Instream Habitat Restoration and Stream Temperature Reduction in a Whirling Disease-Positive Spring Creek in the Blackfoot River Basin, Montana

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Abstract
Anthropogenic warming of stream temperature and the presence of exotic diseases such as whirling disease are both contemporary threats to coldwater salmonids across western North America. We examined stream temperature reduction over a 15-year prerestoration and postrestoration period and the severity of Myxobolus cerebralis infection (agent of whirling disease) over a 7-year prerestoration and postrestoration period in Kleinschmidt Creek, a fully reconstructed spring creek in the Blackfoot River basin of western Montana. Stream restoration increased channel length by 36% and reduced the wetted surface area by 69% by narrowing and renaturalizing the channel. Following channel restoration, average maximum daily summer stream temperatures decreased from 15.7°C to 12.5°C, average daily temperature decreased from 11.2°C to 10.0°C, and the range of daily temperatures narrowed by 3.3°C. Despite large changes in channel morphology and reductions in summer stream temperature, the prevalence and severity of M. cerebralis infection for hatchery Rainbow Trout Oncorhynchus mykiss remained high (98–100% test fish with grade > 3 infection) versus minimal for hatchery Brown Trout Salmo trutta (2% of test fish with grade-1 infection). This study shows channel renaturalization can reduce summer stream temperatures in small low-elevation, groundwater-dominated streams in the Blackfoot basin to levels more suitable to native trout. However, because of continuous high infections associated with groundwater-dominated systems, the restoration of Kleinschmidt Creek favors brown trout Salmo trutta given their innate resistance to the parasite and the higher relative susceptibility of other salmonids.

Degradation of salmonid habitat historically involved physical alterations of streams and rivers from land use activities such as channel degradation, dewatering, and overgrazing (Meehan 1991; Behnke 1992; Thurow et al. 1997; Pierce et al. 2013). However, the additive stressors of anthropogenic warming (e.g., climate change and riparian degradation) have not only elevated the overall need for aquatic restoration, but also the need to refine, implement, and evaluate specific restoration activities associated with these conditions (Rieman et al. 2007; Williams et al. 2009; Pierce et al. 2014). Despite the pressing need for applied studies of this nature, few, if any, long-term field investigations link restoration to stream
HABITAT MODIFICATION AND WHIRLING DISEASE

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Ambient climate (i.e., air temperature) contributes to variability in stream temperatures through heat exchange near the surface of the water (Meisner et al. 1988; Mote 2006). However, groundwater-dominated systems are thermally regulated by groundwater inflow and are therefore less affected by seasonal, elevational, and climatic conditions than basin-fed streams (Melina et al. 2002). Groundwater-induced streams are thereby cooler during summer and warmer during winter, especially near the sources of groundwater inflows (Meisner et al. 1988; Cassie 2006; Pierce et al. 2012). As an example of this, stream temperatures at the source of an artesian spring creek on the floor of the Blackfoot Valley remain at a near constant 7–8°C range of annual temperatures versus <0°C in winter to >23°C during summer in nearby basin-fed streams (Pierce et al. 2002, 2012, 2013). Given the moderating effects of groundwater, stream improvements that renaturalize channels and reduce stream temperatures during the peak of summer may prove increasingly important given projections of climate warming, especially in low-elevation streams where native trout are most at risk (Meisner et al. 1988; Riemann et al. 2007; Williams et al. 2009).

Similar to restoration-induced cooling, the known potential of restoration to moderate the effects of whirling disease is currently limited by localized and short-term field studies (Hansen and Budy 2011; Thompson 2011). Salmonid whirling disease is a parasitic infection cause by the exotic myxosporean Myxobolus cerebralis, which is native to the Eurasian continent and arrived on the North American continent in the 1950s where it spread rapidly (Bartholomew and Reno 2002). Clinical signs of whirling disease include blacktail, radical whirling (tail chasing) behavior and skeletal deformities (MacConnell and Vincent 2002). Whirling disease has been associated with population declines of Rainbow Trout Oncorhynchus mykiss in certain Montana and Colorado rivers (Nehring and Walker 1996; Vincent 1996; Granath et al. 2007; McMahon et al. 2010). Whirling disease may be especially harmful in groundwater-dominated streams where several environmental factors are conducive to the proliferation of M. cerebralis and its obligate aquatic worm host Tubifex tubifex (Burckhardt and Hubert 2005; Neudecker et al. 2012; Pierce et al. 2012).

Habitat conditions favorable for the proliferation of M. cerebralis and T. tubifex generally include (1) high stream temperatures (MacConnell and Vincent 2002; Hansen and Budy 2011), (2) fine sediment (Krueger et al. 2006; Anlauf and Moffitt 2008; McGinnis and Kerans 2013), and (3) elevated nutrient concentrations (Kaer et al. 2006), all of which can increase with the anthropogenic degradation of streams (Zendt and Bergersen 2000; Hansen and Budy 2011; McGinnis and Kerans 2013). As a result, the ability of restoration to offset whirling disease seems to require a reduction of one or more of these conditions, as well as an increasing recognition that mediating environmental conditions tied to whirling disease can vary greatly between basin-fed (Anlauf and Moffitt 2008; Hansen and Budy 2011; McGinnis and Kerans 2013) and groundwater-fed streams (Burckhardt and Hubert 2005; Neudecker et al. 2012; Pierce et al. 2012).

Myxobolus cerebralis has a complex, two-host life cycle and can affect most salmonids, which include trout, whitefish, and salmon (Bartholomew and Wilson 2002). Susceptibility to the pathogen depends on species (Hedrick et al. 1999; MacConnell and Vincent 2002; Vincent 2002), fish age and size (Ryce et al. 2005), and parasite dose at time of exposure (Vincent 2002). Infectious conditions often vary by season (Downing et al. 2002; De La Hoz Franco and Budy 2004; Neudecker et al. 2012) and typically peak in rivers during summer and autumn (MacConnell and Vincent 2002; De La Hoz Franco and Budy 2004; Pierce et al. 2012) at temperatures conducive (10–15°C) to the release of triactinomyxons (TAMs; El-Matbouli et al. 1999; De La Hoz Franco and Budy 2004; Kerans et al. 2005). However, recent studies show high M. cerebralis infection can be continuous across seasons and can occur at much lower temperatures (<5°C) with the moderating influence of groundwater inflows (Neudecker et al. 2012; Pierce et al. 2012). As an example of this elevated infections in groundwater environment, a prior study in the Blackfoot River basin found a majority of Mountain Whitefish Prosopium williamsoni were infected in early spring in the groundwater-induced upper Blackfoot River compared with no concurrent infection a river segment with very little groundwater influence (Pierce et al. 2012). Likewise, a second study found season-long higher infection rates in groundwater-dominated streams (spring creeks) versus receiving waters (Neudecker et al. 2012). High TAM release in groundwater-dominated streams (e.g., spring creeks) relates largely to stable stream temperatures (Neudecker et al. 2012; Pierce et al. 2012), especially where low channel gradients, lack of flushing flows, and high sediment loads are present (Hiner and Moffitt 2002; Hubert et al. 2002; Neudecker et al. 2012).

In the Blackfoot Basin of Western Montana, we monitored summer stream temperatures associated with the restoration of Kleinschmidt Creek over a 15-year before–after period (1998–2012), as well as the prevalence and severity of M. cerebralis infection during a 7-year before–after period (1998–2004). This study expands on a prior study that broadly describes restoration techniques in the Blackfoot basin, including changes in general channel morphology and increases in wild trout abundance in Kleinschmidt Creek (Pierce et al. 2013). The goal of this study is to examine the potential of restoration to alter water temperature in a groundwater-dominated stream and to clarify whether comprehensive stream restoration can mediate M. cerebralis, which is now present in many low-elevation streams of the Blackfoot basin (Pierce et al. 2009, 2012; Neudecker et al. 2012). Our specific study objectives were to (1) examine summer stream temperature changes after the full reconstruction of Kleinschmidt Creek, and (2) identify...
the prevalence and severity of *M. cerebralis* infection before and after stream restoration.

**STUDY AREA**

Kleinschmidt Spring Creek, a spring creek tributary to the lower North Fork of the Blackfoot River, is located on the floor of the Blackfoot River valley in west-central Montana (Figure 1). Discharge in Kleinschmidt Creek ranges from a low of 0.26 m$^3$/s during winter and spring to a high of about 0.42 m$^3$/s during midsummer months (Pierce and Podner 2006). Although Kleinschmidt Creek receives basin-fed runoff upstream of stream kilometer (skm) 3.2, approximately 90% of summer stream flows are generated by groundwater inflows from an alluvial aquifer, most of which surfaces between skm 1.6 and 3.2 (Pierce et al. 2002; Pierce and Podner 2006). To examine stream temperature reduction, we monitored stream temperatures in the North Fork of the Blackfoot River at U.S. Geological Survey (USGS) gauge station 12338300 and treated this as a control site in the study (Figure 1). Although the lower North Fork of the Blackfoot River is much larger and has a snow-fed and basin-fed hydrograph during the spring runoff, like Kleinschmidt Creek, the lower 12 skm of the North Fork of the Blackfoot River receives >80% of late summer (August–September) base flow (mean discharge = 5.8 m$^3$/s) from groundwater inflows (Montana Department of Natural Resource Conservation and USGS, unpublished data) and several small spring creeks entering the North Fork of the Blackfoot River between skm 8 and 10.

To reestablish natural features of a relatively deep and narrow channel (Table 1; Figure 2), the reconstruction of Kleinschmidt Creek was completed in the autumn of 2001.

![Figure 1](image_url)
(Pierce et al. 2013). Channel renaturalization increased channel length by 36% and reduced the wetted surface area of the channel by 69% by narrowing the channel. In addition, stream renaturalization recreated pools and riffles, increased habitat diversity, reduced instream sediment levels, fenced livestock from the riparian corridor, reestablished vegetation and secured instream flows.

Kleinschmidt Creek supports a mixed community of salmonids, though Brown Trout *Salmo trutta* compose about 92% of the salmonid community (Pierce et al. 2013); other salmonids include, in order of decreasing density, Brook Trout *Salvelinus fontinalis*, native Westslope Cutthroat Trout *O. clarkii lewisi*, native Bull Trout *Salvelinus confluentus*, and Rainbow Trout. Prior to the restoration of Kleinschmidt Creek, the exotic parasite *M. cerebralis* was already present at high infection levels (Neudecker et al. 2012). Rainbow Trout are highly susceptible to whirling disease (MacConnell and Vincent 2002), whereas Brook Trout, Westslope Cutthroat Trout, and Bull Trout possess intermediate (i.e., partial) resistance to whirling disease (MacConnell and Vincent 2002). The nonnative Brown Trout is naturally much more resistant to the parasite, given their coevolution on the Eurasian continent (Bartholomew and Reno 2002).

**METHODS**

**Stream temperature change.**—To examine summer stream temperature change, we monitored stream temperatures near the mouth of Kleinschmidt Creek and at skm 4.2 on the lower North Fork of the Blackfoot River between 1 June and 1 October (Figure 2). Concurrent daily monitoring included 3 years prerestoration (1998, 1999, and 2001) and 5 years postrestoration (2002, 2004, 2010, 2012, and 2013) on both Kleinschmidt Creek and the North Fork of the Blackfoot River. For both Kleinschmidt Creek and the North Fork of the Blackfoot River site, we recorded temperatures continuously at 48–72 min intervals using Onset digital thermograph (Onset Computer Corporation, Pocasset, Massachusetts; accuracy = 0.2°C). During the monitoring periods, daily stream temperature statistics (maximum, mean and minimum) from Kleinschmidt Creek were paired with the same daily stream temperature statistics from the North Fork of the Blackfoot River control site. Concurrent daily air temperature statistics (maximum, mean, and minimum) were also extracted for each site before and after periods using TopoWx daily climatological surfaces (TopoWx 2014; J. W. Oyler, University of Montana, and colleagues, unpublished data), except for the year 2013, when climatological data were unavailable.

We used a before–after, control–impact (BACI) design to compare the mean, maximum and range of daily stream temperatures for the control (North Fork of the Blackfoot River)

<table>
<thead>
<tr>
<th>Period</th>
<th>Channel length (km)</th>
<th>Sinuosity</th>
<th>Mean wetted width (m)</th>
<th>Wetted surface area (f)</th>
<th>Number of pools/100 m</th>
<th>Mean maximum pool depth (m)</th>
<th>Number of woody stems/100 m</th>
<th>Percent fine sediment (&lt;2 mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Before</td>
<td>2.5</td>
<td>1.1</td>
<td>12.6</td>
<td>3.2</td>
<td>0.6</td>
<td>0.7</td>
<td>0.03</td>
<td>30a</td>
</tr>
<tr>
<td>After</td>
<td>3.4</td>
<td>1.5</td>
<td>2.9</td>
<td>1.0</td>
<td>4.5</td>
<td>1.0</td>
<td>6.40</td>
<td>21</td>
</tr>
</tbody>
</table>

aData from Neudecker et al. 2012.
and treatment (Kleinschmidt Creek) sites and averaged each temperature metric over the 3 years prerestoration and 11-years postrestoration periods. We selected these stream temperature parameters because they are commonly used in both salmonid and whirling disease studies (e.g., Dunham et al. 2003; Kerans et al. 2005; Pierce et al. 2012). A single-factor ANOVA with before–after restoration periods as a fixed factor was used to test maximum and mean stream temperature change for Kleinschmidt Creek. A two-factor ANOVA with before–after restoration periods and site as fixed factors was used to test for differences in air temperatures, as well as stream temperatures between the control and treatment sites. All statistical analyses were conducted at α = 0.05 in R version 2.15.0 software (R Development Core Team 2013).

Whirling disease testing in Kleinschmidt Creek.—Similar to previous whirling disease studies in the Blackfoot basin (Pierce et al. 2009, 2012; Neudecker et al. 2012), we monitored the prevalence (percent infected) and severity of *M. cerebralis* infection before and after restoration in lower Kleinschmidt Creek using sentinel cage exposures with hatchery Rainbow Trout fry (diploid age-0 cohorts) as surrogates for infection. Test fish ranged in age from 66 to 151 d posthatch, and total lengths ranged from 34 to 53 mm (Table 2). Five exposure trials were undertaken between late winter (March 15) and early summer (July 11) and spanned a 7-year period, which included 2 years prerestoration (1998–1999) and 3 years postrestoration (2002–2004). The March to July span of exposure trials in this study overlaps with hatching, emergence, and early rearing periods (i.e., periods of increased disease vulnerability) for fall-spawning Brown Trout, Brook Trout, and Rainbow Trout, as well as spring-spawning Rainbow Trout and Westslope Cutthroat Trout (Behnke 1992; Ryce et al. 2005; Neudecker et al. 2012; Pierce et al. 2009, 2012). To examine variation of infection among three trout species present in Kleinschmidt Creek, we also completed side-by-side postrestoration exposure trials of age-0 hatchery Brown Trout, Brook Trout, and Rainbow Trout in March 2002 (Table 2).

Following field exposures and a holding period, all fish in this study were killed and heads were histologically examined and scored using the MacConnell–Baldwin grading scale (Hedrick et al. 1999; Baldwin et al. 2000; Ryce et al. 2004). Since 1999, this scale has categorically ranked the severity of infection into one of six qualitative groups: 0 = no infection, 1 = minimal, 2 = mild, 3 = moderate, 4 = high, and 5 = severe. Prior to 1999, grade-5 infections were not distinguished from grade 4 (E. Ryce, Montana Fish, Wildlife and Parks, personal communication). As in prior studies, the severity of infection for each exposure trial was considered high if >50% of exposed trout had histological scores of grades >3 severity (Pierce et al. 2009, 2012; Neudecker et al. 2012). At severity grades >3, *M. cerebralis* digests and destroys cartilage of young fish, which causes inflammation and lesions in the spine and cranium, resulting in skeletal damage as severity of infection increases. This leaves young fish crippled, weak, and unable to feed or evade predators, all of which ultimately elevate mortality (Hedrick et al. 1999; MacConnell and Vincent 2002; Ryce et al. 2004). According to Ryce et al. (2005), age-0 Rainbow Trout are most susceptible if exposed to *M. cerebralis* at <63 d posthatch and at <40 mm TL, after which time the effects of disease are reduced through increased resistance.

### RESULTS

#### Air and Stream Temperature Change

To ensure that changes in stream temperatures before and after restoration were not driven by climatological differences between sites, we performed the same BACI two-factor

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**TABLE 2.** Sentinel exposure results for three salmonid species in lower Kleinschmidt Creek before (1998-99) and after restoration (2002–2004).

<table>
<thead>
<tr>
<th>Species</th>
<th>Exposure date</th>
<th>Mean daily water temperature (°C)</th>
<th>Number histologically examined</th>
<th>Individual histological scores</th>
<th>Group scores (%)</th>
<th>Age of fish (d) at exposure</th>
<th>Length of fish (mm) at exposure</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rainbow Trout</td>
<td>Jul 1–11, 1998</td>
<td>12.5</td>
<td>48</td>
<td>5 3 7 13 20</td>
<td>90</td>
<td>75</td>
<td>37</td>
</tr>
<tr>
<td>Rainbow Trout</td>
<td>Jul 1–11, 1999</td>
<td>11.0</td>
<td>50</td>
<td>5 3 4 18 17</td>
<td>90</td>
<td>78</td>
<td>43</td>
</tr>
<tr>
<td>Rainbow Trout</td>
<td>Mar 15–25, 2002</td>
<td>5.8</td>
<td>48</td>
<td>0 0 3 17 28</td>
<td>100</td>
<td>71</td>
<td>45</td>
</tr>
<tr>
<td>Brown Trout</td>
<td>Mar 15–25, 2002</td>
<td>5.8</td>
<td>43</td>
<td>42 1 0 0 0</td>
<td>2</td>
<td>107</td>
<td>37</td>
</tr>
<tr>
<td>Brook Trout</td>
<td>Mar 15–25, 2002</td>
<td>5.8</td>
<td>50</td>
<td>2 1 3 4 18 22</td>
<td>96</td>
<td>88</td>
<td>115</td>
</tr>
<tr>
<td>Rainbow Trout</td>
<td>Apr 23–May 3, 2003</td>
<td>9.0</td>
<td>50</td>
<td>1 0 0 0 9 40</td>
<td>98</td>
<td>98</td>
<td>151</td>
</tr>
<tr>
<td>Rainbow Trout</td>
<td>Jun 20–30, 2003</td>
<td>—</td>
<td>49</td>
<td>0 0 0 0 3 46</td>
<td>100</td>
<td>100</td>
<td>111</td>
</tr>
</tbody>
</table>

*aNot applicable.*
ANOVA using TopoWx air temperature data as performed in the stream temperature analyses. We found no statistically significant before–after differences between control and treatment sites in average daily mean air temperatures ($F_{1,1226} = 0.0015, P = 0.9691$, Figure 3A), average daily maximum air temperatures ($F_{1,1226} = 0.0052, P = 0.9427$, Figure 3B), and the range in daily maximum and minimum air temperatures ($F_{1,1226} = 0.0186, P = 0.8916$, Figure 3C).

Prior to restoration, daily maximum stream temperatures in Kleinschmidt Creek averaged 15.7°C in contrast to 13.8°C in the North Fork of the Blackfoot River (Figure 4A). During the 11-year postrestoration period (2002–2013), average daily maximum stream temperatures in Kleinschmidt Creek decreased to 12.5°C, significantly lower than the prerestoration (1998–2001) average of 15.7°C ($F_{1, 710} = 647.4, P < 0.0001$). More interestingly, postrestoration daily maximum
stream temperatures in Kleinschmidt Creek were 1.5°C lower than temperatures at the North Fork of the Blackfoot River control site, where prerestoration averages were 1.9°C higher ($F_{1.1420} = 220.9, P < 0.0001$; Figure 4A). This pattern of reduction was consistent for mean daily stream temperatures at the treatment site: prerestoration average = 11.2°C and postrestoration average = 10.0°C ($F_{1, 710} = 391.1, P < 0.0001$). In addition, average daily stream temperatures at the treatment site were 0.5°C higher (i.e., 11.2°C) than the control site prerestoration (i.e., 10.7°C) and 1.1°C lower postrestoration ($F_{1, 1420} = 125.1, P < 0.0001$; Figure 4B). Consistent with both trends in stream temperature reduction, the average range of daily stream temperatures (i.e., difference between daily maximum and minimum) in Kleinschmidt Creek declined 3.3°C from 7.6°C prerestoration to 4.3°C postrestoration. In comparison, differences at the North Fork of the Blackfoot River site were 8.3°C prerestoration and 8.6°C postrestoration, statistically different than those at the treatment site ($F_{1, 1420} = 243.7, P < 0.0001$; Figure 4C).

Sentinel Cage Exposures

Prior to restoration, 90% of the Rainbow Trout test fish were infected with *M. cerebralis*, of which most (69–78%) had high (grade, >3) severity of infection. Following restoration, the prevalence of infection increased to 93–100% of test fish, and the severity of high infection (grade, ≥3) increased to 96–100% during late winter to early summer exposures (Table 2). The side-by-side Brown Trout, Brook Trout, and Rainbow Trout exposure trials showed high (grade, ≥3) severity of infections for both Rainbow Trout (100%) and Brook Trout (88%) versus minimal infection for Brown Trout (2% with grade 1). In addition to high infection, most Rainbow Trout examined exceeded the age (i.e., 63 d) and size (40 mm) at which resistance to whirling disease is conferred (Table 2; Ryce et al. 2005), which further demonstrates infection conditions during the March–July exposure period.

DISCUSSION

This study shows channel renaturalization can reduce summer stream temperatures in small low-elevation, groundwater-dominated streams. Despite full channel restoration and significant reductions in summer stream temperatures, the severity of *M. cerebralis* infection remained high for susceptible salmonids, but low for nonnative Brown Trout, a salmonid with natural immunity to the parasite. Because of the more continuous release of TAMs in spring creeks, it appears unlikely that salmonids other than Brown Trout (due to their increased resistance to *M. cerebralis*) can reproduce and rear successfully in Kleinschmidt Creek due to infectious conditions that overlap with hatching and early rearing windows for spring and fall spawners. Though infectious conditions clearly favor resident brown trout, a reduction in stream temperature may favor age-1 and older native trout in Kleinschmidt Creek, as well as improve thermal habitat in receiving waters of the North Fork of the Blackfoot River, where infections are low (Pierce et al. 2009, 2012; Neudecker et al. 2012).

Channel Restoration and Stream Temperature

Spring creek restoration is important for wild trout because the potential for cool temperatures and stable flows can provide optimum conditions for spawning, rearing, and refugia (Decker-Hess 1985, 1987; Swanberg 1997; Pierce et al. 2014). Though the importance of groundwater influences to salmonid habitat is widely recognized (Brown and Mackay 1995; Baxter and Hauer 2000; Chu et al. 2008), few if any, published field studies examine the efficacy of restoration in buffering anthropogenic warming effects of stream temperatures in areas of strong groundwater inflows (Poole and Berman 2001; Ebersole et al. 2003). This form of temperature reduction is particularly important to coldwater salmonids and may be especially so for migratory native trout of western North America (e.g., Westslope Cutthroat Trout and Bull Trout) because migratory native trout often rely on a patchy network of cold, low-elevation streams for thermal refugia (Swanberg 1997; Rieman et al. 2007; Jones et al. 2014). The North Fork of the Blackfoot River near the Kleinschmidt Creek confluence provides a clear example of important low-elevation refugia. Here, fluvial Bull Trout from the Blackfoot River migrate, in some cases, long distances (>40 km) to summering areas in the lower North Fork of the Blackfoot River, where ambient summer water temperatures are about 5°C cooler than the Blackfoot River (Swanberg 1997; USFWS 2010; Pierce and Podner 2013).

Our study shows active restoration of groundwater-dominated streams can significantly reduce summer stream temperatures to levels suitable to native trout. In the case of Kleinschmidt Creek, a 69% reduction in wetted surface area of the channel preceded a 3.2°C reduction in the average maximum daily temperatures postrestoration, a 1.2°C reduction in mean daily stream temperatures, and a 3.3°C reduction in the range of daily temperatures (Figure 4). Following restoration, summer temperatures on Kleinschmidt Creek declined into the optimal thermal range of bull trout (i.e., maximum temperatures <13°C; Selong et al. 2001; Dunham et al. 2003) with maximum temperatures about 1.5°C colder than those in the North Fork of the Blackfoot River (Figure 4). Likewise, two additional spring creeks to the North Fork of the Blackfoot River have shown similar reductions in maximum temperatures (4–6°C) following full channel reconstruction (Pierce and Podner 2013). Considered together, restored spring creeks of the North Fork of the Blackfoot River show active restoration through reductions in wetted surface area, and revegetation can reduce summer temperatures in small, groundwater-dominated streams. Such buffering may ultimately prove important based on regional climate projections that point to
continued loss of thermal habitat for coldwater salmonids, especially in low-elevation streams like the North Fork of the Blackfoot River (Rieman et al. 2007; Williams et al. 2009; Jones et al. 2014).

Groundwater and *M. cerebralis* Infection

The same groundwater-fed environments that often foster productive trout fisheries also make certain spring creeks more prone to the proliferation of *M. cerebralis* and the release of TAMs (MacConnell and Vincent 2002; Burckhardt and Hubert 2005; Neudecker et al. 2012). In exposure trials of surrogate rainbow trout, we found no restoration-induced moderation in the prevalence or severity of *M. cerebralis* infection, despite more natural channel morphology and reductions in summer stream temperatures. To the contrary, postrestoration exposures revealed higher (grade, ≥3) severity of infection in all Rainbow Trout trials than in prerestoration scores (Table 2). Increases in both the prevalence and severity of infection correspond in time with the *M. cerebralis* enzootic, which intensified in the Blackfoot basin between 1996 and 2005 (Pierce et al. 2009). Yet, our findings of high grades of severity are also consistent with recent studies showing season-long trends of high infection in groundwater-dominated streams (Pierce et al. 2012; Neudecker et al. 2012). Unlike the summer to autumn period of high TAM production in basin-fed streams and larger rivers (e.g., Gilbert and Granath 2001; Downing et al. 2002; Neudecker et al. 2012), high infections in groundwater environments relate to continuous TAM release under the influence of stable groundwater temperatures (Kerans and Zale 2002; Neudecker et al. 2012; Pierce et al. 2012).

Though this study emphasized summer temperature reduction, we also monitored winter stream temperatures prior to (December–March) and during the March 15–25, 2002, sentinel exposures to explore groundwater–disease relationships. This monitoring identified an average temperature of 6.1°C from December through March and 5.8°C during the exposure period (Table 2). These values reveal relatively warm and stable winter temperatures compared with <1.0°C winter temperatures observed in nearby basin-fed streams during the same period (Pierce et al. 2004). These warmer temperatures are colder than the average temperatures (10–15°C) often associated with TAM release (El-Matbouli et al. 1999; Hansen and Budy 2011). Under these temperature conditions, all 48 Rainbow Trout in the 2002 exposure trial showed a high (grade, ≥3) severity of infection, and 28 showed grade-5 severity (Table 2). Similar to Neudecker et al. (2012), the March–July timing of high histological scores in our study overlapped temporally (winter and spring) with that of other Montana spring creeks where infectious conditions extend from autumn into spring. However, our study shows high infections can also extend from spring into summer in groundwater dominated streams. Unlike the summer–autumn peak of high infections for Montana Rivers at warmer water temperatures (i.e., 10–15°C; Gilbert and Granath 2001; Downing et al. 2002; Pierce et al. 2009), we found that high grades of infections in groundwater-dominated streams can occur regardless of season, which confirms high infections at much lower temperatures than in basin-influenced areas (e.g., Hansen and Budy 2011; Neudecker et al. 2012; Pierce et al. 2012). As described by Kerans et al. (2005), TAM release at lower temperatures relates the number of degree days that *T. tubifex* worms were exposed to *M. cerebralis* and that the development of *M. cerebralis* in worms is related to temperature accumulation. This may explain why infection in fish (and TAM production in general) is different in spring creeks where temperatures are high in winter.

Our study further suggests that certain groundwater-dominated streams, like Kleinschmidt Creek, may be predisposed to high infection rates. These conditions clearly contrast in both space and time to streams with more basin influences (Anlauf and Moffitt 2008; Hansen and Budy 2011; McGinnis and Kerans 2013), including the North Fork of the Blackfoot River (where sentinel exposures near the confluence of Kleinschmidt Creek consistently show low to no infection) and the main stem Blackfoot River (where high infections ≥3 in severity occur during summer; Pierce et al. 2009, 2012; Neudecker et al. 2012). For basin-fed streams, infectious conditions often occur in lower-elevation stream valleys with low gradients and fine sediments (De La Hoz Franco and Budy 2004; Anlauf and Moffitt 2008) and where temperatures (10–15°C) favor the seasonal release of TAMs (El-Matbouli et al. 1999; Hansen and Budy 2011). In addition to these natural stream features, human land uses that elevate temperature, sediment, and nutrient regimes (e.g., roads and heavy riparian grazing) have also been implicated in the proliferation of *M. cerebralis* by creating habitat favorable for *T. tubifex*, temperatures favorable to TAM release, or both (Zendt and Bergersen 2000; Anlauf and Moffitt 2008; Hansen and Budy 2011; McGinnis and Kerans 2013). Our study suggests the potential for restoration to mediate whirling disease may apply to streams with more basin influence. It also illustrates the potential for restoration to mitigate high summer stream temperatures or thermally unsuitable habitat, which could be especially important for basin-fed streams where temperatures are not buffered by groundwater influences and are significantly higher during the summer months.

In contrast with our results from a groundwater-dominated stream, Hansen and Budy (2011) showed disease reduction in a small basin-fed stream in a northern Utah watershed, where passive restoration (grazing exclusion) improved riparian condition, reduced total nitrogen and phosphorus levels, and reduced infection rates when mean daily summer stream temperatures fell below 10–15°C. These findings support an assertion that restoration potential varies between groundwater-fed and basin-fed streams. Implications of both studies are, however, limited by the short-term nature of the posttreatment data sets. In our study, exposure trials ended at 3 years.
postrestoration, which may not provide enough time for restoration-induced changes to alter tubificid lineages or otherwise mediate *M. cerebralis* through changes in benthic communities (Kerans et al. 2004; Beauchamp et al. 2005; Nehring et al. 2005). Long-term studies across hydro-physiological landscapes are needed to better explore the mechanisms of whirling disease reduction through restoration and stream temperature reduction.

With the exception of Brown Trout, most postrestoration exposure trials showed grades 4 and 5 severity (Table 2). Conversely, Brown Trout, a species with innate natural immunity, showed very low infection rates, as demonstrated by the side-by-side exposures in this study (Table 2). Following restoration, the abundance of brown trout have increased significantly in Kleinschmidt Creek (Pierce et al. 2012), whereas the presence of more susceptible species (Brook Trout, Rainbow Trout, Bull Trout, and Westslope Cutthroat Trout) remain incidental (Montana Fish, Wildlife and Parks, unpublished data). Though increases in resident Brown Trout can be attributed to habitat improvements, as well as disease resistance, our study suggests the incidental presence of other more susceptible salmonids may be the result of *M. cerebralis*.

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