**TITLE:** An unusual suspect: Do counting fences mediate predator-prey interactions between Bull Trout (*Salvelinus confluentus*) and Sockeye Salmon (*Oncorhyncus nerka*) smolts?

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**Abstract:** Juvenile Sockeye Salmon (*Oncorhynchus nerka*) smolts experience high rates of mortality during their annual outmigration period from freshwater to the ocean. These annual migrations are predictable and present opportunities for predators to aggregate and exploit seasonal prey pulses, feeding extensively on migrants during a short period. Within Chilko Lake, British Columbia, Canada, the outmigration of Sockeye Salmon smolts has been observed to be coupled with the movements and aggregations of Bull Trout (*Salvelinus confluentus*), exploiting prey pulses as they attempt to exit the Chilko system. This study uses Dual-frequency Identification Sonar (DIDSON) acoustic videos to assess fine-scale predator-prey interactions between Sockeye Salmon smolts and Bull Trout. Over 10 days, we found that smolt densities were closely correlated with feeding activity of Bull Trout upstream of a government installed fence, used to estimate smolt numbers. Predator-prey interactions were also closely coupled with previously described nocturnal migratory behaviors of Sockeye Salmon smolts, presumably to deter predation. Total length of Bull Trout obtained from the DIDSON when compared to field estimates differed significantly, likely due to the presence of smaller fish species in the system and the bidirectional movement of Bull Trout. These results provide further evidence for the nocturnal migratory of Sockeye Salmon smolts within the Chilko system to mitigate predation risk, and the potential for anthropogenic structures such as counting fences that don’t inherently affect flow to facilitate predator-prey interactions.

**Introduction:**

Pacific Salmon (*Oncorhynchus spp.)* have incredible ecological, economic, and cultural value. Most Pacific salmon are anadromous and semelparous, and thus will rear in freshwater, migrate into the Pacific Ocean as juvenile salmon smolts, return to their natal streams to spawn after several years, and die shortly after. As juvenile salmon begin their downstream migration into the open ocean, they undergo a suite of behavioral and physiological changes called “smoltification” in order to adapt to higher salinity environments (Young et al. 1989), thus becoming smolts. During this period, smolts are mediated by a variety of factors such as predation (Furey et al. 2015; Zimmerman and Ward 1999), growth and size (Beamish et al. 2008; Beamish et al. 2004; Beamish and Mahnken 2001), and large-scale oceanographic drivers (Thomson et al. 2012). Density-dependent factors such as winds, river discharge, and surface stratification have previously been described as important determinants for food availability and growth, which subsequently impact the early marine survival of smolts (Beamish et al. 2012; Thomson et al. 2012). As a result, the early marine survival of smolts is a critical life-stage that is associated with the productivity of overall salmon populations, and is integral in maintiang healthy and mianitnaing healthy and productive salmon populations (Beamish et al. 2012; Thomson et al. 2012).

As smolts begin their downstream migration towards the ocean, they face predation from piscivorous fishes, avian predators, and mammals such as otters and minks (Beamesderfer et al. 1996; Blackwell and Juanes 1998; Flávio et al. 2020; Furey et al. 2015; Osterback et al. 2013). As a result, smolts exhibit a variety of adaptations to presumably reduce predation risk. For instance, both Sockeye Salmon (*Oncorhynchus nerka*) and Atlantic Salmon (*Salmo salar*, that also undertake seaward migrations) smolts migrate nocturnally (Clark et al. 2016; Furey et al. 2016; Flávio et al. 2020; Ibbotson et al. 2006; Ibbotson et al. 2011). Furthermore, smolts can synchronize their migrations to find safety in numbers or “swamp” predators (Furey et al. 2016a; Furey et al. 2021b). However, it’s less studied how densities of migrating smolts could impact the foraging behavior of predators present.

Chilko Lake, British Columbia, is home to one of the largest populations of Sockeye Salmon in Canada, and consequently this population is intensively studied and is used as an indicator of Sockeye Salmon for the entire Fraser River watershed (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. Using telemetry, the initial migratory corridor, the clear, slow-moving, and pristine waters of the Chilko River, appear high-risk relative to the turbid waters downstream, including the Fraser River (Clark et al. 2016; Rechisky et al. 2020). These high-risk areas are likely attributed to by the presence of predators such as piscivorous Bull Trout (*Salvelinus confluentus*) observed in the area (Clark et al. 2016). Bull Trout in the system are observed toexploit the Sockeye Salmon smolt migrations, feeding extensively on migrating Sockeye Salmon smolts near the Chilko Lake outlet (Furey et al. 2015), and appear to synchronize their movements with the timing of the Sockeye Salmon smolt out-migration period (Furey and Hinch 2017). Furthermore, Bull Trout in Chilko also appear to selectively feed on small smolts or those with specific infections (Furey et al. 2015; Furey et al. 2021), and smolts can reduce their risk of predation by migrating in high densities (Furey et al. 2016; Furey et al. 2020). Thus, this system provides an ideal model for investigating fine-scale predator-prey interactions between Sockeye Salmon smolts and Bull Trout.

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 animal behaviors, including in turbid water and at night (Maxwell and Gove 2007; Moursund et al. 2003; Nichols et al. 2014). This technology can also be used to assess fish size distributions (Burwen et al. 2010; Crossman et al. 2011; Martignac et al. 2015). The present study uses DIDSON at the Chilko Lake-River outlet to: 1) gain a better understanding of predator-prey dynamics between Bull Trout and Sockeye Salmon smolts, 2) investigate site differences and temporal factors influencing Bull Trout feeding activity, and 3) ascertain if the DIDSON system can provide accurate estimates of Bull Trout size distributions.

<A>Methods:

*Study area.* —

This study was conducted at the outlet of Chilko Lake (also known as Tŝilhqox Biny), British Columbia, Canada (Fig. 1). Chilko Lake is a 180 km2, high elevation (~1100 m.a.s.l) lake that has a north-south orientation and stretches ~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). Smolt densities obtained from the counting fence are estimated using digital photographs of smolt passing through the fence at regular time intervals and integrate estimates of smolt speeds as they pass. In 2016, smolt densities were estimated hourly.

*DIDSON deployment and setup.* —

The DIDSON system (Sound Metrics, Bellevue, Washington) was deployed at 5 sites (Fig. 1) from April 20 - April 29 in 2016 during the Sockeye Salmon smolt outmigration. We deployed the DIDSON upstream of the government counting fence (site UF) from April 20 – 21 2016 and April 27 – 29 2016. We also stationed the DIDSON downstream from Chilko River (site DR) from April 21 – 22 2016 and downstream from the counting fence (site DF) from April 23 – 24 2016. Finally, the DIDSON was positioned at a narrow river segment (site N) from April 25 – 26 2016 and April 29, 2016. 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 keep 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 5 sites during the 2016 smolt outmigration (throughout a 10-day period). Video files from the DIDSON were analyzed in 30-minute intervals and were viewed using the DIDSON Control and Display software (Sound Metrics, Bellevue, Washington). In every video, interactions between Bull Trout and out-migrating Sockeye Salmon smolts were recorded. In the case of this study, Bull Trout were identified based on their body shape (elongated) and size relative to out-migrating smolts. Conversely, Sockeye Salmon smolts were identified based on schooling behavior which generated easily identifiable “clouds” of small fish grouped tightly together. Interactions were determined to be any time it appeared that either Bull Trout or smolts (or both) reacted to the presence or proximity of the other within the video. For every interaction that was recorded, the frame number and lengths of Bull Trout were recorded. The total length (TL) of all Bull Trout at a given interaction were recorded using the “Measure” tool to the nearest cm within the DIDSON Control and Display software.

Videos were processed at frame rates of ~25 - 50 frames/s and were played back, slowed down, and/or paused when interactions were detected. This was done to verify interactions and to measure the lengths of interacting Bull Trout. Further, these videos were viewed using the “Background Subtraction” tool to remove potential static background and to better visualize fish passing through the video. Because Bull Trout are the primary piscivorous predator of migrating smolts in this system (Furey et al. 2016b; Furey et al. 2015), we assumed that large fish on the screen were Bull Trout, but there are other fishes (mountain whitefish and rainbow trout primarily) that are present.

*Data analysis.* —

Recorded observations of interactions between Bull Trout and smolts were standardized to per m2 because the window length (~5m vs 10m) and area differed among sites, due to varying landscapes (Table 1). To estimate the window area (~9.87 m2 vs ~29.27 m2), images of the DIDSON were imported and calculated using ImageJ (Schneider et al. 2012). Kruskal-Wallis rank sum tests were used to test for differences in the number of interactions across sites. Non-parametric Wilcoxon rank sum tests were performed to test for differences in the number of interactions between daylight and night times hours (sunrise and sunset determined via <https://www.timeanddate.com/>) both collectively among all sites and with a separate test for each of the five sites. Finally, correlations between smolt densities and interactions between Bull Trout and smolts were tested using Pearson’s correlation coefficient. Here, interactions were pooled every hour to correspond with hourly estimates of smolt densities obtained from the DFO counting fence. Because we were 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 and thus smolt density estimates equaled zero (mostly during daylight hours). Because length measurements of Bull Trout were taken for every interaction detected, it is very likely that individuals were remeasured several times. Furthermore, additional biases could be introduced because Bull Trout in this system were not moving unidirectionally, and Bull Trout are likely to be remeasured (Martignac et al. 2015). In response, this distribution of comprehensive, but likely pseudo-replicated, lengths were compared to a condensed dataset that only consisted of lengths of Bull Trout from the single interaction that had the most Bull Trout in the frame for each deployment night. Non-parametric Wilcoxon rank sum tests were used to test for differences between DIDSON-derived estimates of Bull Trout length and field estimates obtained from prior studies in the system which captured Bull Trout via hook-and-line or dip net for telemetry and diet studies (Furey and Hinch 2017; Furey et al. 2015, Kanigan 2019). All statistical analyses were conducted using R v3.6.3 (R Core Team 2020).

<A>Results:

Interactions between smolts and Bull Trout across all sites ranged from 0 - 4.86 interactions per m2 (mean = 0.63; SD = 0.99). Moreover, the number of interactions m-2 observed between smolts and Bull Trout varied among sites significantly (Kruskal-Wallis rank sum test, χ²= 105; df = 5; p < 0.001). The highest number of interactions per m2 were observed at site Upstream Fence April 27 - 29 (mean = 1.37; SD = 1.18; range = 0 - 4.86) and the lowest was observed at site Narrows April 29 (mean = 0.014; SD = 0.038; range = 0 - 0.10) (Table 1). Furthermore, the number of interactions observed across diel cycles per m2 were also variable. Interactions were highest during night-time hours and ranged from 0 to 4.86 interactions per m2 (mean = 1.19; SD = 1.24) relative to during the day (mean = 0.225, SD = 0.44). When the number of interactions across diel cycles were compared among sites, night-time interactions per m2 were higher than daytime interactions at sites Upstream Fence April 20 - 21 (day-time: mean = 0.05; SD = 0.11, night-time: mean = 0.78; SD = 0.42; W = 11; *P* < 0.01Fig. 2A) and Upstream Fence April 27 - 29 (day-time: mean = 0.54; SD = 0.57, night-time: mean = 2.35; SD = 0.93; W = 79.5; *P* < 0.01 Fig. 2E), and were statistically significant in both cases, relative to other sites.

Smolt density estimates obtained from the DFO enumeration fence ranged from 200 - 882,717 smolts per hour. The number of hourly interactions and smolt densities were not correlated when these data were aggregated across all sites (Pearson’s correlation, r = -0.22; t = -1.73; df = 57;  *P* = 0.08). However, a significant positive correlation did exist between the number of hourly interactions and smolt densities for site Upstream Fence April 27 - 29 (Pearson’s correlation, r = 0.64; t =3.96; df = 22; *P* < 0.001; Fig.2E). This correlation also existed for Site Upstream Fence April 20 - 21 but not significantly (Pearson’s correlation, r = 0.66; t = 2.17; df = 6; *P* = 0.07; Fig.2A).

Additionally, previously obtained field estimates (n = 327) of Bull Trout total length ranged between 41 to 80 cm (mean = 58.1; SD = 6.4; Fig. 3). From the DIDSON, we obtained length estimates of Bull Trout that ranged from 25 cm to 86 cm across all bull trout (n = 462; mean 48.6 cm; SD 10.1 cm) and from 32 cm to 68 cm (n = 41; mean 49.5 cm; 8 cm) for the more conservative subset of lengths (Fig. 3). Bull Trout lengths from both DIDSON-derived datasets were significantly smaller than previously collected field estimates (Wilcoxon rank sum test, W = 2741; *P* < 0.001; Fig. 3).

<A>Discussion:

Interactions between Bull Trout and migrating Sockeye Salmon smolts appeared to increase as the sun set, particularly at sites Upstream Fence April 20 - 21 and Upstream Fence April 27 - 29, located upstream of the counting fence (Fig 2A; Fig 2E). These interactions also appeared to be closely linked to previously described nocturnal migratory behaviors of sockeye smolts in Chilko Lake (Clark et al. 2016; Furey et al. 2016a). Our study provides additional evidence demonstrating that smolts do indeed exhibit nocturnal migrations, presumably to mitigate foraging efficiency from visual predators. We also observed that Bull Trout respond by interacting with smolts during night-time (when smolt migration is densest), demonstrating that Bull Trout synergize their movements and behaviors in response to outmigrant smolts at finer spatial and temporal scales than previously demonstrated (Furey and Hinch 2017; Kanigan 2019). Due to the nature of the DIDSON system, we were unable to quantify the number of smolts consumed per interaction, and the effectiveness of synergized nocturnal movements of smolts (predator swamping). Future studies could couple the use of DIDSON and other methods (i.e., diet studies) to quantify Bull Trout predation rates on smolts and create an index that would account for such losses for management purposes.

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The DIDSON provided smaller estimates of Bull Trout length than those previously collected in the field (Fig. 3). These smaller putative Bull Trout detected were likely fish of smaller species (i.e., rainbow trout), because field estimates of Bull Trout ranged from 41 - 80 cm, and the aforementioned species are also observed in the same system (Clark et al. 2016). Although we found that the length comparisons of Bull Trout were significantly different from each other, we do believe that the DIDSON is capable of producing accurate length estimates per the findings of other DIDSON studies (Burwen et al. 2010; Crossman et al. 2011). Accurate DIDSON length estimates can likely be obtained if fish are only moving in one direction (i.e., upstream, downstream), and if the fish species can be easily identified based on their outline (Martignac et al. 2015).

Although beyond the scope of our study, a variety of factors could affect the predator-prey interactions we observed 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 preferences of predators (Duffy and Beauchamp 2008; Saloniemi et al. 2004; Tucker et al. 2016; West and Larkin 1987). Similarly, smolts in poor body condition (Tucker et al. 2016) or experiencing specific infections (Furey et al. 2021a; Miller et al. 2016; Jeffries et al. 2014) can experience increased predation or mortality. Research could attempt to quantify how predator-based selection of smolts is affected by anthropogenic structures or other alterations to flow.

Human altered landscapes have long been documented to influence the risk landscape for migratory animals, affecting survival rates by introducing non-native predators, anthropogenic structures, etc (Sabal et al. 2021). Altered landscapes through the introduction of anthropogenic structures (e.g., dams) are known to constrict and even at times, obstruct fish movement, and have also been documented to aggregate predators, increasing the mortality of fishes utilizing these habitats (Blackwell and Juanes 1998; Davis et al. 2012; Keefer et al. 2012; Sabal et al. 2016). However, much of this research has been concentrated predominately on dams, culverts, and other barriers to fish passage. There has been some research on landscapes such as narrow streams in increasing aggregation and predation rates of bears (*Ursus. spp*) on adult salmon, likely because these natural landscapes spatially constrict salmon, which may enhance foraging efficiency of bears (Quinn et al. 2017). However, the effects of anthropogenic structures that don’t inherently affect flow (e.g., counting fences, bridges), or prevent fish passage have seldom been studied, but likely still mediate predator-prey interactions, posing a potential threat to migrants, affecting their behavior.

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A picture containing map

Description automatically generated

Figure 1. Map of Chilko Lake, British Columbia, Canada. Aerial image of the upper reaches of Chilko Lake shows the positions of where the DIDSON system was deployed from April 20 - 29th, 2016, during the smolt outmigration period. 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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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.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Site and date(s) | Hours of video footage | Detection window area (m2) | Average number of interactions ± SD  (m2) | Minimum number of interactions (m2) | Maximum number of interactions (m2) |  | Total number of interactions | Total number of smolts per deployment |
| Upstream Fence April 20 – 21 2016 | 14 | 29.27 | 0.444±0.484 | 0 | 1.61 |  | 364 | 1,054,978 |
| Downstream Fence April 21 – 22 2016 | 14.5 | 29.27 | 0.062±0.924 | 0 | 0.376 |  | 52 | 1,082,198 |
| Downstream Fence April 23 – 24 2016 | 22 | 29.27 | 0.008±0.018 | 0 | 0.068 |  | 23 | 5,339,320 |
| Narrows April 25 -26 2016 | 5.5 | 29.27 | 0.016±0.023 | 0 | 0.068 |  | 5 | 26,000 |
| Upstream Fence April 27 – 29 2016 | 41.5 | 9.87 | 1.37±1.18 | 0 | 4.86 |  | 1032 | 2,041,534 |
| Narrows April 29 2016 | 3.5 | 29.27 | 0.015±0.039 | 0 | 0.102 |  | 3 | NA |