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ARTICLE

Characterizing the Flow Regime in Brook Trout Incubation Habitats and Implications for Management in a Hydro-Regulated River

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Abstract

The operation of dams, diversions, and power generation facilities unavoidably influence the ecological function of rivers. We evaluated vertical and horizontal hydraulic gradients and subsequent water temperature changes in the hyporheic zone of a spawning area for Brook Trout *Salvelinus fontinalis* in a managed Lake Superior tributary in Ontario, then conducted a laboratory-based experiment to show the impact of cold shock during incubation on the timing of larval emergence and survival. Upwelling groundwater was observed at the spawning area during the monitoring period (October 28, 2016, to January 11, 2017); hyporheic water temperatures remained above 3.7°C, whereas ambient river temperature above the substrate fell to 1.5°C until water was released from the upstream control dam. After the release event, water level increased by 0.9 m over the spawning area, and within 24 h, vertical and horizontal flow gradients were reversed in the hyporheic zone; downwelling conditions were observed for 30 h between surface and hyporheic water 1.8 m below substrate, and hyporheic water temperature decreased in unison. Hyporheic

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temperatures at shallow inshore sites fell below 1°C for more than 53 h. In the laboratory, applying a worst-case scenario of dam-induced cold shock on Brook Trout redds using historic monitoring records (i.e., <1.0°C for 40 h), we found no appreciable effect on survival and development timing of incubating Brook Trout eggs compared with a control group. Survival from fertilization to hatching was high for both treatment and control groups (>90%) and lower from fertilization to emergence (55%). Overall, our results suggest that standard winter operating procedures on a Lake Superior tributary had little impact on Brook Trout egg survival and development time to hatching and emergence; however, our findings also suggest that staged winter discharges would lessen the reversal of flow in the hyporheic zone and the magnitude of temperature changes experienced at Brook Trout redds.

The Brook Trout Salvelinus fontinalis, endemic to northeastern North America, is a species of socioeconomic and ecological significance (Melstrom et al. 2015; Haxton et al. 2020). Brook Trout populations are in decline across their native range due to many factors, including habitat loss (Haxton et al. 2020) and climate change (Chu et al. 2005). Within the Great Lakes region, particularly in Lake Superior, Brook Trout populations have declined significantly from historic levels, making conservation and rehabilitation efforts a basinwide management priority, including harvest regulation and habitat protection and restoration (Schreiner et al. 2008; Lake Superior Binational Program 2016). Hydroelectric development, which may fragment rivers and alter and impound flows, is also a concern for fish populations (Rosenberg et al. 1997; Renöfält et al. 2010; Haxton et al. 2015) and a potential threat to Brook Trout populations (Schreiner et al. 2008; Kelly et al. 2017). Canada is the fourth largest producer of hydroelectricity in the world. More than 500 hydroelectric structures provide 60% of Canada's total electricity (IHA 2021). In Ontario, 241 dams on 24 river systems produce 50% of the province's hydroelectricity (OPG 2021).

The construction and operation of hydroelectric dams, diversions, and generating facilities is economically important (OPG 2021) but unavoidably influences the ecological function of rivers (Renöfält et al. 2010). Fragmentation and manipulation of water flow in rivers for power generation can alter the physical and chemical characteristics of aquatic habitats, including the hyporheic environments required by fish to maintain suitable incubation environments (Murchie et al. 2008). Interstitial water quality and hyporheic temperature and groundwater flow are directly influenced by the frequency, amplitude, and duration of flow alterations (Malcolm et al. 2004; Arntzen et al. 2006; Casas-Mulet et al. 2015, 2021). For example, water chemistry, temperature, and hyporheic exchange volume were found to fluctuate in response to flow oscillations as much as 15 km downstream of a control dam, where hyporheic exchange penetrates several meters into the substrate (Sawyer et al. 2009). Artificially rising river levels have been shown to reverse groundwater flow at downstream locations and introduce surface water into the riverbank, whereas the recession of river levels increases groundwater

flow potentials in an offshore direction (Curry et al. 1994). In the absence of hydroelectric dam operations, groundwater normally flows through riparian aquifers towards a river, stabilizing water chemistry, temperature, and groundwater flux in the hyporheic zone (Brunke and Gonser 1997; Boulton et al. 1998; Bencala 2000). Filling the knowledge gap, including hyporheic monitoring through various stages of river flow, will allow for the development of minimal-flow models for control structures better suited to the protection of Brook Trout habitat and other ecological processes in porous substrates (Brown and Pasternack 2008).

Brook Trout assess stream depth, substrate type, water velocity, and the presence of discharging groundwater to select spawning habitats for redd construction in the hyporheic zone of rivers (Reiser 1976). In addition, the physical and chemical properties of interstitial water in the hyporheic zone are also important factors in the selection and maintenance of environmental stability at redd sites throughout the incubation period, which is necessary for successful Brook Trout recruitment (Webster and Eiriksdottir 1976; Witzel and MacCrimmon 1983a; Curry and Noakes 1995; Curry et al. 1995). The effects of river regulation and hydropeaking regimes on the hyporheic zone in rivers are important conservation considerations for hydroelectric operations on rivers that support fall-spawning salmonid species (Curry et al. 1994; Curry and Noakes 1995).

Cold shock is a potentially important environmental control on fish performance, survival, and development (Donaldson et al. 2008). In rivers, these shocks may be the result of natural (e.g., rain on snow, ice jams, and ice out) or humancaused (e.g., dam operations) rapid fluctuations in river stage. Groundwater-dependent fishes (like several salmonid species that incubate their eggs in riverbed zones of locally upwelling groundwater) may experience cold shocks when rising flows disrupt baseline groundwater-surface water dynamics. Previous studies have demonstrated increased egg mortality in Brook Trout and other salmonid species resulting from cold shock administered during early incubation periods (i.e., prior to eved stage; Lemoine and Smith 1980; Tang et al. 1987). Cold incubation temperatures may also delay salmonid development timing to egg hatching and larval emergence (Kazakov 1971; McCullough 1999) and cause sublethal

effects, such as induced polyploidy, DNA methylation, and the alteration of gene expression (Lemoine and Smith 1980; Moghadam et al. 2017; Robinson et al. 2019). As such, the particulars of the timing, frequency, and magnitude of cold shock occurrences in nature are all likely very important to incubating fish embryos but are relatively understudied.

The Aguasabon River (Ontario, Canada) contains multiple artificial structures for water diversion, storage, and power generation and supports a recreational fishery that includes Brook Trout. Brook Trout spawning areas downstream from the control dam are potentially impacted by winter flow alterations caused by water releases to the river from an upstream control dam in January of each year. The discharge event temporarily increases flow that results in lower hyporheic temperature conditions (i.e., a decline from approximately 5°C to near 0°C) for the incubation of Brook Trout. Here, we tested the hypotheses that (1) water release from the reservoir was associated with reversal of flow and reduction of temperature in the hyporheic zone (Curry et al. 1994) and that (2) this temperature reduction has a negative impact on Brook Trout incubation duration (i.e., delayed time to egg hatching and larval emergence) and survival. To evaluate these hypotheses, we set out to (1) describe hyporheic flow through the substrate at the Aguasabon River's main Brook Trout spawning location during spawning and incubation periods with normal and with increasing discharge conditions and (2) design a controlled study to expose Brook Trout embryos to cold shock simulating observed maximum thermal changes to spawning redds after water release from the Long Lake reservoir into the Aguasabon River.

METHODS

Study area.—The Aguasabon River flows south from Long Lake in the Thunder Bay District, Ontario, and in its last 609 m drops 63 m at Aguasabon Falls before draining into Lake Superior. In addition to the natural barrier created by the falls, multiple artificial structures for diversion, water storage, and power generation were constructed as part of the Long Lake Diversion Project completed in 1939 (Peet 1978). The diversion was designed in part for transporting logs from the otherwise inaccessible forests around Long Lake. The Kenogami River Control Dam was constructed 16 km north of Long Lake to prevent northward flow and increase water moving through the diversion (Peet 1978). The Long Lake Control Dam (LLCD) was constructed at the south end of Long Lake and controls the southward flow of water through the Aguasabon River as part of the regulation of the Great Lakes water levels and water supply to the Aguasabon Generating Station. Hydroelectricity on the Aguasabon River is produced by regulating streamflow in a winter reservoir system at Long Lake, which involves the storage of water behind the LLCD during high flows (e.g., spring freshet) and controlled or scheduled releases during periods of low flows (e.g., midwinter) to deliver water to generating facilities near the mouth of the river in times of high energy demand (Haxton et al. 2015; Ontario Power Generation, 2017 unpublished report). In the way that it was altered in the past to facilitate the logging industry and is managed today to provide hydroelectricity, Aguasabon River's historic and current management is typical of many major glacial-origin streams in the Great Lakes basin.

There is only one known Brook Trout spawning location in the isolated main channel of the Aguasabon River above the falls and below the LLCD. This site was found by use of radio transmitters implanted in 11 Brook Trout, one of which was tracked at the end of September 2006 to a location in the main channel 1 km south of the Harvey Creek confluence to the west, approximately 20 km north of Terrace Bay, Ontario, and 12 km below the LLCD (Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry, 2016 unpublished report; Figure 1). This fish was observed in the area with other spawning Brook Trout; active redd construction occurred until the end of November. The location of the Brook Trout spawning area is along an artificial gravel bank that was created to allow better passage of timber during log drive operations (Figure 1, see satellite image inset). Water flow at the spawning location is dominated at certain periods by the discharging regime from the LLCD. In previous work, a series of temperature loggers were installed to monitor hyporheic water temperature in the substrate at the spawning location, after 2006. Flow increases during spawning and incubation were found to decrease redd temperature, with unknown consequences for incubating Brook Trout eggs (Figure 2B).

On the Aguasabon River, there are critical flow and reservoir levels that must be maintained above and below the LLCD as part of the commitments made in the water management plan. Currently, flows over the LLCD should not fall less than 5 m³/s for benthic invertebrate protection. However, the current water management plan lacks site-specific advice regarding river regulation and how it affects the vertical and horizontal flow through Brook Trout spawning redds.

Hyporheic-flow monitoring.— Two transects with six piezometers each were installed perpendicular to the shoreline at the spawning site in substrate dominated by sand and gravel and 5 m from a high-water mark near the right river bank (Figure 1). Piezometers were driven directly into the river substrate with a small, manual pile driver. The two transects were labeled north (N) and south (S). Each transect consisted of three piezometer nests: a shoreline nest that would be inundated during high-water conditions and exposed during low conditions (inshore [I]), a nest in deeper water (~6 m offshore) further



FIGURE 1. Location of piezometer transects within the study area along the Aguasabon River, Ontario. The portion of the river with dashed boundaries near the piezometer transects (upper left) is one of several oxbow lakes that formed the river course before straightening occurred for log runs. The arrangement of piezometers in a transect is illustrated in cross section facing upstream in the lower left inset.



FIGURE 2. (A) Brook Trout redd (spawning area) temperature (dashed line) and ambient temperature (gray line) in the Aguasabon River, Ontario, plotted with discharge (solid line) from the Long Lake reservoir in winter 2013 that was used to guide the coldwater exposure experiment and (B) annual midwinter changes in discharge downstream of the Long Lake Control Dam into the Aguasabon River from 2006 to 2007 and corresponding declines in temperature (black triangles) with recovery time (gray squares) to ambient redd temperature. The circle marks the cold treatment with the greatest decrease in temperature and the longest duration of recovery to prerelease temperatures in January 2013. Data are from Ontario Power Generation.

from shore (offshore [O]), and a nest halfway between (middle [M]). Generally, redds have been observed between the areas where the middle and offshore nests were placed. Each nest consisted of a shallow (S; 0.9 m) and deep (D; 1.8 m) piezometer. Hereafter, any individual piezometer is referenced using acronyms that utilize these definitions: for example, "NIS" refers to the piezometer on the north transect, inshore (near the shoreline), and in shallow water. The SMS piezometer data was discarded due to a faulty logger.

Piezometers were cut from 2.5-cm-diameter galvanized steel piping and attached to a stainless steel well screen of

 1.9×15.2 -cm dimension. Each piezometer was equipped with a Solinst EDGE pressure/temperature monitor (Solinst Canada, Georgetown, Ontario) attached to the bottom of the piezometer with aircraft cable. A separate steel rebar was inserted into the river and equipped with a similar data logger (referred to as a river-level station). A barometric pressure and temperature data logger was hung in the nearest tree on shore to the piezometer site. Transit survey equipment was used to relate river level and hydraulic head measurements in piezometers to a common overhead datum.

Vertical and horizontal head gradients.—Hydraulic pressure head at each piezometer was measured at half-

hour intervals; subtracting barometric pressure measured at the same time allowed total pressure above the data loggers to be converted to height of water above the data loggers. Manually employing a Solinst 101 P1 water level meter (Solinist Canada, Georgetown, Ontario) and clock allowed both substrate and river levels to be calibrated to depth below the common datum line. River and hyporheic temperatures were recorded by all data loggers associated with the piezometers, and air temperature was recorded with barometric pressure at half-hour intervals.

Three vertical head gradients (VHGs) were calculated: (1) between the shallow piezometer and the river, (2) between the deep piezometer and the river, and (1) between the deep piezometer and the shallow piezometer. These calculations were repeated for each nest and for both transects. Vertical gradients were measured from the deepest location to the surface water, where positive VHG indicated discharging flux from the substrate to the river. Negative VHG indicated discharging flux from the river to the substrate. Horizontal head gradients (HHGs) were calculated between the shallow and deep piezometers for adjacent nests within the same perpendicular transect (i.e., north nearshore to north middle, and north middle to north offshore). Calculations of VHG and HHG were as follows:

$$Hydraulic gradient = dh/dl,$$
(1)

where dh is the difference in hydraulic head between piezometers and dl is the vertical or horizontal distance between piezometer screens.

Contour mapping the hyporheic zone.— A river cross section at each of the two transects was constructed to estimate the two-dimensional direction of hyporheic flow using SurferV14 software (Golden Software, Golden, Colorado) to map isolines (contour lines of equal potential). Isolines in cross section beneath the substrate were drawn from water elevations measured at the piezometers. Contour maps were created at three specific times: late October during Brook Trout spawning (October 28, 2016), during a period before water release (January 10, 2017), and during the peak water level after the release (January 12, 2017).

Timing of the prolonged cold treatment.— In addition to air and stream temperature, redd temperature was monitored for the period 2006–2016 by burying a single temperature logger (HOBO UA-001-64 Pendant Temperature Data Logger; Onset Computer Corporation, Bourne, Massachusetts) approximately 20 cm below the substrate in the same vicinity of where Brook Trout spawn each year. Flow in the main channel of the Aguasabon River was plotted with redd temperature during the Brook Trout incubation period (October–April) to show declines in temperature together with recovery times to ambient temperature at the redds and to select the worst-case observed scenario to simulate a cold treatment for its effect on Brook Trout incubation (hatching and emergence of alevins). The timing of the cold treatment was early January to generally match the winter water release (from the LLCD) and development stage (eye-up stage) of Brook Trout observed in the Aguasabon River.

Egg incubation experiment.—Egg incubation experiments were conducted at the Dorion Fish Culture Station, operated by the Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry. The station uses water from a spring-fed pond to supply gravity-fed water to a flow-through system for all hatchery operations. Brook Trout eggs were sourced from the Lake Nipigon strain (the broodstock provided by the hatchery), whose origin is a large watershed in northwestern Ontario. Eggs were fertilized using the wet method (i.e., milt mixed with saline solution in a bowl then poured onto eggs and mixed gently), disinfected with ovodine, and water hardened. Eggs from different fish were not pooled together; instead, sperm from only one male and eggs from only one female were mixed. This individual exposure of both eggs and sperm was repeated 12 times, from 12 different pairs of fish (gametes), such that each "family" was considered a replicate treatment and each combination was incubated in an individual hatching box.

The experimental apparatus (i.e., hatching boxes) was placed on aluminum stands inside an empty rearing unit in one of the station's isolation rooms. A power analysis was used to determine the number of replicates needed to detect a 1.5% difference in survival. Twelve replicates (i.e., families, each in separate incubation boxes) were used for both the control and treatment groups. Each box measured $21.5 \times 21.5 \times 13.6$ cm and contained an insert box $(20.5 \times 15.7 \times 10.5 \text{ cm})$. Both boxes were constructed from polyvinyl chloride (PVC). The insert box had a wire mesh screen bottom where the eggs were placed to incubate. This allows the water to flow through the eggs, simulating natural stream conditions. The boxes were covered with lids to maintain dark conditions throughout the entire incubation period. The inflow was extended with a 7.62cm-diameter pipe constructed from acrylonitrile butadiene styrene (ABS) to attach the main water supply line with the main header pipe for the incubation system. Each box had its own 1.27-cm PVC ball valve that allowed the flow to each individual incubation box to be controlled from the main header line. The flow of unfiltered pond water originated from the main pipe and was then split to each replicate box using these valves. Water entered the incubation box, flowed up through the screened portion housing the eggs, and flowed out of the box through a standpipe. Water flow into the main header line was controlled by a 10.16-cm ABS valve. The main header line then emptied into a large garbage pail that sat on the floor between the

upper and lower incubation levels. A second main header line made with ABS pipe was fitted to the garbage pail with 12 valves and pipes connecting to the 12 treatment incubation boxes on the lower level. Water flow through each box was maintained at 1.5-2.0 L/min, measured by holding a 1-L container under the outflow and recording time with a stopwatch. Adjustments to flow were made as needed.Eggs from each mating event were split, with half going to a control replicate and half to a treatment replicate, to create 12 equal box pairs with eggs from the same broodstock (male and female). Once fertilization and water hardening were complete, eggs were placed into their respective incubation boxes on the same day. Each box replicate held 85 eggs, a manageable number to permit the determination of the fate of each individual egg every few days. For the experiment, the total number of control (n = 1.020) and treatment (n = 1.020) eggs that were in incubation was identical. Incoming water temperatures were monitored by the Dorion Fish Culture Station and fluctuated naturally with weather at the head pond source. The main header line temperature to the 12 lower incubation boxes was reduced during the cold treatment to $<1.0^{\circ}$ C by inserting ice blocks (frozen hatchery water) continuously into the large plastic pail thereby decreasing the supply temperature. Therefore, over this 40-h period, the eggs supplied by the upper-level header pipe maintained normal incubating temperatures, while the lower boxes had their temperature reduced to <1.0°C. After completing the 40-h experiment, the environment for the incubating eggs in the treatment boxes was allowed to return to station water temperature. The water temperature during cold treatment was logged using two temperature loggers (Onset HOBO UA-001-64 Pendant Temperature Data Logger; Onset Computer Corporation, Bourne, Massachusetts) at the beginning of each main header pipe to the control and treatment incubation boxes. These loggers were in place from December 20, 2016 to January 24, 2017.

Estimating and comparing hatching and emergence.-Incubation boxes were examined three times weekly to count and remove dead eggs until hatching. Once the eggs reached the eyed-up stage, they were briefly removed to clean the incubation boxes. No egg mortality was observed during this step. Once hatching began, daily observations were made to record the number and timing of hatched alevins. After hatching, the newly hatched alevins were allowed to develop for 3.5 weeks. Boxes were checked two to three times per week to remove dead alevins. After 3.5 weeks, alevins were placed in a PVC ring in the center of their box and buried in 3 cm of aquarium gravel. Alevins were then counted and moved to larger rearing tanks as they emerged. Alevins were considered to have emerged when they were swimming in the box, resting on the gravel surface, or entering into gravel headfirst. After 3 d of no additional emergence, monitoring was ended and all nonemergent cases were recorded as mortalities.

The calculation of trends in hatching of eggs and emergence of alevins to incorporate mortality at any time in both stages used the approach of failure-time analysis, very common in wildlife studies where some data are censored (Pollock et al. 1989). Kaplan-Meier estimators were used to censor the cases of mortality and separately model hatching and alevin emergence for the control and treatment boxes, combining counts from all broodstock replicates. Mean time to hatching and mean time to emergence was calculated as the inflection point for each curve. Kaplan-Meier models were then applied the same way to all the eggs from each broodstock pair, combining counts from control and treatment boxes. Times to hatching and emergence were converted into growing degree-days (GDDs) to examine the accumulated temperature unit differences between control and treatment, using a base temperature of 0°C applied to the incoming water temperature at the hatchery.

To determine differences between cold treatment and controls, mortality counts and counts of nonemergence of alevins at the end of the monitoring were compared with paired *t*-tests. Tests were one-tailed, with the expectation that cold treatment would result in higher mortality and nonemergence. Time to hatching was also compared between the pooled treatment and pooled control boxes using a log-rank test based on the χ^2 distribution. Statistical analysis was conducted using SPSS Statistics for Windows, version 22.0 (IBM, Armonk, New York).

RESULTS

Water Release Effects on Hyporheic Flow Conditions

Monitoring began on October 28, 2016, and ended January 13, 2017, when ice flows disturbed the piezometers. From the period of October 28, 2016, to January 10, 2017, no discharge events occurred from the Long Lake reservoir (Figure 2A); the average estimated mean daily discharge at the spawning site was 17.0 m³/s and ranged from 11.7 m³/s (November 16, 2016) to 25.1 m³/s (November 30, 2016). On January 11, 2017, water was released from the Long Lake reservoir, resulting in a substantial increase in flow for the Aguasabon River. The day prior to water release, daily discharge at the spawning area was estimated at 20.0 m³/s and increased to 67.0 m³/s on January 13, 2017, a change that encompassed minimum to maximum flow conditions for the 2016-2017 winter season. This translated to a 0.9-m increase in river depth over the spawning redds in less than 24 h. On January 11, 2017, water release from the reservoir upstream of the spawning site increased discharge from 18 to $68 \text{ m}^3/\text{s}$.

In both river transects, VHG remained positive (water discharging from the substrate to the river) for the spawning and incubation periods before the water release event occurred (Table 1; Figure 3A–D). When river levels rose on January 11, 2017, all VHGs declined into negative values (net flow of stream water into the substrate) on both transects. The VHG remained negative for a range of 5 to 30 h following water release (Table 1). Negative VHG only occurred during and after water release at the LLCD (Figure 3E, F).

All HHGs measured between nests in the north and south transects remained positive for the entire incubation period before water release. As river levels rose on January 11, 2017, HHGs declined into negative values, indicating flow changes to the opposite horizontal direction, towards the shoreline (Table 2). The exception was the SOS-SMS pair, where HHG began to gradually decline at the time of water release but did not reach negative values during the sampling period (Table 2). The HHGs remained negative for a range of 22 to 50 h (Table 2). The HHG between piezometers NOD and NMD took 10 h longer to reach negative values after water release relative to the other piezometers and did not return to positive values during the sampling period. As was the case for VHG and vertical flux, the LLCD water release was the only factor likely to have altered the horizontal flow through the substrate at the spawning area during the

period of observation. During the spawning season, the overall direction of water flow in the hyporheic zone was directed upwards to the river for both north and south transects (Figure 3A–D). Tight contours around the shallow piezometers in the offshore nests display stronger horizontal movement directed inshore. Similarly, contours surrounding the inshore piezometers indicated flow in an offshore direction. Contour maps after water release of both transects display downward vertical flow of stream water into the river substrate. During both high- and low-water conditions, direction of water flow was predominantly vertical (Figure 3E, F).

At the start of the monitoring period, the average daily temperature of water in all 11 piezometers was >6.0°C on October 28, 2016, while temperature of water measured in the river-level logger just above the substrate over the spawning area was 7.4°C (Table 3). Groundwater temperatures in all piezometers declined slowly from October to January but did not exhibit the diel fluctuations typical of ambient stream water above the river substrate. All groundwater temperatures remained above 3.7° C before the water release event. River temperature exhibited sharp diel fluctuations similarly to air temperature and reached a lowest temperatures then declined during the water release event and were impacted for periods that differed based on the position and depth of the piezometer

| | | | V | | | |
|----------|----------|---------------|----------------|---------------|------------|--------------|
| Transect | Nest | Piezometer | Before release | After release | Difference | Duration (h) |
| North | Inshore | Shallow-river | 0.0532 | -0.0376 | 0.0908 | 14 |
| | | Deep-river | 0.0433 | -0.0391 | 0.0825 | 16 |
| | | Deep-shallow | 0.0336 | -0.0411 | 0.0747 | 20 |
| | Middle | Shallow-river | 0.0994 | -0.0652 | 0.1640 | 18 |
| | | Deep-river | 0.0602 | -0.0454 | 0.1050 | 19 |
| | | Deep-shallow | 0.0245 | -0.0284 | 0.0529 | 21 |
| | Offshore | Shallow-river | 0.0861 | -0.0970 | 0.1830 | 20 |
| | | Deep-river | 0.0530 | -0.0523 | 0.1050 | 19 |
| | | Deep-shallow | 0.0156 | -0.0017 | 0.0173 | 5 |
| South | Inshore | Shallow-river | 0.0351 | -0.0590 | 0.0940 | 30 |
| | | Deep-river | 0.0443 | -0.0534 | 0.0980 | 22 |
| | | Deep-shallow | 0.0547 | -0.0471 | 0.1010 | 18 |
| | Middle | Shallow-river | 0.0690 | -1.22 | 0.1910 | 26 |
| | | Deep-river | | | | |
| | | Deep-shallow | | | | |
| | Offshore | Shallow-river | 0.0706 | -0.1080 | 0.1780 | 24 |
| | | Deep-river | 0.0405 | -0.0567 | 0.0962 | 23 |
| | | Deep-shallow | 0.0079 | -0.0002 | 0.0081 | 0.5 |

TABLE 1. Vertical head gradients (positive values indicate vertical flow from substrate to river) calculated for north- and south-transect piezometers inserted at a Brook Trout spawning area of the Aguasabon River before (January 10, 2017) and after (January 12, 2017) water release downstream of the Long Lake Control Dam. The difference and the duration (h) of the negative horizontal head gradient are given for after this water release.



FIGURE 3. Cross sections of transects through the Brook Trout spawning area of the Aguasabon River, facing upstream. Solid circles represent the location of piezometers in the river channel. Water flow is in the direction of light gray towards darker gray.

TABLE 2. North- and south-transect horizontal head gradients (positive values indicate horizontal flow from deeper nests towards inshore nest) for piezometers at a Brook Trout spawning area before (January 10, 2017) and after (January 12, 2017) discharge downstream of the Long Lake Control Dam at the Aguasabon River and the duration of the negative horizontal head gradient after water release.

| Transect | Nest | Piezometer | Before release | After release | Difference | Duration (h) |
|----------|-----------------|---|----------------|---------------|------------|--------------|
| North | Middle-inshore | Shallow-shallow | 0.0063 | -0.0122 | 0.0185 | 22 |
| | | Deep-deep | 0.0038 | -0.0086 | 0.0124 | 23 |
| | Offshore-middle | Shallow-shallow | 0.0042 | -0.0085 | 0.0127 | 50 |
| | | Deep-deep | 0.0015 | -0.0030 | 0.0045 | 40 |
| South | Middle-inshore | Shallow-shallow | 0.0065 | -0.0200 | 0.0271 | 27 |
| | Offshore-middle | Deep–deep Shallow–shallow Deep–deep | 0.0064 | 0.0010 | 0.0055 | 0 |

TABLE 3. Water temperature (°C) at piezometers and at the river-level station near the Brook Trout spawning area of the Aguasabon River at spawning and before and after water release downstream of the Long Lake Control Dam, showing the duration of the period with water temperature $<1^{\circ}C$ at the piezometers.

| | | | Temperature (°C) | | | |
|---------------------|----------|---------------|------------------|----------------|---------------|-------------------|
| Piezometer transect | Nest | Location | At spawning | Before release | After release | Duration <1°C (h) |
| River station | | River station | 7.4 | 1.5 | 0.2 | >53 |
| North | Inshore | Shallow | 7.4 | 4.1 | 0.3 | >53 |
| | | Deep | 7.0 | 5.1 | 0.9 | 15 |
| | Middle | Shallow | 6.1 | 5.2 | 0.9 | 20 |
| | | Deep | 6.1 | 5.2 | 3.5 | 0 |
| | Offshore | Shallow | 6.1 | 5.3 | 1.8 | 0 |
| | | Deep | 5.7 | 5.2 | 4.6 | 0 |
| South | Inshore | Shallow | 7.2 | 3.7 | 0.5 | 48 |
| | | Deep | 6.4 | 5.0 | 0.1 | 35 |
| | Middle | Shallow | 6.1 | 5.4 | 0.4 | 25 |
| | | Deep | | | | |
| | Offshore | Shallow | 6.1 | 5.1 | 2.0 | 0 |
| | | Deep | 6.1 | 5.4 | 5.0 | 0 |

(Table 3). Temperature reductions were less severe and shorter in duration for the piezometers that were deeper and furthest from shore. For example, at the northern transect, the NOD piezometer decreased in temperature from 5.2°C to 4.6°C during the event, while at NIS, it decreased from 4.1°C to 0.3°C, and the change lasted >53 h at <1°C (the 53-h minimum owes to temperatures at NIS still <1°C at the time when piezometers were disrupted by ice flows). Similarly, for the southern transect, temperature at SOD decreased from 5.4°C to 5.0°C, while at SIS, it decreased from 5.0°C to 0.1°C, the change this time lasting 48 h at <1°C. Temperature at the bottom of the river also decreased from 1.5°C to 0.2°C during the water release event.

Cold Treatment Effects on Brook Trout Hatching, Emergence, and Survival

Increases in discharge at the LLCD corresponding to as much as 30 m^3 /s flow over the dam had little effect on redd temperature, but historical increases higher than 30 m^3 /s were always associated with changes in redd temperature (Figure 2B). The most extreme example was a water release in 2013 that raised discharge by 47 m³/s and lowered hyporheic water temperature to 0.3° C, a drop of 5.3° C (Figure 2A). Following this release of water, recovery to ambient temperature at the redd site took 75 h, with 40 h at temperatures <1°C, which defined the treatment conditions for the laboratory experiment.

The cold treatment was initiated on January 10, 2017, at 1550 hours and lasted until January 12, 2017, at 0750 hours, creating 40 h of temperatures $<1.0^{\circ}$ C (mean = 0.5° C) for the treatment incubation boxes. The initial

temperature before treatment was 5.31°C, and the lowest temperature achieved was 0.2°C, a difference of 5.1°C. The temperature returned to ambient hatchery temperature within 5 h of the cold treatment ending. After hatching was complete, one replicate box failed, leaving emergence to be observed across 11 replicates.

Mean \pm SE egg mortality at the hatchery, prior to cold treatment, was 4.6 ± 1.1 eggs for the control and 5.1 ± 1.4 eggs for the treatment boxes, and the corresponding total mortality was 56 and 61 eggs. Mean \pm SE egg mortality after cold treatment and prior to hatching was 1.6 ± 1.4 eggs and 2.2 ± 2.0 eggs, and the corresponding total mortality was 19 and 26 eggs for the control and treatment replicates, respectively. These differences were not significant either before (paired *t*-test: $t_{11} = 0.37$, P = 0.33) or after ($t_{10} = 1.74$, P = 0.06) the cold treatment was administered. In total, the control replicates had a combined mortality of 75 eggs (7.3%) and the treatment 87 eggs (8.5%).

There was no difference in the length of the period from survival to emergence, comparing broodstocks between treatment and control (paired *t*-test: $t_{10} = 0.20$, P = 0.42). Mortality associated with nonemergence was relatively high when compared with mortality before hatching; from the period of the experiment after cold treatment to emergence, the mean \pm SE number of eggs dying were 33.0 ± 2.3 and 33.0 ± 3.7 and the corresponding total mortality was 368 and 362, for the control and treatment replicates, respectively (Figure 4).

Development to hatching was significantly delayed in eggs experiencing the cold treatment but with a mean difference of <1 d (log rank $\chi^2_1 = 11.4$, P = 0.001; Figure 4A). The mean \pm SE times to hatching for the control and



FIGURE 4. Kaplan–Meier estimates of hatching of Brook Trout alevins (A) in a control (black line; n = 1,020) and coldwater treatment (gray line; n = 1,020) in a hatchery experiment and (B) from 12 broodstock pairs in the same experiment, and Kaplan–Meier estimates of emergence of Brook Trout alevins (C) in the control (black line; beginning with n = 867 eggs) and coldwater treatments (gray line; beginning with n = 855 eggs) in the same experiment and (D) from 11 broodstock pairs in the same experiment (beginning with n = 1,722 eggs).

treatment replicates, in days, were 97.1 ± 0.4 and 97.3 ± 0.4 , respectively. Hatching started 84 d after fertilization and ended at 102 d for both sets of pooled replicates. Differences in time to hatching within broodstock pairs were not statistically significant (paired *t*-test: $t_{11} = 0.39$, P = 0.28). Among the 11 broodstock replicates, 8 had longer mean times to hatching for the cold shock treatment than for the control. The Kaplan-Meier estimates of time to hatching for the control and treatment replicates ranged from 95.5 to 99.4 d and from 94.5 to 99.0 d, respectively. Estimates of time to hatching by broodstock showed greater variation than the difference between the total pooled treatment and control replicates (Figure 4B).

Emergence started 132 d after fertilization for both control and treatment replicates and ended at 142 d in control and at 144 d for treatment replicates. There was no difference in time to emergence between the pooled control and treatment replicates (log rank $\chi^2_1 = 0.4$, P = 0.52; Figure 4C). The mean \pm SE times to emergence for the pooled replicates were 137.7 \pm 0.4 d and 138.4 \pm 0.5 d for control and treatment, respectively. Similar to the case for hatching, functions fitting time to emergence as alevins had greater variation among broodstock than the difference estimated between the treatment and control (Figure 4D).

Time from fertilization to emergence was not statistically different between treatment and control family pairs (paired t-test: $t_{11} = 1.49$, P = 0.14). Among the 11 replicates, 7 had longer times to emergence in the treatment than in the control. The Kaplan-Meier estimates of time to emergence ranged from 135 to 140 d and from 136 to 141 d for the control and treatment replicates, respectively. After the same number of calendar days, the cold treatment reduced the number of GDDs by 6.5 temperature units in the treatment replicates. Accounting for the temperature of water in the Dorion Fish Culture Station, estimates of the mean number of GDDs taken by alevins to hatch and to emerge were 765.6 for control and 764.7 for treatment replicates. The ranges in temperature units to hatching for the control and treatment replicates were 528-549 and 521-542 GDDs, respectively, and to emergence they were 750-774 and 755-783 GDDs, respectively.

DISCUSSION

Despite a single winter monitoring period limited to the Brook Trout redd location, a period that ended just after the water release, we were able to show that reversal of flow and reduction of temperature occurs in the hyporheic zone with water release. The change included a 40-h period of temperatures <1°C, with recovery to ambient water temperature requiring 75 h. However, the same duration of low temperature did not affect incubation period or mortality in Brook Trout eggs monitored in the hatchery. Thus, while we conclude that significant changes in flow direction and temperature on known Brook Trout redds are associated with midwinter hydroelectric water releases, our controlled experiments suggest that low temperatures as experienced on the Auguasabon River are unlikely to have an observable effect on survival to hatch or a meaningful effect on hatch timing for Brook Trout in a winterreservoir-managed system.

The timing and extent of cold shock evaluated in our experiment represents the longest duration to near-freezing temperatures evaluated in literature to our knowledge; however, our result is generally similar to what has been reported from cold treatment experiments on other salmonids despite being much longer in duration (Peterson et al. 1977; Neitzel and Becker 1985; Murray and Beacham 1986, 1987; Tang et al. 1987). Tang et al. (1987) assessed the effects of abrupt temperature reductions of as much as 6.1°C for shorter (8 h) durations on survival of Coho Salmon Oncorhynchus kisutch. These shorter-term temperature reductions did not reduce egg survival, except when temperature reduced from 10.2°C to 4.1°C for a duration of 8 h during an early development stage, suggesting that the timing of cold shock may be a critical aspect in salmonid egg survival. Cold treatments during fertilization or up to 72 h after fertilization can have severe negative impacts on salmonid egg survival if this period includes the water-hardening stage (Wagner et al. 2006). Eggs in the blastula stage during this period are more sensitive to temperature changes (Vernier 1977). Murray and Beacham (1987) tested effects of temperature reductions from higher initial incubation temperatures (both 8°C and 12°C) down to 1°C and found that cold treatment had no effect on survival to hatching but that larger temperature reductions at the prehatch stage did reduce survival of hatched Pink Salmon Oncorhynchus gorbuscha alevins.

The impact of cold shock from hydroelectric activities is likely to be highly dependent on the geological and hydrological attributes of the river, the management practices and timing of water release, and the species of management interest. In the Aguasabon River, Brook Trout spawn between October and November and waterhardening therefore occurs as soon as the eggs are laid and fertilized in redds. In this winter reservoir system, cold

treatment induced by river regulation typically occurs in January, and at this time, Brook Trout eggs will have completed the eye-up stage when they are more resilient to changes in temperature; however, a similar water release and hyporheic response to the one observed on the Aguasabon River may cause increased mortality if the release occurs earlier during the developmental period of salmonid eggs. Earlier winter water releases may be less common for winter-reservoir-managed systems; however, in managed rivers that experience hydropeaking regimes, power is produced during periods of peak power demand, resulting in highly variable monthly and/or daily flows (Haxton et al. 2015). Constant ramping of flow may impact the temperature regime of upwelling spawning habitat during critical early development windows for Brook Trout and other salmonids (i.e., before eye-up stage), in hydropeaking systems more so than winter reservoir systems. Further, hyporheic exchange and temperature recovery may vary greatly between river systems highlighting the need for site-specific hyporheic monitoring (Liu et al. 2018). Peaking regimes may deliver more frequent water releases, resulting in decreased incubation temperatures and therefore a greater probability of delayed hatching and emergence time for salmonids. Water managers should therefore consider the magnitude, frequency, duration, and timing of flow releases to avoid the implications of cold shock on the recruitment of Brook Trout and/or other salmonid species.

Temperature is an influential factor in development timing from fertilization to hatching and emergence in salmonids, and it has been shown that prolonged declines in temperature during the incubation period can lead to delayed hatching times (Murray and McPhail 1988; Beacham and Murray 1990; Marten 1992; McCullough 1999). Relatively small decreases in water temperature resulted in large delays in salmonid development timing (>100 d) when temperatures were decreased towards the lower lethal limits, indicating a nonlinear effect of temperature on development rates in these taxa (Neitzel and Becker 1985; Donaldson et al. 2008). Though the cold treatment experiment in the Dorion hatchery had a statistically significant impact on time from fertilization to hatching for Brook Trout, we conclude that a delay in hatching of <1d is not biologically significant (Baird et al. 2002) given that the variation in time to hatching observed across broodstock pairs within the experiment (a random variable) was greater than differences between treatment and control. However, cold shock and other early life stress can have sublethal effects on fish that go beyond the survival and development timing endpoints evaluated in this study (Donaldson et al. 2008; Angilletta 2009). For example, freshly fertilized Brook Trout eggs cold-shocked to -1.5°C for 2h not only significantly increased egg mortality, but also induced polypoidy (Lemoine and Smith 1980).

Historically, cold shock has been used to induce triploidy in fish, a method to disrupt sexual maturation and produce sterility (Tiwary et al. 2004). Atlantic Salmon *Salmo salar* cold-shocked prior to hatching were found to have modified the expression genes with developmental importance and initiated DNA methylation (Moghadam et al. 2017; Robinson et al. 2019).

The presence of upwellings in the hyporheic zone of rivers is a primary factor in selection of spawning sites by Brook Trout (Webster and Eiriksdottir 1976; Witzel and MacCrimmon 1983a, 1983b; Curry et al. 1995), such that typically low river levels during October generally result in increased potential for groundwater flow, which may amplify the thermal and chemical gradients that Brook Trout select (Curry et al. 1994; Curry and Noakes 1995). In the current study, we confirmed the presence of upwelling water in the hyporheic zone at the only known Brook Trout spawning site on the Aguasabon River. Groundwater discharge creates thermally stable habitat, important for successful spawning and incubation for Brook Trout and other salmonid species (Snucins et al. 1992; Curry and Noakes 1995; Saltveit and Brabrand 2013). During winter, a constant discharge of groundwater onto Brook Trout redds is likely essential for protection against prolonged exposure to colder ambient stream temperatures (<1°C) and prevents the infiltration of anchor ice in spawning substrates (a thick, spongy coating of frazil ice crystals on underwater objects). Anchor ice may have deleterious effects on incubating salmonid eggs by reducing the hyporheic flow supplying oxygen to the eggs (Power et al. 1999; Bisaillon and Bergeron 2009; Sear et al. 2014).

We observed a rapid increase in river flow that resulted in the reversal of vertical and horizontal head gradients and decreases in water temperature up to 1.8 m below the river substrate in the hyporheic zone. According to our observations, the area around Brook Trout redds changed from upwelling to downwelling conditions, likely due to surface water infiltrating the substrate. Depending on the distance of the redd from shore and its depth in the substrate, incubating Brook Trout eggs in a redd would have experienced varied cooling and flow reversal conditions due to water release, with the coldest temperatures and longest durations just beneath the substrate and closest to shore. Similar results were observed previously on the Nipigon River, a northern Ontario river also modified for hydroelectric power generation, which is also known for upwelling environments used by spawning Brook Trout and other salmonids (Curry et al. 1994).

Though our results indicated that a single-event (40-h) reduction in the thermal environment had little impact on Brook Trout egg survival and development timing to hatch and emergence, interstitial water quality is known to be a limiting factor in salmonid egg development (Sternecker et al. 2013). Interstitial water quality is determined

by the source of water that dominates the hyporheic zone (i.e., surface water or groundwater) and the resulting redd environments (Arntzen et al. 2006). Dissolved oxygen, pH, and specific conductance have all been shown to influence the timing and success of hatching and emergence in salmonid eggs (Merz et al. 2004; Soulsby et al. 2009; Sternecker et al. 2013). The reversal of flow in the hyporheic zone altered thermal interstitial water conditions and, although not measured in this study, may have also altered other physical and chemical conditions in the hyporheic zone (Humpesch 1985; Brunke and Gonser 1997). This presents an area for future research, specifically how river regulation affects other interstitial water quality parameters in salmonid incubation habitats and their resulting impact on salmonid recruitment.

Unlike the general pattern of groundwater discharge into rivers, which is typically maximized at the shoreline and declines with distance offshore (Winter and Pfannkuch 1984: Curry et al. 1994), our results demonstrate that this pattern does not generally hold for the Aguasabon River; vertical head gradient in the substrate was strongest in piezometer nests *furthest* from shore, likely due to the straightening of the original river channel, which altered the location of the shoreline interface between surface water and the riverbed. The artificial bank that exists now acts as a barrier between the flowing river and an adjacent oxbow. The presence of the artificial bank likely decreases groundwater potential at the current shoreline-surface water interface, where it likely flows horizontally to the river, forcing groundwater to enter the river at deeper locations. The position of the oxbow presents a challenge for understanding the horizontal flow of groundwater or surface water between it and the river. At the same time, this site presents a unique opportunity to study the effects of discharge over a control structure where an artificial bank may make vertical flow relatively more important in determining upwelling and downwelling conditions in the hyporheic zone, a phenomenon that likely contributes to the Brook Trout spawning habitat found at the site. The construction of artificial banks to stimulate upwelling of warmer groundwater may be a useful mitigation measure in areas where Brook Trout habitat has been compromised.

The spawning and incubation success of Brook Trout in the Aguasabon River is of special concern due to the species-specific spawning requirements of Brook Trout, the limited spawning habitat in the Aguasabon River, and the vulnerability of that habitat to upstream water management practices. While hydroelectric operations vary greatly from one system to another, the results of this study may be applicable to the management of various regulated river systems, with the most significant biological cold-shock-related impacts being delivered in hydropeaking regimes.

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