

Stream temperature variability in headwater beaver dam complexes in relation to hydrologic and environmental factors

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**Abstract**

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Due to their ability to modify their environments, translocation of beaver, along with the construction of human engineered beaver dam analogs (BDAs), have become popular approaches to both stream restoration and climate-change adaptation. However, there is a lack of understanding about how beaver engineering affects aquatic ecosystems. Reported findings of how beaver dam complexes alter one of the most fundamental and important factors, stream temperature, vary considerably, and the drivers of the discrepancy remain unclear. I investigated the longitudinal and vertical variation of stream temperature in and around 24 beaver ponds across 17 headwater streams in the Methow Valley of Washington State (USA). In addition, I

explored possible hydrologic and environmental drivers of observed thermal patterns. Despite considerable variation, I found that on average beaver ponds were associated with an increase in downstream temperatures. The magnitude of this effect increased with total pond hydraulic height, which reflected the number and size of ponds per site. I also found that pond bottoms were cooler than upstream reference reaches for a period of time in the afternoon. Thus, although beaver dam complexes in the Methow watershed do not consistently cool streams—and in fact cause increases in temperatures downstream—the bottom of beaver ponds can create cool water areas during the hottest part of the day. Furthermore, if managers choose to use beaver translocation or BDAs, locations where topography would result in deeper ponds, and where canopy cover of ponds would be maximized may limit harmful temperature effects.

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## Introduction

Temperature is a key environmental variable, regulating biological processes such as metabolism and physiology, the timing of life history events, and community composition and structure (Beschta et al. 1987, Montgomery and Buffington 1998, Quinn 2011). As ectotherms, riverine fish have a narrow range of thermal tolerance, above which growth rates sharply decline due to the high cost of metabolic maintenance (Brett and Grooves 1979). By directly increasing atmospheric energy inputs, as well as reducing the thermal carrying capacity of rivers due to decreasing flow, climate change will increase the temperature of freshwater systems globally, threatening aquatic species (van Vliet et al. 2013). However, groundwater, which is buffered from the diurnal and seasonal fluctuations to which surface water is subjected, along with internal stream structure, can create patches of relatively cool water, or limit the tendency of streams to warm downstream (Poole and Berman 2001). These patches of thermal refugia can allow fish to avoid unsuitable habitat, and persist in streams that are at or near their thermal limits (Berman and Quinn 1991, Torgersen et al. 1999).

To address the impacts of climate change on stream biota, land managers have begun to explore methods for the identification, protection, and restoration of thermal refuges (Torgersen et al. 2012). Beaver (*Castor canadensis*) are being used more regularly as part of adaptation strategies to affect stream temperature and water storage, either through translocation, facilitation of natural recolonization, or mimicking beaver dam building in their historical range. Proponents of these strategies believe ponding by beaver recharges groundwater stores, which can lead to upwelling of cooler water downstream (Pollock et al. 2015). In addition, beaver have been found to increase water storage, attenuate peak flows, reconnect streams to their floodplains, and increase habitat complexity (Naiman et al. 1988, Westbrook et al. 2006, Pollock et al. 2007,

Hood and Bayley 2008, Smith and Mather 2013, Puttock et al. 2017). These effects could have benefits in the face of climate change as drought and extreme flooding events increase and biodiversity declines (Allan and Soden 2012, Bellard et al. 2012, Collins et al. 2012, Littell et al. 2013).

Though there is considerable agreement that some goals of beaver-based restoration and climate adaptation, such as increasing water storage, will be achievable, there is less conclusive evidence that beaver ponds will reduce stream temperature. Some studies have suggested that beaver ponds can provide beneficial thermal effects in the form of buffering extreme temperatures, providing cool water in the ponds themselves, or creating localized cool areas downstream. For example, beaver ponds on Bridge Creek in Oregon were found to dampen summer diel stream temperature extremes, reduce the warming between upstream controls and reaches downstream of beaver impoundments, and to create pockets downstream of dams that averaged 4.1°C cooler than ambient stream temperatures (Pollock et al. 2007, Weber et al. 2017). Additionally, in the Coldwater River in the Fraser watershed, beaver ponds were observed to be cooler than the ambient stream temperatures during the hottest part of the year (Swales and Levings 1989). Cool patches downstream of dams have been attributed to upwelling of shallow groundwater beneath the dam (Pollock et al. 2007, Weber et al. 2017). White (1990) found that ponds increase outseepage of surface water into the streambed, as well as the pressure on subsurface flows. As these flows move downstream of the pond, reductions in pressure from surface water create the potential for groundwater upwelling (White 1990, Poole and Berman 2001). In hot climates, groundwater is typically cooler than surface water in the summer, meaning these areas of upwelling might provide cool pockets of water downstream of beaver ponds (White 1990, Pollock et al. 2007, Weber et al. 2017).

Contrary to these findings, a meta-analysis found that temperatures tend to increase downstream of beaver ponds compared to upstream reference reaches (Ecke et al. 2017). This finding aligns with research showing that beaver impoundments can increase stream temperature through reduced shading, causing an increase in solar radiation (Alexander 1998, Margolis et al. 2001, Avery 2002, Andersen et al. 2011, Majerova et al. 2015, Malison et al. 2015). Other studies, although not finding a conclusive cooling effect, fall short of clearly demonstrating that beaver ponds warm streams (Talabere and Bouska 2002, Machen 2016, Bouwes et al. 2016). The lack of consensus appears to stem from a combination of site-dependent influences and insufficient spatial extents (Cook 1940, McRae and Edwards 1994, Rosell et al. 2005). A limited number of studies have investigated temperature at pond complexes on more than a few streams, making it challenging to explain the drivers behind the observed variation. Overall, we lack a complete understanding of how beaver affect their environment, especially in regard to stream temperature.

As beaver are used more frequently for restoration and climate-change adaptation, it is critical to understand not only how these strategies influence stream temperature, but also what factors are driving the variation in their effect. Doing so will allow land managers interested in beaver-based restoration and adaptation to make more informed decisions about what actions to take, and where to carry them out. In this study, I explored stream temperature in relation to beaver ponds across 17 streams in north-central Washington to evaluate their potential as a solution to climate-induced stream warming. The objectives of this study were to (1) compare longitudinal stream temperatures in and around beaver ponds in the Methow watershed, (2) evaluate vertical temperature patterns within beaver ponds, and (3) investigate what factors are associated with the variation in observed thermal patterns around beaver pond complexes.

## Methods

### *Study area and design*

This study took place in the forested headwater streams within the upper Columbia River watershed in Washington State, USA (Figure 1). This area is home to a beaver translocation program that has been working for over 10 years to increase beaver populations for restoration and climate change adaptation purposes. Two study streams were located in the contiguous Okanogan and Chief Joseph basins. The rest of the streams were located in the neighboring Methow basin, a snowmelt-dominated drainage that starts in the North Cascades at 2,700 m in elevation and eventually meets the Columbia River at an elevation of 240 m. Dry, ponderosa pine (*Pinus ponderosa*)-dominated, mixed conifer forests cover much of the lower elevations, whereas Douglas fir (*Pseudotsuga menziesii*) and subalpine fir (*Abies lasiocarpa*) are common at higher elevations. Black cottonwood (*Populus trichocarpa*), quaking aspen (*Populus tremuloides*), and red alder (*Alnus rubra*) are common in riparian zones. Thirteen percent of the watershed is shrub-steppe, where antelope bitterbrush (*Purshia tridentata*) is common. Mean air temperature during the summer of 2017, when my study took place, was 19.2 °C. Mean daily maximum and minimum air temperatures during the two weeks prior to the period of analysis were 30.6 and 9.3 °C, respectively (NWSFO 2014). Mean annual precipitation for the study area ranges from 15 to 31 cm (PRISM 2015), but summers are very dry. Mean monthly precipitation for the summer of 2017 was 0.05 cm, and no precipitation had occurred in the two weeks prior to or during our period of analysis (NWSFO 2014).

During the summer of 2017, I investigated a convenience sample of 24 sites spread across 17 low-order streams ranging from 387 m to 1,852 m in elevation (Figure 1). Sites varied

from a single pond, to complex clusters of ponds, and individual streams contained between one and six sites. At each site, I identified reaches up- and downstream of beaver ponds, referred to as  $T_u$  and  $T_d$ , respectively (Figure 1). In addition, I assigned at least one pond surface and pond bottom location, referred to as  $T_{ps}$  and  $T_{pb}$ , respectively, in 17 ponds spanning 15 of our study streams (Figure 1).

### *Field data collection*

Field measurements were made between 19-July-2017 and 27-Oct-2017. From 29-Aug-2017 to 14-Sep-2017, I recorded synoptic water temperatures at all locations every 15 minutes with submerged water temperature loggers (HOBO Pendant Temperature/Alarm Data Logger and HOBO Water Temp Pro v2 Data Logger, Onset Computer, Pocasset, Massachusetts, USA).  $T_u$  and  $T_d$  loggers were placed on the streambed in the middle of the channel in flowing water, as close to the pond as possible, while avoiding any direct effect of impounded water. Loggers were positioned to avoid intervening tributaries, but in several cases, when this was not possible, supplementary loggers were deployed in additional channels. Pond loggers were attached to a post secured in the pond bed.  $T_{pb}$  loggers were positioned as close to the sediment-water interface at the base of the pond as possible, while  $T_{ps}$  loggers were attached to the post 20 cm below the pond water surface at the time of deployment.

In addition to water temperature, I made field measurements of hydraulic height and pond dimensions at each site. Hydraulic height, defined as the vertical distance between the water surface of the pond and water surface of the stream immediately downstream of the dam, was measured with an automatic level (AT-G2A, Topcon America Corporation, Paramus, New Jersey, USA) and levelling rod graduated every 0.05 cm, or a real-time kinematic global (RTK) positioning system (R10 LT, Trimble, Sunnyvale, California, USA). I then calculated the

maximum height for each site, as well as the total site hydraulic height by adding together measurements for each dam at a site. The track-log function of a geographic positioning system (GPS) receiver (GPSmap 62sc, Garmin, Olathe, Kansas, USA) was used to delineate ponds, and record elevations and locations of sites and all temperature loggers. I measured pond lengths and widths using a measuring tape or rangefinder (Truepulse 200, Laser Technology, Centennial, Colorado, USA). In addition, I used the levelling rod to record at least three depths per pond, or at least five depths per pond at sites with few ponds.

I collected the remaining field measurements of canopy cover, gradient, discharge, and stream dimensions at the stream level. I estimated average percent canopy at each stream by taking densitometer readings at the location of the pond loggers. I took the average of four measurements made at 0, 90, 180, and 270° to provide a minimum of one estimate per stream. In addition, I calculated gradient using elevation change between two points as far apart as possible, which was measured using the auto-level or RTK as described above for measuring hydraulic heights. I then divided elevation change by the straight-line distance between the two points, which was measured with the rangefinder or measuring tape. I measured velocity up- and downstream of ponds on each stream using a portable flowmeter (Flo-Mate 2000, Marsh-McBirney, Frederick, Maryland, USA) and calculated stream flow using the velocity-area method (Turnipseed and Sauer 2010). I also measured stream depth and width above and below ponds on each stream.

#### *GIS data collection and processing*

As the sites varied substantially in size, complexity, and surrounding vegetation, I used a combination of methods to calculate surface area. In all cases, field measurements of pond dimensions aided in the process. In some instances, sites were clearly visible in satellite imagery

taken in July 2017 available through Google Earth Pro 7.3 (Google, Mountain View, California, USA). In these cases, ponds were digitized and then exported to a geographic information system (GIS), ArcMap 10.6 software (ESRI 2017), where the rest of the spatial data were analyzed. At sites where Google Earth imagery or field measurements were not sufficient, aerial imagery was used instead. Aerial imagery was acquired in the fall of 2017 with a drone (Mavic Pro, DJI, Shenzhen, Guangdong, China) and orthorectified and mosaicked using PhotoScan software (Agisoft 2018). Orthophotographs were uploaded to ArcMap, where ponds were digitized. From the digitized ponds, surface area as well as straight-line distances including pond length, defined as the distance between the inlet and outlet of each pond, and length of non-ponded reaches within each site, were calculated by subtracting the pond length from the distance between  $T_u$  and  $T_d$ .

I used a 10-m resolution digital elevation model (DEM) obtained from the U.S. Geological Survey National Elevation Dataset (USGS 2017) to delineate drainages for each of the study streams using the hydrology toolset in ArcMap as well as to create a hillshade layer. I used these layers to calculate the distance along the main flow path to the watershed divide, as well as upstream basin size for each site. I extracted mean annual precipitation and air temperature for each site using raster data of 30-year normals for 1981 – 2010 from the PRISM Climate Group (PRISM 2015).

### *Data analysis*

As I was more interested in the variation between sites than I was in variation over longer temporal periods, and because there was considerable temporal variation throughout the sampling period, I analyzed temperatures from one day. I identified 30-Aug-2017 as a hot (maximum temperature of 32.2° C), clear day, which had been preceded by a hot day (maximum

temperature of 32.8° C), when groundwater signals would be easy to discern. To evaluate how stream temperature varied longitudinally around beaver complexes, for each 15-minute interval, I subtracted  $T_u$  temperatures from  $T_d$  temperatures for each site, so that (1) a negative difference occurred when water at the downstream site was cooler and (2) a positive difference occurred when temperatures downstream were warmer. All calculated temperature metrics are explained in Table 2. To further investigate longitudinal patterns, I also subtracted  $T_u$  temperatures from associated  $T_{pb}$  temperatures, so that (1) negative differences were found when temperatures were cooler at the bottom of the pond than they were upstream, and (2) positive differences were found when temperatures were warmer at the bottom of the pond than they were upstream. From these instantaneous differences, I found the greatest decrease in temperature, or least increase if no decrease in temperature occurred, for each site. I defined this difference as the greatest downstream cooling of  $T_{pb}$  relative to  $T_u$  (MxNegDif\_UPb). I also found the time this difference occurred (TMxNegDif\_UPb). To evaluate vertical stratification within beaver ponds, I subtracted  $T_{ps}$  temperatures from the associated  $T_{pb}$  temperatures, resulting in negative values when the pond bottom was cooler than the pond surface.

I graphically evaluated relationships between explanatory variables and linear predictors. Based on the pairwise correlation of surface area and MeanDif, I transformed surface area using the natural logarithm so that it displayed a linear relationship with the mean difference. I also calculated pond morphology, defined as the natural logarithm of the quotient of hydraulic height and pond surface area (Fuller and Peckarsky 2011). In this calculation, we used the maximum hydraulic height per site to represent the greatest pressure put on the pond bed at one point. This quotient enabled me to examine the effect of hydraulic height per unit surface area, as well as to allow me to compare our results to previous findings. In addition, I evaluated all pairwise

correlations between initial explanatory variables (see Table 1) for multicollinearity, and reduced potential variables by excluding variables that exhibited multicollinearity or relatively uniform distribution across sites (Table 1).

### Principal component analysis (PCA)

I computed multivariate ordinations with principal component analysis (PCA) to assess patterns in temperature response metrics using PC-ORD software (MjM Software Design 2011). I created a joint plot by overlaying environmental variables in temperature metric space and examined Pearson correlations of environmental variables with ordination axis scores. This allowed me to verify the importance of different temperature metrics and choose a reduced suite of potential predictor variables to explain the variation in temperature among sites.

### Linear regression

I used simple linear regression to model the difference between temperatures at  $T_u$  and  $T_d$  as a function of the reduced set of explanatory variables to determine what factors were most important in explaining the variation in the temperature pattern around beaver ponds. Candidate models were based on prior literature and the joint plot created from the PCA ordination analysis (Table 4). Model selection was based on Akaike's Information Criterion corrected for small sample size bias ( $AIC_c$ ) to identify the 'best approximating' models from all candidates (Akaike 1974, Burnham and Anderson 2002). I used the package `AICcmodav` in R (R Core Team 2013) using the R studio graphical user interface (version 1.1.423, RStudio, Boston, Massachusetts) to calculate the differences in  $AIC_c$  scores between each model and the highest ranked model ( $\Delta AIC_c$ ), and Akaike weights ( $w_i$ ), which indicate the most plausible models given the data. Models with the lowest  $\Delta AIC_c$  and highest  $w_i$  were selected as the best approximating models. I

evaluated how well the selected models fit the data using the Pearson coefficient of determination.

## Results

### *Longitudinal and vertical temperature comparisons*

Temperatures downstream of beaver ponds ( $T_d$ ) were slightly warmer than upstream reference reaches ( $T_u$ ), with a median difference (MedDif) for all sites of 0.3 °C (Figure 2). Of 24 sites, seven displayed mean temperatures (MeanDif) at least 0.5 °C warmer downstream, while only three exhibited mean temperatures more than 0.5 °C cooler. The MeanDif of the remaining 14 sites was less than 0.5 °C in either direction. However, variation occurred across sites, as well as throughout the day within sites. For example, the site that exhibited the greatest cooling effect (MxNegDif) displayed MeanDif of -1.9 °C, whereas the site that exhibited the greatest warming effect (MxPosDif) displayed a MeanDif of 4.6 °C. Throughout the day, non-averaged differences ( $T_{ps} - T_{pb}$ ) within one site differed by a maximum of 9.6 °C, ranging from 6.9 °C cooler to 2.7 °C warmer. Differences between pond surface and bottom temperatures ( $T_{ps} - T_{pb}$ ) revealed pronounced stratification, with a median difference (MedDif\_PsPb) for all ponds of -0.8 °C (Figure 2). Temperatures at  $T_{pb}$  were only slightly warmer than those at  $T_u$  reference locations, with a median difference for all ponds of 0.1 °C (Figure 2).

Although temperatures at  $T_d$  were higher than those at  $T_u$  on average,  $T_d$  temperature ranges were attenuated compared to those at  $T_u$  (Figure 3a). The mean difference in range (DifDTR) at  $T_d$  was 0.95 °C smaller than the range at  $T_u$ . The attenuation was due to an increase in the minimum temperatures at  $T_d$ , which was 0.8 °C greater than the minimum upstream

temperature (DifOfMin). Maximum temperatures did not contribute considerably to the change in range, and only changed by  $-0.1$  °C (DifOfMx) (Figure 3a). In addition, the range at  $T_{pb}$  was reduced by  $2.3$  °C compared to  $T_{ps}$  (DifR\_PsPb). In contrast to differences between  $T_d$  and  $T_u$ , this attenuation was due primarily to a considerable decrease of  $2.5$  °C in the maximum temperature at  $T_{pb}$  (DifOfMx\_PsPb), as opposed to a change in the minimum, which only decreased by a mean of  $0.2$  °C at  $T_{pb}$  (DifOfMin\_PsPb).

### Timing

In addition to higher maximum temperatures at  $T_d$  compared to  $T_u$  (a mean increase of  $0.8$  °C), the maximum was reached later in the day downstream of the ponds (LagMax) (Figure 4). The median LagMax was  $0.9$  hours, with a range among the sites of one hour earlier to  $4.3$  hours later.

Although average temperatures at  $T_{pb}$  were similar to those at  $T_u$  (MeanDif\_UPb), the differences varied over time. Prior to  $10:00$ , temperatures at  $T_{pb}$  in all sites were similar to, or slightly warmer than those at  $T_u$ . However, later in the day, a majority of the sites revealed a distinct decrease in temperature at  $T_{pb}$  relative to  $T_u$  (Figure 5). This pattern is apparent in both the median (MedDif\_UPb) and time of the greatest downstream cooling effect between  $T_{pb}$  and  $T_u$  (TMxNgDif\_UPb), which were  $-1.7$  °C and  $15:30$ , respectively (Figure 5).

### *Environmental associations*

Temperatures at  $T_d$  were warmer with respect to  $T_u$  in relation to increasing total hydraulic height, the number of dams, pond length, and surface area ( $r = 0.69, 0.67, 0.62,$  and  $0.59,$  respectively). MeanDif\_UPb was positively associated with pond length and total hydraulic height ( $r = 0.47$  and  $0.41,$  respectively). Vertically, pond stratification increased, with lower

temperatures at  $T_{pb}$  relative to  $T_{ps}$  in larger ponds.  $T_{pb} - T_{ps}$  was negatively correlated with both maximum pond width and depth were negatively correlated ( $r = -0.82$  and  $-0.70$ , respectively).

### Principal component analysis (PCA)

Axis 1 and 2 of the PCA ordination described 73% of the variation among sites in  $T_d - T_u$  response metric space (Figure 6, Table 3). Positive axis 1 values indicated increasing MeanDif, MedDif, and MaxDif, as well as increases in the greatest warming effect (MxPsDif). Negative axis 1 values indicated a greater number of negative differences per site (CoNegDif). Positive axis 2 values indicated greater DifOfMin and later times of the greatest cooling effect at  $T_d$  (TMxNegDif). Negative axis 2 values indicated greater DifDTR, later times of greatest warming (TMxPosDif), and greater LagMax. Sites in quadrant 1 of the PCA were associated with more ponds and deeper, wider ponds, and sites in quadrants 1 and 2 were associated with higher mean annual air temperatures. Quadrants 2 and 3 were associated with greater canopy cover, and sites in quadrants 3 and 4 were associated with higher amounts of annual precipitation and higher elevations. About 30% of the sites were outside of the main cluster of sites in response metric space, demonstrating the considerable amount of variation of  $T_d - T_u$  temperature metrics among the sites.

### Linear regression and model selection

Candidate models were chosen a priori based on the literature, pairwise correlations, and the PCA ordination results (Table 4). The simple linear regression model with hydraulic height was the highest ranked model describing MeanDif. However, this model was only 1.6 times more likely to be the best model than the next highest ranked model, which included mean annual air temperature along with hydraulic height. The next three highest-ranked models, which all included hydraulic height, and then either elevation, annual precipitation, or maximum pond

width, respectively, differed from the highest ranked model by less than two, demonstrating the importance of these variables. The best approximating model indicated that increases in temperature at  $T_d$  relative to  $T_u$  increased as the total hydraulic height for a site increased, and explained 48% of the observed variation in the mean difference (Table 5, Figure 7a). The highest ranked model was 25 times more likely to be the ‘best approximating model’ than the pond morphology (LnMaxHH\_SA) model (Table 5).

A simple linear regression with annual precipitation was the highest ranked of the candidate models predicting MeanDif, compared to other models using other GIS derived variables (Table 5). This model was only 1.6 times as likely to be the ‘best’ model than the second ranked model, which was a simple linear regression with mean annual air temperature as the single explanatory variable. The model rankings demonstrated that elevation, distance to the divide, and upstream basin size were also important variables. The best approximating model using GIS derived variables indicates that temperatures at  $T_d$  relative to  $T_u$  decreased with greater annual precipitation but only accounted for 17% of the total variation among the sites (Table 5).

## **Discussion**

Rising stream temperatures threaten coldwater fish species such as Pacific salmon and steelhead, and adaptation strategies are needed to mitigate the effects of climate change. Beaver reintroductions and human-constructed beaver-dam analogs have become popular methods of adaptation to both reduce the effects of drought and moderate stream temperatures (Wild 2011, Pollock et al. 2015, Fitch 2016). Yet, there is no conclusive evidence that beaver impoundments cool streams, and the drivers of the discrepancy in published study results remain unclear. I found that on the whole, beaver dams in the Methow watershed in Washington tend to warm

streams. This finding corroborates the conclusion of a recent meta-analysis on 27 studies, which found that beaver ponds are associated with an increase in downstream temperature (Ecke et al. 2017). My results demonstrate that resource managers need to consider how the wide variety of landscape settings of beaver habitat can result in different responses of stream temperature to beaver pond complexes.

Although mean temperatures downstream of beaver ponds were slightly higher overall, I found a large range of spatial and temporal variation in temperature differences above and below beaver ponds. Downstream temperatures ranged from 4.6 °C warmer to 1.8 °C cooler. There was also considerable temporal variation in the differences in up- and downstream temperatures within a site. For example, non-averaged differences at one site ranged over 9 °C, from 2.7 °C warmer to 6.9 °C cooler. On the other hand, several sites, including the three smallest sites, showed narrow ranges in differences throughout the day of  $\pm 1$  °C.

Given the findings of previous studies, I expected that downstream temperatures would vary predictably with pond morphology. Specifically, as was found in streams in the Rocky Mountains in Colorado, I predicted that ponds with high-head dams and a small surface area would have cooler downstream temperatures, whereas ponds with low-head dams and a large surface area would have warmer downstream temperatures (Fuller and Peckarsky 2011). This pattern has been attributed to the fact that beaver ponds, especially those with high-head dams, increase hydraulic pressure, which can increase the outseepage of surface water into the streambed. This outseepage can result in locally elevated water tables (Lowry 1993). After passing under dams, pressure on subsurface flows is reduced. The reduction in pressure, along with elevated water tables, can lead to groundwater upwelling (White 1990, Poole and Berman 2001). For example, in the Swan River basin in Montana, negative vertical hydraulic gradients,

indicative of downwelling, were found upstream of a beaver dam complex, whereas positive gradients, indicative of upwelling, were found for several hundred meters downstream of the ponds (Baxter and Hauer 2000). In the summer, the upwelling of relatively cool groundwater might provide cold-water areas.

Although I hypothesized that downstream temperatures would be negatively correlated with hydraulic height, I also expected to see a positive association between downstream temperature and pond surface area. As the surface area of a pond increases, the proportion of the pond that is shaded by riparian vegetation typically decreases, which could result in warmer temperatures downstream. I predicted that normalizing hydraulic height by surface area would reveal a negative relationship between downstream temperature and hydraulic height. In line with this hypothesis, I found that the natural logarithm of the maximum hydraulic height normalized by surface area ( $\text{LnMaxHH\_SA}$ ) showed a negative relationship with downstream warming ( $r = -0.57$ ). That is, sites with larger maximum hydraulic heights and smaller surface areas displayed cooler downstream temperatures, which corroborates the findings Fuller and Peckarsky (2011).

Although I found a negative relationship between pond morphology and downstream temperature, the linear model describing this relationship was ranked lower than other candidate models. The highest ranked model, which was 25 times more likely to be the ‘best approximating’ model than the pond morphology model, was a single variable model with the total hydraulic height for each site. This model shows that larger total hydraulic heights are positively associated with warmer downstream temperature differences, which is inconsistent with the negative relationship between downstream temperature and pond morphology. However, in this study, total site hydraulic height was highly correlated with site dimension

variables, including surface area and site length (Figure 6). As mentioned previously, larger surface areas are associated with increased solar radiation due to a reduction in the proportion of the pond that is shaded. In addition, during the summer, and without influences from groundwater or tributaries, stream temperature typically increases as it flows downstream. This is due to increased solar radiation and equilibration with air temperature. Therefore, instead of describing the hydraulic pressure put on the streambed, it appears that total hydraulic height reflected the proportion of solar radiation on the pond, and the capacity of the stream to equilibrate with air temperature.

One notable difference between my study and Fuller and Peckarsky (2011) was that their study evaluated individual ponds, whereas we examined a combination of individual ponds and pond complexes. This was due to the fact that many of my study sites were complex clusters of ponds that could not be clearly delineated. Thus, my measurements of hydraulic height included combined measurements of multiple, contiguous ponds. This may have obscured the hypothesized relationship between hydraulic height and downstream temperature because neither the site total hydraulic height, nor average hydraulic height, when normalized by pond surface area displayed a relationship with downstream temperature changes. Unlike total or average hydraulic height, the maximum hydraulic height appeared to be a suitable descriptor of the ability of each site to elevate groundwater, which is why I chose it to describe pond morphology.

In addition to the correlation between downstream warming and hydraulic height, modeling downstream temperature with GIS-derived variables demonstrated that sites with higher annual precipitation were slightly more likely to have cooler temperatures downstream. One possible explanation for this finding is that sites with more precipitation likely have higher water tables, making any potential groundwater upwelling more likely to occur than at sites with

lower groundwater levels. Although precipitation only explained 17% of the variance in temperature, the majority of the study sites were in the same Columbia River sub-basin, where a precipitation gradient exists but is relatively limited in range. With a wider range of precipitation, there may be a stronger relationship precipitation and temperature downstream of pond complexes. In the Skykomish watershed, located on the western slopes of the North Cascades, where precipitation is substantially higher, cooler temperatures have been found downstream of beaver ponds (Dittbrenner 2018). Furthermore, in the arid Southwest (USA), a study found warmer temperatures downstream of beaver ponds (Huey and Wolfrum 1956). To better understand the impact of precipitation inputs on temperature, it may be necessary to investigate beaver pond complexes over a broader precipitation gradient.

Although my results indicate that beaver ponds increased downstream temperatures on average, they may provide thermal refuge in the ponds themselves. Temperatures at the bottom of ponds were consistently cooler than surface temperatures, which were highly sensitive to solar heating and showed marked diurnal fluctuations. It is interesting that although some studies have reported stratification within beaver ponds (Gard 1961), others have not (Huey and Wolfrum 1956, Fuller and Peckarsky 2011). Moreover, when compared to upstream reference reaches, most sites showed lower temperatures at pond bottoms during the afternoons, the time of day when thermal refuge is most critical. This may be due to the buffering of pond bottom temperatures from solar heating. Beaver ponds are often described as warmer bodies of water that can act as heat sinks detrimental to coldwater fish (Rasmussen 1941, Guignion 2009). However, I found that despite warmer surface temperatures, deeper parts of beaver ponds may provide thermal refuge during the hottest part of the day.

The diversity and complexity of my study sites played an important role in the variance of the temperature response. The heterogeneity in the study sites is partly illustrated by the large ranges in many of the environmental variables that I measured. For example, the total ponded area ranged from under 20 m<sup>2</sup> at the smallest site, to over 26,000 m<sup>2</sup> at the largest site. Distance to the watershed divide ranged from under 700 m to over 10,000 m, representing sites very close to the headwaters, as well as sites farther downstream. In addition, canopy cover at the sites ranged from 0 to 80%. These variables represent conditions at 17 different streams spanning the length and elevation of the Methow watershed and therefore encompass more of the variation inherent in beaver-engineered habitat than would have been apparent in investigations conducted over a smaller spatial extent. The majority of previously reported data is based on ponds from a small number of streams, including several studies that only investigated one stream (Smith et al. 1989, Majerova et al. 2015, Weber et al. 2017). I suspect this has been a contributing factor to the contradictory effects of beaver ponds on stream temperature found in the current literature. To avoid making incomplete conclusions, studies covering a broad range of conditions are needed.

My study sites were diverse and highly complex, which made them difficult to measure in a consistent manner. I strove to include only beaver pond complexes that fit a simple upstream reach-pond-downstream reach pattern to facilitate logger placement and reduce confounding effects. However, beaver are known to increase habitat and channel complexity (Naiman et al. 1988, Majerova et al. 2015, Machen 2016, Bouwes et al. 2016). In addition, beaver ponds elevate local water tables, which can lead to areas of upwelling (Gard 1961, White 1990, Lowry 1993). Therefore, easily delineated ponds with simple up- and downstream reaches and no intervening springs were rare. Moreover, the diversity we found was present within one small region of

Washington. Beaver habitat across the species' entire range, which spans almost all of the North America must be even more diverse. The heterogeneity found in beaver pond complexes likely contributes to the diverse temperature responses seen in the reported findings.

Even though the spatial extent of this study was larger than many previous studies, almost all of the streams fell within the same Columbia River sub-basin, so it is difficult to generalize to other geographic regions is limited. This also suggests that some of the relationships that I identified, such as the influence of precipitation on temperature response, may be easier to detect if a set of streams experiencing a wider range of precipitation were considered. In addition, during the three-month field season, I witnessed substantial disturbances at our study ponds. Several sites grew considerably due to beaver activity, while other sites lost entire dams. Moreover, one site was burned in a wildfire, and others experienced significant reductions in flow, to the point where the upstream reach of one pond completely dried up. Therefore, I chose to study temperature effects during a single day, which allowed me to reduce the temporal variation and avoid the influence of confounding disturbances. Initial screening of the data showed no prominent changes in the overall patterns of the data from one day to another, except in the cases of the major disturbances mentioned. Nonetheless, it is possible important insights were missed by limiting the temporal extent to one day.

My findings do not suggest that beaver dams consistently cause a reduction in downstream temperature and, therefore, do not support the use of beaver reintroduction or translocation as a strategy to mitigate the effects of climate-driven stream temperature increases. Nonetheless, I did see a large range in the variation of responses, and many of the beaver complexes did not increase downstream temperatures substantially. If beaver-based restoration or adaptation techniques are to be used, selecting locations where topography would allow for

deeper ponds and greater proportion of shading may be important. Moreover, although temperatures were typically warmer downstream, pond bottoms often provided cool-water refuge during the afternoons. Further investigations into what portion of ponds can provide refuge, in addition to factors influencing the degree and area of cooling, are needed.

Although the results of beaver-based restoration as a strategy to address increasing stream temperature are highly variable, it may still be a valuable climate change-adaptation strategy for other reasons. For example, during drought conditions, the ability of beaver to store surface water and raise the local water table, for which there is ample evidence, may outweigh any potential negative effects on stream temperature (Lowry 1993, Morrison et al. 2014, Majerova et al. 2015). Managers will need to evaluate these methods and consider the potentially harmful temperature effects when deciding whether to use beaver-based restoration.

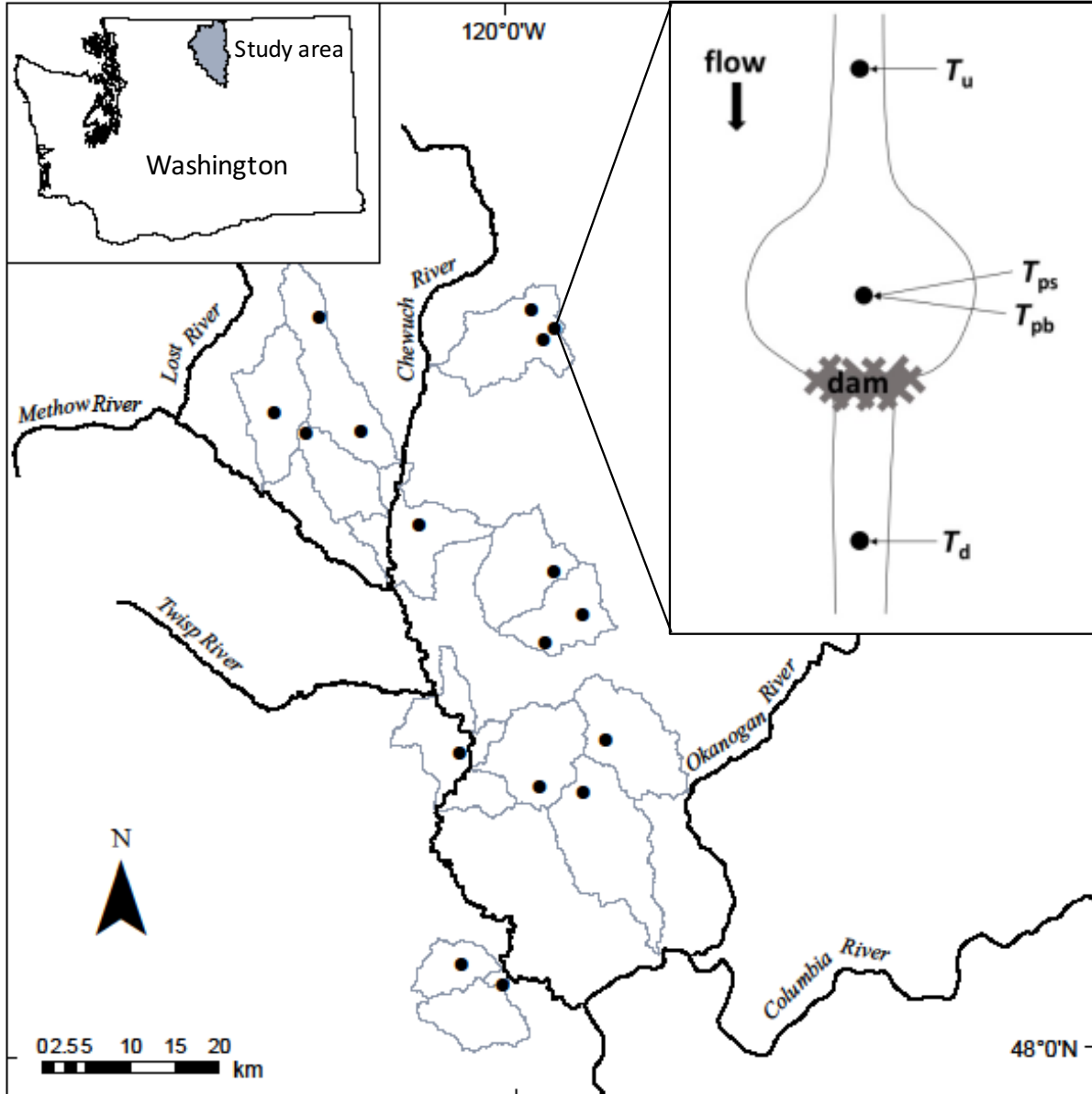


Figure 1. Study area of selected streams in north-central Washington State (USA). Black dots indicate study area(s) on each stream. The number of sites per stream ranged from 1 to 6. The light grey lines delineate the watersheds in which the sites were located. The relative locations of loggers at one site, including upstream ( $T_u$ ), downstream ( $T_d$ ), pond bottom ( $T_{pb}$ ), and pond surface ( $T_u$ ), are displayed in the inset diagram.

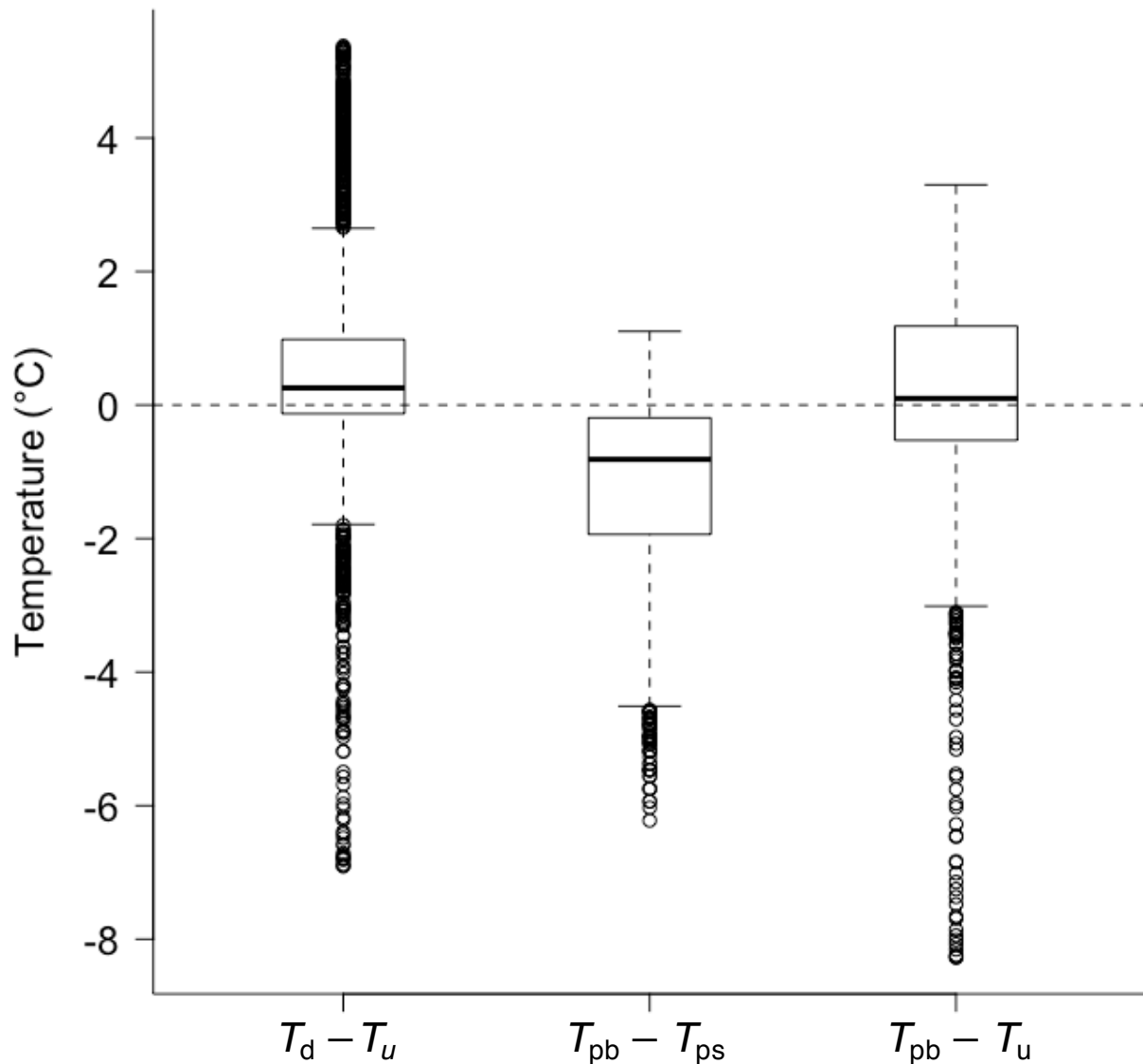


Figure 2. Differences in temperature recorded every 15 minutes on 30-Aug-2017 between  $T_d$  and  $T_u$ ,  $T_{pb}$  and  $T_{ps}$ , and  $T_{pb}$  and  $T_u$  (see Figure 1 for definitions). Sample sizes for the differences are 2304, 1728, and 1632, respectively. Positive differences indicate warmer temperatures further downstream or at the pond bottom compared to temperatures upstream or at the pond surface. A dashed line at a difference of zero has been drawn for reference. Boxes represent the 75th and 25th percentiles and the bold line shows the median. Whiskers indicate either 1.5 times the interquartile range or the maximum (for upper whisker) or minimum (for lower whisker) temperature difference, whichever is less extreme. Outliers are denoted by hollow circles.

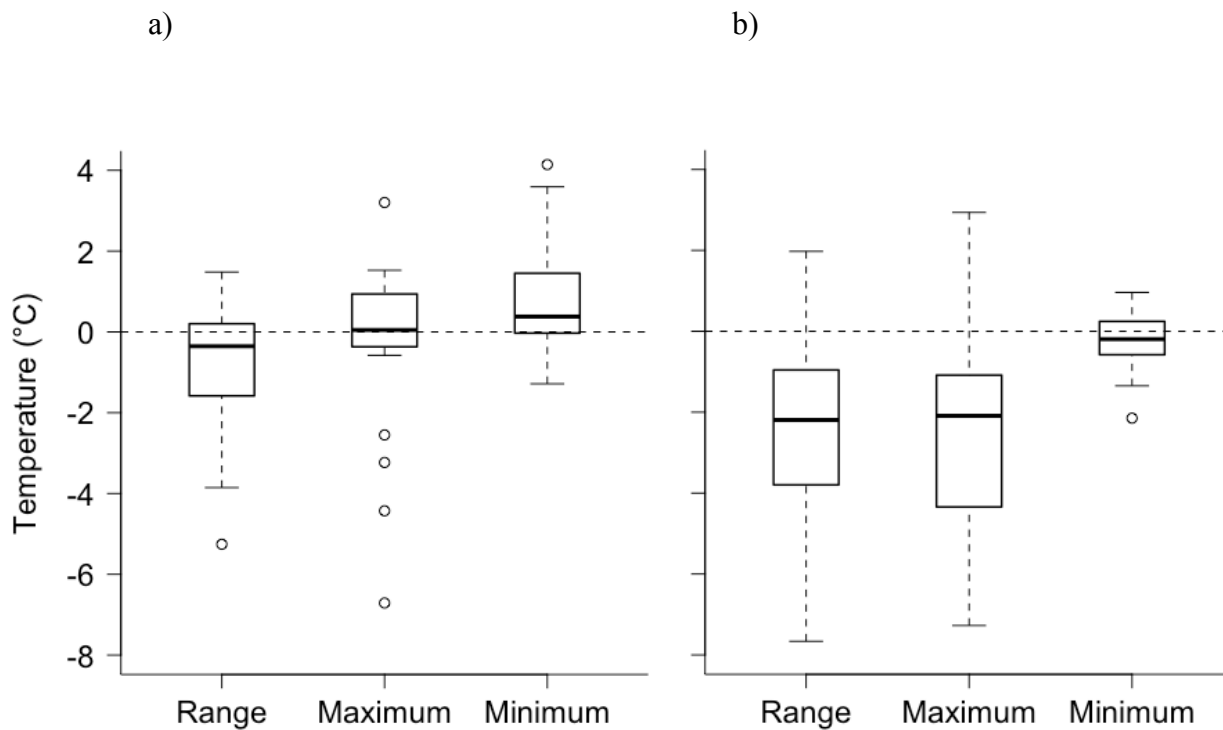


Figure 3. Difference in daily range, maximum, and minimum between  $T_d$  and  $T_u$  (a), and  $T_{pb}$  and  $T_{ps}$  (b) for 30-Aug-2017 (see Figure 1 for definitions). Sample sizes for  $T_d$  and  $T_u$ , and  $T_{pb}$  and  $T_{ps}$  are 24 and 18, respectively. Positive differences indicate warmer temperatures downstream or at the pond bottom compared to temperatures upstream or at the pond surface.

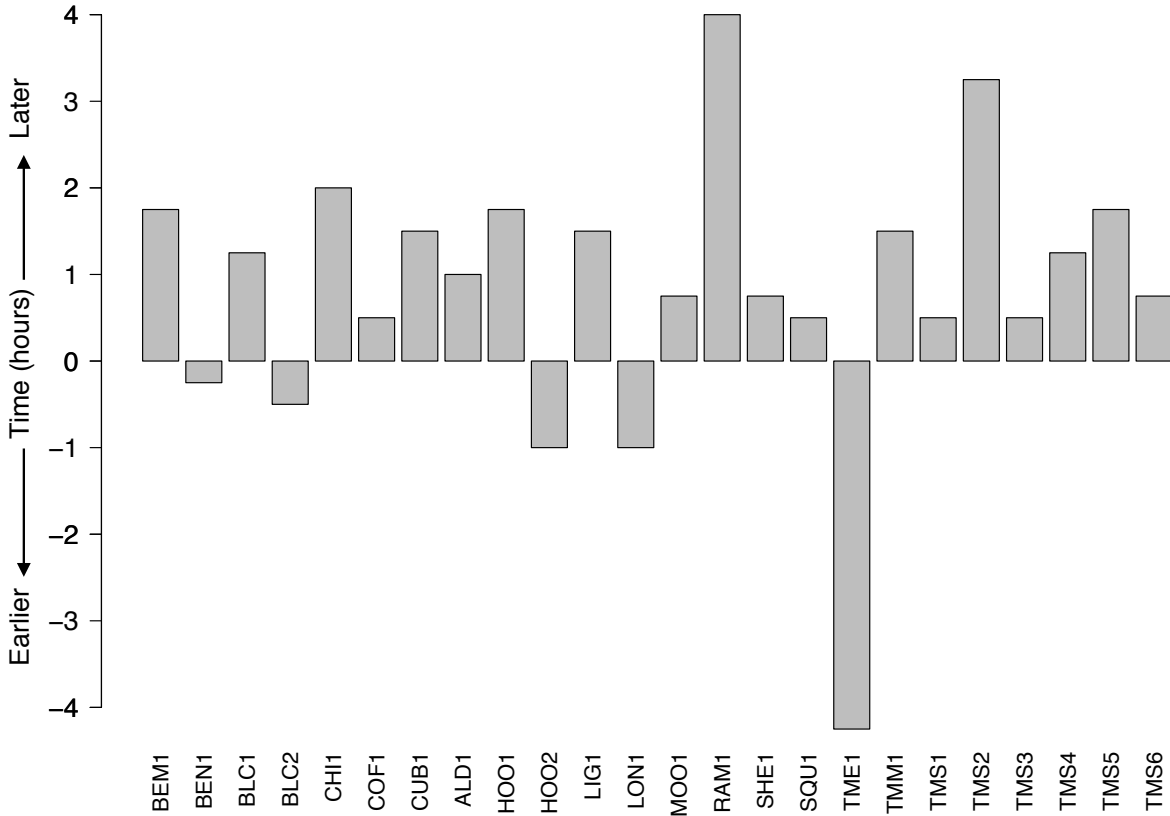


Figure 4. Lag time between maximum at  $T_u$  and  $T_d$  for all 24 sites on 30-Aug-2017 (see Figure 1 for definitions). Sites are denoted by site ID, where the first three letters denote the stream, and the number represents unique sites at each stream. Positive values indicate the maximum occurred at a later time downstream. Maximum temperatures were adjusted for two sites to ensure that the afternoon maximum was used in analysis.

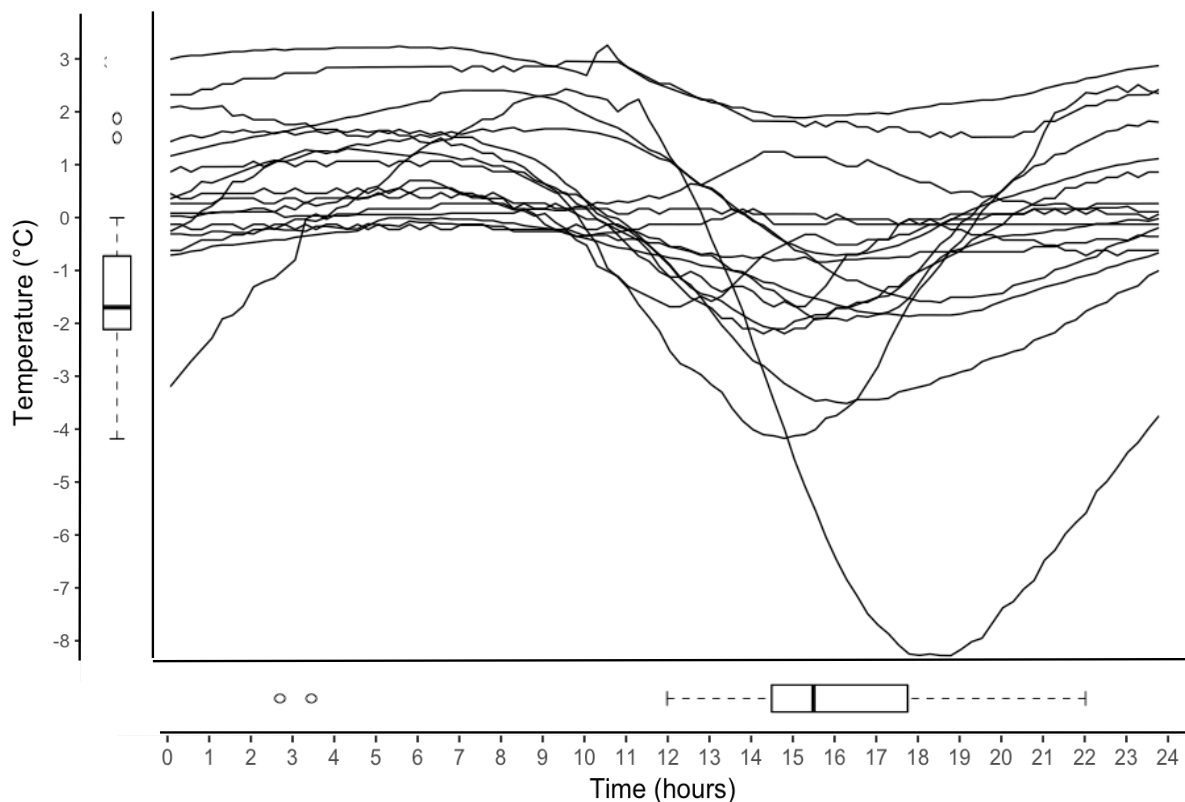


Figure 5. Differences between  $T_{pb}$  and associated  $T_u$  from 17 sites for each 15-minute recording interval on 30-Aug-2017 (see Figure 1 for definitions). The vertical box plot shows the maximum negative difference (MxNegDif\_UPb) reached for each site on that day. Negative differences indicate cooler temperatures at the pond bottom than at the upstream reference. The horizontal box plot shows the time of the maximum negative difference (TMxNegDif\_UPb).

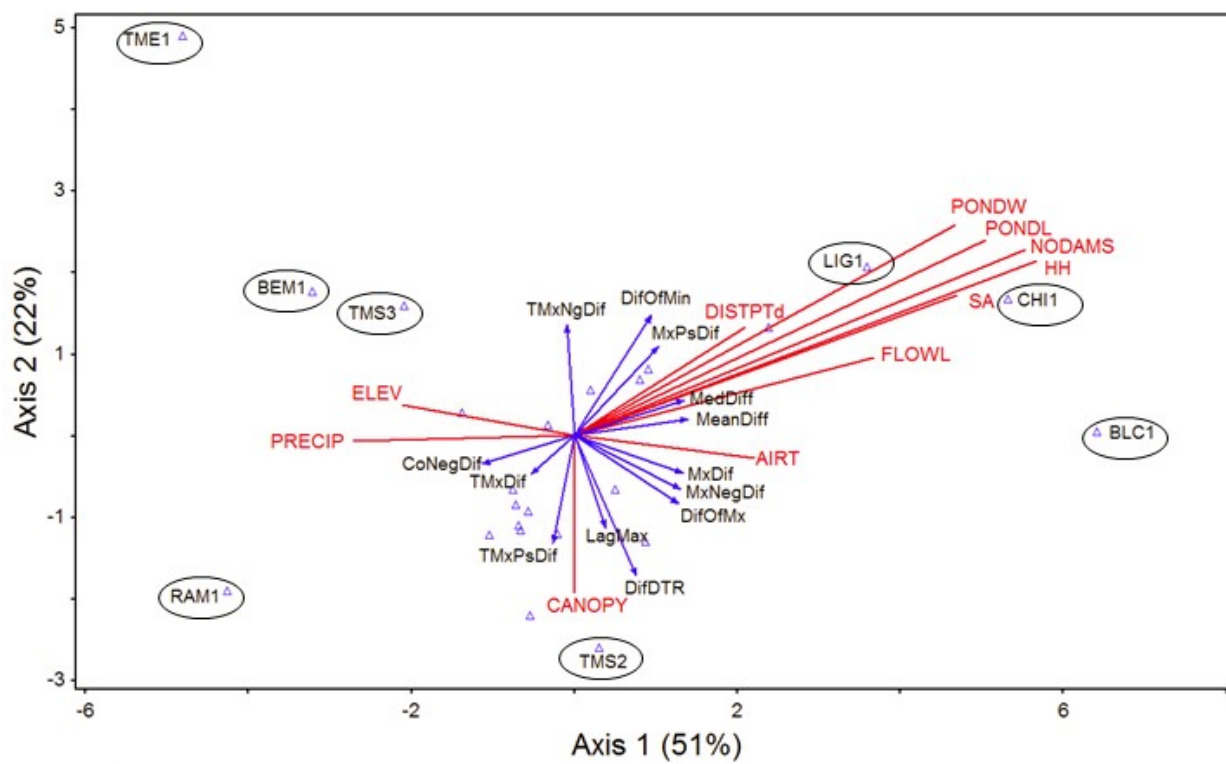


Figure 6. Principal component analysis (PCA) ordination of temperature response metrics. Triangles are sites plotted in temperature space, with outliers labeled and circled for reference. Loadings of temperature metrics with the first two principal components are indicated by blue lines. Explanatory environmental variables, shown by red lines, are overlaid, indicating their degree of correlation to the first two principal components. The amount of variation explained by each ordination axis is shown in parentheses.

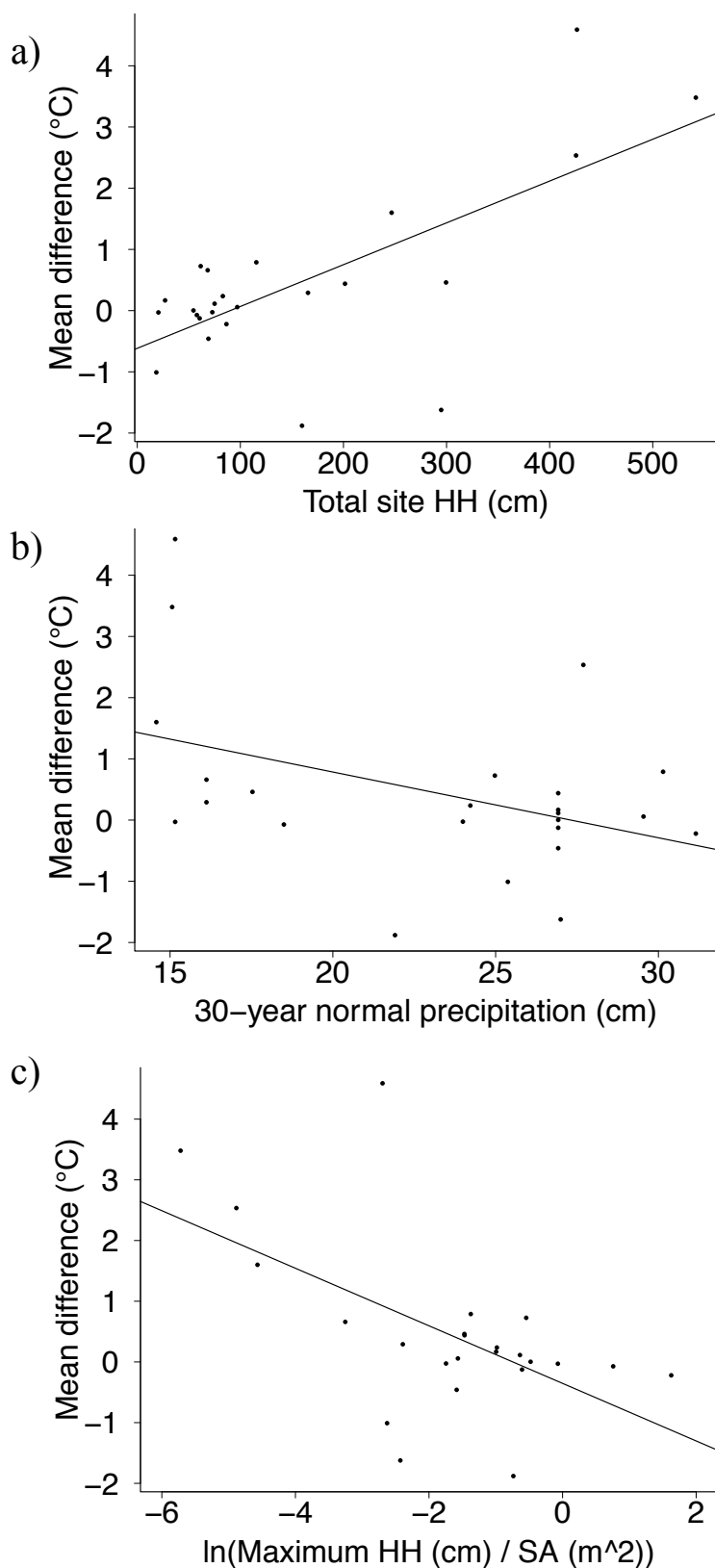


Figure 7. The relationship between MeanDif and a) total site hydraulic height (cm), b) annual precipitation (cm), and c) the natural logarithm of the maximum hydraulic height (cm) normalized by surface area (m<sup>2</sup>). Observed values are from 30-Aug-2017, and are indicated by black dots. Straight lines represent the fitted, simple linear regressions ( $n = 24$  for all three models). Positive differences indicate sites where  $T_d$  was cooler than  $T_u$ , whereas negative differences indicate the opposite (see Figure 1 for definitions).

Table 1. Potential explanatory variables for principal component analysis (PCA) and linear models (LM) to evaluate associations with response temperature metrics. See text for additional information on how each variable was measured and/or calculated.

<i>Variable</i>	<i>Unit/ category</i>	<i>Data type</i>	<i>Abbreviation</i>	<i>Measurement method</i>	<i>Included in PCA</i>	<i>Included in LM</i>
<b><i>Stream scale variables</i></b>						
30-year normal average temperature	°C	Continuous	AirT	Calculated using PRISM data in ArcGIS	yes	no*
30-year normal precipitation amount	mm	Continuous	Precip	Calculated using PRISM data in ArcGIS	yes	yes
Average canopy cover	%	Continuous	Canopy	Field measurements using densiometer 0, 90, 180, and 270° at the location of $T_{pb}$ and $T_{ps}$	yes	no <sup>†</sup>
Average discharge	m <sup>3</sup> /s	Continuous	Disch	Field measurements using area velocity method with flowmeter	yes	no <sup>†</sup> *
Mean stream width	cm	Continuous	StrWMean	Field estimates using levelling rod	no <sup>†</sup>	no <sup>†</sup>
Median stream depth	cm	Continuous	StrDMed	Field estimates using top set wading rod	no <sup>†</sup>	no <sup>†</sup>
Gradient	Percent	Continuous	Grad	Field estimates using auto level or RTK	no <sup>†</sup>	no <sup>†</sup>
<b><i>Site scale variables</i></b>						
Upstream basin size	m <sup>2</sup>	Continuous	Basin	Calculated using digital elevation model and hydrography data in ArcGIS	yes	no <sup>†</sup> *
Beaver presence		Ordinal	Pres_c	Field estimates of how recently beaver were present at site (1 = current, 3 = more than 5 years ago)	no	no <sup>†</sup>
Current	1					
≤ 2 yrs	2					
> yrs ago	3					
Distance between pond and $T_d$	m	Continuous	DistPT <sub>d</sub>	Calculated using digitized ponds in ArcGIS	yes	no <sup>†</sup>
Distance to divide	m	Continuous	DistDiv	Calculated using elevation and hydrography data in ArcGIS	yes	no*
Elevation	m	Continuous	Elev	Field measurements using Garmin GPS	yes	no*

Table 1. (continued)

<i>Variable</i>	<i>Unit/ category</i>	<i>Data type</i>	<i>Abbreviation</i>	<i>Measurement method</i>	<i>Included in PCA</i>	<i>Included in LM</i>
Hydraulic height	cm	Continuous	HH	Field estimates using auto level or RTK	yes	yes
Hydraulic height maximum	cm	Continuous	HHmax	Field estimates using auto level or RTK	no <sup>†</sup>	yes
Length of flowing stream between $T_u$ and $T_d$	m	Continuous	FlowL	Calculated from hydrography data and digitized ponds in ArcGIS	yes	no*
Maximum pond depth	cm	Continuous	PondD	Field estimates using levelling rod	no*	no*
Maximum pond width	m	Continuous	PondW	Calculated from digitized ponds in ArcGIS	yes	no*
Number dams	#	Discrete	NoDams	Field counts of dams between $T_u$ and $T_d$	yes	no*
Pond length	m	Continuous	PondL	Calculated from digitized ponds in ArcGIS	yes	no*
Site age ≤ 2 yrs > 2 yrs, ≤ 5 yrs > 5 yrs	1 2 3	Ordinal	Age_c	Field estimates of site age (1 = less than two years, 3 = older than 5 years)	no <sup>†</sup>	no <sup>†</sup>
Surface area	m <sup>2</sup>	Continuous	SA	Calculated from digitized ponds in ArcGIS	yes	no*
Surface water at dam	y/n	Binary	Surf_water_c	Field estimate of whether surface water flow was present at dam	no <sup>†</sup>	no <sup>†</sup>
Water flow over dam	y/n	Binary	Water_over_c	Field estimate of whether water was flowing over the top of any dams at site	no <sup>†</sup>	no <sup>†</sup>

\* removed based on multicollinearity

† removed based on distribution and simple regressions

Table 2. Response metrics used to evaluate associations with environmental attributes. All metrics without an asterisk were used in principal component analysis (PCA). Metrics were based on 96 observations of  $T_u$  and  $T_d$  from 30-Aug-2017. The difference  $T_u - T_d$  refers to the difference between the two locations at one time step. All calculations were made so that the result shows the change moving downstream (ie, when MeanDif is negative, temperatures were lower at  $T_d$  than at  $T_u$ ). See text for additional information on how each metric was measured and/or calculated.

<i>Metric</i>	<i>Abbreviation</i>	<i>Unit</i>	<i>Data type</i>	<i>Calculation</i>
Mean difference	MeanDif	°C	Continuous	Mean $T_u - T_d$
Median difference	MedDif	°C	Continuous	Median $T_u - T_d$
Lag of maximums	LagMax	hr	Discrete	Time of max $T_u -$ time of max $T_d$
Difference of minimums	DifOfMin	°C	Continuous	Min $T_u -$ min $T_d$
Difference of maximums	DifOfMx	°C	Continuous	Max $T_u -$ max $T_d$
Greatest cooling	MxNegDif	°C	Continuous	Smallest $T_u - T_d$
Time of greatest cooling	TMxNgDif	Decimal hr	Discrete	Time of smallest $T_u - T_d$
Greatest warming	MxPsDif	°C	Continuous	Greatest $T_u - T_d$
Time of greatest warming	TMxPsDif	Decimal hr	Discrete	Time of greatest $T_u - T_d$
Greatest difference	MxDif	°C	Continuous	Greatest $ T_u - T_d $
Time of maximum difference	TMxDif	Decimal hr	Discrete	Time of greatest $ T_u - T_d $
Count of negative differences	CoNegDif	°C	Continuous	Number of negative $T_u - T_d$
Difference in range	DifDTR	°C	Continuous	Range $T_u -$ range $T_d$
Mean difference (pond bottom vs surface)*	MeanDif_PsPb	°C	Continuous	Mean $T_{ps} - T_{pb}$
Median difference (pond bottom vs upstream)*	MedDif_PsPb	°C	Continuous	Median $T_{ps} - T_{pb}$
Mean difference (pond bottom vs upstream)*	MeanDif_UPb	°C	Continuous	Mean $T_u - T_{pb}$
Greatest cooling (pond bottom vs upstream)*	MxNegDif_UPb	°C	Continuous	Smallest $T_u - T_{pb}$
Time of greatest cooling (pond bottom vs upstream)*	TMxNegDif_UPb	Decimal hr	Discrete	Time of smallest $T_u - T_{pb}$
Difference in range (pond bottom vs surface)*	DifR_PsPb	°C	Continuous	Range $T_{ps} -$ range $T_{pb}$
Difference of minimums	DifOfMin_PsPb	°C	Continuous	Min $T_{ps} -$ min $T_{pb}$
Difference of maximums	DifOfMx_PsPb	°C	Continuous	Max $T_{ps} -$ max $T_{pb}$

\* Metric was not included in PCA

Table 3. Pearson correlation coefficients of response metrics and environmental attributes versus axis scores from PCA ordination of response metrics. Abbreviated variable names are explained in Tables 1 and 2.

<b>Variable</b>	<b>Axis 1</b>	<b>Axis 2</b>
<i>Response metrics</i>		
MeanDif	0.99	0.09
MedDif	0.96	0.20
DifOfMx	0.91	-0.39
LagMax	0.27	-0.53
DifOfMin	0.67	0.68
MxNegDif	0.92	-0.31
TMxNgDif	-0.06	0.63
MxPsDif	0.73	0.51
TMxPsDif	-0.19	-0.61
MxDif	0.95	-0.22
TMxDif	-0.38	-0.22
CoNegDif	-0.80	-0.16
DifDTR	0.53	-0.80
<i>Environmental variables</i>		
AirT	0.40	-0.14
Precip	-0.44	-0.07
Canopy	0.02	-0.37
Disch	0.24	0.06
Basin	0.28	0.13
DistPT <sub>d</sub>	0.39	0.31
DistDiv	0.25	0.15
Elev	-0.39	0.16
HH	0.64	0.39
FlowL	0.51	0.26
PondW	0.58	0.43
NoDams	0.63	0.40
PondL	0.60	0.41
SA	0.58	0.35

Table 4. Linear models predicting mean difference between  $T_u$  and  $T_d$  on 30-Aug-2017 using any potential explanatory variable, or using only explanatory variables derived from GIS. Akaike's Information Criterion corrected for small sample bias ( $AIC_c$ ),  $AIC_c$  difference between a given model and the highest ranked model ( $\Delta AIC_c$ ), and Akaike weights ( $w_i$ ) indicate the most plausible models given the data. Models with the lowest  $AIC_c$  and highest  $w_i$  are the best approximating models.

<b>Model Predictors</b>	<b><math>AIC_c</math></b>	<b><math>\Delta AIC_c</math></b>	<b><math>w_i</math></b>
<i>Mean difference using any potential explanatory variables</i>			
1. HH	75.90	0.00	0.25
2. HH + AirT	76.85	0.95	0.16
3. HH + Elev	77.24	1.34	0.13
4. HH + Precip	77.24	1.34	0.13
5. HH + PondW	77.79	1.89	0.10
6. HH + FlowL	78.80	2.90	0.06
7. HH + AirT + PondW	79.56	3.66	0.04
8. HH + Elev + PondW	80.03	4.12	0.03
9. HH + Precip + PondW	80.03	4.12	0.03
10. HH + PondW + FlowL	80.86	4.96	0.02
11. lnSA	81.73	5.83	0.01
12. lnMaxHH_SA	82.21	6.31	0.01
13. HH + AirT + PondW + FlowL	82.92	7.02	0.01
14. HH + Elev + PondW + FlowL	83.39	7.49	0.01
15. HH + Precip + PondW + FlowL	83.39	7.49	0.01
16. maxHH + lnSA	84.52	8.62	0.00
17. maxHH	90.28	14.38	0.00
<i>Mean difference using GIS derived explanatory variables</i>			
1. Precip	86.90	0.00	0.29
2. AirT	87.81	0.91	0.18
3. Elev	87.96	1.06	0.17
4. Precip, DistDiv	88.69	1.79	0.12
5. Precip, BasinSz	88.86	1.96	0.11
6. Precip, AirT	89.70	2.80	0.07
7. Precip, Elev	89.73	2.83	0.07

Table 5. Linear regression parameter estimates, standard error (SE), coefficient of determination ( $R^2$ ), and p-value for the ‘best approximating’ models predicting mean difference between  $T_u$  and  $T_d$  on 30-Aug-2017.

Parameter	Estimate	SE	Model $R^2$	Model p-value
<i>Field and GIS-derived explanatory variables</i>			0.477	0.0002
Intercept	-0.616	0.321	-	-
HH	0.007	0.002	-	-
<i>GIS-derived explanatory variables</i>			0.173	0.043
Intercept	2.934	1.191	-	-
Precip	-0.107	0.050	-	-
<i>Pond morphology variable (Fuller and Peckarsky 2011)</i>			0.319	0.004
Intercept	-0.353	0.350	-	-
Ln(MaxHH/SA)	-0.474	0.148	-	-

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