

Whirling Disease and Native Cutthroat Trout of the Yellowstone Lake Ecosystem

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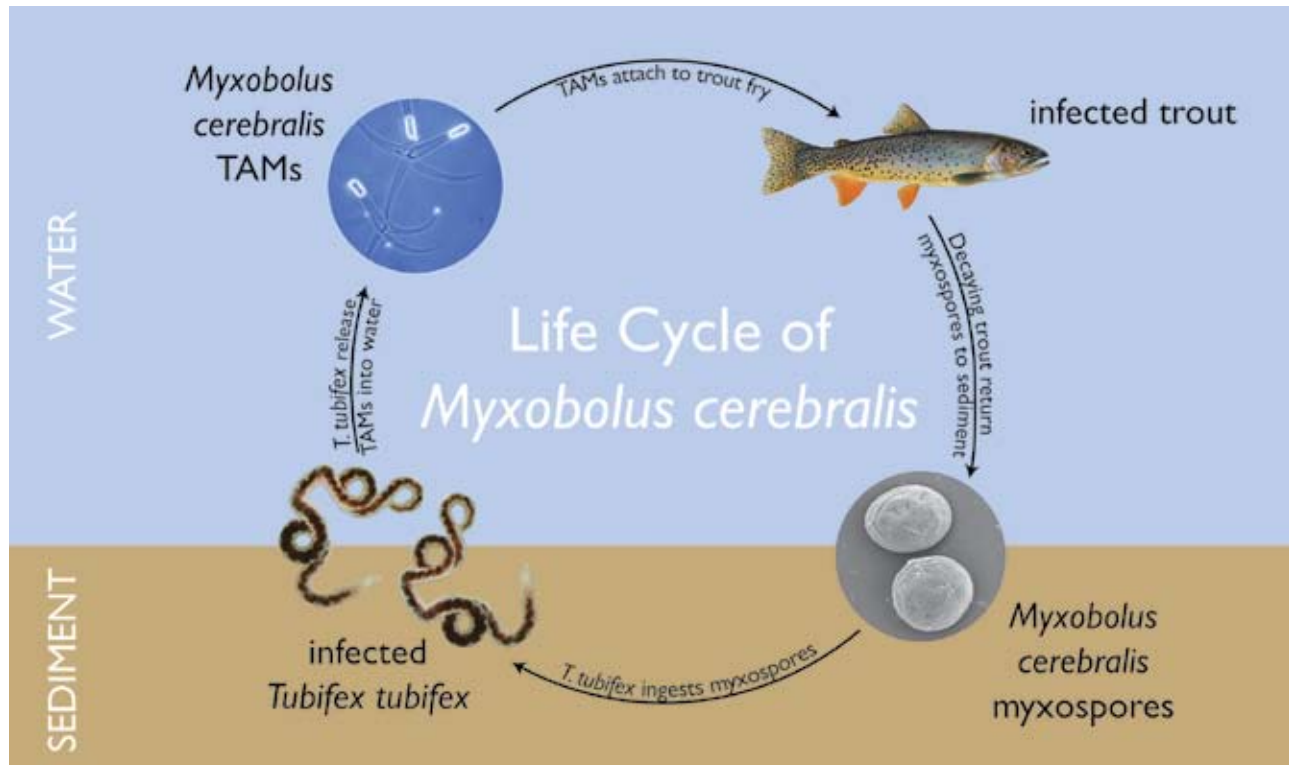


Figure 1. The life cycle of *Myxobolus cerebralis*, the causative agent of whirling disease in fish of the family Salmonidae. *M. cerebralis*, a microscopic parasite, infects two hosts, including native Yellowstone cutthroat trout, and *Tubifex tubifex*, a common aquatic worm found in the park. The primitive life forms of *M. cerebralis* include a triactinomyxon (TAM), which is a relatively fragile, free-floating form carried by water currents, and a myxospore, which is a highly resistant form that may remain viable within sediments of aquatic systems for decades. (Adapted from M. El Matbouli et al., 1992, *Annual Review of Fish Diseases* 3:367–402; TAM and myxospore images by Ron Hedrick, University of California–Davis, *Tubifex tubifex* photo by Kendra Kinnin.)

WHIRLING DISEASE, caused by the exotic parasite *Myxobolus cerebralis*, is responsible for severe declines in wild trout populations in the Intermountain West (Bartholomew and Reno 2002). In Colorado (Nehring and Walker 1996) and other states where infection has been severe, whirling disease has had a significant negative economic impact on the recreational fishing industry. In Montana, the number of wild rainbow trout (*Oncorhynchus mykiss*) in the Madison River declined 70–90% after the introduction of *M. cerebralis* (Vincent 1996). The parasite has spread to many other drainages in the western part of the state, resulting in population-level effects (E. R. Vincent, personal communication). The parasite was first documented in Wyoming waters

in 1988 and has spread to at least seven river drainages there.

In Yellowstone National Park (YNP), examination of wild trout for whirling disease began in earnest in 1995 through the U.S. Fish and Wildlife Service's Wild Fish Health Survey. *Myxobolus cerebralis* was first detected in the park in 1998 in native Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvierii*) collected from Yellowstone Lake. The Yellowstone cutthroat trout is considered a keystone species in the Greater Yellowstone Ecosystem. It provides a significant source of protein for the grizzly bear (*Ursus arctos*) during the spring and midsummer (Reinhart and Mattson 1990; Gunther 1995). The diet of the threatened bald eagle (*Haliaeetus leucocephalus*) in the park consists of about 25% fish (Swenson et al. 1986).

Many other avian and terrestrial species in the Yellowstone Lake ecosystem use Yellowstone cutthroat trout as an energy source (Schullery and Varley 1995).

The life cycle of *M. cerebralis* involves two hosts, including fish from the family Salmonidae and an aquatic worm (the oligochaete *Tubifex tubifex*; Wolf et al. 1986; Gilbert and Granath 2003; Figure 1). Myxospores within the infected salmonid become available and are ingested by *T. tubifex* upon a fish's death and decay. Within *T. tubifex*, the parasite proliferates and assumes a second form, known as a triactinomyxon (TAM). The TAMs are released by tubificids into the water column where they suspend and are carried by the current. Upon contact with a salmonid, the TAMs attach and infect them, completing the parasite's life cycle. Compared to other species, Yellowstone cutthroat trout appear to be highly susceptible to whirling disease when challenged with triactinomyxons in the laboratory (Hedrick et al. 1999) and in the field (Murcia et al. 2006). Recent studies have indicated that whirling disease susceptibility of *T. tubifex* varies among genetically distinct strains (Kerans et al. 2004). However, no previous studies have examined the genetic composition of *T. tubifex* in the park, but samples from the Madison River in Montana indicated the presence of a clade that is moderately susceptible to the transmission of whirling disease (Kerans et al. 2004).

The waters of YNP provide a unique opportunity to study whirling disease in native cutthroat trout. The spawning streams vary widely in their thermal, hydrological, and geological characteristics within a relatively undisturbed region that is free from the confounding effects of land use. We hypothesized that *M. cerebralis* infection prevalence and severity in the upper Yellowstone Lake basin (above the upper falls of the Yellowstone River), would be related to Yellowstone cutthroat trout life history strategies; the presence, abundance, and infection of tubificid oligochaetes (worms); and stream environmental gradients. The overall goal of this study was to describe patterns in infection risk of Yellowstone cutthroat trout. Specific objectives were to (1) determine the prevalence and spatial extent of *M. cerebralis* infection in Yellowstone cutthroat trout within Yellowstone Lake, (2) assess the *M. cerebralis* infection risk of age-0 Yellowstone cutthroat trout in spawning tributaries, (3) determine the relative abundance, phylogeny, and *M. cerebralis* infection of tubificid oligochaetes in spawning tributaries, and (4) relate the *M. cerebralis* infection risk to basic environmental characteristics of spawning tributaries. Improving our understanding of relationships among whirling disease infection and ecological factors will allow resource managers to focus efforts and funding on waters that have high disease potential.

Study Area

At an elevation of 2,357 m, Yellowstone Lake is the largest high-elevation lake in North America. Yellowstone cutthroat trout of the upper Yellowstone Lake basin primarily exhibit

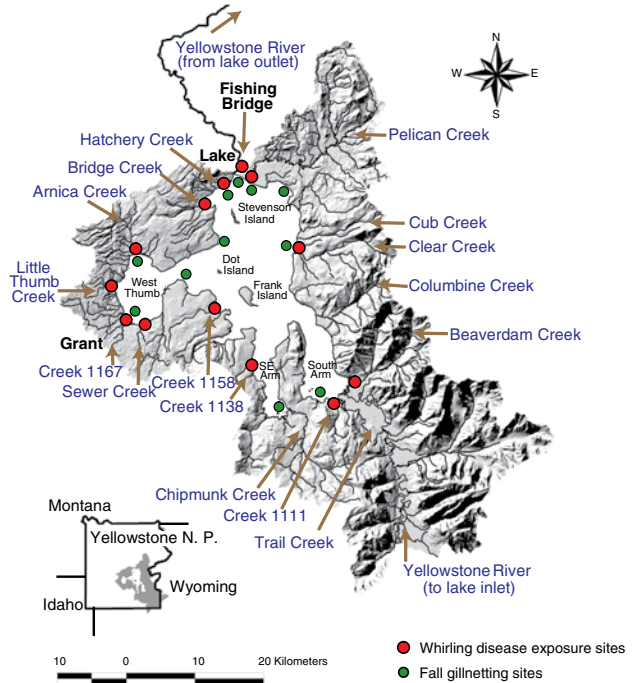


Figure 2. Map of Yellowstone Lake and the upper Yellowstone River drainage within Yellowstone National Park, showing the locations of the 11 cutthroat trout lake gill-netting sites, the 12 streams, and the Yellowstone River near Fishing Bridge, where Yellowstone cutthroat trout sentinel fry exposure and tubificid studies were conducted, 1999–2001.

an adfluvial life history strategy (Gresswell and Varley 1988), although other movement patterns exist (Kaeding and Boltz 2001). Spawning has been documented in 68 tributaries, but 16 of them are used only during years with above-average stream discharge (Jones et al. 1987; Gresswell et al. 1997). Many tributary basins have been influenced by natural fire disturbance (Farnes 1996), potentially influencing their suitability for *M. cerebralis* through nutrient (nitrogen and phosphorus) enrichment (Brass et al. 1996; Robinson and Minshall 1996) or changes in retention of organic matter (McIntyre and Minshall 1996).

Methods

Infection prevalence in Yellowstone Lake. Juvenile and adult Yellowstone cutthroat trout were collected from 1999 to 2001 using gill nets set overnight in September at 11 sites located throughout the lake in waters 2–6 m deep (Figure 2; Koel et al. 2005). Yellowstone cutthroat trout that were incidentally killed during gill netting for lake trout in waters primarily 45–50 m deep were also examined for *M. cerebralis* (Bigelow et al. 2003). Each Yellowstone cutthroat trout was screened by the pepsin–trypsin digest (PTD) method for the presence of myxospores (Andree et al. 2002). Because another *Myxobolus*

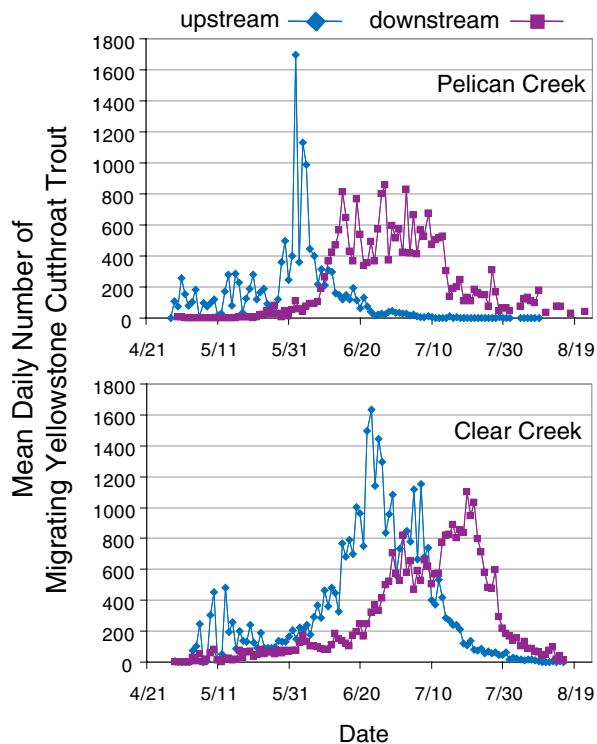


Figure 3. The mean daily number of Yellowstone Lake adfluvial Yellowstone cutthroat trout that were enumerated at migration traps while moving upstream or downstream in Pelican Creek (1964–1983) and Clear Creek (1977–2001).

species is also known to infect Yellowstone cutthroat trout, if *M. cerebralis* was suspected by PTD screening, the spore digest suspension was used for confirmation of *M. cerebralis* by the nested polymerase chain reaction (PCR) technique (Andree et al. 1998).

Infection risk in tributary streams. Information on basin size, aspect, slope, precipitation yield, stream order and length at specific elevations, geological characteristics, and forest composition was compiled for 54 known Yellowstone cutthroat trout spawning tributaries to Yellowstone Lake. We conducted principal components analysis (PCA; Krebs 1999) to determine similarities among spawning stream watersheds and selected 12 tributaries and the Yellowstone River near the lake outlet (Figure 2) to best represent the ranges in large-scale environmental gradients (including temperature and flow), given the logistical challenges of conducting sentinel fish exposures in remote areas of the Yellowstone Lake basin.

The daily mean numbers of upstream- and downstream-migrating Yellowstone cutthroat trout spawners were compiled for Pelican and Clear creeks from National Park Service historical records (migrating Yellowstone cutthroat trout were counted daily at fixed weirs located near the stream mouth during 1964–1983 at Pelican Creek and 1977–2001 at Clear Creek; Figure 3). Potential fry emergence dates were estimated based on known incubation periods for Yellowstone cutthroat trout at various temperatures. Sentinel fish exposure periods

from mid-July through mid-October were selected to encompass the times when the fry would be emerging and vulnerable to *M. cerebralis* infection in tributary streams.

Sentinel cage exposures were conducted on the selected streams during 1999–2001 (Figure 2) using cylindrical enclosures constructed of 5-mm galvanized wire mesh. Yellowstone cutthroat trout fry (60–80 per cage) obtained from the Wyoming Game and Fish Department broodstock (LeHardys Rapids, Yellowstone River origin) were exposed during 10-day periods within each study stream starting after peak flows and spawning. After the exposure periods, the fry were maintained in aquaria at 138°C for 90 days (El-Matbouli et al. 1999) and then lethally sampled after anesthetization. Half of the head of each fish was preserved for histological analysis to describe pathology associated with the presence of *M. cerebralis* in cranial cartilage (Baldwin et al. 2000). The other half was screened for *M. cerebralis* following procedures similar to those used for the fish sampled from Yellowstone Lake (described above).

Tubificid and actinosporean examination. Each exposure stream was sampled for live tubificids three times during 2001. To the extent possible, collections occurred when Yellowstone cutthroat trout fry were being held in sentinel cages. Oligochaetes were collected by sieving sediments within 30 m upstream of each cage location. If an oligochaete was detected within one hour, the collection effort would persist for one additional hour or until 300 oligochaetes were collected, whichever occurred first. If no oligochaetes were detected within one hour, a 30-m reach downstream of the sentinel cage was sampled.

The collected oligochaetes were examined under a microscope. Those with an external morphology similar to that of *T. tubifex* (with hair chaetae; Kathman and Brinkhurst 1998) were placed into wells of tissue culture plates and periodically examined for seven days for actinospore production. (Actinospores include triactinomyxons and other kinds of parasitic spores released by aquatic invertebrates.) Tubificids that produced actinospores, the actinospores themselves, and randomly selected non-actinospore-producing tubificids from each collection site were prepared for DNA extraction and *M. cerebralis* PCR analysis.

Environmental characteristics of tributaries. In 2001, water temperatures were recorded hourly to determine daily and seasonal thermal regimes near the sentinel cages of each exposure stream. Recent and historical hydrological characteristics of the Yellowstone Lake basin were assessed based on information provided by the U.S. Geological Survey stream discharge gauge on the Yellowstone River downstream of the lake outlet. Habitat assessments were conducted by assessing the relative quantity and quality of natural structures that could provide ecological niches (Barbour et al. 1999).

Water samples were collected from the lower reaches of all exposure streams during July and September 2001. Analyses to determine nutrient and other chemical characteristics of waters

were conducted by the Great Lakes Water Center, University of Wisconsin–Milwaukee. Measurements of dissolved oxygen concentration, percent oxygen saturation, and specific conductance were collected at each sentinel cage site during the exposure periods in 2001.

Results

Infection prevalence. Of the 453 juvenile and adult Yellowstone cutthroat trout collected from within Yellowstone Lake by gillnetting in 1999–2001, 89 were infected by *M. cerebralis*. In general, these infected fish showed no significant external signs of disease and otherwise appeared healthy.

Yellowstone cutthroat trout fry exposed in spawning tributaries that tested positive for the presence of *M. cerebralis* were first obtained from the Yellowstone River in August 1999 (Table 1). None of the other 12 exposure streams examined that year showed evidence of the parasite. In 2000, *M. cerebralis* was found in Pelican Creek (strong infection) and Clear Creek (weak infection). Infection was not found in fish in the Yellowstone River or the other four streams tested that year, even though multiple exposure periods were used in an attempt to span peak infection periods. The 2001 results provided further evidence of a severe

infection in Pelican Creek; infection was found during all exposure periods and the fry showed clinical signs of the disease. All of the fish exposed during the mid-July period were infected; the mean histological ranking of severity was 4.00 (maximum of 5.00) on the MacConnell–Baldwin scale (Table 1). A weak infection was found in the Yellowstone River, but none of the other streams examined in 2001 showed evidence of the parasite.

Tubificid and actinosporean examination. A high number of tubificids was found in Beaverdam, Sewer, and Little Thumb creeks and Creek 1167, especially in late August and early September of 2001. Few of the 3,037 collected tubificids were sexually mature, making morphological identification difficult. The mature oligochaetes with hair chaetae were identified as *T. tubifex*, *Ilyodrilus templetoni*, and individuals of the genus *Rhyacodrilus*. The 17 mature *T. tubifex* were found in three geographically distant streams (Pelican and Beaverdam creeks and Creek 1167; Figure 2).

Only 20 of the collected tubificids produced actinospores during the 7-day observation periods. Arnica Creek exhibited the highest prevalence of infection: 7.50–9.43% of the 93 observed tubificids (Table 2). Repeated nested PCR assays did not detect *M. cerebralis* in any of the infected or immature worms or any actinosporean preparations. (We were able to detect *M. cerebralis* in actinosporean-producing

Stream	Year	Period	Dates	Prev (%)	Severity
Pelican Creek	2000	1	09/12–09/23	94	2.76
		2	08/07–08/17	75	1.00
	2001	1	07/12–07/23	100	4.00
		3	08/29–09/07	94	2.72
Clear Creek	1999	1	08/12–08/23	0	0.00
	2000	1	09/12–09/23	2	0.02
		2	09/25–10/05	0	0.00
		3	10/09–10/19	0	0.00
	2001	1	07/12–07/23	0	0.00
		2	08/07–08/17	0	0.00
		3	08/29–09/07	0	0.00
Yellowstone River	1999	1	08/12–08/23	14	0.20
	2000	1	09/12–09/23	0	0.00
		2	09/25–10/05	0	0.00
		3	10/09–10/19	0	0.00
	2001	1	07/14–07/23	20	0.40
		2	08/07–08/17	7	0.07
3		08/29–09/07	0	0.00	

Table 1. Results of sentinel fry exposure studies from streams in which Yellowstone cutthroat trout fry tested positive for *Myxobolus cerebralis* during 1999–2001. Prevalence (prev) is the proportion of individuals examined that were infected. Severity is the average histological score from laboratory examination and is based on a scale of 0–5 (5 = the most severe infection). Pelican Creek was not tested in 1999. A single exposure period occurred on all tested streams in 1999 and on Pelican Creek in 2000.

Orientation Stream	Tubificids to cage	Producing per hour	Number (%) of Tubificids		
			Observed	Mc positive Actinospores	by PCR
Pelican Creek	upstream	94.5	189	0	1
	downstream	28.0	28	0	0
Clear Creek	upstream	0.0	0	0	0
	downstream	0.3	1	0	0
Beaverdam Creek	upstream	259.0	777	1 (0.13)	0
	downstream	ns	ns	ns	ns
Creek 1111	upstream	13.3	40	0	0
	downstream	ns	ns	ns	ns
Creek 1138	upstream	84.3	253	0	0
	downstream	ns	ns	ns	ns
Creek 1158	upstream	47.0	141	0	0
	downstream	ns	ns	ns	ns
Sewer Creek	upstream	0.0	0	0	0
	downstream	200.0	200	1 (0.50)	0
Creek 1167	upstream	139.0	278	1 (0.36)	0
	downstream	132.0	264	0	0
Little Thumb Creek	upstream	40.0	80	1 (1.25)	0
	downstream	196.0	392	1 (0.26)	0
Arnica Creek	upstream	17.7	53	5 (9.43)	0
	downstream	40.0	40	3 (7.50)	0
Bridge Creek	upstream	61.3	184	6 (3.26)	0
	downstream	51.0	51	0	0
Hatchery Creek	upstream	0.0	0	0	0
	downstream	10.0	10	0	0
Yellowstone River	upstream	17.0	34	1 (2.94)	0
	downstream	22.0	22	0	0
Total			3,037	20	1
Mean		64.6	38	1	0

Table 2. Numbers of tubificids with hair chaetae selected from bulk live oligochaete samples taken near Yellowstone cutthroat trout cage sites over three time periods and observed for actinospore production for seven days. Areas not sampled are indicated "ns". Triactinomyxon-type actinospores were produced by all infected tubificids except those isolated from Beaverdam Creek, which produced synactinomyxon-type actinospores. The diagnostic *Myxobolus cerebralis* (Mc) nested polymerase chain reaction test was used to assay for Mc infection.

tubificids collected from other *M. cerebralis* endemic areas and in our positive plasmid controls.) However, one sexually mature *T. tubifex* collected from Pelican Creek in early July that was not shedding triactinomyxons tested positive for *M. cerebralis* by PCR analysis, indicating the presence of infected worms in that stream. The mature *T. tubifex* were most abundant in early summer and genetically homogeneous, belonging to an mtDNA lineage that has been associated with high levels of whirling disease (Beauchamp et al. 2002).

Discussion

Biological aspects of Myxobolus cerebralis infection risk. The Yellowstone cutthroat trout fry in exposure cages in Pelican and Clear creeks and the Yellowstone River were infected by *M. cerebralis* during at least one exposure period. Whereas the infections at the Yellowstone River site (1999 and 2001) and Clear Creek (2000) were relatively light, the fish exposed at Pelican Creek were severely infected and showed clinical signs of whirling disease in laboratory aquaria. These streams are located along the north and east-central shores of Yellowstone Lake; the other exposure streams tested negative for *M.*

cerebralis. The higher infection prevalence in the northern and central sections of the lake in 1999 may have been due to Pelican Creek and, to a lesser extent, the Yellowstone River and Clear Creek as sources of *M. cerebralis*.

Only two of the 89 infected fish detected during the 1999–2001 study period within Yellowstone Lake were found in 2001; the reason for this significant temporal variation is not known. Our results suggest at least some resilience of this cutthroat trout subspecies to whirling disease; a significant number have evidently been surviving and recruiting to the spawning population even though infected (perhaps at an older age) by *M. cerebralis*. Population-level declines have only recently been noticed, and it is likely that *M. cerebralis* has only recently invaded this system. A serious concern is the potential for this parasite to increase in its prevalence, further diminishing the ability of Yellowstone cutthroat trout to survive to spawning age.

Recent studies in Idaho and Colorado have suggested a relationship between infection risk in salmonids and the abundance of *T. tubifex* (Hiner and Moffitt 2001; Nehring and Thompson 2003) and between infection risk and the density of infected worms (Krueger 2002). However, our results from Pelican Creek may indicate that even low numbers of tubificids can support severe infection of native Yellowstone cutthroat trout. Alternatively, the distribution of infected tubificids may be clumped or the infection source may exist some distance upstream from our exposure site. The finding of an infected tubificid from Pelican Creek that belongs to an mtDNA lineage associated with high salmonid infection levels in whirling disease endemic regions (Beauchamp et al. 2002) is consistent with severe infection rates in Pelican Creek.

Actinosporean production was low among streams except Arnica Creek, where prevalence was relatively high at 7.5–9.4% of the 93 tubificids observed. Low infection rates have also been reported in Montana (2.6%, Rognlie and Knapp 1998) and Colorado (0.4–1.5%, Beauchamp et al. 2002). None of the actinosporeans examined by this study tested positive for the presence of *M. cerebralis* genes. The stocking of non-native fishes early in the history of Yellowstone National Park (Varley 1981), before *M. cerebralis* was introduced in the United States, could have contributed to the introduction of relatively unknown myxozoans.

Environmental aspects of *Myxobolus cerebralis* infection risk. Pelican Creek, where infection was most severe, is a fourth-order stream and the largest tributary to Yellowstone Lake in terms of stream length (53.5 km), total drainage size (17,656 ha), and precipitation yield. It also has more length at lower elevations (<2,396 m) than the other exposure streams. Chemical analysis of surface waters indicated that Pelican



Fisheries technician Scott Favrot checks a sentinel cage holding cutthroat trout fry on Clear Creek. After exposure to the creek for 10 days, the fry were examined for *Myxobolus cerebralis*.

Creek generally had much higher concentrations of ammonium, chloride, sulfate, and phosphorus than did the other streams, suggesting that Pelican Creek had the highest potential for biological productivity. Specific conductivity was also much higher in Pelican and Beaverdam creeks and may indicate the higher overall productive potential of these streams. This parameter has been significantly correlated with *M. cerebralis* infection prevalence in Oregon, where specific conductivities were in the same range as those of Yellowstone Lake tributaries (Sandell et al. 2001).

During the first exposure period in 2000, a single Yellowstone cutthroat trout fry at Clear Creek was lightly infected by *M. cerebralis*, but the parasite was not detected in this stream in 2001. Peak spawning migrations at Clear Creek took place several weeks after those at Pelican Creek. The emergence of fry much later in the season and the environmental setting at Clear Creek may be somewhat incompatible with successful *M. cerebralis* life cycle establishment.

In Montana (Baldwin et al. 2000) and Oregon (Sandell et al. 2001), the prevalence of infection has varied seasonally and was significantly higher later in the calendar year. In Yellowstone Lake tributaries, however, sentinel fry infection was most prevalent and severe early in the season (mid-July). The fry infection did not seem to correlate with tubificid abundance at exposure sites, as most tubificids were collected in late August and early September, and only one tubificid, collected in early July, tested positive for *M. cerebralis* infection.

Interpretation of stream characteristics in 2001 must take into consideration the conditions of extreme drought present in Yellowstone National Park that year. Many tributary streams decreased to zero or near-zero surface flow and became disconnected from the lake. Peak discharge was 46% below

the long-term average. Although other studies in the Intermountain West have demonstrated the relationship between *M. cerebralis* infection and stream temperature (Baldwin et al. 2000; Hiner and Moffitt 2001; Krueger 2002), mean water temperatures during the exposure periods were 6.2–10.8°C. The water in Pelican Creek, which has a drainage aspect largely to the south, warmed to above 20°C in June 2001, and elevated temperatures (>15°C) remained through early September. The first of the three exposure periods in Pelican Creek had the highest mean temperature (18.1°C) and the highest infection severity. A temperature of 15°C has been considered optimal for triactinomyxon development, but an increase to 20°C has stopped the production of *T. tubifex* in laboratory incubations (El-Matbouli et al. 1999). Pelican Creek was well above 20°C during parts of most days of exposure periods 1 and 2. However, tubificids in Pelican Creek could be releasing triactinomyxons during the night, when water temperatures declined somewhat.

Conclusions

Pelican Creek, which once supported nearly 30,000 upstream-migrating Yellowstone cutthroat trout (Jones et al. 1982), now appears to be the center of *M. cerebralis* infection in the upper Yellowstone Lake basin. There has been significant variation in infection prevalence and severity in the exposed fry at Pelican Creek and other infected streams, and the host–parasite and ecological interactions in this system have been unclear. The *T. tubifex* strain found during this study is genetically similar to laboratory strains known to produce moderate to high levels of triactinomyxons (Kerans et al. 2004), suggesting that the establishment of whirling disease in the Yellowstone *T. tubifex* populations poses a substantial threat to the Yellowstone cutthroat trout. Moreover, other myxozoans that exist in the lake basin are infecting tubificids and unknown fish hosts.



Pelican Creek whirling disease site.

Evidence from this study suggests that *M. cerebralis* tolerates higher mean water temperatures than have been documented for most other systems. The unique geothermal influences of Pelican Creek have perhaps concentrated tubificids and *M. cerebralis* infection. Many areas upstream of the exposure reach are thermally heated and remain without ice cover throughout the winter. Management action to reduce *M. cerebralis* infection risk in this stream could be taken if more information about infected tubificid locations in Pelican Creek were obtained, especially if the distribution is highly clumped. The temperature effects on *M. cerebralis* in both hosts are of interest, and studies aimed at relating infection prevalence in *T. tubifex* and Yellowstone cutthroat trout to temperature and other environmental characteristics would be useful for predicting the risk of whirling disease establishment in other park watersheds.

Vincent (2001) predicted population-level losses of wild rainbow trout in systems with histological infection grades exceeding 2.5. This study has shown that infection rates during the emergence of Yellowstone cutthroat trout fry in Pelican Creek have the potential to significantly affect this fishery. Angler survey data from throughout the stream and recent efforts to capture upstream-migrating adult Yellowstone cutthroat trout are indicating a substantial decline in this spawning population; the Yellowstone Lake population overall is currently at extremely low levels (Koel et al. 2004, 2005). The establishment and the potential proliferation of *M. cerebralis* add a significant threat to a Yellowstone cutthroat trout population that is already imperiled due to predation and competition by non-native lake trout. Although laboratory challenges and previous field studies have suggested that Yellowstone cutthroat trout are only moderately susceptible to *M. cerebralis* infection, the results of our research indicate that this subspecies may be very susceptible. Additional work should be done to compare the *M. cerebralis* resistance among potentially unique cutthroat trout from isolated populations. Perhaps inherent resistance to this parasite exists and could be used to support ongoing broodstock development programs for conservation efforts in Yellowstone National Park and the surrounding region.

Authors' Note

During the years 2002–2007, our collaborative research on whirling disease in Yellowstone National Park has continued. We have determined that infection prevalence and severity of exposed fry extends to the upper reaches of the Pelican Creek watershed, suggesting that whirling disease risk for Yellowstone cutthroat trout extends far upstream in the valley. In contrast, however, Montana State University PhD student Julie Alexander has observed patchy patterns of *M. cerebralis* infection in tubificids from sites sampled throughout the watershed, suggesting that for *T. tubifex*, at least, the risk of whirling disease varies spatially. Additional work has confirmed the

presence of *M. cerebralis* in the Yellowstone River proper in its Hayden Valley reach, and in the lower reaches of several tributaries there. What remains uncertain are the mechanisms responsible for 1) dissemination of *M. cerebralis* among waters, and 2) allowing *M. cerebralis* to persist in these habitats and proliferate, causing losses of cutthroat trout. The highly variable patterns of oligochaetes and abundance of infected *T. tubifex* relative to habitat types warrants further research. Potential vectors of whirling disease dissemination are also being investigated, particularly the role of avian piscivores such as American white pelican (*Pelicanus erythrorhynchos*), great blue heron (*Ardea herodias*), and double-crested cormorant (*Phalacrocorax auritus*). In the pristine environment of Yellowstone National Park, improving our understanding of *M. cerebralis* ecology and life history strategies should increase our ability to mitigate for this harmful disease in the future.

This article has been adapted with permission from the American Fisheries Society. It was originally published as "Myxobolus cerebralis in Native Cutthroat Trout of the Yellowstone Lake Ecosystem" by Todd M. Koel, Daniel L. Mahony, Kendra L. Kinnan, Charlotte Rasmussen, Crystal J. Hudson, Silvia Murcia, and Billie L. Kerans in the Journal of Aquatic Animal Health 18(3):157–175 (September 2006).

Ertel and Michael Ruhl, National Park Service, assisted with field studies and compiled historical spawning migration information. Carmen Aguilar and Russel Cuhel, Great Lakes WATER Institute, conducted chemical analyses of water. Thanks also to Patricia Bigelow, Davina White, and many other biological technicians and volunteers who assisted with field studies. We are grateful to Jim Winton, U.S. Geological Survey, for laboratory facilities and helpful discussions that greatly contributed to the success of this project. This project was partially funded by the Whirling Disease Foundation and by the Montana Water Center through the National Partnership for the Management of Wild and Native Coldwater Fisheries, Whirling Disease Initiative.



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Acknowledgments

Steve Sharon and other Wyoming Game and Fish Department staff provided fry for sentinel exposure studies. Jeff Bagdanov and E. Richard Vincent, Montana Fish, Wildlife and Parks, assisted with transportation of exposed fry. Cal Frasier, Montana Water Center, Wild Trout Research Laboratory, held fry in laboratory aquaria during disease development periods. Linda Staton, U.S. Fish and Wildlife Service, conducted extensive laboratory investigations of sentinel fry and adult fish from Yellowstone Lake. Brian

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The printing of *Yellowstone Science* is made possible through a generous annual grant from the nonprofit Yellowstone Association, which supports education and research in the park. Learn more about science in Yellowstone through courses offered by the Yellowstone Association Institute and books available by visiting www.YellowstoneAssociation.org.



The production of *Yellowstone Science* is made possible, in part, by a generous grant to the Yellowstone Park Foundation from Canon U.S.A., Inc., through *Eyes on Yellowstone* is made possible by Canon. This program represents the largest corporate donation for wildlife conservation in the park.