2022

Dammed water quality—Longitudinal stream responses below beaver ponds in the Umpqua River Basin, Oregon

John R. Stevenson

Jason B. Dunham

Steven M. Wondzell

Jimmy Taylor

Received: 18 October 2021 | Revised: 10 March 2022 | Accepted: 12 May 2022

DOI: 10.1002/eco.2430

RESEARCH ARTICLE

WILEY

Dammed water quality—Longitudinal stream responses below beaver ponds in the Umpqua River Basin, Oregon

John R. Stevenson[1] | Jason B. Dunham[2] | Steven M. Wondzell[3] | Jimmy Taylor[4]

[1]Department of Fisheries, Wildlife & Conservation Sciences, Oregon State University, Corvallis, Oregon, USA

[2]Forest and Rangeland Ecosystem Science Center, U.S. Geological Survey, Corvallis, Oregon, USA

[3]Pacific Northwest Research Station, U.S. Forest Service, Corvallis, Oregon, USA

[4]National Wildlife Research Center, U.S. Department of Agriculture, Corvallis, Oregon, USA

Correspondence
John Stevenson, Department of Fisheries, Wildlife & Conservation Sciences, Oregon State University, Corvallis, Oregon, USA.
Email: john.stevenson@oregonstate.edu

Funding information
North Umpqua Foundation; U.S. Department of Agriculture, National Wildlife Research Center

Abstract

Beaver-related restoration (BRR) has gained popularity as a means of improving stream ecosystems, but the effects are not fully understood. Studies of dissolved oxygen (DO) and water temperature, key water quality metrics for salmonids, have demonstrated improved conditions in some cases, but warming and decreased DO have been more commonly reported in meta-analyses. These results point to the contingencies that can influence outcomes from BRR. We examined water quality related to beaver ponds in a diverse coastal watershed (Umpqua River Basin, OR, USA). We monitored water temperature 0–400 m above and below beaver ponds and at pond surfaces and bottoms across seven study sites from June through September of 2019. DO was also recorded at two sites at pond surfaces and pond bottoms. Downstream monthly mean daily maximum temperatures were warmer than upstream reference locations by up to 1.9°C at beaver dam outlets but this heating signal attenuated with downstream distance. Downstream warming was greatest in June and July and best predicted by pond bottom temperatures. DO at pond surfaces and bottoms were hypoxic (≤5 mg/L) for more than half of the 32-day monitoring period. Water temperatures increased for short distances below monitored beaver ponds and observed oxygen conditions within ponds were largely unsuitable for salmonid fishes. These findings contrast with some commonly stated expectations of BRR, and we recommend that managers consider these expectations prior to implementation. In some cases, project goals may override water quality concerns but in streams where temperature or DO restoration are objectives, managers may consider using BRR techniques with caution.

KEYWORDS

Castor canadensis, dissolved oxygen, stream restoration, stream temperature, water quality

1 | INTRODUCTION

North American beaver (*Castor canadensis*) are considered ecosystem engineers because they can fundamentally transform stream and riparian ecosystems through a number of their activities, most notably, creating ponds by building dams and impounding water (Jones et al., 1996; Larsen et al., 2021; Wright et al., 2002). These attributes have inspired much interest in the potential for beaver to play a role in process-based stream restoration (Ciotti et al., 2021; Johnson et al., 2020; Pollock et al., 2015). This approach is often termed 'beaver-related restoration' or BRR. Expectations from practitioners of BRR can be wide ranging and even evolve over the course of a project (Nash et al., 2021) but include restoration of incised streams by decreasing streamflow velocities for sediment retention (Cluer & Thorne, 2014;

Pollock et al., 2014), creation of environmental conditions suitable for aquatic species (Bouwes et al., 2016), increases in late summer streamflow through surface and subsurface storage and improvements to stream temperature (Bennett et al., 2019; Pollock et al., 2015).

Evaluating the expected benefits of BRR is challenging because it is often implemented without formal study (Pilliod et al., 2017). When BRR efforts are evaluated, reports are highly variable across watersheds (Collen & Gibson, 2000) or through time (Clark, 2020) particularly with regard to stream temperature. A meta-analysis of studies considering the effect of beaver ponds on stream temperature indicated that downstream warming was the most common response (Ecke et al., 2017). Accordingly, many important questions about BRR remain to be fully addressed, including (1) the consistency of quantifiable benefits of ponds among locations and through time and (2) possible unintended or undesirable outcomes (Dilling et al., 2015; Lautz et al., 2019).

Understanding beaver dam influences on stream temperature and associated water quality parameters presents an excellent example of the potential costs and benefits of BRR. In the western United States, summer stream temperature is particularly important because warm water can push coldwater taxa, such as salmon and trout, to their physiological limits (Richter & Kolmes, 2005). Evidence from empirical evaluation of beaver dams suggests that maximum summer water temperature may cool below beaver dams in some cases (Fuller & Peckarsky, 2011; Weber et al., 2017) but warm in others (Avery, 2002; Majerova et al., 2015) by as much as 9°C (Margolis et al., 2001). Differences in how downstream changes are reported among studies also add to uncertainty in determining the effect of beaver dams on stream temperature. For example, temperature analyses have reported results during critical periods of time for coldwater species, spanning from a single day (Means, 2018) to weeks (Majerova et al., 2020), to a month (Dittbrenner, 2019) and across seasons (Weber et al., 2017) and years (Clark, 2020). It is also possible that changes in other water quality parameters, especially dissolved oxygen (DO), may be influenced by BRR (Ecke et al., 2017). Declining concentrations of DO are often associated with warmer stream temperatures, leading to potentially interacting stresses on coldwater fishes. For example, water with low DO can lead to mobilization of mercury into food webs (Ecke et al., 2017), limit juvenile fish growth (Davis, 1975) and lead to changes in fish behaviour that could increase their vulnerability to predators (Vinson & Levesque, 1994). In severe cases, low DO concentrations have led to mass die-offs of aquatic species (La & Cooke, 2011).

Overall, existing research suggests that beaver ponds have variable influences on water quality that may or may not align with human desired outcomes. Furthermore, existing research has focused on more proximate impacts of ponds by studying conditions within these systems or just immediately downstream of them (e.g., Dittbrenner, 2019; Majerova et al., 2015; Means, 2018; Weber et al., 2017). This leaves important questions unanswered regarding the longitudinal extent and duration of any potential influences of beaver ponds on downstream reaches (e.g., Roon, Dunham, & Torgersen, 2021).

In this study, we evaluated changes in stream temperature below beaver dams and DO in beaver ponds, as well as the downstream extent of thermal influences among watersheds over the summer when many species are limited by oxygen and coldwater habitat. Specifically, our objectives were to consider (1) the magnitudes and longitudinal extents of changes in maximum stream temperature below beaver dams; (2) how these changes varied over the summer; (3) the influence of pond bottom and pond surface temperatures on downstream changes; and (4) how DO concentrations at pond surfaces and bottoms varied relative to biological thresholds for salmonids.

2 | METHODS

2.1 | Study area

The study area (Figure 1) for this research is the Umpqua River Basin, OR (hereafter Umpqua). The Umpqua is in south-western Oregon and is the second largest coastal river in the state (catchment area of 12,124 km^2). Elevations range from a high of 2799 m in the Cascade Mountains to sea level where it enters the Pacific Ocean. Many management priorities within the basin focus on improving spawning and juvenile rearing conditions for anadromous salmon and trout (*Oncorhynchus spp.*) such as Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Oncorhynchus mykiss*). The basin also supports other culturally and ecologically important species such as Pacific lamprey (*Entosphenus tridentata*), endemic species including the Umpqua chub (*Oregonichthys kalawatseti*) and other non-salmonid fishes (Markle, 2019). Each of these species faces unique threats but a common challenge that managers must address is water quality, particularly as it relates to temperature impairment (focused on supporting coldwater taxa such as salmonids, Falke et al., 2016) which is of particular concern in the Umpqua. For example, in its most recent assessment, the State of Oregon reported that more than 85% (81 of 93) of monitoring locations across the Umpqua with sufficient data violated maximum temperature standards between 2016 and 2019 (Donald et al., 2020).

2.2 | Study sites

We monitored water temperature in seven streams (hereafter sites) in the Umpqua with known beaver dams and sign of current beaver occupancy, including recent vegetation clippings, scat or scent mounds. We compared water temperatures above, below and in the beaver ponds (surface and bottom temperatures in ponds). We also monitored dissolved oxygen concentrations in beaver ponds at two sites, one of which was included in the temperature analysis and one that was not (Table 1). In total, observations from eight study sites were used in the temperature and DO analyses.

2.3 | Watershed characteristics

Watershed and stream reach characteristics (Table 1) for each site were based on Netmap,[1] described by Benda et al., 2007. All study

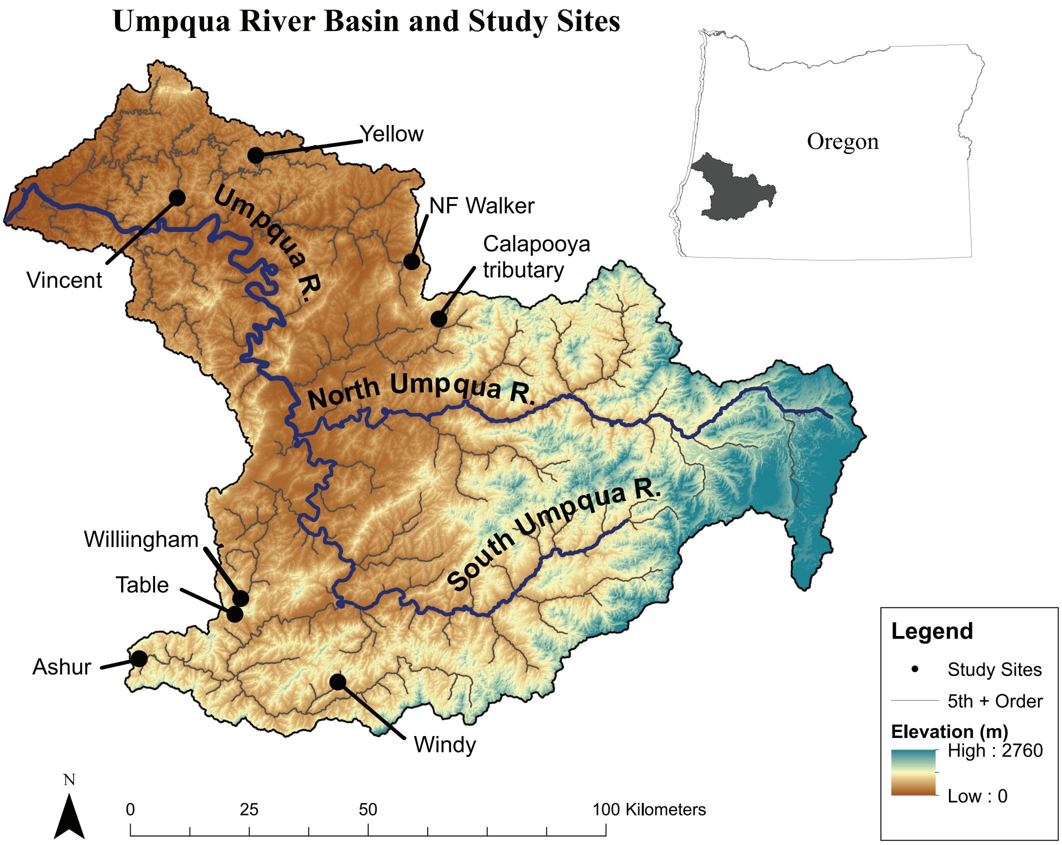

FIGURE 1 Basin topography, hydrography and eight study sites with beaver ponds or complexes in the Umpqua Basin in southwest Oregon. Note that '5th order +' refers to all 5th order or higher streams based on the Strahler stream order classification

sites were on low order streams and nested in small watersheds less than 15 km^2. Pond surface area was measured directly with measuring tape or, in the case of sites on Willingham and Windy creeks, which each supported multiple ponds, hand-held GPS observations around the circumference of all wetted pond surface areas.

2.4 | Stream temperature

We recorded water temperature in streams on an hourly basis to capture the daily thermal maxima (Dunham et al., 2005) from 1 June 2019 to 15 September 2019 using data loggers (Onset Hobo Water Temperature Pro v2 Data Logger (U22-001); www.onsetcomp.com) shielded from direct solar influence with white 2.5 × 5 inch PVC housing. We verified that all temperature data loggers were operating within the manufacturer's specified accuracy range of ±0.2°C prior to field deployment following Heck et al. (2018). Data loggers that recorded temperatures outside of this range were not used.

We quantified reference water temperature upstream of beaver ponds along a 400-m stream reach that was instrumented at five locations spaced at 100-m intervals (Figure 2). The same design was used to monitor downstream water temperature, beginning at the dam outlet to 400 m downstream every 100 m. In cases where there were more than one dam and pond, the upstream reach ended at the furthest upstream pond, and the downstream reach began at the outlet of the furthest downstream dam (Majerova et al., 2015). We refer to each downstream position as 0, 100, 200, 300 and 400 m based on the respective distances downstream of the dam outlet. Stream temperature data loggers were placed in the channel thalweg along the upstream and downstream reaches in free flowing current (Heck et al., 2018) and tethered to a sandbag or iron stake anchors. We verified temperature data logger accuracy with hand-held measurements (ThermoWorks Precision Plus Thermometer (https://www.thermoworks.com/Precision-Plus; accuracy: ±0.05°C)). Handheld readings were recorded five times throughout the study period at each instream temperature data logger to verify that the automated temperature observations were within the ±0.2°C accuracy range.

2.5 | Pond temperature

In addition to longitudinal sampling of stream temperatures, we also recorded pond bottom and surface temperatures at each site. We monitored the pond with the greatest surface area at sites where more than one pond was present. We secured pond temperature data loggers 5 cm below the surface and 5 cm above the pond bottom using a sandbag anchor and chain tether held vertically in the water column with a surface float.

TABLE 1 Study site characteristics

	Ash	Cal	NFW[a]	Vin	Tab[b]	Wil	Win	Yel	Mean
Total pond(s) surface area (ha)	0.03	0.08	0.13	0.18	0.93	1.13	3.85	0.82	0.9
Total pond/complex length (m)	296	303	207	249	413	566	616	421	383.9
Total # ponds	1	2	2	1	2	>10	>10	1	na
Pond depth at Pb (cm)	31	81	75	43	65	45	95	73	63.5
Total head (m)	0.11	5.84	1.37	1.06	1.37	5.64	5.33	11.25	4.0
Pond morphology ratio	1.23	3.21	0.39	1.80	0.30	3.77	1.55	1.07	1.7
Catchment area (km^2)	3.8	4.8	5.3	8.5	2.4	8.8	14.9	6.4	6.9
Stream order	3	4	4	4	3	4	5	4	3.9
Mean annual precip (m)	1.9	1.6	1.6	1.5	1.2	1.2	1.1	1.5	1.5
Mean annual discharge (m^3/s)	0.09	0.13	0.17	0.2	0.02	0.15	0.2	0.15	0.1
Bankfull discharge (m^3/s)	2.9	6.4	4.4	4.9	2.5	6.2	9.9	5.2	5.3
Stream power (watts/m)	456	1801	707	480	1889	1,272	3,185	636	1303
Bankfull flow velocity (m/s)	1.9	2.7	1.9	1.5	2.5	1.8	2.2	1.8	2
Gradient	0.02	0.03	0.02	0.01	0.06	0.01	0.02	0.01	0.02
Bankfull width (m)	4.0	4.7	5.0	5.6	2.2	4.9	5.6	5.1	4.6
Bankfull depth (m)	0.4	0.5	0.5	0.5	0.3	0.6	0.6	0.5	0.5
Valley width (m)	60	36	91	72	88	74	71	55	68
Floodplain width (m)	32	23	53	48	56	47	45	41	43
Azimuth	67	78	222	192	219	98	200	192	158
Sinuosity	1.1	1.0	1.1	1.0	1.0	1.0	1.1	1.0	1.0

Note: Catchment, stream and pond or pond complex attributes for eight study sites. All other sites included only in longitudinal temperature analysis. Pond surface area, complex length, pond frequency, and hydraulic head were measured in situ in early June 2019. All other site characteristics are based on Netmap products (http://www.netmaptools.org) described by Benda et al. (2007). Hydraulic head was based on total vertical drop (m) measured from upstream extent of upper most pond surface water to the bottom of the downstream most dam. Pond morphology ratio is the natural log ratio of the hydraulic head to surface area (ha) described by Fuller & Peckarsky, 2011.

[a]Site included in longitudinal temperature and DO analyses.

[b]Site included only in DO analysis.

2.6 | Dissolved oxygen

We monitored DO concentrations and temperature simultaneously in the furthest downstream pond at Table Creek (TC) and North Fork Walker Creek (NFWC) study sites between 20 August 2019 and 21 September 2019 using DO data loggers (Onset Hobo Dissolved Oxygen Data Logger: U26-001; www.onsetcomp.com). We verified that DO measurements were calibrated using the manufacturer's 100% saturation method prior to deployment. Data logger accuracy was within the manufacturer's ±0.2-mg/L range. We recorded DO and temperature 5 cm below pond surfaces and 5 cm above pond bottoms at 5-min intervals. Surface and bottom DO loggers were located adjacent to dams where pond depths were greatest (TC = 65 cm; NFWC = 75 cm).

2.7 | Discharge

Stream gage data were not available for any of the study sites so discharge was estimated using a drainage area ratio method to a nearby reference gage station (Archfield & Vogel, 2010):

$$Qu_t = \frac{Au}{Ag} Qg_t,$$

where Qu_t is discharge at the ungaged site on day t; Au = area of ungaged site; Ag = area of gaged site; Qg_t = discharge at gaged site on day t. This estimation method assumes that there is a linear relationship between catchment size and discharge through time. Ratios of gaged catchments have explained more than 90% of nested, ungaged catchments (Gianfagna et al., 2015). Daily discharge from reference gages was retrieved from StreamStats[2] provided by U.S. Geological Survey and Douglas County, OR Public Works.[3] We estimated catchment area for each study site using StreamStats basin delineation tool based on the most downstream temperature data logger coordinates.

2.8 | Precipitation and temperature

We estimated the mean daily precipitation and temperature anomaly among sites as a percentage of the 30-year climate normals (1981–2010) for precipitation and temperature for each month of the 2019 water year (1 October 2018 to 30 September 2019) using PRISM 4-km^2 gridded data[4] (Daly et al., 1994, 2008). We selected PRISM

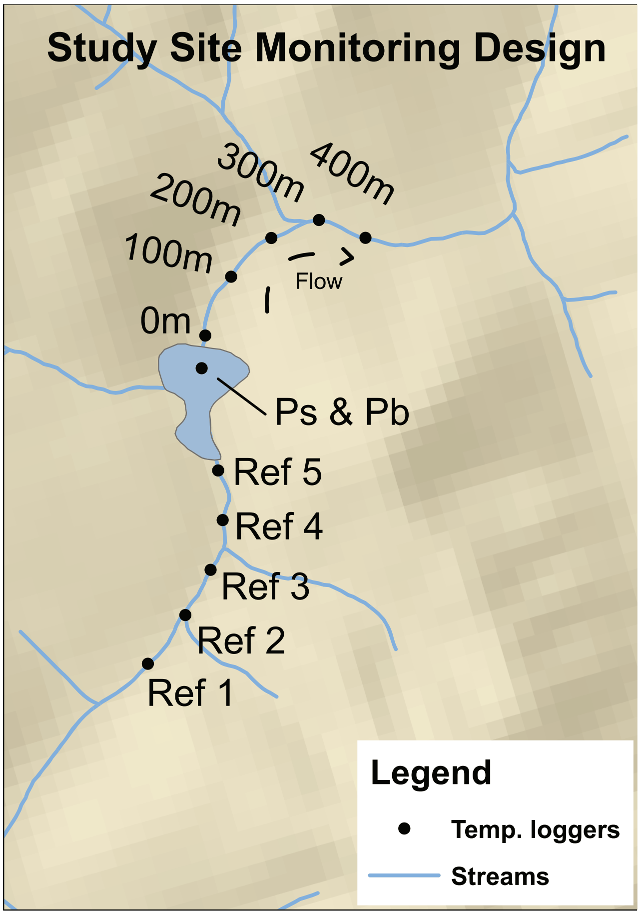

FIGURE 2 Hypothetical illustration of monitoring design across study sites. 0–400 m refers to monitoring positions based on downstream distance from dam outlet. Ps and Pb refer to pond surface and bottom monitoring positions. Upstream reference conditions based on mean of reference positions. 1–5

grids based on coordinates for each site's pond or most downstream pond.

3 | DATA ANALYSIS

All temperature analyses were conducted using R statistical software (R Core Team, 2020).

3.1 | Longitudinal temperature model

The response variable was mean daily maximum temperature for each month across all positions at each study site. To account for site level differences, responses were analysed using a linear mixed-effects model (Brown, 2021; Zuur et al., 2009) with two fixed-effect factor variables and their interaction: (1) month as a four-level predictor variable for each month that observations were recorded (June–September); and (2) temperature data logger position as a six-level predictor, reduced from 10 by averaging the upstream positions into a single upstream 'reference' level. Sites and the site-by-month interaction were used as random effects. Site and watershed level factors were not used as predictor variables because they had limited statistical power due to the number of site replicates and limited temporal variation relative to the response variable. We evaluated model residuals for independence, equal variance, and normality to determine if these data met our assumption for the analysis. Assumptions of independence were not met among observations in time and space. To address this, correlation among temperature data loggers within sites was corrected with a Matérn function (Rousset & Ferdy, 2014) based on Euclidean distance from the upstream midpoint and downstream positions and thalweg distance among downstream positions. Negative correlation among months was observed at lag 1 but was not improved with inclusion of an autoregressive (AR1) function, so we made no adjustment for correlation among months in the model. The negative autocorrelation resulted in larger confidence bounds for parameter estimates of differences between months. We concluded this was acceptable for the analysis because our focus was on longitudinal differences within months. All pairwise comparisons of positions within months were estimated from the model, using a Tukey-adjustment for a family of six comparisons.

3.2 | Pond outlet models

We estimated the relationships of maximum daily temperature between water in ponds and water immediately downstream (0 m) of the dams (i.e., pond outlets) using linear mixed-effects models. Models were fit separately for each of the 4 months of the study. One set of monthly models used maximum daily temperature at the pond surface as the fixed effect variable and the other set used maximum daily temperature at pond bottoms as a fixed effect variable. All eight models used study site as a seven-level random effect. We evaluated each model's residuals for independence, equal variance and normality to determine if these data met our assumption for the analysis. Assumptions of independence were not met among observations in time and were addressed with an autoregressive (AR1) function in all models. We calculated marginal and conditional coefficients of determination (pseudo R^2) based on Nakagawa and Schielzeth (2013). We also compared differences in daily maximum temperature of pond bottoms and reference conditions. Normality assumptions for the distribution of differences were not met based on a Shapiro–Wilk test. Differences between daily maximum temperatures of pond bottoms and references were reported as medians with associated p values from a paired-samples Wilcoxon test.

3.3 | Dissolved oxygen

DO was monitored at only two sites so we provide only descriptive summaries of daily temperature and DO mean, minimum and

TABLE 2 Monthly mean maximum daily temperature by stream position

Position	June *T*	June 95% CI	July *T*	July 95% CI	August *T*	August 95% CI	September *T*	September 95% CI
Ref	14.8	*13.9, 15.7*	15.9	*15.0, 16.8*	16.5	*15.6, 17.4*	15.1	*14.3, 16.0*
0 m	16.7	*15.8, 17.6*	17.6	*16.7, 18.5*	17.3	*16.4, 18.2*	15.8	*14.9, 16.7*
100 m	16.2	*15.3, 17.1*	16.9	*16.1, 17.8*	16.7	*15.8, 17.6*	15.6	*14.7, 16.5*
200 m	15.8	*14.9, 16.7*	16.6	*15.7, 17.5*	16.6	*15.7, 17.5*	15.4	*14.6, 16.3*
300 m	15.5	*14.6, 16.4*	16.4	*15.5, 17.3*	16.5	*15.6, 17.4*	15.3	*14.4, 16.2*
400 m	15.4	*14.5, 16.3*	16.3	*15.4, 17.2*	16.6	*15.7, 17.5*	15.3	*14.4, 16.2*
Comparison	**Δ*T***	**95% CI**	**Δ*T***	**95% CI**	**Δ*T***	**95% CI**	**Δ*T***	**95% CI**
0 m-Ref	**1.9**	*0.8, 2.9*	**1.7**	*0.6, 2.7*	0.8	*−0.2, 1.8*	0.6	*−0.4, 1.7*
100 m-Ref	**1.4**	*0.3, 2.4*	1.0	*0.0, 2.1*	0.2	*−0.9, 1.3*	0.4	*−0.6, 1.5*
200 m-Ref	1.0	*−0.1, 2.0*	0.7	*−0.4, 1.8*	0.1	*−1.0, 1.2*	0.3	*−0.8, 1.4*
300 m-Ref	0.7	*−0.4, 1.8*	0.4	*−0.6, 1.5*	0.0	*−1.1, 1.0*	0.1	*−1.0, 1.2*
400 m-Ref	0.6	*−0.4, 1.7*	0.4	*−0.7, 1.5*	0.1	*−1.0, 1.2*	0.1	*−0.9, 1.2*

Note: Model estimates and Tukey-adjusted 95% confidence intervals (gray italics) for monthly mean maximum daily temperature (°C) by (top) position and (bottom) differences of downstream positions from reference mean. (Bottom) Bold indicates that associated 95% CI for differences do not include zero.

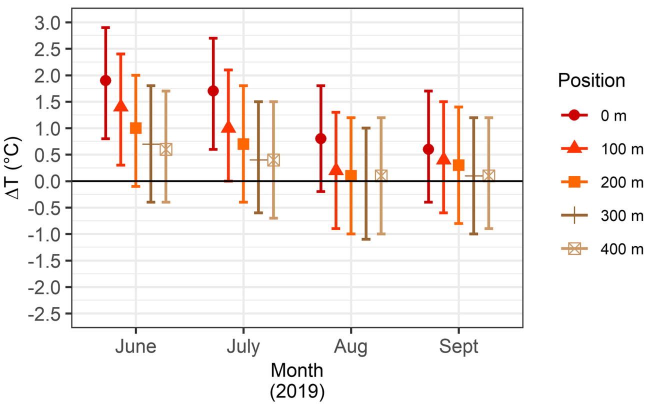

FIGURE 3 Model estimates with Tukey-adjusted 95% confidence intervals for difference in mean (shape) daily maximum stream temperature (°C) by month (2019) between downstream positions (colour/shape) and upstream references (downstream position–Reference) among sites sampled (Figure 1). Positive and negative values indicate warming or cooling relative to the mean reference temperatures. Positions are labelled based on downstream distances from dam outlets (Figure 2)

maximum. In addition to descriptive summaries, we calculated percent saturation as the fraction of maximum saturation based on observed pond temperature and average barometric pressure during the monitoring period at Roseburg Regional Airport, OR weather station (KRBG). Maximum DO saturation was estimated using DO solubility tables provided by U.S. Geological Survey DOTABLES[5] assuming zero specific conductance for freshwater.

4 | RESULTS

4.1 | Longitudinal temperature change

Estimated differences in mean monthly maximum daily temperature among downstream positions relative to the upstream reference (Table 2 and Figure 3) indicate that temperatures downstream of beaver ponds in June warmed by 1.9°C (Tukey-adjusted 95% CI: 0.8–2.9) at 0 m downstream and by 1.4°C (Tukey-adjusted 95% CI: 0.3 to 2.4) at 100 m downstream. Model estimates also indicate mean warming in June at 200, 300, and 400 m but confidence bounds suggest these differences were statistically inconclusive. In July, temperatures warmed at 0 m (1.7°C, Tukey-adjusted 95% CI 0.6 to 2.7), and followed a pattern similar to June with mean warming downstream of 100 m, but these differences were statistically inconclusive. Estimated differences in means among downstream positions relative to the reference in August and September showed a similar longitudinal trend to those observed in June and July but were statistically inconclusive at all downstream positions.

4.2 | Pond outlet temperature

The estimated marginal R^2 for daily maximum temperature at 0 m downstream of pond outlets was greatest among the four pond bottom models (Table 3). Fixed effects from the pond bottom models (pond bottom daily maximum temperature) for June and July explained 72% and 79% of water temperature variation at 0 m below

TABLE 3 Pond surface and bottom models for daily maximum temperature of pond outflow water

Model	Month	Slope	95% CI	R^2m	R^2c	df
0 m ~ $P_{surface}$	*June*	0.39	*0.32, 0.46*	0.23	0.29	131
	July	0.39	*0.34, 0.44*	0.42	0.64	205
	Aug	0.22	*0.18, 0.26*	0.14	0.78	204
	Sept	0.29	*0.24, 0.34*	0.32	0.32	132
0 m ~ P_{bottom}	*June*	0.99	*0.87, 1.10*	0.72	0.91	131
	July	0.90	*0.78, 1.01*	0.79	0.88	205
	Aug	0.54	*0.39, 0.68*	0.27	0.73	204
	Sept	0.92	*0.79, 1.04*	0.80	0.80	132

Note: Results from eight linear mixed models estimating relationship between daily maximum temperatures (°C) of pond surfaces and pond bottoms with pond outlets at 0 m downstream for each of the 4 months during the monitoring period. Slopes for models based on pond bottom temperatures were greater than those for pond surface models. Pond surface and bottom model slopes were smallest in August. R^2*marginal*: variance explained by the model's fixed effects (pond position). R^2*conditional*: variance explained by both the model's fixed (pond position) and random (site) effects.

TABLE 4 Comparison of median montly maxium pond bottom to reference temperatures

Comparison	Month	ΔT	p
Pb-ref	*June*	0.81	<0.001
	July	0.45	0.001
	Aug	−0.57	<0.001
	Sept	−0.05	0.05

Note: Median monthly difference and associated *p* values from paired-samples Wilcoxon test for daily maximum temperatures (°C) between pond bottom (Pb) and reference (Ref) positions (Pb-Ref). Comparisons were paired by site.

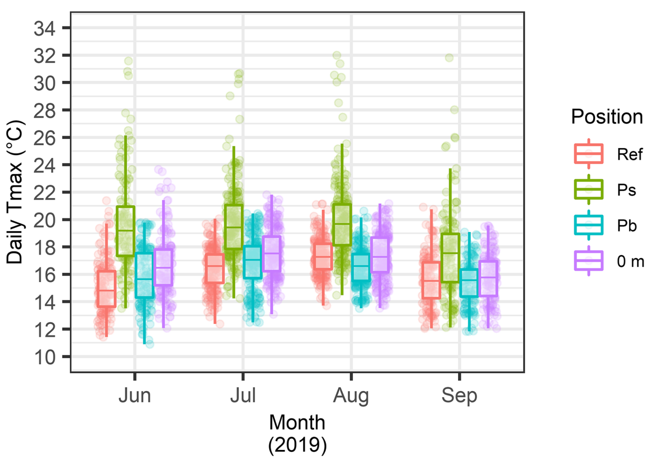

FIGURE 4 Maximum daily temperature (°C) of monitoring positions for each month of study period: Upstream reference mean (Ref), pond surfaces (Ps), pond bottoms (Pb) and pond outlets at 0 m downstream of dams (0 m). Circles represent daily maximum temperature observations for each position (colour). Boxplots represent the median and inter-quartile range (25th to 75th percentiles). Upper and lower whiskers represent the maximum daily temperature observations up to 1.5 of the inter-quartile range. Points are horizontally jittered

TABLE 5 Daily temperature, DO concentration and DO saturation at North Walker and Table creeks

	NF Walker Creek		Table Creek	
Mean daily:	$P_{surface}$	P_{bottom}	$P_{surface}$	P_{bottom}
DO_{min}	2.2	1.6	3.3	1.1
DO_{mean}	3.9	3.3	4.8	2.8
DO_{max}	6.7	6.5	6.4	4.3
DO_{range}	4.5	4.9	3.1	3.2
% time $_{\leq 5\ mg/L}$	75%	78%	57%	88%
% time P_s & $P_{b\ \leq 5\ mg/L}$	66%	66%	57%	57%
T_{min}	15.9	15.8	13.9	13.7
T_{mean}	17.9	16.6	15.1	14.0
T_{max}	20.7	17.4	17.3	14.6
T_{range}	4.8	1.6	3.4	0.9
Sat_{min}	22%	16%	34%	10%
Sat_{mean}	40%	33%	49%	26%
Sat_{max}	72%	66%	64%	41%
Sat_{range}	50%	50%	31%	31%

Note: Pond surface ($P_{surface}$) and bottom (P_{bottom}) mean daily minimum, mean, maximum and range for (DO) dissolved oxygen concentrations (mg/L), (*T*) temperature (°C) and (Sat) oxygen saturation (%) at NF Walker and Table creeks from 20 August 2019 to 21 September 2019. Pond depths were 75 and 65 cm for NF Walker and Table creeks, respectively.

the dams, respectively. Fixed effects from the pond surface models for June and July explained 23% and 42% of downstream variation respectively. Results from the September models were similar to those in June and July.

The models for August generally explained the least amount of variation in 0 m temperature with 14% and 27% using pond surface and pond bottom temperatures as predictors. The conditional R^2 for August that includes both the fixed effects of pond position and random effects of site accounts for 78% and 73% of downstream

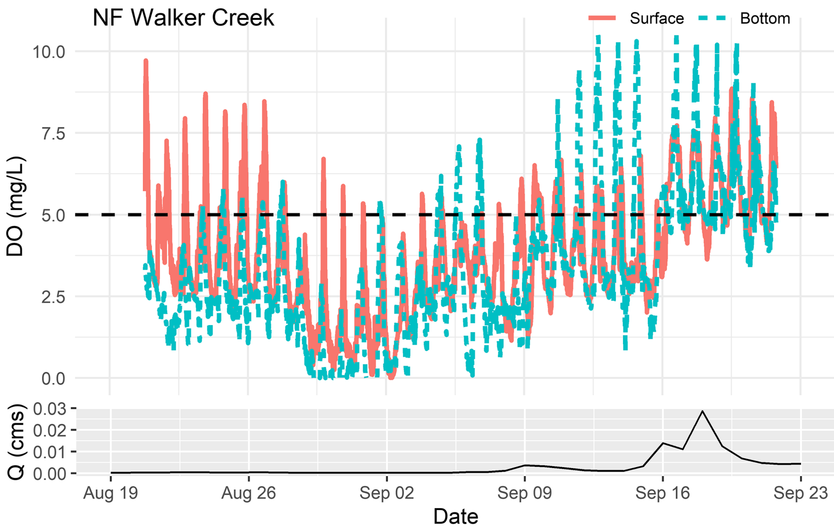

FIGURE 5 (top) Dissolved oxygen concentrations (mg/L) for the pond surface and bottom at North Fork Walker Creek from 20 August 2019 to 21 September 2019. Dashed horizontal represents minimum biological threshold. (bottom) Estimated stream discharge (m^3/s) for North Fork Walker Creek

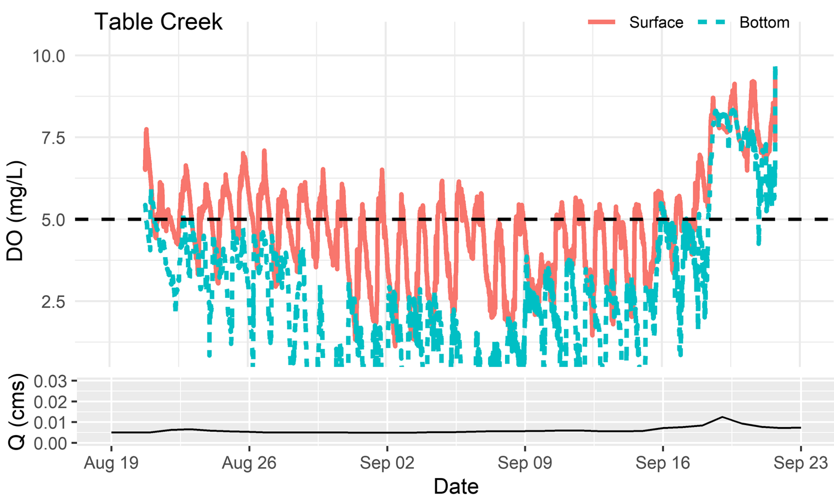

FIGURE 6 (top) Dissolved oxygen concentrations (mg/L) for the pond surface and bottom at Table Creek from 20 August 2019 to 21 September 2019. Dashed horizontal represents minimum biological threshold. (bottom) Estimated stream discharge (m^3/s) for Table Creek

TABLE 6 Comparison of monitoring period temperature and preciption to the 30-year climate normals

	Precipitation		Tmean		Tmin		Tmax	
	Normal	% Normal	Normal	Δ	Normal	Δ	Normal	Δ
Jun	48.8	26	16.5	1.3	8.8	0.4	24.3	2.2
Jul	13.6	42	18.4	−0.5	11.2	0.1	25.6	−1.1
Aug	16.3	143	19.9	0.9	12.4	1.6	27.4	0.2
Sep	38.5	345	15.9	−0.8	10.5	1.2	21.3	−2.9

Note: Estimated monthly climate normals (1980-2010) and 2019 anomalies across study studies for total precipitation (mm), and mean (Tmean), minimum (Tmin) and maximum (Tmax) temperature (°C). Precipitation anomalies were calculated as the ratio of 2019 mean monthly total precipitation to the 30-year precipitation normal. Percent normal precipitation values above or below 100% indicate wetter or drier than normal conditions. All temperature anomalies were calculated by subtracting the 2019 monthly mean from the 30-year normal monthly mean. Positive and negative temperature anomalies indicate above and below average conditions.

temperature variance in August for pond surface and bottom models. This suggests that site level factors explained a greater portion of downstream variance than pond surface or bottom temperature during August. Monthly comparisons of median daily maximum temperature differences between pond bottoms and reference positions (Table 4 and Figure 4) indicated warmer water at pond bottoms in

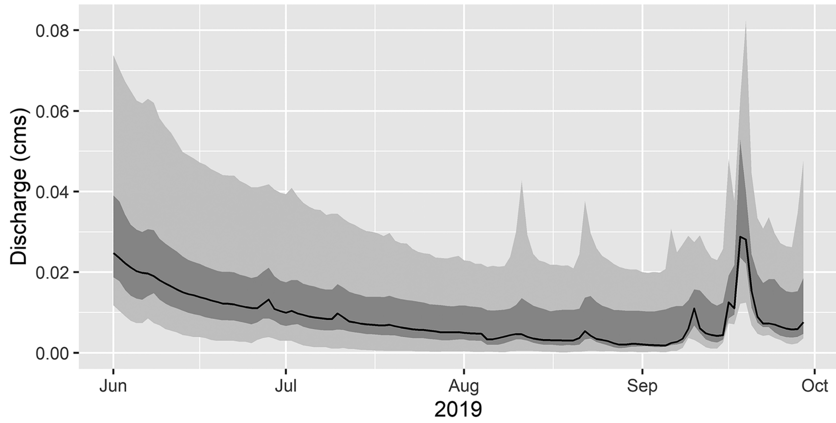

FIGURE 7 Estimated mean daily discharge (cubic meters per second; cms) across study sites during the study period, 1 June 2019 to 30 September 2019, with 50th (black curve) and 25th to 75th (dark grey band) percentiles and minimum and maximum (light grey band) discharge

June (0.81°C, $p < 0.001$) and July (0.45°C, $p = 0.001$), cooler water in August (−0.57°C, $p < 0.001$) and nearly no change September (−0.05°C, $p = 0.05$).

4.3 | Dissolved oxygen

Observed DO concentrations (Table 5 and Figures 5 and 6) indicated that hypoxic conditions prevailed during the monitoring period based on a 5 mg/L minimum threshold that we used for biological significance (Davis, 1975). Mean daily DO at NFWC was 3.9 and 3.3 mg/L at the pond surface and bottom. Mean DO concentrations at TC were also below the biological threshold but with greater differences between pond surface and bottom than at NFWC.

Pond bottoms at both sites were below the 5-mg/L DO threshold for 78% and 88% of the monitoring period at NFWC and TC. Pond surface DO concentrations at NFWC and TC were below the threshold 75% and 57% of the monitoring period. We also found that DO concentrations at the pond surface and bottom were simultaneously below the biological threshold for 66% and 57% of the monitoring period at NFWC and TC. Observed DO concentrations at the bottom and surface of both ponds increased towards the end of the monitoring period, concurrent with increased streamflow discharge in September (Figures 5 and 6).

Oxygen saturation at both ponds also remained low during the study period. Mean daily oxygen saturation at NFWC was 40% at the pond surface and 33% at the pond bottom, with mean maximum daily oxygen saturation of 72 (surface) and 66% (bottom). At TC, surface and bottom mean daily oxygen saturation was 49% and 26%; mean maximum daily oxygen saturation was 64% (surface) and 41% (bottom).

4.4 | Surface air temperature, precipitation and stream discharge

Mean temperature and precipitation anomalies from the 30-year average (hereafter normal) across our study sites (Table 6) generally indicated that conditions were warmer and drier during early summer when our study period began and wetter and cooler during early fall when the study period ended. Estimated mean monthly maximum surface air temperatures were greater than normal in June (2.2°C), below normal in July (−1.1°C), near normal in August (0.02°C) and below normal in September (−2.9°C). In comparison, June and July received 26% and 42% of the normal precipitation. The second half of the monitoring season was abnormally wet with 143% and 345% of normal precipitation in August and September. Stream discharge (Figure 7) shows consistent recession of median flows across sites from just over 0.02 m^3/s in early June to the seasonal minima of less than 0.005 m^3/s in late August. Median discharge increased to nearly 0.03 m^3/s in early and mid-September, corresponding to the timing of above normal late season precipitation.

5 | DISCUSSION

We observed variable influences of beaver ponds on water quality across a diverse river network. Stream temperatures warmed immediately downstream of the beaver pond outlets and the degree of warming decreased with distance downstream. Further, the warming observed at 0 m below the dam/dam complexes appeared to be most strongly related to pond bottom temperatures. Dissolved oxygen (DO) concentrations in the two beaver ponds that we monitored were frequently below tolerance thresholds for salmon and trout throughout the late summer and early fall. We discuss each of these findings below, as well as implications for expectations associated with desired outcomes for beaver-related restoration (BRR).

5.1 | Downstream warming

Our results agree with many other studies of the overall effects of beaver ponds on stream temperature (Avery, 2002; Collen & Gibson, 2000; Ecke et al., 2017; Johnson-Bice et al., 2018; Means, 2018). Our results contrast, however, with results reported from some western North American studies, where decreased maximum summer stream temperatures have been observed below beaver ponds (Dittbrenner, 2019; Weber et al., 2017, but see Jones et al., 2018). The divergent findings from these studies likely point to a host of context-specific or contingent outcomes that may be expected from beaver-constructed ponds on streams (Ciotti et al., 2021; Nash et al., 2021; Pilliod et al., 2017).

Stream temperatures warmed downstream of beaver ponds in early and mid-summer across the ponds we monitored in the Umpqua. Although some studies have reported cooling of stream temperatures related to beaver ponds or BDAs, warming is the most prevalent response reported in meta-analyses of upstream versus downstream comparisons (Ecke et al., 2017). Relative to the references we used, however, mean warming declined with downstream distance from ponds, particularly at 200, 300 and 400 m. Although we did not quantify light or shading in this study, increases in the surface area of water (i.e., transformation of the stream into a single or series of ponds by beaver) and consumption of riparian trees by beaver should be expected to increase inputs of solar radiation and associated stream heating as noted in other studies (Majerova et al., 2015; Moore, Spittlehouse, & Story, 2005).

The longitudinal extent of downstream warming associated with beaver ponds has not been well studied but our findings are similar to Alexander (1998) who found warming signals persisted several hundred meters downstream of ponds. These results are also consistent with studies of stream warming following forest harvests (Groom et al., 2011; Moore, Spittlehouse, & Story, 2005). For example, Roon, Dunham, & Torgersen et al., (2021) reported the magnitude of warming and downstream extent of heated water was proportional to the length of stream reach adjacent to harvests. Water temperatures eventually cooled with distance below the harvest units, once the streams were again shaded by riparian vegetation. We did not estimate how warming varied by pond area, but warming was shown to increase in relation to pond area in other studies (Fuller & Peckarsky, 2011) and remains a topic for future research. Like Roon, Dunham, & Torgersen et al., (2021), however, we expect that the distance over which warmer stream temperatures persisted downstream was related to the magnitude of warming.

Our estimates of pond influences on downstream temperatures suggest associations with both pond surfaces and bottoms but a stronger coupling between water at pond bottoms and water at 0 m downstream. Impounding water above a beaver dam will force water to downwell through the pond bottom and flow under the dam. These subsurface flows are described by Darcy's Law, where the amount of water flowing under the dam will be a function of (1) the hydraulic gradient which will be the difference between the water surface elevation in the pond and the water surface elevation in the stream, divided by the horizontal distance between the two points; (2) the hydraulic conductivity of the substrate which is a function of the sediment size distribution; and (3) the cross-sectional area of the subsurface zone through which water flows—effectively determined by the depth and width of sediment filling the valley (Hester et al., 2009). Clearly, a basic hydrogeologic mechanism exists that will drive flows of hyporheic water under the beaver dam which then upwells into the stream. The magnitude of this effect will depend on the height of the dam and the texture of the valley floor sediment. Tall dams built over coarse valley fills would be expected to promote extensive hyporheic flows, like those observed by Baxter and Hauer (2000) in a glacially formed valley segment. They noted, however, that hyporheic flows were likely to be much more limited in non-glaciated landscapes where alluvial sediment in low-gradient, wide valleys is likely to be relatively fine textured. White (1990) also examined hyporheic flowpaths beneath dams in sand-bedded streams and showed that hyporheic upwelling below the dam was confined to a short distance (<1 m) downstream of dams.

The temperature of these hyporheic exchange flows will be dependent on the temperature of the downwelling water and the residence time of the water on the hyporheic flow path. Short flowpaths would be expected to reflect the temperature of the pond bottom water with little time lag. The temperature of upwelling water from very long flow paths, however, will reflect the temperature of the pond bottom water days, weeks or even months previously, but modified by any thermal exchanges that occur along the flowpath. These thermal exchanges are dependent on (1) the temperature gradient between water and the substrate (during the summer temperatures decrease with depth); (2) the thermal conductivity of the substrate that influences how efficiently energy is transferred; and (3) the length of time that water remains in the subsurface for these heat exchanges to occur (Anderson, 2005; Conant, 2004).

Because of the differences in site conditions among locations, we should expect that, in some places, exchange flows beneath beaver dams should have a cooling effect on summer stream temperatures for some distance downstream of the dam (Caissie, 2006; Conant, 2004; Mayer, 2012). In our case, the water that downwelled from the pond bottom was warm, relative to the upstream reference, prior to downwelling. Moreover, based on the persistence of the downstream heating anomalies we expect that the cooling influence of subsurface heat exchanges were limited. This may have been due, in part, to shallow subsurface flows where temperature gradients between water and substrate were small, short subsurface residence time between points of downwelling and upwelling, or a combination of both factors. This explanation is corroborated by our comparisons that show daily maximum pond bottom temperatures were warmer than reference temperatures in June and July when downstream heating at 0 m was greatest and cooler in August when heating at 0 m was smallest. This pattern is also consistent with results from the monthly pond regression models showing strong coupling of pond bottom temperatures with 0 m temperatures in June and July and weak coupling in August. In sum, these two lines of evidence suggest that warming at 0 m may have been the result of hyporheic flows that transported heated water from pond bottoms beneath pond dams into the downstream channel.

The declining heat signal we observed with distance downstream from the dam suggests that water temperatures were warmer than the equilibrium temperature for the conditions along the stream below the dam. Under these conditions, streams lose heat through a variety of thermal fluxes—especially from evaporation (sensible heat losses) and longwave radiation losses (Davis et al., 2016; Moore, Sutherland, et al., 2005). Summer cooling of streams due to influxes of colder subsurface water and increases in subsurface flows from adjacent floodplains are often cited as expectations for BRR. Past studies have reported increased water table elevations following construction of beaver dams or BDAs (Dittbrenner, 2019; Munir & Westbrook, 2020; Orr et al., 2020; Scamardo & Wohl, 2020) along with increases in downstream discharge (Majerova et al., 2015, 2020; Westbrook et al., 2006) and/or temperature decreases (Dittbrenner, 2019; Weber et al., 2017).

Groundwater seems an unlikely explanation for the declining heat signal we observed with distance downstream of the dams. We did not monitor water table elevations nor make the other measurements that would allow us to directly estimate the potential groundwater influence on stream temperatures. However, we do know that subsurface water temperature with a long residence time would be much colder than the monthly average of the daily maximum stream temperature in summer. Thus, if upwelling water had a substantial effect on stream temperatures, we would not expect temperatures to converge towards the upstream reference temperature with distance downstream. In fact, we would expect maximum daily temperatures to be colder than the upstream reference because groundwater contributions should have the greatest thermal influence in summer when discharge is low. Simply put, it would be highly unlikely that the net effect of groundwater inflows, combined with all other thermal exchanges, would allow downstream mean daily maximum water temperatures to converge to almost exactly the same temperature as observed in the upstream reference reach.

Although we cannot definitively reject groundwater influences, a more parsimonious explanation is that heated water exiting the ponds simply lost energy downstream as it returned to the streams' mean temperature expected for the downstream reach (Davis et al., 2016). Garner et al. (2014) reported decreased rates of downstream heating in a stream without notable groundwater inputs as water moved out of solar-exposed moorland into a forested reach, owing to reduced energy fluxes. As discussed earlier, similar patterns were observed in streams where forest harvests opened riparian canopies and resulted in localized or moderately extended pulses of heat that declined with distance from the opening (Davis et al., 2016; Roon, Dunham, & Groom, 2021; Wondzell et al., 2019). Thus, we think the most likely explanation for the patterns we observed is warm water from the beaver ponds re-equilibrating to the ambient conditions of the downstream reaches. We would also, in general, expect the equilibrium temperatures of the upstream reference reach to be similar to the downstream reach. Consequently, we would expect the water temperature in the downstream reach to converge towards the reference temperature with distance downstream. This expected pattern is largely consistent with our results.

We also found strong intra-seasonal differences in longitudinal temperature patterns downstream of the beaver ponds during the monitoring period. As we discussed above, observable warming was greatest in June and July near the dam but declined in magnitude and downstream extent during August and September. This temporal pattern appears inversely related to seasonal streamflow and somewhat counter to our expectations that pond residence times would increase during the seasonal flow minima, resulting in greater pond heating and downstream warming (Caissie, 2006; Moore, Sutherland, et al., 2005). Whereas pond surface temperatures in August seem to validate these expectations, they do not explain why this energy did not manifest as downstream warming. One explanation is that pond stratification increased during seasonal flow minimums and may have isolated energy gains at the surface from pond bottoms in comparison to previous months. Comparisons showing that mean daily maximum temperatures at the pond bottoms were warmer than the reference in June and July but cooler in August support this explanation.

It is also possible that the minimal discharges observed in August led to a proportionally larger influence of local heat exchanges downstream when streams become hydrologically disconnected during low flow periods (Gendaszek et al., 2020). During these periods, temperature shifts can occur over short distances (Johnson, 2004) when summer stream velocity and thermal mass are limited (Moore, Spittlehouse, & Story, 2005). This explanation is consistent with the results from our pond models that showed the importance of site level factors on downstream temperature in August relative to other months. The influence of limited late summer stream discharge, combined with the variability of coupling between heated water at the pond bottoms across the summer, offer the most probable explanation of the temporal pattern of downstream heating that we observed.

Overall, our temperature findings add to syntheses of previous studies that reported warming stream temperatures below beaver dams (Collen & Gibson, 2000; Ecke et al., 2017; Johnson-Bice et al., 2018). The warming we observed downstream suggests that transfer of heat from ponds, particularly from pond bottoms, was more important than conductive heat losses to the subsurface in the streams we studied. We also found that the longitudinal extent of these effects appeared to decline with downstream distance and are seasonally dependent which we posit may be partially influenced by streamflow recession.

These findings point to the context-dependency of downstream effects that beaver dams may generate (Larsen et al., 2021). We emphasize the role that watershed and site level factors likely have on downstream responses. Our analysis points to the importance of pond water on associated downstream temperatures and helps narrow consideration of possible geomorphic characteristics defining how surface energy is exchanged within ponds and ultimately downstream. The context-dependency of downstream effects is also influenced by study design, including how reference temperatures were estimated and, perhaps more importantly, over what timeframes upstream and downstream reaches were compared. In this study, we employed a multi-point sampling design to capture energy fluxes along a greater longitudinal transect to improve representation of equilibrium temperatures. This design should improve the robustness of reference temperatures used for downstream comparisons. We also reported our findings at multiple intervals within summer and early fall seasons when high stream temperature can limit available habitats for coldwater species. These timesteps showed a variable temporal and longitudinal heating signal below beaver ponds that points to the non-stationarity of physical processes driving downstream responses.

5.2 | Dissolved oxygen

Increases in stream temperature below beaver dams can reduce the concentration of DO in the stream water, leading to adverse ecological impacts. Hypoxia can impose physiological stress on aquatic organisms and has resulted in mass die-off events in both marine (Diaz & Rosenberg, 2008; Stauffer et al., 2012) and freshwater environments (La & Cooke, 2011). Davis (1975) reported that freshwater fishes may begin experiencing stress at DO concentrations below 7 mg/L and severe harm below 5 mg/L. The results from our monitoring suggest that extremely hypoxic conditions persisted throughout much of 32-day monitoring period based on a 5-mg/L threshold and frequently dropped to 0 mg/L near pond bottoms. These observations indicate that hypoxia was more severe and frequent at the pond bottoms, but we also found that both the surface and bottom locations (and likely the entire water column) within each pond was below the 5-mg/L threshold for more than half of the monitoring period. If these vertical patterns were representative of spatial extents across the ponds, then behavioural adaptations such as diel migrations (Chapman & Mckenzie, 2009; Rahel & Nutzman, 1994) would have been ineffective at escaping hypoxic conditions. Instead, individuals may need to concentrate in areas of inflowing water with elevated DO—if such supplies existed, exit the ponds, which can be difficult during low discharge periods of the year, or face mortality. Overall, our results indicate that conditions within these ponds were unsuitable for salmonids for more than half of the monitoring period.

The patterns of low DO appear consistent with expectations associated with the demands of respiration and limited stream inflows to replenish DO in ponds. The diel pattern of DO was consistent with expectations of small lentic systems when DO decreases during non-photic hours of the day as oxygen production from photosynthesis declined (Hanson et al., 2006), but oxygen consumed via respiration continued (Chang & Ouyang, 1988). We also estimated that mean daily maximum saturation across the study period was below 100%. This suggests that concentrations of DO may have been limited by the supply of oxygen, though we did not measure DO in streams flowing into the ponds, and as well as declining solubility of oxygen as water temperatures increased. Our interpretation of processes driving DO in ponds is consistent with observations that DO rose appreciably following storms and increased discharge in September.

It is also notable that during this period at NF Walker Creek, pond bottom DO was greater than DO at the pond surface. We do not have an entirely satisfactory explanation for this observation. It is possible that oxygenated stream discharge flowing into the pond may not have mixed evenly and could have disproportionally influenced DO at the pond bottom. Incoming discharge would need to have been relatively dense to underride or wedge below pond surface water for this to have occurred. The likelihood of such an explanation is unclear but could have been possible with large enough temperature gradients between incoming discharge and pond water.

5.3 | Biological impacts

The potential biological implications of water quality responses we report here may run counter to the expectation that BRR unconditionally benefits coldwater species such as salmonids (Nash et al., 2021). In practice, many conditions likely influence impacts of BRR on these species. In the streams we studied, both mean maximum daily temperature and DO concentrations indicated unfavourable habitat conditions for the survival of salmonids. Other studies in the region reported that greater thermal heterogeneity downstream of beaver ponds could benefit individual fitness by offering a wider range of habitat availability (Bouwes et al., 2016; Weber et al., 2017). In those cases, however, temperatures cooled downstream of natural and artificial beaver dams and offered late season thermal refuge, via lateral groundwater inputs or hyporheic upwelling. Whereas in our system, changes to the diversity of downstream habitats were driven by warming. In another study, temperature increases similar to the findings reported here (1–2°C) were associated with greater growth among coho (*O. kisutch*) and Chinook (*O. tshawytschwa*) salmon juveniles (Malison et al., 2015). However, temperatures in that study did not exceed 12°C, suggesting the fitness benefits to juvenile salmon from warming occurred because the system did not reach temperatures likely to cause stress in salmonids (Richter & Kolmes, 2005). Although we observed warming in beaver ponds and below dams in this study, the downstream extent of this response was spatially limited. Warming was also most pronounced earlier in summer and temperatures in that timeframe were warm enough to produce stress in salmonids.

Without reference data, we cannot definitively attribute the hypoxic DO conditions that we observed in the two ponds as unique to the respective upstream reaches. Our observations, however, are consistent with expectations that respiration would deplete DO in isolated lentic environments such as aquaculture ponds (Chang & Ouyang, 1988; Romaire et al., 1978) and described in reviews (Collen & Gibson, 2000) and meta-analysis (Ecke et al., 2017) of beaver pond influences on streams. Hypoxic conditions in the two beaver ponds we observed appear much more limiting to salmonids than the thermal impacts discussed above. Under hypoxic conditions, the partial pressure required for oxygen exchange across gill surfaces is decreased, which can cause decreased mobility and growth among juvenile fishes (Davis, 1975) and have been reported as a leading cause of fish kills (La & Cooke, 2011). Low oxygen concentrations can also impact aquatic health indirectly by favouring microbial processes that produce methylmercury (MeHg), a biologically available form of mercury (Bigham et al., 2017; Hsu-Kim et al., 2013). Elevated MeHg has been observed in beaver pond water (Ecke et al., 2017; Roy et al., 2009) and in dam structures (Čiuldienė et al., 2020) with other studies demonstrating that MeHg can bioaccumulate in aquatic organisms and spill over to terrestrial food webs (Jackson et al., 2020). Summer hypoxia in beaver ponds can impact salmonids through at least two pathways. Hypoxic conditions could act as movement barriers for individuals seeking to move through the stream network. Such restrictions on movement could constrain the capacity of individuals to seek complementary habitats or summer refuges (e.g., deeper or cooler water, Snyder et al., 2020). It is also possible that beaver ponds that produce seasonal hypoxia may serve as ecological traps (Battin, 2004; Robertson & Hutto, 2006), where fish may be attracted to conditions within ponds that eventually turn lethal if they are unable to move to suitable conditions elsewhere. Although others have reported beaver ponds to provide important habitats for juvenile salmonids by providing refuge from high winter flows or low summer flows (Leidholt-Bruner et al., 1992; Pollock et al., 2004), our findings indicate caution is warranted in extending these observations to systems where specific responses are not known.

6 | CONCLUSION

The results of this work reinforce findings from reviews of the effects of beavers on streams that report a range of outcomes for water quality, with respect to water temperature and DO (Collen & Gibson, 2000; Ecke et al., 2017). This highlights the notion of contingency-based restoration (Nash et al., 2021): that is, that meeting restoration expectations, such as decreased downstream temperature, may be contingent on a specific set of hydrological and geomorphic processes that generate sufficient cold-subsurface inputs to overcome solar heating. Such contingencies can be critical to consider if BRR treatments (Pilliod et al., 2017) are implemented with the expectation that a common set of outcomes will result (Johnson-Bice et al., 2018; Nash et al., 2021). For example, if beaver ponds are viewed as a means of improving water quality in systems such as those in this study, whether in response to a perceived lack of beaver on the landscape, climate adaptation, or other response, beaver ponds may not only fail to meet desired outcomes, but produce results contrary to common restoration objectives (Ciotti et al., 2021; Dilling et al., 2015).

With these and similar findings in mind, improved guidance for BRR would help to avoid undesirable outcomes from well-intended efforts (Lautz et al., 2019). Instead, BRR outcomes may be improved by further research on what factors lead to lower water quality conditions and offer strategies to manage these risks through site selection and treatment design. It is also worth considering the prevalence of beaver and associated influences within entire riverscapes, as the influences of local changes to water quality observed here attenuated relatively rapidly in a downstream direction, as reported for other localized changes such as thinning of forests in riparian zones (Roon, Dunham, & Groom, 2021). Finally, other objectives (e.g., sediment retention, creation of wetlands or restoration of beavers populations per se; Nash et al., 2021; Pollock et al., 2015) may be more important to stakeholders than the responses we studied here. Overall, findings of this work highlight the complexities and trade-offs associated with influences of beaver and BRR in streams and the context-dependency of possible project outcomes.

7 | STATEMENT OF SIGNIFICANCE

Despite popular expectations that beaver dams consistently lead to watershed improvements that benefit aquatic biota, such outcomes may be contingent on the specific physical processes or biological requirements of a stream. Our study design was observational and cannot be used to make causal inferences related to beaver pond influences on downstream conditions, per se. Our results are consistent, however, with meta-analyses of similar studies and showed that water quality declined in and below beaver dams. While benefits of BRR may override water quality concerns in other contexts, the evidence suggests that managers implementing BRR practices do so with caution in streams limited by water quality or where improving water quality is an explicit goal.

ACKNOWLEDGEMENTS

Funding for this work was supported by a cooperative agreement between the U.S. Department of Agriculture, National Wildlife Research Center and Oregon State University and donations from the North Umpqua Foundation Scholarship Fund. Equipment and in-kind support was provided by the U.S. Bureau of Land Management, Medford OR District, the U.S. Fish and Wildlife Service, Roseburg OR Field Office and the Aquatic and Riparian Effectiveness Monitoring Plan of the Regional Ecosystem Office for the Northwest Forest Plan. Publication of the paper was supported, in part, by the Henry Mastin Graduate Student Fund. Many thanks to Ariel Muldoon for providing generous advice on R programming and statistical modeling techniques and to Vanessa Petro and Derek Allen for suffering through thorny thickets to help collect these data. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

DATA AVAILABILITY STATEMENT

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

ENDNOTES

[1] http://www.netmaptools.org

[2] https://streamstats.usgs.gov

[3] https://www.douglascountyor.us/streamreadings/streamsnws.asp

[4] PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created Jan. 18, 2021.

[5] https://water.usgs.gov/water-resources/software/DOTABLES/

REFERENCES

Alexander, M. D. (1998). *Effects of beaver (Castor canadensis) impoundments on stream temperature and fish community species composition and growth in selected tributaries of Miramichi River*. Canadian technical report of fisheries and aquatic sciences. https://publications.gc.ca/site/eng/79463/publication.html

Anderson, M. P. (2005). Heat as a ground water tracer. *Groundwater*, *43*(6), 951–968. https://doi.org/10.1111/j.1745-6584.2005.00052.x

Archfield, S. A., & Vogel, R. M. (2010). Map correlation method: Selection of a reference streamgage to estimate daily streamflow at ungaged catchments. *Water Resources Research*, *46*(10), W10513. https://doi.org/10.1029/2009WR008481

Avery, E. (2002). *Fish community and habitat responses in a northern Wisconsin brook trout stream 18 years after beaver dam removal*. Wisconsin Department of Natural Resources. https://fyi.extension.wisc.edu/beaver/files/2011/10/Avery-2002-WDNR-18-year-Beaver-Dam-Removal-Study.pdf

Battin, J. (2004). When good animals love bad habitats: Ecological traps and the conservation of animal populations. *Conservation Biology*, *18*(6), 1482–1491. https://doi.org/10.1111/j.1523-1739.2004.00417.x

Baxter, C. V., & Hauer, F. R. (2000). Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (Salvelinus confluentus). *Canadian Journal of Fisheries and Aquatic Sciences*, *57*(7), 1470–1481. https://doi.org/10.1139/f00-056

Benda, L., Miller, D., Andras, K., Bigelow, P., Reeves, G., & Michael, D. (2007). NetNetMap: A newtool in support of watershed science and resource management. *Forest Science*, *53*(2), 206–219.

Bennett, S. N., Wheaton, J. M., Bouwes, N., Jordan, C. E., Macfarlane, W. W., Maestas, J. D., Portugal, E., & Shahverdian, S. M. (2019). Chapter 3: Planning for low-tech process-based restoration. In J. M. Wheaton, S. N. Bennett, N. Bouwes, J. D. Maestas, & S. M. Shahverdian (Eds.), *Low-tech process-based restoration of riverscapes: Design manual* (p. 57). Utah State University Restoration Consortium. https://doi.org/10.13140/RG.2.2.15815.75680

Bigham, G. N., Murray, K. J., Masue-Slowey, Y., & Henry, E. A. (2017). Biogeochemical controls on methylmercury in soils and sediments: Implications for site management. *Integrated Environmental Assessment and Management*, *13*(2), 249–263. https://doi.org/10.1002/ieam.1822

Bouwes, N., Weber, N., Jordan, C. E., Saunders, W. C., Tattam, I. A., Volk, C., Wheaton, J. M., & Pollock, M. M. (2016). Ecosystem experiment reveals benefits of natural and simulated beaver dams to a threatened population of steelhead (*Oncorhynchus mykiss*). *Scientific Reports*, *6*, 1–12. https://doi.org/10.1038/srep28581

Brown, V. A. (2021). An introduction to linear mixed-effects modeling in R. *Advances in Methods and Practices in Psychological Science*, *4*(1), 2515245920960351. https://doi.org/10.1177/2515245920960351

Caissie, D. (2006). The thermal regime of rivers: A review. *Freshwater Biology*, *51*(8), 1389–1406. https://doi.org/10.1111/j.1365-2427.2006.01597.x

Chang, W. Y. B., & Ouyang, H. (1988). Dynamics of dissolved oxygen and vertical circulation in fish ponds. *Aquaculture*, *74*(3), 263–276. https://doi.org/10.1016/0044-8486(88)90370-5

Chapman, L. J., & Mckenzie, D. J. (2009). Chapter 2 Behavioral responses and ecological consequences. In J. G. Richards, A. P. Farrell, & C. J. Brauner (Eds.), *Fish physiology* (Vol. 27, pp. 25–77). Academic Press. https://doi.org/10.1016/S1546-5098(08)00002-2

Ciotti, D. C., Mckee, J., Pope, K. L., Kondolf, G. M., & Pollock, M. M. (2021). Design criteria for process-based restoration of fluvial systems. *BioScience*, *71*(8), 831–845. https://doi.org/10.1093/biosci/biab065

Čiuldienė, D., Vigricas, E., Belova, O., Aleinikovas, M., & Armolaitis, K. (2020). The effect of beaver dams on organic carbon, nutrients and methyl mercury distribution in impounded waterbodies. *Wildlife Biology*, *2020*, wlb.00678. https://doi.org/10.1111/wlb.00678

Clark, T. (2020). *Impacts of beaver dams on mountain stream discharge and water temperature*. Utah State University. https://digitalcommons.usu.edu/gradreports/1485

Cluer, B., & Thorne, C. (2014). A stream Evolution model integrating habitat and ecosystem benefits. *River Research and Applications*, *30*(2), 135–154. https://doi.org/10.1002/rra.2631

Collen, P., & Gibson, R. J. (2000). The general ecology of beavers (Castor spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish – A review. *Reviews in Fish Biology and Fisheries*, *10*(4), 439–461. https://doi.org/10.1023/A:1012262217012

Conant, B. (2004). Delineating and quantifying ground water discharge zones using streambed temperatures. *Groundwater*, *42*(2), 243–257. https://doi.org/10.1111/j.1745-6584.2004.tb02671.x

Daly, C., Halbleib, M., Smith, J. I., Gibson, W. P., Doggett, M. K., Taylor, G. H., Curtis, J., & Pasteris, P. P. (2008). Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*, *28*(15), 2031–2064. https://doi.org/10.1002/joc.1688

Daly, C., Neilson, R. P., & Phillips, D. L. (1994). A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology and Climatology*, *33*(2), 140–158. https://doi.org/10.1175/1520-0450(1994)033<0140:ASTMFM>2.0.CO;2

Davis, J. (1975). Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: A review. *Journal of the Fisheries Research Board of Canada*, *32*(12), 2295–2332.

Davis, L. J., Reiter, M., & Groom, J. D. (2016). Modelling temperature change downstream of forest harvest using Newton's law of cooling. *Hydrological Processes*, *30*(6), 959–971. https://doi.org/10.1002/hyp.10641

Diaz, R. J., & Rosenberg, R. (2008). Spreading dead zones and consequences for marine ecosystems. *Science*, *321*(5891), 926–929. https://doi.org/10.1126/science.1156401

Dilling, L., Daly, M. E., Travis, W. R., Wilhelmi, O. V., & Klein, R. A. (2015). The dynamics of vulnerability: Why adapting to climate variability will not always prepare us for climate change. *WIREs Climate Change*, *6*(4), 413–425. https://doi.org/10.1002/wcc.341

Dittbrenner, B. J. (2019). *Restoration potential of beaver for hydrological resilience in a changing climate*. University of Washington. https://search.proquest.com/docview/2290954308?pq-origsite=summon

Donald, C., Grund, Y., & Michie, R. (2020). *Oregon statewide status and trends report*. Oregon Department of Environmental Quality. https://www.oregon.gov/deq/wq/programs/Pages/wqstatustrends.aspx

Dunham, J., Chandler, G., Rieman, B., & Martin, D. (2005). *Measuring stream temperature with digital data loggers: A user's guide. Gen. Tech. Rep. RMRS-GTR-150*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 15, 150. https://doi.org/10.2737/RMRS-GTR-150

Ecke, F., Levanoni, O., Audet, J., Carlson, P., Eklöf, K., Hartman, G., McKie, B., Ledesma, J. L. J., Segersten, J., Truchy, A., & Futter, M. (2017). Meta-analysis of environmental effects of beaver in relation to artificial dams. *Environmental Research Letters*, *12*, 113002. https://doi.org/10.1088/1748-9326/aa8979

Falke, J. A., Dunham, J. B., Hockman-Wert, D., & Pahl, R. (2016). A simple prioritization tool to diagnose impairment of stream temperature for Coldwater fishes in the Great Basin. *North American Journal of Fisheries Management*, *36*(1), 147–160. https://doi.org/10.1080/02755947.2015.1115449

Fuller, M. R., & Peckarsky, B. L. (2011). Ecosystem engineering by beavers affects mayfly life histories. *Freshwater Biology*, *56*(5), 969–979. https://doi.org/10.1111/j.1365-2427.2010.02548.x

Garner, G., Malcolm, I. A., Sadler, J. P., & Hannah, D. M. (2014). What causes cooling water temperature gradients in a forested stream reach? *Hydrology and Earth System Sciences*, *18*(12), 5361–5376. https://doi.org/10.5194/hess-18-5361-2014

Gendaszek, A. S., Dunham, J. B., Torgersen, C. E., Hockman-Wert, D. P., Heck, M. P., Thorson, J., Mintz, J., & Allai, T. (2020). Land-cover and climatic controls on water temperature, flow permanence, and fragmentation of Great Basin stream networks. *Water*, *12*(7), 1962. https://doi.org/10.3390/w12071962

Gianfagna, C. C., Johnson, C. E., Chandler, D. G., & Hofmann, C. (2015). Watershed area ratio accurately predicts daily streamflow in nested catchments in the Catskills, New York. *Journal of Hydrology: Regional Studies*, *4*, 583–594. https://doi.org/10.1016/j.ejrh.2015.09.002

Groom, J. D., Dent, L., Madsen, L. J., & Fleuret, J. (2011). Response of western Oregon (USA) stream temperatures to contemporary forest management. *Forest Ecology and Management*, *262*(8), 1618–1629. https://doi.org/10.1016/j.foreco.2011.07.012

Hanson, P. C., Carpenter, S. R., Armstrong, D. E., Stanley, E. H., & Kratz, T. K. (2006). Lake dissolved inorganic carbon and dissolved oxygen: Changing drivers from days to decades. *Ecological Monographs*, *76*(3), 343–363. https://doi.org/10.1890/0012-9615(2006)076[0343:LDICAD]2.0.CO;2

Heck, M. P., Schultz, L. D., Hockman-Wert, D., Dinger, E. C., & Dunham, J. B. (2018). *Monitoring stream temperatures—A guide for* *non-specialists. In monitoring stream temperatures—A guide for non-specialists (USGS numbered series no. 3-A25; techniques and methods)* (Vol. 3-A25, p. 84). U.S. Geological Survey. https://doi.org/10.3133/tm3A25

Hester, E. T., Doyle, M. W., & Poole, G. C. (2009). The influence of in-stream structures on summer water temperatures via induced hyporheic exchange. *Limnology and Oceanography*, *54*(1), 355–367. https://doi.org/10.4319/lo.2009.54.1.0355

Hsu-Kim, H., Kucharzyk, K. H., Zhang, T., & Deshusses, M. A. (2013). Mechanisms regulating mercury bioavailability for methylating microorganisms in the aquatic environment: A critical review. *Environmental Science & Technology*, *47*(6), 2441–2456. https://doi.org/10.1021/es304370g

Jackson, A. K., Eagles-Smith, C. A., & Emery, C. (2020). Spatial variation in aquatic invertebrate and riparian songbird mercury exposure across a river-reservoir system with a legacy of mercury contamination. *Ecotoxicology*, *29*(8), 1195–1204. https://doi.org/10.1007/s10646-019-02043-z

Johnson, M. F., Thorne, C. R., Castro, J. M., Kondolf, G. M., Mazzacano, C. S., Rood, S. B., & Westbrook, C. (2020). Biomic river restoration: A new focus for river management. *River Research and Applications*, *36*(1), 3–12. https://doi.org/10.1002/rra.3529

Johnson, S. L. (2004). Factors influencing stream temperatures in small streams: Substrate effects and a shading experiment. *Canadian Journal of Fisheries and Aquatic Sciences*, *61*(6), 913–923. https://doi.org/10.1139/f04-040

Johnson-Bice, S. M., Renik, K. M., Windels, S. K., & Hafs, A. W. (2018). A review of beaver–salmonid relationships and history of management actions in the western Great Lakes (USA) region. *North American Journal of Fisheries Management*, *38*(6), 1203–1225. https://doi.org/10.1002/nafm.10223

Jones, C. G., Lawton, J. H., & Shachak, M. (1996). Organisms as Ecosystem Engineers. In F. B. Samson & F. L. Knopf (Eds.), *Ecosystem management: Selected readings* (pp. 130–147). Springer. https://doi.org/10.1007/978-1-4612-4018-1_14

Jones, K., White, J., Smith, C., Poor, E., Doyle, M., Costello, A., & Rounds, S. (2018). *Overview of the Tualatin urban beaver dam study*. https://prd-wret.s3.us-west-2.amazonaws.com/assets/palladium/production/atoms/files/1_Overview_final_Feb%209%202018_0.pdf

La, V. T., & Cooke, S. J. (2011). Advancing the science and practice of fish kill investigations. *Reviews in Fisheries Science*, *19*(1), 21–33. https://doi.org/10.1080/10641262.2010.531793

Larsen, A., Larsen, J. R., & Lane, S. N. (2021). Dam builders and their works: Beaver influences on the structure and function of river corridor hydrology, geomorphology, biogeochemistry and ecosystems. *Earth-Science Reviews*, *218*, 103623. https://doi.org/10.1016/j.earscirev.2021.103623

Lautz, L., Kelleher, C., Vidon, P., Coffman, J., Riginos, C., & Copeland, H. (2019). Restoring stream ecosystem function with beaver dam analogues: Let's not make the same mistake twice. *Hydrological Processes*, *33*(1), 174–177. https://doi.org/10.1002/hyp.13333

Leidholt-Bruner, K., Hibbs, D., & McComb, B. (1992). Beaver dam locations and their effects on distribution and abundance of coho salmon fry in two coastal Oregon streams. *Northwest Science*, *66*(4), 218–223.

Majerova, M., Neilson, B. T., & Roper, B. B. (2020). Beaver dam influences on streamflow hydraulic properties and thermal regimes. *Science of the Total Environment*, *718*, 134853. https://doi.org/10.1016/j.scitotenv.2019.134853

Majerova, M., Neilson, B. T., Schmadel, N. M., Wheaton, J. M., & Snow, C. J. (2015). Impacts of beaver dams on hydrologic and temperature regimes in a mountain stream. *Hydrology and Earth System Sciences*, *19*(8), 3541–3556. https://doi.org/10.5194/hess-19-3541-2015

Malison, R. L., Eby, L. A., & Stanford, J. A. (2015). Juvenile salmonid growth, survival, and production in a large river floodplain modified by beavers (Castor canadensis). *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(11), 1639-1651 https://doi.org/10.1139/cjfas-2015-0147

Margolis, B. E., Castro, M. S., & Raesly, R. L. (2001). The impact of beaver impoundments on the water chemistry of two Appalachian streams. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(11), 2271–2283. https://doi.org/10.1139/f01-166

Markle, D. F. (2019). Drainage evolution and freshwater fish zoogeography in coastal Oregon and Washington. *Northwestern Naturalist*, *100*(2), 71–89. https://doi.org/10.1898/NWN-18-18

Mayer, T. D. (2012). Controls of summer stream temperature in the Pacific northwest. *Journal of Hydrology*, *475*, 323–335. https://doi.org/10.1016/j.jhydrol.2012.10.012

Means, C. (2018). *Stream temperature variability in headwater beaver dam complexes in relation to hydrologic and environmental factors [thesis]*. University of Washington. https://digital.lib.washington.edu:443/researchworks/handle/1773/43064

Moore, R. D., Spittlehouse, D. L., & Story, A. (2005). Riparian microclimate and stream temperature response to forest harvesting: A review. *JAWRA Journal of the American Water Resources Association*, *41*(4), 813–834. https://doi.org/10.1111/j.1752-1688.2005.tb03772.x

Moore, R. D., Sutherland, P., Gomi, T., & Dhakal, A. (2005). Thermal regime of a headwater stream within a clear-cut, coastal British Columbia, Canada. *Hydrological Processes*, *19*(13), 2591–2608. https://doi.org/10.1002/hyp.5733

Munir, T. M., & Westbrook, C. J. (2020). Beaver dam analogue configurations influence stream and riparian water table dynamics of a degraded spring-fed creek in the Canadian Rockies. *River Research and Applications*, *37*(3), 1–13. https://doi.org/10.1002/rra.3753

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Nash, C. S., Grant, G. E., Charnley, S., Dunham, J. B., Gosnell, H., Hausner, M. B., Pilliod, D. S., & Taylor, J. D. (2021). Great expectations: Deconstructing the process pathways underlying beaver-related restoration. *BioScience*, *71*(3), 249–267. https://doi.org/10.1093/biosci/biaa165

Orr, M. R., Weber, N. P., Noone, W. N., Mooney, M. G., Oakes, T. M., & Broughton, H. M. (2020). Short-term stream and riparian responses to beaver dam analogs on a low-gradient channel lacking woody riparian vegetation. *Northwest Science*, *93*(3–4), 171–184. https://doi.org/10.3955/046.093.0302

Pilliod, D. S., Rohde, A. T., Charnley, S., Davee, R. R., Dunham, J. B., Gosnell, H., Grant, G. E., Hausner, M. B., Huntington, J. L., & Nash, C. (2017). Survey of beaver-related restoration practices in rangeland streams of the western USA. *Environmental Management*, *61*, 58–68. https://doi.org/10.1007/s00267-017-0957-6

Pollock, M. M., Beechie, T. J., Wheaton, J. M., Jordan, C. E., Bouwes, N., Weber, N., & Volk, C. (2014). Using beaver dams to restore incised stream ecosystems. *BioScience*, *64*(4), 279–290. https://doi.org/10.1093/biosci/biu036

Pollock, M. M., Lewallen, G., Woodruff, K., Jordan, C. E., & Castro, J. M. (2015). *The beaver restoration guidebook: Working with beaver to restore streams, wetlands, and floodplains, Version 1.02* (p. 189). United States Fish and Wildlife Service, Portland, OR.

Pollock, M. M., Pess, G. R., Beechie, T. J., & Montgomery, D. R. (2004). The importance of beaver ponds to coho salmon production in the Stillaguamish River basin, Washington, USA. *North American Journal of Fisheries Management*, *24*(3), 749–760. https://doi.org/10.1577/M03-156.1

R Core Team. (2020). *R: A language and environment for statistical computing*. R foundation for statistical computing. https://www.R-project.org/

Rahel, F. J., & Nutzman, J. W. (1994). Foraging in a lethal environment: Fish predation in hypoxic waters of a stratified lake. *Ecology*, *75*(5), 1246–1253. https://doi.org/10.2307/1937450

Richter, A., & Kolmes, S. A. (2005). Maximum temperature limits for Chinook, coho, and chum salmon, and steelhead trout in the Pacific northwest. *Reviews in Fisheries Science*, *13*(1), 23–49. https://doi.org/10.1080/10641260590885861

Robertson, B. A., & Hutto, R. L. (2006). A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, *87*(5), 1075–1085. https://doi.org/10.1890/0012-9658(2006)87[1075:AFFUET]2.0.CO;2

Romaire, R. P., Boyd, C. E., & Collis, W. J. (1978). Predicting nighttime dissolved oxygen decline in ponds used for Tilapia culture. *Transactions of the American Fisheries Society*, *107*(6), 804–808. https://doi.org/10.1577/1548-8659(1978)107<804:PNDODI>2.0.CO;2

Roon, D. A., Dunham, J. B., & Groom, J. D. (2021). Shade, light, and stream temperature responses to riparian thinning in second-growth redwood forests of northern California. *PLoS ONE*, *16*(2), e0246822. https://doi.org/10.1371/journal.pone.0246822

Roon, D. A., Dunham, J. B., & Torgersen, C. E. (2021). A riverscape approach reveals downstream propagation of stream thermal responses to riparian thinning at multiple scales. *Ecosphere*. *Ecosphere*, *12*(10): e03775.

Rousset, F., & Ferdy, J.-B. (2014). Testing environmental and genetic effects in the presence of spatial autocorrelation. *Ecography*, *37*, 781–790. https://doi.org/10.1111/ecog.00566

Roy, V., Amyot, M., & Carignan, R. (2009). Beaver ponds increase methylmercury concentrations in Canadian shield streams along vegetation and pond-age gradients. *Environmental Science & Technology*, *43*(15), 5605–5611. https://doi.org/10.1021/es901193x

Scamardo, J., & Wohl, E. (2020). Sediment storage and shallow groundwater response to beaver dam analogues in the Colorado front range, USA. *River Research and Applications*, *36*(3), 398–409. https://doi.org/10.1002/rra.3592

Snyder, M. N., Schumaker, N. H., Dunham, J. B., Keefer, M. L., Leinenbach, P., Brookes, A., Palmer, J., Wu, J., Keenan, D., & Ebersole, J. L. (2020). Assessing contributions of cold-water refuges to reproductive migration corridor conditions for adult salmon and steelhead trout in the Columbia River, USA. *Journal of Ecohydraulics*, *0*(0), 1–13. https://doi.org/10.1080/24705357.2020.1855086

Stauffer, B. A., Gellene, A. G., Schnetzer, A., Seubert, E. L., Oberg, C., Sukhatme, G. S., & Caron, D. A. (2012). An oceanographic, meteorological, and biological 'perfect storm' yields a massive fish kill. *Marine Ecology Progress Series*, *468*, 231–243. https://doi.org/10.3354/meps09927

Vinson, M., & Levesque, S. (1994). Redband trout response to hypoxia in a natural environment. *The Great Basin Naturalist*, *54*(2), 150–155.

Weber, N., Bouwes, N., Pollock, M. M., Volk, C., Wheaton, J. M., Wathen, G., Wirtz, J., & Jordan, C. E. (2017). Alteration of stream temperature by natural and artificial beaver dams. *PLoS ONE*, *12*(5), e0176313. https://doi.org/10.1371/journal.pone.0176313

Westbrook, C. J., Cooper, D. J., & Baker, B. W. (2006). Beaver dams and overbank floods influence groundwater–surface water interactions of a Rocky Mountain riparian area. *Water Resources Research*, *42*(6), W06404. https://doi.org/10.1029/2005WR004560

White, D. S. (1990). Biological relationships to convective flow patterns within stream beds. *Hydrobiologia*, *196*(2), 149–158. https://doi.org/10.1007/BF00006106

Wondzell, S. M., Diabat, M., & Haggerty, R. (2019). What matters most: Are future stream temperatures more sensitive to changing air temperatures, discharge, or riparian vegetation? *Journal of the American Water Resources Association*, *55*(1), 116–132. https://doi.org/10.1111/1752-1688.12707

Wright, J. P., Jones, C. G., & Flecker, A. S. (2002). An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, *132*(1), 96–101. https://doi.org/10.1007/s00442-002-0929-1

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Introduction. In A. F. Zuur, E. N. Ieno, N. Walker, A. A. Saveliev, & G. M. Smith (Eds.), *Mixed effects models and extensions in ecology with R* (pp. 1–10). Springer. https://doi.org/10.1007/978-0-387-87458-6_1

How to cite this article: Stevenson, J. R., Dunham, J. B., Wondzell, S. M., & Taylor, J. (2022). Dammed water quality—Longitudinal stream responses below beaver ponds in the Umpqua River Basin, Oregon. *Ecohydrology*, *15*(4), e2430. https://doi.org/10.1002/eco.2430