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MANAGEMENT BRIEF

Acoustic Imaging Observes Predator–Prey Interactions between Bull Trout and Migrating Sockeye Salmon Smolts

Matthew L. H. Cheng*

Department of Biological Sciences, University of New Hampshire, 46 College Road, Durham, New Hampshire 03824, USA; and Department of Fisheries at Lena Point, College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 17101 Point Lena Loop Road, Juneau, Alaska 99801, USA

Scott G. Hinch

Pacific Salmon Ecology and Conservation Laboratory, Department of Forest and Conservation Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada

Francis Juanes 

Department of Biology, University of Victoria, Post Office Box 1700 Station CSC, Victoria, British Columbia V8W 2Y2, Canada

Stephen J. Healy and Andrew G. Lotto

Pacific Salmon Ecology and Conservation Laboratory, Department of Forest and Conservation Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada

Sydney J. Mapley and Nathan B. Furey 

Department of Biological Sciences, University of New Hampshire, 46 College Road, Durham, New Hampshire 03824, USA

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, prior telemetry and stomach content analyses suggested that the out-migration of Sockeye Salmon *Oncorhynchus nerka* smolts influences the movements and aggregations of Bull Trout *Salvelinus confluentus* that feed extensively on smolts during their out-migration. 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 d during the 2016 smolt out-

migration. 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.

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

*Corresponding author: mat.cheng412@gmail.com
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1 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).

9 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, Sockeye Salmon smolts can migrate nocturnally (Clark et al. 2016; Furey et al. 2016a), presumably to minimize detection by visual predators. 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.

26 One method to passively observe predator–prey interactions is dual-frequency identification sonar (DIDSON). The DIDSON system uses acoustic imaging to passively observe fish behaviors, size distributions, and relative abundances, including in turbid waters and at night (Moursund et al. 2003; Maxwell and Gove 2007; Burwen et al. 2010; Crossman et al. 2011; Nichols et al. 2014; 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.

37 Chilko Lake (or T ilhqox Biny, traditional territory of the Xeni Gwet'in First Nations, one of the six communities forming the T ilhqot'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 million to more than 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 Canada (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 out-migration 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 versus other locales upstream and downstream).

METHODS

Study area.—This study was conducted at the outlet of Chilko Lake, British Columbia (51.294, −124.077; Figure 1). Chilko Lake is a 180-km², high-elevation (~1,100 m above sea level) lake that has a north–south orientation and is approximately 65 km long. Each spring, DFO installs a counting fence to estimate the numbers of out-migrant smolts. The DFO counting fence is located approximately 1.3 km downstream from Chilko Lake (Figure 1; Figure S1 in the supplement in the online version of this article) 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; this resulted in time intervals with zero smolts.

Deployment of DIDSON.—The DIDSON system (Sound Metrics, Bellevue, Washington) was deployed at five different locations (Figure 1) from April 20 to April 29 in 2016 during the Sockeye Salmon smolt out-migration (Table 1). We deployed the DIDSON upstream of the counting fence (site UF; 51.625, −124.142; Figure 1) 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; Figure 1) April 21–22, 2016, and downstream of the counting fence (site DF; 51.625, −124.141; Figure 1) April 23–24, 2016. Finally, the DIDSON was positioned at the outflow of Chilko Lake (site N; 51.615, −124.152; Figure 1) April 25–26, 2016, and April 29, 2016

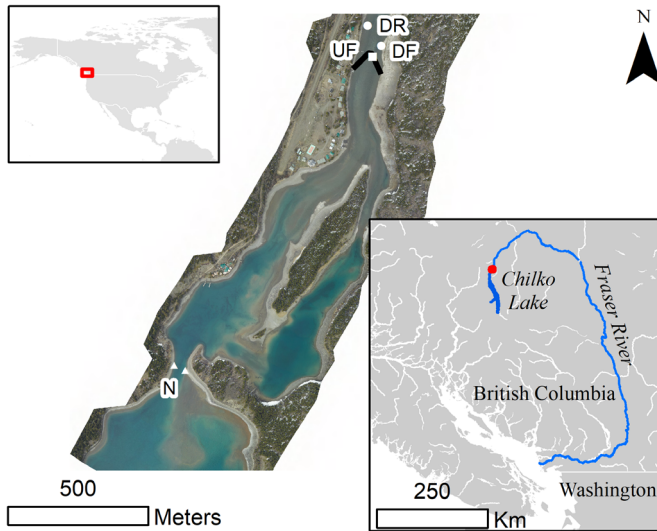


FIGURE 1. Map of Chilko Lake, British Columbia (51.294, -124.077). Aerial image of the upper reaches of Chilko Lake shows the positions (white shapes) of where the DIDSON system was deployed April 20–29, 2016, during the smolt out-migration period. The white square indicates DIDSON deployments upstream 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.

(site N; 51.615, -124.151; Figure 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 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 m and the second to 10 m into the river channel (Table 1); we used both configurations for exploratory purposes.

Data collection and video processing.—Approximately 100 h of DIDSON acoustic sonar videos were recorded and evaluated across the deployments. Video files from the DIDSON were analyzed in 30-min 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., Videos 1, 2 in the supplement in the online version of this article). Sockeye Salmon smolts were easily identified as “clouds” of small fish on the DIDSON. We also measured the total length (TL) to the nearest centimeter 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 *Prosopium williamsoni* and Rainbow Trout *Oncorhynchus mykiss* 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 (N. B. Furey, unpublished data). Nevertheless, Bull Trout lengths from each interaction were measured to understand the potential for bias resulting from observations of smaller fish 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 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 square meter (counts of interactions per m²) because the window length of the DIDSON (~5 m versus 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-min

TABLE 1. Summary data for DIDSON deployments in Chilko Lake, British Columbia, during a Sockeye Salmon smolt out-migration period (April 20–29 in 2016). The detection window area (m^2) represents the approximate area observed by the DIDSON. The total number of interactions is the sum of all interactions detected for a given deployment. The total number of smolts per deployment is 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 \pm SD number of interactions (m^{-2} per 30 min)	Minimum number of interactions (m^{-2} per 30 min)	Maximum number of interactions (m^{-2} per 30 min)	Total number of interactions	Total number of smolts per deployment
Upstream fence (UF) April 20–21	14	29.27	0.444 ± 0.484	0	1.61	364	1,054,978
Downstream river (DR) April 21–22	14.5	29.27	0.062 ± 0.924	0	0.376	52	1,082,198
Downstream fence (DF) April 23–24	22	29.27	0.008 ± 0.018	0	0.068	23	5,339,320
Narrows (N) April 25–26	5.5	29.27	0.016 ± 0.023	0	0.068	5	26,000
Upstream fence (UF) April 27–29	41.5	9.87	1.37 ± 1.18	0	4.86	1,032	2,041,534
Narrows (N) April 29	3.5	29.27	0.015 ± 0.039	0	0.102	3	

intervals that had zero interactions between Bull Trout and Sockeye Salmon smolts at parallel sites (UF2021, 29.27 m^2 ; UF272829, 9.87 m^2); if bias occurred, a smaller detection range would result in a larger number of zero interactions observed.

Data analysis.—For the following analyses, nonparametric 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-min interval, standardized to per square meter 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-min 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 min, 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 version 3.6.3 (R Core Team 2021).

RESULTS

Interactions between smolts and Bull Trout throughout all deployments ranged from 0 to 4.86 interactions/ m^2 among 30-min intervals (mean = $0.63/\text{m}^2$; SD = 0.99). 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 site UF April 20–21 and site UF 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 site DR April 21–22 deployment and the site DF 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 square meter were observed when the DIDSON was deployed upstream of the counting fence (site UF; mean = $1.14/\text{m}^2$; SD = 1.12; range = $0\text{--}4.86/\text{m}^2$), followed by sites that occurred downstream of the counting fence (site DR and DF; mean = $0.029/\text{m}^2$; SD = 0.065; range = $0\text{--}0.376/\text{m}^2$) and the narrow river segment (site N; mean = $0.015/\text{m}^2$; SD = 0.029; range = $0.102/\text{m}^2$).

The number of standardized interactions among 30-min intervals varied with the diel cycle when aggregated across all deployments ($W = 2693.5$; $P < 0.01$; Figure 2);

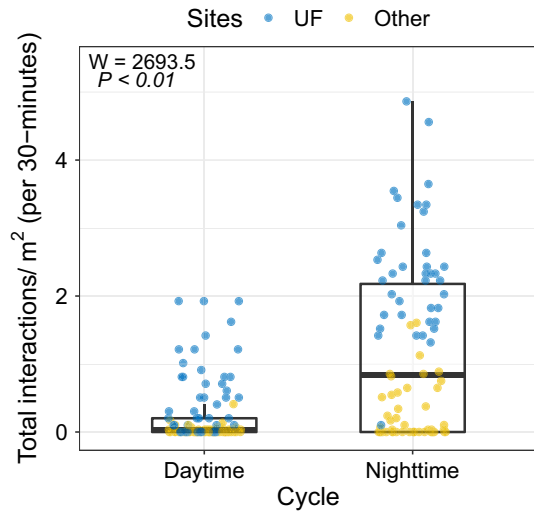


FIGURE 2. Total interactions (per m^2) among 30-min intervals detected between Bull Trout and smolts throughout all DIDSON deployments. Each observation represents a 30-min interval within a diel period (daytime: $n=116$; nighttime: $n=86$). Daylight and nighttime hours were determined via <https://www.timeanddate.com/>. 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 (site 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.

interactions were higher during nighttime hours and ranged from 0 to 4.86 interactions/ m^2 (mean = 1.19/ m^2 ; SD = 1.24) than during daytime hours (mean = 0.225/ m^2 , SD = 0.44). For individual deployments, nighttime interactions (per m^2) were significantly higher than daytime interactions during the site UF April 20–21 deployment (daytime mean = 0.05/ m^2 , SD = 0.11; nighttime mean = 0.78/ m^2 , SD = 0.42; $W = 11$, $P < 0.01$; Figure 3A), the site DR April 21–22 deployment (daytime mean = 0.02/ m^2 , SD = 0.05; nighttime mean = 0.10/ m^2 ; SD = 0.11; $W = 49.5$, $P = 0.01$; Figure 3B), and the site UF April 27–29 deployment (daytime: mean = 0.54/ m^2 , SD = 0.57; nighttime: mean = 2.35/ m^2 , SD = 0.93; $W = 79.5$, $P < 0.01$; Figure 3E), but other deployments did not demonstrate this relationship.

Smolt density estimates obtained from the DFO counting fence ranged from 200 to 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 site UF April 20–21 deployment (Spearman's correlation: $\rho = 0.87$, $P < 0.001$; Figure 3A) and the site

UF April 27–29 deployment (Spearman's correlation: $\rho = 0.76$, $P < 0.001$; Figure 3E).

We directly compared the proportion of 30-min 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 UF April 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 of 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 to 87 cm across all interactions ($n = 3,025$; mean = 50.7 cm; SD = 9.99). 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 ≤ 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; Figure S2 in the supplement in the online version of this article).

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 (Furey et al. 2015, 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 d), 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

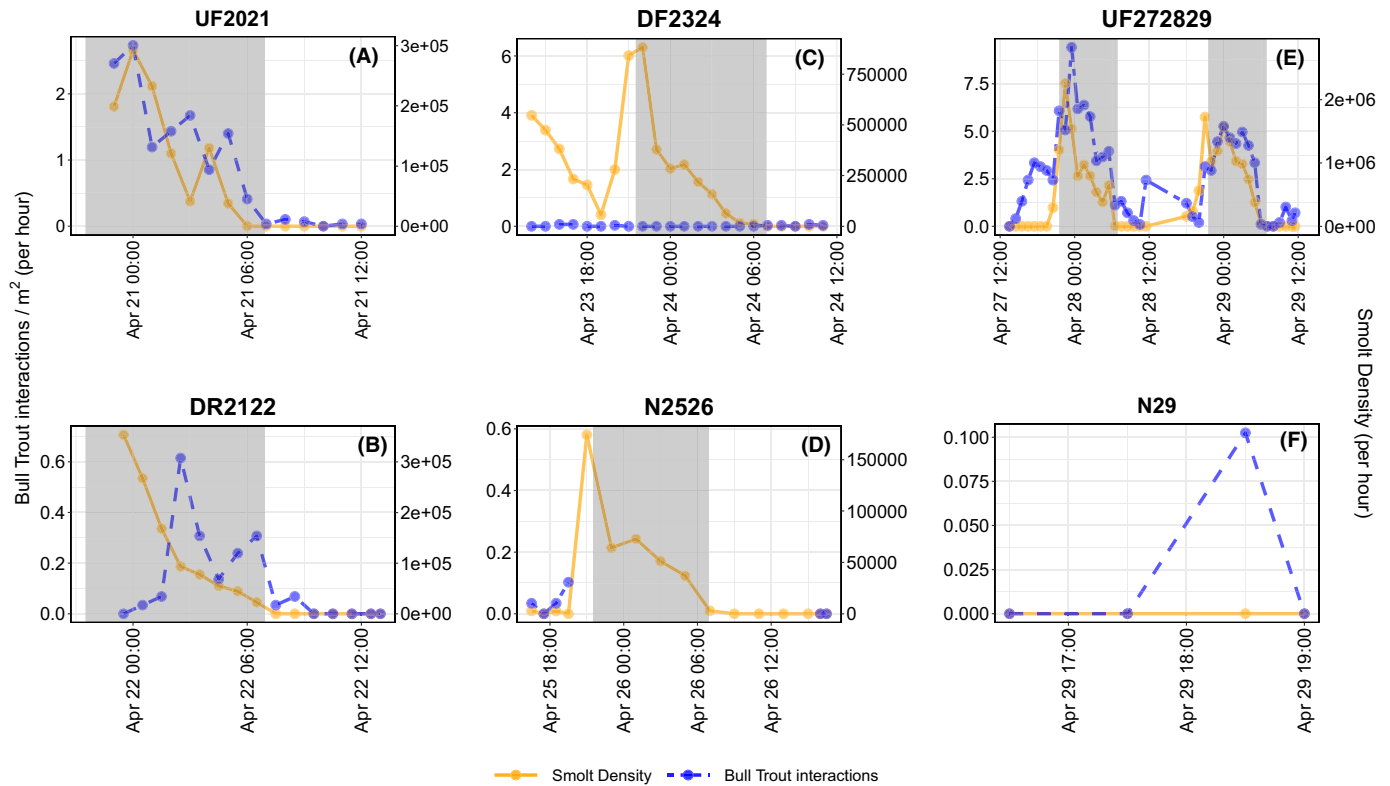


FIGURE 3. The number of interactions per square meter and per unit time (1 h) detected between Bull Trout and smolts (blue lines and points, left y-axis) plotted alongside hourly smolt density estimates (orange lines and points, right y-axis) across time. Note that during certain hours, smolt densities are not observed because the fence is physically closed to migrants (when orange points are at zero). Gray shading indicates nighttime hours. Panels (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 April 25 at 16:30–19:30 h and April 26 at 16:00–16:30 h for site N2526 and thus other times are presented as missing observations.

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 out-migrant 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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ORCID

Francis Juanes  <https://orcid.org/0000-0001-7397-0014>
Nathan B. Furey  <https://orcid.org/0000-0002-8584-7889>

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.