ADVANCING EARTH AND SPACE SCIENCE

Water Resources Research

RESEARCH ARTICLE
10.1029/2021WR031887

**Key Points:**

- Telemetry results aligned with known biological/life history characteristics for fluvial or fluvial-adfluvial potadromous species
- Rainbow trout had a significantly higher total dissolved gas exposure risk relative to mountain whitefish
- Sufficient depth refugia was available to mitigate exposure risk and gas bubble trauma occurrence in both species

**Supporting Information:**

Supporting Information may be found in the online version of this article.

**Correspondence to:**

D. A. Algera,
dirkalgera@cmail.carleton.ca

**Citation:**

Algera, D. A., Kamal, R., Ward, T. D., Pleizier, N. K., Brauner, C. J., Crossman, J. A., et al. (2022). Exposure risk of fish downstream of a hydropower facility to supersaturated total dissolved gas. *Water Resources Research*, *58*, e2021WR031887. https://doi.org/10.1029/2021WR031887

Received 23 DEC 2021
Accepted 25 MAY 2022



# Exposure Risk of Fish Downstream of a Hydropower Facility to Supersaturated Total Dissolved Gas

**Dirk A. Algera[1], Rajib Kamal[2], Taylor D. Ward[1], Naomi K. Pleizier[3], Colin J. Brauner[3], James A. Crossman[4], Alf Leake[5], David Z. Zhu[2], Michael Power[6], and Steven J. Cooke[1]**

[1]Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, Ottawa, ON, Canada, [2]Department of Civil and Environmental Engineering, University of Alberta, Edmonton, AB, Canada, [3]Department of Zoology, University of British Columbia, Vancouver, BC, Canada, [4]Fish and Aquatics, Castlegar, BC, Canada, [5]BC Hydro, Burnaby, BC, Canada, [6]Department of Biology, University of Waterloo, Waterloo, ON, Canada

**Abstract** Fish exposed to supersaturated total dissolved gas (TDG) levels can develop gas bubble trauma (GBT) which can lead to sublethal effects or mortality. Access to refugia in areas of high TDG that allows for hydrostatic (depth) compensation can mitigate exposure risk and GBT occurrence. The goals for this study were to examine resident fish habitat and depth use and assess exposure risk to elevated TDG levels related to hydropower operations in the Columbia-Kootenay system in British Columbia. Modeling was used to predict TDG levels for three operational cases (low, medium, and high spill rates). Acoustic telemetry was used to track rainbow trout *Oncorhynchus mykiss* (RT) and mountain whitefish *Prosopium williamsoni* (MW) reach and depth residency. Telemetry results did not differ among operational scenarios and aligned with known biological/life history characteristics for fluvial or fluvial-adfluvial species. Within-species MW reach residency appeared to be reflective of seasonal habitat selection for spawning, foraging, and refuge movements. Within-species RT reach residency appeared to follow habitat association patterns reflective of RT ecology. A risk assessment revealed that RT had a significantly higher TDG exposure risk relative to MW, but sufficient depth refugia habitat was available to mitigate exposure risk and GBT occurrence in both species. The results suggested that TDG exposure risk and actual risk depend on the interplay between species-specific ecology and TDG patterns generated by hydropower facilities. The ecological and TDG patterns in this study suggested that system- and species-specific studies will be required to generate detailed TDG exposure predictions for management decision-making.

## 1. Introduction

Dams convey water to downstream environments through turbines for power generation or through spillways and related infrastructure during seasonal high flow events, for safety purposes, during periods of reduced energy demand, or for meeting conservation requirements such as maintaining minimum flows to mitigate stranding events and/or provide attraction flows and enhance fish passage (Nagrodski et al., 2012; Travnichek et al., 1995). Spilling water to mitigate aquatic impacts can be beneficial from a conservation standpoint, but the process of spilling water can also generate supersaturated total dissolved gas (TDG) levels in the downstream environment. Water passing over hydropower infrastructure such as spillways can entrain bubbles containing atmospheric gases (i.e., nitrogen, oxygen, and other trace gases) that are plunged to depth and then dissolved in water in proportion to their partial pressures, resulting in elevated TDG levels. If that water rises to the surface, TDG exceeds the surrounding hydrostatic pressure, resulting in supersaturated TDG levels. The latter can result in gas bubble formation in the surrounding water and within aquatic organisms inhabiting the water (Pleizier, Algera, et al., 2020).

Exposure to TDG supersaturation >110% in surface waters is known to produce gas bubble trauma (GBT) and fish mortality, although the severity is dependent on species, life stage, and exposure duration (Cao et al., 2019; Deng et al., 2020; Ji et al., 2019; Pleizier, Algera, et al., 2020; Wang et al., 2015; Weitkamp & Katz, 1980). Exposure at low to moderate TDG levels (i.e., 105%–120% supersaturation) in surface waters can have sub-lethal effects (Pleizier, Algera, et al., 2020; Pleizier, Nelson, et al., 2020), with fitness related implications (i.e., survival) for fishes residing below large hydro dams (McGrath et al., 2006). Since TDG supersaturation is a function of pressure (depth), hydrostatic compensation is possible such that a 1 m increase in depth roughly compensates for the effects of about 10% increase in TDG supersaturation (Bouck, 1980; Pleizier, Algera, et al., 2020; Pleizier, Nelson, et al., 2020). Thus, a fish positioned at 1 m depth is compensated for the effects at 110% TDG supersaturation. Through hydrostatic (depth) compensation, fish can endure increased TDG levels with no ill effects or GBT occurrence (Dawley et al., 1976). However, symptoms of GBT can manifest with loss of depth compensation.

Generation of TDG is greatly influenced by a hydropower facility's operational conditions, where the degree of spillage is the primary factor in elevating TDG (Qu et al., 2011). Dissipation of TDG occurs via air-water contact, so turbulent waters dissipate TDG more rapidly than flat, standing tailwaters where TDG can remain elevated for considerable distances downstream from the dam (Qu et al., 2011; Urban et al., 2008). Consequently, fish immediately downstream of the dam are at greatest risk of exposure to higher TDG levels, with exposure risk diminishing with distance from the dam (Qu et al., 2011). Mitigating supersaturated TDG levels involves preventing the production of TDG by avoiding water spillage, or rapidly increasing downstream dissipation through operational modifications or infrastructure installations that increase tailwater turbulence (Kamal et al., 2020). Passing water through turbines for power generation can minimize TDG supersaturation by reducing the volume of water passed over spillways, but is not always an option under high flow scenarios. Maximum allowable TDG levels have been included in water quality standards and TDG reduction strategies, such as installing spillway deflectors or changing the timing of spillway operations during fish migrations, have been implemented in some jurisdictions (Fidler & Miller, 1994; McGrath et al., 2006). However, in systems with large tributaries or waterfalls upstream of hydropower facilities, or in highly impounded systems with multiple hydropower facilities in series such as the Columbia River system, TDG levels may be already elevated in the receiving waters (e.g., Kamal et al., 2020). Consequently, elevated TDG levels remain a persistent problem in these systems (Ma et al., 2018; McGrath et al., 2006).

Fish behavior may mitigate TDG exposure, either through direct avoidance or through habitat preferences that make them less susceptible to elevated TDG (e.g., benthic species). Pelagic silver carp *Hypophthalmichthys molitrix* and resident cyprinid and catostomid fishes in the Yangtze River system exhibited strong detection and avoidance abilities when TDG was high (i.e., >130%, Ji et al., 2021, 145%, Wang et al., 2020). Some salmonids, common focal species for TDG management and conservation actions in North America (Backman & Evans, 2002), appear able to detect high TDG levels and, in some instances, exhibit lateral movement avoidance behaviors (Pleizier et al., 2021; Stevens et al., 1980). Another method of TDG avoidance is through depth compensation, however, salmonid responses are varied (Dawley et al., 1976; Lund & Heggberget, 1985) and remain largely understudied. Habitat use and residency may increase exposure risk to elevated TDG levels. Mature fish that are spawning may spend more time in certain areas of a watercourse during the spawning season. Furthermore, many salmonids are territorial (Bachman, 1984; Gunnarsson & Steingrímsson, 2011) and body size can influence behaviors, with larger individuals typically occupying higher quality habitats (i.e., with higher resource abundance) and defending territory against smaller conspecifics attempting to occupy the same habitats (Bridcut & Giller, 1993; Gunnarsson & Steingrímsson, 2011; Pert & Erman, 1994). If preferred or critical habitats (e.g., territorial, spawning) are in areas with elevated TDG levels, avoidance may not be possible and individuals may face increased exposure risk and probability of developing GBT.

Although studies tracking individual fish movements in relation to elevated TDG levels and hydrostatic compensation have been conducted (Johnson et al., 2005, 2010; Weitkamp et al., 2003), knowledge of TDG exposure risk as it relates to behavioral traits such as site residency is limited. Most studies have focused on migratory salmon and trout, with few investigating resident fishes that could experience increased TDG exposure multiple times a year. Furthermore, to our knowledge no studies have conducted a risk analysis correlating TDG exposure to fish movement behavior. In this study, three TDG profiles were developed based on operational scenarios for two hydropower facilities located on the Columbia River Basin. Fish movements (location, depth) of two resident species, rainbow trout *Oncorhynchus mykiss* and mountain whitefish *Prosopium williamsoni*, were tracked using acoustic biotelemetry to determine whether fish movement behavior mitigated or aggravated exposure risk to TDG. More specifically, the goal was to examine relationships between fish seasonal reach residency and depth use and assess exposure risk to elevated supersaturated TDG levels under operational scenarios with high spillway use. It was hypothesized that: (a) reach and depth residency would vary by body length, species, and season; (b) exposure risk would differ by species and location within the system. It was further predicted that: (a) smaller mountain whitefish and rainbow trout reach residency would be more widespread in the system when compared

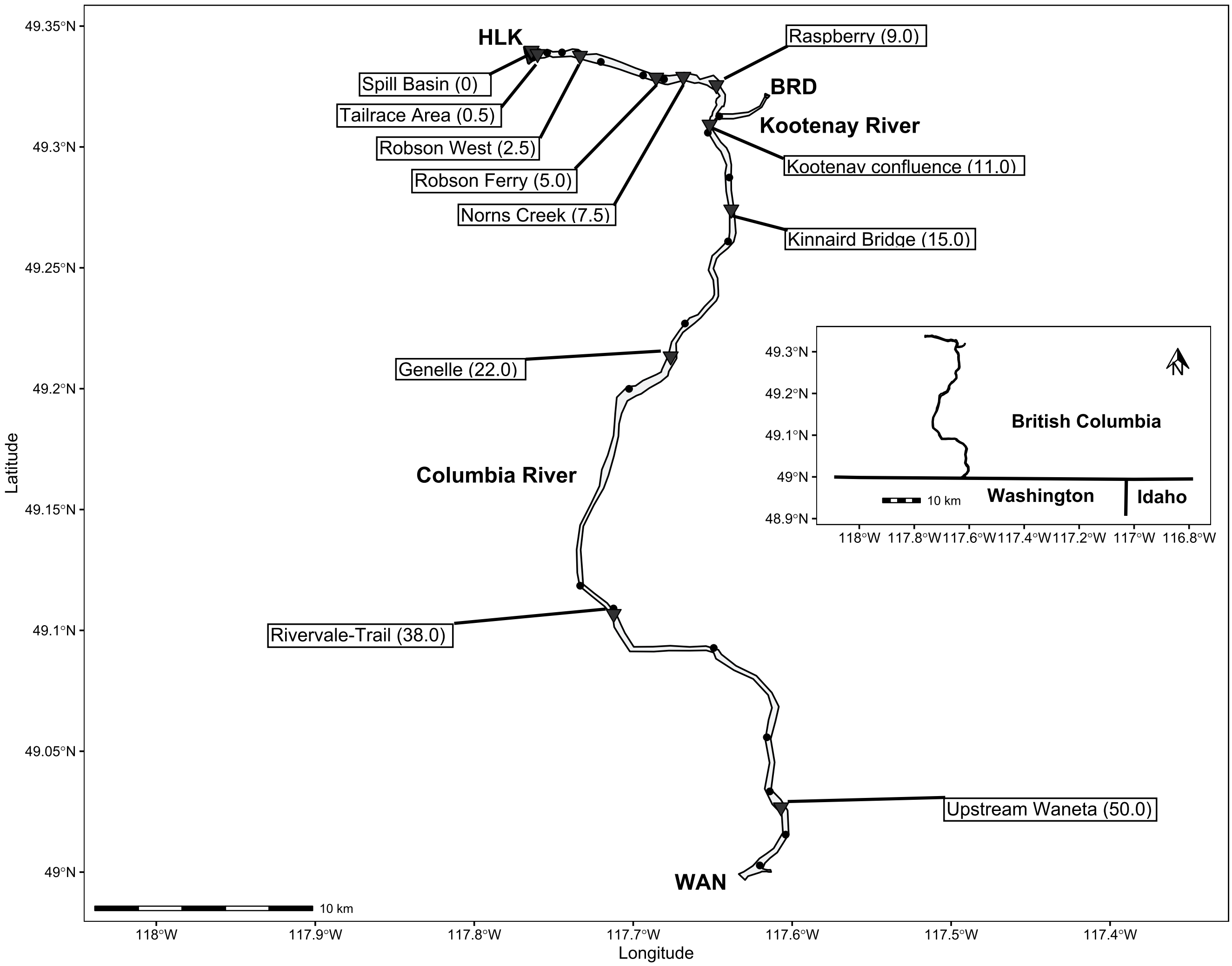


**Figure 1.** The Lower Columbia study system which included the ∼56 km reach that extends from the Hugh L. Keenleyside Dam (HLK) on the Columbia River, Brilliant Dam (BRD) on the Kootenay River, and Waneta Dam (WAN) at the Pend d'Oreille River confluence. Filled circles denote receiver sites; filled triangles denote locations used in analyses with location names and downstream distance (∼river km) from HLK indicated in textboxes.

with larger conspecifics occupying preferred habitats; (b) mountain whitefish and rainbow trout seasonal reach residency would correspond to the species-specific pre- and post-spawning areas; (c) owing to increased water levels, mountain whitefish and rainbow trout would occupy deeper habitats in fall and spring and shallower habitats in winter; (a) benthic oriented mountain whitefish would be fully depth compensated more frequently than predominantly drift-feeding rainbow trout; and (b) species-specific elevated TDG exposure risk would be highest at locations closer to dams.

## 2. Methods

### 2.1. Study Site

Acoustic telemetry data were collected on the Columbia River and Kootenay River systems located near Castlegar, British Columbia (Figure 1). The Columbia River segment included the ∼56 km stretch downstream of Hugh L. Keenleyside Dam (HLK; 49°20'30″N 117°46'25"W) to Waneta Dam (WAN) at the Pend d'Oreille River confluence (49°00'15"N 117°37'12"W) near the Canada-United States border. The HLK facility, which impounds the Arrow Lakes Reservoir, consists of a 52 m dam, eight low-level outlet gates on either side of a four-bay spillway, and a 185 MW generating station (two low head Kaplan turbines) on the left bank. The HLK dam, which was constructed as part of the Columbia River Treaty for water regulation purposes, is owned and

10.1029/2021WR031887

operated by BC Hydro, whereas the powerhouse (Arrow Lakes Generating Station) is owned and operated by the provincially owned Columbia Power Corporation. The Kootenay River segment includes the ~2.8 km stretch downstream of Brilliant Dam (BRD; 49°19′29″N 117°37′13″W) to the confluence with the Columbia River. The BRD facility, also owned and operated by Columbia Power Corporation, is a run-of-the-river facility with a 140 MW generating station (four vertical Francis turbines) on the right bank, an eight-bay gated spillway, and a 120 MW capacity generating station (one Kaplan turbine) 150 m downstream on the left bank.

### 2.2. Fish Capture and Tagging

Rainbow trout (RT) and mountain whitefish (MW) were captured in October 2016 and October 2017 (surface water temperatures of 8°C–11°C). The 2016 fish were captured via angling ($n = 31$) or electrofishing ($n = 42$). Angled fish were captured in the Columbia River ~7–18 km downstream of HLK. Fish caught by electrofishing at night received a passive integrated transponder (PIT) tag prior to surgery. The 2017 fish ($n = 19$) were all captured via angling ~7–8 km downstream of HLK.

Fish were immobilized for surgery using electric fish handling gloves (EFHG) or anaesthetized using clove oil. Immobilization with EFHG (Smith Root, Inc., Vancouver, and Washington) was achieved using the lowest power settings (i.e., 4 or 6.3 mA) that induced immobilization. Fish that were anaesthetized by clove oil were immersed in a 40 mg $L^{-1}$ clove oil solution (1 part clove oil: 9 parts 95% ethanol) until loss of equilibrium was achieved. Once immobilized or anaesthetized, fish were measured for body length (total length [TL], nearest mm), and surgically implanted with an acoustic transmitter (Thelma Biotel, Trondheim, Norway). Betadine was used to disinfect transmitters and surgery equipment prior to surgery and between each fish. Small (~15 mm) incisions were made along the midline, just anterior to the pelvic girdle and closed using 3 simple-interrupted absorbable sutures (3/0 monofilament PDSII, Ethicon Inc., Somerville, New Jersey). During surgery, fish were held in a 100 L cooler containing ambient temperature river water, and the entire surgery procedure took <5 min for each fish. A wide range of fish body lengths were targeted for tagging to examine if movement data differed between large and small conspecifics. Body lengths for RT ranged from 307 to 504 mm TL and for MW from 310 to 499 mm TL. Weights were not taken to limit air exposure and handling time, but published length-weight relationships suggest that estimated weights for RT ranged from ~315 to 1,737 g (Simpkins & Hubert, 1996) and for MW ranged from ~300 to 1,275 g (Rogers et al., 1996).

Two types of transmitters were used (ADT LP-9-LONG, 9 × 38.5 mm, 6.8 g dry weight, 30–90 s duty cycle, 143 dB power output, expected battery life 30 months; ADT LP-7.3-LONG, 7.3 × 27 mm, 2.9 g dry weight, 90–120 s duty cycle, 139 dB power output, expected battery life 12 months). Both transmitter types were outfitted with depth sensors and transmitted using the 69 kHz transmitter frequency. The larger 6.8 g LP-9 transmitters ($n = 73$) were implanted into fish in the 307–540 mm TL range. The body length range equates to a weight range of ~315–1,737 g and a maximal tag weight of 2% of the fish's body weight. The smaller 2.9 g LP-7.3 transmitters ($n = 19$) were implanted into fish in the 310–506 mm TL range, which equates to a weight range of ~300–1,427 g and a maximal tag weight of 1% of the fish's body weight. Transmitter weights 2% of fish body weight are consistent with the assumption that tag burden would not impede swimming behavior (Brown et al., 1999). The LP-9 tags accounted for 79% of the tags in the study and were implanted into fish in October 2016, whereas the LP-7.3 tags accounted for 21% of the tags in the study and were implanted in October 2017. Surgeries were performed as close to the capture location as feasible and fish were released after recovery at the surgery location. During recovery, fish were held at a low density (i.e., <10 kg $m^{-3}$) in a 100 L cooler containing ambient river water and released once they gained equilibrium.

### 2.3. Telemetry Array

An array of 27 omni-directional hydrophone acoustic telemetry receivers (VR2W, Vemco/Innovasea, Halifax, Nova Scotia, Canada) deployed downstream of HLK and BRD was used to track fish movements (Figure 1). The telemetry array was active from October 2016 through to April 2019. Thirteen receivers were deployed in October 2016 and the remainder were already in place as part of long-term monitoring program in the Columbia River. As the lower Columbia River is relatively shallow, receivers were secured to a nylon rope anchor line at ~1 m depth under a large surface buoy and oriented such that the hydrophone listening component was pointed toward the substrate.

**Table 1**
*Date Range, Spillage Rate at Brilliant Dam (BRD) and Description of Selected Water Spillage Scenarios*

| Scenario | Date range | BRD spillage ($m^3s^{-1}$) | Description |
|---|---|---|---|
| 1 | May 01–31, 2016 | 895.5 | Low |
| 2 | June 01–10, 2017 | 1,837.8 | Moderate |
| 3 | May 26–27, 2018 | 2375.5 | High |

Range and detection efficiency testing were conducted in July 2018 using an array of three VR2W receivers and the LP-7.3 acoustic transmitter model. The LP-9 transmitters were not tested, however, the LP-7.3 model has a longer duty cycle and a lower power output than the LP-9 model. Therefore, the resulting range and detection efficiencies of the LP-9 model were expected to be similar or exceed the LP-7.3 model. For testing, the LP-7.3 transmitter was anchored at a location ~300 m downstream of the HLK dam face and receivers were anchored 50, 100, and 150 m from the transmitter. The receivers remained anchored for the duration of the range and detection efficiency testing. Since the transmitter depth sensor values recorded by the receivers were reported as unitless values, a depth calculation for the sensor values was required. During range and detection efficiency testing the transmitter was anchored at six depth intervals (0.5, 2, 5, 10, 15, and 17 m) for time periods between ~21 and ~73 hr. A standard calibration curve was developed by plotting the six depth intervals against the reported unitless depth sensor values, and the resulting Equation 1, which yielded a good fit to the data ($R^2 = 0.99$, $F_{1,13} = 1{,}056$, $P < 0.001$), was used to calculate telemetry depth data.

$$\text{Depth} = 0.3892(\text{sensor value}) - 2.9175 \tag{1}$$

### 2.4. Total Dissolved Gas Modeling

In the present study, three TDG scenarios for the Columbia-Kootenay sector (henceforth Lower Columbia) were modeled using a TDG dissipation methodology following Kamal et al. (2019, 2020, 2021). See Appendix A in Text S1 for a more detailed description of the TDG modeling methodology. Hourly operational data (discharge per water conveyance structure) for the facilities were provided by BC Hydro. Scenarios were chosen based on HLK and BRD operating conditions during periods of interest in 2016 and 2018. Acoustic tags were active for these periods except for Scenario 1. Data exploration of the HLK and BRD facilities revealed there was substantially higher variation in BRD spillage relative to HLK, so scenarios were selected based on BRD operating conditions (Table 1). Time periods for a given scenario were selected where the spillage rate was relatively consistent (coefficient of variation <15%, all scenarios) to enhance TDG dissipation modeling outputs. Low, moderate, and high spillage scenarios that occurred in May and June were selected. These scenarios were chosen because they represented relevant scenarios that resident fishes would experience annually during spring high flows. The dissipation modeling output resulted in TDG point data for transects in the Lower Columbia system, which were extrapolated across the entire ~56 km section using the Ordinary Kriging function in QGIS (version 2.142).

### 2.5. Data Analysis

Telemetry data, statistical analyses, and maps were processed in *R* Studio (version 1.2.5042) using *R* (version 3.6.3). False negative detections, defined as transmitter IDs that were not implanted into fish, were removed prior to data analysis. False positive detections, existing transmitter IDs deemed erroneous, were removed from the data set by applying a minimum lag method whereby a pre-determined, biologically relevant minimum detection number within a specified time interval was used to identify and remove false positive detections (Pincock, 2012). Since the duty cycle differed for the two transmitter types (LP-9 = 30–90 s, LP-7.3 = 90–120 s), the minimum lag was calculated separately for each of the transmitter types. In the present study a minimum of two detections within a one-hour period were considered "true" detections (Papastamatiou et al., 2010). Fish detection data were verified by visually inspecting individual abacus plots. Maximum detection range was determined by examining range testing data. Detection efficiency percentage was calculated at each distance and depth interval as the quotient of the number of observed detections divided by the number of possible detections while the receivers were active. The mean duty cycle of the two transmitter types (i.e., 105 s) was used to determine the number of expected detections for a given time period. Range and detection efficiency testing results were not applied to telemetry data during analysis, but are presented to provide the level of certainty for interpretation of the detection data (see Appendix B Table B1 in Table S1).

The individual receiver sites (stations) were grouped based on geographical proximity and location in similar fish habitat. The mean coordinates (latitude and longitude) of each receiver group (location) were calculated for mapping purposes. If a location's mean coordinates fell outside of the river boundary on terrestrial habitat (five instances), the latitude was retained, and the longitude was manually adjusted to a point in the middle of the river. In total there were 11 locations used for analyses (Figure 1, Table B2 in Table S1).

### 2.6. Reach Residency Index

A residence index (RI) was used to quantify site residency as a measure of reach use for individual fish. A residence index was selected to infer site residency over use of raw detection data because a RI reduces the potential for bias, that is, in cases where mean site residency was primarily driven by a few individuals generating high numbers of detections at a given site (Kessel et al., 2016). To calculate RI, daily fish detections were enumerated within a 24 hr time-bin at each location and divided by the total number of time-bins in which the fish was detected anywhere in system. A fish was considered "resident" at a site if there were >9 detections within a 24 hr time-bin at the location. Time-bins that did not meet the threshold were excluded from analyses. The detection threshold cut-off was selected based on the distribution of the telemetry data (based on visualizations of patterns of detections) and gave us confidence that fish were resident within the assigned reach without sacrificing useable data. The RI values vary between 0 and 1, with a value of 1 indicating that at least one fish was resident at that location for that 24 hr period. The daily RI was summed for each fish at each location within a season and divided by the total number of days corresponding to each season to calculate a seasonal RI value. In the present study September-November was considered as fall, December–February as winter, March–May as spring, and June–August as summer. The data set encompassed seasons over multiple years (e.g., spring 2017, spring 2018). A Kruskal-Wallis rank sum test found no statistical difference among inter-annual seasonal RI data in the MW data (Kruskal-Wallis chi-squared = 13.128, d$f$ = 9, $P$ = 0.157). An overall inter-annual statistical difference was found for RT seasonal RI data (Kruskal-Wallis chi-squared = 19.1068, d$f$ = 9, $P$ = 0.02), but a Dunn's test with a Bonferroni correction factor for pairwise comparisons revealed that no relevant pairwise comparisons (e.g., winter 2017 and 2018) were statistically different ($P$ > 0.05 all cases). Consequently, seasonal data were pooled across years. To account for the difference in the number of receivers that could contribute to fish detections at a given location, the seasonal RI was weighted at each location by dividing the seasonal RI by the number of stations at the location (see Table B2 in Table S1 for maximum weighted RI values at each location).

### 2.7. Depth Residency Index

A depth RI was determined at each location following the same procedure as described for the reach use RI. Telemetry depth values were categorized into 1 m incremental bins (e.g., 0–0.9, 1–1.9 m, etc.). Depth RI was calculated by enumerating the number of detections grouped by depth-bin at a location divided by the total number of detections independent of location and depth bins. An overall inter-annual statistical difference in depth use was found for MW data (Kruskal-Wallis chi-squared = 19.1068, d$f$ = 9, $P$ = 0), but a Dunn's test with a Bonferroni correction factor revealed no significant differences in pairwise comparisons ($P$ > 0.05 all cases). An overall inter-annual statistical difference was found for RT data (Kruskal-Wallis chi-squared = 28.569, d$f$ = 9, $P$ = 0). A Dunn's test with a Bonferroni correct factor revealed only one significant pairwise comparison (spring 2018 and 2019: $P$ = 0.011). Consequently, seasonal depth RI data were pooled across years to retain sample sizes.

### 2.8. Risk Assessment

The modeled TDG levels in the present study are a discrete representation at a given location, and thus the TDG exposure risk resulting in harmful outcomes can be assessed as a function of reach and depth residency (i.e., reach use and hydrostatic compensation). The TDG exposure risk for MW and RT were analyzed separately and only included spring (March, April, and May) reach RI and depth RI data. Spring data were chosen because they represent the high flow season when increased water spillage events are most likely and presumably associated with relatively greater TDG exposure risk (Fidler, 2003). A Monte Carlo method (MCM) was used to generate probability distributions of reach, depth, and TDG level occurrence using input distributions derived from the reach residency, depth residency, and TDG level data. For the reach occurrence input distribution, an empirical density function (EDF) was applied to MW and RT reach residency data to determine the cumulative probability of occurrence at a given location for each species. For the MCM reach residency output distribution, a uniform distribution of 100,000 randomly generated numbers between 0 and 1 was generated. The input reach residency cumulative probability distribution was then applied to the uniform distribution such that the location assigned to the randomly generated value corresponded to the cumulative proportion range for that location. For example, if EDF determined the spill basin location accounted for 0.25 of the total proportion and the tailrace for 0.25, random number values between 0 and 0.25 (inclusive) in the uniform distribution were assigned as occurring in the spill basin and those >0.25 but ≤0.50 were assigned to the tailrace. For depth occurrence input distributions, an EDF was applied to MW and RT depth residency data at each location to determine the cumulative probability of occurrence at a given location for each species. For the MCM depth residency output distribution, a uniform distribution of 100,000 randomly generated numbers between 0 and 1 was generated for each location. The input depth residency cumulative probability distribution was then applied to the uniform distribution in the same manner as for reach occurrence above. For TDG occurrence, TDG levels were categorized into 5% incremental bins (e.g., 100%–104%, 105%–109%, etc.) at each location and an EDF was applied to the TDG data determine the cumulative probability of TDG occurrence at each location. The MCM TDG output followed the same uniform distribution and cumulative proportion process as for depth occurrence. The location-conditional cumulative probability process used for depth and TDG occurrence ensured that values represented real possibilities at the corresponding locations. All EDF were determined using the "ecdfPlot" function in the EnvStats package (Millard & Kowarik, 2020) and all uniform distributions were generated using the "runif" function in the *R* base stats package.

The within-species realized risks for MW and RT were assessed by calculating the cumulative proportion of compensation occurring at a given location compared against the mean TDG and depth RI values for that location. The degree of compensation achieved by fish was determined using the 10% TDG supersaturation compensation per meter of depth rule (Pleizier, Algera, et al., 2020; Pleizier, Nelson, et al., 2020). For example, a depth RI bin value of 2–2.9 m would compensate for all TDG levels <130%. A TDG level of 110% was chosen as the benchmark to evaluate risk because 110% TDG is the threshold above which GBT effects begin to be observed (Pleizier, Algera, et al., 2020) and British Columbia has a water quality objective requiring that TDG not exceed 110% (Fidler & Miller, 1994).

### 2.9. Statistical Analysis

For all statistical analyses the significance threshold was set $\alpha = 0.05$. A Pearson's Chi-square test with Yate's continuity correction was used to determine if there was a difference in the relative proportions of transmitter types that were detected in the array. The weighted seasonal reach RI data (reach RI hereafter) were used to test for statistical differences in seasonal MW and RT reach use. Low detection numbers precluded inclusion of location in the statistical model, so testing focused on overall drivers of residency. Because the response data were bounded by 0 and 1, a generalized linear mixed model (GLMM) with a beta distribution and logit link function was used to test for differences in seasonal reach RI among species (categorical), season (categorical), and body length (TL, continuous). A random intercept for individual fish (fish ID) was included in the GLMM because there were multiple observations from each individual fish. The GLMM was modeled using the "glmmTMB" function in the glmmTMB package (Magnusson et al., 2020). Model fit was verified by plotting the residuals against the fitted values for all the factors. A Type III Wald Chi-square analysis of deviance test was used to determine the significance of main factor effects on response variables. Multiple comparisons were conducted with a Tukey's HSD method using the "lsmeans" function in the eemeans package (Length et al., 2020).

The weighted depth residency RI data (depth RI hereafter) were used to test for statistical differences in seasonal MW and RT depth use. A GLMM with a beta distribution and logit link function was used to test for differences in seasonal depth RI among species (categorical), season (categorical), location (categorical), depth bin (categorical), and body length (TL, continuous). A depth bin interaction term with species, season, or location was of primary interest for the purposes of this study, but sample sizes were either not sufficient for testing or interaction terms were not found significant and consequently removed from further statistical testing. A random intercept for individual fish (fish ID) was included in the GLMM because there were multiple observations from each individual fish. The GLMM model, analysis of deviance for main effects, and any multiple comparisons were completed using the same functions and packages for reach RI data. Model fits were verified as outlined above for reach RI data.

10.1029/2021WR031887

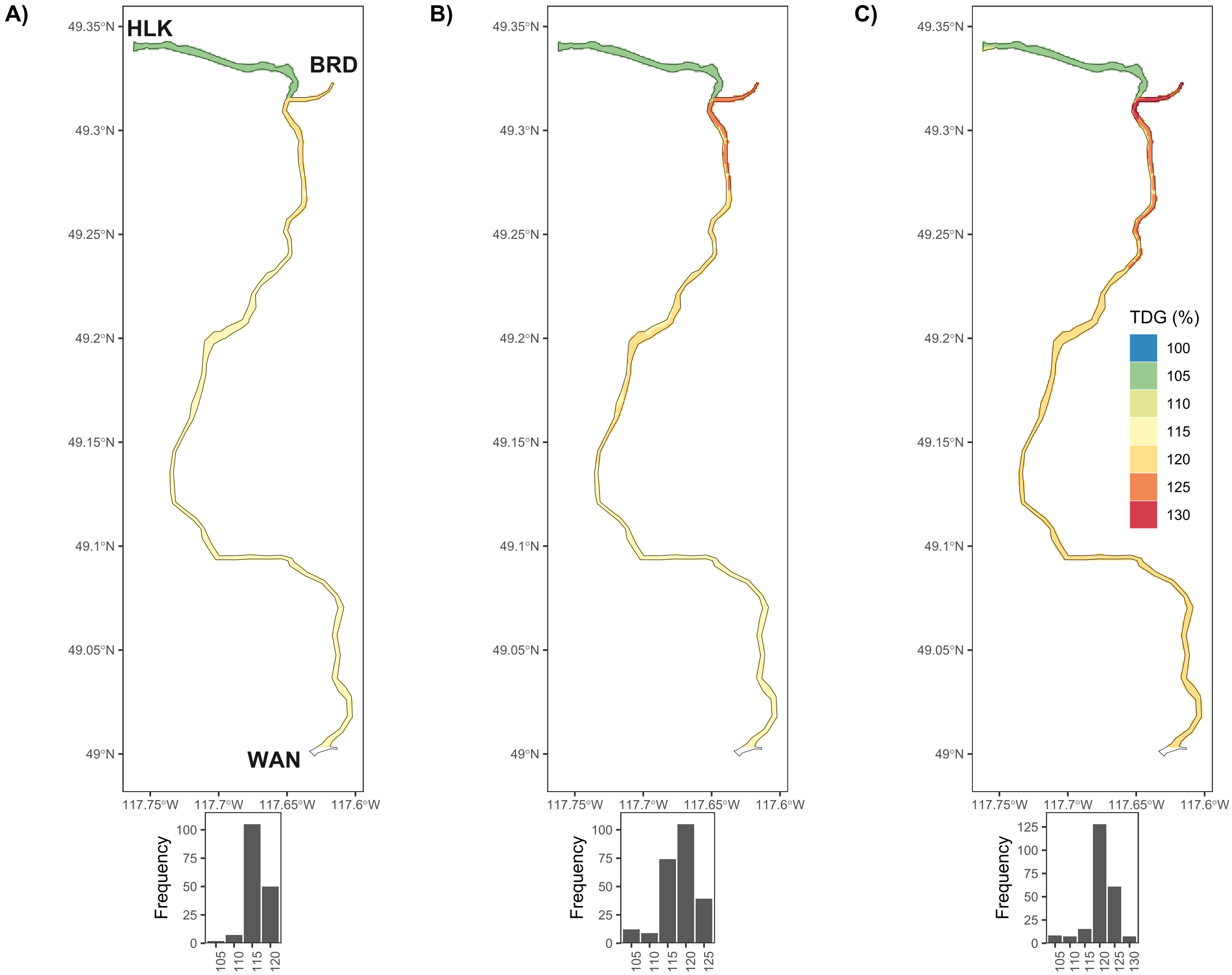


**Figure 2.** Modeled total dissolved gas (TDG) profile for the Lower Columbia system and frequency of TDG levels for Scenario 1 (a), Scenario 2 (b), and Scenario 3 (c). The corresponding date ranges for each Scenario are described in Table 1.

A Pearson's Chi-square test with Yate's continuity correction was used to test if there was a difference in overall depth compensation between species (i.e., independent of location). To test if there was a difference in TDG exposure risk at a given location, within-species cumulative proportions were compared using a Marascuilo method for pairwise multiple comparisons (Wagh & Razvi, 2016). Briefly, the absolute value of the difference between two cumulative proportions was compared to a critical range value. The difference was considered statistically significant if the absolute value was greater than the critical range value. Locations with an occurrence of <110% TDG were automatically categorized as low regardless of fish depth compensation because the 110% guideline threshold was not exceeded. If the TDG exceeded 110%, risk was categorized according to depth compensation percentages whereby 0%–25% compensation was considered high risk, 26%–50% as of concern, 51%–75% as moderate, and 76%–100% as low risk.

## 3. Results

### 3.1. TDG Models and Detection Data

The range (mean ± SD) of TDG levels varied among and within the three scenarios (Figure 2). Scenario 2 and 3 produced the highest TDG levels, ranging from 107% to 129% (120 ± 4.3) and 108% to 131% (122 ± 4.6),

**Table 2**
*Summary of Statistical Test Outputs for the Effect of Species, Season, Body Length, Binned Depth and Location on Seasonal Reach Residence Index (RI) and Depth RI*

| Response | Factor | $\chi^2$ | df | $P$ |
|---|---|---|---|---|
| Reach RI | **Intercept** | **44.475** | **1** | **<0.001** |
| | Species | 0.001 | 1 | 0.974 |
| | Season | 6.158 | 3 | 0.104 |
| | Body Length | 1.812 | 1 | 0.178 |
| Depth RI | **Intercept** | **27.479** | **1** | **<0.001** |
| | Species | 0.026 | 1 | 0.871 |
| | **Season** | **26.542** | **3** | **<0.001** |
| | Body Length | 2.839 | 1 | 0.092 |
| | Depth Bin | 5.989 | 4 | 0.200 |
| | **Location** | **59.711** | **10** | **<0.001** |

*Note.* Depth bins are in increments of 1 m. Locations are found in Figure 1. Significant terms are denoted in bold. Multiple comparisons for significant interaction terms are described in the text.

respectively. Scenario 1 produced relatively lower TDG levels that ranged from 108% to 124% (118 ± 2.5). The highest TDG levels were generated at the Kootenay confluence or downstream thereof.

A total of 92 (RT = 51, MW = 41) fish were tagged and released. After removing false negative and positive detections, a total of 66 of the 92 tagged fish were detected in the receiver array, resulting in 1,265,723 detections. The relative proportion of the LP-9 and LP-7.3 transmitters detected were similar (LP-9 = 76%, LP-7.3 = 24%) to the relative proportion originally deployed for the study (LP-9 = 79%, LP-7.3 = 21%) and were statistically equivalent ($\chi^2 = 1.145$, d$f$ = 1, $P = 0.285$).

Maximum detection range was >150 m. Detection efficiency was lowest when near the surface, and increased until 10 m depth, where it remained relatively high across depths and distances (Table B1 in Table S1).

### 3.2. Reach Residency Index

Reach and depth RI calculation criteria (i.e., fish with >9 detections) further excluded five fish, resulting in 61 fish (RT = 42, MW = 19) included for RI analyses. The body length of the 61 fish ranged from 307 to 540 mm TL.

The GLMM model revealed no statistical differences in seasonal reach RI among any of the factors included in the model (Table 2). Examining location-based fish reach residency (Figure 3), MW were most commonly observed in the upper half of the ~56 km Lower Columbia sector in all seasons, with the majority of fish resident at locations upstream of the Genelle location (rkm 22). Residency downstream of Genelle in the lower reaches of the system was only observed in the fall. The highest MW residency was in the spring at Raspberry (rkm 9) and Norns Creek (rkm 7.5). Residency was lowest in summer, which also produced the fewest detections of MW throughout the system overall. Genelle, Robson Ferry (rkm 5), and Kinnaird Bridge (rkm 15) had moderate MW residency in the spring and winter seasons. Rainbow trout residency was documented at locations upstream of Genelle in all seasons (Figure 3). During the study period, the highest RT residency occurred at Norns Creek in spring and Raspberry in the summer. Fall RT residency was evenly distributed among all locations, and primarily at/or upstream of Kootenay confluence in winter.

### 3.3. Depth Residency Index

The GLMM revealed that season and location had an effect on depth residency, but both were independent of species, body length, and depth bin (Table 2). Examining species-pooled depth residency among locations and seasons (Figure 4), fish exhibited relatively consistent within-season residency at each location, with consistently higher residency values in winter and spring across depth bins. Multiple comparisons for season revealed that fish exhibited higher depth residency in the winter compared to fall and summer ($P < 0.001$, all cases), and in spring compared to fall ($P = 0.011$) and summer ($P = 0.003$). Fish at Norns Creek, the Tailrace, and Raspberry consistently produced the highest within-location depth residency values. Multiple comparisons for location revealed that fish exhibited higher depth residency at Norns Creek area compared to Kootenay confluence ($P = 0.007$), Robson Ferry ($P < 0.001$), Robson West ($P = 0.016$), and the Spill Basin ($P = 0.012$), and at Raspberry compared to Robson Ferry ($P < 0.001$). Of primary interest in this study was depth use (i.e., hydrostatic compensation). The GLMM revealed no significant interaction terms between depth bin and any of the other factors, meaning that the fish in this study did not exhibit a depth preference according to season, species, location, or body size. Graphical representations of the main effects differences in depth residency among seasons and locations are presented in Appendix C (Figure C1 in Figure S1).

### 3.4. Risk Assessment

The MCM TDG frequency distributions resulted in TDG levels that fell entirely within the 105%–109% range at locations downstream of HLK but upstream of the Kootenay confluence (Figure 5a). The highest TDG values

10.1029/2021WR031887

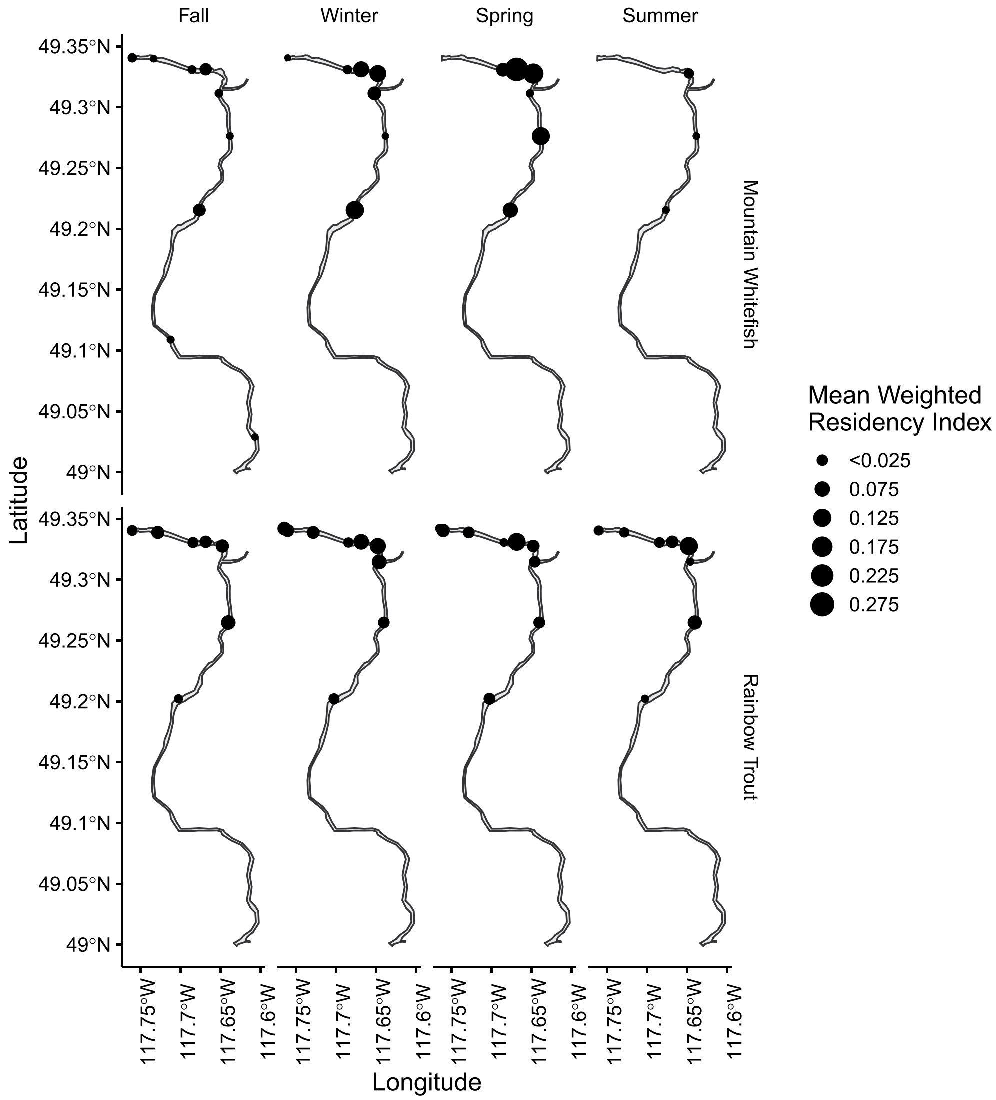


**Figure 3.** Mountain whitefish and rainbow trout seasonal reach residency index at each location in the Lower Columbia system. See Figure 1 for location details and Table B2 in Table S1 for minimum/maximum possible residency index values at each location.

were produced at the Kootenay confluence and Kinnaird Bridge locations. Kinnaird Bridge had an even frequency distribution of TDG levels and the highest mean TDG level, and thus posed the highest risk purely from a TDG exposure standpoint (i.e., when not incorporating consideration of reach or depth use). The TDG values at locations upstream from the Kootenay confluence fell within the 110% water quality guidelines whereas locations at or downstream of the Kootenay confluence did not.

The reach use distributions revealed that MW occurrence would extend from Robson Ferry downstream to Genelle (Figure 5b). The highest frequency of MW occurrence was at Genelle (>25%), but the spatial mean of MW occurrence was at Raspberry and cumulatively occurred more frequently (>50%) in the locations directly upstream of the Kootenay confluence (Figure 5b). The Kootenay confluence location produced the lowest MW occurrence. The MCM revealed that RT occurrence extended from the spill basin downstream to Genelle. The highest frequency (>35%) and spatial mean frequency of RT occurrence were at Norns Creek, with the occurrence distribution being fairly equal upstream and downstream of Norns Creek.

The depth use distributions revealed mountain whitefish depth occurrence that varied by location (Figure 5c). Depth use at locations upstream of the Kootenay confluence were most frequently in the 0–0.9 m range. Mean

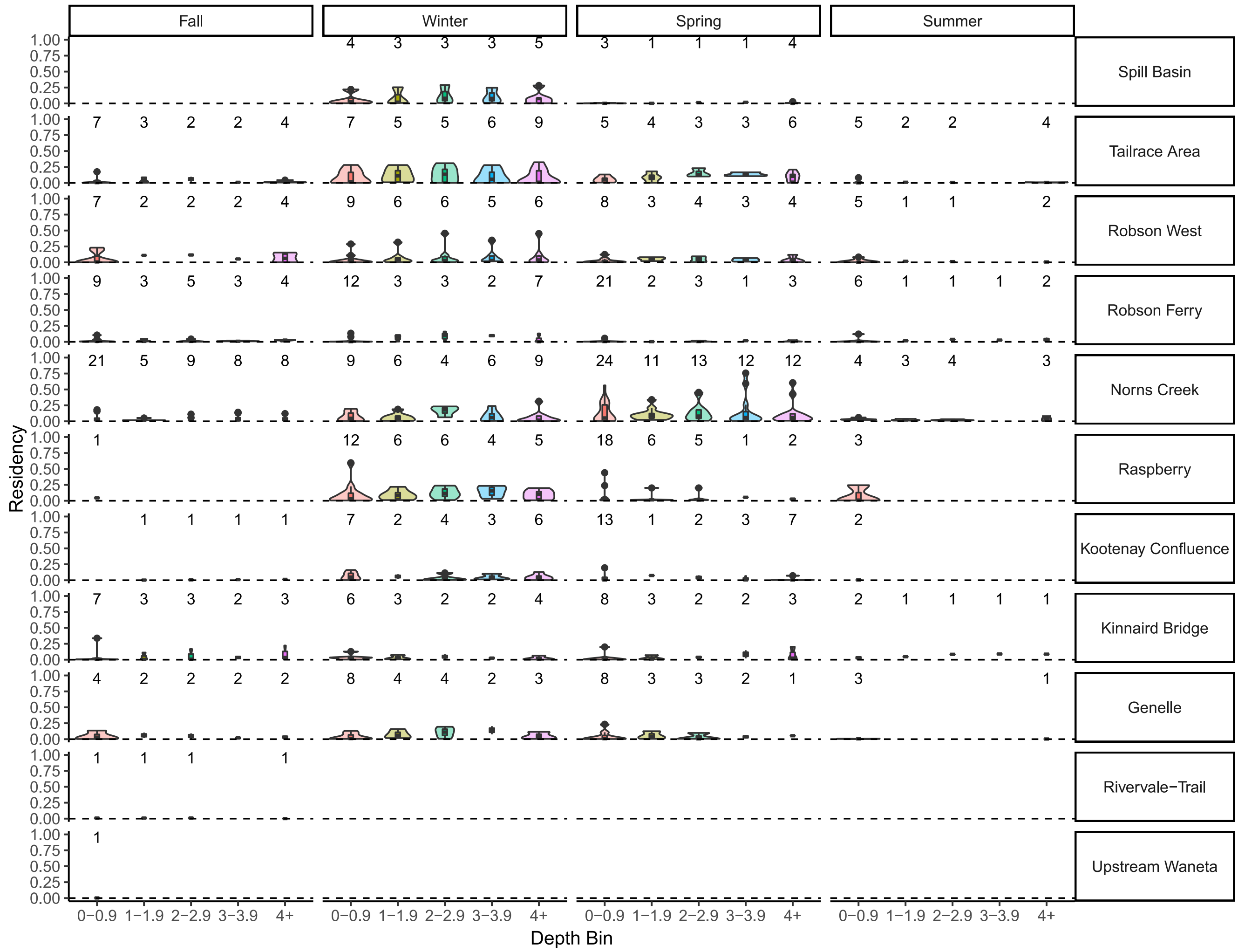


**Figure 4.** Seasonal depth Residency Index (RI) at each 1-m depth bin and location in the Lower Columbia system. Mountain whitefish and rainbow trout data are pooled for each season and location. Numbers below the dashed *x*-axes indicate the number of individual fish detected at each depth bin within each location. Statistical testing revealed no significant differences among depth bin-location interaction terms. For main effects of season and location see Figure C1 in Figure S1.

depth use for MW was in the 0–0.9 m depth range at all locations except for the Kootenay confluence and Kinnaird Bridge areas, where MW were deeper, being predominantly confined to ≥3 m depth at these locations. The MCM also indicated RT depth use varied according to location. In the areas directly downstream of HLK, RT mean depth use in the Spill Basin and Tailrace areas was ≥3 m, and <2 m in the other locations. Rainbow trout depth occurrence was deepest in the Spill Basin area and largely confined to the 4+ m depth bin. Depth occurrence was fairly evenly distributed among depth bins at the Tailrace, Robson West and Norns Creek areas, and was largely confined to shallower 0–0.9 depth bins at Robson Ferry, Raspberry, Kootenay confluence, Kinnaird Bridge, and Genelle locations.

Mountain whitefish were more frequently depth compensated than RT (MW = 43%, RT = 39%), and this difference was statistically significant ($\chi^2 = 2263.800$, d$f$ = 1, $P < 0.001$). Mountain whitefish cumulative depth compensation and risk level varied by location (Table 3). The highest risk locations were at Norns Creek and Raspberry in terms of compensation, but the TDG level was <110% at these locations so they were assigned a low risk categorization. Genelle was the only location for MW occurrence where TDG levels consistently exceeded compensation and thus risk was high. Within-species multiple comparisons revealed that MW depth compensation percentages were statistically different among the locations in all cases except for the Norns Creek-Robson Ferry comparison (i.e., both 0%). Rainbow trout were most frequently compensated at the Spill Basin and Tailrace locations, which also had <110% TDG, and fish were considered at a low exposure risk in these locations. At

10.1029/2021WR031887

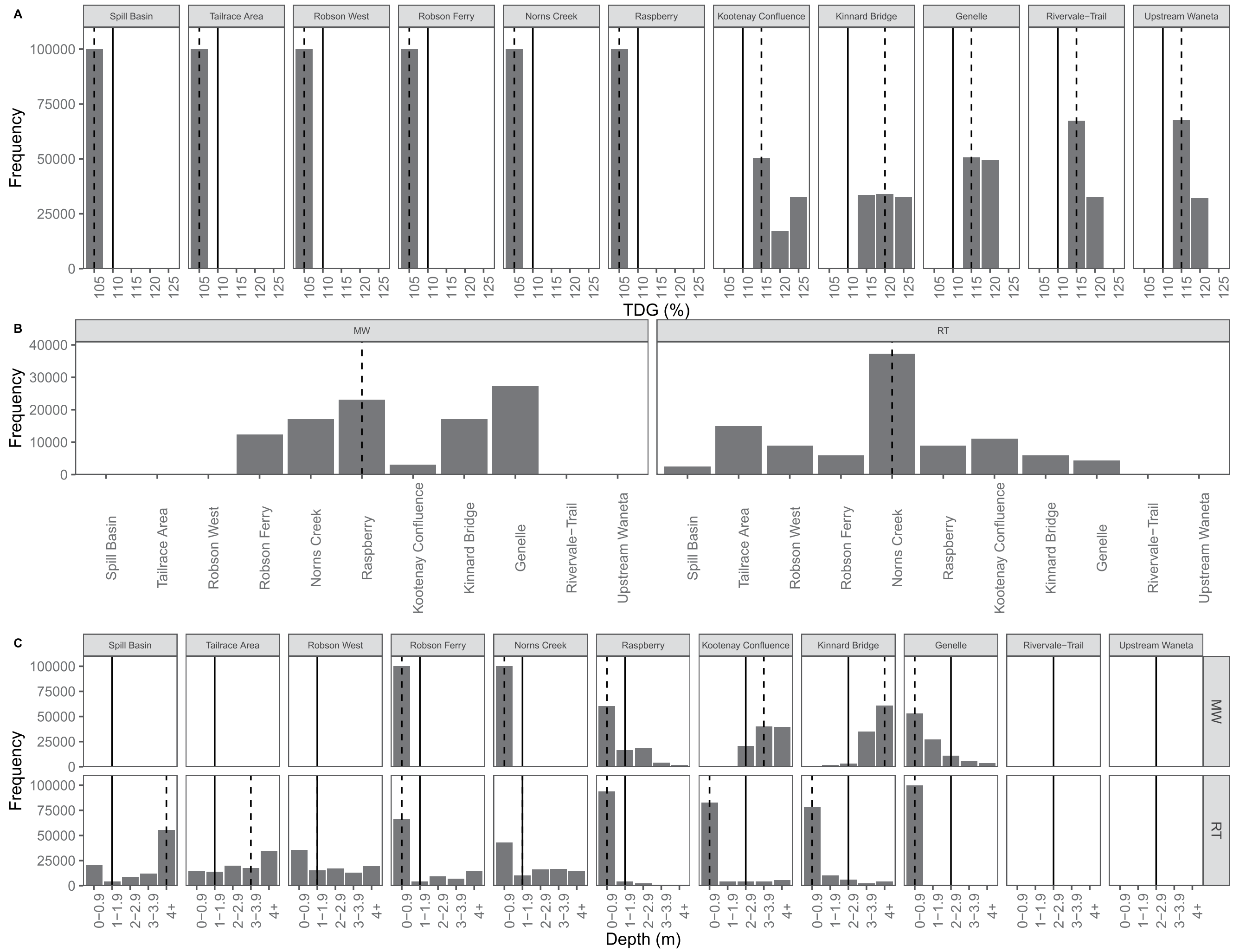


**Figure 5.** Monte Carlo model risk assessment frequency distribution outputs for total dissolved gas (TDG) level occurrence (a), reach occurrence (b), and depth occurrence (c) of mountain whitefish (MW) and rainbow trout (RT) at each location. The dashed line denotes the mean value. The solid line in (a) denotes the 110% TDG threshold. Values to the left of this line met the provincial TDG guideline and fish occupying areas meeting the guideline were considered compensated. The solid line in (c) denotes the depth bin required for compensation at that location. Values to the right of the line indicate lack of depth compensation.

the Robson West, Robson Ferry, Norns Creek, and Raspberry locations, RT were infrequently or minimally depth compensated but the TDG level was <110% so they were assigned low risk. The high risk locations for RT were the Kootenay confluence and downstream where TDG levels consistently exceeded sufficient depth compensation. Within-species multiple comparisons revealed that RT depth compensation percentages were statistically different among the locations in all cases.

## 4. Discussion

Acoustic telemetry was used to examine and quantify the reach and depth residency of resident MW and RT in a system impounded by two hydropower facilities. This analysis enabled us to estimate the location-based risk exposure in relation to TDG levels for each species. The reach residency analysis revealed no differences in residency between MW and RT, or according to season or body length. The depth residency analysis revealed that there was a difference among seasons and locations, partially supporting the hypothesis that depth use would vary by species, season, body length, and depth bin. As hypothesized, the risk assessment revealed that MW were fully depth compensated more frequently than RT. The risk assessment also revealed that MW and RT were at highest TDG exposure risk at locations close to or downstream of BRD. The result thus only partially supported the hypothesis that species-specific elevated TDG exposure risk would be highest for fish at locations closer to dams.

**Table 3**
*The Mean Total Dissolved Gas (TDG) Level, Cumulative Depth Compensation (Comp) and Exposure Risk Level of Mountain Whitefish (MW) and Rainbow Trout (RT) at Each Location As Determined Using a Monte Carlo Simulation*

| Location (~rkm) | Mean TDG (%) | Comp depth-bin (m) | MW comp (%), risk level | RT comp (%), risk level |
|---|---|---|---|---|
| Spill Basin (0)* | 105–109 | 1.0–1.9 | - | 80, low |
| Tailrace Area (0.5)* | 105–109 | 1.0–1.9 | - | 86, low |
| Robson West (2.5)* | 105–109 | 1.0–1.9 | - | 64, low |
| Robson Ferry (5)* | 105–109 | 1.0–1.9 | 0, low | 34, low |
| Norns Creek (7.5)* | 105–109 | 1.0–1.9 | 0, low | 57, low |
| Raspberry (9)* | 105–109 | 1.0–1.9 | 40, low | 6, low |
| Kootenay confluence (11) | 115–119 | 2.0–2.9 | 100, low | 14, high |
| Kinnard Bridge (15) | 120–124 | 2.0–2.9 | 99, low | 12, high |
| Genelle (22) | 115–119 | 2.0–2.9 | 20, high | 0, high |
| Rivervale-Trail (38) | 115–119 | 2.0–2.9 | - | - |
| Upstream Waneta (50) | 115–119 | 2.0–2.9 | - | - |

*Note.* The compensation depth-bin value indicates the minimum depth-bin interval occurrence required for compensation at that location. Locations denoted with * indicate that the 110% threshold was not exceeded and were assigned a low risk level regardless of compensation %. If the TDG level exceeded 110% at a location, risk was categorized according to cumulative depth compensation whereby 0%–25% was considered as high exposure risk, 26%–50% as of-concern, 51%–75% as moderate, and 76%–100% as low risk. No telemetry observations were noted at the Rivervale-Trail or Upstream Waneta locations for MW and RT. Within-species Marascuilo pairwise multiple comparisons revealed compensation was statistically different at all locations except MW Norns Creek-Robson Ferry.

### 4.1. Reach and Depth Residency

Fish movement and migration decisions are ultimately made at the individual level (Chapman et al., 2012). Although interesting from a biological perspective, a TDG management approach catered to individual fish movement patterns is not feasible from a hydropower operational perspective. Nevertheless, a greater understanding of movement patterns of fish populations or for specific behaviors (e.g., spawning movements or fish arriving at passage facilities) would allow hydropower managers to better understand how to adjust operations to mitigate TDG exposure. For this reason, the focus was on examining location-based residency patterns independent of individual fish movements. Mountain whitefish can substantially vary in their seasonal movement patterns among systems and within the same population (Baxter, 2002; Ford et al., 1995). In the present study, within-species trends in MW reach residency appeared to be reflective of habitat selection for seasonal spawning, foraging, and refuge movements characteristic of fluvial or fluvial-adfluvial potadromous species (Northcote, 1997). Mountain whitefish reach and depth residency at locations within the Lower Columbia were comparable in winter-spring relative to the other seasons. The timing of MW spawning tends to be population specific, driven largely by temperature (Benjamin et al., 2014) and varies according to altitude and longitude of the system (Boyer et al., 2017; Pettit & Wallace, 1975; Thompson & Davies, 1976; Wydoski, 2001). The main spawning season for MW in the Lower Columbia system, or those close by, occurs between late October and February with a peak in January (Ford et al., 1995; Irvine et al., 2017). Mountain whitefish were most often resident at Norns Creek, Kinnaird Rapids, and the Kootenay confluence areas in the winter, which have been identified as primary and secondary spawning locations in the system (Golder Associates Ltd., 2014). Boyer et al. (2017) found no evidence that MW select for specific depths, water velocity or substrate composition at spawning sites in a Montana river system. This was evident in the fish in this study which showed increased depth residency in winter and spring, but no depth bin preference. In the spring, MW in the present study were largely resident in the same locations as winter, which contrasts with the post-spawning movements of adult MW reported in other systems (Benjamin et al., 2014; Pierce et al., 2012; Thompson & Davies, 1976; Wydoski, 2001). However, these studies were conducted on MW populations in high elevation streams or tributaries where spawning timing is earlier (October/November) than in the Lower Columbia (January/February) (Ford et al., 1995) and overwintering in the spawning habitats in some of these systems may not be possible. Furthermore, these systems have more pronounced differences in upstream-downstream habitat relative to the Lower Columbia system. With the later spawning timing in the Lower Columbia system and the relatively system-wide habitat homogeneity, the sustained winter-spring residency suggests that larger, potentially spawning MW in this study do not undertake post-spawn migrations from the spawning areas. Alternatively, the MW included in this study may have been facultative spawners which did not spawn. Pierce et al. (2012) noted that over 30% of the adult MW showed no migratory spawning movements during the spawning season. Boyer et al. (2017) also noted that a proportion of adult MW remained close to spawning grounds throughout the spawning period. Specimens were not directly monitored to confirm spawning activity, thus it is also possible that MW selected these locations for foraging or overwintering purposes (Northcote, 1997). As movement can be energetically costly relative to residency (Forseth et al., 1999; Morinville & Rasmussen, 2003), environments supporting both spawning and overwintering requirements are likely to be occupied for both purposes as data from the fish in this study suggest.

There was a lack of summer MW reach and depth residency data, thus it was somewhat unclear where MW spent their time in Lower Columbia during the summer season. In other systems, fluvial/fluvial-adfluvial MW migrate to deeper, slower moving areas for foraging (Benjamin et al., 2014; Pettit & Wallace, 1975). Pettit and Wallace (1975) found MW exhibited a high degree of residency in deep pools throughout the summer months. There was an increased residency at sites across the study system in the fall, including in the lower reaches where they were absent in the other seasons. Hence, this may suggest that MW in this study moved to foraging areas in the summer and fall in the downstream reaches of the system, thereby evading detection in the summer. As MW seasonal movement patterns appeared to largely follow that of their key life history activities, a TDG abatement strategy for the Lower Columbia MW should consider seasonal movement patterns to lower exposure risk.

Rainbow trout exhibited consistent residency in the same locations across seasons, as previously demonstrated by BC Hydro long-term monitoring studies where RT exhibited high (50%–75%) site fidelity (Golder Associates Ltd. et al., 2016, 2018). Consistent locational residency made it difficult to discern patterns in RT seasonal movements. However, RT reach residency appeared to follow habitat association patterns reflective of RT ecology. For example, previous research on the Kootenai River in northern Idaho found that RT were positively associated with faster water velocities, shallower depths, and cobble-boulder riverbanks and substrates (Smith et al., 2016). The reach from Kinnaird Bridge upstream to HLK, that accounted for the bulk of the RT residency in this study consists largely of faster water habitats with deep riffle, pool and back eddy areas with varying substrate types. Many of these habitat characteristics align with those reported in Smith et al. (2016), suggesting that areas downstream of HLK to the Kootenay confluence provide habitats sufficient for year-round RT refuge, foraging, and spawning activities.

### 4.2. Risk Assessment

Residency patterns of MW and RT were examined to determine if TDG exposure risk differed according to species and the location of hazardous areas for each species. As predicted, RT exhibited less cumulative depth compensation and were found to be at a greater TDG exposure risk relative to MW. Some species and life stages are more likely than others to experience harmful outcomes from exposure to elevated TDG levels owing to differences in physiology, morphology, or habitat use (Beeman et al., 2003; Fidler & Miller, 1997; Jensen et al., 1986; Weitkamp & Katz, 1980; Weitkamp et al., 2003). Rainbow trout appear to be one of the more susceptible salmonids based on both field and lab studies. In a field study at Bonneville Dam, Backman and Evans (2002) found that adult steelhead rainbow trout and sockeye salmon *O. nerka* had a higher incidence of GBT relative to chinook salmon *O. tshawytscha* despite the latter's exposure to higher TDG levels. In lab experiments, Mesa et al. (2000) reported that juvenile steelhead rainbow trout mortality occurred in shorter timespans than juvenile chinook salmon exposed to the same TDG levels. Dawley and Ebel (1975) also noted that larger steelhead rainbow trout were less tolerant than small chinook salmon to elevated TDG levels.

The TDG risk in the spring season varied by location for each species within the Lower Columbia. Upstream of the Kootenay confluence to HLK, the TDG levels fell within the 110% guidelines, and despite RT and MW lacking complete depth compensation at these locations the risk of GBT occurrence was considered low, in part because degassing occurs throughout this reach (Kamal et al., 2019) and deeper refugia habitat are available year-round. Previous research has found that TDG levels <110% are generally not lethal for salmonids even when they are lacking complete depth compensation (Antcliffe et al., 2002; Ryan et al., 2000; Weitkamp et al., 2003). Downstream of the Kootenay confluence to the United States border had TDG levels that posed greater risk to fish in the Lower Columbia. The highest TDG levels exceeding the 110% guideline (120%–124% in the present study) are associated with mortality and other harmful effects when fish are not fully depth compensated and exposed for extended periods (Pleizier, Algera, et al., 2020; Pleizier, Nelson, et al., 2020). In lab experiments, Mesa et al. (2000) reported that 20% of steelhead rainbow trout died ($LT_{20}$) within 25–30 hr exposure to 120% TDG and within 5–7 hr at 130% when lacking depth compensation. However, previous field studies in other hydropower impounded systems have found most fish to be depth compensated during TDG exposure. Weitkamp et al. (2003) reported minimal GBT symptoms in salmonids and non-salmonids exposed to 120%–130% because fish were sufficiently depth compensated. Studies on the Columbia River in the United States that tracked depth use of migrating rainbow trout and chinook salmon in relation to modeled TDG levels found that they used water depths sufficient for full depth compensation (Johnson et al., 2005, 2007, 2010). The high risk areas in the Lower Columbia have sufficient habitat available for full depth compensation, but the risk assessment results in the present study indicated that MW and RT occurrence in those deeper waters is relatively low.

The TDG risk for the BRD/HLK operational regime in the present study appeared to be divided into two zones—upstream and downstream of the Kootenay confluence. The timing of freshet in the Kootenay and Columbia systems differs, with freshet in the Kootenay occurring in the spring and freshet flows in the Columbia occurring in the summer. Accordingly, exposure patterns to elevated TDG can differ upstream and downstream of the confluence. The fish seasonal residency results generally followed this same pattern, suggesting that the Kootenay confluence may be a transition zone in the Lower Columbia and that RT and MW follow known zonation (i.e., ranges within the longitudinal section of the river) and habitat association patterns in the region (Smith et al., 2016). Dividing a watercourse into zones according to habitat associations and the functional guilds of the fish assemblage (i.e., fish zonation) may be an effective tool for managing TDG risk outcomes. Using fish zonation for avoiding or mitigating the negative effects of fish exposure to elevated TDG levels is not common, but similar frameworks exist for other hydropower management outcomes. For example, European regulators and environmental managers have explored using a fish zonation approach to assess the ecological status of rivers and to support decision making for restoring river connectivity for diadromous and potadromous fishes (Breve et al., 2014; Lasne et al., 2007). There, fish assemblages were categorized into ecological fish guilds to identify their sensitivities and habitat requirements, then fish zonation (via spatial analyses) was used to identify the most disruptive connectivity barriers for the fish guilds. Other European fish-based assessment methods used a combination of environmental data, ecological guilds, reference sites, impact sites, and spatial based modeling to assess the human disturbance of rivers (Schmutz et al., 2007; Virbickas & Kesminas, 2007). These fish zonation and other fish-based methods have broad applicability and could likely be scaled for facility level operations such as TDG management strategies.

## 5. Management Implications

The telemetry and risk assessment results indicated that TDG exposure risk depends on the interplay between species ecologies and the patterns of TDG generated by the hydropower facilities. While the risk assessment results indicated that RT were at a higher TDG exposure risk relative to MW, the high habitat suitability reaches near hydropower facilities are likely to pose an increased risk for both species if higher TDG water is unavoidable. Given that spring is the high flow season, the risk assessment results reported here probably represent a worst-case scenario for the operational regimes used in this study. Risk levels would likely change under other operational regimes, such as high-water years where the duration of spill operations are extended. The ecological and TDG patterns suggested that system-specific studies, in combination with further field-based studies into TDG biological responses will be necessary if detailed TDG exposure predictions are required for decision-making. In the interim, hydropower operators should focus on reducing the frequency and duration of operations that generate high TDG and be particularly diligent when rivers have limited refugia in which fish can TDG compensate.

**Acknowledgments**

The authors thank M. Marrello of Terraquatic Resource Management, D. Ford, C. King and other staff at Golder Associates, and R. Zavaduk and others in the West Kootenay Fly Fishing club for their assistance with fish collections. The authors acknowledge L. Masson for help with fish telemetry data collation for the Columbia-Kootenay system and E. Ledee and B. Hlina for their help with telemetry data analysis. This project was funded by a Natural Sciences and Engineering Research Council Collaborative Research and Development grant to Colin J. Brauner, David Z. Zhu, Michael Power, and Steven J. Cooke in partnership with BC Hydro. Dirk A. Algera, Taylor D. Ward, and Naomi K. Pleizier were supported by an NSERC Post-Graduate Scholarship. Fish were collected under permits CB16-237424 and CB17-280969 issued by the British Columbia Ministry of Forests, Lands, and Natural Resource Operations. Handling and surgical procedures performed during this study were conducted in accordance with the Canadian Council of Animal Care regulations as administered by Carleton University under protocol 110723. We thank two referees for thoughtful comments on our manuscript.

## Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

## Data Availability Statement

The data and data analysis code (R scripts) used in the creation of this manuscript are freely available via the Carleton University Dataverse (Algera, 2021). The software and *R* functions used in the data and statistical analyses are cited in Section 2.

## References

Algera, D. (2021). Replication data for: TDG biotelemetry project [Dataset]. https://doi.org/10.5683/SP3/NHS9WE

Antcliffe, B. L., Fidler, L. E., & Birtwell, I. K. (2002). Effect of dissolved gas supersaturation on the survival and condition of Juvenile Rainbow Trout (Oncorhynchus mykiss) under static and dynamic exposure scenarios. *Canadian Technical Report of Fisheries and aquatic Sciences 2370, Fisheries and oceans Canada, Ottawa, Ontario, Canada*.

Bachman, R. A. (1984). Foraging behavior of free-ranging wild and hatchery brown trout in a stream. *Transactions of the American Fisheries Society*, *113*, 1–32. https://doi.org/10.1577/1548-8659(1984)113<1:fbofwa>2.0.co;2

Backman, T. W. H., & Evans, A. F. (2002). Gas bubble trauma in adult salmonids in the Columbia River Basin. *North American Journal of Fisheries Management*, *22*(2), 579–584. https://doi.org/10.1577/1548-8675(2002)022<0579:gbtiia>2.0.co;2

Baxter, C. V. (2002). *Fish movement and assemblage dynamics in a Pacific Northwest riverscape*. (Ph.D. dissertation). Oregon State University.

Beeman, J. W., Venditti, D. A., Morris, R. G., Gadomski, D. M., Adams, B. J., Vanderkooi, S. P., et al. (2003). Gas bubble disease in resident fish below Grand Coulee Dam. *Final report of research. Western fisheries Research Center*. Columbia River Research Laboratory, USGS.

Benjamin, J. R., Wetzel, L. A., Martens, K. D., Larsen, K., & Connolly, P. J. (2014). Spatio-temporal variability in movement, age, and growth of mountain whitefish (Prosopium williamsoni) in a river network based upon PIT tagging and otolith chemistry. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*(1), 131–140. https://doi.org/10.1139/cjfas-2013-0279

Bouck, G. R. (1980). Etiology of gas bubble disease. *Transactions of the American Fisheries Society*, *109*(6), 703–707. https://doi.org/10.1577/1548-8659(1980)109<703:eogbd>2.0.co;2

Boyer, J. K., Guy, C. S., Webb, M. A. H., Horton, T. B., & McMahon, T. E. (2017). Reproductive ecology, spawning behaviour, and juvenile distribution of Mountain Whitefish in the Madison River, Montana. *Transactions of the American Fisheries Society*, *146*(5), 939–954. https://doi.org/10.1080/00028487.2017.1313778

Breve, N. W., Buijse, A. D., Kroes, M. J., Wanningen, H., & Vriese, F. T. (2014). Supporting decision-making for improving longitudinal connectivity for diadromous and potadromous fishes in complex catchments. *The Science of the Total Environment*, *496*, 206–218. https://doi.org/10.1016/j.scitotenv.2014.07.043

Bridcut, E. E., & Giller, P. S. (1993). Movement and site fidelity in young Brown trout Salmo trutta populations in a southern Irish stream. *Journal of Fish Biology*, *43*(6), 889–899. https://doi.org/10.1111/j.1095-8649.1993.tb01163.x

Brown, R. S., Cooke, S. J., Anderson, W. G., & McKinley, R. S. (1999). Evidence to challenge the "2% Rule" for biotelemetry. *North American Journal of Fisheries Management*, *19*(3), 867–871. https://doi.org/10.1577/1548-8675(1999)019<0867:etctrf>2.0.co;2

Cao, L., Li, Y., An, R., Wang, Y., Li, K., & Buchmann, K. (2019). Effects of water depth on GBD associated with total dissolved gas supersaturation in Chinese sucker (Myxocyprinus asiaticus) in upper Yangtze River. *Scientific Reports*, *9*(1), 6828. https://doi.org/10.1038/s41598-019-42971-8

Chapman, B. B., Skov, C., Hulthen, K., Brodersen, J., Nilsson, P. A., Hansson, L.-A., & Bronmark, C. (2012). Partial migration in fishes: Definitions, methodologies and taxonomic distribution. *Journal of Fish Biology*, *81*(2), 479–499. https://doi.org/10.1111/j.1095-8649.2012.03349.x

Dawley, E. M., & Ebel, W. J. (1975). Effects of various concentrations of dissolved atmospheric gas on juvenile chinook salmon and steelhead trout. *Fisheries Bulletin*, *73*, 787–796.

Dawley, E. M., Schiewe, M., & Monk, B. (1976). Effects of long term exposure to supersaturation of dissolved atmospheric gases on juvenile chinook salmon and steelhead trout in deep and shallow test tanks. In D. H. Fickeisen, & J. Schneider (Eds.), *Gas bubble disease*, *Technical information center* (pp. 1–20). Office of Public Affairs Energy Research and Development Administration.

Deng, Y., Cao, C., Liu, X., Yuan, Q., Feng, C., Shi, H., et al. (2020). Effect of total dissolved gas supersaturation on the survival of Bighead Carp (Hypophthalmichthys Nobilis). *Animals*, *10*(1), 166. https://doi.org/10.3390/ani10010166

Fidler, L. E. (2003). *TGP performance measures for the Columbia River WUP. A brief summary. Prepared for BC Hydro, Castlegar, B.C.* Retrieved from http://criemp.org/pdfs/tgp_performance-measures.pdf. Accessed 20 March 2021.

Fidler, L. E., & Miller, S. B. (1994). *British Columbia water quality guidelines for dissolved gas supersaturation*. Prepared for: BC Ministry of Environment, Canada Department of Fisheries and Oceans, and Environment Canada. Retrieved from https://www2.gov.bc.ca/gov/content/environment/air-land-water/water/water-quality/water-quality-guidelines/approved-water-quality-guidelines. Accessed 08 March 2021.

Fidler, L. E., & Miller, S. B. (1997). *British Columbia water quality guidelines for the protection of aquatic biota from dissolved gas supersaturation—technical report*. Aspen Applied Sciences Limited report to the BC Ministry of Environment, Lands and Parks, Environment Canada, Department of Fisheries and Oceans.

Ford, B. S., Higgins, P. S., Lewis, A. F., Cooper, K. L., Watson, T. A., Gee, C. M., et al. (1995). *Literature reviews of the Life History, Habitat Requirements and Mitigation/compensation Strategies for Thirteen Sport Fish Species in the Peace, Liard and Columbia River Drainages of British Columbia* (Vol. 2321, p. xxiv+342). Canadian Manuscript Report of the Fisheries and Aquatic Sciences.

Forseth, T., Nasje, T. F., Jonsson, B., & Harsaker, K. (1999). Juvenile migration in brown trout: A consequence of energetic state. *Journal of Animal Ecology*, *68*(4), 783–793. https://doi.org/10.1046/j.1365-2656.1999.00329.x

Golder Associates Ltd. (2014). *Lower Columbia River whitefish life history and egg Mat monitoring program: Year 5 interpretive Report*. Report prepared for BC Hydro, Castlegar, BC Golder (Report No. 11-1492-0111F). 102 p. + 5 app.

Golder Associates Ltd., & Okanagan Nation Alliance, and Poisson Consulting Ltd. (2016). *CLBMON-45 Lower Columbia River Fish Population Indexing Survey 2015 Report. Report prepared for BC Hydro Generation, Water License Requirements*. 75 pages + 8 app.

Golder Associates Ltd., & Okanagan Nation Alliance, and Poisson Consulting Ltd. (2018). *CLBMON-45 Lower Columbia River Fish Population Indexing Survey 2017 Report. Report prepared for BC Hydro Generation, Water License Requirements*. 70 pages + 8 app.

Gunnarsson, G. S., & Steingrímsson, S. O. (2011). Contrasting patterns of territoriality and foraging mode in two stream-dwelling salmonids, Arctic char (Salvelinus alpinus) and Brown trout (Salmo trutta). *Canadian Journal of Fisheries and Aquatic Sciences*, *68*(12), 2090–2100. https://doi.org/10.1139/f2011-127

Irvine, R. L., Thorley, J. L., & Porto, L. (2017). When do mountain whitefish (Prosopium williamsoni) spawn? A comparison of estimates based on gonadosomatic indices and spawner and egg counts. *The Open Fish Science Journal*, *10*(1), 12–22. https://doi.org/10.2174/1874401x01710010012

Jensen, J. O. T., Schnute, J., & Alderdice, D. F. (1986). Assessing juvenile salmonids response to gas supersaturation using a general multivariate dose—Response model. *Canadian Journal of Fisheries and Aquatic Science*, *43*(9), 1694–1709. https://doi.org/10.1139/f86-213

Ji, Q., Li, K., Wang, Y., Liang, R., Feng, J., Yuan, Q., et al. (2021). Total dissolved gases induced tolerance and avoidance behaviors in pelagic fish in the Yangtze River, China. *Ecotoxicology and Environmental Safety*, *216*, 112218. https://doi.org/10.1016/j.ecoenv.2021.112218

Ji, Q., Xue, S., Yuan, Q., Yuan, Y., Wang, Y., Liang, R., et al. (2019). The tolerance characteristics of resident fish in the Upper Yangtze River under varying gas supersaturation. *International Journal of Environmental Research and Public Health*, *16*(11), 2021. https://doi.org/10.3390/ijerph16112021

Johnson, E. L., Clabough, T. S., Bennett, D. H., Bjornn, T. C., Peery, C. A., Caudill, C. C., & Stuehrenberg, L. C. (2005). Migration depths of adult spring and summer chinook salmon in the lower Columbia and Snake Rivers in relation to dissolved gas supersaturation. *Transactions of the American Fisheries Society*, *134*(5), 1213–1227. https://doi.org/10.1577/t04-116.1

Johnson, E. L., Clabough, T. S., Caudill, C. C., Keefer, M. L., Peery, C. A., & Richmond, M. C. (2010). Migration depths of adult steelhead Oncorhynchus mykiss in relation to dissolved gas supersaturation in a regulated river system. *Journal of Fish Biology*, *76*(6), 1520–1528. https://doi.org/10.1111/j.1095-8649.2010.02578.x

Johnson, E. L., Clabough, T. S., Perry, C. A., Bennett, D. H., Bjornn, T. C., Caudill, C. C., & Keefer, M. L. (2007). Estimating adult Chinook Salmon exposure to dissolved gas supersaturation downstream of hydroelectric dams using telemetry and hydrodynamic models. *River Research and Applications*, *23*(9), 963–978. https://doi.org/10.1002/rra.1019

Kamal, R., Zhu, D. Z., Crossman, J. A., & Leake, A. (2020). Case study of total dissolved gas transfer and degasification in a prototype ski-jump spillway. *ASCE Journal of Hydraulic Engineering*, *146*(9), 05020007. https://doi.org/10.1061/(asce)hy.1943-7900.0001801

Kamal, R., Zhu, D. Z., Crossman, J. A., & Leake, A. (2021). A system model for total dissolved gas risk assessment due to multidam spill operations. *Journal of Water Resources Planning and Management*, *147*(12), 04021086. https://doi.org/10.1061/(asce)wr.1943-5452.0001487

Kamal, R., Zhu, D. Z., Leake, A., & Crossman, J. A. (2019). Dissipation of supersaturated total dissolved gases in the intermediate mixing zone of a regulated river. *ASCE Journal of Environmental Engineering*, *145*(2), 04018135. https://doi.org/10.1061/(asce)ee.1943-7870.0001477

Kessel, S. T., Hussey, N. E., Crawford, R. E., Yurkowski, D. J., O'Neill, C. V., & Fisk, A. T. (2016). Distinct patterns of Arctic cod (Boreogadus saida) presence and absence in a shallow high Arctic embayment, revealed across open-water and ice-covered periods through acoustic telemetry. *Polar Biology*, *39*(6), 1057–1068. https://doi.org/10.1007/s00300-015-1723-y

Lasne, E., Berngerot, B., Lek, S., & Lafaille, P. (2007). Fish zonation and indicator species for the evaluation of the ecological status of rivers: Example of the Loire Basin (France). *River Research and Applications*, *23*(8), 1–14. https://doi.org/10.1002/rra.1030

Length, R., Buerkner, P., Herve, M., Love, J., Riebl, H., & Singmann, H. (2020). *Estimated Marginal means, aka Least-Squares means* version 1.5.2-1.

Lund, M., & Heggberget, T. G. (1985). Avoidance response of two-year-old rainbow trout, Salmo gairdneri Richardson, to air-supersaturated water: Hydrostatic compensation. *Journal of Fish Biology*, *26*(2), 193–200. https://doi.org/10.1111/j.1095-8649.1985.tb04256.x

Ma, Q., Li, R., Feng, J., Lu, J., & Zhou, Q. (2018). Cumulative effects of cascade hydropower stations on total dissolved gas supersaturation. *Environmental Science and Pollution Research*, *25*(14), 13536–13547. https://doi.org/10.1007/s11356-018-1496-2

Magnusson, A., Skaug, H., Anders, N. A., Berg, C., Kristensen, K., Martin, M. M., et al. (2020). *Generalized Linear mixed models using Template model builder* version 1.0.2.1.

McGrath, K. E., Dawley, E. M., & Geist, D. R. (2006). *Total dissolved gas effects on fishes of the Lower Columbia River. Final Report* (p. 46). Prepared for U.S. Army Corps of Engineers. Contract DE-AC05-76RL01830.

Mesa, M. G., Weiland, L. K., & Maule, A. G. (2000). Progression and severity of gas bubble trauma in juvenile salmonids. *Transactions of the American Fisheries Society*, *129*(1), 174–185. https://doi.org/10.1577/1548-8659(2000)129<0174:pasogb>2.0.co;2

Millard, S. P., & Kowarik, A. (2020). *EnvStats: Package for environmental statistics, including US EPA guidance*.version 2.4.0.

Morinville, G. R., & Rasmussen, J. B. (2003). Early juvenile bioenergetic differences between anadromous and resident brook trout (Salvelinus fontinalis). *Canadian Journal of Fisheries and Aquatic Sciences*, *60*(4), 401–410. https://doi.org/10.1139/f03-036

Nagrodski, A., Raby, G. D., Hasler, C. T., Taylor, M. K., & Cooke, S. J. (2012). Fish stranding in freshwater systems: Sources, consequences, and mitigation. *Journal of Environmental Management*, *103*, 133–141. https://doi.org/10.1016/j.jenvman.2012.03.007

Northcote, T. G. (1997). Potamodromy in Salmonidae—Living and moving in the fast lane. *North American Journal of Fisheries Management*, *17*(4), 1029–1045. https://doi.org/10.1577/1548-8675(1997)017<1029:pisami>2.3.co;2

Papastamatiou, Y. P., Itano, D. G., Dale, J. J., Meyer, C. G., & Holland, K. N. (2010). Site fidelity and movements of sharks associated with ocean-farming cages in Hawaii. *Marine and Freshwater Research*, *61*(12), 1366–1375. https://doi.org/10.1071/mf10056

Pert, E. J., & Erman, D. C. (1994). Habitat use by adult rainbow trout under moderate artificial fluctuations in flow. *Transactions of the American Fisheries Society*, *123*(6), 913–923. https://doi.org/10.1577/1548-8659(1994)123<0913:hubart>2.3.co;2

Pettit, S. W., & Wallace, R. L. (1975). Age, growth, and movement of mountain whitefish, Prosopium willamsoni (Girard), in the North Fork Clearwater river, Idaho. *Transactions of the American Fisheries Society*, *104*(1), 68–76. https://doi.org/10.1577/1548-8659(1975)104<68:agamom>2.0.co;2

Pierce, R., Davidson, M., & Podner, C. (2012). Spawning behavior of mountain whitefish and cooccurrence of Myxobolus cerebralis in the Blackfoot river Basin, Montana. *Transactions of the American Fisheries Society*, *141*(3), 720–730. https://doi.org/10.1080/00028487.2012.675900

Pincock, D. H. (2012). *Application Note. False detections: What they are and how to remove them from detection data*. Document #: DOC-004691 Version 03.

Pleizier, N. K., Algera, D., Cooke, S. J., & Brauner, C. J. (2020). A meta-analysis of gas bubble trauma in fish. *Fish and Fisheries*, *21*(6), 1175–1194. https://doi.org/10.1111/faf.12496

Pleizier, N. K., Nelson, C., Cooke, S. J., & Brauner, C. J. (2020). Understanding gas bubble trauma in an era of hydropower expansion: How do fish compensate at depth? *Canadian Journal of Fish and Aquatic Sciences*, *77*(3), 556–563. https://doi.org/10.1139/cjfas-2019-0243

Pleizier, N. K., Rost-Komiya, B., Cooke, S. J., & Brauner, C. J. (2021). The lack of avoidance of total dissolved gas supersaturation in juvenile rainbow trout. *Hydrobiologia*, *848*(20), 4837–4850. https://doi.org/10.1007/s10750-021-04676-w

Qu, L., Li, R., Li, J., Li, K., & Deng, Y. (2011). Field observation of total dissolved gas supersaturation of high-dams. *Science China Technological Sciences*, *54*(1), 156–162. https://doi.org/10.1007/s11431-010-4217-8

Rogers, K. B., Bergsted, L. C., & Bergersen, E. P. (1996). Standard weight equation for mountain whitefish. *North American Journal of Fisheries Management*, *16*(1), 207–209. https://doi.org/10.1577/1548-8675(1996)016<0207:mbswef>2.3.co;2

Ryan, B. A., Dawley, E. M., & Nelson, R. A. (2000). Modeling the effects of supersaturated dissolved gas on resident aquatic biota in the man-stem Snake and Columbia rivers. *North American Journal of Fisheries Management*, *20*(1), 192–204. https://doi.org/10.1577/1548-8675(2000)020<0192:mteosd>2.0.co;2

Schmutz, S., Cowx, I. G., Haidvogl, G., & Pont, D. (2007). Fish-based methods for assessing European running waters: A synthesis. *Fisheries Management and Ecology*, *14*(6), 369–380. https://doi.org/10.1111/j.1365-2400.2007.00585.x

Simpkins, D. G., & Hubert, W. A. (1996). Proposed revision of the standard-weight equation for rainbow trout. *Journal of Freshwater Ecology*, *11*(3), 319–325. https://doi.org/10.1080/02705060.1996.9664454

Smith, C. D., Quist, M. C., & Hardy, R. S. (2016). Fish assemblage structure and habitat associations in a large wester river system. *River Research and Applications*, *32*(4), 622–638. https://doi.org/10.1002/rra.2877

Stevens, D. G., Nebeker, A. V., & Baker, R. J. (1980). Avoidance responses of salmon and trout to air-supersaturated water. *Transactions of the American Fisheries Society*, *109*(6), 751–754. https://doi.org/10.1577/1548-8659(1980)109<751:arosat>2.0.co;2

Thompson, G. E., & Davies, R. W. (1976). Observations on the age, growth, reproduction, and feeding of Mountain Whitefish (Prosopium Williamsoni) in the Sheep River, Alberta. *Transaction of the American Fisheries Society*, *105*, 208–219.

Travnichek, V. H., Bain, M. B., & Maceina, M. J. (1995). Recovery of a warmwater fish assemblage after the initiation of a minimum-flow release downstream from a hydroelectric dam. *Transactions of the American Fisheries Society*, *124*(6), 836–844. https://doi.org/10.1577/1548-8659(1995)124<0836:roawfa>2.3.co;2

Urban, A. L., Gulliver, J. S., & Johnson, D. W. (2008). Modeling total dissolved gas concentrations downstream of spillways. *Journal of Hydraulic Engineering*, *134*(5), 550–561. https://doi.org/10.1061/(asce)0733-9429(2008)134:5(550)

Virbickas, T., & Kesminas, V. (2007). Development of fish-based assessment method for the ecological status of rivers in the Baltic region. *Fisheries Management and Ecology*, *14*(6), 531–539. https://doi.org/10.1111/j.1365-2400.2007.00572.x

Wagh, S. T., & Razvi, N. A. (2016). Marascuilo method of multiple comparisons (an analytical study of caesarean section delivery). *International Journal of Contemporary Medical Research*, *3*, 1137–1140.

Wang, Y., Li, K., Li, J., Li, R., & Deng, Y. (2015). Tolerance and avoidance characteristics of Prenant's Schizothoracin Schizothorax prenanti to total dissolved gas supersaturated water. *North American Journal of Fisheries Management*, *35*(4), 827–834. https://doi.org/10.1080/02755947.2015.1052160

Wang, Y., Liang, R., Li, K., & Li, R. (2020). Tolerance and avoidance mechanisms of the rare and endemic fish of the upper Yangtze River to total dissolved gas supersaturation by hydropower stations. *River Research and Applications*, *36*(7), 993–1003. https://doi.org/10.1002/rra.3677

Weitkamp, D. E., & Katz, M. (1980). A review of dissolved gas supersaturation literature. *Transactions of the American Fisheries Society*, *109*(6), 659–702. https://doi.org/10.1577/1548-8659(1980)109<659:arodgs>2.0.co;2

Weitkamp, D. E., Sullivan, R. D., Swant, T., & DosSantos, J. (2003). Gas bubble disease in resident fish of the lower Clark Fork river. *Transactions of the American Fisheries Society*, *132*(5), 865–876. https://doi.org/10.1577/t02-026

Wydoski, R. S. (2001). Life history and fecundity of Mountain Whitefish from Utah streams. *Transactions of the American Fisheries Society*, *130*(4), 692–698. https://doi.org/10.1577/1548-8659(2001)130<0692:lhafom>2.0.co;2