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[Article]

Correlation of Fluvial Rainbow Trout Spawning Life History with Severity of Infection by *Myxobolus cerebralis* in the Blackfoot River Basin, Montana

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Abstract.—To assess the exposure of Blackfoot River rainbow trout *Oncorhynchus mykiss* to the exotic parasite *Myxobolus cerebralis*, the causal agent of whirling disease, we investigated the spawning life histories of adult rainbow trout with respect to the distribution and severity of infection in spawning and early rearing areas in two distinct reaches of the Blackfoot River. Radiotelemetry confirmed that Blackfoot River rainbow trout express a fluvial life history and migrate from wintering sites within the Blackfoot River to spawning sites in the lower reaches of tributaries. Spawning peaked in late April, and fry emergence was estimated to occur within a narrow window of time in early July during the known period of high parasite exposure. However, the severity of infection varied between study reaches. Spawning of lower Blackfoot River rainbow trout was dispersed among the lowermost reaches of smaller, colder, higher-gradient tributaries, most of which fell below our ability to detect infection. By contrast, a majority of the telemetered rainbow trout in the middle Blackfoot River spawned higher in the drainage and within a single, low-gradient stream where fry emerged under infectious conditions. For fluvial rainbow trout, the risk of infection varies from the tributary to the subbasin scale and relates to the geographical arrangement and properties of the tributaries, the longitudinal relationship of the pathogen to spawning and early rearing areas, and the rate and timing of dispersing age-0 fry to downstream parasite-positive waters. Before the introduction of *M. cerebralis*, the middle Blackfoot River was identified as having recruitment limitations caused by winter mortality and anthropogenic activities. According to our results, riparian restoration and habitat enhancement with emphasis on migratory native fish within and upstream of the pathogen may buffer fish from the effects of the disease.

Whirling disease, a parasitic infection caused by the myxosporean *Myxobolus cerebralis*, has been associated with significant declines in introduced rainbow trout *Oncorhynchus mykiss* populations in certain streams in the western United States (Nehring and Walker 1996; Vincent 1996). Whirling disease was first detected in Montana in 1994 within the renowned Madison River following large and unexplained declines in rainbow trout abundance. Soon thereafter, whirling disease was described as one of the single greatest threats to wild trout (MWDTF 1996). Yet with the passage of time and the expansion of *M. cerebralis*, it appears the influences of the pathogen on interior populations of rainbow trout are highly variable within and across watersheds (Nehring and Walker 1996; Modin 1998; Granath et al. 2007). *Myxobolus cerebralis* has a complex, two-host life cycle involving the aquatic oligochaete worm *Tubifex tubifex* and most salmonids, including trout, whitefishes, and salmon. 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). Young trout, particularly rainbow trout, are most vulnerable when infected at less than 9 weeks of age (Ryce et al. 2004). The concurrence of this vulnerable period with the release of the infective triactinomyxon (TAM) stage of the parasite, largely determines the degree of exposure for young fish and ultimate population effects (MacConnell and Vincent 2002). High mortality and recruitment collapse can occur in highly exposed populations (Nehring and Walker 1996; but see Sandell et al. 2001).

Although whirling disease has resulted in large population declines of rainbow trout in certain Montana (Vincent 1996) and Colorado rivers (Nehring and Walker 1996), population effects are regionally variable. In Montana, previous studies of rainbow trout vulnerability to whirling disease have focused on the tailwater fishery of the Madison River where trout

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spawn in side-channels (Downing et al. 2002; Krueger et al. 2006). Across regions, high variation of infection has been identified within drainages throughout the western United States (Nehring and Walker 1996; Modin 1998; Sandell et al. 2001), yet this variation seems to include a common pattern of lower infection in headwater areas than in downstream reaches (Hiner and Moffit 2001; Allen and Bergerson 2002; De la Hoz and Budy 2004).

Since hatchery stocking of introduced trout ceased in Montana in 1979, the Blackfoot River, like all rivers in western Montana, has been managed for self-sustaining salmonids, including both introduced and native species, under the philosophy of "wild trout" management. Following rainbow trout declines in the Madison River and the 1995 detection of *M. cerebralis* in the Blackfoot River basin, Montana Fish, Wildlife and Parks began to assess whirling disease risks in the Blackfoot River basin using controlled (sentinel) exposures of age-0 hatchery rainbow trout as surrogates for free-ranging salmonids. Between 1998 and 2006, exposures of rainbow trout at 32 fixed monitoring sites identified the range expansion of *M. cerebralis* and an increasing intensity of infection among many, but not all, of the low-elevation streams of the Blackfoot River valley (Pierce and Podner 2006; Pierce et al. 2008). Tributaries to the Blackfoot River provide spawning and rearing for several free-ranging salmonids, which possess various levels of disease susceptibility according to controlled studies (Hedrick et al. 1999; MacConnell and Vincent 2002; Vincent 2002). These include (1) rainbow trout, a species that is highly susceptible to whirling disease, (2) salmonids of intermediate susceptibility (westslope cutthroat trout *O. clarkii lewisii* and brook trout *Salvelinus fontinalis*), and (3) those of low susceptibility (bull trout *Salvelinus confluentus* and brown trout *Salmo trutta*), as well as (4) mountain whitefish *Prosopium williamsoni*, a species whose susceptibility remains in question. Rainbow trout occupy the lower basin, and population densities increase in the downriver direction (Pierce and Podner 2006). Although rainbow trout occupy only about 15% of the Blackfoot River basin, they comprise about 70% of the trout community in the lower Blackfoot River where they contribute to a high-value recreational fishery.

In western Montana, significant declines in rainbow trout in Rock Creek, a large tributary to the upper Clark Fork River near Missoula, coincided with the introduction and expansion of *M. cerebralis* (Granath et al. 2007). Likewise, rainbow trout in lower Cottonwood Creek, a tributary to the middle Blackfoot River, have declined by 50% since the first occurrence of the parasite (Peters 1990; Smith 1998; Pierce et al. 2004). Both Rock Creek and lower Cottonwood Creek have experienced community-level shifts toward brown trout, a species with partial disease resistance. These observations suggest some risk of population- or community-level changes where the severity of infection has increased in known spawning streams (Pierce and Podner 2006).

Several studies have identified rainbow trout reproduction and rearing within tributaries of the Blackfoot River (Peters and Spoon 1989; Peters 1990; Pierce et al. 1997); however, the relative importance of tributary stocks to the main-stem population has not been fully evaluated, nor has the influence and spatial extent of possible disease effects upon fluvial rainbow trout of the Blackfoot River. To investigate these questions, we assessed exposure of *M. cerebralis* with fluvial rainbow trout in known spawning streams. Our study objectives were to identify (1) the spawning life histories of fluvial adult rainbow trout of the Blackfoot River; (2) the relative use of spawning tributaries by fluvial stocks of the Blackfoot River; and (3) the severity of infection in spawning streams and early rearing areas using sentinel exposures of surrogate age-0 hatchery rainbow trout. Our larger aims were to (1) assess disease risk for migratory rainbow trout stocks for two distinct reaches of the Blackfoot River, (2) gain a better understanding of fluvial rainbow trout, and (3) identify management measures that could buffer possible rainbow trout declines within rivers of western Montana.

Study Area

The Blackfoot River, a fifth-order tributary (Strahler 1957) of the upper Columbia River, lies in west-central Montana and flows west 212 river kilometers (rkm) from the Continental Divide to its confluence with the Clark Fork River in Bonner, Montana (Figure 1). The River drains a 5,998-km^2 heterogeneous watershed through 3,038 rkm of perennial streams and generates a mean annual discharge of 44.8 m^3/s (U.S. Geological Survey, unpublished data). The Blackfoot River flows freely to its confluence with the Clark Fork River where Milltown Dam, a run-of-the-river hydroelectric facility, prevented upstream fish passage to the Blackfoot River from 1907 to 2008, when the dam was removed. The physical geography of the watershed is geostructurally controlled and 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. Primary tributaries of the Blackfoot River upstream of the Clearwater River flow through a broad upper valley and alluvial bottomlands. Downstream from the Clearwater River, mountains constrict the

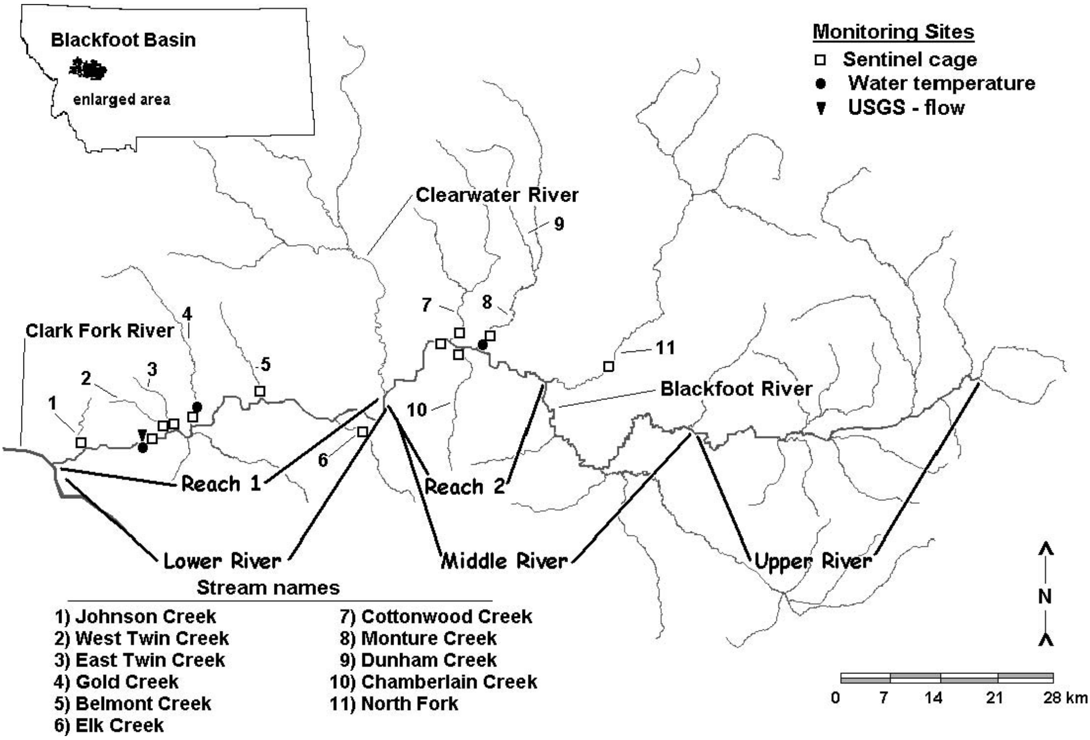

FIGURE 1.—Map of the Blackfoot River basin showing the locations of the sentinel cages, water temperature and flow monitoring sites, and main-stem study area (reaches 1 and 2) and demarcations of the lower, middle, and upper reaches of the Blackfoot River.

Blackfoot River to a narrow canyon. With some exceptions, numerous small tributaries enter the lower Blackfoot River through this mountainous area with confined forested channels, steeper gradients, and colder summer temperatures. Land ownership in the Blackfoot River basin is approximately 42% National Forest, 25% private, 19% Plum Creek Timber Company, 7% state of Montana, and 6% U.S. Bureau of Land Management. Public lands and large tracts of industrial forestlands generally comprise the mountainous areas, while private lands occupy the foothills and bottomlands where traditional uses of the land include mining, timber harvest, cattle ranching, and recreation.

Our study area emphasized the Blackfoot River upstream and downstream from the mouth of the Clearwater River. The lower Clearwater River flows through a series of natural lakes, has high summer temperatures (>27°C), and supports very limited rainbow trout reproduction (Peters 1990; Pierce et al. 2002). This river demarcates the approximate midpoint of rainbow trout distribution within the Blackfoot River and separates the Blackfoot River basin into two general subbasins based on physical differences of tributaries. The lower reach of the Blackfoot River (reach 1) extends from the Clearwater River confluence 55.8 rkm downstream to the Blackfoot River confluence with the Clark Fork River. Except for the uppermost tributary to reach 1 (Elk Creek), rainbow trout spawning tributaries originate in a mountainous region and tend toward smaller (second- and third-order), higher-gradient streams with colder summer temperatures. Conversely, Elk Creek, a low-gradient stream within an agricultural valley, experiences water quality (temperature and sediment) impairments (Montana Department of Environmental Quality 2007). The Blackfoot River between the confluence of the Clearwater River and North Fork Blackfoot River (reach 2) supports fewer but generally larger (third- and fourth-order) rainbow trout spawning streams that flow within wider channels, have broader floodplains with lower gradients, and experience warmer summer temperatures. An exception is the North Fork, a stream of wilderness origin that is larger and colder than all other tributaries in reach 2 (Pierce and Podner 2006).

Methods

Radiotelemetry.—We assessed the migration patterns, relative use of tributaries, timing of migration events, and location of rainbow trout spawning upstream and downstream from the mouth of the Clearwater River using radiotelemetry. Twenty-five rainbow trout were captured in the Blackfoot River, phenotypically identified as rainbow trout, implanted with continuous (12-h on–off cycle) Lotek radio transmitters on 8 March 2004 ($n = 4$), between 28 February and 8 March 2005 ($n = 10$), and 7–22 March 2006 ($n = 11$), and tracked to spawning areas within tributaries. These fish ranged from 34.0 to 49.0 cm in total length (TL; mean, 41.4 cm) and from 408 to 1,270 g in weight (mean, 680 g). We selected larger, "plump" female fish (based on the absence of a kype) to increase the likelihood that telemetered fish were sexually mature and more accurately identify the timing and location of spawning events. Visual identification was later verified for 21 of the 25 fish collected in 2005–2006 through genetic analysis of fin clips using 17 fragments of nuclear DNA at the University of Montana, Trout and Wild Salmon Genetics Laboratory (Boecklen and Howard 1997).

Transmitters were evenly distributed among fish in the lower 35.4 rkm of reach 1 ($n = 12$), whereas telemetered fish were captured only in a 6.4-rkm section in reach 2 ($n = 13$) owing to shelf ice and limited river access. Fish were captured by electrofishing in suspected wintering pools before their spawning migrations. Individually coded transmitters weighed 7.7 g, had an estimated life of 450 d, emitted an individual coded signal, did not exceed 2% of fish weight (Winter 1997), and were implanted following standard surgical methods (Swanberg et al. 1999).

Technicians located telemetered fish on foot using a hand-held, three-element Yagi antenna or by truck using an omnidirectional whip antenna. We located fish weekly before migrations, 2–3 times per week during migrations and spawning, once per week after spawning, and generally once per month thereafter.

All river locations and movements of rainbow trout were referenced by river kilometer. Fish were assumed to have spawned at their uppermost location if they ascended a stream with suitable spawning habitats during the spring spawning period. Spawning sites were confirmed by observations of spawning activity and the presence of age-0 rainbow trout from previous surveys of all spawning streams (Peters and Spoon 1989; Peters 1990; Pierce et al. 1997, 2004, 2006). We estimated the timing of migration and spawning events as the median date between two contacts for a given event, and the peak of spawning was identified as the median spawning date (Downing et al. 2002; Pierce et al. 2007).

Water temperature and flows.—Water temperatures and flows were measured in the Blackfoot River to assess their influences on rainbow trout migrations (Figure 1). Thermographs (Onset) were placed (2005–2006) at rkm 12.7 at the U. S. Geological Survey gauging station (number 1234000). We used both mean daily discharge and temperature to examine potential relationships with rainbow trout movements. Thermographs were also placed in the primary reach 1 (Gold Creek, 2005–2006) and reach 2 (Monture Creek, 2004–2006) spawning streams during the migration period, and mean daily temperatures were calculated to identify the relationships between tributary movements and spawning across river reaches. All thermographs recorded at 48-min intervals. To predict the timing of fry emergence in the primary reach 1 (Gold Creek) and reach 2 (Monture Creek) spawning streams, we first calculated the incubation period using an accumulation of 350 (Celsius) degree-days (Piper 1982) using thermographs within each stream. This calculation began with the estimated spawning date for each individual fish per stream, and emergence was estimated at 3 weeks posthatch.

Analyses of life histories.—Because of the small samples size and skew within data sets, certain analyses of life history traits relied on a related pair of nonparametric tests. These included Mann–Whitney rank sum tests for unpaired groups and Kruskal–Wallis one-way analysis of variance (ANOVA) by ranks to test equality of population medians among three or more groups (Zar 1984). For comparisons between reaches, we used Mann–Whitney tests to analyze (1) the start date of migration, (2) the dates spawners entered tributaries, (3) the upstream distance to spawning sites upon entering a tributary, (4) the estimated spawning dates, and (5) the dates spawners exited tributaries. To test spawner use of streams by stream size, we used Kruskal–Wallis ANOVA to test the relationships between stream order and the date of entry and number of days spawners spent within tributaries. For the total group of 25 fish, we also used linear regressions to explore associations between (1) the start date of migration and distance (rkm) to spawning sites; (2) the total duration (number of days) and total distance (rkm) of migrations; and (3) the date spawners returned to the Blackfoot River and the total migration period (number of days). All tests were performed in Statistica (version 7) software and evaluated at the $\alpha = 0.05$ level of significance.

Severity of M. cerebralis infection.—During the summer of 2005, we conducted sentinel exposures of 50 hatchery rainbow trout fry (diploid age-0 cohorts) at 10 known rainbow trout spawning streams to test for variation in *M. cerebralis* infection among streams (Figure 1). Uninfected fish of the commercial Trout Lodge strain were exposed at 98–103 d posthatch at a mean length of 36 mm. Exposures were completed in July within 9 weeks of the estimate posthatch period for free-ranging fish. This timing coincides with the age of high rainbow trout susceptibility (Ryce et al. 2004), emergence of rainbow trout fry in the wild, and the corresponding peak TAM production period as a seasonal (temperature driven) occurrence within rivers of western Montana (Vincent 2000). The exposure period for each live cage was standardized at 10 d. At the end of that time, fry were transferred to a state whirling disease research facility at Pony, Montana, where they were held for an additional 80 d at a constant 10°C to ensure that whirling disease, if present, would reach maximum intensity (Vincent 2000). At the end of the holding period, all surviving fish were killed and sent to the Washington State University Animal Disease Diagnostic Laboratory where fish heads were histologically analyzed and scored using the MacConnell–Baldwin grading scale (Hedrick et al. 1999; Ryce et al. 2004). Cartilaginous tissues (cranium, gill arches, jaw, vertebrae, and nares) were examined for the presence of the parasite and associated lesions. The abundance of parasites, cartilage damage, inflammation, extent of lesions, involvement of other tissues, and bone distortion were categorized into one of six qualitative categories and scored as follows: (0) no infection, (1) minimal, (2) mild, (3) moderate, (4) high, or (5) severe. Data for each exposure group were tabulated by individual fish scores and by mean grade scores following Downing et al. (2002). Sentinel exposures were considered high if a majority (percent) of exposed rainbow trout had histological scores of at least 3. At a score of 3 or higher, cartilage damage and a dispersed inflammatory response occur, which can be severe in infected fish (Hedrick et al. 1999; Vincent 2002).

Results

Migratory Life Histories and Spawning

For 25 telemetered rainbow trout, we made a total of 1,594 contacts with an average of 64 contacts (range, 12–129) per fish. All 25 rainbow trout were successfully tracked to spawning tributaries from March 2004 to December 2006 (Table 1). Of the 20 fish that underwent genetic analysis, 14 were identified as post-F_1 rainbow trout–westslope cutthroat trout hybrids, with a predominant rainbow trout genetic contribution; the remaining 6 were identified as genetically unaltered rainbow trout (Robb Leary, Montana Fish, Wildlife and Parks, personal communication). Four migrants captured in 2004 that later entered Monture Creek ($n = 3$) and the North Fork ($n = 1$) were untested.

River temperatures and flows increased incrementally during the 2004–2006 rainbow trout prespawning migrations. In these years, migrations began between 19 March and 15 April on the rising limb of the hydrograph as mean daily temperatures approached 5°C (Figure 2). With the onset of migration, 24 rainbow trout moved upriver and 1 moved downriver. In 9 d telemetered rainbow trout traveled a median of 6.8 rkm to their respective spawning tributary. Rainbow trout from reach 1 moved a (median) distance of 10.0 rkm (range, 0.5–56.8 rkm) compared with 6.6 rkm (range, 2.7–21.4 rkm) for the trout from reach 2.

For the total group, there was no relationship between the date migrations began and the total distance to spawning sites (linear regression: $R^2 = 0.008$, $P = 0.89$). However, rainbow trout with longer prespawning distance (starting locations to spawning sites) underwent migrations of longer duration (linear regression: $R^2 = 0.20$, $P = 0.04$) and returned to the river later than fish exhibiting movements of shorter duration (linear regression: $R^2 = 0.36$, $P = 0.003$).

Spawners spent an average of 17 d (range, 3–63 d) in tributaries and ascended a median of 3.0 rkm (range, 0.2–19.8 rkm) to their spawning grounds, where they held for an average of 6 d (range, 1–14 d) before returning to the Blackfoot River. We observed that reach 2 fish migrated significantly farther up tributaries to spawning sites than did reach 1 fish (median, 7.1 versus 1.0 rkm; Mann–Whitney test: $P = 0.005$). Based on the distance between winter pools and spawning sites, fish moved a median distance of 12.1 rkm overall, with medians of 10.6 rkm (range, 1.1–63.2 rkm) for reach 1 fish and 12.6 rkm (range, 6.0–27.5 rkm) for reach 2 fish.

Rainbow trout from reach 2 began their migrations 8 d earlier than did reach 1 fish (median, 9 April versus 17 April, respectively; Mann–Whitney test: $P = 0.17$), entered tributaries 9 d earlier (median, 17 April versus 26 April; Mann–Whitney test: $P = 0.10$), and spawned 6 d earlier (median, 28 April versus 4 May; Mann–Whitney test: $P = 0.40$). However, the duration of tributary use was 5 d longer for reach 2 fish than for reach 1 fish (median, 17 versus 12 d), and reach 2 fish exited tributaries 6 d later (median, 15 May versus 9 May; Mann–Whitney test: $P = 0.24$).

Rainbow trout spawned in six tributaries ranging from 2nd to 4th order, the Monture Creek watershed and Gold Creek supporting the highest proportion of spawners ($n = 12$ [48%] and $n = 5$ [20%], respectively; Table 1). Fish from reach 1 spawned in four tributaries: Gold Creek ($n = 5$), Belmont Creek ($n = 4$), East Twin Creek ($n = 2$), and Monture Creek ($n = 1$). Reach 2 fish spawned in Monture Creek ($n = 10$) and its tributary, Dunham Creek ($n = 2$), and only one spawned outside of the Monture Creek basin, within the North Fork. Based on stream order, spawners entered larger

TABLE 1.—Summary of migration and spawning events, including start of river migration, migration time and distance, tributary spawning (dates and locations) and total migration distance for 25 telemetered rainbow trout in two reaches of the Blackfoot River.

Fish number[a]	Start of river migration		Prespawning river migration		Tributary spawning				
	rkm	Date	Total rkm	Total d	Tributary	rkm to spawning site	Estimated spawning data	Days in tributary	Date exited
1	6	22 Apr 2006	11.4	24	East Twin Creek	0.2	18 May 2006	12	28 May 2006
2	16.9	2 May 2005	0.5	1	East Twin Creek	0.6	6 May 2005	6	9 May 2005
3	4.7	4 Apr 2006	17.5	5	Gold Creek	0.3	16 Apr 2006	14	23 Apr 2006
4	5.5	13 Apr 2006	16.7	11	Gold Creek	0.3	1 May 2006	12	6 May 2006
5	19	7 Apr 2005	3	9	Gold Creek	0.5	18 Apr 2005	11	27 Apr 2005
6	14	27 Apr 2006	8.2	4	Gold Creek	1	15 May 2006	22	23 May 2006
7	17.7	2 Apr 2006	4.5	2	Gold Creek	3.1	18 Apr 2006	23	27 Apr 2006
8	26.6	15 May 2006	8.7	1	Belmont Creek	0.2	17 May 2006	5	20 May 2006
9	17.1	30 Apr 2006	18.2	20	Belmont Creek	0.2	23 May 2006	8	28 May 2006
10	38.8	7 Apr 2005	3.4	17	Belmont Creek	1.5	26 Apr 2005	5	28 Apr 2005
11	24	11 Apr 2006	11.3	16	Belmont Creek	3.4	15 May 2006	31	28 May 2006
12	67.3	23 Apr 2004	6.6	4	Monture Creek	0.3	29 Apr 2004	3	30 Apr 2004
13	70.3	10 Apr 2006	3.5	10	Monture Creek	2.4	28 Apr 2006	16	6 May 2006
14	66	7 Apr 2005	5.5	11	Monture Creek	3.2	29 Apr 2005	17	5 May 2005
15	67.1	30 Mar 2004	6.8	6	Monture Creek	5.3		11	
16	70.3	25 Mar 2006	3.5	15	Monture Creek	5.6	23 Apr 2006	22	1 May 2006
17	17.1	9 Apr 2005	56.8	14	Monture Creek	6.4	26 Apr 2005	63	25 Jun 2005
18	67.1	26 Apr 2005	6.8	7	Monture Creek	6.9	11 May 2005	11	14 May 2005
19	66.8	19 Mar 2004	7.1	5	Monture Creek	7.1	1 Apr 2004	13	6 Apr 2004
20	67.1	24 Mar 2005	6.8	10	Monture Creek	7.1	17 Apr 2005	20	23 Apr 2004
21	70.3	8 Apr 2006	3.5	8	Monture Creek	7.2	7 May 2006	29	15 May 2006
22	71.1	8 Apr 2005	2.7	9	Monture Creek	9.8	28 Apr 2005	17	4 May 2005
23	66	25 Apr 2005	7.9	10	Dunham Creek	19.6	20 May 2005	20	25 May 2005
24	69	25 Apr 2005	4.8	10	Dunham Creek	19.8	16 May 2005	17	22 May 2005
25	65.5	7 Apr 2004	21.4	3	North Fork Blackfoot River	1.9	13 Apr 2004	6	16 Apr 2004

[a] See Figure 1.

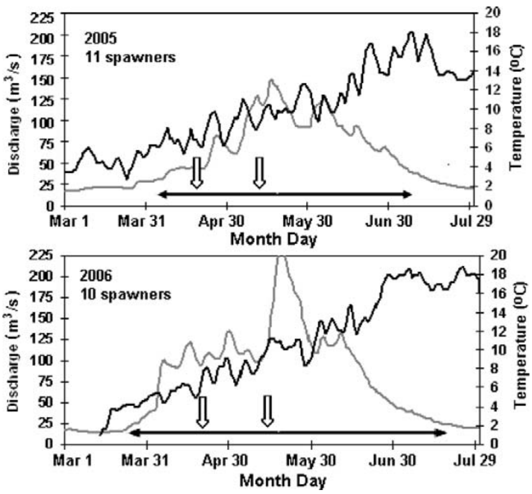

FIGURE 2.—Mean daily discharge (gray lines) and water temperature (black lines) at U.S. Geological Survey gauging station 12340000 in the Blackfoot River during rainbow trout spawning migrations in 2005 and 2006. The total migration periods are indicated by the arrowed horizontal lines; the vertical arrows show the median dates on which spawners entered and exited tributaries.

tributaries earlier than smaller tributaries (ANOVA: df = 2, $P = 0.02$). However, there was no significant difference with stream order and time spent in tributaries (ANOVA: df = 2, $P = 0.20$).

During the period of prespawning river migration (19 March to 15 April), mean water temperatures in the Blackfoot River were higher in 2005 (5.6°C) than in 2006 (4.9°C). Thirteen rainbow trout entered Monture Creek and five entered Gold Creek at a mean water temperature of 5.6°C (range, 3.6–8.1°C), and rainbow trout spawned at a mean temperature of 5.2°C (range, 3.4–8.0°C) in these drainages (Figure 3).

After spawning, all fish with active radio transmitters ($n = 24$) exited the tributaries. Three (12%) of the 24 postspawners (fish 4, 5, and 22; Figure 4) moved downstream from Milltown Dam into the Clark Fork River during peak flow (May through July), including two spawners from Gold Creek and one that moved downriver more than 74 rkm after spawning in Monture Creek. However, the majority ($n = 18$ [76%]) either returned to ($n = 9$) or were within ($n = 9$) 1.6 rkm of their original start locations; three (12%) moved downriver a mean of 14.0 rkm (range, 4.3–23.7 rkm) from their starting locations.

We monitored 17 fish at summering sites within the

TABLE 1.—Extended.

	End of migration	
Fish number[a]	Date migration ended	Date returned to starting location
1	17 Jun 2006	
2	9 May 2005	
3	23 Apr 2006	23 Apr 2006
4		
5	4 May 2005	
6	17 Jun 2006	28 May 2006
7	29 Apr 2006	29 Apr 2006
8	31 May 2006	
9	23 Jul 2006	
10	7 May 2005	7 May 2005
11	28 May 2006	28 May 2006
12	6 May 2004	
13	6 May 2006	6 May 2006
14	6 May 2005	6 May 2005
15		
16	15 May 2006	
17	7 Jul 2005	7 Jul 2005
18	26 May 2005	26 May 2005
19	28 Apr 2004	
20	28 Apr 2004	
21	17 Jun 2006	
22		
23	26 Jun 2005	26 Jun 2005
24	12 Jun 2005	12 Jun 2005
25	23 Apr 2004	

Blackfoot River. A majority of these ($n = 11$, or 65%) showed either no movement ($n = 5$) or remained within ($n = 6$) 1.6 rkm of their starting locations; six (35%) summered an average of 9.3 rkm (range, 2.6–23.7 rkm) from their original starting sites. All 15 fish tracked into the winter remained within 0.3 rkm of their summer locations. We also observed a few rainbow trout moving laterally to the margins of the shoreline and into flooded vegetation during high spring runoff, an apparent refuge-seeking response to high river flows.

Emergence and Disease Severity

Estimated fry emergence was complete by 11 July (2005 and 2006) for both Gold and Monture creeks. Sentinel exposures and histological examinations were successfully completed for six tributaries in reach 1, four in reach 2, and both study reaches of the Blackfoot River. Histological examinations identified infections within exposure groups that ranged from 0% to 100%, and mean scores ranged from 0 to 4.82 on the MacConnell–Baldwin scale (Table 2). Of the six rainbow trout–bearing streams tested within reach 1, five recorded low histological scores (majority < grade 3), and of those most ($n = 4$) showed no infection despite the near proximity (within 0.3 rkm) of mild to moderate levels of histological scores identified in the

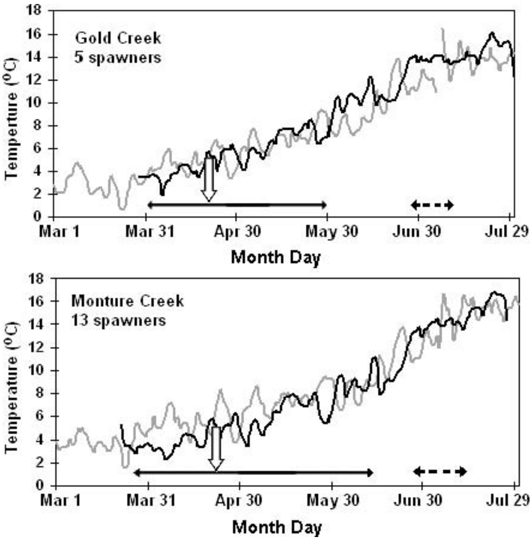

FIGURE 3.—Water temperature in Gold and Monture creeks in 2005 (gray lines) and 2006 (black lines). The time that fish spent within tributaries (2004–2006) and the estimated emergence periods for the 18 spawners are indicated by the solid and dashed arrowed horizontal lines. The median spawning dates are indicated by vertical arrows. Note the similarity between years and spawning streams.

Blackfoot River (Table 2). Conversely, sentinel exposures in three of the four spawning streams in reach 2 recorded a high severity (majority $\geq$ grade 3) and only the North Fork recorded a low severity. The percentage of Blackfoot River fish with high severity ($\geq$grade 3) was 43% in the reach 1 trial compared with 66% in the reach 2 sentinel exposure.

Discussion

A similar study east of the Continental Divide in Montana investigated rainbow trout spawning life history and whirling disease risk to juvenile survival within the "tailwater" section of the Madison River (Downing et al. 2002). By contrast, our study, undertaken west of the Continental Divide, examined fluvial life history and disease risk within a "free-flowing" river system. Common to both areas are (1) predictable migratory strategies involving prespawning migrants holding within wintering areas before upriver movement, (2) the fidelity of most postspawners to their initial tagging location, (3) upstream migrations of similar distances (mean, 14.5 versus 18.7 rkm) to spawning grounds, and (4) fry emergence during the vulnerable, highly infectious period (Vincent 2000; Downing et al. 2002) at temperatures conducive (12–15°C) to the release of TAMS (El-Matbouli et al. 1999; Kerans et al. 2005). Life history differences between

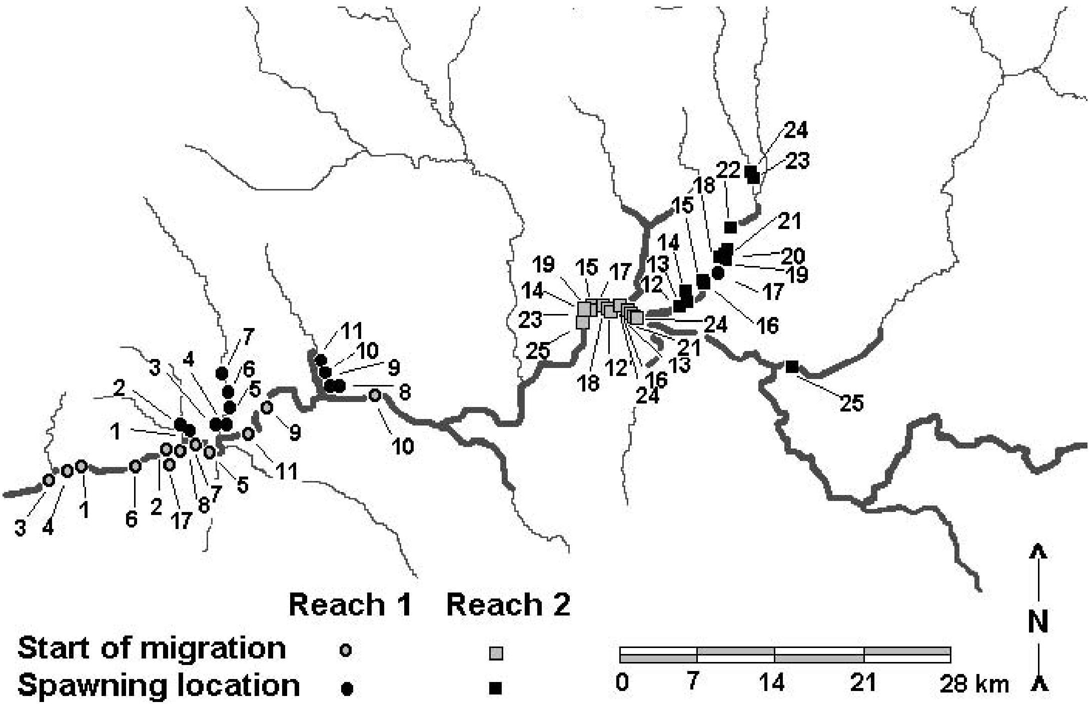

FIGURE 4.—The start of river migrations (gray symbols) and tributary spawning locations (black symbols) for reach 1 (circles) and reach 2 (square) spawners. The bold lines show the known distribution of waters testing positive for *Myxobolus cerebralis* (Pierce et al. 2006).

the Madison and Blackfoot River sites involve primarily main-stem spawning within the Madison River versus tributary spawning within the Blackfoot River basin. Although histological scores in tested rainbow trout varied within the main stem of the Madison River (Downing et al. 2002; Krueger et al. 2006), our study identifies a wide range of histological scores in rainbow trout among spawning streams. This variation among streams adheres to a predictable local pattern of increasing infection in the downstream direction (Smith 1998; Pierce et al. 2008), as generally observed across the intermountain west (Sandell et al. 2001; Allen and Bergerson 2002; Hubert et al. 2002; De la Hoz and Budy 2004).

As in an Idaho study (Anlauf and Moffit 2008), Smith (1998) initially identified the longitudinal distribution of *Tubifex tubifex* in the Blackfoot River basin, there being no infections in upper glacial valleys but an abundance of the tubificid worms and high histological scores in exposed rainbow trout in lower

TABLE 2.—Sentinel cage exposure results in 2005 for 10 rainbow trout spawning streams.

					Individual histological scores						Group	
Reach	Stream	Tributary confluence (rkm)	Cage site (rkm)	Number histologically examined	0	1	2	3	4	5	Percent infected	Mean grade
1	Blackfoot River		20.9	47	8	9	10	13	6	1	83	2.06
	Johnson Creek	4.8	0.2	49	49	0	0	0	0	0	0	0
	West Twin Creek	17	0.2	50	50	0	0	0	0	0	0	0
	East Twin Creek	14.7	0.2	48	48	0	0	0	0	0	0	0
	Gold Creek	21.7	0.3	38	38	0	0	0	0	0	0	0
	Belmont Creek	35.2	0.2	33	0	7	10	10	5	1	100	2.48
	Elk Creek	46.2	4.8	43	1	0	0	0	3	39	98	4.82
2	Blackfoot River		72.4	50	2	5	10	18	11	4	96	2.86
	Cottonwood Creek	60	1.6	46	0	0	0	9	20	17	100	4.17
	Chamberlain Creek	70.7	0.2	50	3	1	7	5	11	23	94	3.78
	Monture Creek	73.9	3.2	32	0	0	1	1	1	29	100	4.81
	North Fork	87.1	11.3	44	39	2	0	2	1	0	13	0.27

Cottonwood Creek. More recently, the presence of infected rainbow trout in tributaries of the Blackfoot River basin was correlated with warmer water, lower stream gradients, and accumulations of fine sediment (Pierce et al. 2008), all natural features of *T. tubifex* habitat (El-Matbouli et al. 1999; Arndt et al. 2002; Anlauf and Moffitt 2008) present in alluvial valleys in the Blackfoot River basin. Known human conditions favoring the worm host (and pathogen) can involve organic enrichment (Kaeser and Sharpe 2006), elevated sediment, and water temperature (Zendt and Bergersen 2000; De la Hoz and Budy 2004), all of which are conditions present within the riparian bottomlands of the Blackfoot River basin (Montana Department of Environmental Quality 2007).

In the lower Blackfoot River canyon (reach 1) area, telemetry identified several overlapping stocks of rainbow trout in the Blackfoot River and spawning dispersed in lower portions of three morphologically similar (cold, high-gradient) tributaries. Among these are three additional similar tributaries (Johnson, East Twin, and Bear creeks), which support known (Peters and Spoon 1989; Montana Fish, Wildlife and Parks, unpublished data) but limited rainbow trout spawning (based on our telemetry findings) and low to no detectable infection. From Belmont Creek (rkm 35.4) downriver, this concentrated group of relatively "clean" tributaries enters the Blackfoot River at a mean interval of one stream per 5.9 rkm of river. Sentinel exposures within this group of tributaries consistently test at low levels ($<$grade 3 or not detectable) versus reach 2 tributaries where exposure groups consistently rank at high levels ($\geq$grade 3) of severity (Pierce and Podner 2006). Rainbow trout densities in the lower Blackfoot River remain stable (Pierce and Podner 2006) despite an apparent annual loss of about 15–20% of lower River spawners over Milltown Dam as identified in this study.

By contrast, the 51.5-rkm reach of the Blackfoot River between Belmont Creek and the North Fork (reach 2) contain fewer (five) rainbow trout spawning streams, and of these, most (four) enter a limited (17.8 rkm) section of the Blackfoot River between Cottonwood Creek (rkm 69.2) and the North Fork (rkm 86.9). Consequently, rainbow trout recruitment sources over a majority (33.8 rkm) of the Blackfoot River between Belmont and Cottonwood creeks are limited. Elk Creek enters this reach, but it experiences water quality impairments, supports fish with high histological scores in exposure trials, and has shown declines of rainbow trout abundance in recent years (Pierce et al. 2004). Of the five rainbow trout spawning streams upstream from Belmont Creek, only the North Fork supports low histological scores, yet it supports limited rainbow trout reproduction (this study) and recruits relatively fewer age-0 rainbow trout to the Blackfoot River than do downstream tributaries (Peters and Spoon 1989).

Unlike dispersed lower-river spawning, over 90% of telemetered rainbow trout in the middle Blackfoot River spawned in Monture Creek. Within this stream, more than 95% of the 2005 sentinel exposure group exceeded grade 3 in severity. At a severity category of at least 3, granulomatous lesions in infected rainbow trout can be large and severely affect bone tissue, causing distortion and breakage (Hedrick et al. 1999; Ryce 2004), which leaves the fish weak and less able to compete for food and habitat, and ultimately increases chances of mortality (Vincent 2002). Infections in Monture Creek increased from nondetectable during exposures in 1999 to a severe (mean) histological score of 4.8 in this study. This escalation in the severity of infection overlaps in time with increased cranial deformities (a sublethal clinical sign of whirling disease) and a rainbow trout decline in the middle Blackfoot River downstream from the Monture Creek confluence (Pierce and Podner 2006).

Similar to what occurs in the Madison River (Downing et al. 2002), age-0 (and older) rainbow trout in the Blackfoot River basin rear within and downstream from their spawning grounds. In our study area, fry also disperse into the Blackfoot River where they tend to concentrate below natal tributaries by midsummer (Peters and Spoon 1989). Fry thereby express a more discrete distribution in middle river tributaries with adjacent patchy areas of concentrated fry in the main-stem Blackfoot River and more dispersed rearing across several lower river tributaries and an increasing trend in fry densities in the downriver direction. These diverse distributions identify vulnerable fry as variously juxtaposed with *M. cerebralis*, but also capable of developing disease resistance at many sites where both *M. cerebralis* and rearing life histories overlap.

To develop enhanced resistance, emergent fry must be both 9 weeks old (posthatch) and 40 mm in fork length at the time of parasite exposure (Ryce et al. 2005). The potential to confer resistance thus involves not only the spatial characteristics of *M. cerebralis* and vulnerable fry but also associated the temporal conditions related to TAM release or periods of spawning, emergence, and dispersion, all of which can vary within and across the watersheds of the intermountain west (Bartholomew and Wilson 2002; Benke 2002; this study).

As in a Colorado study (Allen and Bergerson 2002), basin-fed (e.g., Blackfoot River basin) and tailwater (e.g., Madison River) rivers in Montana show higher TAM production during summer and fall than winter and spring (Downing et al. 2002). Yet a recent study of Montana spring creeks found TAM exposures were often high in winter and low in the summer, which may allow spring spawners, such as rainbow trout, some ability to avoid severe exposure during periods of high TAM production (Anderson 2004). Across regions, rainbow trout spawning can also vary from January to June (Benke 2002), and periods of emergence in waters where *M. cerebralis* is present can extend into August as identified in spring creeks of Montana (Anderson 2004) and the high country of Colorado (Allen and Bergerson 2002). Within Montana, rainbow trout emergence occurs from April through August in spring creeks (Anderson 2004) and from May to July in the tailwaters of Madison River (Downing et al. 2002), as opposed to July in tributaries in the Blackfoot River basin (this study). Between reaches of the Blackfoot River, earlier spawning was detected in reach 2 spawning streams (i.e., Monture Creek) versus reach 1 tributaries, although differences were not significant, and emergence windows were small in both reach 1 (Gold Creek) and reach 2 (Monture Creek) study streams. Our findings suggest the ability to confer resistance appears greatly diminished where small windows of emergence overlap in both time and space and high TAM production (e.g., lower Monture Creek and middle Blackfoot River) compared with what occurs in the lower river environment.

Before the invasion of *M. cerebralis*, Peters and Spoon (1989) identified Monture Creek as a primary source of rainbow trout recruitment but considered the middle Blackfoot River as recruitment limited. While our study confirmed this spawning relationship, we also identified spawning occurred significantly higher in the Monture Creek basin compared with all other spawning streams. The sentinel cage, however, was located downstream (rkm 3.2) from the central (median) spawning site located at rkm 6.9 (range, 0.3–19.8 rkm). To clarify infection at the central and upper spawning areas, we further examined *M. cerebralis* exposures in Monture Creek at both rkm 7.4 and rkm 20.8 with additional sentinel exposures in 2006. Exposure results confirmed the high severity (95% $\geq$ grade 3) at the central spawning area, but detected no infection in the area of upper spawning. These findings, like other longitudinal relationships associated with *M. cerebralis*, identify exposure risk for the upper segment of the Monture Creek spawning stock as relatively low and subject to early dispersal rates into parasite-positive waters.

Although environmental conditions and the life histories traits of migratory rainbow trout can either contribute to or buffer fluvial stocks from *M. cerebralis*, other parasite–host interactions may influence whirling disease in salmonids. Although untested in the Blackfoot River basin, distinct *T. tubifex* lineages occupy various habitats in the intermountain west (Kerans et al. 2004; Beauchamp et al. 2005), among which are *M. cerebralis*-resistant strains as well as strains prone to *M. cerebralis* infection and high TAM production. In the presence of infected worms, not only can the tubificid composition shift from infected to resistant strains, such shifts can diminish TAM production (Beauchamp et al. 2005; Nehring et al. 2005). Among salmonids, an inherent immune response that partially limits infection is variously present among species (MacConnell and Vincent 2002) and among certain strains of rainbow trout (Hedrick et al. 2003; Wagner et al. 2005). An immune response can develop through crossbreeding susceptible strains with resistant strains of rainbow trout (Schisler et al. 2006) or by genetic (natural) selection, as is now hypothesized in the Madison River (Vincent 2006).

For this study, we used a susceptible strain (Trout Lodge) of rainbow trout for the sentinel exposures (Hedrick et al. 2003) in contrast to free-ranging rainbow trout in the Blackfoot River that are considered "undifferentiated" by strain. Thus, inferences of potential disease effects from surrogate test fish to fluvial rainbow trout in the Blackfoot River are somewhat difficult. Most fish visually identified as rainbow trout in this study were, in fact, mildly introgressed with native westslope cutthroat trout, which is common in Montana rivers west of the Continental Divide. Physiological resistance of rainbow trout–westslope cutthroat trout hybrids to whirling disease is untested, but it may be possible that F_1 hybrids possess some intermediate level of resistance between the low resistance of rainbow trout and the moderate resistance of westslope cutthroat trout (Hedrick et al. 1999; MacConnell and Vincent 2002), a relationship identified in F_1 crosses between resistant and susceptible strains of rainbow trout (Schisler et al. 2006).

Management Implications

Management implications vary by river reach and involve the potential for an additive loss of recruitment, primarily in the middle Blackfoot River. The middle Blackfoot River was previously identified as having trout recruitment problems brought on by drought and winter mortality, limited spawning areas, and degradation of existing spawning and rearing areas caused by agricultural and other land uses.

Based on the community-level changes in Rock and Cottonwood creeks, brown trout clearly have the potential for expansion in western Montana within environments conducive to high infection in rainbow trout. This naturally more resistant species has also shown significant population increases in highly infected spring creeks within the middle Blackfoot River basin after limiting factors related to physical habitat were corrected (Pierce et al. 2006). Like brown trout, native westslope cutthroat trout and bull trout could thrive within waters supporting *M. cerebralis*. While these native salmonids seem to possess partial resistance to the pathogen, they both also possess life history strategies that help avoid exposure of *M. cerebralis* at early life stages by spawning and rearing in headwaters of the Blackfoot River basin (including Monture Creek) where contact with *M. cerebralis* at critical stages (age 0) is reduced. Young cutthroat trout and bull trout migrate to downstream waters at more disease-resistant stages (age 1 and older). Both species migrate extensively within the Blackfoot River basin (Swanberg 1997; Schmetterling 2001; Pierce et al. 2007) and occupy sections of the Blackfoot River prone to limited rainbow trout recruitment and high TAM production (Pierce and Podner 2006).

Conclusions

Although many conditions (e.g., environmental conditions, anthropogenic actions, rainbow trout life histories, and host resistance) make future population (and community) effects difficult to fully predict, our study clearly indicates that whirling disease risks to Blackfoot River fluvial rainbow trout vary from the tributary to subbasin scales. Our study identified rainbow trout from Belmont Creek upriver to be at a higher risk of recruitment loss due to a higher severity of *M. cerebralis* infections over a majority of spawning and rearing areas and the reliance of most reach 2 fluvial rainbow trout on a single spawning stream. Stocks of rainbow trout in certain valley floor streams (e.g., Elk, Cottonwood, and Monture creeks) spawn and rear in streams that favor the pathogen. These and many other streams are subject to anthropogenic disturbances that may either favor the pathogen or adversely influence the quality of spawning and rearing habitats, or both. By contrast, spawning of lower Blackfoot River fish was dispersed among higher-gradient mountain streams within environments poorly suited to *T. tubifex* and *M. cerebralis*. To offset potential rainbow trout losses in tributaries of the middle Blackfoot River basin, stakeholders must (1) better manage riparian areas for channel stability, increased shade, and erosion reduction; (2) promote native fish recovery and migratory life histories; and (3) restore (or enhance) habitats favoring salmonid life stages less affected by the pathogen.

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