



**Acoustic imaging observes predator-prey interactions
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Sockeye Salmon (*Oncorhynchus nerka*) smolts**

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TITLE: Acoustic imaging observes predator-prey interactions between Bull Trout (*Salvelinus confluentus*) and migrating Sockeye Salmon (*Oncorhynchus nerka*) smolts

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Abstract:

Annual migrations by juvenile Pacific Salmon (*Oncorhynchus spp.*) smolts are predictable, presenting opportunities for predators to exploit these seasonal prey pulses. Directly observing predator-prey interactions to understand factors affecting predation may be possible via Dual-frequency Identification Sonar (DIDSON) acoustic imaging. Within Chilko Lake, British Columbia, Canada, prior telemetry and stomach content analyses suggested the outmigration of Sockeye Salmon (*Oncorhynchus nerka*) smolts influences the movements and aggregations of Bull Trout (*Salvelinus confluentus*) that feed extensively on smolts during their outmigration. Bull Trout captured at the government-installed counting fence exhibited high consumption of smolts, but it is only assumed that feeding occurred directly at the fence. We used DIDSON to assess fine-scale predator-prey interactions between Sockeye Salmon smolts and Bull Trout over 10 days during the 2016 smolt outmigration. We found that smolt-Bull Trout interactions were correlated with smolt densities at the counting fence, consistent with the prior diet studies in the system. Predator-prey interactions were also coupled with nocturnal migratory behaviors of Sockeye Salmon smolts, presumably to minimize predation risk. These results demonstrate that DIDSON technology can record interactions between predators and migrating prey at a resolution to identify variability in space and time, and provide insight on the role of anthropogenic structures (e.g., counting fences) in mediating such interactions.

43 Introduction:

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45 Pacific Salmon (*Oncorhynchus spp.*) are integral to the culture, livelihoods, and identity of First
46 Nations and represent valuable recreational and commercial fisheries (Gislason et al. 2017).
47 Ecologically, Pacific salmon mediate trophic relationships, where adult carcasses contribute
48 significant nutrients to both stream and riparian ecosystems (Naiman et al. 2002). However,
49 many species of Pacific Salmon, including Sockeye Salmon (*O. nerka*) of the Fraser River basin
50 in British Columbia, have experienced substantial population-level declines (Peterman and
51 Dorner 2012), resulting in threatened or endangered populations (COSEWIC 2017).

52 Sockeye Salmon juveniles typically rear in freshwater lakes for 1-3 years before they
53 begin their seaward migration as smolts, a migration that requires a suite of behavioral and
54 physiological changes (i.e., smoltification; Young et al. 1989) to cope with saltwater. While
55 migrating, smolts also face predation from piscivorous fishes, birds, and mammals
56 (Beamesderfer et al. 1996; Blackwell and Juanes 1998; Osterback et al. 2013; Furey et al. 2015).
57 As such, smolts exhibit a variety of behaviors to reduce their predation risk. For instance,
58 Sockeye Salmon smolts can migrate nocturnally (Clark et al. 2016; Furey et al. 2016a),
59 presumably to minimize detection by visual predators. Given that predation is often the ultimate
60 source of mortality for a variety of proximate factors (Miller et al. 2014), methods that allow for
61 direct monitoring of predator-prey interactions are valuable.

62 One method to passively observe predator-prey interactions is Dual-Frequency
63 Identification Sonar (DIDSON). The DIDSON system uses acoustic imaging to passively
64 observe of fish behaviors, size distributions, and relative abundances, including in turbid waters
65 and at night (Burwen et al. 2010; Crossman et al. 2011; Martignac et al. 2015; Moursund et al.
66 2003; Maxwell and Gove 2007; Nichols et al. 2014). Here, we use DIDSON in a system with

known smolt-predator relationships to determine if the technology can provide *in situ* passive observations of predator-prey interactions.

Chilko Lake (or T̓silhqox Biny, traditional territory of the Xení Gwet'in First Nations, one of the six communities forming the T̓silhqot'in Nation), British Columbia, is home to one of the largest populations of Sockeye Salmon in Canada, and consequently this population is intensively studied (Bradford et al. 2000; Irvine and Akenhead 2013). Each spring, 10 - >40 million Sockeye Salmon smolts (~96% age-1 smolts, ~4% age-2 smolts; Irvine and Akenhead 2013) emigrate from the lake towards the ocean. Acoustic telemetry revealed that the initial migratory corridor in the Chilko River (clear and slow-moving water) is high-risk relative to the turbid waters of the Chilcotin and Fraser Rivers downstream (Clark et al. 2016; Rechisky et al. 2019). Bull Trout (*Salvelinus confluentus*) feed extensively on migrating Sockeye Salmon smolts (Furey et al. 2015), with Bull Trout caught at the Fisheries and Oceans (DFO) counting fence near the Chilko Lake outlet feeding at the highest rates (Furey et al. 2016b). Thus, the fence may be facilitating predator-prey interactions, but fine-scale observations at the fence and other sites are needed to confirm that Bull Trout are actively foraging directly at this structure. Smolts, presumably to minimize predation risk, migrate nocturnally and synchronize their movements to numerically overwhelm or swamp predators in the clear upper-river reaches of Chilko Lake (Clark et al. 2016; Furey et al. 2016a). Thus, this system is ideal for investigating fine-scale predator-prey interactions. The present study investigates if DIDSON can be successful at observing and quantifying predator-prey interactions at the Chilko Lake-River outlet during the smolt outmigration by determining: 1) where Bull Trout are most frequently interacting with migrating Sockeye Salmon smolts, 2) if Bull Trout activity is synchronized with Sockeye

Salmon migrations and 3) if any such synchrony is location-specific (at the counting fence, vs other locales upstream and downstream).

Methods:

Study area.—

This study was conducted at the outlet of Chilko Lake, British Columbia, Canada (51.294, -124.077; Fig. 1). Chilko Lake is a 180 km², high elevation (~1100 m.a.s.l) lake that has a north-south orientation and is approximately 65 km long. Each spring, Fisheries and Oceans Canada (DFO) installs a counting fence to estimate the numbers of outmigrant smolts. The DFO counting fence is located approximately 1.3-km downstream from Chilko Lake (Fig. 1; Fig. S1) and has been deployed annually since the early 1950s, with the exception of 2017 and 2020 (Irvine and Akenhead 2013). Smolts are funneled through a constriction and pass over a white background where digital photographs are taken at regular time intervals to estimate hourly densities. If no smolts were present, the fence was closed and smolts could not physically pass; these resulted in time intervals with zero smolts.

DIDSON deployment.—

The DIDSON system (Sound Metrics, Bellevue, Washington) was deployed at five different locations (Fig. 1) from April 20 - April 29 in 2016 during the Sockeye Salmon smolt outmigration (Table 1). We deployed the DIDSON upstream of the counting fence (site UF; 51.625, -124.142; Fig. 1) from April 20 – 21 2016 and April 27 – 29 2016, approximately 1-m from the fence's edge. We also stationed the DIDSON downstream of Chilko River (site DR;

51.626, -124.142; Fig. 1) from April 21 – 22 2016 and downstream of the counting fence (site DF; 51.625, -124.141; Fig. 1) from April 23 – 24 2016. Finally, the DIDSON was positioned at the outflow of Chilko Lake (site N; 51.615, -124.152; Fig. 1) from April 25 – 26 2016 and April 29, 2016 (site N; 51.615, -124.151; Fig. 1). The DIDSON was deployed on a custom-built metal tripod. This frame allowed the DIDSON to be placed ~0.5-m above the riverbed and kept the sensor between level to the water's surface and -15° and perpendicular to the flow. Given that DIDSON deployments occurred before freshet, flows were generally low but increasing from ~20 m³/s to ~30 m³/s between the first and last deployments (Water Office of Canada station 08MA002). Site N at the outflow of Chilko Lake is much deeper (~9-m maximum depth) than the river sites (~0.75 – 1-m deep); the river width varies from ~50-m wide (at the lake outflow; site N) to ~80-m wide at other sites. We used two different configurations of the DIDSON: the first constrained the detection range to ~5 meters and the second to 10 meters into the river channel (Table 1); we used both configurations for exploratory purposes.

DIDSON data collection and video processing.—

Approximately 100 hours of DIDSON acoustic sonar videos were recorded and evaluated across the deployments. Video files from the DIDSON were analyzed in 30-minute intervals and viewed using the DIDSON Control and Display software (Sound Metrics, Bellevue, Washington). In each video, interactions between Bull Trout and out-migrating Sockeye Salmon smolts were recorded. We defined interactions by the following criteria: 1) Bull Trout were actively moving towards Sockeye Salmon smolts or 2) the proximity of Bull Trout resulted in Sockeye Salmon smolts dispersing or changing direction or speed rapidly (e.g., Supplementary Videos 1 & 2). Sockeye Salmon smolts were easily identified as “clouds” of small fish on the

DIDSON. We also measured the total length (TL) to the nearest cm of each Bull Trout using the “measure” tool. Bull Trout are the dominant piscivore present during the migration to feed on smolts (Furey et al. 2015, 2016b) and are generally much larger in body size (we measured at ~25-85 cm in length) than other fishes present at lower abundances (Mountain Whitefish and Rainbow Trout primarily, which when observed were < 30 cm), and thus were generally identifiable on the DIDSON. For deployments near the counting fence, Bull Trout were observed visually, confirming DIDSON observations. In addition, Rainbow Trout and Mountain Whitefish do not appear to consume smolts consistently (Furey, unpublished data). Nevertheless, Bull Trout lengths from each interaction were measured to understand the potential for bias resulting from observations of smaller fishes that may not have been Bull Trout. In response, we assessed the empirical cumulative distribution function of presumed Bull Trout lengths (cm) measured in this study, comparing the DIDSON length estimates to those obtained in the field from prior studies in the system. Specifically, we compared both minimum (41.5 cm) and maximum (79.5 cm) length estimates from Kanigan (2019), which captured Bull Trout via hook-and-line sampling, to provide a probability threshold of observations that are not consistent with lengths of Bull Trout captured by angling.

Videos were processed at frame rates of ~25 - 50 frames·s⁻¹ and were played back, slowed down, and/or paused when interactions were detected. This was done to verify interactions between Bull Trout and Sockeye Salmon smolts. Further, these videos were viewed using the “Background Subtraction” tool to remove potential static background and to better visualize fish passing through the video. Recorded observations of interactions between Bull Trout and smolts were standardized to per m² (counts of interactions per m²) because the window length of the DIDSON (~5 m vs 10 m) and thus area observed, differed among deployments (Table 1). To

estimate the window area observed by the DIDSON (~9.87 m² for the 5-m window length and ~29.27 m² for the 10-m window length), images of the DIDSON were imported and window area calculated using ImageJ (Schneider et al. 2012). Considering the differences in DIDSON configuration and resulting window area observed, we quantified the proportion of 30-minute intervals that had zero interactions between Bull Trout and Sockeye Salmon smolts at parallel sites (UF2021; 29.27 m², UF272829; 9.87 m²); if bias occurred, a smaller detection range would result in a larger number of zero interactions observed.

Data analysis.—

For the following analyses, non-parametric tests were used due to violations of model assumptions (i.e., homogeneity of variance, normally distributed residuals, etc.). Kruskal-Wallis rank sum tests were used to test for differences in the number of interactions per 30-minute interval, standardized to per m² among all deployments. Separate pairwise Wilcoxon rank sum tests tested for differences in the number of interactions between each of the five individual deployments with a Holm-Bonferroni correction to account for multiple comparisons. Wilcoxon rank sum tests were also performed to test for differences in the number of standardized interactions (m⁻² in each 30-minute interval) between daylight hours and nighttime hours (daytime hours were considered as between sunrise and sunset determined via <https://www.timeanddate.com/>; nighttime was considered as sunset to sunrise) both collectively among all deployments, and with a separate test for each of the five individual deployments. Finally, correlations between migrating smolt densities (collected from the DFO counting fence) and standardized interactions (per hour, instead of every 30 minutes, to match the resolution of smolt density data from the counting fence) between Bull Trout and smolts were tested both

collectively among all deployments and individually for each of the five different deployments using Spearman's rank order correlation coefficient. All statistical analyses were conducted using R v3.6.3 (R Core Team 2021).

<A>Results:

Interactions between smolts and Bull Trout throughout all deployments ranged from 0 - 4.86 interactions per m² among 30-minute intervals (mean = 0.63 m⁻²; SD = 0.99 m⁻²). The number of standardized interactions observed between smolts and Bull Trout varied among deployments significantly (Kruskal-Wallis rank sum test, $\chi^2 = 105$; df = 5; $P < 0.001$). Pairwise Wilcoxon tests indicated that the number of standardized interactions between the Upstream Fence April 20 – 21 and Upstream Fence April 27 – 29 deployments differed significantly from each other and all other deployments ($P < 0.05$). Significant differences in the number of interactions were also detected between the Downstream River April 21 – 22 deployment and the Downstream Fence April 23 – 24 deployment ($P < 0.05$); however, neither of these deployments were significantly different from the two deployments that occurred at site N. In general, the highest number of interactions per m² was observed when the DIDSON was deployed upstream of the counting fence (site UF; mean = 1.14 m⁻²; SD = 1.12 m⁻²; range = 0 - 4.86 m⁻²), followed by sites that occurred downstream of the counting fence (site DR and DF; mean = 0.029 m⁻²; SD = 0.065 m⁻²; range = 0 - 0.376 m⁻²), and the narrow river segment (site N; mean = 0.015 m⁻²; SD = 0.029 m⁻²; range = 0.102 m⁻²).

The number of standardized interactions among 30-minute intervals varied with the diel cycle when aggregated across all deployments ($W = 2693.5$; $P < 0.01$; Fig. 2); interactions were higher during nighttime hours and ranged from 0 to 4.86 interactions per m² (mean = 1.19 m⁻²; SD = 1.24 m⁻²) than during daytime hours (mean = 0.225 m⁻², SD = 0.44 m⁻²). For individual

deployments, nighttime interactions (per m^2) were significantly higher than daytime interactions during the Upstream Fence April 20 - 21 deployment (daytime mean = 0.05 m^{-2} ; SD = 0.11 m^{-2} , nighttime mean = 0.78 m^{-2} ; SD = 0.42 m^{-2} ; $W = 11$; $P < 0.01$; Fig. 3A), the Downstream River April 21 – 22 deployment (daytime mean = 0.02 m^{-2} ; SD = 0.05 m^{-2} , nighttime mean = 0.10 m^{-2} ; SD = 0.11 m^{-2} ; $W = 49.5$; $P = 0.01$; Fig. 3B), and the Upstream Fence April 27 – 29 deployment (daytime: mean = 0.54 m^{-2} ; SD = 0.57 m^{-2} , nighttime: mean = 2.35 m^{-2} ; SD = 0.93 m^{-2} ; $W = 79.5$; $P < 0.01$; Fig. 3E), but other deployments did not demonstrate this relationship.

Smolt density estimates obtained from the DFO counting fence ranged from 200 - 882,717 smolts per hour when smolts were actively migrating (i.e., when the counting fence was not physically closed). The number of hourly interactions and smolt densities were not correlated when these data were aggregated across all deployments (Spearman's correlation, $\rho = 0.12$; $P = 0.21$). However, a significant and strong positive correlation did exist between the number of hourly interactions and smolt densities for the Upstream Fence April 20 - 21 deployment (Spearman's correlation, $\rho = 0.87$; $P < 0.001$; Fig. 3A) and the Upstream Fence April 27 - 29 deployment (Spearman's correlation, $\rho = 0.76$; $P < 0.001$; Fig. 3E).

We directly compared the proportion of 30-minute time windows without any interactions (e.g., equal to zero) between deployments at the UF site with the two viewing window sizes and did not find evidence that the larger viewing window results in more observed interactions. Specifically, the Upstream Fence 20 – 21 deployment had a larger proportion of zeros (0.25; detection window area of 29.27 m^2), relative to the deployment spanning April 27 – 29 (0.12; detection window area: 9.87 m^2), contrary to what would be expected if biases were present. Lengths of Bull Trout (cm) as measured from the DIDSON ranged from 25 cm to 87 cm

across all interactions ($n = 3025$; mean 50.7 cm; SD 9.99 cm). Compared to minimum and maximum lengths of Bull Trout captured via hook-and-line sampling (41 cm - 79.5 cm; Kanigan 2019), we found that the cumulative probability of observing presumed Bull Trout ≤ 41 cm from DIDSON interactions was $\sim 19\%$. Additionally, maximum lengths from hook-and-line angling (79.5 cm) were similar to those measured from the DIDSON (87 cm; Fig. S2).

Discussion:

The DIDSON successfully observed predator-prey interactions between Bull Trout and migrating Sockeye Salmon, with these interactions occurring most frequently just upstream of the counting fence, suggesting this anthropogenic structure facilitates predation behavior. Consumption was higher (e.g., at *ad libitum*) for Bull Trout collected at the counting fence relative to other locales (Furey et al. 2016b), and the DIDSON confirms that predator-prey interactions at this site can be intense and tightly coupled to migrating smolt densities; thus, feeding intensity is likely consistent with prior diet studies (Fuery et al. 2015; Furey et al. 2016b). As a result, the counting fence may create a spatial bottleneck for migrant smolts to pass. It is possible that the constriction of the counting fence, and potentially the presence of Bull Trout, may concentrate smolts within a small area and increase the foraging efficiency of Bull Trout. However, further research could better quantify how smolts behave as they pass through the counting fence relative to other landscapes, and quantify mortality, potentially via telemetry tracking upstream of the fence (all telemetry work in this system occurred downstream of the fence). Given the short duration of our study (10 days), which was due to opportunistic use of the DIDSON during other field programs, we believe our conclusions could be better supported by monitoring the site upstream of the fence more intensively (i.e., additional days), with concurrent

comparisons of other sites. We also acknowledge that with only one DIDSON unit, we were unable to compare differences in predator-prey interactions between or among sites simultaneously; in particular, sampling in systems without counting fences would be informative as to how anthropogenic structures affect behavior of salmonid predators more broadly.

Diel differences in the frequency of interactions were also strongest for deployments close to the counting fence, albeit sample sizes were low throughout our deployments. Given that the smolt migration is largely nocturnal (Clark et al. 2016; Furey et al. 2016a), it is intuitive that nighttime hours would provide the most opportunities for predator-prey interactions. Smolts likely exhibit nocturnal migrations to mitigate foraging efficiency from visual predators, as seen in other salmonid migrations in fresh water (Ibbotson et al. 2006; 2011; Haraldstad et al. 2017). Bull Trout likely synchronize their movements and behaviors in response to outmigrant smolts at fine spatial and temporal scales, as they do at broader scales (Furey and Hinch 2017; Kanigan 2019), but confirmation would require increased tracking of movements and behavior during daytime periods. Due to the resolution of the DIDSON system, we were unable to confirm actual predation events, estimate the number of smolts consumed, or quantify the effectiveness of synchronized nocturnal movements of smolts (i.e., predator swamping; Furey et al. 2016a; Furey et al. 2021b). Future studies could couple the use of acoustic imaging, which is consistently improving, and other methods (e.g., diet studies or high-resolution telemetry) to quantify Bull Trout predation rates on smolts.

Human-altered landscapes can influence the risk landscape for migratory animals (Sabal et al. 2021). Dams and other barriers are well known to constrict and even at times, obstruct fish movement, and can aggregate predators, increasing mortality of migrant fishes (Blackwell and

Juanes 1998; Davis et al. 2012; Keefer et al. 2012; Sabal et al. 2016). However, temporary structures such as counting fences or weirs are commonly used, but generally less studied than permanent structures, even though they can affect predator-prey interactions (Furey et al. 2016b). Our study suggests that a temporary counting fence, even one that has been relied on for management (Irvine and Akenhead 2013), can mediate predator-prey interactions and pose a potential challenge to migrants by affecting predator or prey behavior. Thus, the impacts of temporary structures on fish behavior and predator-prey interactions likely deserve more attention given that they are often used during times of important life history events such as migrations.

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- Table 1. Summary data for DIDSON deployments in Chilko Lake, British Columbia, Canada, from April 20 – 29, 2016 during a Sockeye Salmon smolt outmigration period. The detection window area (m²) represents the approximate area observed by the DIDSON. The total number of interactions are the sum of all interactions detected for a given deployment. The total number of smolts per deployment are the sum of smolt densities (estimated hourly) for a given night from the counting fence.

DIDSON deployment (Site and date)	Hours of video footage	Detection window area (m ²)	Average number of interactions ± SD (m ⁻² per 30 minutes)	Minimum number of interactions (m ⁻² per 30 minutes)	Maximum number of interactions (m ⁻² per 30 minutes)	Total number of interactions	Total number of smolts per deployment
Upstream Fence (UF) April 20 – 21 2016	14	29.27	0.444±0.484	0	1.61	364	1,054,978
Downstream River (DR) April 21 – 22 2016	14.5	29.27	0.062±0.924	0	0.376	52	1,082,198
Downstream Fence (DF) April 23 – 24 2016	22	29.27	0.008±0.018	0	0.068	23	5,339,320
Narrows (N) April 25 -26 2016	5.5	29.27	0.016±0.023	0	0.068	5	26,000
Upstream Fence (UF) April 27 – 29 2016	41.5	9.87	1.37±1.18	0	4.86	1032	2,041,534
Narrows (N) April 29 2016	3.5	29.27	0.015±0.039	0	0.102	3	NA

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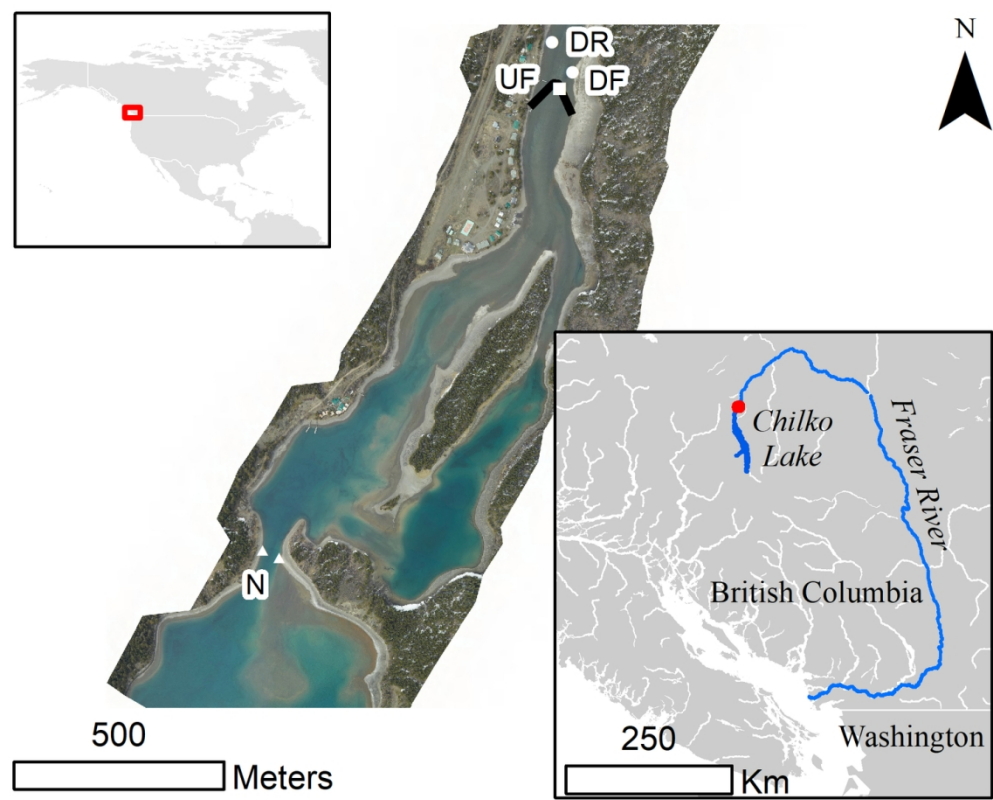
419 Figures:
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421 Figure 1. Map of Chilko Lake, British Columbia, Canada (51.294, -124.077). Aerial image of the
422 upper reaches of Chilko Lake shows the positions (white shapes) of where the DIDSON system
423 was deployed from April 20 - 29th, 2016, during the smolt outmigration period. The white
424 square indicates DIDSON deployments upstream of the government operated counting fence
425 (UF), white circles denote deployments downstream from Chilko River (DR) and downstream
426 from the counting fence (DF), and white triangles indicate deployments at the narrow river
427 segments (N). See Table 1 for more information on deployments. The government operated
428 counting fence is denoted in black. The red dot in the lower right inset represents the
429 approximate position of where the study was conducted. The red square on the upper left inset
430 denotes the location of Chilko Lake in North America.

431

Figure 2. Total interactions (m^{-2}) among 30-minute intervals detected between Bull Trout and smolts throughout all DIDSON deployments. Each observation represents a 30-minute interval within a diel period (Daytime: $n = 116$; Nighttime: $n = 86$). Daylight and nighttime hours were determined via <https://www.timeanddate.com/>. Results from the Wilcoxon rank sum test are displayed on the left upper corner. Points are jittered horizontally for visibility. Observations originating from sites upstream of the fence (UF) are in blue and those from other sites are in yellow. The lines in the middle of the boxplots indicate the median, and the left and right edges represent the 25th and 75th percentiles respectively. Whiskers represent 1.5-times the interquartile range.

Figure 3. The number of interactions per m^2 and per unit time (1 hour) detected between Bull Trout and smolts (blue lines and points, left y-axis) plotted alongside hourly smolt density estimates (orange lines and points, right y-axis) across time. Note that during certain hours, smolt densities are not observed because the fence is physically closed to migrants (when orange points are at zero). Grey shading indicates nighttime hours. Plots A - F display interactions and smolt density estimates across different deployment-night combinations (refer to Table 1 for additional information on deployments). The DIDSON was only deployed from 04-25 16:30 – 19:30 and 04-26 16:00 – 16:30 for site N2526 and thus are presented as missing observations.



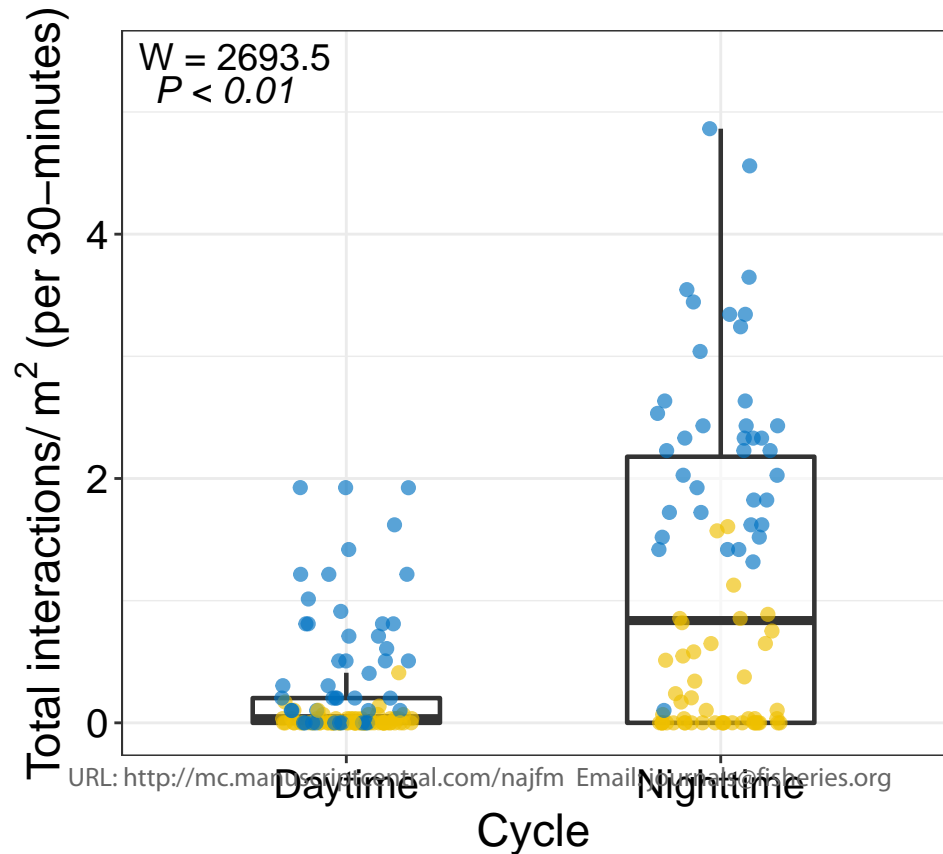
Map of Chilko Lake, British Columbia, Canada (51.294, -124.077). Aerial image of the upper reaches of Chilko Lake shows the positions (white shapes) of where the DIDSON system was deployed from April 20 - 29th, 2016, during the smolt outmigration period. The white square indicates DIDSON deployments upstream of the government operated counting fence (UF), white circles denote deployments downstream from Chilko River (DR) and downstream from the counting fence (DF), and white triangles indicate deployments at the narrow river segments (N). See Table 1 for more information on deployments. The government operated counting fence is denoted in black. The red dot in the lower right inset represents the approximate position of where the study was conducted. The red square on the upper left inset denotes the location of Chilko Lake in North America.

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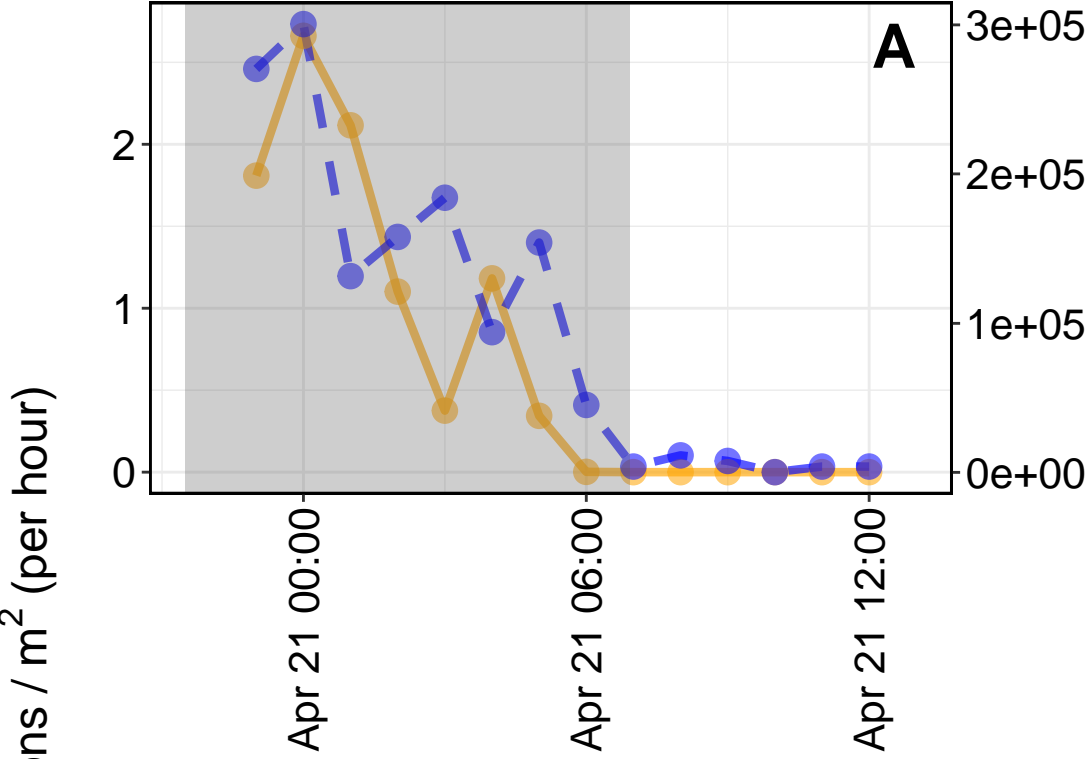
Sites

UF

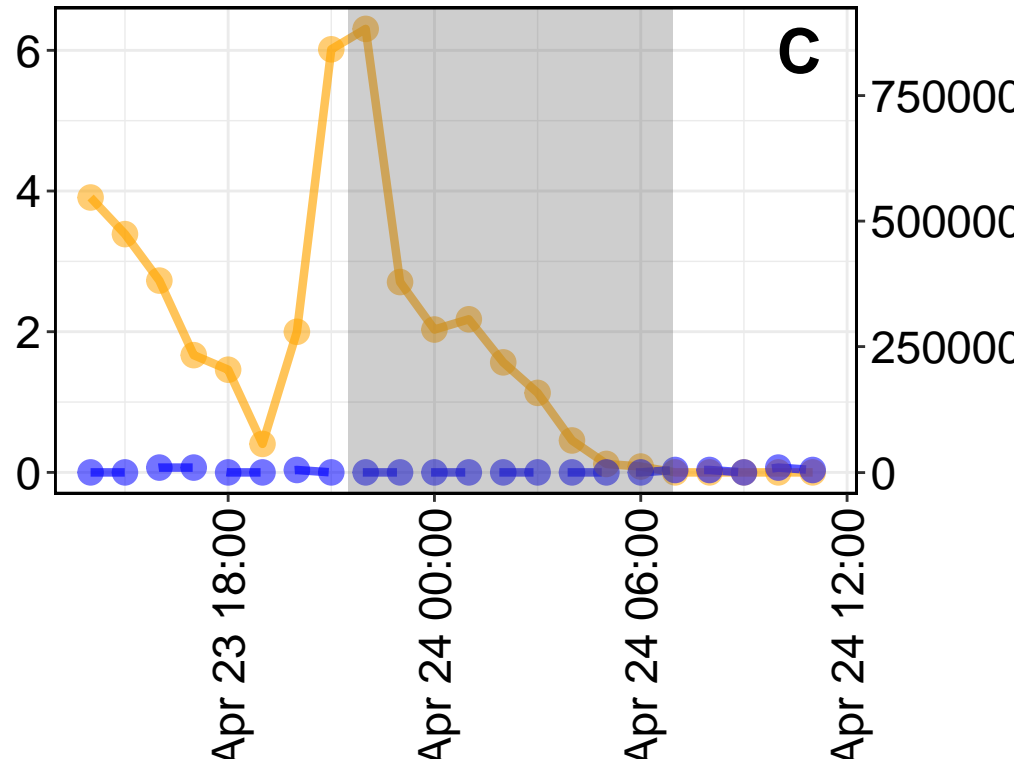
Other



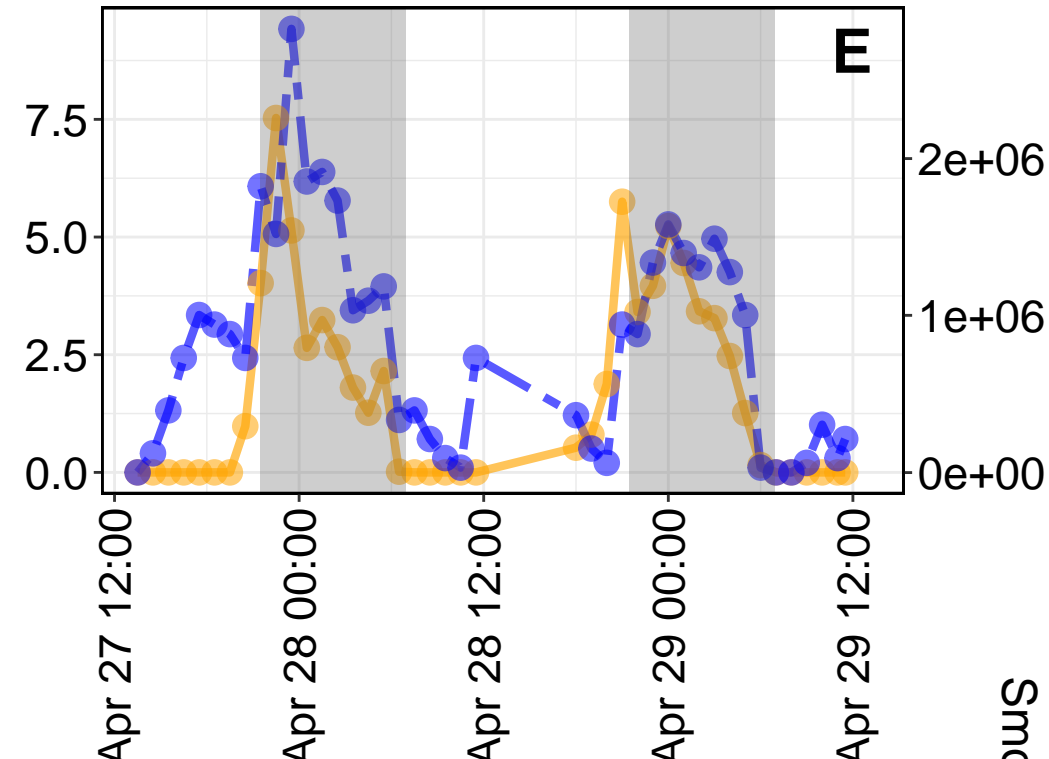
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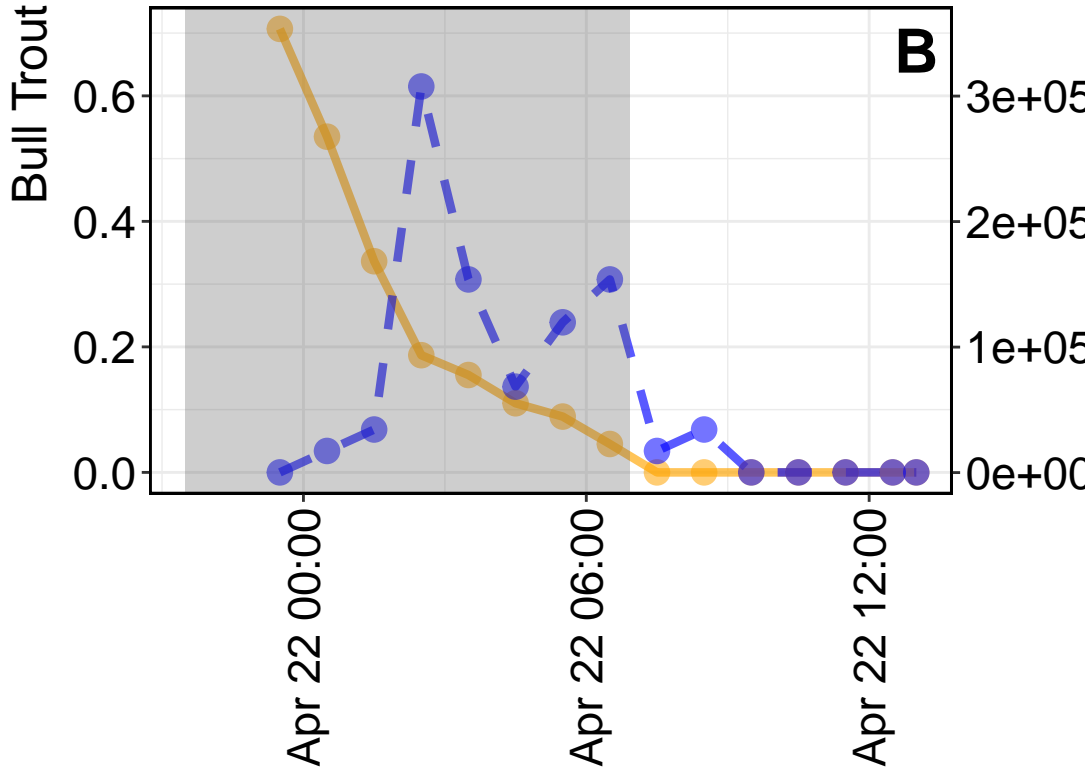
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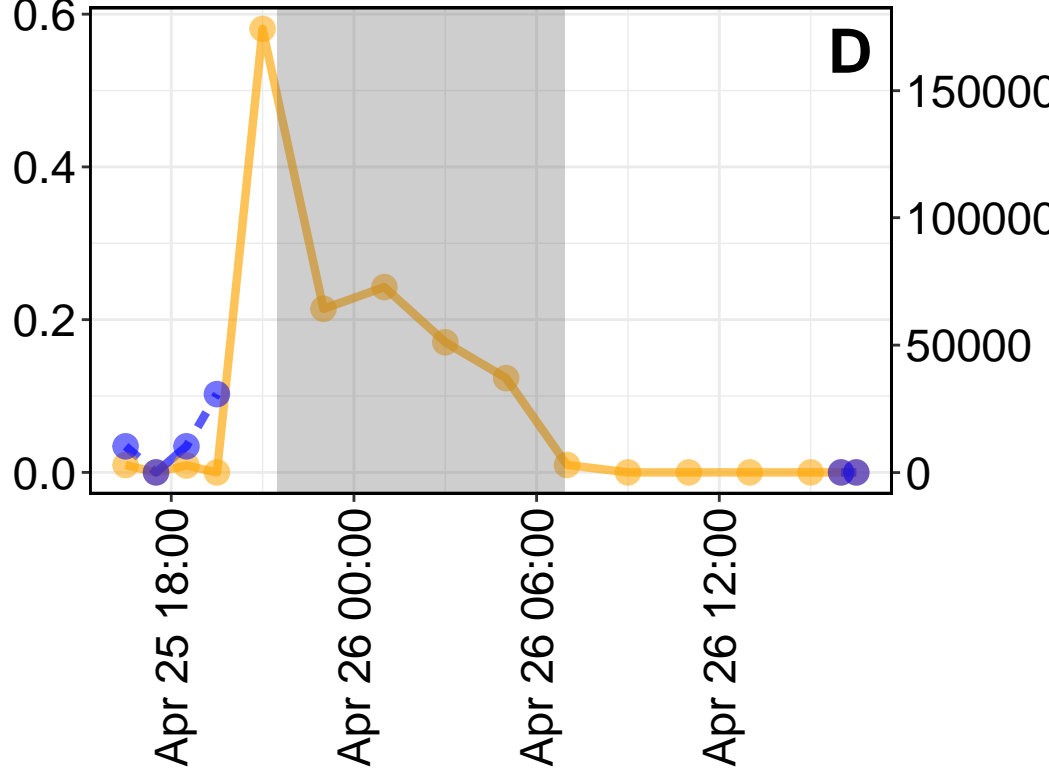
UF272829



DR2122



N2526



N29

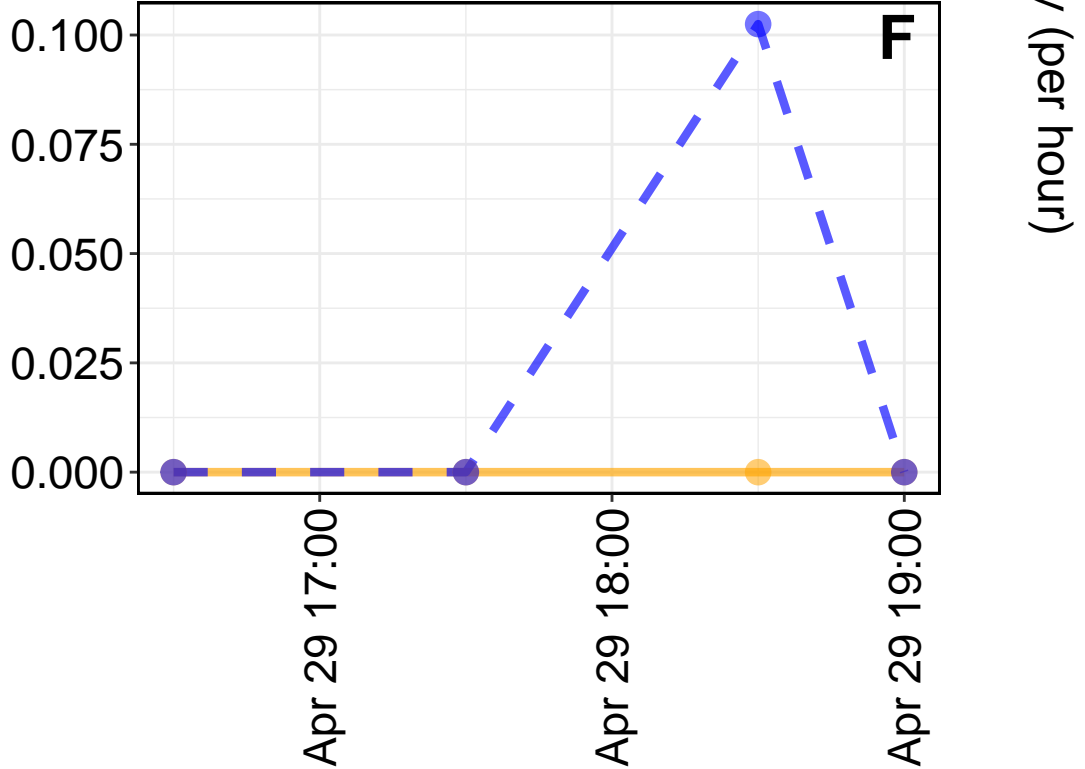
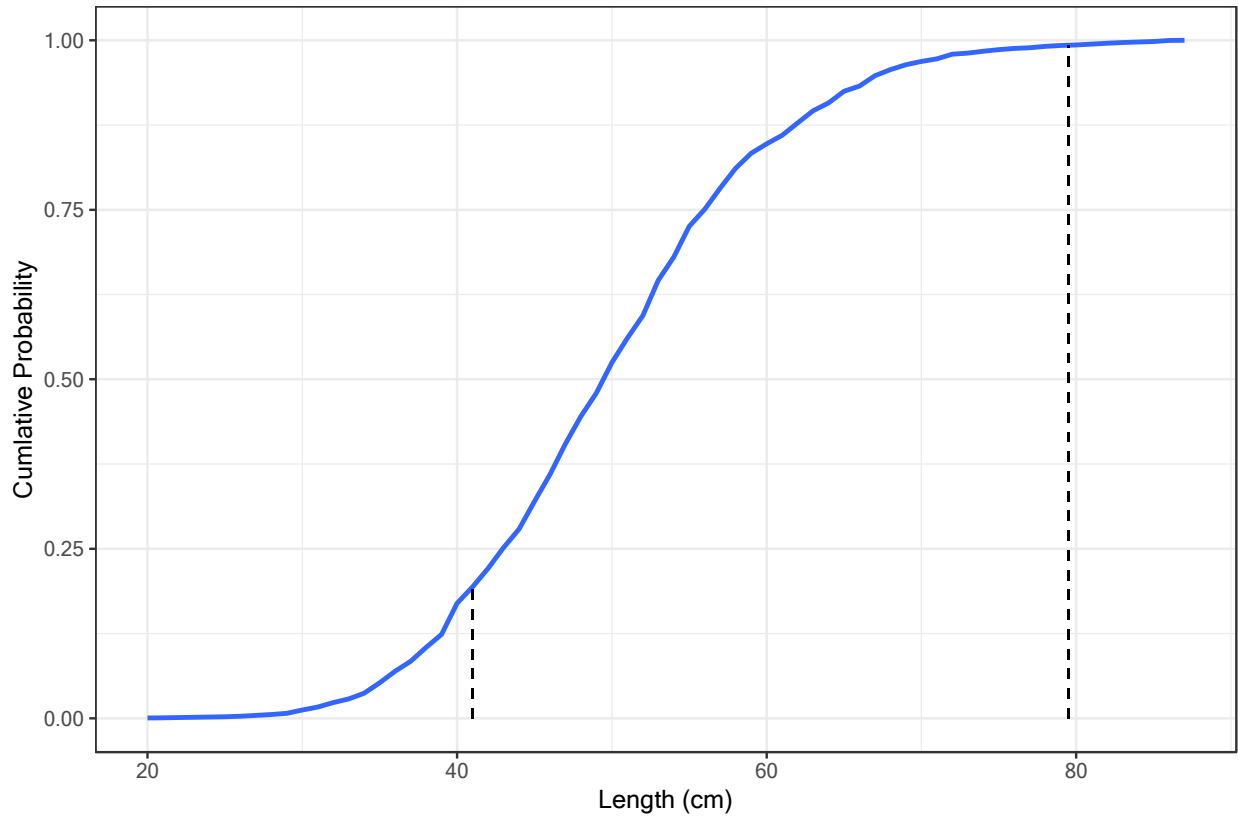




Fig. S1. Counting fence configuration deployed by the Fisheries and Oceans Canada, located in Chilko Lake (T̓silhqox Biny, traditional territory of the Xeni Gwet'in First Nations, one of the six communities forming the T̓silhqot'in Nation), British Columbia, Canada. The counting fence is used to estimate densities of outmigrant smolts and is closed when no smolts are present.

Photo by Marika Gale.



11
12 Fig S2. Empirical cumulative distribution function of presumed Bull Trout lengths (cm)
13 measured for every record interaction. The blue-line is smoothed for visualization purposes.
14 Black dashed-lines represent the minimum (41.5 cm) and maximum (79.5 cm) lengths of Bull
15 Trout observed in Kanigan 2019, which were sampled via hook-and-line and dip netting for
16 telemetry studies.

Response to Reviewers

Please note that while responding to reviewer comments, all line number positions we reference are in the tracked-changes document.

Reviewer 1

Comment #1: Response to "standardized interactions observed between smolts and Bull Trout varied among deployments"; Didson sonar placement details are insufficiently described to allow a more comprehensive understanding of site conditions relative to observations, recommendations and subsequent analysis - i.e. velocities, stream depths, or additional factors that might be considered when reflecting on results. Presented as a proof of concept on a limited study duration as this one might suggest that additional time and resources are needed to meet full publication - this currently would seem to be within an extension note type of publication.

Author response #1: We have reframed our manuscript as a Management Brief – presenting our findings and use of DIDSON as a proof of concept for observing and quantifying predator-prey interactions at fine spatial scales (L127 - 154), but also with a more focused story regarding the fence (in response to the Associate Editor's comments). We have also added text (Methods L176, 188 - 193) that provides further environmental context (site depth, width, and river discharge) for our data.

Comment #2: Line 36: might be good to articulate "broader scale" - assume this is elsewhere?

Author response #2: Thank you for the suggestion. We have clarified "broader scale" to be more direct – that our results corroborate the prior telemetry and diet studies (L33,41) in the same system.

Comment #3: Line 136: generally identifiable - given piscivore rainbow occur in Chilko is there further comment that could be provided on the ability to provide frequency of occurrence or distinction of species - i.e. acknowledgement of uncertainty, reconciled against video and Didson timestamps?

Author response #3: We have provided further comment on the occurrence of smaller sized fish observed via DIDSON (L220-230). In short, these other (non Bull Trout) fishes are indeed of smaller body size (from angling as well as GoPro footage) and do not appear to eat on smolts, at least regularly (from unpublished diet data); thus, they are unlikely to "interact" with smolts in the way we describe and observe via the DIDSON. Furthermore, we provide a relative estimate of uncertainty with respect to individuals observed that may not have been from Bull Trout by comparing the empirical cumulative density function of measured DIDSON Bull Trout lengths and minimum size estimates of Bull Trout in the same system obtained via hook-and-line sampling (Kanigan 2019); 19% of fish identified of Bull Trout are of small enough size to potentially be another species (Fig. S2 and text from L354-369). This 19% is likely an overestimate, as angling from Kanigan 2019 likely targets larger bull trout; thus many of these smaller fish are also likely bull trout.

Reviewer 2

Comment #1: *Lines 91 – 94: The 2 objectives are redundant. Recommend rewording to: “to investigate spatial and temporal differences in potential Bull Trout feeding activity relative to smolt density” Or “determine if Bull Trout activity is synchronized with Sockeye Salmon migrations.” I prefer the latter.*

Author response #1: We have used the reviewer’s second suggestion. However, the spatial variability is still important – it is possible that in one site Bull Trout activity is synchronized, and others not (indeed, this is what we observed). So, we added a third objective, but it is more specific (“determine if such synchrony is location-specific”). (L129-154). We also added an objective to simply compare amount of activity among sites to better match our statistics and in response to comments from the Associate Editor.

Comment #2: *Supplementary Figure: A photo of the counting fence set up at site would be helpful to readers to understand how constricting the fence may be and where the array was set up relative to the fence*

Author response #2: We have added a supplementary figure of the counting fence, as suggested (Fig. S1).

Comment #3: *Lines 113 and 116: Include distance between fence and array*

Author response #3: We have provided more details on the location of the DIDSON deployments (L176-177).

Comment #4: *Lines 121-123, Table 1: The detection window area for the second deployment at UF is much smaller than during the first deployment and all other locations. Why was the detection window changed between deployments of UF and could this inconsistency impact your conclusions?*

Author response #4: We used different window areas purely for exploratory reasons (to see if one window would perform better or not; however, our ability to identify bull trout and predator-prey interactions were consistent across window sizes (larger window did not result in a large enough loss of resolution to impair our abilities). Furthermore, we standardize our metrics for statistical tests per unit area (per m² per time interval) which should help address such bias. However, if this inconsistency were to impact our conclusions, we would expect to find a larger proportion of zeros (no interactions over a 30-minute time window) observed in the smaller detection window compared to the larger one. However, this was not the case when comparing between parallel sites (UF2021: 29.27 m²; UF272829: 9.87 m²). Specifically, UF2021 with the larger window (0.25) had a greater proportion of zeroes than UF272829 (0.12) with the smaller window. We added this qualitative comparison to our text (L354-369).

Comment #5: *Lines 131-133 : What does “reacted to” mean? I assume you could visualize the cloud of smolts moving rapidly away from a larger shape? Please include more detail so these methods could be easily replicated by another researcher.*

Author response #5: We have clarified what “reacted to” means to hopefully improve replicability. Furthermore, we have attached supplementary videos to provide a couple examples of what constituted an interaction (L203-206, Supplementary Video 1 and 2).

Comment #6 *Lines 135-137: “We measured...”. Did you measure Bull Trout as part of this study? If so, please add to methods and results. If not, please clarify. Provide specific size ranges of Mountain Whitefish and Rainbow Trout to strengthen your argument that larger fish were probably Bull Trout. Or, be more clear that you assumed larger fish (over a specific size, or characterized by a specific presentation in the video) were Bull Trout. Discuss this assumption and the implications in the discussion.*

Author response #6: We did measure Bull Trout as part of this study and have provided methods and results associated with these measurements. We do not have direct length measurements of Mountain Whitefish and Rainbow Trout, but they tend to be smaller (15-30 cm length) in these habitats and during the smolt emigration, such that only the largest individuals overlap with the smallest potential bull trout (24 cm) measured via DIDSON. We also use measurements of Bull Trout length observed in the field via hook-and-line sampling (Kanigan 2019), to compare the lower bound of an empirical cumulative density function to understand the probability of observing a Bull Trout individual that was ≤ 41 cm (about 19%) (minimum Bull Trout size captured by hook-and-line). Note that this uncertainty estimate is conservative considering that Bull Trout of smaller length are very likely to exist in the Chilko system (but anecdotally tend not be present in the system at this time, potentially due to competition with larger bull trout(?) as well as less likely to be caught by angling). We have added text to the Methods (L221 - 230) and Results (L354-369) to provide these details. Also see response to Reviewer #1, Comment #3.

Comment #7: *Line 167: As you are investigating temporal patterns of Bull Trout activity relative to smolt migration, the fact that the fence is closed during the day is a pretty important element to the study design. Do you mean the fence is physically closed to migrating fish? If so, please add this to Paragraph 100-107 so readers can keep this in mind while considering the data. Could also clarify in Figure 3 – I’m not sure if smolt densities were naturally zero during the day or if the fence was physically closed. The only day time fence closure mentioned in Figure 3 was for N29.*

Author response #7: Thank you for pointing out these important details. We have clarified that the fence was closed when smolts were not present at the counting fence site – typically during the day (L168 - 169). We have added this clarification to the requested paragraph and the figure caption. Furthermore, we have added points to Figure 3 to better convey periods where the counting fence was closed, which is also reflected in the figure caption.

Comment #8: *Line 182: Mean value is missing unit*

Author response #8: Thank you for pointing this out. Missing units have been corrected throughout.

Comment #9: *Lines 199-213: Although a significant relationship between diel cycle and interactions was found when the data were aggregated, follow-up analysis showed that this was only observed at the location upstream of the fish fence. Therefore, I don't agree there is enough evidence to support the general conclusion that interactions increase during nighttime hours.*

Author response #9: We appreciate this comment. However, we believe that context is important for the other deployments that did not show significant differences in interactions between day and night. For example, we could not make diel comparisons for two of the three non-significant deployments, as we only had data for daytime periods in both (N2526 and N29). For DF2334's deployment, very few interactions were observed regardless of diel period and thus overall low bull trout activity. And after including zeros (as requested by the Associate Editor; comment 7), deployment DR2122 is now also significant (daytime mean = 0.02 m^{-2} ; SD = 0.05 m^{-2} , nighttime mean = 0.10 m^{-2} ; SD = 0.11 m^{-2} ; $W = 49.5$; $P = 0.01$; Fig. 3B). We have changed the text to reflect this (L335 – 336). Regardless, we do think we have evidence of more bull trout activity at night than during the day broadly. However, given how weak our power is throughout the study, we recognize the need to be careful with our tone. Thus, we have modified these sentences to be softer in our language (L395 - 396) to recognize caveats.

Comment #10: *Lines 225-231: Would also recommend monitoring Bull Trout x smolt interactions in systems with no fish fences.*

Author response #10: We appreciate the excellent suggestion – we have added this to the end of this paragraph (L393 - 394).

Comment #11: *Figure 1: One of the white triangles appears to be on land, is this correct?*

Author response #11: Thank you for catching this error – a couple of our locations were misplaced (N deployments); fixed in the revised manuscript.

Comment #12: *Figure 2: Recommend color coding data from UF site versus all other sites so readers understand diel pattern was observed at UF site only.*

Author response #12: Thank you for the suggestion. We have color-coded observations from the UF site to better articulate that the diel pattern was observed only at the UF site.

Comment #13: *Figure 3: Recommend using similar range for Y axes as much as possible, or at least group deployments with similar Y axes in the same row. Remove yellow line from N29, as fence was closed. Missing period of Bull Trout interactions in N2526.*

Author response #13: Figure 3 has been altered such that ranges for the Y axes are as similar as possible across group deployments. The missing period of Bull Trout interactions in N2526 are present because the DIDSON was not deployed during that period (clarified in the figure caption). Nonetheless, we have indicated and clarified this in the caption associated with Figure

3. We chose not to remove the yellow line from N29 to reflect fence closures and to keep Figures 3A-F consistent.

Associate Editor

Comment #1: **Overview:** I don't see a clear hypothesis being tested, nor uncertainty that you are resolving. Potentially cool work, but please put it in a specific context of a *problem* that you *solved*. As written and described, I don't see much new knowledge here; bulls are known to be nocturnal sometimes, predators feed on available prey, we knew the diet of bulls near the counting fence was seriously on sockeye. What is the key point of this data/study? Where is the novel finding?

I think there is something here, but it needs significant re-crafting to focus on a problem/solution. Simply looking at the graphs, it looks like only one set of scans/counts can be used show an interesting pattern (Figure 3e). The other data is more or less fragmentary.

Find a clear test or problem, and re-work your data to answer that. Could be a neat little paper.

Author response #1: We appreciate the Associate Editor's thoughtful comment, and we feel the revised manuscript is improved due to this suggestion. We have simplified our context – we want to determine or demonstrate if DIDSON can be used to observe and quantify predator-prey interactions in a system where they are known to occur at broader scales (the general lake-river outlet), and to assess if feeding behaviors occur directly at the fence to verify/confirm prior studies (these previous studies provided gut contents, but not confirmation of where behaviors/consumption occurred). In response, our objectives (L129-154) are simplified but also clearer. We have edited text throughout the manuscript to reflect our new focus.

Comment #2: **Title:** consider stating key finding, rather than method, in a title. Makes it easier to attract interested readers.

Author response #2: We have modified the title slightly to be more active. But given this paper is largely methods-focused, we kept the essence similar ("Acoustic imaging to observe predator-prey interactions between Bull Trout (*Salvelinus confluentus*) and migrating Sockeye Salmon (*Oncorhynchus nerka*) smolts"). We felt adding in additional findings (fence-based details) would make the title too long while still including the method. We also felt that specifically mentioning the fence in the title might be too strong given our limited sample sizes.

Abstract:

Comment #3: L31- odd concept "uncertain if these predator-prey patterns exist at finer spatial scales" One would assume they must exist. Specifically, where is the uncertainty that you are resolving? And finer spatial scale is not your key finding. It was temporal scale.

Author response #3: We acknowledge our original text was vague. First, we have restructured text to make it clear that we are testing DIDSON's capabilities in a system where we know predator-prey interactions are occurring (L32 – 37). Second, although stomach contents revealed bull trout captured at the fence to have more smolts in their stomachs, this assumes that such consumption occurred at or close to the location of capture (i.e., that bull trout feed heavily on smolts at the fence). Although likely a valid assumption, the DIDSON confirms that predator-prey interactions here are more frequent than elsewhere. Further, consumption and feeding activity might not have a direct relationship (if feeding is "easier" in one location vs another, or if bull trout are feeding elsewhere prior to being captured in prior diet studies) (L38). We have integrated these ideas into the text throughout and removed "uncertain if these predator-prey patterns exist at finer spatial scales".

Comment #4: L38 – *do you mean daylight risk? If predation is high at night, they haven't avoided risk.*

Author response #4: Thank you for pointing this out. We have clarified this to reflect presumed minimized predation risk during the daytime (L42).

Intro:

Comment #5: L68-69 – *why do we need to know this information? So far, the whole intro is about Sockeye.*

Author response #5: We have removed ancillary information on Atlantic Salmon for clarity, given the focus on Sockeye Salmon smolts. We have also removed information on predator-swamping here to be more concise.

Comment #6: L70 – *I appreciate your use of First Nations language as place name (well done!). Whose territory and language?*

Author response #6: Chilko Lake is under the territory of the Xeni Gwet'in first Nations and the first language of the Xeni Gwet'in is the Tsilhqot'in language. The text has been altered to reflect this – thank you for this point (L111 – 112).

Comment #7: L81 – *circular argument. We don't know smolts responded. Do they migrate in daylight everywhere without Bull Trout? You see night predation and migration. Do we have evidence of what caused which? Are smolts responding to something else? In my experience, Bull Trout can also be nocturnal in systems without prey fish. Picky point, but you've jumped to a conclusion, and should ponder alternates.*

Author response #7: We have softened our language to clearly state that we presume nocturnal smolt movements and synchronization is to reduce predation (L123 – 124). The relationship does seem likely, given that once smolts are in more turbid waters (Chilcotin and Fraser Rivers), they no longer migrate nocturnally but at all times of the day (Clark et al. 2016).

Comment #8: *L83 – still don't know why this is important to your “problem – solution” questions.*

Author response #8: Although we removed sentences of a similar notion in an earlier section, we chose not to remove information on predator-swamping here, given that the observed phenomenon provides additional context for Chilko Lake being an ideal study system to observe predator-prey interactions using DIDSON (it requires an immense number of prey to be able to “swamp” predators. Please also see our response to your comment #1 regarding clarifying our objectives.

Comment #9: *L85-91: methods are described before we know what question is being answered. It seems like this is a sonar project as its priority, rather than an “understand something important and useful about fish” project.*

Author response #9: We have reframed our text to reflect our problem-solution question of our study to better accommodate this text. Specifically, we illustrate that the present study is a sonar project as its priority, and our aims are to: determine if DIDSON can indeed observe predator-prey interactions in our model system, particularly where we assume intensive consumption is occurring (the fence) to ground-truth prior studies, and determine if such observed predator-prey interactions have correlates either by location or time (diel periods or across prey densities). (L129 – 154).

Comment #10: *L92-94 – state what you were trying to answer, or disprove. “Investigate” is too vague. Was the synchronicity in doubt? What is the value in showing non-synchronicity? It can be assumed that predators will hunt prey when the prey is available. Why do we need a study? Just ponder that and find an answer, and make it clear to the readers why this data/study matters.*

Author response #10: We have clarified this section. We now explicitly state the aims of this study and attempt to better convey the value of the study (L129 – 154).

Methods:

Comment # 11: *L136- any direct evidence of sonar images = bull trout?*

Author response #11: Yes, for some deployments (sites near the fence) we were able to at times use flashlights to see the bull trout sitting by the DIDSON. We also use GoPros in the system to confirm bull trout in the areas of bull trout deployment, and that bull trout were the primary species present. We have conducted work in this system for ~ a decade, and bull trout are consistently seen in the positions detected by the DIDSON.

Comment #12: *L158 – was day just when sun in sky, or was twilight included? Hence, were interactions crepuscular, rather than purely nocturnal or diurnal?*

Author response #12: Interactions classified as purely diurnal and nocturnal. We have since clarified this in the text (L272-273).

Comment #13: *L144-148 – using quite two different sampling frames and correcting down to per m² might be introducing bias. i.e., the small frame would have more zeros. Were the differences in large and small frame data checked for this bias?*

Author response #13: We believe that potential biases introduced from using two different sampling frames and correcting down to per m² are negligible. For example, when comparing the proportion of zeros between the same sites (UF) observed with different areas (UF2021: 29.27 m²; UF272829: 9.87 m²), we found that UF2021 (0.25) had a larger proportion of zeros had a smaller proportion of zeros (0.12), relative to UF272829 (0.12). We have reflected this in the text (results; L348 – 354).

Comment #14: *L165-168 – Your point was to show bull trout feed at night, but you exclude most day data. Really? Explain why this is not a potential source of bias?*

Author response #14 : The goal of this analysis was to assess degree of correlation between the number of Bull Trout interactions and smolt densities (i.e., to understand whether Bull Trout are responding to higher smolt densities). Nevertheless, we recognize that there is potential to bias our results by simply removing observations where smolts were not passing through the counting fence. Thus, we have removed this statement and re-ran our analyses (same analysis, but with zeros included) to reflect this change. These changes did not result in differences in the interpretation of results, but text in the Methods and Results were amended.

Results

Comment #15: *L178 – lowest number of interactions, but no smolts on graph. If the smolts were absent, how did interactions occur? What other metric of smolt abundance is more useful?*

Were there no bull trout below the fence? Figure 3c suggests so. Or where there no sockeye at the Narrows (fig 3f)

Author response #15: Although no smolts were observed to pass through the counting fence during the daytime periods, we observed smolts milling below the fence, and thus, interactions could occur (zero smolts passing through the fence is not the same as zero smolts in the system). At present, we do not have another metric of smolt abundance that may be more useful. We have clarified in the text that smolts can be present despite the fence being closed if they are downstream of the fence. We have also further clarified that the fence is typically closed during daytime hours (L168 – 169).

With respect to Figure 3C, very few (but more than zero) Bull Trout were observed below the fence. However, both Bull Trout and interactions occurred at low numbers compared to other sites and times during which the DIDSON was deployed (so it appears to be at zero, but if you look closely, the blue points often fall just above zero). Furthermore, no Sockeye Smolts were observed at the counting fence during the period where the DIDSON was deployed at Narrows (Fig 3F), which is why smolt density estimates are reported as zeros. We have provided additional clarification in the figure caption.

Comment #16: L182 – confused, based on methods statement. Did you use daylight data or partial daylight data, or what? You show daylight data.

The whole results section would be much clearer if you were testing a hypothesis, or describing a pattern in relation to a hypothesized patterns. As it reads, it is not very informative.

Author response #16: We use both daytime and nighttime data to evaluate how the number of bull trout interactions might differ across sites and diel periods. We have clarified the specific hypotheses and objectives throughout our manuscript, and hope that makes our results section clearer.

Comment #17: L426 (caption) – what do n-values represent? I don't understand that many "diel cycles" can be fit into 10 days in April.

Author response #17: The number of observations made across 30-minute intervals/deployments throughout our study and are differentiated between daytime interactions and nighttime interactions observed. We have clarified this in the caption.

Discussion

Comment #18: L200 – if this is a result, put it in that section and only discuss, not present. Or state it as an interpretation of previously shown graphs/data. And, to my eyes, only graphs a and e show that relationship. The others make you wonder "where were the bulls, where were the smolts?" I would be more interested in the pattern of increasing/decreasing smolts and bulls, and not a simple day/night comparison, with the day data being incomplete, and the night data actually quite thin (only one set of data shows pattern over day and night, = graph e).

Author response #18: We have restructured our Discussion to more tightly link to the utility of the DIDSON and the impacts of the counting fence. We believe that the day-night comparison still remains valuable given the strong diel nature of this system and have decided to keep it within the manuscript, but focus more on the fence vs elsewhere (and the relationships between bull trout and smolt densities remain as in the original manuscript)

Comment #19: L205-208: sort of circular. You don't present data to show bulls are diurnal at other times, without smolts. Did they respond by changing a normal pattern, or do bulls feed on prey when prey is available? And why does this matter? Predators eat prey when prey are available, and we already knew bulls eat sockeye. I'm having trouble seeing a novel finding here.

Author response #19: We have simplified this statement, acknowledging that we are simply observing Bull Trout being more active when prey are available, and that further studies would be needed to examine Bull Trout behavior at other times (L373-375, 391 - 394).

Comment #20: L214-232: Odd. We knew that bulls feed a lot near the fence, so what is the point of this paragraph?

Author response #20: Although Bull Trout captured near the fence do indeed contain large numbers of smolts in their stomach, it is unclear whether these prey items originated from predation events at the counting fence (which had been assumed up to this point) or elsewhere. We have reflected this point throughout the manuscript, and thus believe it justifies retaining this section within the text.

Comment #21: L233-240: *not really necessary here. Not part of this study, not a data set easily collected by this methods, so...not relevant here. Unless I missed a point, so change my mind.*

Author response #21: We have removed this paragraph as we agree that this is not a data set easily collected by the methods used in this study and tangential for this short Brief.

Comment #22: L251-252 – *if this is the main conclusion (i.e., bulls feed more at the counting fence), how does it differ from Furey et al. 2016b? Why is this a new conclusion from your data?*

Author response #22: Our results differ from Furey et al. 2016b because conclusions drawn resulted from bioenergetic simulations and stomach content analyses (diet studies provide a snapshot of what is in the guts, with assumptions being made in terms of the time period over which contents were consumed AND where consumption occurred). Thus, although it was assumed Bull Trout were indeed more easily consuming smolts at the fence, the DIDSON confirms that feeding activity here is intense. We have carried this point throughout the manuscript to better communicate the novelty of the present study.

TITLE: ~~Using~~ Aacoustic imaging ~~to observe potential~~ observes predator-prey interactions between Bull Trout (*Salvelinus confluentus*) and migrating Sockeye Salmon (*Oncorhynchus nerka*) smolts

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Abstract:

Annual migrations by juvenile Pacific Salmon (*Oncorhynchus spp.*) smolts are predictable, and presenting present opportunities for predators to aggregate and exploit these seasonal prey pulses. Directly observing predator-prey interactions to understand factors affecting predation may be possible via Dual-frequency Identification Sonar (DIDSON) acoustic imaging. Within Chilko Lake, British Columbia, Canada, prior large-scale telemetry and stomach content analyses suggested the outmigration of Sockeye Salmon (*Oncorhynchus nerka*) smolts influences the movements and aggregations of Bull Trout (*Salvelinus confluentus*) that feed extensively on smolts during their outmigration. Bull Trout captured at the government-installed counting fence exhibited high consumption of smolts, but it is only assumed that feeding occurred directly at the fence. It is uncertain if these predator-prey patterns exist at finer spatial scales. We used Dual-frequency Identification Sonar (DIDSON) acoustic imaging to assess fine-scale predator-prey interactions between Sockeye Salmon smolts and Bull Trout over 10 days during the 2016 smolt outmigration. We found that smolt-Bull Trout interactions were correlated with smolt densities were correlated with feeding activity of Bull Trout upstream of a governmentat installedthe counting fence used to estimate smolt numbers, consistent with observations at broader the prior diet studies in the system. Predator-prey interactions were also closely coupled with nocturnal migratory behaviors of Sockeye Salmon smolts, presumably to minimize predation risk. These results demonstrate that DIDSON technology can record interactions between predators and migrating prey at a resolution to identify variability in space and time. Furthermore, we provide further evidence that the migrations of Sockeye Salmon smolts affect the behavior of Bull Trout.

47 Furthermore, this fine-scale imagery and are important to this predator's ecology and, and
48 provides insight on the role of anthropogenic structures (e.g., counting fences) in mediating
49 predator-preysuch interactions.

For Peer Review Only

Introduction:

Pacific Salmon (*Oncorhynchus spp.*) are integral to the culture, livelihoods, and identity of First Nations and represent valuable recreational and commercial fisheries (Gislason et al. 2017). Ecologically, Pacific salmon mediate trophic relationships, where adult carcasses contribute significant nutrients to both stream and riparian ecosystems (Naiman et al. 2002). However, many species of Pacific Salmon, including Sockeye Salmon (*O. nerka*) of the Fraser River basin in British Columbia, have experienced substantial population-level declines (Peterman and Dorner 2012), resulting in threatened or endangered populations (COSEWIC 2017).

Sockeye Salmon juveniles typically rear in freshwater lakes for 1-3 years before they begin their seaward migration as smolts, a migration that requires a suite of behavioral and physiological changes (i.e., smoltification; Young et al. 1989) to cope with saltwater. While migrating, smolts also face predation from piscivorous fishes, birds, and mammals (Beamesderfer et al. 1996; Blackwell and Juanes 1998; Osterback et al. 2013; Furey et al. 2015;). As such, smolts exhibit a variety of behaviors to reduce their predation risk. For instance, both Sockeye Salmon and Atlantic Salmon (*Salmo salar*, which also undertake seaward migrations) smolts can migrate nocturnally (Ibbotson et al. 2006, 2011; Clark et al. 2016; Furey et al. 2016a), presumably to minimize detection by visual predators. Furthermore, smolts can synchronize their migrations to find safety in numbers or “swamp” predators with large pulses of conspecific migrants (Furey et al. 2016a, 2021b). However, how densities of migrating smolts could impact the foraging behavior of predators is less well studied. Given that predation is often the ultimate source of mortality for a variety of proximate factors ((Miller et al. 2014), methods that allow for direct monitoring of predator-prey interactions are valuable.

One method to passively observe predator-prey interactions is Dual-Frequency Identification Sonar (DIDSON). The DIDSON system uses acoustic imaging, ~~allow ingto~~ ~~passively~~ observe of fish behaviors, size distributions, and relative abundances, including in turbid waters and at night (Burwen et al. 2010; Crossman et al. 2011; Martignac et al. 2015; Moursund et al. 2003; Maxwell and Gove 2007; Nichols et al. 2014). ~~This technology can also be used to assess fish size distributions and relative abundances (Burwen et al. 2010; Crossman et al. 2011; Martignac et al. 2015).~~ Here, we use DIDSON in a system with known smolt-predator relationships to determine if the technology can provide *in situ* passive observations of predator-prey interactions.

Chilko Lake (or T̓silhqox Biny, traditional territory of the Xenigwet' in First Nations, one of the six communities forming the T̓silhqot' in Nation), British Columbia, is home to one of the largest populations of Sockeye Salmon in Canada, and consequently this population is intensively studied (Bradford et al. 2000; Irvine and Akenhead 2013). Each spring, 10 - >40 million Sockeye Salmon smolts (~96% age-1 smolts, ~4% age-2 smolts; Irvine and Akenhead 2013) emigrate from the lake towards the ocean. Acoustic telemetry revealed that the initial migratory corridor in the Chilko River (clear and slow-moving water) is high-risk relative to the turbid waters of the Chilcotin and Fraser Rivers downstream (Clark et al. 2016; Rechisky et al. 2019). Bull Trout (*Salvelinus confluentus*) feed extensively- on migrating Sockeye Salmon smolts (Furey et al. 2015), with Bull Trout caught at the Fisheries and Oceans (DFO) counting fence near the Chilko Lake outlet feeding at the highest rates (Furey et al. 2016b). Thus, the fence may be facilitating predator-prey interactions, but fine-scale observations at the fence and other sites are needed to confirm that indeed Bull Trout are actively foraging directly at this structure. ~~and appear to synchronize their movements with the timing of the Sockeye Salmon~~

smolt out-migration period (Furey and Hinch 2017; Kanigan 2019). Furthermore, Bull Trout in Chilko also appear to selectively feed on small smolts or those with specific infections (Furey et al. 2015, 2021a). In response, smolts, presumably to minimize predation risk, migrate nocturnally and synchronize their movements to numerically overwhelm or swamp predators in the clear upper-river reaches of Chilko Lake (Clark et al. 2016; Furey et al. 2016a). Thus, this system is ideal for investigating fine-scale predator-prey interactions.

One method to passively observe predator-prey interactions is Dual-Frequency Identification Sonar (DIDSON). The DIDSON system uses acoustic imaging to allow for passive observations of fish behaviors, size distributions, and relative abundances, including in turbid water and at night (Burwen et al. 2010; Crossman et al. 2011; Martignac et al. 2015; Moursund et al. 2003; Maxwell and Gove 2007; Nichols et al. 2014). This technology can also be used to assess fish size distributions and relative abundances (Burwen et al. 2010; Crossman et al. 2011; Martignac et al. 2015). The present study uses DIDSON to investigate the present study investigates if DIDSON can be successful at observing and quantifying predator-prey interactions at the Chilko Lake-River outlet during the smolt outmigration by determining: 1) where Bull Trout are most frequently interacting with migrating Sockeye Salmon smolts, 2) if Bull Trout activity is synchronized with Sockeye Salmon migrations investigate both spatial and temporal differences in potential Bull Trout feeding activity and 3) determine if any such synchrony is location-specific (at the counting fence, vs other locales upstream and downstream) Bull Trout activity is synchronized with Sockeye Salmon migrations.

<A>Methods:

Study area.—

This study was conducted at the outlet of Chilko Lake, British Columbia, Canada (51.294, -124.077; Fig. 1). Chilko Lake is a 180 km², high elevation (~1100 m.a.s.l) lake that has a north-south orientation and is approximately 65 km long. Each spring, Fisheries and Oceans Canada (DFO) installs a counting fence to estimate the numbers of outmigrant smolts. The DFO counting fence is located approximately 1.3-km downstream from Chilko Lake (Fig. 1; Fig. S1) and has been deployed annually since the early 1950s, with the exception of 2017 and 2020 (Irvine and Akenhead 2013). Smolts are funneled through a constriction and pass over a white background where digital photographs are taken at regular time intervals to estimate hourly densities. If no smolts were present, the fence was closed and smolts could not physically pass; these resulted in time intervals with zero smolts.

DIDSON deployment.—

The DIDSON system (Sound Metrics, Bellevue, Washington) was deployed at five different locations (Fig. 1) from April 20 - April 29 in 2016 during the Sockeye Salmon smolt outmigration (Table 1). We deployed the DIDSON upstream of the counting fence (site UF; 51.625, -124.142; Fig. 1) from April 20 – 21 2016 and April 27 – 29 2016, approximately 1-m from the fence's edge. We also stationed the DIDSON downstream of Chilko River (site DR; 51.626, -124.142; Fig. 1) from April 21 – 22 2016 and downstream of the counting fence (site DF; 51.625, -124.141; Fig. 1) from April 23 – 24 2016. Finally, the DIDSON was positioned at the outflow of Chilko Lake (site N; 51.615, -124.152; Fig. 1) from April 25 – 26 2016 and April 29, 2016 (site N; 51.615, -124.151; Fig. 1). The DIDSON was deployed on a custom-built metal tripod. This frame allowed the DIDSON to be placed ~0.5-m above the riverbed and kept the

sensor between level to the water's surface and -15° and perpendicular to the flow. Given that DIDSON deployments occurred before freshet, flows were generally low but increasing from $\sim 20 \text{ m}^3/\text{s}$ to $\sim 30 \text{ m}^3/\text{s}$ between the first and last deployments (Water Office of Canada station 08MA002). Site N at the outflow of Chilko Lake is much deeper ($\sim 9\text{-m}$ maximum depth) than the river sites ($\sim 0.75 - 1\text{-m}$ deep); the river width varies from $\sim 50\text{-m}$ wide (at the lake outflow; site N) to $\sim 80\text{-m}$ wide at other sites. We used two different configurations of the DIDSON: the first constrained the detection range to ~ 5 meters and the second to 10 meters into the river channel (Table 1); ~~we used both configurations for exploratory purposes, with the outlet or river width 70-100 m depending upon the site.~~

DIDSON data collection and video processing.—

Approximately 100 hours of DIDSON acoustic sonar videos were recorded and evaluated across the deployments. Video files from the DIDSON were analyzed in 30-minute intervals and viewed using the DIDSON Control and Display software (Sound Metrics, Bellevue, Washington). In each video, interactions between Bull Trout and out-migrating Sockeye Salmon smolts were recorded. ~~For the purposes of this study, w~~We defined interactions by the following criteria: 1) Bull Trout were actively moving towards Sockeye Salmon smolts; or 2) the proximity of Bull Trout resulted in Sockeye Salmon smolts dispersing or changing direction or speed rapidly; (e.g., and 3) Sockeye Salmon smolts actively swam away from a Bull Trout when in proximity (Supplementary Videos 1 & 2). Sockeye Salmon smolts were easily identified as “clouds” of small fish on the DIDSON. ~~as any instance when it appeared that either Bull Trout or Sockeye Salmon smolts (or both) reacted to the presence or proximity of the other within the video.~~ We also measured the total length (TL) to the nearest cm of each Bull Trout using the

“measure” tool. Bull Trout are the dominant piscivore present during the migration to feed on smolts (Furey et al. 2015, 2016b) and are generally much larger in body size (we measured at ~25-85 cm in length) than other fishes present at lower abundances (~~mountain~~ Mountain whitefish Whitefish and ~~R~~rainbow ~~T~~trout primarily, which when observed were < 30 cm), and thus were generally identifiable on the DIDSON. For deployments near the counting fence, Bull Trout were observed visually, confirming DIDSON observations. In addition, rainbow Rainbow trout Trout and ~~mountain~~ Mountain whitefish Whitefish do not appear to consume smolts consistently (Furey, unpublished data). However Nevertheless, Bull Trout lengths from each interaction were measured to understand the potential for bias resulting from observations of smaller fishes that ~~were~~ may not have been Bull Trout. In response, we assessed the empirical cumulative distribution function of presumed Bull Trout lengths (cm) measured in this study, comparing the DIDSON length estimates to those obtained in the field from prior studies in the system. Specifically, we compared both minimum (41.5 cm) and maximum (79.5 cm) length estimates from Kanigan (2019), which captured Bull Trout via hook-and-line sampling, to provide a probability threshold of observations that are not consistent with lengths of Bull Trout captured by angling. ~~Sockeye Salmon smolts present as “clouds” of small fish on the DIDSON and are easily identifiable.~~

Videos were processed at frame rates of ~25 - 50 frames·s⁻¹ and were played back, slowed down, and/or paused when interactions were detected. This was done to verify interactions between Bull Trout and Sockeye Salmon smolts. Further, these videos were viewed using the “Background Subtraction” tool to remove potential static background and to better visualize fish passing through the video. Recorded observations of interactions between Bull Trout and smolts were standardized to per m² (counts of interactions per m²) because the window length of the

DIDSON (~5 m vs 10 m) and thus area observed, differed among deployments (Table 1). To estimate the window area observed by the DIDSON (~9.87 m² for the 5-m window length and ~29.27 m² for the 10-m window length), images of the DIDSON were imported and window area calculated using ImageJ (Schneider et al. 2012). Considering the differences in DIDSON configuration and resulting window area observed, we quantified the proportion of 30-minute intervals that had zero interactions between Bull Trout and Sockeye Salmon smolts at parallel sites (UF2021; 29.27 m², UF272829; 9.87 m²); if bias occurred, a smaller detection range would result in a larger number of zero interactions observed.

Data analysis.—

For the following analyses, non-parametric tests were used due to violations of model assumptions (i.e., homogeneity of variance, normally distributed residuals, etc.). Kruskal-Wallis rank sum tests were used to test for differences in the number of interactions per 30-minute interval, standardized to per m² across among all deployments; ~~note that intervals containing zero interactions were included in this analysis.~~ Separate pairwise Wilcoxon rank sum tests tested for differences in the number of interactions between each of the five individual deployments with a Holm-Bonferroni correction to account for multiple comparisons. ~~Non-parametric Wilcoxon~~ rank sum tests were also performed to test for differences in the number of standardized interactions (m⁻² in each 30-minute interval) between daylight hours and nighttime hours (daytime hours were considered as between sunrise and sunset determined via <https://www.timeanddate.com/>; nighttime was considered as sunset to sunrise) both collectively among all deployments, and with a separate test for each of the five individual deployments. Finally, correlations between migrating smolt densities (collected from the DFO counting fence)

and standardized interactions (per hour, instead of every 30 minutes, to match the resolution of smolt density data from the counting fence) between Bull Trout and smolts were tested both collectively among all deployments and individually for each of the five different deployments using Spearman's rank order correlation coefficient. ~~Furthermore, because we were only focused on predator-prey interactions during times of active smolt migrations, we removed any time period when smolts were not migrating due to fence closure (mostly during daylight hours), to better capture potential correlations between Bull Trout and smolt densities for these specific analyses.~~ All statistical analyses were conducted using R v3.6.3 (R Core Team 2021).

<A>Results:

Interactions between smolts and Bull Trout throughout all deployments ranged from 0 - 4.86 interactions per m² among 30-minute intervals (mean = 0.63 m⁻²; SD = 0.99 m⁻²). The number of standardized interactions observed between smolts and Bull Trout varied among deployments significantly (Kruskal-Wallis rank sum test, $\chi^2 = 105$; df = 5; $P < 0.001$). Pairwise Wilcoxon tests indicated that the number of standardized interactions between the Upstream Fence April 20 – 21 and Upstream Fence April 27 – 29 deployments differed significantly from each other and all other deployments ($P < 0.05$). Significant differences in the number of interactions were also detected between the Downstream River April 21 – 22 deployment and the Downstream Fence April 23 – 24 deployment ($P < 0.05$); however, neither of these deployments were significantly different from the two deployments that occurred at site N. In general, the highest number of interactions per m² was observed during the when the DIDSON was deployed upstream of the counting fence Upstream Fence April 27 – 29 deployment (site UF; mean = 1.1437 m⁻²; SD = 1.128 m⁻²; range = 0 - 4.86 m⁻²), followed by and the lowest was observed during the Narrows April 29 deployment sites that occurred downstream of the counting fence (site DR and DF;

mean = 0.02914 m⁻²; SD = 0.06538 m⁻²; range = 0 - 0.37610 m⁻²; ~~Table 1~~), and the narrow river segment (site N; mean = 0.015 m⁻²; SD = 0.029 m⁻²; range = 0.102 m⁻²).

~~Furthermore, the~~ The number of standardized interactions among 30-minute intervals varied with the diel cycle when aggregated across all deployments ($W = 2693.5$; $P < 0.01$; Fig. 2); ~~i~~Interactions were highest-higher during night-time hours and ranged from 0 to 4.86 interactions per m² (mean = 1.19 m⁻²; SD = 1.24 m⁻²) ~~relative to~~than during ~~the day~~daytime hours (mean = 0.225 m⁻², SD = 0.44 m⁻²). ~~Among For~~ individual deployments, nighttime interactions (per m²) were significantly higher than daytime interactions during the Upstream Fence April 20 - 21 deployment (daytime mean = 0.05 m⁻²; SD = 0.11 m⁻², nighttime mean = 0.78 m⁻²; SD = 0.42 m⁻²; $W = 11$; $P < 0.01$; Fig. 3A), the Downstream River April 21 – 22 deployment (daytime mean = 0.02 m⁻²; SD = 0.05 m⁻², nighttime mean = 0.10 m⁻²; SD = 0.11 m⁻²; $W = 49.5$; $P = 0.01$; Fig. 3B), and the Upstream Fence April 27 – 29 deployment (daytime: mean = 0.54 m⁻²; SD = 0.57 m⁻², nighttime: mean = 2.35 m⁻²; SD = 0.93 m⁻²; $W = 79.5$; $P < 0.01$; Fig. 3E), but other deployments did not demonstrate ~~such a diel~~this relationship (~~$P > 0.05$~~).

Smolt density estimates obtained from the DFO counting fence ranged from 200 - 882,717 smolts per hour when smolts were actively migrating (~~i.e., when the counting fence was not physically closed~~). The number of hourly interactions and smolt densities were not correlated when these data were aggregated across all deployments (Spearman's correlation, $\rho = -0.2012$; $P = 0.4421$). However, a significant and strong positive correlation did exist between the number of hourly interactions and smolt densities for the Upstream Fence April 20 - 21 deployment (Spearman's correlation, $\rho = 0.87$; $P < 0.001$; Fig. 3A) and the Upstream Fence April 27 - 29 deployment (Spearman's correlation, $\rho = 0.76$; $P < 0.001$; Fig. 3E).

the Upstream Fence April 27–29 deployment (Spearman's correlation, $\rho = 0.68$; $P < 0.001$; Fig. 3E). A similar positive correlation also existed for the Upstream Fence April 20–21 deployment, but was not significant (Spearman's correlation, $\rho = 0.52$; $P = 0.19$; Fig. 3A).

We directly compared the proportion of 30-minute time windows without any interactions (e.g., equal to zero) between deployments at the UF site with the two viewing window sizes and did not find evidence that the larger viewing window results in more observed interactions. Specifically, the Upstream Fence 20–21 deployment had a larger proportion of zeros (0.25; detection window area of 29.27 m²), relative to the deployment spanning April 27–29 (0.12; detection window area: 9.87 m²), contrary to what would be expected if biases were present. Lengths of Bull Trout (cm) as measured from the DIDSON ranged from 25 cm to 87 cm across all interactions ($n = 3025$; mean 50.7 cm; SD 9.99 cm). Compared to minimum and maximum lengths of Bull Trout captured via hook-and-line sampling (41 cm - 79.5 cm; Kanigan 2019), we found that the cumulative probability of observing presumed Bull Trout ≤ 41 cm from DIDSON interactions was ~19%. Additionally, maximum lengths from hook-and-line angling (79.5 cm) were similar to those measured from the DIDSON (87 cm; Fig. S2).

Discussion:

The DIDSON successfully observed predator-prey interactions between Bull Trout and migrating Sockeye Salmon, with these interactions occurring most frequently just upstream of the counting fence, suggesting this anthropogenic structure facilitates predation behavior. Consumption was higher (e.g., at *ad libitum*) for Bull Trout collected at the counting fence relative to other locales (Furey et al. 2016b), and the DIDSON confirms that predator-prey interactions at this site can be intense and tightly coupled to migrating smolt densities; thus,

feeding intensity is likely consistent with prior diet studies (Fuery et al. 2015; Furey et al. 2016b). As a result, the counting fence may create a spatial bottleneck for migrant smolts to pass. It is possible that the constriction of the counting fence, and potentially the presence of Bull Trout, may concentrate smolts within a small area and increase the foraging efficiency of Bull Trout. However, further research could better quantify how smolts behave as they pass through the counting fence relative to other landscapes, and quantify mortality, potentially via telemetry tracking upstream of the fence (all telemetry work in this system occurred downstream of the fence). Given the short duration of our study (10 days), which was due to opportunistic use of the DIDSON during other field programs, we believe our conclusions could be better supported by monitoring the site upstream of the fence more intensively (i.e., additional days), with concurrent comparisons of other sites. We also acknowledge that with only one DIDSON unit, we were unable to compare differences in predator-prey interactions between or among sites simultaneously; in particular, sampling in systems without counting fences would be informative as to how anthropogenic structures affect behavior of salmonid predators more broadly.

Diel linkages differences in the frequency of interactions were also strongest for deployments close to the counting fence, albeit sample sizes were low throughout our deployments. -smolts appeared to increase during nighttime hours, particularly upstream of the counting fence (Fig. 3A; Fig. 3E). Given that the smolt migration is largely nocturnal (Clark et al. 2016; Furey et al. 2016a), it is intuitive that nighttime hours would provide the most opportunities for predator-prey interactions. Smolts likely exhibit nocturnal migrations to mitigate foraging efficiency from visual predators, as seen in other salmonid migrations in fresh water (Ibbotson et al. 2006; 2011; Haraldstad et al. 2017). In response to nocturnal migrations of prey, Bull Trout were observed interacting to interact with smolts more often at night, particularly

~~at the fence.~~ We also observed that Bull Trout respond by actively interacting with smolts during nighttime (when smolt migration is densest), demonstrating that Bull Trout likely synchronize their movements and behaviors in response to outmigrant smolts at fine spatial and temporal scales, as they do at broader scales (Furey and Hinch 2017; Kanigan 2019), but confirmation would requires increased tracking of movements and behavior during daytime periods. Due to the resolution of the DIDSON system, we were unable to confirm actual predation events, estimate the number of smolts consumed, or quantify the effectiveness of synchronized nocturnal movements of smolts (i.e., predator swamping; Furey et al. 2016a; Furey et al. 2021b). Future studies could couple the use of acoustic imaging, which is consistently improving, and other methods (e.g., diet studies or high-resolution telemetry) to quantify Bull Trout predation rates on smolts.

~~Activity of Bull Trout was most tightly linked with smolt migration densities for deployments when the DIDSON was deployed just upstream of the counting fence (Fig. 3E). Potential feeding activity of Bull Trout was most positively correlated with smolt densities upstream of the fence, but not elsewhere in the system. Thus, it appears smolt-Bull Trout interactions are most tightly coupled just upstream of this anthropogenic structure. In fact, Bull Trout feed at higher rates (e.g., at *ad libitum*) at the counting fence relative to other locales (Furey et al. 2016b), and it appears that fine-scale behaviors (i.e., actively pursuing smolts as they appear as observed by the DIDSON) likely reflect these observations of feeding intensity. As a result, the counting fence may create a spatial bottleneck for migrant smolts to pass. It is possible that the constriction of the counting fence, and potentially the presence of Bull Trout, may concentrate smolts within a small area, slowing the movement speeds of smolts, and thus, increasing the foraging efficiency of Bull Trout. However, further research could better quantify~~

how smolts behave as they pass through the counting fence relative to other landscapes, and if mortality is higher at the fence, potentially via telemetry tracking upstream of the fence. Given the short duration of our study (10 days), which was due to opportunistic use of the DIDSON during other field programs, we believe our conclusions could be better supported by monitoring the upstream fence site more intensively (i.e., additional days), with concurrent comparisons of other sites. We also acknowledge that with only one DIDSON unit, we were unable to compare differences in predator-prey interactions between or among sites simultaneously.

Although beyond the scope of our study, a variety of factors could affect the predator-prey interactions between Sockeye Salmon smolts and Bull Trout. Several studies have found that smaller smolts tend to have lower survival rates, likely due to size-dependent predation (West and Larkin 1987; Saloniemi et al. 2004; Duffy and Beauchamp 2008; Tucker et al. 2016). Similarly, smolts in poor body condition (Tucker et al. 2016) or experiencing specific infections (Miller et al. 2014; Jeffries et al. 2014; Furey et al. 2021a) can experience increased predation or mortality. Further research could attempt to quantify behavioral mechanisms of predation-based selection processes and how such selection might be affected by anthropogenic structures.

Human-altered landscapes can influence the risk landscape for migratory animals (Sabal et al. 2021). Dams and other barriers are well known to constrict and even at times, obstruct fish movement, and can aggregate predators, increasing mortality of migrant fishes (Blackwell and Juanes 1998; Davis et al. 2012; Keefer et al. 2012; Sabal et al. 2016). However, temporary structures such as counting fences or weirs are commonly used, but generally less studied than permanent structures, even though they can affect predator-prey interactions (Furey et al. 2016b). Our study suggests that a temporary counting fence, even one that has been relied on for management (Irvine and Akenhead 2013), can mediate predator-prey interactions and pose a

potential challenge to migrants by affecting predator or prey behavior. Thus, the impacts of temporary structures on fish behavior and predator-prey interactions likely deserve more attention given that they are often used during times of important life history events such as migrations.

<A> Acknowledgements:

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Table 1. Summary data for DIDSON deployments in Chilko Lake, British Columbia, Canada, from April 20 – 29, 2016 during a Sockeye Salmon smolt outmigration period. The detection window area (m²) represents the approximate area observed by the DIDSON. The total number of interactions are the sum of all interactions detected for a given deployment. The total number of smolts per deployment are the sum of smolt densities (estimated hourly) for a given night from the counting fence.

DIDSON deployment (Site and date)	Hours of video footage	Detection window area (m ²)	Average number of interactions \pm SD (m ⁻² per 30 minutes)	Minimum number of interactions (m ⁻² per 30 minutes)	Maximum number of interactions (m ⁻² per 30 minutes)	Total number of interactions	Total number of smolts per deployment
Upstream Fence (UF) April 20 – 21 2016	14	29.27	0.444 \pm 0.484	0	1.61	364	1,054,978
Downstream River (DR) April 21 – 22 2016	14.5	29.27	0.062 \pm 0.924	0	0.376	52	1,082,198
Downstream Fence (DF) April 23 – 24 2016	22	29.27	0.008 \pm 0.018	0	0.068	23	5,339,320
Narrows (N) April 25 -26 2016	5.5	29.27	0.016 \pm 0.023	0	0.068	5	26,000
Upstream Fence (UF) April 27 – 29 2016	41.5	9.87	1.37 \pm 1.18	0	4.86	1032	2,041,534
Narrows (N) April 29 2016	3.5	29.27	0.015 \pm 0.039	0	0.102	3	NA

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Figures:

Figure 1. Map of Chilko Lake, British Columbia, Canada (51.294, -124.077). Aerial image of the upper reaches of Chilko Lake shows the positions (white shapes) of where the DIDSON system was deployed from April 20 - 29th, 2016, during the smolt outmigration period. The white square indicates DIDSON deployments upstream of the government operated counting fence (UF), white circles denote deployments downstream from Chilko River (DR) and downstream from the counting fence (DF), and white triangles indicate deployments at the narrow river segments (N). See Table 1 for more information on deployments. The government operated counting fence is denoted in black. The red dot in the lower right inset represents the approximate position of where the study was conducted. The red square on the upper left inset denotes the location of Chilko Lake in North America.

Figure 2. Total interactions (m^{-2}) among 30-minute intervals detected between Bull Trout and smolts throughout all DIDSON deployments. Each observation represents a 30-minute interval within a diel period (~~Observations were made across diel cycles~~) (Daytime: $n = 116$; Nighttime: $n = 86$). Daylight and nighttime hours were determined via <https://www.timeanddate.com/>. Results from the Wilcoxon rank sum test are displayed on the left upper corner. Points are jittered horizontally for visibility. Observations originating from sites upstream of the fence (UF) are in blue and those from other sites are in yellow. The lines in the middle of the boxplots indicate the median, and the left and right edges represent the 25th and 75th percentiles respectively. Whiskers represent 1.5-times the interquartile range.

Figure 3. The number of interactions per m² and per unit time (1 hour) detected between Bull Trout and smolts (blue lines and points, left y-axis) plotted alongside hourly smolt density estimates (orange lines and points, right y-axis) across time. Note that during certain hours, smolt densities are not observed because the fence is physically closed to migrants (when orange points are at zero). Grey shading indicates nighttime hours. Plots A - F display interactions and smolt density estimates across different deployment-night combinations (refer to Table 1 for additional information on deployments). The DIDSON was only deployed from 04-25 16:30 – 19:30 and 04-26 16:00 – 16:30 for site N2526 and thus are presented as missing observations. Smolt densities were not observed for plot F due to fence closures during the daytime.

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