelinus malma) in Southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 50(2):312-315.

Evans, A. F., Q. Payton, A. Turecek, B. Cramer, K. Collis, D. D. Roby, P. J. Loschl, L. Sullivan, J. Skalski, M. Weiland, and C. Dotson. 2016. Avian Predation on Juvenile Salmonids: Spatial and Temporal Analysis

Based on Acoustic and Passive Integrated Transponder Tags. Transactions of the American Fisheries Society 145(4):860-877.

Evans, A. F., D. D. Roby, K. Collis, B. M. Cramer, J. A. Sheggeby, L. J. Adrean, D. S. Battaglia, and D. E. Lyons. 2011. Recovery of Coded Wire Tags at a Caspian Tern Colony in San Francisco Bay: A Technique to Evaluate Impacts of Avian Predation on Juvenile Salmonids. North American Journal of Fisheries Management 31(1):79-87.

Furey, N. B., S. G. Hinch, A. L. Bass, C. T. Middleton, V. Minke-Martin, and A. G. Lotto. 2016. Predator swamping reduces predation risk during nocturnal migration of juvenile salmon in a high-mortality landscape. Journal of Animal Ecology 85(4):948-959.

Gaston, K. J., J. Bennie, T. W. Davies, and J. Hopkins. 2013. The ecological impacts of nighttime light pollution: a mechanistic appraisal. Biological Reviews 88(4):912-927.

Gaston, K. J., J. P. Duffy, S. Gaston, J. Bennie, and T. W. Davies. 2014a. Human alteration of natural light cycles: causes and ecological consequences. Oecologia 176(4):917-931.

Gaston, K. J., S. Gaston, J. Bennie, and J. Hopkins. 2014b. Benefits and costs of artificial nighttime lighting of the environment. Environmental Reviews 23(1):14-23.

Gregory, R. S., and C. D. Levings. 1998. Turbidity Reduces Predation on Migrating Juvenile Pacific Salmon. Transactions of the American Fisheries Society 127(2):275-285.

Grossman, G. D. 2016. Predation on fishes in the Sacramento–San Joaquin Delta: current knowledge and future directions. San Francisco Estuary and Watershed Science 14(2).

Henderson, M. J., I. S. Iglesias, C. J. Michel, A. J. Ammann, and D. D. Huff. 2019. Estimating spatial–temporal differences in Chinook salmon outmigration survival with habitat- and predation-related covariates. Canadian Journal of Fisheries and Aquatic Sciences 76(9):1549-1561.

Hiemstra, P.H., Pebesma, E.J., Twenhofel, C.J.W. and G.B.M. Heuvelink, 2008. Real-time automatic interpolation of ambient gamma dose rates from the Dutch Radioactivity Monitoring Network. Computers & Geosciences. dx.doi.org/10.1016/j.cageo.2008.10.011

Hölker, F., T. Moss, B. Griefahn, W. Kloas, C. C. Voigt, D. Henckel, A. Hänel, P. M. Kappeler, S. Völker, A. Schwope, S. Franke, D. Uhrlandt, J. Fischer, R. Klenke, C. Wolter, and K. Tockner. 2010a. The Dark Side of Light A Transdisciplinary Research Agenda for Light Pollution Policy. Ecology and Society 15(4).

Hölker, F., C. Wolter, E. K. Perkin, and K. Tockner. 2010b. Light pollution as a biodiversity threat. Trends in Ecology & Evolution 25(12):681-682.

Horodysky, A. Z., R. W. Brill, E. J. Warrant, J. A. Musick, and R. J. Latour. 2010. Comparative visual function in four piscivorous fishes inhabiting Chesapeake Bay. The Journal of Experimental Biology 213(10):1751-1761.

Ingebritsen, S., M. Ikehara, D. Galloway, and D. Jones. 2000. Delta subsidence in California: the sinking heart of the state. Geological Survey (US), 2327-6932.

Jechow, A., and F. Hölker. 2019. How dark is a river? Artificial light at night in aquatic systems and the need for comprehensive night-time light measurements. WIREs Water 6(6):e1388.

Jordan, R. C., and D. V. Howe. 2007. Photopigment Spectral Absorbance in Four Hudson River Fishes. Journal of Freshwater Ecology 22(1):155-157.

Lehman, B. M., M. P. Gary, N. Demetras, and C. J. Michel. 2019. Where Predators and Prey Meet: Anthropogenic Contact Points Between Fishes in a Freshwater Estuary. San Francisco Estuary and Watershed Science 17(4).

Lindley, S. T., C. B. Grimes, M. S. Mohr, W. T. Peterson, J. E. Stein, J. J. Anderson, L. W. Botsford, D. L. Bottom, C. A. Busack, and T. K. Collier. 2009. What caused the Sacramento River fall Chinook stock collapse. NOAA-TM-NMFS-SWFSC-447, National Oceanic and Atmospheric Administration, Santa Cruz, CA.

Martín-Olalla, J. M. 2018. Latitudinal trends in human primary activities: characterizing the winter day as a synchronizer. Scientific Reports 8(1):5350.

Mazur, M. M., and D. A. Beauchamp. 2003. A comparison of Visual Prey Detection Among Species of Piscivorous Salmonids: Effects of Light and Low Turbidities. Environmental biology of fishes 67(4):397-405.

Mazur, M. M., and D. A. Beauchamp. 2006. Linking piscivory to spatial–temporal distributions of pelagic prey fishes with a visual foraging model. Journal of fish biology 69(1):151-175.

McMahon, T. E., and S. H. Holanov. 1995. Foraging success of largemouth bass at different light intensities: implications for time and depth of feeding. Journal of fish biology 46(5):759-767.

Michel, C. J., M. J. Henderson, C. M. Loomis, J. M. Smith, N. J. Demetras, I. S. Iglesias, B. M. Lehman, and D. D. Huff. 2020a. Fish predation on a landscape scale. Ecosphere 11(6):e03168.

Michel, C., J. Smith, N. Demetras, D. Huff, and S. Hayes. 2018. Non-Native Fish Predator Density and Molecular-Based Diet Estimates Suggest Differing Impacts of Predator Species on Juvenile Salmon in the San Joaquin River, California. San Francisco Estuary and Watershed Science 16(4).

Michel, C. J., A. J. Ammann, E. D. Chapman, P. T. Sandstrom, H. E. Fish, M. J. Thomas, G. P. Singer, S. T. Lindley, A. P. Klimley, and R. B. MacFarlane. 2013. The effects of environmental factors on the migratory movement patterns of Sacramento River yearling late-fall run Chinook salmon (Oncorhynchus tshawytscha). Environmental biology of fishes 96(2):257-271.

Michel, C. J., A. J. Ammann, S. T. Lindley, P. T. Sandstrom, E. D. Chapman, M. J. Thomas, G. P. Singer, A. P. Klimley, and R. B. MacFarlane. 2015. Chinook salmon outmigration survival in wet and dry years in California's Sacramento River. Canadian Journal of Fisheries and Aquatic Sciences 72(11):1749-1759.

Michel, C. J., J. M. Smith, B. M. Lehman, N. J. Demetras, D. D. Huff, P. L. Brandes, J. A. Israel, T. P. Quinn, and S. A. Hayes. 2020b. Limitations of Active Removal to Manage Predatory Fish Populations. North American Journal of Fisheries Management 10.1002/nafm.10391.

Mitchem, L. D., S. Stanis, M. Zhou, E. Loew, J. M. Epifanio, and R. C. Fuller. 2018. Seeing red: color vision in the largemouth bass. Current Zoology 65(1):43-52.

Monsen, N. E., J. E. Cloern, and J. R. Burau. 2007. Effects of flow diversions on water and habitat quality: Examples from California's highly manipulated Sacramento–San Joaquin Delta. San Francisco Estuary and Watershed Science 5(3).

Monsivais, D., A. Ghosh, K. Bhattacharya, R. I. M. Dunbar, and K. Kaski. 2017. Tracking urban human activity from mobile phone calling patterns. PLOS Computational Biology 13(11):e1005824.

Mount, J., and R. Twiss. 2005. Subsidence, sea level rise, and seismicity in the Sacramento–San Joaquin Delta. San Francisco Estuary and Watershed Science 3(1).

Navara, K. J., and R. J. Nelson. 2007. The dark side of light at night: physiological, epidemiological, and ecological consequences. Journal of Pineal Research 43(3):215-224.

Nichols, F. H., J. E. Cloern, S. N. Luoma, and D. H. Peterson. 1986. The Modification of an Estuary. science 231(4738):567-573.

Osterback, A.-M. K., D. M. Frechette, A. O. Shelton, S. A. Hayes, M. H. Bond, S. A. Shaffer, and J. W. Moore. 2013. High predation on small populations: avian predation on imperiled salmonids. Ecosphere 4(9):1-21.

Poe, T. P., H. C. Hansel, S. Vigg, D. E. Palmer, and L. A. Prendergast. 1991. Feeding of Predaceous Fishes on Out-Migrating Juvenile Salmonids in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120(4):405-420.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. 1991. Estimated Loss of Juvenile Salmonids to Predation by Northern Squawfish, Walleyes, and Smallmouth Bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120(4):448-458.

Riensche, D. L., M. L. Elliott, and S. H. Euing. 2012. Breeding Status, Nesting Densities & Diet Trends of Two Endangered California Least Tern Colonies. Journal of Environmental Science and Engineering. B 10:1135-1145.

Riley, W. D., P. I. Davison, D. L. Maxwell, and B. Bendall. 2013. Street lighting delays and disrupts the dispersal of Atlantic salmon (Salmo salar) fry. Biological Conservation 158:140-146.

Sabal, M., S. Hayes, J. Merz, and J. Setka. 2016. Habitat Alterations and a Nonnative Predator, the Striped Bass, Increase Native Chinook Salmon Mortality in the Central Valley, California. North American Journal of Fisheries Management 36(2):309-320.

Schroeder, R. K., L. D. Whitman, B. Cannon, and P. Olmsted. 2015. Juvenile life-history diversity and population stability of spring Chinook salmon in the Willamette River basin, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 73(6):921-934.

Sherker, Z. T. 2020. Predation by Pacific great blue herons on juvenile salmon. University of British Columbia. https://open.library.ubc.ca/cIRcle/collections/ubctheses/24/items/1.0390460

Tabor, R. A., A. T. C. Bell, D. W. Lantz, C. N. Gregersen, H. B. Berge, and D. K. Hawkins. 2017. Phototaxic Behavior of Subyearling Salmonids in the Nearshore Area of Two Urban Lakes in Western Washington State. Transactions of the American Fisheries Society 146(4):753-761.

Tabor, R. A., G. S. Brown, and V. T. Luiting. 2004. The Effect of Light Intensity on Sockeye Salmon Fry Migratory Behavior and Predation by Cottids in the Cedar River, Washington. North American Journal of Fisheries Management 24(1):128-145.

Therneau, T. M. 2015. A Package for Survival Analysis in S. version 2.38, https://CRAN.R-project.org/package=survival.

Underwood, E. C., M. J. Mulitsch, J. A. Greenberg, M. L. Whiting, S. L. Ustin, and S. C. Kefauver. 2006. Mapping Invasive Aquatic Vegetation in the Sacramento-San Joaquin Delta using Hyperspectral Imagery. Environmental Monitoring and Assessment 121(1):47-64.

Vogel, J. L., and D. A. Beauchamp. 1999. Effects of light, prey size, and turbidity on reaction distances of lake trout (Salvelinus namaycush) to salmonid prey. Canadian Journal of Fisheries and Aquatic Sciences 56(7):1293-1297.

Williams, J. G. 2006. Central Valley salmon: a perspective on Chinook and steelhead in the Central Valley of California. San Francisco Estuary and Watershed Science 4(3).

Williams, T. H., B. C. Spence, D. A. Boughton, R. C. Johnson, E. G. R. Crozier, N. J. Mantua, M. R. O'Farrell, and S. T. Lindley. 2016. Viability assessment for Pacific salmon and steelhead listed under the Endangered Species Act: Southwest. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-564.

Yoshiyama, R. M., F. W. Fisher, and P. B. Moyle. 1998. Historical Abundance and Decline of Chinook Salmon in the Central Valley Region of California. North American Journal of Fisheries Management 18(3):487-521.

Yurk, H., and A. W. Trites. 2000. Experimental Attempts to Reduce Predation by Harbor Seals on Out-Migrating Juvenile Salmonids. Transactions of the American Fisheries Society 129(6):1360-1366.

Zapata, M. J., S. M. P. Sullivan, and S. M. Gray. 2019. Artificial Lighting at Night in Estuaries—Implications from Individuals to Ecosystems. Estuaries and Coasts 42(2):309-330.

Zeug, S. C., M. Beakes, J. Wiesenfeld, M. Greenwood, L. Grimaldo, J. Hassrick, A. Collins, S. Acuña, and M. Johnston. 2020. Experimental Quantification of Piscivore Density and Habitat Effects on Survival of Juvenile Chinook Salmon in a Tidal Freshwater Estuary. Estuaries and Coasts.

[A]Tables

Table 1. Results of predator density generalized linear mixed models (GLMM) for all data, early-night (1 - 3 hours past sunset), and late night-data subsets (3 - 5 hours past sunset). Coefficient estimates of the presence

of ALAN (ALAN), minutes past sunset (Min), and their interaction. Exponentiated estimates (e^{est}), standard error (*se*), *t*, and *p* values are also reported for each parameter.

All Data	Estimate	e^{est}	se	t	p
ALAN	-0.310	0.734	0.448	-0.691	0.490
Min	-0.015	0.985	0.060	-0.254	0.799
ALAN x Min	0.212	1.237	0.090	2.358	0.018
Early Data					
ALAN	0.207	1.230	0.280	0.740	0.459
Min	0.022	1.022	0.108	0.201	0.841
Late Data					
ALAN	1.376	3.957	0.297	4.627	< 0.001
Min	0.108	1.114	0.140	0.771	0.441

Table 2. Results of Cox proportional hazard models for all data, early-night (1 - 3 hours past sunset), and late-night (3 - 5 hours past sunset) data subsets. Predictor variables include lux (light intensity) or lux at depth (Lux [Depth]), minutes past sunset (Min), and 30 minute predator (fish ≥ 200 mm) density (Pred Den). The coefficient (*coef*) column indicates the direction (positive vs. negative) of the effect of each predictor variable on relative predation risk and coefficient standard error (*se* [*coef*]) is reported. The e^{coef} columns reports the relative predation risk change for each unit increase in predictor variables of both raw and scaled variables. The *z* column is the Wald statistic value and evaluates whether the coefficient of a given variable is significantly different from 0 and the significance value is indicated in the *p* column. The *p* value for the cox.zph test is also reported in the *p_zph* column.

All Data	*coef*	raw e^{coef}	*se* (*coef*)	scaled e^{coef}	*z*	*p*	*p_zph*
Lux	-0.061	0.940	0.041	0.670	-1.494	0.135	0.782
Lux (Depth)	-0.220	0.803	0.147	0.670	-1.494	0.135	0.782
Min	-0.004	0.996	0.001	0.472	-3.123	0.002	0.227
Pred Den	42.309	2.369×10^{18}	4.228	1.843	10.006	< 0.001	0.590
Lux x Min	0.0004	1.0004	0.0002	1.625	2.228	0.026	0.696
Early Data							
Lux	-0.006	0.994	0.022	0.964	-0.267	0.789	0.879
Lux (Depth)	-0.021	0.979	0.078	0.964	-0.267	0.789	0.879
Min	-0.006	0.994	0.004	0.429	-1.723	0.085	0.490
Pred Den	41.111	7.150×10^{17}	6.501	1.708	6.323	< 0.001	0.591
Late Data							
Lux	0.029	1.030	0.009	1.217	3.017	0.003	0.770
Lux (Depth)	0.105	1.111	0.035	1.217	3.017	0.003	0.770
Min	-0.006	0.994	0.003	0.252	-1.902	0.057	0.281
Pred Den	44.156	1.502×10^{19}	5.979	1.987	7.385	< 0.001	0.404

[A]Figure Captions

Figure 1. Experimental sites within the Sacramento - San Joaquin Delta. The top left panel is the state of California and Central Valley rivers. Sacramento (SAC), Stockton (ST), and San Francisco (SF) are major cities along salmonid outmigration routes denoted by gray diamonds. The lower left panel is the extent of the Sacramento - San Joaquin Delta and the main panel has our experimental sites.
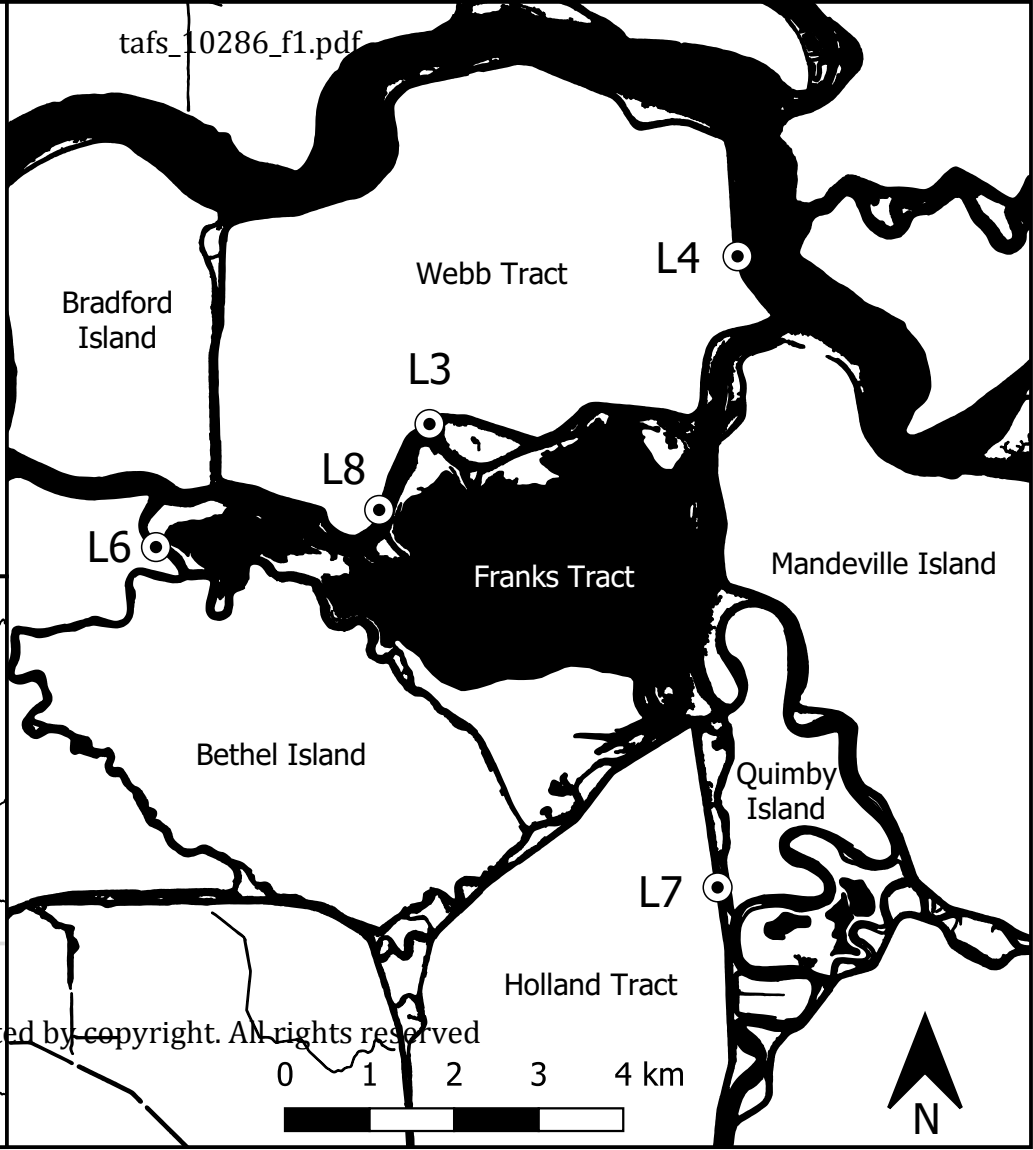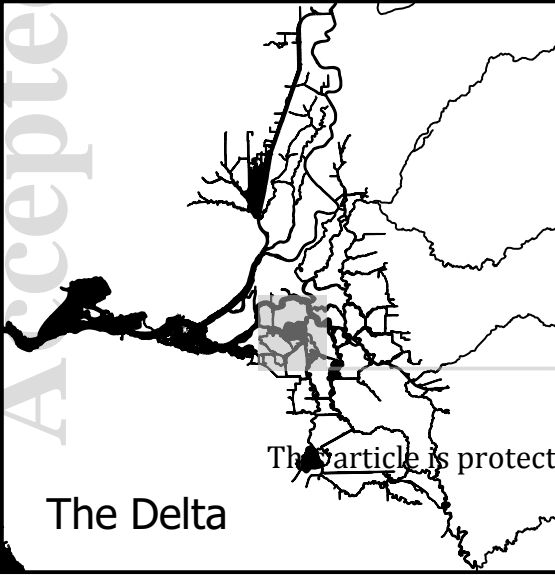
Figure 2. Schematic of an experimental study reach. We positioned floating lines parallel to the shoreline to ensure predation event recorders (PERs, cylinders) drifted through water that our introduced LED light source (yellow triangle) illuminated. Largemouth Bass and Striped Bass represent potential predators. ARIS cameras and the artificial light source are depicted at their respective positions within the experimental design.

Figure 3. Interpolated lux values for site L4 on sampling night 8 (L4_8). Predation proportion rasters for late-night (≥ 180 minutes past sunset) and all-night datasets. We produced predation proportion rasters by generating kernel densities of all predation event recorder (PER) predation events and dividing these by kernel densities of all PER GPS positions.

Figure 4. Mean large fish (≥ 200 mm, likely predators) density (Large Fish m^{-3} 30 min^{-1} [± 1 SE]) across each time bin within both light and dark treatments (A). Mean large fish density across each experimental night (±

1 SE) within both light and dark treatments (B) and the estimated nightly mean PER predation risk (filled circles) from the overall Cox model. Continuous lines under experimental nights represent consecutive experimental nights at a given site.

Figure 5. The nightly mean percentage (± 1 SE) of PER observations when predation events occurred binned across increasing lux values (top row) for early-night (1 - 3 hours after sunset, column 1) and late-night (3 - 5 hours past sunset, column 2) data subsets. Predicted relative predation risk of increasing lux (row 2) and large fish (≥ 200 mm, likely predators) density (row 3). Predictions (solid black line) above the horizontal dashed line (risk = 1) indicate increased relative predation risk and below the dashed line represent decreased risk with 95% confidence intervals in gray. Where the solid black line crosses the dashed line is the mean observation of each variable within each model.
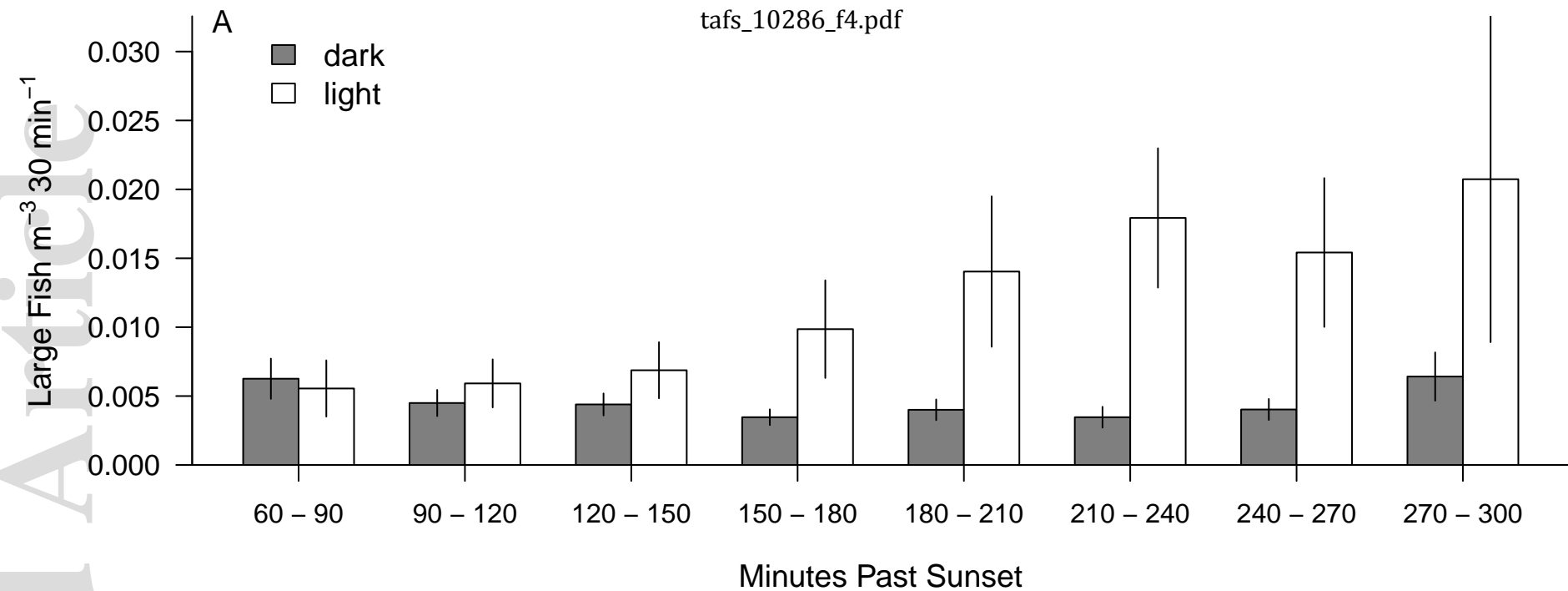
California

SAC

SF   ST

The Delta

Bradford Island

Webb Tract

L4

L3

L8

L6

Franks Tract

Mandeville Island

Bethel Island

Quimby Island

L7

Holland Tract

0   1   2   3   4 km

N

Light Source tafs_10286_f2.pdf

0m 50m 100m 150m

ARIS

ARIS

Tidal Flow Direction

Lux

0.5

68

○ Light
Source

0 m

20

40

60

80

100

120

140

160

180

200

220

Lux

Late Night

All Night

Predation Proportion

No PER
Sampling

0

0.01

Early Night

Late Night