Received: 13 May 2019 | Revised: 17 January 2020 | Accepted: 26 February 2020

DOI: 10.1002/rra.3617

RESEARCH ARTICLE

WILEY

# A comparison of turbine entrainment rates and seasonal entrainment vulnerability of two sympatric char species, bull trout and lake trout, in a hydropower reservoir

Philip M. Harrison[1,2] | Taylor Ward[1] | Dirk A. Algera[1] | Brad Culling[3] | Ted Euchner[3] | Alf Leake[4] | James A. Crossman[5] | Steven J. Cooke[1] | Michael Power[6]

[1]Department of Biology, Carleton University, Ottawa, Ontario, Canada

[2]Department of Biology, Canadian Rivers Institute, University of New Brunswick, Fredericton, New Brunswick, Canada

[3]Diversified Environmental Services, Fort St. John, British Columbia, Canada

[4]Fish and Aquatic Issues, Environment, BC Hydro, Burnaby, British Columbia, Canada

[5]Fish and Aquatic Issues, Environment, BC Hydro, Castlegar, British Columbia, Canada

[6]Department of Biology, University of Waterloo, Waterloo, Ontario, Canada

**Correspondence**
Philip M. Harrison, Carleton University, Ottawa, ON, Canada.
Email: pharriso@unb.ca

**Funding information**
Canada Research Chairs Program; HYCANOR; Natural Sciences and Engineering Research Council of Canada

## Abstract

Potadromous salmonids that reside in hydropower reservoirs often have a high recreational and conservation value. However, the potential seasonal turbine entrainment vulnerability patterns of potadromous salmonids are not well understood. Here, we use acoustic telemetry to test the hypothesis that adults of two species of the *Salvelinus* genus (bull trout and lake trout) differ in their seasonal patterns of entrainment and entrainment vulnerability over a 2-year period. Our results show that while both species were entrained at similarly low annual rates (~1%), these two salmonids differed in their patterns of forebay residency and proximity, with implications for entrainment risk. Bull trout occupied the forebay at low rates across all seasons, with no clear seasonal pattern of forebay proximity. In contrast, lake trout displayed a strongly seasonal pattern of entrainment vulnerability with a distinct movement away from the forebay during the summer, and a large increase in forebay proximity and use in the winter and spring. These findings provide a novel species-specific demonstration of the potential entrainment vulnerability of lake trout. The seasonal patterns of entrainment vulnerability seen in previous bull trout studies, where bull trout occupied top pelagic predator niches, were not replicated in our study where bull trout occur in sympatry with another top pelagic predator. These findings, which indicate that species composition plays an important role determining entrainment vulnerability, have important implications for the conservation of indigenous lake trout and bull trout populations, and together highlight the need for a site-specific approach to entrainment quantification.

KEYWORDS

acoustic telemetry, connectivity, downstream passage, freshwater fish ecology, hydropower dams, *Salvelinus*, spatial ecology

## 1 | INTRODUCTION

Turbine entrainment (i.e., the displacement of fish downstream from reservoirs through hydroelectric turbines) can influence fish populations residing upstream and downstream of hydropower reservoirs (Coutant & Whitney, 2000; Martins et al., 2013). As upstream passage facilities are rare, entrained fish often represent a loss to the upstream population (Harrison et al., 2019). Furthermore, because turbine entrainment mortality is frequently <100%, and often ~30% (Pracheil, DeRolph, Schramm, & Bevelhimer, 2016; Wilkes, Webb, Baumgartner, et al., 2018), entrainment survivors can disperse into downstream environments and can augment downstream populations (Harrison et al., 2019). While the vulnerability of anadromous salmonid populations to turbine entrainment has been well studied (e.g., Calles & Greenberg, 2009; Silva et al., 2017), less is known about the turbine entrainment vulnerability of potadromous fish populations (Rytwinski et al., 2017). Accordingly, estimation of entrainment rates (i.e., the proportion of a fish population annually removed from the reservoir by turbine entrainment) represents an important first step in understanding the impacts of hydropower on freshwater fish populations.

In addition to quantification of entrainment rates, an understanding of the seasonal nature of turbine entrainment risk is necessary to design effective mitigation strategies (Coutant & Whitney, 2000). When the number of entrained individuals is high, seasonal patterns of entrainment vulnerability can be quantified directly (Smith & Brown, 2002). However, when the number of observable entrainment events are restricted due to sample size, seasonal patterns of forebay (the area of a reservoir in the vicinity of the dam) occupancy, can be used as proxy for entrainment vulnerability (Harrison et al., 2019; Martins et al., 2013). Furthermore, given that fish that are located close to the dam forebay are likely at higher risk of entrainment than fish that are located a long distance away, fish proximity to the forebay, can also be used a measure of entrainment vulnerability, and to help understand seasonal patterns of entrainment vulnerability (Harrison et al., 2019).

In the cold-water inland hydropower reservoirs typical of Canada and the northern western United States, potadromous salmonids, such as bull trout *Salvelinus confluentus*, and lake trout, *Salvelinus namaycush*, are top predators, and often grow to large sizes (>1 m in length Gutowsky, Harrison, Landsman, Power, & Cooke, 2011; Johnson & Martinez, 2000). Accordingly, bull trout and lake trout are prized by anglers (Nitychoruk et al., 2013; Post, Mushens, Paul, & Sullivan, 2003). Bull trout are a generalist species and include both river resident and lacustrine adfluvial populations. Adfluvial populations perform late summer/early fall spawning migrations into tributary systems. Bull trout have a high conservation value (Gutowsky et al., 2011) as they are considered a species of special concern throughout much of their range in western Canada (Committee on the Status of Endangered Wildlife in Canada, 2012) and threatened throughout much of their United States range (Dunham, Gallo, Shively, Allen, & Goehring, 2011). Lake trout are generally lacustrine, fall spawners, endemic to Arctic drainages in Western North America. Introduced lake trout populations have thrived in North American Pacific drainages, often with negative impacts on native fish populations (Martinez et al., 2010).

Despite the presence of numerous hydropower facilities in western Canada, our understanding of the effects of hydropower fragmentation on bull trout populations remains relatively poor. We could find no previous studies investigating or documenting lake trout turbine entrainment. Quantitative estimates of bull trout turbine entrainment rates and seasonal patterns of vulnerability have been limited to a single study by Martins et al. (2013). Martins et al. (2013) showed that bull trout in Kinbasket Reservoir, British Columbia, were entrained at a rate of 3.4% per year, and displayed increased fall/winter forebay residency, in comparison to spring and summer. Given uncertainties in how entrainment risk may vary between reservoirs or species, baseline information on both entrainment rates and seasonal patterns of entrainment vulnerability is important for quantifying the risk of hydropower activities. While the specific aspects of behaviour and ecology that determine entrainment vulnerability are not well understood (Harrison et al., 2019), we do know that sympatric species often differ in their entrainment vulnerability (Čada & Schweizer, 2012; Martins et al., 2013).

Here, we use acoustic telemetry to investigate turbine entrainment rates and turbine entrainment vulnerability of sympatric populations of bull trout and lake trout through the WAC Bennet Dam, in north eastern British Columbia, Canada. Upstream fish passage facilities do not exist at our study site, and thus, all entrained fish, irrespective of their passage mortality, represent a loss to the upstream population. We hypothesise that bull trout and lake trout differ in their annual entrainment rates, seasonal patterns of forebay residency, and seasonal proximity to the dam forebay. We tested these hypotheses through the installation of a dam tailrace telemetry array, which we used to determine entrainment rates, a forebay based array, which we used to determine forebay residency, and a lake-wide array which we used to quantify seasonal patterns of proximity to the forebay.

## 2 | METHODS

### 2.1 | Study site

Williston Reservoir (56°01′00″N, 122°12′02″W), is the largest body of freshwater in British Columbia (surface area 1761 km$^2$). The reservoir was created in 1968 by the construction of the WAC Bennett dam on the upper Peace River for hydroelectricity production. The reservoir is comprised of three reaches (Figure 1): the Finlay Reach which flooded the valley formed by the southward flowing Finlay River, the Parsnip Reach which filled the valley formed by the northward flowing Parsnip River, and the Peace Reach which encompasses the eastward flowing Peace River valley between the confluence of the Parsnip and Finlay tributaries and the dam forebay (the area in close vicinity of the dam face). Each "reach" is >120 km in length.

The reservoir is deep (mean depth 41.7 m, max depth 166 m), ultra-oligotrophic and cold (maximum of 19°C in summer) (Stockner, Langston, Sebastian, & Wilson, 2005). The reservoir typically stratifies between June and October, with an epilimnion depth of 15–25 m in the Peace Reach and a temperature range of 13–19°C. Hypolimnetic temperatures range from 4 to 6°C. The reservoir is operated on an annual cycle (see Figure S1), with maximum reservoir elevations typically occurring in during the summer period. The reservoir is then drawn down over the fall and winter, when power requirements are

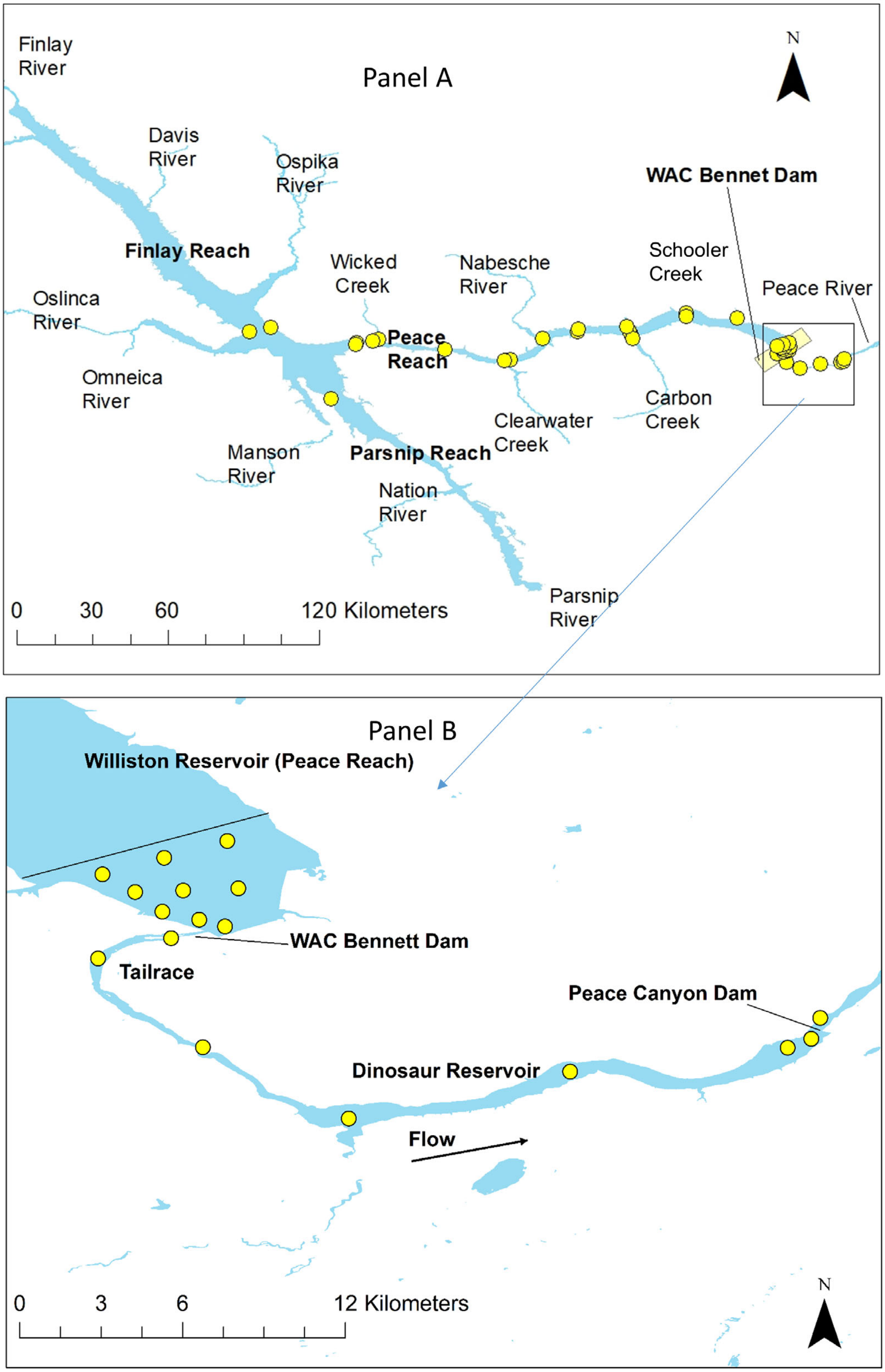


**FIGURE 1** Map of Williston Reservoir, British Columbia, Canada. Panel A depicts reservoir wide telemetry array, with receiver locations (filled circles), and black line depicting forebay. Panel B provides a close-up view of forebay and tailrace telemetry arrays (filled circles) and 750 m receiver ranges (wider filled circles) [Colour figure can be viewed at wileyonlinelibrary.com]

highest, with highest turbine flows occurring in late fall/early winter (December to January). Lowest reservoir elevations occur late April to early May. Reservoir draw-downs average ~11 m per year. The reservoir is then filled in the late spring and summer (Stockner et al., 2005). The reservoir is operated to ensure that spill events are exceedingly rare (once a decade or less).

The powerhouse at the WAC Bennett Dam consists of 10 Francis turbines (5 × 275 MW, 3 × 310 MW and 2 × 306 MW), which together can provide a total capacity of 2,730 MW with a combined release of 1982 $m^3/s$ (the position of the turbine intakes can be seen in Figure S2). Intakes for turbines 1–3 are situated at depths between 61 and 78 m and turbines 4–10 are situated at depths between 27 and 44 m (Stockner et al., 2005). A full list of species known to occur in Williston Reservoir can be found in the supplementary material.

## 2.2 | Capture

Angling was used to target both bull trout and lake trout. We cast and trolled spoons and lures, both from the bank and by boat. Angling effort occurred across the entire Peace reach. Most bull trout (70 of 99) were captured in Peace Reach and associated tributaries (see Figure S5). However, 13 bull trout were captured at Scott Creek on the Parsnip Reach and 16 were caught at the mouth of the Omineca River on the Finlay Reach. Bull trout were captured in littoral habitat within the reservoir and in sections of tributaries close to the reservoir, by casting spoons from the bank. Bull trout were captured in the fall of 2015 ($n$ = 10), early summer to fall 2016 ($n$ = 71), and early summer to fall 2017 ($n$ = 18). Six lake trout were captured in littoral habitats. The remaining lake trout were captured in deeper pelagic habitats, using spoons trolled or jigged from a boat ($n$ = 33). All lake trout ($n$ = 39) were captured between May and June 2016. Capture locations can be seen in Figures S7 and S8.

## 2.3 | Tagging

In total, 138 captured fish were tagged with acoustic transmitters (99 bull trout and 39 lake trout). Previous research on bull trout (Gutowsky et al., 2011) and lake trout (Loftus, Taylor, & Keller, 2009) has revealed that these species are relatively robust to recreational fisheries/tagging interactions and exhibit low levels of immediate hooking mortality (0.79 and 14.9%, respectively). Captured fish were either anaesthetised in clove oil (bull trout $n$ = 52, lake trout $n$ = 39), or sedated using electric-gloves (bull trout $n$ = 47). Chemically, anesthetised fish were immersed in a 40 mg/L clove oil solution that contained 1 part clove oil to 9 parts 95% ethanol. When using electric gloves (Electric Fish Handling Gloves, Smith-Root, Inc., Vancouver, Washington) we followed the methods described in Ward et al. (2017) and applied low-voltage DC (<30 V) during the entirety of the surgical procedure. Following loss of equilibrium (in the case of clove oil) or immobilisation (in the case of the electric gloves), fish were measured to the nearest mm, and then surgically implanted with pressure sensing acoustic transmitters (V13P, 45 mm × 13 mm, 6 g in water, signal transmission rate 60–180 s, average 120 s, expected battery life 1,028 days, VEMCO, Halifax, Nova Scotia, Canada). Tags and surgical gear were disinfected with Betadine prior to surgery. Small (~20 mm) incisions were made along the midline, just anterior to the pelvic girdle and anal pore. Fish were visually sexed where possible, by direct observation of the gonad in the body cavity. However, since 63 of the 138 tagged fish (12 lake trout and 51 bull trout) could not be assigned a sex, sex was not included as a factor in any models. Incisions were closed using 2 or 3 simple-interrupted absorbable sutures (3/0 monofilament PDSII, Ethicon Inc., Somerville, New Jersey). Recirculating lake water was applied to the gills throughout the entire procedure, which took <5 min. Fish were released at capture locations, as soon as they had gained equilibrium (<5 min post-surgery). Tagged bull trout ranged from 370 to 885 mm and were thus considered adult (>200 mm; Al-Chokhachy, Budy, & Schaller, 2005). Tagged lake trout ranged from 590 to 992 mm and were thus considered adult (>500 mm; Trippel, 1993).

## 2.4 | Telemetry array

During the study we deployed 29 omni-directional hydrophone acoustic telemetry receivers (VR2W, VEMCO Division) for 3 years (June 2015 to June 2018) (Figure 1, Panel A). Of these 29 receivers, nine were deployed in the dam forebay (Figure 1, Panel B). A beacon tag (constant 90 s ping rate) was deployed in the forebay to assess forebay array detection efficiency (see Table S8 and Figure S2 for full detail). An additional seven receivers were deployed downstream of Williston Reservoir in the Dinosaur Reservoir, to capture detections of fish post-entrainment (Figure 1, Panel B). All receivers were deployed using three sandbags attached to polypropylene rope, with a surface buoy (on date of deployment). Receivers were located at one-third of the total depth at site (e.g., if the depth was 100 m the receiver was deployed at 30 m; Heupel, Semmens, & Hobday, 2006). These receiver depths ranged from 5 to 40 m, with an average of 25 m. Detection efficiency estimates for the forebay array, the reservoir array, and the downstream array are provided in the supplementary material.

## 2.5 | Data processing

Telemetry datasets were processed in R (version 3.5.2. https://cran.r-project.org/bin/windows/base/). Detections which did not contain sensor information (depth) were assigned a false positive status and removed from the dataset. All detections within 7 days following the date of surgery were removed from our dataset to avoid short-term post-surgery effects (Rogers & White, 2007). Depth distributions were plotted for all tagged fish to identify fish that appeared to have died or shed tags and to determine the date of mortality/shedding. Deceased individuals/tag losses were identified by long detection records at near constant depth (after accounting for changes in reservoir elevation). Detections following mortality/shed dates were censored. Fish that were never detected in the array ($n$ = 21 bull trout) were censored from the entire dataset.

We defined the dam forebay as the area which is within ~3 km of the dam face, which represents 0.63% of the surface area of the reservoir. Forebay presence was determined at the 24-hr scale. We used a minimum of two detections per 24 hr period in the forebay array (nine receivers) to assign forebay presence, rather than the standard two detections per hour, which is designed to minimise the likelihood of false positives, typically in very large datasets. We took this more precautionary approach to minimise the chance of removing true forebay presence as a result of overly conservative filtering, in our somewhat sparse forebay residency dataset. Accordingly, temporal resolution was not sufficient to estimate forebay presence at the diel scale.

Following Martins et al. (2013), seasons were defined as: Winter (January to March), Spring (April to June), Summer (July to September) and Fall (October to December). Sampling years were defined as: Year 0 (July 2015 to June 2016), Year 1 (July 2016 to June 2017), and Year 2 (July 2017 to June 2018). All analyses were restricted to Years 1 and 2 due to the low sample size of 10 bull trout and zero lake trout in Year 0. No entrainment events were recorded in Year 0.

## 2.6 | Data analysis

### 2.6.1 | Entrainment rates

We took a three staged approach to quantifying entrainment rates (the annual, or 2-year cumulative proportion of the population that are entrained), which involved the calculation of: *forebay entry*, the probability of a tagged fish entering the forebay, *tailrace entry*, the probability that a forebay user is detected downstream, and *overall entrainment*, the probability of a tagged fish becoming entrained. These three probabilities were reported at both annual (yearly) and 2-year cumulative (study period) scales. The number of at-risk individuals, for each metric, that is, the denominator, was determined at the seasonal scale, to account for censoring.

*Forebay entry* was estimated using Kaplan–Meier time to event analysis (Harrell, 2001), where the first forebay entry event was defined as the first day on which a fish was deemed present in the forebay. Notably this metric is a binary measure (1 = entered the forebay, 0 = never entered the forebay), and thus does not capture the time spent in the forebay. Time spent in the forebay was estimated using our forebay residency metric (described below).

*Tailrace entry* was also estimated using Kaplan–Meier time to event analysis. A receiver located in the immediate vicinity of the turbine tailrace recorded detections from fish which were subsequently detected moving throughout the reservoir, indicating that some transmissions were making it through the dam structure. Accordingly, we investigated each of these detections, and only assigned a tailrace entry event to individuals that were both: detected at multiple downstream receivers, and never recorded again in the reservoir. The number of at risk individuals, that is, the denominator, was limited to forebay users (Harrison et al., 2019).

*Overall entrainment* was then calculated following Harrison et al. (2019) as the product of forebay entry and tailrace entry.

### 2.6.2 | Forebay residency

Forebay residency (a proportionate measure of forebay use) was modelled using generalised linear mixed effects models (GLMMs). This forebay residency metric was designed to act as proxy for entrainment vulnerability. The proxy is based on two assumptions: (a) presence in the forebay area carries a higher risk of entry (be that accidental or deliberate) into the fish entrainment zone (FEZ) (the area immediately surrounding intakes where flows are sufficiently high to ensure entrainment probability is >90%; Johnson, Hedgepeth, Skalski, & Giorgi, 2004), in comparison to presence in the rest of the reservoir (Harrison et al., 2019) and (b) increased forebay residency (greater proportion of time spent in the forebay), results in an increased likelihood of entry into the FEZ.

An individual was coded as 1, on dates (24-hr periods) when present in the forebay (≥2 detections in forebay array). Individuals were assigned an absent status (0) on any date, between the first detection date (7 days post-surgery) and final detection date, when the sum of forebay detections was <2. Accordingly, the output from our models provides the probability of being present in the forebay at the level of our fixed effects.

An abundance of zeros in the dataset meant that we limited our analysis of forebay residency to those individuals that were detected in the forebay ($n$ = 46). That is, we excluded fish from this forebay residency analysis that were never detected in the forebay. Random intercepts were fitted for each fish. Season, year, and species and the 3-way interaction of these variables were fitted as fixed effects. The variables season and species and associated interactions were fitted to test our hypotheses. The variable year and all associated interactions were fitted to ensure that results were not a function of inter-annual variation. These small within-species samples sizes meant we could not realistically fit body length as a fixed effect in these models. The high proportion of zeros in our response variable resulted in the need to fit our models using a complimentary log–log distribution (Gelman & Hill, 2007). Lake trout were completely absent from the forebay during the summer period of both years, which caused inflation of the Wald confidence intervals. Accordingly, we used the *R* package *Blme* (https://cran.r-project.org/web/packages/blme/index.html) to fit Bayesian GLMMs using penalized maximum likelihood (Laplace approximation) and uninformative zero mean normal fixed effects priors (Gelman & Hill, 2007). Backwards selection for both the fixed and random effects parameters was performed using small sample size corrected $AIC_c$ model selection, where models with $\Delta AIC_c < 4$ in comparison with competing models are considered competitive with the top model (Burnham & Anderson, 2002). Post hoc comparison among fixed effects interaction levels was performed using the *lsmeans* package for *R* (https://cran.r-project.org/web/packages/lsmeans/index.html).

In order to better plot our observed forebay presence/absence data, we converted these binary terms into a forebay residency index for each fish. This metric provides the probability of forebay residency, with 1 equal to 100% residency and 0 = 0%. This residency index is calculated by:

$$\text{Forebay residency index} = \frac{\text{number of days present in forebay}}{\text{number of days present in forebay} + \text{number of days absent}}.$$

## 2.7 | Forebay proximity

"Forebay proximity" (the distance from current location to the dam) is a broad-scale entrainment vulnerability proxy, designed to capture reservoir wide movement in relation to the forebay, and to support and complement forebay residency metrics (Harrison et al., 2019). Forebay proximity can capture variation in movement towards or away from the forebay, which is expected to correlate with increased or decreased entrainment vulnerability respectively. For example, observation of low forebay proximity (i.e., fish that are located many km from the forebay), can complement and help explain observations of low forebay residency. Likewise, a pattern of high forebay proximity can help explain elevated forebay residency.

Forebay proximity was estimated using centre of activity (COA) analysis. We used a minimum of two detections per 24 hr period at a receiver or receiver group to determine positive detections. All detections not meeting these criteria were removed from our COA dataset. Monthly COA positions were estimated for each fish following the methods described in Simpfendorfer et al. (2002). Given the broadly linear nature of our study reach, straight line Euclidean distances were used to estimate the distance (km) between the COA and the forebay, a metric henceforth termed forebay proximity.

Forebay proximity (distance from the dam in km) was fitted using linear mixed effects models using the package *nlme* for R (https://cran.r-project.org/web/packages/nlme/index.html). In our full model (prior to selection), fixed effects included year, season, species and mean centered total length (cm), and all 2-way, and 3-way interactions. Total length and associated interactions were modelled to ensure that results were not an artefact of body size differences. The variable year and all associated interactions were fitted to ensure that results were not a function of inter-annual variation. Individual fish were fitted as random intercepts. Heteroscedasticity of variance across season-year-species levels was detected in the residuals of our model, and thus we use the *varIdent* weights structure to allow variance to vary among these levels (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Significant temporal autocorrelation was observed within individuals across our monthly levels. Thus, we coded each month × year combination as a numeric value, and fitted a temporal correlation structure (Zuur et al., 2009). Following Zuur et al. (2009) we chose the most simple autocorrelation structure available, a continuous autoregressive at lag point 1 (*CAR1 in nlme*). ACF plotting was used to confirm that this structure adequately accounted for temporal correlation, and structure fit was assessed using AIC comparison (between models with and without the structure). Backwards selection was performed using the marginal *F* test (Zuur et al., 2009). Post hoc comparisons of interaction levels were performed using the *lsmeans* package for *R*.

# 3 | RESULTS

## 3.1 | Entrainment rates

Of the 138 tagged fish (99 bull trout and 39 lake trout), 46 fish were detected in the forebay array (32 bull trout and 14 lake trout). After accounting for censored fish at a seasonal scale (those which appeared to have died, shed their tag, or were no longer detected in our array), these detections resulted in a 2-year cumulative forebay entry rate (the proportion of tagged fish that enter the forebay at least once during the 2-year period) of 0.54 for bull trout and 0.37 for lake trout (see Table 1 for confidence intervals).

Two fish were observed to be entrained during the 2-year study period. On October 17, 2017, a 820-mm female bull trout, tag ID 1231881 was entrained. This fish was tagged at Schooler Creek in June 11, 2016. Bull trout 1,231,881 entered the forebay on June 25, 2016 was then detected exclusively in the forebay prior to entrainment (1,222 times). Bull trout 1,231,881 was recorded at eight different receivers in the forebay prior to entrainment, indicating that it was mobile and thus alive prior to entrainment. On March 3, 2018 a 741-mm male lake trout was also entrained. This lake trout (ID 1245452) was tagged on a shoal east of Carbon Creek on June 16, 2016. Lake trout 1,245,452 was highly mobile during its time at large prior to entrainment, visiting both the forebay and the far western end of our array. Lake trout 1,245,452 made its final visit to the forebay on February 23, 2018 and was detected 516 times in the forebay at eight different receivers prior to entrainment. These entrainment events resulted in a 2-year cumulative tailrace entry rate (the proportion of forebay users that were detected in the tailrace over the 2-year period) of 2% for bull trout and 4% for lake trout (after accounting for censuring). Accordingly, bull trout and lake trout were entrained at an annual rate of 0.5 and 1% respectively (see Table 1 for full details).

**TABLE 1** Kaplan–Meier estimates of entrainment vulnerability for bull trout and lake trout in Williston Reservoir, British Columbia, Canada (lower and upper 95% confidence intervals in parentheses)

| Species | Forebay entry | Tailrace entry | Entrain V |
|---|---|---|---|
| Bull trout (2-year cumulative) | 0.54 (0.40, 0.69) | 0.04 (0, 0.10) | 0.02 (0, 0.07) |
| Lake trout (2-year cumulative) | 0.37 (0.21, 0.51) | 0.03 (0, 0.20) | 0.01 (0, 0.10) |

### 3.2 | Forebay residency

Our forebay residency model also relied on a sample size of 46 fish (14 lake trout and 32 bull trout) and included 24,791 daily observations of residency over the 2-year period, with an average of 538 daily observations per fish. Our best model included a 3-way interaction among year, season and species, indicating that forebay residency was a function of the combination of sampling year, season, and species ($\Delta AIC_c = -12.98$ between models with and without the 3-way interaction term). Lake trout forebay residency was higher than bull trout during the winter of both years (all $p < .001$, see Figure 2 for observed data, Figure 3 for model estimates and visualisation of post hoc comparisons, and Table S1 with among-species within year × season level comparisons). While bull trout forebay residency was low during the summer in both years, rates were higher than for lake trout, who were completely absent from the forebay in the summer during both years (Figures 2 and 3). No significant among-species differences in forebay residency were detected in the fall of Year 1 and Year 2 (Table S1). However, while bull trout and lake trout were shown to have similar forebay residencies in the spring of Year 1, lake trout residency was significantly higher than bull trout in the spring of Year 2 (Table S1).

Bull trout forebay residency was observed to be low across all seasons and years, with an average residency index (of all individuals) of 0.03, and a median of 0. The maximum average observed residency index of any bull trout was 0.20. Our models show that in Year 1, bull trout had higher forebay residencies in winter and spring in comparison to summer and fall (See Figure 2 for observed data, Figure 3 for the model estimates and visualisation of multiple comparisons, and Table S2 for full details of multiple comparisons at the within-bull trout, within-year, across-season scale.) This pattern was not consistent across years, with bull trout in Year 2 displaying higher residency in the fall in comparison to all other seasons (Table S2). Significant inter-annual differences in forebay residency were detected in fall, spring, and winter (all $p < .05$, Figure 3 and Table S4). However, while the among-season and among-year differences described above were deemed statistically significant (Tables S2 and S4), the effect sizes of this variation were small, ranging from a minimum season × year forebay residency model estimate of 0.003 in summer of Year 1 to a maximum season × year model estimate of 0.05 in spring of Year 1 (Figure 3).

Lake trout had an average (observed) forebay residency index of 0.10 (median 0), and the maximum overall (observed) residency index of any lake trout was 0.40. Lake trout forebay residency varied more across seasons than bull trout (Figure 3). Lake trout had higher rates of forebay residency in spring and winter than the fall and summer in both years (Figures 2 and 3 and Table S3). Furthermore, lake trout were completely absent from the forebay in the summer of both sampling years. However, lake trout also displayed some inter-annual variability in forebay residency, with lake trout exhibiting significantly different forebay residency across years in all seasons except summer (Figures 2 and 3 and Table S4).

Analysis of forebay depth detections (supplementary material and Figure S2) show that bull trout and lake trout used depths within the range of turbine entrance depths (27–78 m).

### 3.3 | Forebay proximity

Our forebay proximity model was based on a large sample size ($n$ = 106, 39 lake trout and 67 bull trout), and featured 1,324 monthly forebay distance observations, with an average of 12.37 monthly distance observations per fish. Our best model showed that the

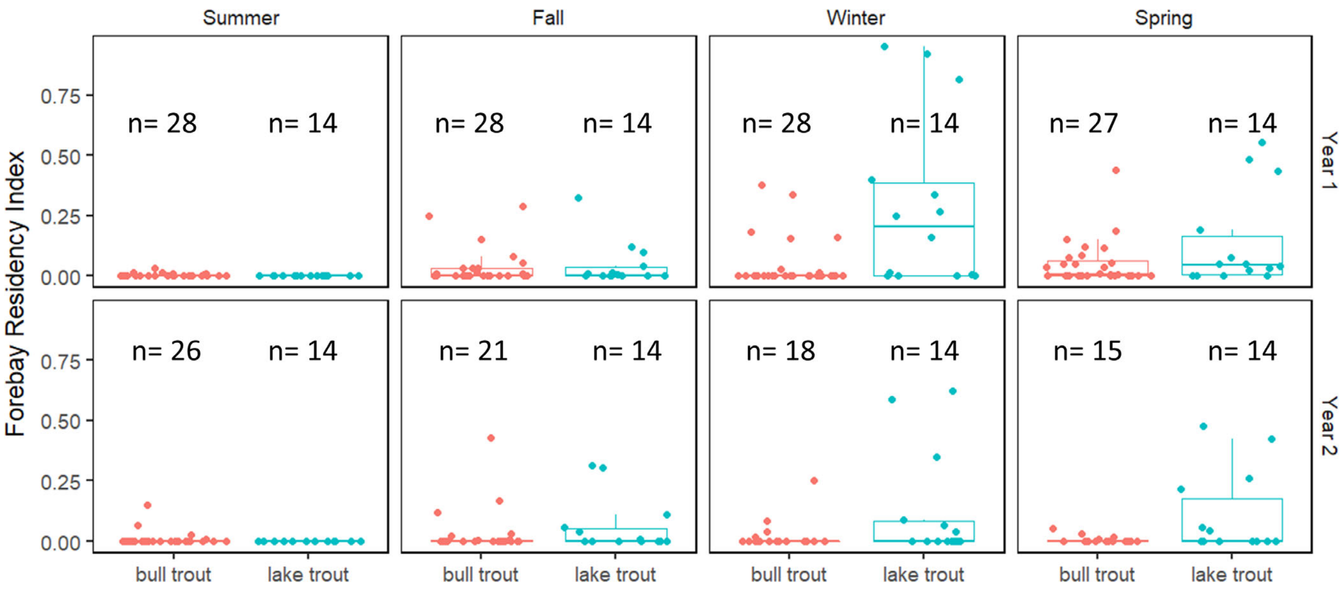


**FIGURE 2** Observed forebay residency indexes of bull trout ($n$ = 32) and lake trout ($n$ = 14) in Williston reservoir. Filled circles represent individual residency indexes from the observed data (days detected in the forebay/days at large) and boxes and associated error bars provide inter-quantile estimates [Colour figure can be viewed at wileyonlinelibrary.com]

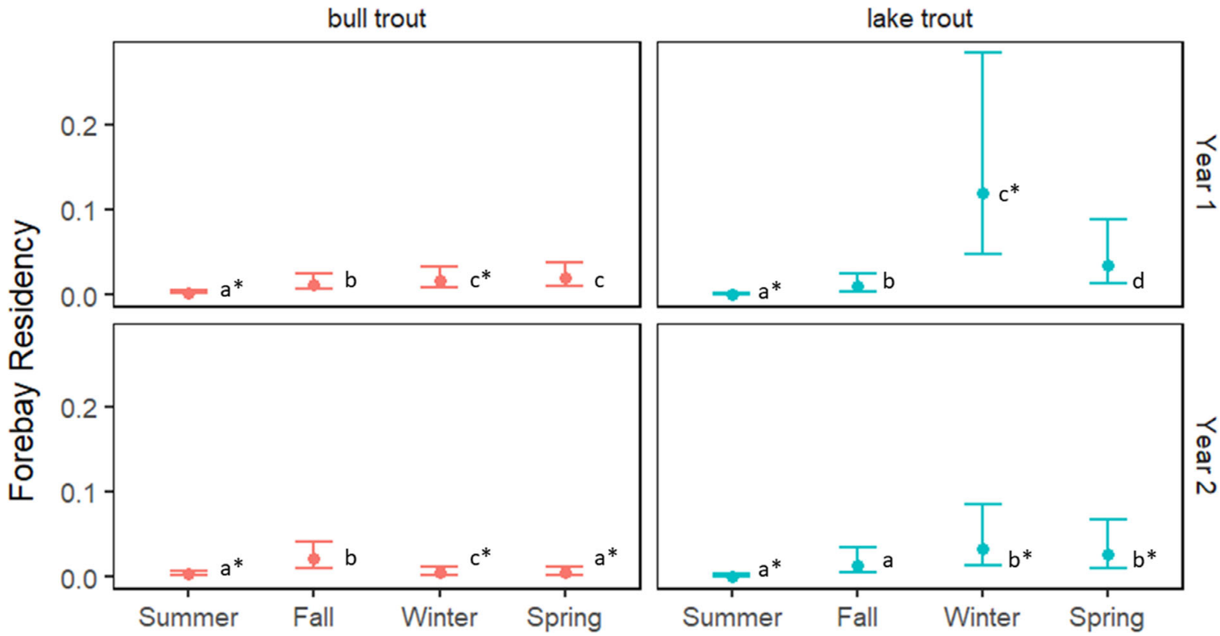


**FIGURE 3** Seasonal patterns of forebay residency of bull trout ($n$ = 32) and lake trout ($n$ = 14) in Williston Reservoir. Filled circles represent model estimates and error bars portray modelled 95% confidence intervals. Differing letters identify significant within-year, within-species among-season differences. Asterisks indicate significant differences between species at the within season and year level [Colour figure can be viewed at wileyonlinelibrary.com]

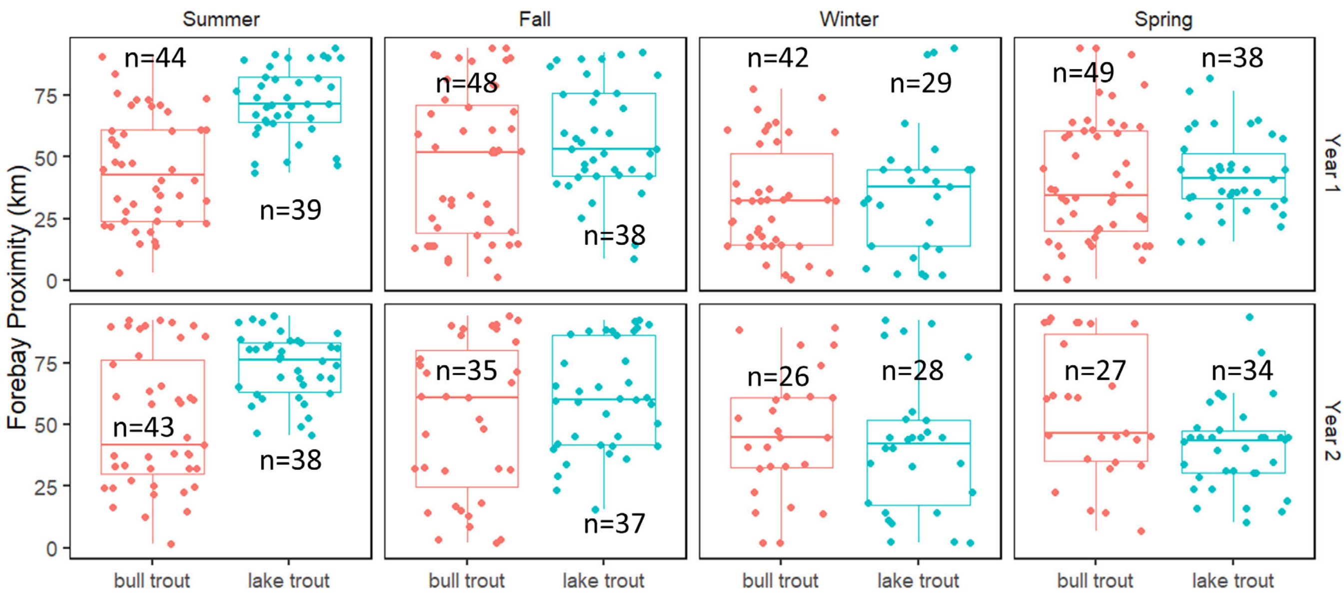


**FIGURE 4** Observed forebay proximity of bull trout ($n$ = 67) and lake trout ($n$ = 39) in Williston Reservoir. Filled circles represent individual means from the observed data, and boxes and associated error bars provide inter-quantile estimates [Colour figure can be viewed at wileyonlinelibrary.com]

interaction between species and season explained a significant proportion of variation in forebay proximity (see Figure 4 for observed data and Figure 5 for model estimates and visualisation of multiple comparisons, Table 2 for model selection details). Body length and sampling year, and all interactions involving body length and sampling year were not found to be significant predictors of forebay proximity (all $p$ > .05, see Table 2 for full details of backwards selection). Significant temporal autocorrelation (*Phi* = 0.71) was detected and accounted for in our final model (ΔAIC = −475 between models with and without correlation structure). Significant heteroscedasticity was observed at the species × season× year scale and was accounted for using the *varIdent* function for *nlme* (ΔAIC = −95.56 between models with and without variance weights).

Post hoc multiple comparisons between levels of our interaction variable season × species (Figure 5 and Table S5) showed that bull trout were located closer to the forebay during the summer than lake

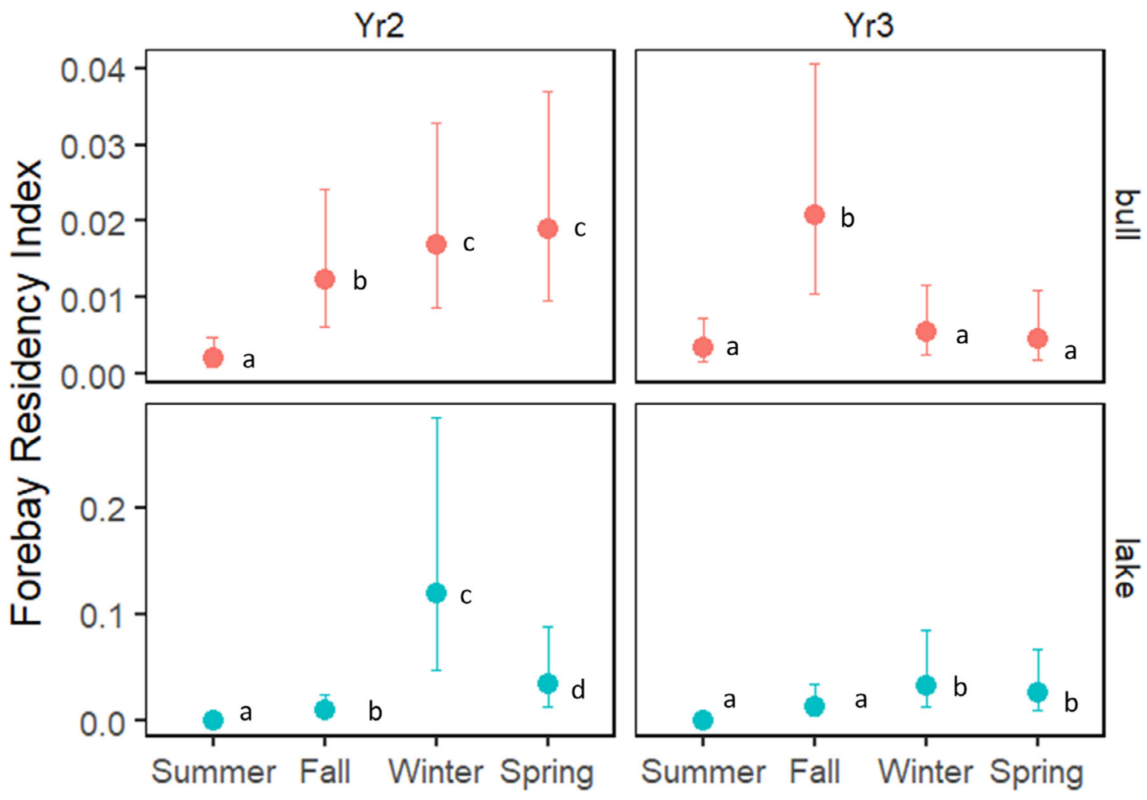


**FIGURE 5** Seasonal patterns of forebay proximity of bull trout ($n$ = 67) and lake trout ($n$ = 39) in Williston Reservoir. Filled circles represent model estimates and error bars portray 95% confidence intervals. Differing letters identify significant within-year, within-species among-season differences. Asterisks indicate significant differences between species at the within season and year level [Colour figure can be viewed at wileyonlinelibrary.com]

**TABLE 2** Significance of predictor terms used to model forebay proximity for lake trout and bull trout in Williston Reservoir, British Columbia, determined using the marginal *F* test

| Term | | numDf | numDF | *F*-value | *p*-Value |
|---|---|---|---|---|---|
| Intercept | Kept | 1 | 1,211 | 256.36 | <.001 |
| Season | Kept | 3 | 1,211 | 10.61 | <.0001 |
| Species | Kept | 1 | 105 | 2.06 | .15 |
| Season × species | Kept | 3 | 1,211 | 5.76 | .0007 |
| Year | Eliminated | 1 | 1,210 | 1.87 | .17 |
| Year × species | Eliminated | 1 | 1,209 | 2.14 | .15 |
| Year × season | Eliminated | 3 | 1,206 | 0.77 | .51 |
| Year × season × species | Eliminated | 3 | 1,203 | 2.36 | .07 |
| Body length | Eliminated | 1 | 104 | 0.02 | .89 |
| Body length × season | Eliminated | 3 | 1,200 | 0.96 | .41 |
| Body length × year | Eliminated | 1 | 1,199 | 1.49 | .22 |
| Body length × species | Eliminated | 1 | 103 | 0.13 | .72 |
| Body length × season × year | Eliminated | 3 | 1,196 | 2.28 | .08 |
| Body length × year × species | Eliminated | 1 | 1,195 | 0.77 | .38 |

trout. However, forebay proximity did not differ among species in the fall, winter and spring (Figure 5 and Table S5). At the within species scale, bull trout were located closer to the forebay in winter in comparison to the summer and fall. Bull trout were located further from the forebay in summer in comparison to the spring (Figure 5 and Table S6).

Lake trout displayed a more distinct seasonal pattern of forebay proximity than bull trout (Figure 5 and Table S7). Lake trout were located furthest from the forebay in the summer, in comparison to all other seasons (Figure 5 and Table S7). Lake trout were located further from the forebay in the fall in comparison to the winter and spring (Figure 5 and Table S7). Lake trout were located closest to the forebay in winter and spring, and proximities did not differ significantly between these seasons (Figure 5).

## 4 | DISCUSSION

We used acoustic telemetry to quantify and compare turbine entrainment rates and seasonal patterns of turbine entrainment vulnerability between two mature adult life-stage members of the *Salvelinus* genus (lake trout and bull trout), in a large hydropower reservoir. Our data, which demonstrate that adult bull trout and lake trout were entrained at a similarly low rates (0.5 and 1% annual minimum estimates, respectively) over our 2-year study period, lead us to reject our hypothesis of species differences in entrainment rates. However, our data which showed that these two species differed in their seasonal patterns of forebay residency and proximity, confirm our hypothesis concerning inter-specific variation in seasonal entrainment vulnerability patterns. The patterns seen in our forebay residency dataset were confirmed and supported by our forebay proximity analysis. Bull trout displayed no clear seasonal pattern of forebay residency and proximity, indicating that entrainment vulnerability did not vary by season and was consistently low year-round. In contrast, lake trout showed a distinct seasonal pattern of forebay occupancy and proximity, with increased forebay residency and forebay proximity during the winter and spring, and decreased forebay residency and proximity during the summer and fall. These findings suggest that for lake trout turbine entrainment vulnerability is highest during the winter and early spring.

### 4.1 | Entrainment rates

The bull trout annual entrainment rate recorded in this study (0.5%) was lower than the 3.4% annual rate recorded by Martins et al. (2013) through Mica Dam, in Kinbasket Reservoir, British Columbia. Our study site, Williston Reservoir (74 km$^3$) has approximately three times the total volume capacity of Kinbasket Reservoir (25 km$^3$), and annual power generation at Williston (13,100 GWh) is almost double that of Kinbasket Reservoir (7,202 GWh) (Stockner et al., 2005). Accordingly, in terms of bull trout entrainment per GWh of electricity production, values are considerably lower at Williston Reservoir than at Kinbasket Reservoir. However, given the wide array of ecological and physical differences between study sites, which include differing species compositions, and differing temperature regimes, it is difficult to determine the factors that drive these site-specific differences in entrainment rates. Our receiver detection efficiency testing that occurred in our downstream receiver arrays suggest that our downstream array was relatively efficient. Moreover, the fact that we have installed eight receivers in this downstream reach, meant that the chances of detecting entrained fish in this array was high. We acknowledge that no telemetry system is 100% efficient, and sample sizes were small, therefore we must treat all entrainment rates as minimum estimates. Nonetheless, our findings do provide an additional information to support previous findings (Martins et al., 2013), which show that bull trout turbine entrainment at hydropower reservoirs is potentially low.

We could find no previous studies documenting turbine entrainment in lake trout. Accordingly, while our data show entrainment rates are low, our findings provide a novel indication that adult lake trout are vulnerable to turbine entrainment. Moreover, given that our telemetry array may not capture 100% of turbine entrainment events, these entrainment rates represent a minimum. Lake trout have been widely introduced into cold water reservoirs outside of their native range (Martinez et al., 2010), where they have caused declines in native fish populations (Yule & Luecke, 1993). Our findings which show that hydropower turbines can provide a potential downstream dispersal route for lake trout, suggest that the management practice of stocking of non-native lake trout in reservoirs may pose a threat to native salmonid populations residing in lacustrine habitats below hydropower.

Without data concerning the population dynamics of reservoir lake trout populations, it is difficult to determine the population level consequences of the observed entrainment rates on upstream reservoir populations. Nonetheless, several investigations into lake trout suppression have demonstrated population resilience to annual removal rates much higher (>15%) than the observed entrainment rate (1%) (Ng, Fredericks, & Quist, 2016; Syslo et al., 2011). Accordingly, we hypothesise that lake trout populations are likely resilient to current entrainment rates. Likewise, in a population simulation, Underwood & Cramer (2007) showed that a population of bull trout in Tieton Reservoir, Washington, would be resilient to similar entrainment removal rate (i.e., 0.5%) to what we observed here. However, the slow growth and late maturity of bull trout may make them sensitive to removals (Johnston & Post, 2009; Post et al., 2003). Moreover, the tendency of bull trout populations to adopt non-consecutive annual spawning may further reduce resilience to removals (Johnston et al., 2007). Further research is now needed to: assess the resilience of bull trout populations to removals, particularly in more northerly, cold, ultra-oligotrophic reservoir populations, such as our study system, where growth may be slower than in more productive systems; and to better understand how these entrainment removals influence reservoir metapopulation dynamics. Furthermore, given that turbine passage mortality is likely <100%, research is needed to determine the impacts of bull trout that survive entrainment on downstream bull trout populations, including research into the impacts of entrained individuals on downstream metapopulation dynamics and geneflow (Wilkes, Webb, Pompeu, et al., 2018).

### 4.2 | Seasonal patterns of entrainment vulnerability

The distinct seasonal pattern of forebay residency and proximity suggest that lake trout entrainment vulnerability is likely lowest during the summer and fall, and highest during winter and spring. While our sample size of observed entrainment events was low, the single lake trout entrainment event also occurred during winter. Indeed, the seasonal patterns of lake trout entrainment vulnerability are potentially useful for guiding any potential mitigation policy. Our findings suggest that any forebay based mitigation efforts (e.g., deterrence or avoidance devices, or operational changes) should be concentrated on the winter and spring period. Thus, research to determine the underlying causes of these seasonal movements, has potential to inform on the design of any successful mitigation. Given that entrainment vulnerability occurs in the winter and spring when the reservoir is being rapidly drawn down and then quickly filled, further research to investigate the possible role of hydropower operations in forebay residency, is also warranted.

The lack of a consistent seasonal pattern of bull trout forebay residency differed from the findings of Martins et al. (2013), who found that bull trout showed a distinct seasonal pattern of fall winter forebay residency in Kinbasket Reservoir, British Columbia. The lack of a seasonal movement pattern for bull trout in Williston Reservoir, may be a function of interspecific competition with lake trout. When bull trout occur in sympatry with lake trout, lake trout often establish themselves as the dominant pelagic piscivore (Donald & Alger, 1993; Ferguson, Taper, Guy, Syslo, & Tonn, 2012; Guy et al., 2011). Accordingly, further research into diet, space-use and niche overlap between these two species in our study system, may help to explain the observed inter-specific differences in entrainment vulnerability. Moreover, at the site-specific scale our findings suggest that if managers do decide to attempt bull trout entrainment mitigation, then no one season would likely be more effective than another.

### 4.3 | Study limitations

Dam forebays are noisy environments, and thus detection efficiency of acoustic telemetry receivers located in dam forebays can be highly variable and often reduced in comparison to less noisy environments (Kessel et al., 2014; Martins et al., 2013). Some previous studies have attempted to account for the influence of variable detection efficiency on forebay residency, through the installation of large sentinel tag arrays (Martins et al., 2013). In this study, economic constraints meant we were only able to deploy a single sentinel tag in the forebay. Moreover, a mishap during the deployment of this sentinel tag resulted in poor performance (see supplementary material for further detail). Consequently, our ability to determine receiver detection efficiency in the forebay was severely compromised, and we were not able to adjust our forebay residency estimates as a function of detection efficiency. Thus, we cannot be sure that seasonal variation in detection efficiency is not influencing our estimates of forebay residency. Nonetheless, our findings were supported by our forebay proximity analysis, which was less susceptible to detection efficiency issues and on a much larger sample size than our forebay residency analysis. For bull trout, the absence of a clear pattern of seasonal forebay residency was reflected in our forebay proximity data, which showed that bull trout were distributed throughout the study reach and showed no clear pattern of seasonal movement towards the forebay. Similarly, our finding that lake trout were completely absent from the forebay during the summer of both study years, was confirmed and complimented by our finding that lake trout were all found more than 40 km away from the dam during this period. Likewise, our finding that lake trout forebay residency was increased during the winter and spring, was supported by our finding that lake trout also exhibit a pronounced movement towards the forebay during these periods.

In non-migrating fish, it is difficult to determine the fate of entrained fish using acoustic telemetry (Harrison et al., 2019). Indeed, in fast flowing water typical of tailraces, movement may be a function of drift, rather than an indication of survival. Indeed, if a transmitter remains in a single location for a long period at a fixed depth (which we did not observe), this can indicate death, however the absence of this pattern cannot necessarily be attributed to survival. Accordingly, we cannot speculate about the fate of entrained fish in our study. Nonetheless, given that no upstream passage facilities are available at the WAC Bennet Dam, the impacts of entrainment removals on upstream reservoir populations are independent of the fate of entrained individuals.

## 5 | CONCLUSIONS

While our data show that bull trout and lake trout were entrained at similarly low rates, population-specific assessments of impacts of observed entrainment rates will be necessary to fully understand risks to reservoir populations. Our novel demonstration of lake trout turbine entrainment suggests that turbine passage can provide a potential downstream dispersal route, with implications for the control of introduced and invasive reservoir lake trout populations. Furthermore, our findings, which suggest that lake trout entrainment vulnerability is highest during winter and early spring when the reservoir is being drawn down, suggest the periods are important for entrainment mitigation strategies. Our findings which showed that seasonal patterns of forebay residency noted in previous studies of bull trout vulnerability, were not replicated in our study, suggest species interactions can influence entrainment vulnerability, highlighting the need for site specific investigations into entrainment risk.

ACKNOWLEDGEMENTS

P. M. H. is supported by a NSERC CRD to S. J. C. and M. P. in conjunction with BC Hydro. S. J. C. is supported by NSERC and the Canada Research Chairs Program. HYCANOR supported collaborations between authors. Field assistance was provided by BC Hydro staff Randy Zemlak and Bleu Rowe, and Cooke lab associates Lee Gutowsky, James Monaghan, Brittany Sullivan and Naomi Pleizier. Lake trout tagging was performed by Brad Culling and Ted Euchner of Diversified Environmental Services.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

## ORCID

*Philip M. Harrison* https://orcid.org/0000-0002-4791-3232

## REFERENCES


Al-Chokhachy, R., Budy, P., & Schaller, H. (2005). Understanding the significance of Redd counts: A comparison between two methods for estimating the abundance of and monitoring bull trout populations. *North American Journal of Fisheries Management*, *25*, 1505–1512.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information—Theoretic approach* (2nd ed.). New York: Springer.

Calles, O., & Greenberg, L. (2009). Connectivity is a two-way street: The need for a holistic approach to passage problems in regulated rivers. *River Research and Applications*, *1286*, 1268–1286.

Čada, G., & Schweizer, P. E. (2012). *The application of traits-based assessment approaches to estimate the effects of hydroelectric turbine passage on fish populations*. Oak Ridge, TN, USA: Oak Ridge National Laboratory.

Committee on the Status of Endangered Wildlife in Canada. (2012). Assessment and Status Report on the Bull Trout (Salvelinus confluentus) in Canada. COSEWIC, Ottawa.

Coutant, C. C., & Whitney, R. R. (2000). Fish behavior in relation to passage through hydropower turbines: A review. *Transactions of the American Fisheries Society*, *129*, 351–380.

Donald, D. B., & Alger, D. J. (1993). Geographic distribution, species displacement, and niche overlap for lake trout and bull trout in mountain lakes. *Canadian Journal of Zoology*, *71*, 238–247.

Dunham, J., Gallo, K., Shively, D., Allen, C., & Goehring, B. (2011). Assessing the feasibility of native fish reintroductions: A Framework applied to threatened bull trout. *North American Journal of Fisheries Management*, *31*, 106–115.

Ferguson, J. M., Taper, M. L., Guy, C. S., Syslo, J. M., & Tonn, W. (2012). Mechanisms of coexistence between native bull trout (*Salvelinus confluentus*) and non-native lake trout (*Salvelinus namaycush*): Inferences from pattern-oriented modeling. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*, 755–769.

Gelman, A., & Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models*. Cambridge, MA: Cambridge University Press.

Gutowsky, L. F. G., Harrison, P. M., Landsman, S. J., Power, M., & Cooke, S. J. (2011). Injury and immediate mortality associated with recreational troll capture of bull trout (*Salvelinus confluentus*) in a reservoir in the Kootenay-Rocky Mountain region of British Columbia. *Fisheries Research*, *109*, 379–383.

Guy, C. S., McMahon, T. E., Fredenberg, W. A., Smith, C. J., Garfield, D. W., & Cox, B. S. (2011). Diet overlap of top-level predators in recent sympatry: Bull trout and nonnative lake trout. *Journal of Fish and Wildlife Management*, *2*, 183–189.

Harrell, F. E. (2001). *Regression modelling strategies: With applications to linear models, logistic regression and survival analysis*. New York: Springer.

Harrison, P. M., Martins, E. G., Algera, D. A., Rytwinski, T., Mossop, B., Leake, A. J., … Cooke, S. J. (2019). Turbine entrainment and passage of Potadromous fish through hydropower dams: Developing conceptual frameworks and metrics for moving beyond turbine passage mortality. *Fish and Fisheries*, *20*(3), 1–16.

Heupel, M. R. A., Semmens, J. M. B., & Hobday, A. J. D. (2006). Automated acoustic tracking of aquatic animals: Scales, design and deployment of listening station arrays. *Marine and Freshwater Research*, *57*, 1–13.

Johnson, B. M., & Martinez, P. J. (2000). Trophic economics of lake trout management in reservoirs of differing productivity. *North American Journal of Fisheries Management*, *20*, 127–143.

Johnson, G. E., Hedgepeth, J. B., Skalski, J. R., & Giorgi, A. E. (2004). A Markov chain analysis of fish movements to determine entrainment zones. *Fisheries Research*, *69*, 349–358.

Johnston, F. D., & Post, J. R. (2009). Density-dependent life-history compensation of an Iteroparous salmonid. *Ecological Applications*, *19*, 449–467.

Johnston, F. D., Post, J. R., Mushens, C. J., Stelfox, J. D., Paul, A. J., & Lajeunesse, B. (2007). The demography of recovery of an overexploited bull trout, *Salvelinus confluentus*, population. *Canadian Journal of Fisheries and Aquatic Sciences*, *64*, 113–126.

Kessel, S. T., Cooke, S. J., Heupel, M. R., Hussey, N. E., Simpfendorfer, C. A., Vagle, S., & Fisk, A. T. (2014). A review of detection range testing in aquatic passive acoustic telemetry studies. *Reviews in Fish Biology and Fisheries*, *24*, 199–218.

Loftus, A. J., Taylor, W. W., & Keller, M. (2009). An evaluation of lake trout (*Salvelinus namaycush*) hooking mortality in the upper Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *45*, 1473–1479.

Martinez, P. J., Bigelow, P. E., Deleray, M. A. L., Fredenberg, W. A., Hansen, B. S. S. K., Horner, N. J., … Viola, A. E. (2010). Western lake trout woes. *Fisheries*, *34*, 424–442.

Martins, E. G., Gutowsky, L. G., Harrison, P. M., Patterson, D. A., Power, M., Zhu, D. Z., … Cooke, S. J. (2013). Forebay use and entrainment rates of resident adult fish in a large hydropower reservoir. *Aquatic Biology*, *19*, 253–262.

Ng, E. L., Fredericks, J. P., & Quist, M. C. (2016). Population dynamics and evaluation of alternative management strategies for nonnative lake trout in Priest Lake, Idaho. *North American Journal of Fisheries Management*, *36*, 40–54.

Nitychoruk, J. M., Gutowsky, L. F. G., Harrison, P. M., Hossie, T. J., Power, M., & Cooke, S. J. (2013). Sexual and seasonal dimorphism in adult adfluvial bull trout (*Salvelinus confluentus*). *Canadian Journal of Zoology*, *91*, 480–488.

Post, J. R., Mushens, C., Paul, A., & Sullivan, M. (2003). Assessment of alternative harvest regulations for sustaining recreational fisheries: Model development and application to bull trout. *North American Journal of Fisheries Management*, *23*, 22–34.

Pracheil, B. M., DeRolph, C. R., Schramm, M. P., & Bevelhimer, M. S. (2016). A fish-eye view of riverine hydropower systems: The current understanding of the biological response to turbine passage. *Reviews in Fish Biology and Fisheries*, *26*, 153–167.

Rogers, K. B., & White, G. C. (2007). Analysis of movement and habitat use from telemetry data. In M. Brown & C. Guy (Eds.), *Analysis and interpretation of freshwater fisheries data* (pp. 625–627). Bethesda, MA: American Fisheries Society.

Rytwinski, T., Algera, D. A., Taylor, J. J., Smokorowski, K. E., Bennett, J. R., Harrison, P. M., & Cooke, S. J. (2017). What are the consequences of fish entrainment and impingement associated with hydroelectric dams on fish productivity? A systematic review protocol. *Environmental Evidence*, *6*, 1–9.

Silva, A. T., Lucas, M. C., Castro-Santos, T., Katopodis, C., Baumgartner, L. J., Thiem, J. D., … Cooke, S. J. (2017). The future of fish passage science, engineering, and practice. *Fish and Fisheries*, *19*(2), 340–362.

Simpfendorfer, C. A., Heupel, M. R., & Hueter, R. E. (2002). Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*, 23–32.

Smith, K. A., & Brown, M. L. (2002). Seasonal composition and abundance of Ichthyoplankton entrained through Big Bend Dam, South Dakota. *Journal of Freshwater Ecology*, *17*, 199–207.

Stockner, J., Langston, A., Sebastian, D., & Wilson, G. (2005). The limnology of Williston reservoir: British Columbia's largest lacustrine ecosystem. *Water Quality Research Journal of Canada*, *40*, 28–50.

Syslo, J. M., Guy, C. S., Bigelow, P. E., Doepke, P. D., Ertel, B. D., & Koel, T. M. (2011). Response of non-native lake trout (*Salvelinus namaycush*) to 15 years of harvest in Yellowstone Lake, Yellowstone National Park. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*, 2132–2145.

Trippel, E. A. (1993). Relations of fecundity, maturation, and body size of lake trout, and implications for management in Northwestern Ontario Lakes. *North American Journal of Fisheries Management*, *13*, 64–72.

Underwood, K., & Cramer, S. R. (2007). Simulation of human effects on bull trout population dynamics in Rimrock reservoir, Washington. *American Fisheries Society Symposium*, *53*, 191–207.

Ward, T. D., Brownscombe, J. W., Gutowsky, L. F. G., Ballagh, R., Sakich, N., McLean, D., … Cooke, S. J. (2017). Electric fish handling gloves provide effective immobilization and do not impede reflex recovery of adult largemouth bass. *North American Journal of Fisheries Management*, *37*, 652–659.

Wilkes, M., Webb, J. A., Baumgartner, L., Boys, C., Silva, L. G. M., Connor, J. O., … Link, O. (2018). Fish-Net: Probabilistic models for fishway planning, design and monitoring to support environmentally sustainable hydropower. *Fish and Fisheries*, *19*, 677–697.

Wilkes, M. A., Webb, J. A., Pompeu, P. S., Silva, L. G. M., Vowles, A. S., Baker, C. F., … Kemp, P. S. (2018). Not just a migration problem: Metapopulations, habitat shifts, and gene flow are also important for fishway science and management. *River Research and Applications*, *35*(10), 1688–1696.

Yule, D. L., & Luecke, C. (1993). Lake trout consumption and recent changes in the fish assemblage of flaming gorge reservoir. *Transactions of the American Fisheries Society*, *122*, 1058–1069.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Harrison PM, Ward T, Algera DA, et al. A comparison of turbine entrainment rates and seasonal entrainment vulnerability of two sympatric char species, bull trout and lake trout, in a hydropower reservoir. *River Res Applic*. 2020;36:1033–1045. https://doi.org/10.1002/rra.3617