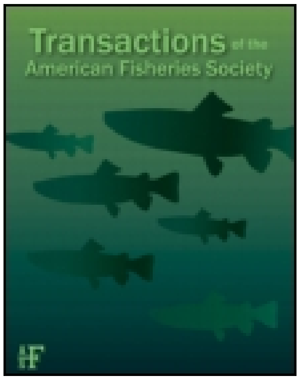

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ARTICLE

Spawning Behavior of Mountain Whitefish and Co-occurrence of *Myxobolus cerebralis* in the Blackfoot River Basin, Montana

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Abstract
To assess the exposure of Blackfoot River mountain whitefish *Prosopium williamsoni* to the exotic parasite *Myxobolus cerebralis*, the cause of salmonid whirling disease, we investigated the spawning behavior of 49 adult mountain whitefish and their overlap with *M. cerebralis* within the Blackfoot River basin, Montana. A majority of the mountain whitefish radio-tagged in the Blackfoot River migrated upstream (range, 0.1–79.0 km) to spawning sites located primarily in the main stem of the Blackfoot River. Spawning ranged from 31 October in the lower river to 9 November in the upper river and occurred across a range of substrate and channel types. Despite later spawning in the upper river, eggs hatched earlier under the warming influence of groundwater inflows. Here, a majority of wild mountain whitefish fry (65%) tested positive for *M. cerebralis* infection during the immediate posthatch period of mid-April. Conversely, mountain whitefish fry from the lower river, downstream of the groundwater influence, showed no detectable infection. June exposure trials using surrogate rainbow trout *Oncorhynchus mykiss* in nine tributaries supporting mountain whitefish showed *M. cerebralis* infection rates ranging from 0% to 100% as well as a pattern of high triactinomyxon (TAM) exposure throughout the main-stem Blackfoot River. For mountain whitefish, the co-occurrence with *M. cerebralis* varied spatially across the basin and temporally within the main-stem Blackfoot River at the most vulnerable early life stages. This variability appears to buffer age-0 mountain whitefish from infectious conditions across large areas of the basin. However, continuous TAM release from groundwater-influenced environments coinciding with mountain whitefish hatch and early rearing may impose pathogenic conditions on mountain whitefish in the upper Blackfoot River.

Mountain whitefish *Prosopium williamsoni*, an endemic salmonid in the Pacific Northwest, occupy a range of environments, including medium to large rivers as well as lake and reservoir environments. In the Blackfoot River basin of western Montana, mountain whitefish occupy streams and rivers and interconnected natural lakes at the low elevations of the basin, a distribution that broadly overlaps with that of the parasite *Myxobolus cerebralis*. Despite the ubiquitous and often abundant presence of mountain whitefish in the large river systems, the life histories, population status, and potential effects of *M. cerebralis* on mountain whitefish populations are rarely studied and poorly understood. Even so, mountain whitefish are ecologically important as forage for upper trophic predators such as native bull trout *Salvelinus confluentus*, a species listed as threatened under the Endangered Species Act (USFWS 2010).

Whirling disease, a parasitic infection caused by the myxosporean *M. cerebralis*, is known to infect six genera of salmonids, including the genus *Prosopium*, which includes mountain whitefish. *Myxobolus cerebralis* has a complex, two-host life cycle involving the aquatic oligochaete worm *Tubifex tubifex* and a salmonid host. Salmonid susceptibility to the pathogen varies by 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; Schisler 2010). Mountain whitefish are considered less susceptible to severe infection than other susceptible salmonids (MacConnell and Vincent 2002). However, age-0 mountain whitefish

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are highly susceptible to injury-related mortality when exposed to *M. cerebralis* at a very young age (MacConnell and Vincent 2002; Schisler 2010).

Following the detection of *M. cerebralis* in the Blackfoot River basin in 1995, Montana Fish, Wildlife and Parks (FWP) began monitoring the extent of the range of *M. cerebralis* using sentinel exposures of age-0 hatchery rainbow trout *Oncorhynchus mykiss* as surrogates for infection in wild salmonids. Between 1998 and 2009, exposures of rainbow trout at 32 fixed monitoring sites identified the range expansion of *M. cerebralis* among certain low-elevation streams of the Blackfoot River valley (Pierce et al. 2009), including the upper Blackfoot River, where summer exposures have consistently demonstrated a high severity of infection since 2005 (FWP, unpublished data). Concurrent with the expansion of *M. cerebralis*, reports of possible disease-related mountain whitefish declines across the American West have been mounting (Burkhardt 2002; Vincent 2009; Schisler 2010), laboratory research has demonstrated high *M. cerebralis*–induced mortality of age-0 mountain whitefish (MacConnell et al. 2000; Schisler 2010), and field-based research has suggested similar high age-0 mortality in the wild (Hubert et al. 2002a; Schisler 2010).

Because *M. cerebralis* poses the greatest threat to salmonids during the early life stages (MacConnell and Vincent 2002; Ryce et al. 2005), the timing and location of spawning and early rearing sites and the co-occurrence of *M. cerebralis* essentially determine susceptibility to whirling disease (Bartholomew and Wilson 2002; Koel et al. 2006). Fish are most vulnerable if they hatch during the peak release of *M. cerebralis* triactinomyxons (TAMs), which typically occurs during the months of June through September (Thompson and Nehring 2000; Gilbert and Granath 2001; Downing et al. 2002) at water temperatures near 12–15°C (El-Matbouli et al. 1999; Kerans et al. 2005). Conversely, species that spawn in the fall and hatch during late winter or early spring (e.g., mountain whitefish) prior to the seasonal peak in TAMs, are usually older, larger and more resistant when they first encounter high parasite abundance at conducive temperatures and thus are less likely to develop whirling disease than spring spawners (Vincent 2000; Ryce et al. 2004). However, in groundwater-influenced environments, where water temperatures are moderated and more constant, high infection can occur in the late winter and early spring (Anderson 2004). This early exposure elevates the infection potential for fall spawners in general as well as injury-related mortality in the case of mountain whitefish (Hubert et al. 2002a, 2002b; Schisler 2010).

Although the distributions of mountain whitefish and *M. cerebralis* overlap at the low elevations of the Blackfoot River basin (Figure 1), the exposure risk of age-0 mountain whitefish to *M. cerebralis* at the critical early rearing stages is poorly understood. To investigate this exposure, we assessed the spawning behavior of mountain whitefish and the overlap with *M. cerebralis* within the main-stem Blackfoot River and several tributaries supporting mountain whitefish. The study objectives were to (1) identify the spawning movements, locations of spawning sites, and hatching periods for mountain whitefish in the Blackfoot River, (2) test for *M. cerebralis* infection at the early life stages across distinct spawning and early rearing areas of the Blackfoot River, and (3) examine the spatial overlap of *M. cerebralis* across mountain whitefish habitat within the basin. Our broader purpose was to gain a better understanding of mountain whitefish life history as well as the risks of *M. cerebralis* exposure in order to better manage mountain whitefish within parasite-positive rivers of western Montana.

STUDY AREA

The Blackfoot River, a free-flowing fifth-order tributary (Strahler 1957) of the upper Columbia River, lies in west-central Montana and flows west 212 km from the Continental Divide to its confluence with the Clark Fork River at Bonner, Montana (Figure 1). The River drains a 5,998-km^2 watershed through 3,038 km of perennial streams and generates a mean annual discharge of 44.8 m3/s (U.S. Geological Survey, unpublished data). The physical geography of the watershed is regionally variable, with subalpine forests dominating the high mountains, montane woodlands at the mid elevations, and semiarid glacial (pothole and outwash) topography on the valley floor. The primary tributaries of the Blackfoot River include the Clearwater River, North Fork, and Nevada Creek. Public lands and large tracts of industrial forestlands generally comprise the mountainous areas, while private lands comprise most of the foothills and bottomlands where traditional uses of the land include mining, timber harvest, cattle ranching, and recreation.

Within the Blackfoot River basin, the distribution of mountain whitefish includes the main-stem Blackfoot and Clearwater rivers, the larger, colder tributaries, the glacially formed lakes on the floor of the Clearwater River valley, and the lower reaches of small streams where age-0 mountain whitefish tend to concentrate during summer (Pierce et al. 2008). The total distribution of mountain whitefish in the Blackfoot basin spans about 450 km of rivers and streams. Although mountain whitefish occupy only about 15% of streams in the Blackfoot basin, they support a majority of the salmonid biomass in the main-stem Blackfoot River and comprise as much as 70% of the salmonid community (Pierce and Podner 2011). The mountain whitefish distribution overlaps with that of *M. cerebralis* at the lower elevations of the Blackfoot basin as well as with the general distribution of bull trout (USFWS 2010; Figure 1), where the mountain whitefish is considered an important forage fish (Bjornn 1991; McPhail and Troffe 2001).

For this study, we divided the main-stem Blackfoot River into three reaches downstream of river kilometer (rkm) 174 based on morphological features of the river environment. The lower river reach includes the lower 55.8 km of the main-stem Blackfoot River between the mouth and its confluence with the Clearwater River. This lower reach has a confined, higher-gradient channel with gravel to boulder substrate and deep bedrock and boulder-formed pools through a narrow canyon and is fed primary by higher-gradient tributaries. The middle reach extends

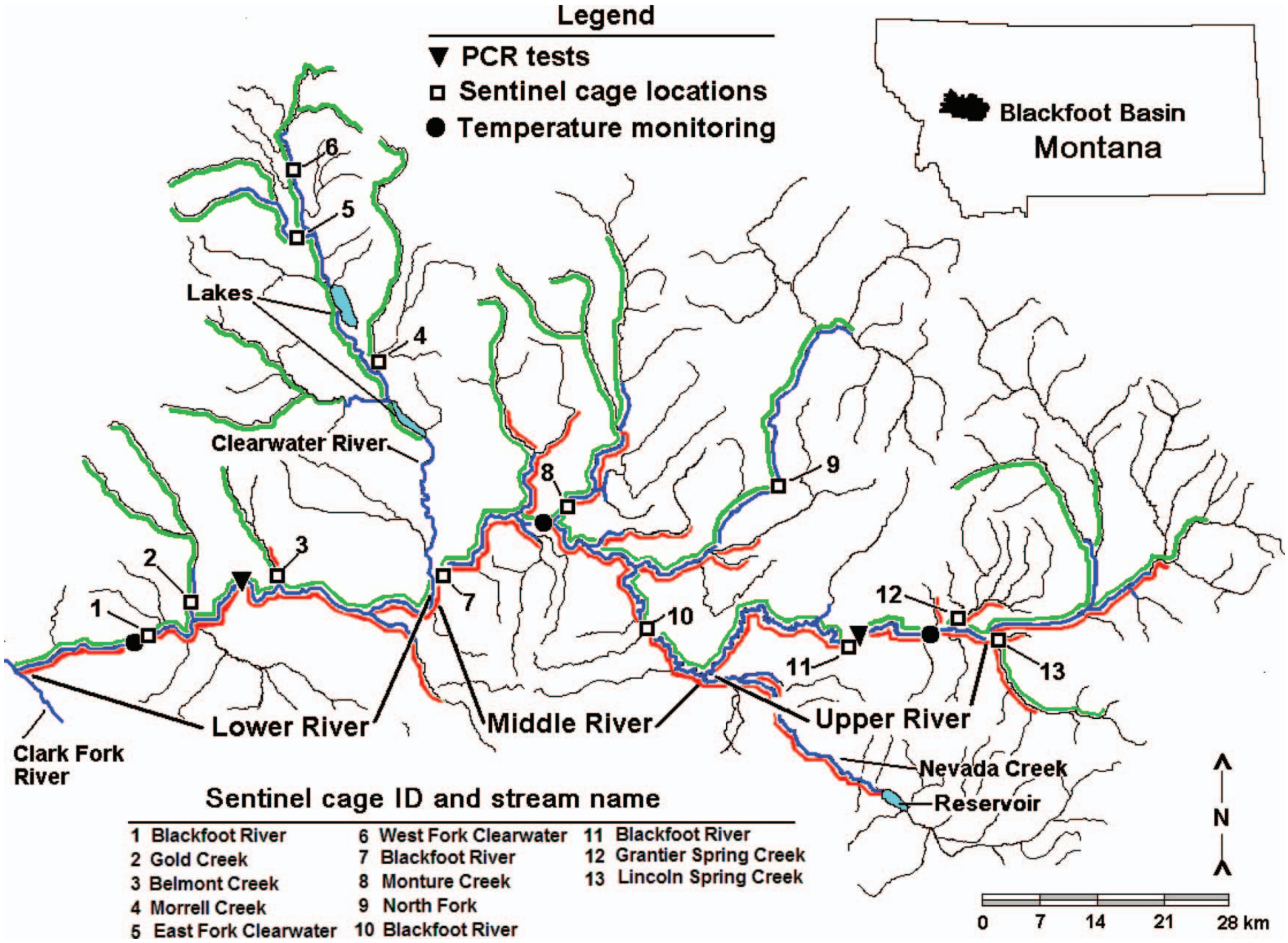

FIGURE 1. Map of the Blackfoot River basin showing the approximate overlap of bull trout (bold green lines), mountain whitefish (bold blue lines), and *M. cerebralis* (bold red lines) distributions (USFWS 2010; Pierce and Podner 2011). Also shown are the sentinel cage sites, water temperature monitoring sites, and locations of fish sampled by PCR for *M. cerebralis*, along with the demarcations of the lower, middle, and upper reaches of the Blackfoot River. The numbers assigned to the sentinel cages correspond to those in Table 2. [Figure available online in color.]

from the mouth of the Clearwater River 53.3 km upstream to the mouth of Nevada Creek. Here the channel is less confined, with deep pools with similar coarse substrate and is fed by larger lower-gradient tributaries. The upper reach extends 64.9 km from Nevada Creek to an intermittent (seasonally dry) section of the Blackfoot River located at km 174 (Figure 1). This upper reach is a sinuous, lower-gradient, unconfined alluvial channel with a primarily gravel substrate. The upper portion of the upper reach is groundwater induced and fed via several spring creeks and groundwater seeps, which collectively create stable river flows and moderate water temperatures during base flow (August–May) periods.

METHODS

Radiotelemetry: Migration and spawning.—To identify the spawning migrations and the timing and location of spawning sites, we tracked 49 adult mountain whitefish in the three study reaches of the Blackfoot River using radiotelemetry. These fish were captured using electrofishing in the Blackfoot River, implanted with continuous (12 h on : 12 h off) Lotek (Lotek Wireless, Newmarket, Ontario) radio transmitters (model NTC-6-2) on 10–11 June 2008 ($n = 13$) and between 4 and 17 June 2009 and tracked from early June ($n = 36$) through the end of the spawning period in late November (in 2009) or December (in 2008). These fish ranged from 305 to 485 mm in total length (mean, 388 mm) and from 274 to 1,146 g in weight (mean, 623 g). Transmitters were evenly allocated among the three reaches. Fish were captured in the spring during high, turbid flow conditions at water temperatures ranging from 6.1°C to 13.8°C. Transmitters weighed 4.5 g, and each emitted a unique coded signal. Transmitters weighed less than 2% of the mass of recipient fish (Winter 1996) and were implanted following standard surgical methods (Swanberg et al. 1999).

We located fish on foot using a handheld three-element Yagi antenna or by truck using an omnidirectional whip antenna. We located fish weekly prior to migrations

(June–August), 3–4 times per week during migrations and spawning (September–November), and once per week following spawning (November–December). All river locations and movements of mountain whitefish were referenced by rkm. As in a previous study (Pierce et al. 2009), we assumed that fish spawned if they followed a prespawning migration pattern common to other migrants in this study. The most upstream or downstream location for each fish expressing movement during the spawning window was the assumed spawning site. Spawning was visually confirmed in the upper Blackfoot River where viewing conditions allowed but not in the lower river due to poor viewing conditions. For individual fish, we estimated the timing of spawning movement and spawning as the central date between two contacts. Among reaches, the peak of spawning was identified as the median spawning date (Pierce et al. 2009).

Of the 49 radioed mountain whitefish, 18 nonmigrants showed no movement beyond the boundary of the habitat unit and were removed from the analyses of migration and spawning. Because of small sample sizes between reaches and similar spawning dates in both 2008 and 2009 (i.e., median spawning date = 5 November in both years), we grouped the remaining 31 mountain whitefish and used linear regressions to explore the relationships between the start date of migration and (1) the distance (km) to the spawning sites and (2) the total duration (number of days) of spawning-related migrations. To compare spawning dates among the three river reaches, we used an analysis of variance test (Kruskal–Wallis one-way ANOVA by ranks). These tests were performed in Statistica (version 7) software and evaluated at the $\alpha = 0.05$ level of significance.

Water temperature and hatching.—To further assess the timing of mountain whitefish migration and spawning and to estimate the timing of the mountain whitefish egg hatch, we used mean daily water temperatures measured with digital thermograph recorders (Onset Computer Corporation, Pocasset, Massachusetts) located in each of the three reaches (km 12.7, 73.5, and 169.0) of the Blackfoot River (Figure 1). Following Pierce et al. (2009), all thermographs recorded at 48-min intervals. To estimate the timing of the hatch for each of the three main-stem study reaches, we first averaged daily temperature readings from each of the three thermographs to calculate degree-days. Because the total degree-days (°C) necessary for incubating mountain whitefish eggs varies with temperature regime, we then used two calculations to estimate the timing of the hatch based on the thermal conditions specific to each river reach. We used a total of 258°C degree-days for mountain whitefish eggs incubated at 2°C mean daily temperature (Schisler 2010) to estimate the timing of the hatch in both lower river reaches where colder winter water temperatures prevail. For the upper reach, where winter water temperatures are higher, we used a total of 320°C degree-days for mountain whitefish eggs incubated at a mean daily temperature of 3.5°C (Jody Hupka, Pony Fish Hatchery, FWP, personal communication). Depending on the reach, we then estimated the hatching date of each fish within each reach of the Blackfoot River using an accumulation of either 258°C or 320°C degree-days, beginning with the estimated spawning date of each migrant mountain whitefish. The two migrant mountain whitefish that ascended the lower North Fork during the spawning period were excluded from estimates of hatching dates due to temperature data gaps during the winter incubation period.

Overlap of Myxobolus cerebralis with mountain whitefish.—We used two methods to investigate the overlap of *M. cerebralis* with mountain whitefish. One method was a basin-scale assessment of *M. cerebralis* in streams supporting mountain whitefish using sentinel cage exposures of hatchery rainbow trout as surrogates for *M. cerebralis* infection. Following Pierce et al. (2009), 50 hatchery rainbow trout of the Fish Lake strain (diploid age-0 cohorts; mean total length = 34 mm) were placed in sentinel cages at 13 sites 36–39 d posthatch to test for parasite exposure (Figure 1). Field exposures ran between 15 and 24 June 2009, a time that corresponds with the typical peak TAM production period for rivers of western Montana (Downing et al. 2002; Krueger et al. 2006; Pierce et al. 2009). Following sentinel exposures, test fish were held in pathogen-free water for another 186–217 d to allow *M. cerebralis*, if present, to mature, at which time all surviving fish were killed and sent to the Washington State University Animal Disease Diagnostic Laboratory at Pullman, where fish heads were histologically analyzed and scored using the MacConnell–Baldwin grading scale to determine infection and disease severity (Baldwin et al. 2000). This scale classifies infection into one of six categorical groups, ranging from 0 (nondetected) to 5 (severe). For this study, TAM exposure was considered high if a majority (>50%) of exposed trout had histological scores of at least grade 3. At grade 3 or higher, cartilage damage and inflammation of tissue can be severe in infected fish (Hedrick et al. 1999; Vincent 2002; Ryce et al. 2004).

The second method involved a polymerase chain reaction (PCR) test specific to *M. cerebralis* infection in wild mountain whitefish from the Blackfoot River. For this test, we collected 20 age-0 mountain whitefish from lower reach (km 29.1) downriver of the groundwater discharge area and 20 age-0 mountain whitefish from the upper reach (km 153.7) within the groundwater influence area (Figure 1). Fish were collected on 19–20 April 2010 during the early posthatch period. We did not test mountain whitefish in the middle reach due to geomorphic and water temperature similarities with the lower reach. These 40 fish (average total length = 18 mm; range, 14–24 mm) were placed in 95% ethanol and sent to the Colorado Division of Wildlife fish health laboratory for PCR analyses. For the PCR test, the head of each fish was removed and placed in an individual centrifuge to extract DNA. The sample DNA was examined for the presence of the *M. cerebralis Hsp70* gene segment by single-round PCR amplification (Schisler et al. 2001). Based on positive correlations between PCR amplification and spore counts, *M. cerebralis* infection of individual mountain whitefish was then grouped into one of following five categories: (1) below detection levels, (2) weak positive signal, (3) positive

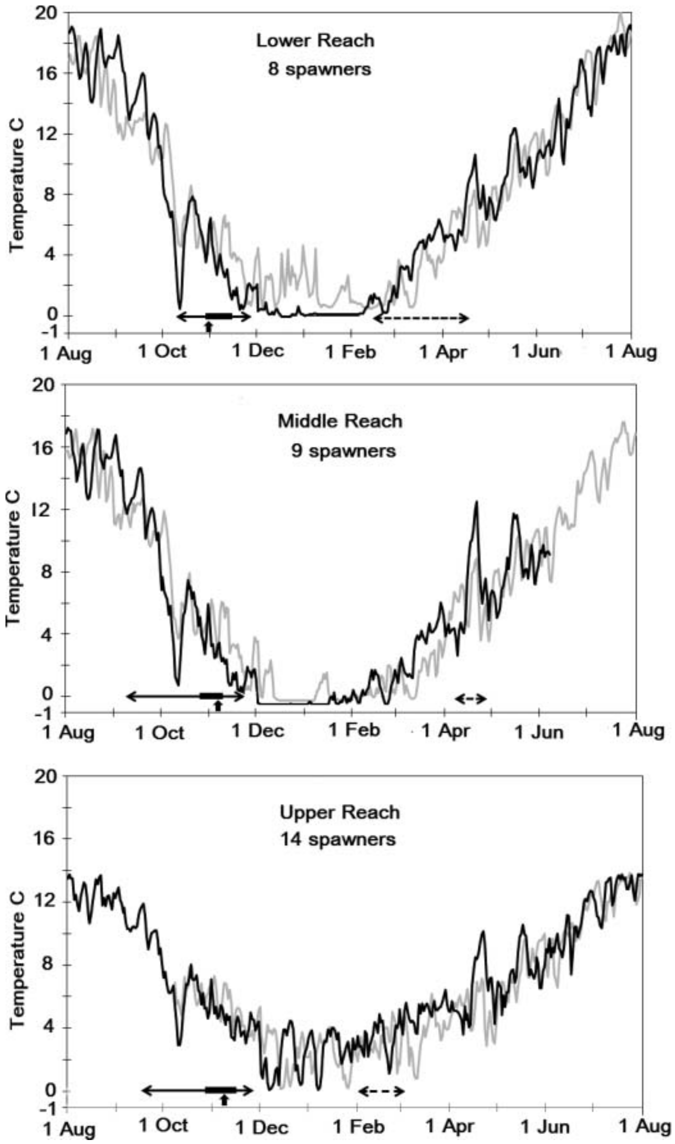

FIGURE 2. Mean daily water temperatures for the three reaches of the Blackfoot River from 1 August 2008 to 1 August 2009 (grey lines) and from 1 August 2009 to 1 August 2010 (black lines). The total period of spawning migrations is shown by the horizontal black arrowed lines. The thickened areas on the migration lines show the spawning windows, and the vertical arrows show the median spawning dates. The horizontal dashed lines show the estimated hatching period for an accumulated 258°C temperature units (lower and middle reaches) and 320°C temperature units (upper reach). Note the relatively warm winter temperatures in the upper reach.

signal, (4) strong positive signal, and (5) very strong positive signal (Schisler et al. 2001).

RESULTS

Spawning Behavior

To identify migrations and the locations and timing of spawning events, we tracked 49 radio-tagged mountain whitefish from early June though the postspawning period in late November. We made a total of 1,887 contacts, with an average of 39 contacts (range, 22–47) per fish. Of these 49 fish, most ($n = 31$) mountain whitefish expressed spawning-related migrations (0.1–79.0 km) beginning in early September, which culminated with spawning between 25 October and 26 November. Of these 31 mountain whitefish, most ($n = 29$) spawned within the main stem of the Blackfoot River and only 2 ascended a tributary (i.e., the North Fork; Figure 1). Over the course of this spawning, the remaining 18 mountain whitefish were identified as nonmigrants based on movements within the habitat unit but no detectable migration beyond the habitat unit. Across the three river reaches, the number of migrant mountain whitefish relative to the total number of radio-tagged mountain whitefish was 9 of 17 (53%), 11 of 15 (73%), and 11 of 17 (65%) for the lower, middle, and upper reaches, respectively.

Migrant mountain whitefish began their prespawning migrations as daily average water temperatures declined to 12°C (Figure 2). With the onset of migration, 27 mountain whitefish traveled upriver and 4 traveled downriver (Figure 3). These 31 fish migrated a median of 3.2 km (average = 12.2 km, range = 0.1–79.0 km) to spawning sites, where they spent an average of 12 d (range, 1–98). Fish that began spawning migrations earlier traveled a longer total (pre- and postspawning) distance ($R^2 = 0.14$, $P = 0.036$) over a longer period of time ($R^2 = 0.66$, $P < 0.0001$) than fish that began their migrations later. Mountain whitefish from the lower and upper reaches migrated short (median) distances of 1.0 km (range, 0.1–79.0 km) and 2.5 km (range, 0.4–10.2 km), respectively, compared with 8.4 km (range, 0.8–73.0 km) for mountain whitefish in the middle reach. As daily average water temperatures decreased from 12°C to 6°C, migrations attenuated to staging in large schools followed by evening spawning in aggregates of typically 4–10 fish (based on observations in the upper reach), which ensued at an average daily temperature of 5.0°C (range, 3.2–7.1°C). The peak of spawning was 31 October in the lower reach, versus 6 and 9 November in the middle and upper reaches (ANOVA: df = 2, $P = 0.15$).

After spawning, most migrant mountain whitefish ($n = 21$) migrated to downriver wintering areas, six moved short distances upriver, and four remained in the habitat unit used for spawning. Of the 21 fish that migrated downriver, most ($n = 11$) returned to their original premigration start location, including 1 that returned downriver 73.2 km to its original premigration location. Twelve others returned to within 1.6 km of their original start locations.

Water Temperatures and Hatching

For 29 migrant mountain whitefish that spawned in the Blackfoot River, the estimated hatch varied between 1 February and 27 April. However, this timing varied by river reach (Figure 2; Table 1). Despite later spawning in the upper reach, the eggs in the upper reach hatched earlier (1 February to 4 March) due to higher winter water temperature in this groundwater-influenced reach. In the middle reach, where water temperatures were consistently colder, the hatch occurred later (10–27 April). Winter temperatures were more variable in the lower reach, and the

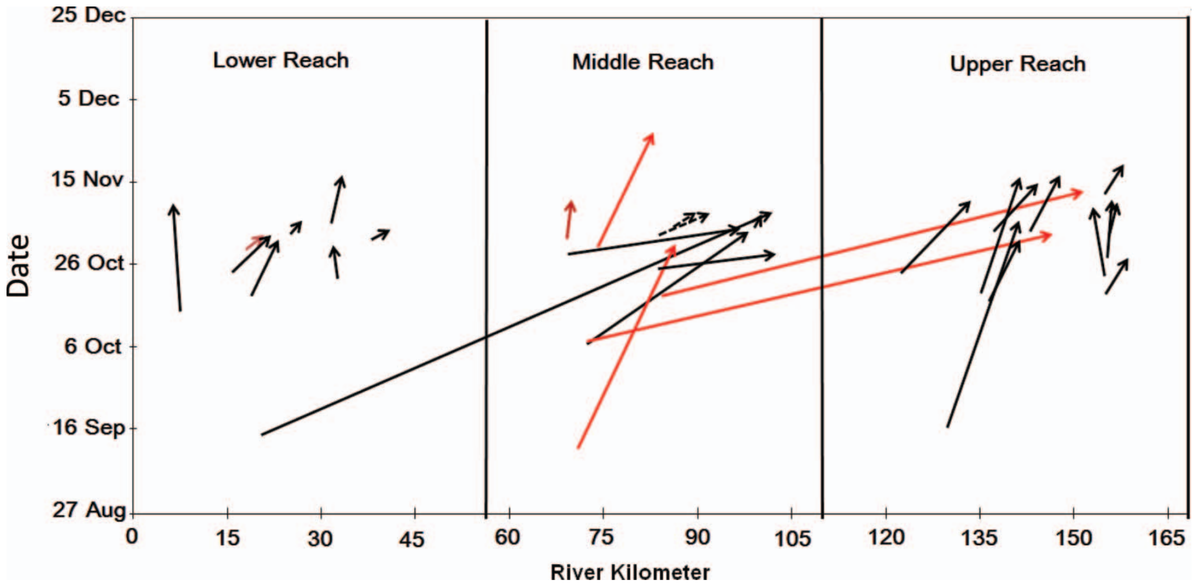

FIGURE 3. Migrations to spawning reaches of 31 mountain whitefish radio-tagged in three reaches of the main-stem Blackfoot River in 2008 (red arrows) and 2009 (black arrows). The arrows show where the migrations began and ended. The dashed lines in the middle reach represent two tributary (North Fork) spawners. [Figure available online in color.]

estimated hatching window was relatively wide (9 February to 22 April).

Histological scores and *M. cerebralis* Infection in Mountain Whitefish

Sentinel exposures and histological examinations of surrogate rainbow trout were completed for all 13 monitoring sites (Table 2). Histological examinations identified infection rates for exposure groups ranging from 0% to 100% during the June 2009 exposure. Seven of 13 exposures groups had high histological scores with ≥50% of the individual exposures scoring at grade ≥3 severity (Table 2). High exposure scores were recorded in all four monitoring sites on the Blackfoot River and one tributary entering each of the three reaches. Four exposure groups did not detect *M. cerebralis* at the three sites in the Clearwater River drainage and Gold Creek. The remaining two streams (Grantier Spring Creek and the North Fork) had low histological scores, with a majority of fish at <grade 3 severity. The PCR tests of newly hatched mountain whitefish tested during April did not detect *M. cerebralis* in the 20 fish collected in the lower Blackfoot River. However, a majority (65%; $n = 13$) of the 20 mountain whitefish from the upper Blackfoot River tested positive for *M. cerebralis*, of which 25% ($n = 5$) of the upper-river sample scored a strong positive signal.

DISCUSSION

Spawning Behavior

Brown (1952) was the first to identify nonmigratory spawning behavior in the larger rivers of Montana. Yet other studies report resident mountain whitefish in smaller streams (Wydoski 2001), residents among migratory populations (Baxter 2002), and highly migratory behavior across larger river systems (Pettit and Wallace 1975). In our study, migrations ranged from very short distances (<1 km) to long distances across river reaches (Figure 3). Within the larger metapopulation of the Blackfoot basin, additional spawning life history variation (e.g., resident fish) is expected across tributaries where mountain whitefish are consistently sampled (Pierce et al. 2008) but were not clearly linked in this study, with the exception of the lower North Fork. The Clearwater River chain of lakes also support lake-dwelling mountain whitefish; however, that life history has not been studied. Life history variation across tributaries, rivers, and lakes is recognized as high across the range of mountain whitefish (Brown 1952; Pettit and Wallace 1975; Northcote and Ennis 1994; McPhail and Troffe 1998; Wydoski 2001), which includes metapopulation function (migration and genetic exchange) at a broad regional scale (Whitely et al. 2006).

In addition to highly variable spawning movements within the main-stem Blackfoot River, mountain whitefish spawned across a diversity of physical channel features. In the upper study area, we observed aggregates of mountain whitefish broadcast spawning along the margins of pools and glides of an alluvial channel with gravel substrate and groundwater inflow. However, spawning areas in the mid- and lower Blackfoot River were morphologically variable and included large boulder-laden and bedrock pools with cobble to boulder substrate and little, if any, direct groundwater influence. Although we were unable to observe spawning in the larger, deeper confined channels of the mid- and lower Blackfoot River, radio-tracking indicated an increasing intensity of movement of both migrant and nonmigrant mountain whitefish within the large runs and pools (similar to the upper river) during peak spawning periods. Observations and collections of age-0 fry during the immediate posthatch period

TABLE 1. Spawning locations, estimated hatching dates for 258°C and 320°C degree-days, and average daily hatching temperatures for individual fish from the three study reaches and the North Fork (NF).

Spawning reach	River km	Spawning date	Temperature at spawning	Hatching date: At 258°C	Hatching date: At 320°C	Average daily incubation temperature (°C)
Lower	20.9	30 Oct 2008	4.8	19 Feb 2009		2.3
	32.7	28 Oct 2009	4.4	3 Apr 2010		1.7
	41.2	31 Oct 2009	6	5 Apr 2010		1.6
	20.9	30 Oct 2009	6.7	5 Apr 2010		1.7
	21.2	31 Oct 2009	6	5 Apr 2010		1.7
	6.8	8 Nov 2009	4	12 Apr 2010		1.7
	33	15 Nov 2009	1.1	15 Apr 2010		1.7
	26.2	4 Nov 2009	3.2	22 Apr 2010		1.7
Middle	83	29 Oct 2008	5.4	10 Apr 2009		1.6
	69	8 Nov 2008	6.9	19 Apr 2009		1.6
	81.4	26 Nov 2008	6.7	27 Apr 2009		1.7
	100.3	25 Oct 2009	5.5	13 Apr 2010		1.5
	97.8	27 Oct 2009	5.2	15 Apr 2010		1.5
	95.6	1 Nov 2009	4.9	17 Apr 2010		1.6
	139	6 Nov 2009	5.4	18 Apr 2010		1.6
	98.8	9 Nov 2009	4.2	19 Apr 2010		1.6
NF	1	6 Nov 2009	6.2			
	1.3	6 Nov 2009	6.2			
Upper	150.5	11 Nov 2008	5.9		28 Feb 2009	2.9
	144.5	1 Nov 2008	6.2		8 Feb 2009	3
	144.5	15 Nov 2009	3.2		3 Mar 2010	2.9
	139	5 Nov 2009	4.8		19 Feb 2010	3
	139.9	30 Oct 2009	7.1		10 Feb 2010	3.1
	143.2	14 Nov 2009	3.2		3 Mar 2010	2.9
	138.9	15 Nov 2009	3.2		3 Mar 2010	2.9
	132	10 Nov 2009	4.6		27 Feb 2010	2.9
	155	16 Nov 2009	3.2		4 Mar 2010	2.9
	151.8	2 Nov 2009	6		15 Feb 2010	3
	156.1	25 Oct 2009	5.5		1 Feb 2010	3.2
	152.6	8 Nov 2009	4.7		25 Feb 2010	2.9
	154.5	4 Nov 2009	4.6		17 Feb 2010	3

seem to confirm local spawning. Consistent with our tracking and fry observations, mountain whitefish spawn across a range of habitat types with little, if any, selection for stream substrate composition (Brown 1952; Daily 1971).

Parasite Distribution and the Influence of Groundwater

The 2009 sentinel cage exposures of surrogate rainbow trout showed highly variable histological scores in June across mountain whitefish habitat. Infection rates ranged from 0% to 100% in the tributaries occupied by mountain whitefish as well as a pattern of high TAM exposure (67–76% of group scores ≥ grade 3) throughout the main stem of the Blackfoot River. This variation among streams conforms to a basin-scale pattern of increasing infection in the downstream direction (Pierce et al. 2009), as broadly observed across the Intermountain West (Sandell et al. 2001; de la Hoz Franco and Budy 2004; Anlauf and Moffitt 2008). In our study area, the low-elevation presence of *M. cerebralis* largely overlaps with the distribution of mountain whitefish with the exception of the Clearwater River, which flows through a series of glacially formed lakes as well as cold, rocky, basin-fed, forested streams with low levels of fine instream sediment, such as Gold Creek and the North Fork Blackfoot River.

Unlike Montana rivers in which TAMs are typically released during summer (Vincent 2000; Downing et al. 2002), groundwater-induced stream (i.e., spring creek) environments

TABLE 2. Severity of *Myxobolus cerebralis* infection based on histology of sentinel cage exposures of surrogate rainbow trout in 13 locations in the Blackfoot basin. Scores in bold italics denote high TAM exposures with a majority of the exposed fish at ≥grade 3 severity. Sentinel cage site locations are indicated in Figure 1.

				Individual histological scores						Group scores	
Cage ID	Stream name	Exposure period	Number rainbow histologically examined	0	1	2	3	4	5	Percent infected	% ≥grade 3
1	Blackfoot River	15–24 June	46	5	6	4	12	17	2	89	***67***
2	Gold Creek	15–24 June	50	50	0	0	0	0	0	0	0
3	Belmont Creek	15–24 June	38	4	0	0	0	4	30	89	***89***
4	Morrell Creek	15–24 June	50	50	0	0	0	0	0	0	0
5	East Fork Clearwater	15–24 June	43	43	0	0	0	0	0	0	0
6	West Fork Clearwater	15–24 June	44	44	0	0	0	0	0	0	0
7	Blackfoot River	15–24 June	38	2	2	5	7	16	6	94	***71***
8	Monture Creek	15–24 June	45	2	2	6	6	22	6	100	***95***
9	North Fork	15–24 June	33	32	0	0	0	1	0	3	3
10	Blackfoot River	15–24 June	45	2	3	6	6	22	6	95	***76***
11	Blackfoot River	15–24 June	43	4	3	7	6	23	0	90	***67***
12	Grantier Spring Creek	15–24 June	34	1	1	2	0	6	24	97	***88***
13	Lincoln Spring Creek	15–24 June	39	28	4	3	3	1	0	28	14

can release TAMS from late winter through spring and into summer (Hubert et al. 2002b; Anderson 2004). This early release relates to stable flow and temperature regimes. However, the low channel gradients, high sediment loading, and organic enrichment typical of spring creeks also tend to create ideal habitat for *T. tubifex* and thus foster high TAM production (Hiner and Moffitt 2002; Hubert et al. 2002a). Similar to reports of early TAM release in smaller spring creeks (Anderson 2004), the April PCR test confirmed positive infection prevalence in the upper study reach in a larger groundwater-induced river environment. In the upper study reach, the temperature sensor recorded a mean daily temperature of 4.6°C (range, 1.1–8.7°C) between the estimated start of the mountain whitefish hatch on 1 February and the 19 April and PCR fry collection date. These low temperatures contrast with reports of TAM viability occurring at higher water temperatures of 7–15°C (El-Matbouli et al. 1999; Sandell et al. 2001; Hiner and Moffitt 2002) and reports of much warmer (12–15°C) temperatures during the typical peak in TAM release for river environments (Vincent 2000; Downing et al. 2002; de la Hoz Franco and Budy 2004), including waters (>20°C) influenced by geothermal input (Koel et al. 2006). Though it may be that high worm abundance can increase TAM release at colder water temperatures (Hiner and Moffitt 2002), high TAM release in spring creeks during winter and spring may also relate to an accumulation of degree-days versus a range of water temperatures (Anderson 2004). With the upper river being warmer, accumulated temperature units would occur faster than in the cooler temperatures of the lower Blackfoot River. Consistent with these mechanisms, most PCR-tested age-0 mountain whitefish (65%) in the upper Blackfoot River tested positive for *M. cerebralis* in early spring. Conversely, the lack of *M. cerebralis* detection in the lower-river PCR test indicates consistency with the typical water temperatures and seasonality of TAM release in a rivers unaffected by direct groundwater inflow.

As shown by the PCR test and sentinel cage exposure in the upper Blackfoot River, groundwater environments can extend parasite exposure from the early spring into summer. With earlier, more continuous exposure, newly hatched mountain whitefish are prone not only to early infection but also to a heightened potential of injury-induced mortality relative to other salmonids (Schisler 2010). This heightened sensitivity to injury reflects the more fragile nature of the newly hatched fry and the invasive nature of the parasite, which causes injury when the sporoplasm penetrates the epithelium. This injury causes osmotic imbalance, plasma leaks, and avenues for secondary infection, which ultimately increases the potential for elevated mortality (MacConnell et al. 2000; Schisler 2010).

Avoidance of the Parasite and Other Mechanisms of Risk Reduction

With the exception of those in groundwater-induced streams, mountain whitefish appear to be separated from *M. cerebralis* over large areas of the basin during the critical early posthatch period. This separation can either help them avoid exposure or slow the progression of infection prior to the onset of seasonally high TAM releases, depending on the spawning and hatching windows and/or the early dispersion of age-0 mountain whitefish.

Though this study identifies spawning and hatching windows in the main-stem Blackfoot River, the early dispersion and other aspects of age-0 mountain whitefish life history are poorly understood. Elsewhere, mountain whitefish fry seek protected backwaters along stream margins once the eggs hatch and then passively disperse downstream during early summer when the water is warmer and food availability is higher (Brown 1952; Grove and Johnson 1978; Northcote and Ennis 1994). In our study area, downriver dispersion of this type would likely place age-0 mountain whitefish from the upper reach in more continuously contact with *M. cerebralis*, first during the spring (posthatch) in groundwater areas and then during summer, when TAM concentrations are seasonally elevated (Table 2). Conversely, downstream dispersion of age-0 mountain whitefish from the mid to lower reaches would avoid early exposure associated with groundwater. In addition, several "clean" mountain whitefish–bearing tributaries enter all study reaches, and these seem to provide more continuous refugia from the parasite.

As with other susceptible salmonids, the time between hatching and parasite exposure may allow mountain whitefish to reach a size or age that is less susceptible to *M. cerebralis* infection and the secondary effects of disease. Though the ability of mountain whitefish to develop physiological resistance to *M. cerebralis* requires further research (MacConnell and Vincent 2002), a reduction in infection prevalence has been detected in mountain whitefish exposed after 5 months of age (Schisler 2010). Other species (e.g., rainbow trout) develop an immune response as early as 9 weeks of age (Ryce et al. 2005). For mountain whitefish, a salmonid with relatively large, platy scales, it may be that scale development at 3–4 months posthatch or 30–45 mm in fork length (Thompson and Davies 1976) provides some protection (i.e., armor) from infection or injury. Under these conditions, early hatching (e.g., February–March) could reduce parasite contact in basin-fed streams prior to the typical summer peak in TAM production.

As shown at a basin scale in this study, the co-occurrence of mountain whitefish and *M. cerebralis* can vary broadly across both time and space. In other areas, spawning windows, for example, extend from late September through February across the range of mountain whitefish depending on elevation and latitude (Brown 1952; Thompson and Davies 1976; McPhail and Troffe 1998; Wydoski 2001). Likewise, fry emergence varies from early February (this study) to as late as early June (McPhail and Troffe 2001). Winter water temperatures greatly influence the timing of the hatch, as described by Schisler (2010), who reported that the degree-days for mountain whitefish egg incubation ranged from 258°C at an average temperature of 2°C to about 444°C at an average temperature of 6°C. In our study area, the mean daily water temperature during the mountain whitefish incubation period varied by year and by up to 4°C depending on the river reach and the influx of groundwater (Figure 2). Similarly, interannual temperature variation can either accelerate or delay the hatch, as shown by two mountain whitefish in the lower reach, one that spawned on 30 October 2008 and the other on 30 October 2009. Under milder winter temperatures, the estimated hatch of the 2008 spawning event occurred on 19 February 2009, as opposed to 5 April 2010 for the 2009 spawner, a difference of 45 d. Interestingly, natural hydrologic events such as spring flooding may also trigger early hatching (McPhail and Troffe 1998).

Conclusions

Mountain whitefish are considered common in many rivers of western Montana, widespread elsewhere, and secure over large areas of their geographic range (McPhail and Troffe 1998; Baxter 2002; Meyer et al. 2009). However, populations are also in decline in many areas of western North America, and in some river systems the declines have been dramatic (Meyer et al. 2009; Vincent 2009; Schisler 2010). Despite their high ecological value, mountain whitefish rarely receive much attention from anglers or resource managers. As a result, evaluations of perceived mountain whitefish declines are generally insufficient to determine whether *M. cerebralis* is causing population-level declines. In our study area, mountain whitefish appear to be separated from *M. cerebralis* over large areas of the basin during the critical early posthatch period, with the exception of the groundwater-induced upper Blackfoot River. Here, winter water temperatures are higher than those in the lower river and remain largely above freezing. This seems to result in earlier and ongoing parasite exposure relative to other areas, such as the lower Blackfoot River and cold, rocky basin-fed streams with low levels of fine instream sediment. Our results suggest that groundwater-induced areas make newly hatched mountain whitefish more likely to be exposed to *M. cerebralis* before the development of scales or other avoidance mechanisms that lower the risk of parasite contact.

While *M. cerebralis* may be deleterious at a local scale in our study area, several other, more direct human-mediated conditions are clearly contributing to the declining mountain whitefish populations. As reported in Idaho and Colorado, dam building and other water projects as well as the recent introduction of exotic predators are all implicated in mountain whitefish declines (Meyer et al. 2009; Schisler 2010). Within the Clearwater River basin of our study area (where *M. cerebralis* has not been detected), sharp declines in the abundance of lake-dwelling mountain whitefish followed the illegal introduction the northern pike *Esox lucius* in the Clearwater lakes. Likewise, the construction of Nevada Reservoir in the Blackfoot Valley preceded the local extirpation of mountain whitefish from upper Nevada Creek prior to the introduction of *M. cerebralis*. Mountain whitefish have also been identified in irrigation canals from the larger, low-elevation streams of the Blackfoot basin (FWP, unpublished data).

In the Blackfoot Valley, the distribution of mountain whitefish overlaps that of bull trout, an imperiled native salmonid (USFWS 2010), and species with moderate susceptibility (MacConnell and Vincent 2002). Interestingly, bull trout also spawn in the fall in areas of groundwater inflow (Baxter and Hauer 2000), which could elevate the *M. cerebralis* infection potential for this fish in parasite-positive waters. Like those of bull trout, the life histories of mountain whitefish require clean, cold water and open migratory corridors to a variety of habitat conditions. Ongoing recovery activities targeting bull trout, such as the screening of irrigation canals, stream flow improvement projects, and improvements to water quality likely benefit mountain whitefish.

In addition to continued stream improvements in mountain whitefish–bull trout habitat, we recommend (1) expanded disease testing of age-0 mountain whitefish in groundwater environments, (2) evaluations of age-0 life histories within the context of *M. cerebralis* overlap, and (3) expanded monitoring of mountain whitefish populations in parasite-positive waters in order to elucidate long-term population trends.

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