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

Journal:	*North American Journal of Fisheries Management*
Manuscript ID	UJFM-2022-0102
Manuscript Type:	Research Article
Keywords:	predator-prey interactions, anthropogenic structures, sockeye salmon, bull trout

SCHOLARONE™
Manuscripts

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

Author information:

Matthew L.H. Cheng[1,2], Scott G. Hinch[3], Francis Juanes[4], Stephen J. Healy[3], Andrew G. Lotto[3], Sydney J. Mapley[1], and Nathan B. Furey[1]

[1] Department of Biological Sciences, University of New Hampshire, 46 College Road, Durham, NH, 03824, USA

[2] Department of Fisheries at Lena Point, College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 17101 Point Lena Loop Rd, Juneau, AK 99801, USA

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

[4] Department of Biology, University of Victoria, PO Box 1700 Station CSC, Victoria, British Columbia V8W 2Y2, Canada

For Peer Review Only

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. It is uncertain if these predator-prey patterns exist at finer spatial scales. We used Dual-frequency Identification Sonar (DIDSON) acoustic imaging to assess fine-scale predator-prey interactions between Sockeye Salmon smolts and Bull Trout over 10 days during the 2016 smolt outmigration. We found that smolt densities were 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 nocturnal migratory behaviors of Sockeye Salmon smolts, presumably to minimize predation risk. These results provide further evidence that the migrations of Sockeye Salmon smolts affect the behavior of Bull Trout and are important to this predator's ecology and provides insight on the role of anthropogenic structures (e.g., counting fences) in mediating predator-prey interactions.

For Peer Review Only

Introduction:

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

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

Chilko Lake (or Tŝilhqox Biny), British Columbia, is home to one of the largest populations of Sockeye Salmon in Canada, and consequently this population is intensively studied (Bradford et al. 2000; Irvine and Akenhead 2013). Each spring, 10 - >40 million Sockeye

For Peer Review Only

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

One method to passively observe predator-prey interactions is Dual-Frequency Identification Sonar (DIDSON). The DIDSON system uses acoustic imaging to allow for passive observations of fish behaviors, size distributions, and relative abundances, including in turbid water and at night (Burwen et al. 2010; Crossman et al. 2011; Martignac et al. 2015; Moursund et al. 2003; Maxwell and Gove 2007; Nichols et al. 2014). This technology can also be used to assess fish size distributions and relative abundances (Burwen et al. 2010; Crossman et al. 2011; Martignac et al. 2015). The present study uses DIDSON at the Chilko Lake-River outlet during the smolt outmigration to: 1) investigate both spatial and temporal differences in potential Bull Trout feeding activity and 2) determine if Bull Trout activity is synchronized with Sockeye Salmon migrations.

URL: http://mc.manuscriptcentral.com/najfm Email: journals@fisheries.org

<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 km^2, 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, 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.

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

For Peer Review Only

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. For the purposes of this study, we defined interactions as any instance when it appeared that either Bull Trout or Sockeye Salmon smolts (or both) reacted to the presence or proximity of the other within the video. Bull Trout are the dominant piscivore present during the migration to feed on smolts (Furey et al. 2015, 2016b) and are generally much larger in body size (we measured at ~25-85 cm in length) than other fishes present at lower abundances (mountain whitefish and rainbow trout primarily) and thus generally identifiable on the DIDSON. Sockeye Salmon smolts present as "clouds" of small fish on the DIDSON and are easily identifiable.

Videos were processed at frame rates of ~25 - 50 frames·s^{-1} and were played back, slowed down, and/or paused when interactions were detected. This was done to verify interactions between Bull Trout and Sockeye Salmon smolts. Further, these videos were viewed using the "Background Subtraction" tool to remove potential static background and to better visualize fish passing through the video. Recorded observations of interactions between Bull Trout and smolts were standardized to per m^2 (counts of interactions per m^2) because the window length of the DIDSON (~5 m vs 10 m) and thus area observed, differed among deployments (Table 1). To

For Peer Review Only

146 estimate the window area observed by the DIDSON (~9.87 m^2 for the 5-m window length and
147 ~29.27 m^2 for the 10-m window length), images of the DIDSON were imported and window
148 area calculated using ImageJ (Schneider et al. 2012).
149
150 *Data analysis.—*
151
152 For the following analyses, non-parametric tests were used due to violations of model
153 assumptions (i.e., homogeneity of variance, normally distributed residuals, etc.). Kruskal-Wallis
154 rank sum tests were used to test for differences in the number of interactions per 30-minute
155 interval, standardized to per m^2 across all deployments; note that intervals containing zero
156 interactions were included in this analysis. Non-parametric Wilcoxon rank sum tests were
157 performed to test for differences in the number of standardized interactions (m^{-2} in each 30-
158 minute interval) between daylight and nighttime hours (sunrise and sunset determined via
159 https://www.timeanddate.com/) both collectively among all deployments, and with a separate
160 test for each of the five individual deployments. Finally, correlations between migrating smolt
161 densities (collected from the DFO counting fence) and standardized interactions (per hour,
162 instead of every 30 minutes, to match the resolution of smolt density data from the counting
163 fence) between Bull Trout and smolts were tested both collectively among all deployments and
164 individually for each of the five different deployments using Spearman's rank order correlation
165 coefficient. Furthermore, because we were only focused on predator-prey interactions during
166 times of active smolt migrations, we removed any time period when smolts were not migrating
167 due to fence closure (mostly during daylight hours), to better capture potential correlations
168 between Bull Trout and smolt densities for these specific analyses. All statistical analyses were
169 conducted using R v3.6.3 (R Core Team 2021).

For Peer Review Only

<A>Results:

Interactions between smolts and Bull Trout throughout all deployments ranged from 0 - 4.86 interactions per m^2 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, χ^2= 105; df = 5; $P < 0.001$). The highest number of interactions per m^2 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 m^2 (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 m^2) were significantly higher than daytime interactions during the Upstream Fence April 20 - 21 deployment (daytime mean = 0.05 m^{-2}; SD = 0.11 m^{-2}, nighttime mean = 0.78 m^{-2}; SD = 0.42 m^{-2}; W = 11; $P < 0.01$; Fig. 3A) 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 counting 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

For Peer Review Only

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).

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

Activity of Bull Trout was most tightly linked with smolt migration densities for deployments when the DIDSON was deployed just upstream of the counting fence (Fig. 3E). Potential feeding activity of Bull Trout was most positively correlated with smolt densities upstream of the fence, but not elsewhere in the system. Thus, it appears smolt-Bull Trout

For Peer Review Only

interactions are most tightly coupled just upstream of this anthropogenic structure. In fact, Bull Trout feed at higher rates (e.g., at *ad libitum*) at the counting fence relative to other locales (Furey et al. 2016b), and it appears that fine-scale behaviors (i.e., actively pursuing smolts as they appear as observed by the DIDSON) likely reflect these observations of feeding intensity. As a result, the counting fence may create a spatial bottleneck for migrant smolts to pass. It is possible that the constriction of the counting fence, and potentially the presence of Bull Trout, may concentrate smolts within a small area, slowing the movement speeds of smolts, and thus, increasing the foraging efficiency of Bull Trout. However, further research could better quantify how smolts behave as they pass through the counting fence relative to other landscapes, and if mortality is higher at the fence, potentially via telemetry tracking upstream of the fence. Given the short duration of our study (10 days), which was due to opportunistic use of the DIDSON during other field programs, we believe our conclusions could be better supported by monitoring the upstream fence site more intensively (i.e., additional days), with concurrent comparisons of other sites. We also acknowledge that with only one DIDSON unit, we were unable to compare differences in predator-prey interactions between or among sites simultaneously.

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

URL: http://mc.manuscriptcentral.com/najfm Email: journals@fisheries.org

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

<A> Acknowledgements:

We gratefully acknowledge the Xeni Gwet'in First Nation for providing access to the field site. We would also like to thank Fisheries and Oceans Canada for providing field and logistical support and for providing access to counting fence data. Purchase of the DIDSON was funded by grants from CFI and BCKDF to Juanes. This project was supported by the Pacific Salmon Foundation as part of the Salish Sea Marine Survival Project (Publication number XX), the Fisheries Society of the British Isles Small Grants Program, Canada's Ocean Tracking Network, and grants from the Natural Sciences and Engineering Research Council of Canada to Hinch. During field work, Furey was supported via the Vanier Canada Graduate Scholarships Program. Furey is currently supported by the Class of 1937 Professorship in Marine Biology from the School of Marine Sciences and Ocean Engineering at the University of New Hampshire.

For Peer Review Only

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.

COSEWIC. 2017. COSEWIC assessment and status report on the sockeye salmon, Oncorhynchus nerka, 24 designatable units in the Fraser River drainage basin, in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.

For Peer Review Only

287 Crossman, J. A., G. Martel, P. N. Johnson, and K. Bray. 2011. The use of Dual-frequency
288 IDentification SONAR (DIDSON) to document white sturgeon activity in the Columbia
289 River, Canada. Journal of Applied Ichthyology 27:53–57.
290 Davis, J. P., E. T. Schultz, and J. C. Vokoun. 2012. Striped Bass Consumption of Blueback
291 Herring during Vernal Riverine Migrations: Does Relaxing Harvest Restrictions on a
292 Predator Help Conserve a Prey Species of Concern? Marine and Coastal Fisheries
293 4(1):239–251.
294 Duffy, E. J., and D. A. Beauchamp. 2008. Seasonal Patterns of Predation on Juvenile Pacific
295 Salmon by Anadromous Cutthroat Trout in Puget Sound. Transactions of the American
296 Fisheries Society 137(1):165–181.
297 Flávio, H., P. Caballero, N. Jepsen, and K. Aarestrup. 2021. Atlantic salmon living on the edge:
298 Smolt behaviour and survival during seaward migration in River Minho. Ecology of
299 Freshwater Fish 30(1):61–72.
300 Furey, N. B., A. L. Bass, K. M. Miller, S. Li, A. G. Lotto, S. J. Healy, S. M. Drenner, and S. G.
301 Hinch. 2021a. Infected juvenile salmon can experience increased predation during
302 freshwater migration. Royal Society Open Science 8(3):rsos.201522, 201522.
303 Furey, N. B., and S. G. Hinch. 2017. Bull Trout Movements Match the Life History of Sockeye
304 Salmon: Consumers Can Exploit Seasonally Distinct Resource Pulses. Transactions of
305 the American Fisheries Society 146(3):450–461.
306 Furey, N. B., S. G. Hinch, A. L. Bass, C. T. Middleton, V. Minke-Martin, and A. G. Lotto.
307 2016a. Predator swamping reduces predation risk during nocturnal migration of juvenile
308 salmon in a high-mortality landscape. Journal of Animal Ecology 85(4):948–959.

For Peer Review Only

309 Furey, N. B., S. G. Hinch, A. G. Lotto, and D. A. Beauchamp. 2015. Extensive feeding on
310 sockeye salmon *Oncorhynchus nerka* smolts by bull trout *Salvelinus confluentus* during
311 initial outmigration into a small, unregulated and inland British Columbia river. Journal
312 of Fish Biology 86(1):392–401.
313 Furey, N. B., S. G. Hinch, M. G. Mesa, and D. A. Beauchamp. 2016b. Piscivorous fish exhibit
314 temperature-influenced binge feeding during an annual prey pulse. Journal of Animal
315 Ecology 85(5):1307–1317.
316 Furey, N. B., E. G. Martins, and S. G. Hinch. 2021b. Migratory salmon smolts exhibit consistent
317 interannual depensatory predator swamping: Effects on telemetry-based survival
318 estimates. Ecology of Freshwater Fish 30(1):18–30.
319 Gislason, G., E. Lam, G. Knapp, and M. Guettabi. 2017. Economic Impacts of Pacific Salmon
320 Fisheries. Report to the Pacific Salmon Commission GSGislason & Associates Ltd.
321 Haraldstad, T., F. Kroglund, T. Kristensen, B. Jonsson, and T. O. Haugen. 2017. Diel migration
322 pattern of Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) smolts: an
323 assessment of environmental cues. Ecology of Freshwater Fish 26(4):541–551.
324 Ibbotson, A. T., W. R. C. Beaumont, and A. C. Pinder. 2011. A size-dependent migration
325 strategy in Atlantic salmon smolts: Small smolts favour nocturnal migration.
326 Environmental Biology of Fishes 92(2):151–157.
327 Ibbotson, A. T., W. R. C. Beaumont, A. Pinder, S. Welton, and M. Ladle. 2006. Diel migration
328 patterns of Atlantic salmon smolts with particular reference to the absence of crepuscular
329 migration. Ecology of Freshwater Fish 15(4):544–551.
330 Irvine, J. R., and S. A. Akenhead. 2013. Understanding Smolt Survival Trends in Sockeye
331 Salmon. Marine and Coastal Fisheries 5(1):303–328.

For Peer Review Only

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.

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.

For Peer Review Only

354 Moursund, R. A., T. J. Carlson, and R. D. Peters. 2003. A fisheries application of a dual-
355 frequency identification sonar acoustic camera. ICES Journal of Marine Science
356 60(3):678–683.
357 Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific Salmon, Nutrients,
358 and the Dynamics of Freshwater and Riparian Ecosystems. Ecosystems 5(4):399–417.
359 Nichols, O. C., E. Eldredge, and S. X. Cadrin. 2014. Gray Seal Behavior in a Fish Weir
360 Observed Using Dual-Frequency Identification Sonar. Marine Technology Society
361 Journal 48(4):72–78.
362 Osterback, A.-M. K., D. M. Frechette, A. O. Shelton, S. A. Hayes, M. H. Bond, S. A. Shaffer,
363 and J. W. Moore. 2013. High predation on small populations: avian predation on
364 imperiled salmonids. Ecosphere 4(9):art116.
365 Peterman, R. M., and B. Dorner. 2012. A widespread decrease in productivity of sockeye salmon
366 (*Oncorhynchus nerka*) populations in western North America. Canadian Journal of
367 Fisheries and Aquatic Sciences 69(8):1255–1260.
368 R Core Team. 2021. R: A Language and Environment for Statistical Computing. R Foundation
369 for Statistical Computing, Vienna, Austria.
370 Rechisky, E. L., A. D. Porter, T. D. Clark, N. B. Furey, M. K. Gale, S. G. Hinch, and D. W.
371 Welch. 2019. Quantifying survival of age-2 Chilko Lake sockeye salmon during the first
372 50 days of migration. Canadian Journal of Fisheries and Aquatic Sciences 76(1):136–
373 152.
374 Sabal, M. C., M. S. Boyce, C. L. Charpentier, N. B. Furey, T. M. Luhring, H. W. Martin, M. C.
375 Melnychuk, R. B. Srygley, C. M. Wagner, A. J. Wirsing, R. C. Ydenberg, and E. P.

For Peer Review Only

Palkovacs. 2021. Predation landscapes influence migratory prey ecology and evolution. Trends in Ecology & Evolution:S0169534721001245.

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.

For Peer Review Only

401 Tables:
402
403 Table 1. Summary data for DIDSON deployments in Chilko Lake, British Columbia, Canada,
404 from April 20 – 29, 2016 during a Sockeye Salmon smolt outmigration period. The detection
405 window area (m^2) represents the approximate area observed by the DIDSON. The total number
406 of interactions are the sum of all interactions detected for a given deployment. The total number
407 of smolts per deployment are the sum of smolt densities (estimated hourly) for a given night
408 from the counting fence.

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

409

410

For Peer Review Only

411 Figures:
412

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

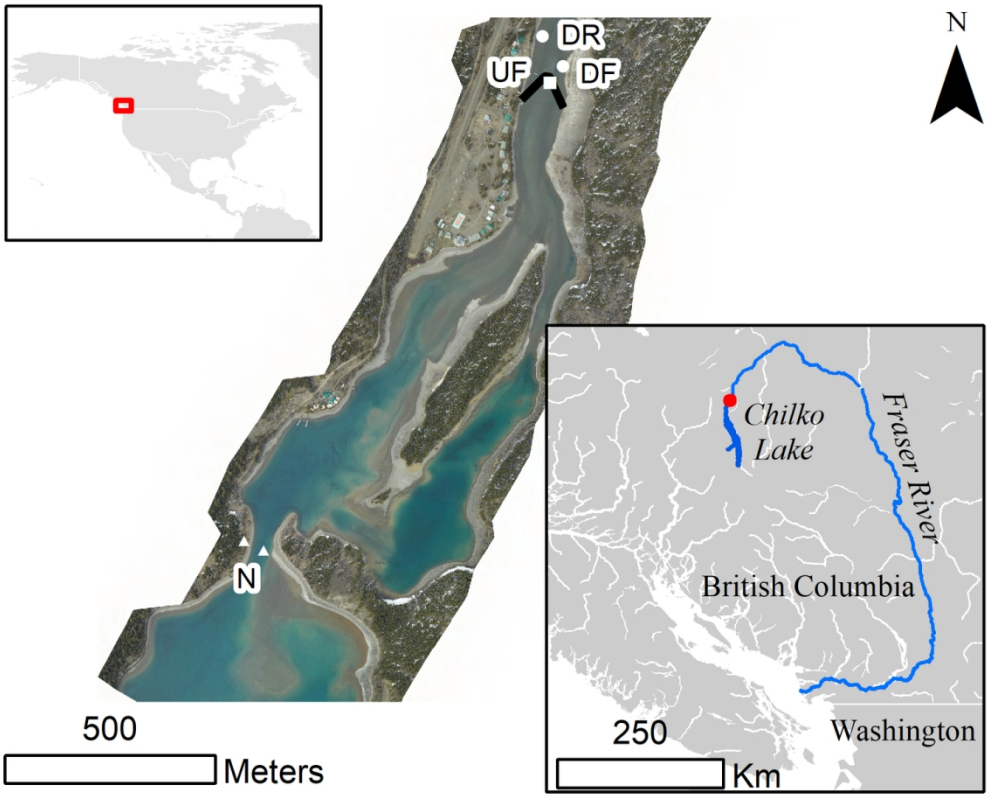
For Peer Review Only

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.

For Peer Review Only

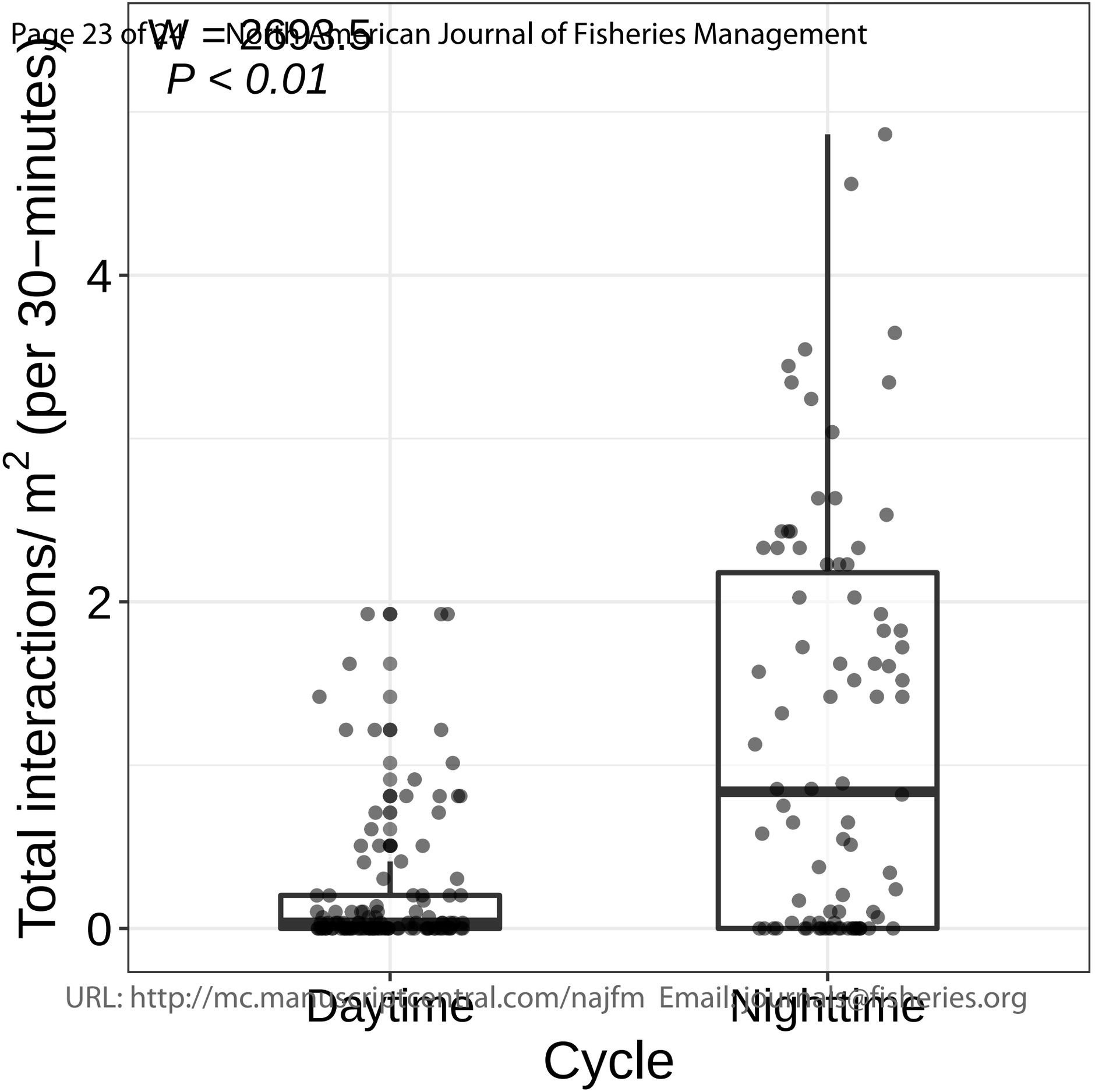
Figure 3. The number of interactions per m^2 and per unit time (1 hour) detected between Bull Trout and smolts (blue, left y-axis) plotted alongside hourly smolt density estimates (orange, right y-axis) across time. Grey shading indicates nighttime hours. Plots A - F display interactions and smolt density 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.

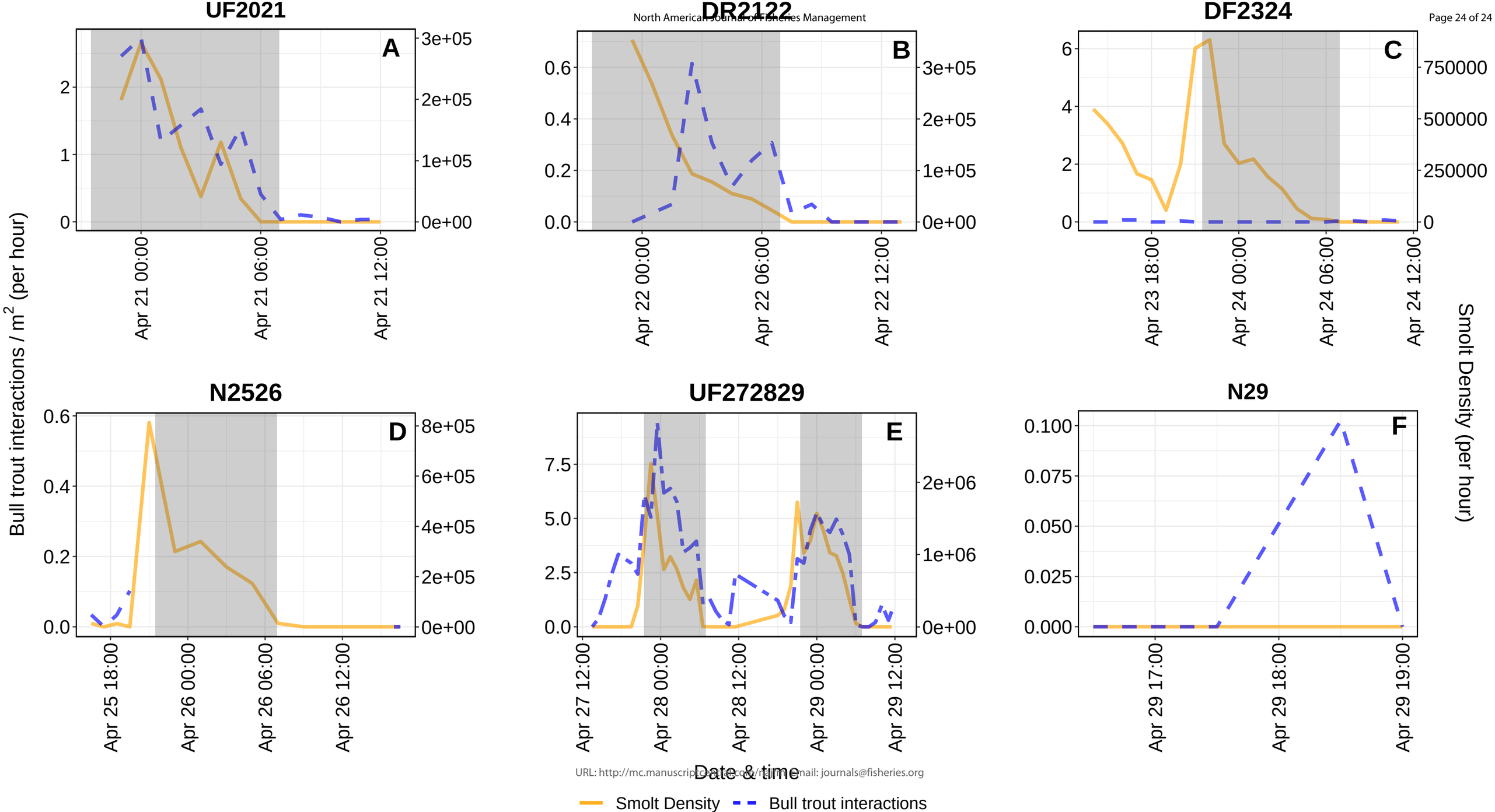
For Peer Review Only



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.

127x101mm (300 x 300 DPI)


W = 2693.5
P < 0.01
Total interactions/ m2 (per 30−minutes)
0
2
4
Daytime
Nighttime
Cycle



URL: http://mc.manuscriptcentral.com/nafm Email: journals@fisheries.org