**TITLE:** Using acoustic imaging to observe potential 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 present opportunities for predators to aggregate and exploit these seasonal prey pulses. Within Chilko Lake, British Columbia, Canada, large-scale telemetry and stomach content analyses suggest 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, especially at a counting fence. However, it is unclear whether Bull Trout from these studies were consuming smolts elsewhere before they were captured near the counting fence. 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 densities were correlated with feeding activity of Bull Trout upstream of a government installed fence used to estimate smolt numbers, consistent with observations from broad-scale telemetry studies. Predator-prey interactions were also closely coupled with nocturnal migratory behaviors of Sockeye Salmon smolts, presumably to minimize predation risk during the daytime. These results provide a conceptual framework for future studies that wish to assess predation risk, evidence that the migrations of Sockeye Salmon smolts affect the behavior of Bull Trout and are important to this predator’s ecology, and provides additional insight on the role of anthropogenic structures (e.g., counting fences) in mediating predator-prey interactions, strengthening hypotheses from previous studies.

# 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). These population-level declines have been hypothesized to be a result of a variety of factors, including mortality from pathogens, contamination from industrial effluents, and predation (Miller et al. 2014; COSEWIC 2017). Among these factors, juvenile Salmon can experience immense predation from piscivorous fishes, birds, and mammals (Beamesderfer et al. 1996; Osterback et al. 2013; Furey et al. 2015; Flávio et al. 2021), and these interactions can potentially be facilitated by the presence of anthropogenic structures such as dams and culverts (Blackwell and Juanes 1998; Sabal et al. 2016; Alcott et al. 2020). Considering that sources of natural mortality (predation) for fish species are difficult to observe (Miller et al. 2014) but important to account for, there remains a need to validate methods and develop frameworks that allow for the monitoring of predator-prey interactions, facilitated by the presence of anthropogenic structures.

that could potentially be an invaluable non-invasive tool for observing predator-prey interactions is Here, we use Chilko Lake (or Tŝilhqox Biny; territory of the Xeni Gwet’in First Nations), British Columbia as a case study to illustrate the utility of the DIDSON in providing *in situ* passive observations of predator-prey interactions at an anthropogenic structure.

Chilko Lake represents an ideal study system to assess predation risk resulting from anthropogenic structures because it is home to one of the largest populations of Sockeye Salmon in Canada, consequently this population is intensively studied (Bradford et al. 2000; Irvine and Akenhead 2013). In Chilko Lake, most Sockeye Salmon juveniles rear for one winter in the lake (~95%) before they begin their seaward migration as smolts (Bradford et al. 2000), a migration that requires a suite of behavioral and physiological changes (i.e., smoltification; Young et al. 1989) to cope with saltwater. For instance, it has been hypothesized that smolts migrate nocturnally to minimize predation from visual predators in the clear upper-river reaches of Chilko Lake (Clark et al. 2016; Quinn 2018). Each spring, 10 - 40 million Sockeye Salmon smolts (~95% age-1 smolts, ~4% age-2 smolts; Irvine and Akenhead 2013) emigrate from the lake towards the ocean, during which Bull Trout (*Salvelinus confluentus*) appear to synchronize their movements with the timing of this out-migration period, presumably to exploit this unique prey-pulse (Furey and Hinch 2017; Kanigan 2019). Furthermore, Bull Trout in Chilko captured near a government counting fence installed by Fisheries and Oceans Canada (DFO) were found to feed at higher rates (e.g., at *ad libitum*)relative to other locales (bioenergentic simulations; Furey et al. 2016b), with a large number of Sockeye Salmon smolts found in their diets (Furey et al. 2015). However, it remains unclear whether Bull Trout from the aforementioned studies were consuming Sockeye Salmon smolts elsewhere before they were captured near the counting fence. Consequently, additional confirmatory video evidence of *in situ* predator-prey interactions may provide further confidence in those findings. Thus, this system is ideal for investigating fine-scale predator-prey interactions.

The present study uses DIDSON at the Chilko Lake-River outlet during the smolt outmigration to: 1) assess whether higher predation risk occurs at a counting fence, 2) determine if Bull Trout activity is synchronized with Sockeye Salmon smolt migrations across both spatial and temporal (diurnal cycles) scales, and 3) develop a conceptual framework to observe predation events using passive acoustic imaging, thereby allowing for an assessment of potential predation risk at anthropogenic structures.

# <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) and has been deployed annually since the early 1950s (Irvine and Akenhead 2013), with the exception of 2017 and 2020. 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. Note that during certain daytime hours, the counting fence is closed. Thus, when smolt densities are denoted as zeros in our subsequent analyses, they indicate that zero smolts are actively passing through the counting fence. However, smolts that occur downstream of the fence can still be observed despite the counting fence being closed, and thus interactions can occur during certain daytime hours as well (see *DIDSON data collection and video processing*).

## *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. 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. 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), 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 and lengths of each Bull Trout were measured using the “measure” tool to the nearest cm. Bull Trout are the dominant piscivore present during the migration to feed on smolts (Furey et al. 2015, 2016b), and their identification were based upon their much larger body size compared to other fishes present at lower abundances (mountain whitefish and rainbow trout primarily). Considering the presence of smaller fishes, Bull Trout lengths from each interaction were measured to understand the potential for bias resulting from observations of smaller fishes that were not Bull Trout. In general, studies have found that the DIDSON can provide reliable estimates of fish length (Burwen et al. 2010; Crossman et al. 2011). To this end, 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 and maximum size estimates from Kanigan 2019, which captured Bull Trout via hook-and-line sampling, to provide a probability threshold of observations that might not have originated from Bull Trout individuals. In addition, Sockeye Salmon smolts were easily identified as “clouds” of small fish on the DIDSON. We defined interactions given the following criteria: 1) Bull Trout were actively pursuing Sockeye Salmon smolts, 2) the proximity of Bull Trout resulted in Sockeye Salmon smolts dispersing, and 3) Sockeye Salmon smolts actively swam away from a Bull Trout when in proximity (Supplementary Video 1 & 2 online).

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). Given the differences in DIDSON configuration, we also assessed the potential for bias to understand whether a smaller detection range would result in a larger number of zero interactions observed between parallel sites (UF2021; 29.27 m2, UF272829; 9.87 m2).

## *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.). To better understand whether higher predation risk occurs near the counting fence, non-parametric Wilcoxon rank sum tests were performed to test for differences in the number of standardized interactions (m-2 in each 30-minute interval) between UF sites and all other sites (Fig. 1). Here, data from UF2021 and UF272829 were aggregated to reflect sites near the counting fence, and deployments DR2122, DF2324, N2526, and N29 were aggregated to reflect “other” sites. To evaluate the degree of synchrony between Bull Trout and Sockeye Salmon smolt migrations across temporal (diel cycles) scales, non-parametric Wilcoxon rank sum tests were performed to test for differences in the number of standardized interactions (m-2 in each 30-minute interval) between daylight and nighttime hours (sunrise and sunset determined via <https://www.timeanddate.com/> and reflect diurnal and nocturnal periods respectively) both collectively among all deployments, and with a separate test for each of the four individual deployments, because only daytime observations were made at deployments N2526 and N29. 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. This was done to assess the degree of spatial synchrony of Bull Trout activity is synchronized with Sockeye Salmon smolt migrations. All statistical analyses were conducted using R v3.6.3 (R Core Team 2021).

# <A>Results:

Lengths of Bull Trout (cm) as measured from the DIDSON ranged from 25 cm to 86 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 -79.5 cm; Kanigan 2019), we found that the cumulative probability of observing presumed Bull Trout ≤ 41cm from DIDSON interactions was about 19%. Additionally, maximum lengths from hook-and-line angling (79.5 cm) were similar to those measured from the DIDSON (Fig. S1). Comparisons of parallels sites with differences in detection window area indicated that site UF2021 (25% zeros; detection window area: 29.27 m2) had a larger percentage of zeros relative to UF272829 (12% zeros; detection window area: 9.87 m2), contrary to what would be expected if significant biases from differential detection areas did exist.

Interactions between smolts and Bull Trout differed significantly between UF sites and sites that were classified as “other” (UF mean = 1.14 interactions m-2; SD = 1.12 interactions m-2, “Other” mean = 0.026 interactions m-2; SD = 0.06 interactions m-2; W = 1199; *P* < 0.01). In addition, the highest number of interactions per m2 was observed during the Upstream Fence April 27 - 29 deployment (mean = 1.37 m-2; SD = 1.18 m-2; range = 0 - 4.86 m-2) and the lowest was observed during the Narrows April 29 deployment (mean = 0.014 m-2; SD = 0.038 m-2; range = 0 - 0.10 m-2; Table 1). The number of standardized interactions among 30-minute intervals differed significantly between daytime and nighttime hours when aggregated across all deployments, where interactions were highest during nighttime hours (W = 2693.5; *P* < 0.01; Fig. 2). Among individual deployments, temporal synchrony in diel cycles of Bull Trout activity depended on the site. Specifically, 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) 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). However, other deployments did not demonstrate such a diel 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 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).

# <A>Discussion:

Interactions observed by the DIDSON between Bull Trout and migrating Sockeye Salmon smolts occurred at higher rates upstream of the counting fence when compared to other sites, suggesting that the counting fence likely facilitates these interactions between consumer and prey in the Chilko system. As previously mentioned, Bull Trout captured near the counting fence in Chilko feed at *ad libitum* rates, which were determined from bioenergetic simulations (Furey et al. 2016b). However, it was unclear whether these individuals consumed smolts elsewhere, prior to being captured. Thus, our study directly reflects observations of high feeding intensity and predation risk occurring at the counting fence (Supplementary Video 1 & 2 online), and further strengthens the assertion that the counting fence facilitates predator-prey interactions in the Chilko system. Similarly, Bull Trout activity was most tightly synchronized with the Sockeye Salmon smolt migration upstream of the counting fence (Fig. 3A; Fig. 3E) and potential feeding activity of Bull Trout was most positively correlated with smolt densities upstream of the fence, but not elsewhere in the system. Although significant correlations were not detected elsewhere in the system, it could have resulted from suboptimal placement of the DIDSON at these sites or the presence of Bull Trout potentially aggregated at other sites (e.g., the counting fence). As a result, strategic placement of the DIDSON and simultaneous observations of other sites would be important considerations for future studies. Nevertheless, this potentially demonstrates that Bull Trout, despite being highly visual predators, may synchronize their movements and behaviors in response to higher densities of outmigrant smolts (during nighttime hours) at finer spatial and temporal scales, as they do at broader scales (Furey and Hinch 2017; Kanigan 2019). It is possible that the constriction of the counting fence, may concentrate smolts within a small area, slowing the movement speeds of smolts, and thus mediate this predator-prey interaction, thereby 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.

Although differences in temporal behavior of Bull Trout activity were significant when tested among all deployments, subsequent analyses demonstrated higher predation risk occurring during the nighttime was largely driven by observations made upstream of the fence (Fig. 2). Thus, conclusions describing this temporal behavior of Bull Trout and Sockeye Salmon smolts is limited to observations made upstream of the counting fence. Nevertheless, considering that the smolt migration is largely nocturnal in the Chilko system (Clark et al. 2016; Furey et al. 2016a), it is intuitive that nighttime hours would provide the most opportunities for predator-prey interactions. As previously described, Sockeye Salmon smolts presumably exhibit nocturnal migrations in the Chilko system 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; Quinn 2018).

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. However, given diet and behavioral studies of Bull Trout in the same system, we are confident that Bull Trout were indeed predating on Sockeye Salmon smolts during our study period (Furey et al. 2015, 2016b; Furey and Hinch 2017). Furthermore, although there may be potential for misidentification of fish species and associated interactions, we believe conclusions drawn from this study are robust to the aforementioned biases, considering there was about 19% probability of observing Bull Trout that were smaller than estimates of minimum size obtained from the field - Bull Trout are likely to occur at even smaller sizes (41 cm; Kanigan 2019) (Fig. S1).

Considering the limited duration of our study (10 days), which was due to the opportunities use of the DIDSON during other field programs, the purpose of this study

is to provide a conceptual framework to observe predation events using passive acoustic sonar, that would allow for an assessment of potential predation risk. Herein, we provide further research recommendations and potential management implications. The framework presented in the current study allows for researchers to “ground-truth” potential predator-prey interactions that might be suspected in a non-invasive manner and allows for observations of predation events that would otherwise be difficult. Future research could extend this framework by monitoring predator-prey interactions in locations with and without anthropogenic structures simultaneously, which may allow researchers to better understand the predation risk of certain structures, and potential benefits of removing them (i.e., dams). Furthermore, given the wide use of temporary anthropogenic structures (e.g., weirs, counting fences) for enumerating and tagging migrant fishes, our framework can be extended to understand the potential for mortality (i.e., post-release, mortality via passage) at these structures. Given the duration of our study, we believe that 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 and further emphasize the value of being able to monitor multiple sites simultaneously.

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 have been proposed to affect predator-prey interactions (Furey et al. 2016b). The current study validates diet observations made by prior studies (Furey et al. 2015, 2016b), and thus strengthens previous hypotheses 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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Tables:

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.

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| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| DIDSON deployment (Site and date) | Hours of video footage | Detection window area (m2) | 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 |

# 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. Individual points for observations made across 30-minute intervals from during the daytime and nighttime were n = 116 and n = 86 respectively.

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 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. Grey shading indicates nighttime hours. Note that during certain daytime hours, smolt densities are not observed because of fence closures (when orange points are at zero). 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 are presented as missing observations.