**TITLE:** Using acoustic imaging to observe potential predator-prey interactions between Bull Trout (*Salvelinus confluentus*) and migrating Sockeye Salmon (*Oncorhyncus 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, the outmigration of Sockeye Salmon (*Oncorhynchus nerka*) smolts appears to influence the movements and aggregations of Bull Trout (*Salvelinus confluentus*) that feed extensively on smolts during their outmigration. However, previous studies used telemetry or Bull Trout stomach contents, and thus it is unclear if prior observations on smolt and Bull Trout behavior occurs 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 spring outmigration. 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, consistent with observations at broader scales. Predator-prey interactions were also closely coupled with previously described nocturnal migratory behaviors of Sockeye Salmon smolts, presumably to minimize predation risk. 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. These results provide further evidence that the migrations of Sockeye Salmon smolts affect the behavior of native Bull Trout and are likely important to this predator’s ecology, and the potential for anthropogenic structures such as counting fences that do not dramatically affect flow to mediate predator-prey interactions.

# Introduction:

Pacific Salmon (*Oncorhynchus spp.)* are ecologically, economically, and culturally valuable (Oke et al. 2020). 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. 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; Osterback et al. 2013; Furey et al. 2015; Flávio et al. 2021). 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 (Ibbotson et al. 2006, 2011; Clark et al. 2016; Furey et al. 2016a). Furthermore, smolts can synchronize their migrations to find safety in numbers or “swamp” predators (Furey et al. 2016a, 2021b). However, it is 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. Acoustic telemetry revealed the initial migratory corridor, the clear, slow-moving, and pristine waters of the Chilko River, as high-risk relative to the turbid waters downstream, including the Fraser River (Clark et al. 2016; Rechisky et al. 2019). Native Bull Trout (*Salvelinus confluentus*) exploit the Sockeye Salmon smolt migrations, feeding extensively on migrating Sockeye Salmon smolts near the Chilko Lake outlet (Furey et al. 2015) at high rates (Furey et al. 2016b) 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, 2021a).

In response, smolts migrate nocturnally and synchronize their movements to numerically overwhelm or swamp predators (Clark et al. 2016; Furey et al. 2016a), 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 (Moursund et al. 2003; Maxwell and Gove 2007; 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 during the smolt outmigration to: 1) investigate both spatial and temporal differences in potential Bull Trout feeding activity, 2) determine if Bull Trout activity is synchronized with Sockeye Salmon migrations, and 3) determine if the DIDSON system can provide accurate estimates of Bull Trout length distributions.

# <A>Methods:

## *Study area.* —

This study was conducted at the outlet of Chilko Lake (also known as Tŝilhqox Biny), 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 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 smolts 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.* —

The DIDSON system (Sound Metrics, Bellevue, Washington) was deployed at 5 different locations (Fig. 1) from April 20 - April 29 in 2016 during the Sockeye Salmon smolt outmigration. We deployed the DIDSON upstream of the counting fence (site UF; 51.625, -124.142) from April 20 – 21 2016 and April 27 – 29 2016. We also stationed the DIDSON downstream from Chilko River (site DR; 51.626, -124.142) from April 21 – 22 2016 and downstream from the counting fence (site DF; 51.625, -124.141) from April 23 – 24 2016. Finally, the DIDSON was positioned at a narrow river segment (site N2526; 51.615, -124.152) from April 25 – 26 2016 and April 29, 2016 (site N29; 51.615, -124.151). 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 the 5 sites. Video files from the DIDSON were analyzed in 30-minute intervals and viewed using the DIDSON Control and Display software (Sound Metrics, Bellevue, Washington). Bull Trout were identified based on their body shape (elongated) and large 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. In each video, interactions between Bull Trout and out-migrating Sockeye Salmon smolts were recorded. For the purposes of this study, we defined interactions as any instance when 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 date and time 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. 2015, 2016b), 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 (see Discussion). Recorded observations of interactions between Bull Trout and smolts were standardized to 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).

## *Data analysis.* —

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 all deployments. Intervals that contained zero interactions were included in this analysis. 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/>) 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.

Bull Trout TL were measured in each recorded interaction. Because length measurements of Bull Trout were measured for every interaction and Bull Trout in this system were not moving unidirectionally, it is nearly certain that individuals were remeasured several times. as they passed through the DIDSON’s viewing window from both upstream and downstream directions (Martignac et al. 2015). In response, this distribution of comprehensive, but likely pseudo-replicated, TLs were compared to a subset of TLs that only consisted 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 et al. 2015; Furey and Hinch 2017; Kanigan 2019). 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, χ²= 105; df = 5; p < 0.001). 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). Furthermore, 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 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 m-2, SD = 0.44 m-2). Among 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) 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 relationship (P > 0.05).

Smolt density estimates obtained from the DFO enumeration fence ranged from 200 - 882,717 smolts per hour when smolts were actively migrating. The number of hourly interactions and smolt densities were not correlated when these data were aggregated across all deployments (Spearman’s correlation, rho = -0.20; *P* = 0.11). However, a significant and strong positive correlation did exist between the number of hourly interactions and smolt densities for 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).

Previously obtained field estimates (n = 327) of Bull Trout total length ranged between 41 to 79.5 cm (mean = 58.1 m-2; SD = 6.4 m-2; Fig. 4). From the DIDSON, we obtained length estimates of Bull Trout that ranged more broadly 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; SD 8 cm) from the more conservative subset of lengths (Fig. 4). 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. 4).

# <A>Discussion:

Interactions between Bull Trout and migrating Sockeye Salmon 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). We also observed that Bull Trout respond by interacting with smolts during nighttime (when smolt migration is densest), demonstrating that Bull Trout 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). Due to the resolution of the DIDSON system, we were unable to confirm actual predation events or quantify the number of smolts consumed, and the effectiveness of synergized 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. 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 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 high-resolution telemetry tracking. 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.

More broadly, acoustic imaging can be valuable in providing estimates of fish length (Burwen et al. 2010; Crossman et al. 2011). However, in our system the DIDSON consistently provided smaller estimates of Bull Trout length than those previously collected in the field (Fig. 3). These smaller lengths (i.e., 20 - 40 cm) were likely accurate, but were measuring smaller-bodied fishes (e.g., rainbow trout or mountain whitefish) instead of Bull Trout. Direct field estimates of Bull Trout ranged from 41 - 80 cm, and the aforementioned species are regularly observed in the system. However, it is possible that smaller bull trout could be present in the system but under-sampled in the field (i.e. via hook and line). More accurate length estimates and species identification can more likely be obtained via acoustic imaging 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 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 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, the effects of anthropogenic structures that do not inherently affect flow (e.g., counting fences, bridges) or prevent fish passage have been studied less. Nonetheless, these structures can still aggregate predators (Yurk and Trites 2000) and narrow rivers can facilitate predation even in natural systems (Quinn et al. 2017). Thus, it is possible that anthropogenic structures, even if they don’t alter flow or affect fish passage directly, can still mediate predator-prey interactions and pose a potential challenge to migrants by affecting predator or prey behavior.

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# References:

Beamesderfer, R. C. P., D. L. Ward, and A. A. Nigro. 1996. Evaluation of the biological basis for a predator control program on northern squawfish (*Ptychocheilus oregonensis*) in the Columbia and Snake rivers. Canadian Journal of Fisheries and Aquatic Sciences 53:2898–2908.

Blackwell, B. F., and F. Juanes. 1998. Predation on Atlantic Salmon Smolts by Striped Bass after Dam Passage. North American Journal of Fisheries Management 18(4):936–939.

Bradford, M. J., B. J. Pyper, and K. S. Shortreed. 2000. Biological Responses of Sockeye Salmon to the Fertilization of Chilko Lake, a Large Lake in the Interior of British Columbia. North American Journal of Fisheries Management 20:661–671.

Burwen, D. L., S. J. Fleischman, and J. D. Miller. 2010. Accuracy and Precision of Salmon Length Estimates Taken from DIDSON Sonar Images. Transactions of the American Fisheries Society 139(5):1306–1314.

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

Crossman, J. A., G. Martel, P. N. Johnson, and K. Bray. 2011. The use of Dual-frequency Identification SONAR (DIDSON) to document white sturgeon activity in the Columbia River, Canada: Use of DIDSON for monitoring white sturgeon activity. Journal of Applied Ichthyology 27:53–57.

Davis, J. P., E. T. Schultz, and J. C. Vokoun. 2012. Striped Bass Consumption of Blueback Herring during Vernal Riverine Migrations: Does Relaxing Harvest Restrictions on a Predator Help Conserve a Prey Species of Concern? Marine and Coastal Fisheries 4(1):239–251.

Duffy, E. J., and D. A. Beauchamp. 2008. Seasonal Patterns of Predation on Juvenile Pacific Salmon by Anadromous Cutthroat Trout in Puget Sound. Transactions of the American Fisheries Society 137(1):165–181.

Flávio, H., P. Caballero, N. Jepsen, and K. Aarestrup. 2021. Atlantic salmon living on the edge: Smolt behaviour and survival during seaward migration in River Minho. Ecology of Freshwater Fish 30(1):61–72.

Furey, N. B., A. L. Bass, K. M. Miller, S. Li, A. G. Lotto, S. J. Healy, S. M. Drenner, and S. G. Hinch. 2021a. Infected juvenile salmon can experience increased predation during freshwater migration. Royal Society Open Science 8(3):rsos.201522.

Furey, N. B., and S. G. Hinch. 2017. Bull Trout Movements Match the Life History of Sockeye Salmon: Consumers Can Exploit Seasonally Distinct Resource Pulses. Transactions of the American Fisheries Society 146(3):450–461.

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

Furey, N. B., S. G. Hinch, A. G. Lotto, and D. A. Beauchamp. 2015. Extensive feeding on sockeye salmon Oncorhynchus nerka smolts by bull trout Salvelinus confluentus during initial outmigration into a small, unregulated and inland British Columbia river: binge feeding on smolts by s. confluentus. Journal of Fish Biology 86(1):392–401.

Furey, N. B., S. G. Hinch, M. G. Mesa, and D. A. Beauchamp. 2016b. Piscivorous fish exhibit temperature-influenced binge feeding during an annual prey pulse. Journal of Animal Ecology 85(5):1307–1317.

Furey, N. B., E. G. Martins, and S. G. Hinch. 2021b. Migratory salmon smolts exhibit consistent interannual depensatory predator swamping: Effects on telemetry‐based survival estimates. Ecology of Freshwater Fish 30(1):18–30.

Haraldstad, T., F. Kroglund, T. Kristensen, B. Jonsson, and T. O. Haugen. 2017. Diel migration pattern of Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) smolts: an assessment of environmental cues. Ecology of Freshwater Fish 26(4):541–551.

Ibbotson, A. T., W. R. C. Beaumont, and A. C. Pinder. 2011. A size-dependent migration strategy in Atlantic salmon smolts: Small smolts favour nocturnal migration. Environmental Biology of Fishes 92(2):151–157.

Ibbotson, A. T., W. R. C. Beaumont, A. Pinder, S. Welton, and M. Ladle. 2006. Diel migration patterns of Atlantic salmon smolts with particular reference to the absence of crepuscular migration. Ecology of Freshwater Fish 15(4):544–551.

Irvine, J. R., and S. A. Akenhead. 2013. Understanding Smolt Survival Trends in Sockeye Salmon. Marine and Coastal Fisheries 5(1):303–328.

Jeffries, K. M., S. G. Hinch, M. K. Gale, T. D. Clark, A. G. Lotto, M. T. Casselman, S. Li, E. L. Rechisky, A. D. Porter, D. W. Welch, and K. M. Miller. 2014. Immune response genes and pathogen presence predict migration survival in wild salmon smolts. Molecular Ecology 23(23):5803–5815.

Kanigan, A. M. 2019. The movements and distribution of bull trout (*Salvelinus confluentus*) in response to Sockeye Salmon (*Oncorhynchus nerka*) migrations in the Chilko Lake system, British Columbia. University of British Columbia, Master’s Thesis:92 pp.

Keefer, M. L., R. J. Stansell, S. C. Tackley, W. T. Nagy, K. M. Gibbons, C. A. Peery, and C. C. Caudill. 2012. Use of Radiotelemetry and Direct Observations to Evaluate Sea Lion Predation on Adult Pacific Salmonids at Bonneville Dam. Transactions of the American Fisheries Society 141(5):1236–1251.

Martignac, F., A. Daroux, J.-L. Bagliniere, D. Ombredane, and J. Guillard. 2015. The use of acoustic cameras in shallow waters: new hydroacoustic tools for monitoring migratory fish population. A review of DIDSON technology. Fish and Fisheries 16(3):486–510.

Maxwell, S. L., and N. E. Gove. 2007. Assessing a dual-frequency identification sonars’ fish-counting accuracy, precision, and turbid river range capability. The Journal of the Acoustical Society of America 122(6):3364–3377.

Miller, K. M., A. Teffer, S. Tucker, S. Li, A. D. Schulze, M. Trudel, F. Juanes, A. Tabata, K. H. Kaukinen, N. G. Ginther, T. J. Ming, S. J. Cooke, J. M. Hipfner, D. A. Patterson, and S. G. Hinch. 2014. Infectious disease, shifting climates, and opportunistic predators: cumulative factors potentially impacting wild salmon declines. Evolutionary Applications 7(7):812–855.

Moursund, R. A., T. J. Carlson, and R. D. Peters. 2003. A fisheries application of a dual-frequency identification sonar acoustic camera. ICES Journal of Marine Science 60(3):678–683.

Nichols, O. C., E. Eldredge, and S. X. Cadrin. 2014. Gray Seal Behavior in a Fish Weir Observed Using Dual-Frequency Identification Sonar. Marine Technology Society Journal 48(4):72–78.

Oke, K. B., C. J. Cunningham, P. A. H. Westley, M. L. Baskett, S. M. Carlson, J. Clark, A. P. Hendry, V. A. Karatayev, N. W. Kendall, J. Kibele, H. K. Kindsvater, K. M. Kobayashi, B. Lewis, S. Munch, J. D. Reynolds, G. K. Vick, and E. P. Palkovacs. 2020. Recent declines in salmon body size impact ecosystems and fisheries. Nature Communications 11(1):4155.

Osterback, A.-M. K., D. M. Frechette, A. O. Shelton, S. A. Hayes, M. H. Bond, S. A. Shaffer, and J. W. Moore. 2013. High predation on small populations: avian predation on imperiled salmonids. Ecosphere 4(9):art116.

Quinn, T. P., C. J. Cunningham, and A. J. Wirsing. 2017. Diverse foraging opportunities drive the functional response of local and landscape-scale bear predation on Pacific salmon. Oecologia 183(2):415–429.

Rechisky, E. L., A. D. Porter, T. D. Clark, N. B. Furey, M. K. Gale, S. G. Hinch, and D. W. Welch. 2019. Quantifying survival of age-2 Chilko Lake sockeye salmon during the first 50 days of migration. Canadian Journal of Fisheries and Aquatic Sciences 76(1):136–152.

Sabal, M. C., M. S. Boyce, C. L. Charpentier, N. B. Furey, T. M. Luhring, H. W. Martin, M. C. Melnychuk, R. B. Srygley, C. M. Wagner, A. J. Wirsing, R. C. Ydenberg, and E. P. Palkovacs. 2021. Predation landscapes influence migratory prey ecology and evolution. Trends in Ecology & Evolution 36: 737-749.

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

Saloniemi, I., E. Jokikokko, I. Kallio-Nyberg, E. Jutila, and P. Pasanen. 2004. Survival of reared and wild Atlantic salmon smolts: size matters more in bad years. ICES Journal of Marine Science 61(5):782–787.

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9(7):671–675.

Tucker, S., J. Mark Hipfner, and M. Trudel. 2016. Size- and condition-dependent predation: a seabird disproportionately targets substandard individual juvenile salmon. Ecology 97(2):461–471.

West, C. J., and P. A. Larkin. 1987. Evidence for Size-Selective Mortality of Juvenile Sockeye Salmon (*Oncorhynchus nerka*) in Babine Lake, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 44(4):712–721.

Young, G., B. Th. Björnsson, P. Prunet, R. J. Lin, and H. A. Bern. 1989. Smoltification and seawater adaptation in coho salmon (*Oncorhynchus kisutch*): Plasma prolactin, growth hormone, thyroid hormones, and cortisol. General and Comparative Endocrinology 74(3):335–345.

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

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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 (UF2021 and UF272829), white circles denote deployments downstream from Chilko River (DR2122) and downstream from the counting fence (DF2324), and white triangles indicate deployments at the narrow river segments (N2526 and N29). 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.

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 (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 April 20 – 21 2016 (UF 2021) | 14 | 29.27 | 0.444±0.484 | 0 | 1.61 |  | 364 | 1,054,978 |
| Downstream River April 21 – 22 2016 (DR2122) | 14.5 | 29.27 | 0.062±0.924 | 0 | 0.376 |  | 52 | 1,082,198 |
| Downstream Fence April 23 – 24 2016 (DF2324) | 22 | 29.27 | 0.008±0.018 | 0 | 0.068 |  | 23 | 5,339,320 |
| Narrows April 25 -26 2016 (N2526) | 5.5 | 29.27 | 0.016±0.023 | 0 | 0.068 |  | 5 | 26,000 |
| Upstream Fence April 27 – 29 2016 (UF272829) | 41.5 | 9.87 | 1.37±1.18 | 0 | 4.86 |  | 1032 | 2,041,534 |
| Narrows April 29 2016 (N29) | 3.5 | 29.27 | 0.015±0.039 | 0 | 0.102 |  | 3 | NA |

Figure 2. Total interactions (m-2) among 30-minute intervals detected between Bull Trout and smolts throughout all DIDSON deployments. 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. 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 (30 minutes) detected between Bull Trout and smolts (blue, left y-axis) plotted alongside hourly smolt density estimates (orange, right y-axis) across time. 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). Smolt densities were not observed for plot F due to fence closures during the daytime.

Figure 4. Total lengths (cm) of Bull Trout measured via two different methods. Upper panel shows unfiltered DIDSON length measurements of Bull Trout across deployments. Lower panel shows Bull Trout length measurements aggregated among deployments (n = 462; refer to Table 1 for more information on deployments). DIDSON measurements (n = 41) indicate estimates that were subsetted to provide a conservative estimate of Bull Trout length (see Methods). Field estimates of Bull Trout (n = 327) were obtained from previous studies conducted in the same system (Furey and Hinch 2017; Furey et al. 2015; Kanigan 2019). Points are jittered for visibility. Lines in the middle of the boxplots represent the median, the left and right edges represent the 25th and 75th percentile respectively, and the whiskers represent values 1.5-times the interquartile range. Black dashed lines represent the minimum (41 cm) and maximum (79.5 cm) sizes of Bull Trout measured in the field.