Spawning and rearing ecology of Madison River rainbow trout in relation to whirling disease infection risk

by Daniel Charles Downing

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish and Wildlife Management
Montana State University

Abstract:
This study examined the relationship between rainbow trout Oncorhynchus mykiss spawning and rearing on whirling disease infection risk in the Madison River. Nearly 80% of the 1,705 observed redds and 59% (10 of 17) of the mainstem spawning radiotagged fish were concentrated in the upper 11 km of the study area. Additionally, 4 of 21 (19%) radiotagged fish spawned in tributaries. Peak spawning occurred April 30 in 1998 and May 1 in 1999, but spawning was observed from late March to early June. Emergence in the mainstem occurred over 3 weeks during late June and early July. Age-0 rainbow trout densities in September 1999 were positively correlated with redd densities ($r2 = 0.91$, $P = 0.01$) suggesting no large scale migration during their first summer. Whirling disease severity, measured using sentinel cage fish, was highly spatially and temporally variable throughout the upper Madison River. Mean whirling disease severity grades of 0.11 and 3.48 were recorded in sites located on opposite sides of the river during the same sampling period. Additionally, mean severity grades ranged from 0.19 to 3.55 within a single site monitored between May and October. This study found rainbow trout spawning and rearing concentrations were spatially diverse. This finding linked to the concomitant finding that whirling disease infection risk was also spatially diverse and not apparently related to spawning site locations, suggests that spawning and rearing in low infection risk areas would limit exposure to whirling disease.

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APPROVAL

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Daniel Charles Downing

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

This study examined the relationship between rainbow trout *Oncorhynchus mykiss* spawning and rearing on whirling disease infection risk in the Madison River. Nearly 80% of the 1,705 observed redds and 59% (10 of 17) of the mainstem spawning radiotagged fish were concentrated in the upper 11 km of the study area. Additionally, 4 of 21 (19%) radiotagged fish spawned in tributaries. Peak spawning occurred April 30 in 1998 and May 1 in 1999, but spawning was observed from late March to early June. Emergence in the mainstem occurred over 3 weeks during late June and early July. Age-0 rainbow trout densities in September 1999 were positively correlated with redd densities ($r^2 = 0.91$, $P = 0.01$) suggesting no large scale migration during their first summer. Whirling disease severity, measured using sentinel cage fish, was highly spatially and temporally variable throughout the upper Madison River. Mean whirling disease severity grades of 0.11 and 3.48 were recorded in sites located on opposite sides of the river during the same sampling period. Additionally, mean severity grades ranged from 0.19 to 3.55 within a single site monitored between May and October. This study found rainbow trout spawning and rearing concentrations were spatially diverse. This finding linked to the concomitant finding that whirling disease infection risk was also spatially diverse and not apparently related to spawning site locations, suggests that spawning and rearing in low infection risk areas would limit exposure to whirling disease.

Introduction

Whirling disease outbreaks in premier salmonid fisheries of the intermountain West of the United States have caught the attention of fishery managers and scientists of the region (Vincent 1996; Nehring and Walker 1996). The disease has the ability to cause severe population declines, but population level effects have not been observed in all cases where the disease has been detected. Severe population declines have been reported in some trout populations in the intermountain West, but little or no effects have been documented in the Pacific Coast, Columbia River basin, and eastern and central United States fisheries where whirling disease is present (Nehring and Walker 1996; Modin 1998). Idaho, Colorado, and Montana have reported varying wild trout population responses among whirling disease positive waters (Elle 1998; Nehring et al. 1998; McMahon et al. 1999; Vincent and Byorth 1999). Idaho, for instance, has reported significant rainbow trout *Oncorhynchus mykiss* population declines in the Big Lost River while rainbow trout populations in the Big Wood River have remained stable in the presence of the disease (Elle 1998).

Variation in disease severity among salmonid populations is partially a consequence of the complex life cycle of the disease. The life cycle of the whirling disease parasite *Myxobolus cerebralis* depends upon two alternate hosts, *Tubifex tubifex,* an oligochaete worm, and salmonids, to complete its life cycle. Despite inhabiting a wide range of habitats including sediments of mountain streams and highly polluted environments (Hedrick et al. 1998), *T. tubifex* distribution and abundance varies spatially and temporally (Lazim and Learner 1986, 1987; Zendt and Bergersen 2000). *M. cerebralis* spores are ingested by the tubificid worms, which in turn produce the waterborne stage of the parasite. The production of the waterborne stage is hypothesized to vary spatially with worm density and temporally with water temperature (Hedrick et al. 1998; El-Matbouli et al. 1999). When exposed to the waterborne stage, which attaches itself to the fish, fish become infected and serve as the host for the spore developmental stage of the parasite. In this stage, the parasite migrates from the skin of the fish to cartilage in the head region and digests the cartilage (Hedrick et al. 1999). Cartilage is abundant in the developing young salmonids; therefore, they are extremely susceptible to the effects of the disease, whereas older fish are not (Hedrick et al. 1998). Fish exposed to the parasite during the early fry stage can suffer severe effects from whirling disease infection including spinal and head deformation, "whirling" behavior, and mortality (Markiw 1991). This "vulnerable period" or relatively narrow window of time (2 to 3 months after hatching depending on water temperature, E. Ryce, Montana State University, personal communication) that fish are susceptible to whirling disease induced mortality, coupled with the high temporal and spatial variability in infection from the parasite (Vincent 2000), suggests many factors may contribute to variable salmonid population responses to whirling disease.

Life history variation in the salmonid host has been proposed as a contributing factor to observed variability in wild trout population responses (McMahon et al. 1999). This hypothesis proposes that variation in life history traits that influence when and where fish occur during their vulnerable period will affect the degree of exposure of young fish to the disease. Timing and location of spawning and rearing in relation to infection risk could therefore influence the severity of whirling disease infection. For instance, fish whose vulnerable period occurs during periods or in areas of low infection risk will have limited exposure to the disease. In contrast, fish whose vulnerable period occurs during periods and in areas of high infection risk will likely show high incidence of whirling disease related mortality, including population level responses. The timing and location of life history events such as spawning, emergence, and rearing will thus influence exposure to the disease.

There is wide variation among salmonids in the life history traits that may affect their exposure to whirling disease. Salmonids have a high degree of variation in both spawning timing and location both within and among populations (Heggberget 1988; Quinn and Unwin 1993; Healey and Prince 1995). For example, Brown and Mackay (1995) found that although a population of cutthroat trout *O. clarki* in the North Ram River, Alberta share overwintering and summer habitat, one group spawned in tributaries and the other spawned in the mainstem and side channels. Distances moved to spawning areas and post spawning movements also differed between the two life histories. Rainbow trout, Yellowstone cutthroat trout *O. clarki bouvieri*, and rainbow trout x cutthroat trout hybrids in the South Fork Snake River, Idaho also spawned in mainstem side channels as well as in tributaries (Henderson 1999). Timing of spawning also differed: tributary spawning cutthroat trout spawned slightly later than mainstem spawning cutthroat trout, whereas rainbow trout showed the opposite trend (Henderson 1999). Additionally, Webb and McLay (1996) noted that Atlantic salmon *Salmo salar* spawning began progressively later at downstream sites over 120 km of the Aberdeenshire Dee, Scotland.

The most significant effect of spawning timing on the vulnerable period of young trout is its influence on emergence timing. There is a link between water temperature and spawning timing that results in hatching and emergence of fry at an optimal time for survival (Heggberget 1988; Quinn and Unwin 1993). Water temperature is the principal environmental variable regulating embryonic and larval development (Taylor 1991). Webb and McLay (1996) suggest emergence is timed to coincide with favorable flow, temperature, and food availability, thus maximizing length of the growth period. They found multiple emergence times within the same river which suggests that optimal conditions occur at different times among sites within a river system. Adaptive responses to differing water temperature regimes result in differing larval survival and developmental rate among salmonid populations (Murray et al. 1989; Taylor 1991).

In addition to the plasticity evident in timing and location of salmonid spawning, there is also considerable variation in life histories of juvenile salmonids after emergence. Northcote (1992) reported high species and stock variability in the extent of migration after emergence in stream-dwelling trout populations. For example, newly emerged cutthroat trout fry from a tributary to Strawberry Reservoir, Utah, displayed two life history strategies: one group migrated to the reservoir soon after emergence, whereas another reared in the stream for 1 to 2 years (Knight et al. 1999). Rainbow trout fry from Lake Taupo and Lake Alexandrina, New Zealand, showed similar variation in migration and rearing (Rosenau 1991; Hayes 1995). Consequently, these wide ranging life history variations could prove to have equally diverse effects on levels of exposure to whirling disease and thus, disease severity within a population. For example, in a system with high whirling disease infection risk in the mainstem but little risk in tributaries, a tributary rearing life history would limit exposure to whirling disease throughout the vulnerable period, thus reducing the probability of a severe population decline caused by whirling disease.

Rainbow trout in the Madison River, Montana, provide an example of severe population effects that have been attributed to whirling disease. Since 1991, several population monitoring sections of the upper Madison River have shown a severe decline of rainbow trout populations compared with historic averages (Vincent 1996; Vincent and Byorth 1999; Clancey 2000). Although the disease has had a severe effect, the Madison River rainbow trout population appears to have stabilized near 25% of its historic abundance. Because no rainbow trout strains have immunity (Vincent 1997), this suggests that at least some fish in the population have life history characteristics enabling them to elude the severe effects of whirling disease.

Study of the relationships between fish life history characteristics and whirling disease infection risk may indicate the influence spawning and rearing life history have on disease severity within a population. This knowledge could be used to develop management strategies that encourage spawning and rearing in low infection risk conditions. In addition, this information may allow researchers to predict salmonid population response to whirling disease infection based on the life history characteristics of the population. Furthermore, such investigations may provide insight as to why some salmonid populations show severe reductions in the face of whirling disease and others do not.

The purpose of this study was to investigate why the rainbow trout population response has been so severe in the Madison River and alternatively, what allows some fish to persist in this whirling disease infected system. Its overall goal was to test the hypothesis that life history characteristics of rainbow trout influence whirling disease infection risk in the Madison River. The approach was to determine rainbow trout spawning timing and location, fry emergence, and juvenile rearing location, and relate these life history variables to temporal and spatial variation in whirling disease infection risk within the upper Madison River.

Study Area

The Madison River, encompassing a total drainage area of 6,475 km^2, originates in Yellowstone National Park and enters Montana in the southwestern portion of the state. The river flows 195 km northward where it joins the Gallatin and Jefferson rivers to form the Missouri River near the town of Three Forks.

This study was conducted on a 46 km section of the Madison River from Hebgen Dam to McAtee Bridge (Figure 1). This section of the river ranges from 1,995 m to 1,665 m in elevation. Flows peak in May and June and are generally stable the rest of the year because of regulation by Hebgen Dam. Annual discharge at Madison (Ennis) Dam averages 48 m^3/s. Minimum and maximum flows at Kirby Ranch, 28 km downstream from Hebgen Dam, are 17 and 99 m^3/s respectively. The majority of the study section is characterized by riffle habitat. Substrate is dominated by cobble in the main channel and cobble and gravel in the side channels throughout the study area. Side channels are common in the upper 35 km below Quake Lake, limited for the next 30 km, and extensive throughout the remainder of the river to the inlet of Ennis Lake. The meadow community type dominates the floodplain vegetation.

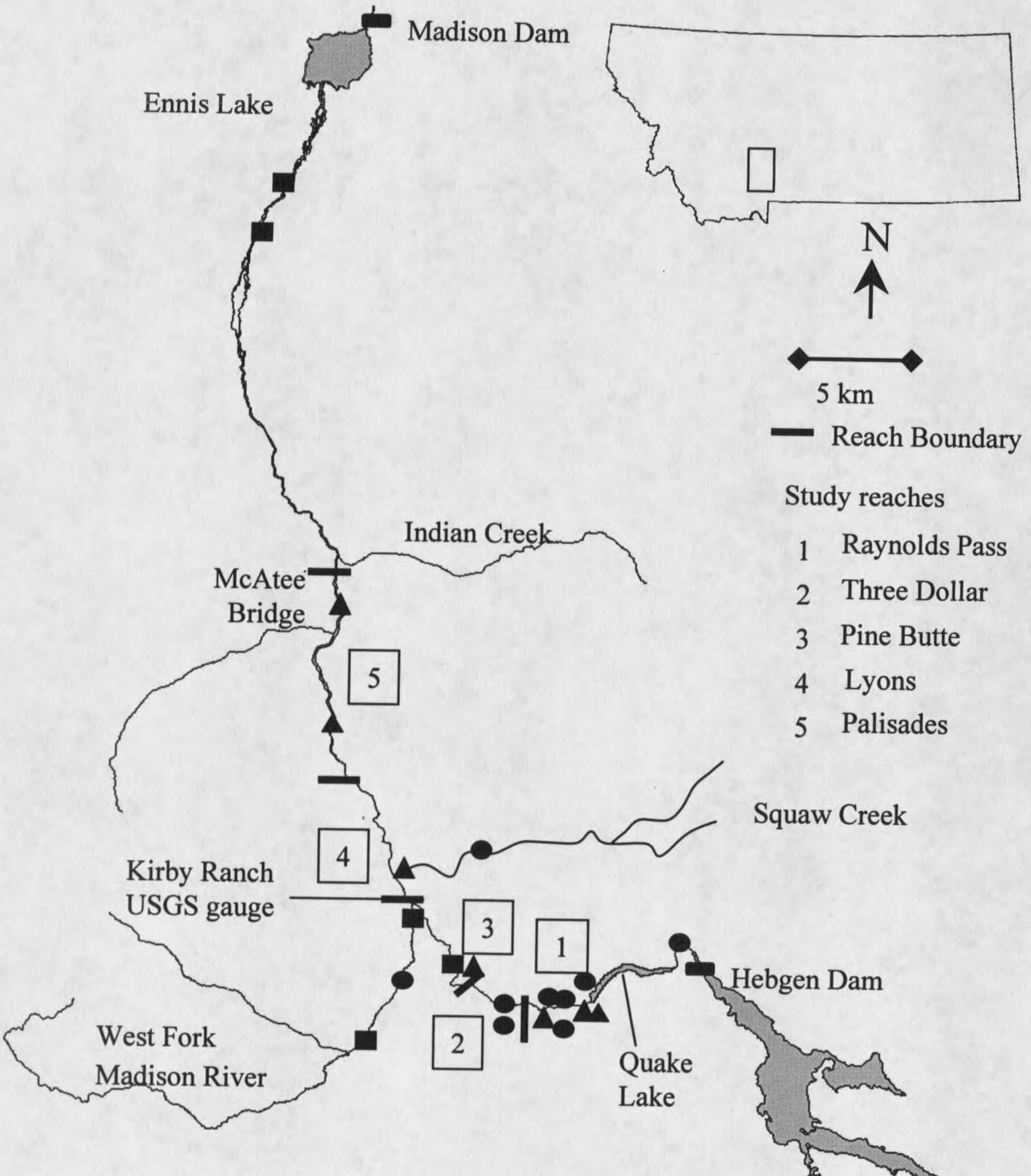

Figure 1. Study reaches and radiotagged rainbow trout spawning locations in the upper Madison River, Montana. Spawning locations are shown for fish tagged upstream from West Fork Madison River (WF) (●), between Indian Creek and WF (▲), and downstream from Indian Creek (■). Study reach boundaries are delineated by solid lines (▬).

Native fish species in the study area include westslope cutthroat trout *O. clarki lewisi*, mountain whitefish *Prosopium williamsoni*, Arctic grayling *Thymallus arcticus*, white sucker *Catastomus commersoni*, longnose sucker *C. catastomus*, mountain sucker *C. platyrhynchus*, longnose dace *Rhinichthys cataractai*, and mottled sculpin *Cottus bairdi*. Nonnative species include rainbow trout, brown trout *S. trutta*, brook trout *Salvelinus fontinalis,* and Utah chub *Gila atraria* (FERC 1997). Rainbow and brown trout were stocked extensively from 1948 to 1974 when stocking was discontinued as studies suggested the wild trout populations increase in number and biomass in the absence of stocked fish (Vincent 1987). Since the discontinuation of stocking, the Madison River has been managed as a wild rainbow and brown trout fishery. The upper Madison River has been designated a Class I fishery (outstanding fishery resource) in the state (FERC 1997).

Methods

Spawning

Spawning timing and location were assessed using a combination of radiotelemetry and redd surveys. Radiotelemetry data revealed spawning migration patterns and location and timing of spawning not detected with redd surveys, which were limited in periods of high flow and turbidity. Redd surveys indicated the duration of the spawning period and allowed quantitative estimation of the relative importance of spawning areas.

Radiotelemetry. Radio transmitters were implanted into 32 adult rainbow trout in an effort to describe spawning and migration behavior during the 1999 spawning season. To ensure the monitoring period encompassed prespawning movements, 28 fish were initially tagged in October 1998. Of these, four transmitters were reimplanted in March 1999 due to pre-spawning mortality. I captured fish by electrofishing, surgically implanted the radio transmitters following procedures outlined by Hart and Summerfelt (1975), Brown and Mackay (1995), and Garrett and Bennett (1995), and released the fish within 0.5 km of their capture location. The size of radiotagged fish ranged from 343 to 460 mm (mean = 396 mm) and from 408 to 998 g (mean = 667 g; Appendix A). I selected larger adults to increase the likelihood that radiotagged fish were sexually mature fish and to ensure that transmitter weight would not exceed 2% body weight of the fish (Winter 1996). On average, I tagged one fish for every 3 river km throughout the section from Quake Lake outlet downstream to the inlet of Ennis Lake to ensure that adults distributed throughout the mainstem were represented (Figure 1).

Each transmitter (model 10 – 28; Advanced Telemetry Systems Inc., Isanti, MN) weighed between 8.13 and 8.28 g, had a 300 mm long external antenna, and a unique frequency for identification ranging from 150.011 to 150.764 MHz. Transmitters had a battery life of 275 d and were programmed to switch on for 4 d and off for 26 d from September 21, 1998 through February 19, 1999, and every day thereafter until July 6, 1999. When switched on, the transmitters were on 9 h each day and off 15 h. This on/off cycle was designed to maximize battery life and provide data through the entire spawning season.

Radiotagged fish were relocated monthly from October 1998 through February 1999 and twice weekly from March 1999 through July 6, 1999. Most fish were relocated from roads paralleling the river by using a whip antenna mounted on a truck. On two occasions (March 30 and May 8), an airplane was used to relocate tagged fish that could not be found from the ground. Fish positions were obtained by triangulation from the riverbank using a directional handheld H antenna (Niemela et al. 1993; Garrett and Bennett 1995). To verify transmitter retention and condition of the fish, I disturbed fish that had remained stationary for 3 to 4 weeks. During this time, I observed fish could easily be relocated to within 10 m using triangulation from distances up to about 30 m. Locations of all tagged fish were recorded on 1:24,000 quadrangle maps to the nearest 0.1 river km, and mean monthly (October to early February) or mean weekly (late February to July) movement of fish was calculated.

The timing and location of spawning were estimated based on a characteristic movement pattern of a period of rapid movement in the spring, a 1 to 2 week period of little movement, followed again by another period of more extensive movement. Spawning was assumed to occur during the period of little movement (Swanberg 1997; Henderson 1999). All radiotagged fish that moved from the main channel into a side channel or migrated into a tributary where spawning habitat or redds were observed were assumed to have spawned (Brown and Mackay 1995; Swanberg 1997; Henderson 1999). Fish were categorized as either mainstem spawners or tributary spawners. Mainstem spawners were further characterized by the reach where spawning occurred. Each spawning location was defined based on the furthest extent of migration and as an area where the fish remained for at least several days. The spawning timing was defined as the duration from the time a fish entered its spawning location until it moved toward its original tagging location. There were several days between relocations, so I defined the initial migration date as midway between the date I first observed the fish migrating and the date of the previous location. The same method was used to estimate the spawning period, and the midpoint of the spawning period was used as the spawning date. Dates (Julian days) of initial migration and spawning as well as duration of spawning period were compared between mainstem spawners and tributary spawners with t-tests.

Redd surveys. The 46 km section of river between Quake Lake and McAtee Bridge was hiked and floated in April 1998 to identify potential spawning sites by the presence of suitable spawning gravel (Magee et al. 1996; Webb and McLay 1996; Kondolf 2000). This section was then divided into five reaches ranging in length from 5.6 to 15.9 km. Reach boundaries were delineated by changes in gradient, side channel development, or presence of tributary junctions (Figure 1). Redd surveys were attempted in tributaries during April 1998; however, high flows and turbidity made redd counts difficult or impossible for much of the period between April and July. Consequently, tributary redd count data were unavailable in this study.

Redd surveys were conducted every 4 to 9 d in each mainstem reach from April 16 to June 9, 1998 and February 21 to June 9, 1999. The 1998 redd surveys were conducted over a greater proportion of each reach to better investigate spawning distribution, whereas in 1999 a smaller proportion of each reach was sampled but over a longer period to better assess spawning timing. I conducted redd surveys by hiking the riverbank and wading the river while wearing polarized sunglasses. Deep (>1 m), swift areas of the main channel could not be effectively surveyed, but I observed that most of these areas had large, embedded substrates that would make spawning difficult, thus I believe the majority of redds were observed. Redds were identified by characteristic pit (upstream depression) and tailspill (downstream mound of disturbed substrate) formation and lighter color than the surrounding undisturbed substrate (Chapman 1988; Thurow and King 1994; DeVries 1997). Each redd location was marked using painted rocks on the riverbed and surveyor's flags on the adjacent riverbank to avoid counting redds more than once. To assess observer misidentification in redd detection and number of false redds, about 10% of redds were randomly chosen and partially excavated to check for the presence of ova (Witzel and MacCrimmon 1983; Knapp and Vredenburg 1996).

Spawning timing was assessed by comparing the number of new redds between each survey. The spawning rate for each interval and reach was expressed as the number of new redds found per day since the last survey. The greatest new redds per day value indicated the peak spawning period for each study reach. Since the large majority of redds were observed in side channels, the total number of redds found in each reach was divided by the side channel area surveyed to compute a mean redd density for each reach. Redd density was then multiplied by the total side channel area for each reach to estimate the proportion of spawning within each reach. The side channel area was calculated using length of side channel and mean width, calculated from 2 to 70 equidistant transects along each side channel. Simple linear regression was used to assess associations between redd density and side channel density, which was defined as hectare of side channel area per km of study reach length.

<u>Emergence</u>

Emergence timing was investigated using redd caps. The caps were 1 m by 2 m nets tapered toward a perforated PVC pipe trap and secured over redds with pins at upstream and downstream ends. The side edges were lined with cobble to seal possible escape routes of emergent fry. Water flowing through the netting and over a redd carried emergent fry into the detachable PVC trap.

Redd capping took place from early May through August in 1998 and 1999. I selected redds that were not immediately adjacent to other redds, contained ova or sac fry, and were accessible during high flows. The number of redds capped was proportional to the number of redds found within each week of the spawning season and each study reach. Caps were cleaned and checked for emergent fry at 1 to 7 d intervals. Emergent fry were identified to species (Weisel 1966), counted, measured (total length in mm), and released. Fry emergence was defined as the first in a succession of sampling days in which a cumulative total of 10 fry were captured. After emergence, caps were removed and placed on another redd of later construction. Thermal units (degree days) from spawning to emergence were calculated by summing mean daily water temperatures (^{o}C) between the dates of redd construction and emergence. Mean daily temperatures were calculated from water temperature data collected by seven Optic StowAway thermographs that were placed 3 to 5 km apart throughout the study area. To account for temperature differences between the redd and the water column caused by upwelling (Hansen 1975; Ringler and Hall 1975; Beard and Carline 1991), thermograph data were supplemented with temperature monitoring of each individual redd capped in 1999. Temperature was recorded 10 cm below the water surface and 10 cm below the surface of the redd substrate using an electronic probe. The mean difference between the water column and redd temperatures was used to adjust the thermal units to emergence derived from the thermograph data. Mean thermal units to emergence were compared between years using a t-test and among reaches using analysis of variance (ANOVA). Temperature differences between the water column and redd substrate were compared among reaches using ANOVA.

Rearing

Trends in age-0 rainbow trout densities within and among reaches over time allow insight into movement and relative abundance of juveniles during the vulnerable period to whirling disease. Backpack electrofishing in a 1 m wide band along the banks of side channels and the main channel was used to determine relative abundances of age-0 rainbow trout. Sites with shallow, low velocity stream margin habitat were selected for age-0 sampling (Baltz et al. 1991; Bozek and Rahel 1991; Tabor and Wurtsbaugh 1991). Age-0 trout were identified to species, measured (total length in mm), and released. In 1998, seven monitoring sites between Quake Lake outlet and McAtee Bridge (Figure 1) were sampled once each in July and August. Relative abundances of age-0 rainbow trout were determined using catch per unit effort (CPUE) values calculated as number caught per 300 s of sampling. In 1999, eight monitoring sites, including four sites sampled in 1998, were sampled for a longer period and more intensively. Each site was sampled four times every 2 to 3 weeks from July through September. Within each site, I randomly chose four 15 m long sampling sections along the 1 m nearest the bank. Because juvenile trout could have occupied most of the side channel area, sampling sections were indices of juvenile abundance. Three pass depletion estimates were conducted for each section. Population estimates and 95% confidence intervals were calculated using depletion method procedures with MicroFish software (Van Deventer and Platts 1989; Griffith and Smith 1993). The number of fish caught per 300 s in the first pass of sampling allowed comparison between years. CPUE was positively correlated with the estimated density of each 15 m^2 sampling section using three-pass depletion (CPUE = 3.30 + 0.114 density, $r^2 = 0.72$, $P < 0.001$, $n = 119$), thus validating the use of the catch per unit effort method for measuring relative abundance. Simple linear regression was used to assess association between fry density and redd density.

Habitat Characteristics

Potential effects of varying flow releases from Hebgen Dam on egg survival and age-0 trout rearing habitat were assessed using two methods. Scour chains (Nawa and Frissell 1993) were used to measure the degree of scour and fill in spawning areas. Scour chains were 42 cm long devices implanted vertically into the substrate with a pipe and a post driver. The scour chains consisted of 40 cm of number 2 chain connected to a weighted end constructed from galvanized pipe fittings and a 4 mm machine screw. The weighted end consisted of a 75 mm long nipple screwed into a bell reducer with a 13 mm plug. An access hole was drilled into the driver pipe flush with the upper extent of the chain to allow parachute cord tied to the uppermost link of chain to exit the pipe. The cord was secured to the pipe to ensure the chain remained elongated during the implanting procedure. The pipe was driven into the substrate to the level of the access hole ensuring the chain was implanted such that the uppermost link was flush with the substrate surface. A total of 18 chains in 1998 and 14 chains in 1999 were installed adjacent to aggregations of redds prior to peak flow in April and May. Scour chains were placed in spawning areas of each study reach. Two pins driven into the riverbank allowed triangulation of the chain location in the streambed. The chains were recovered in October 1998 and August 1999 by carefully excavating the streambed. The depth of substrate moved to uncover the chain was recorded as fill material, and the length of chain laying horizontally was recorded as scour (Nawa and Frissell 1993). Scour and fill measurements were compared between years using t-tests, and combined data from both years were compared among reaches using ANOVA.

To assess effects of low flows on side channels important to spawning and rearing, wetted widths of five side channels were monitored during late July and late October 1999. Mean daily discharges recorded at the USGS gauging station near Hebgen Dam during these periods were 25 m^3/s and 37 m^3/s, respectively. To determine how frequently these flows occurred, I summarized the relative frequency of historical (1980 to 1999) mean daily discharges during the summer rearing period (July 1 to September 30). I selected side channels that were surveyed for redds and age-0 abundance. Two of the side channels were located in the Raynolds Pass study reach, two in Pine Butte, and one in the Lyons study reach. In each side channel, I established a channel cross section in a riffle with the highest streambed elevation, and therefore would reflect habitat available to the entire side channel. I defined habitat availability as the proportion of wetted width to bankfull width. Cross section profiles were determined by measuring the vertical distance to the substrate from a level line to estimate bankfull width. The distinguishing feature of the bankfull level was the abrupt change in bank slope from near vertical to near horizontal (Parrett et al. 1983). Changes in wetted width were reported as changes in proportion of wetted width to bankfull width in relation to discharge.

Whirling Disease Severity

Whirling disease infection risk was evaluated using juvenile rainbow trout in sentinel cages following the protocol developed by Montana Fish, Wildlife and Parks (Vincent 2000). These data were collected by Montana Fish, Wildlife and Parks, reported by Vincent (2000), and described here to relate rainbow trout spawning and rearing life history to risk of infection from whirling disease. A sentinel cage consisted of a 0.5 m diameter by 0.6 m deep screen-covered cylinder containing 60 uninfected 35 to 60 mm hatchery rainbow trout. Fish were held in cages for 10 d, then transported to a laboratory, and held for 80 d to ensure full development of infection and spore formation of the *M. cerebralis* parasite (Baldwin et al. 1998). At the end of this period, the fish were sacrificed and their heads sent to Washington State University Animal Disease Diagnostic Laboratory at Pullman, Washington, for histological examination. Infection severity was scored for each fish using the MacConnell – Baldwin scale of 0 (no infection) to 4 (extensive cartilage damage) (Vincent 2000). The mean infection grade and percent of fish infected within a cage determined infection risk.

Eleven sites in 1998 and 18 sites in 1999 between Hebgen Dam and McAtee Bridge were sampled to assess spatial variability of whirling disease severity among sites. Cages were placed in stream margins along the stream bank in easily accessible locations throughout the study section. There were three sampling periods in 1998, May 25 to June 4, July 8 to July 18, and September 28 to October 8, and two sampling periods in 1999, May 25 to June 4 and June 24 to July 5. These periods corresponded to temperatures and periods when peak infection has been observed in the Madison River and other systems (D. Vincent, FWP Bozeman, personal communication). The periods best corresponding to peak emergence timing were used for whirling disease severity comparison between years. To evaluate infection risk in tributaries, two sentinel cages were also deployed in the West Fork of the Madison River in 1998 during three sampling periods: June 14 to 24, July 9 to 17, and September 17 to 25. To assess temporal variation in whirling disease infection, one site (Kirby Bridge) was used as a "time sequence" site for both years. For this, 10-d infection tests were run consecutively from May 5 to July 25 and from September 16 to October 18 in 1998 and from April 15 to July 15 in 1999.

Results

Spawning

Radiotelemetry. A total of 818 relocations were made on 32 fish implanted with radio transmitters from October 1998 until transmitter failure in July 1999. I obtained spawning data on 21 radiotagged fish; the remainder were lost to predation (N = 9) and transmitter malfunction or loss (N = 2).

Radiotagged fish generally remained near their initial tagging location prior to prespawning movements which began in March. From October 1998 through February 1999, the average weekly movement for all radiotagged fish was < 0.5 km. Apparent spawning migrations began in late March, when average weekly movement increased markedly to 6.1 km per week. Spawning migrations ranged from 0 to 66.3 km for all radiotagged fish. The direction of the spawning migration was upstream for all but one radiotagged fish.

Fish that spawned in the mainstem initiated migration about 6 weeks earlier than tributary spawners (March 23 versus May 6; P < 0.01; Table 1). Tributary spawning fish averaged nearly 30 km greater migration distance than mainstem spawning fish (P = 0.03; Table 1). Five mainstem spawning fish showed no movement throughout the monitoring period. These fish were assumed to have spawned in their respective locations, but timing of spawning could not be determined and they were omitted from estimates of spawning timing. Mainstem spawning fish entered their spawning area and spawned about 30 d earlier than tributary spawning fish (P = 0.02, < 0.01, respectively) but the length of the spawning period was similar (4 to 13 d; P= 0.11; Table 1). Most fish returned to locations near their initial tagging location after spawning.

Table 1. Comparisons of spawning timing attributes between mainstem and tributary spawning radiotagged rainbow trout during the 1999 spawning season on the Madison River, Montana. The P values are from two sample t-tests. Bold type indicates significance at $\alpha = 0.05$. Sample sizes differ among spawning attributes due to mortality and loss of tagged fish.

	Mainstem			Tributary			
Variable	N	Mean	Range	N	Mean	Range	P value
Initial migration	10	3/23	2/11 – 5/18	3	5/6	4/30 – 5/18	**0.002**
Enter spawning area	11	4/21	2/11 – 5/29	4	5/21	5/15 – 5/24	**0.018**
Spawning date	12	4/30	3/12 – 6/1	4	5/27	5/21 – 5/31	**0.006**
Leave spawning area	12	5/11	4/2 – 6/11	4	6/3	5/27 – 6/9	**0.010**
Spawning period (d)	11	23	4 - 58	4	13	10 - 17	0.110
Migration period (d)	9	63	7 - 117	3	41	27 - 51	0.130
Migration distance (km)	16	14.1	0 – 55.0	3	43.2	13.0 – 66.3	**0.027**

Of the 12 radiotagged fish that survived and were relocated throughout the entire period from October to July, 9 (75%) moved back to within 2 km of their original tagging location after spawning (Figure 2). The majority (17 of 21 or 81%) of radiotagged fish spawned in the mainstem while the remaining 19% spawned in tributaries of the Madison River. Mainstem spawners spawned over an 82.1 km section of the mainstem, ranging from 9.5 km upstream from the Quake Lake outlet to 72.6 km downstream from the Quake Lake outlet (Figure 1). However, nearly half (8 of 17 or 47%) spawned in the 3.3 km Raynolds Pass study reach, and 11 of 17 (65%) spawned in the upper 11 km of the river. Fish tagged in all study reaches moved into this upper section to spawn. Of tributary spawning fish, three of the four spawned in the West Fork Madison River system, and one in Squaw Creek (Figure 1).

Redd surveys. Redd surveys were conducted on 13.2 km of side channel habitat in 1998 and 8.7 km in 1999 throughout the entire study area. Percentages of total side channel area surveyed varied among study reaches (range 55 – 100% in 1998 and 20 – 88% in 1999). Redd surveys were conducted 6 or 7 times in 1998 and 10 times in 1999. Generally, conditions upstream from the West Fork Madison River were good for visually identifying redds except for brief (1 to 2 d) periods of high flow and turbidity. Visibility was completely obscured in the lower two study reaches (Lyons and Palisades) after May 11, 1998 and May 24, 1999 because of turbid runoff from the West Fork Madison River; however, most spawning had occurred prior to these dates.

A total of 1,705 redds was observed during the two field seasons. Despite the large number of redds found, incidence of superimposition, or multiple redds formed on

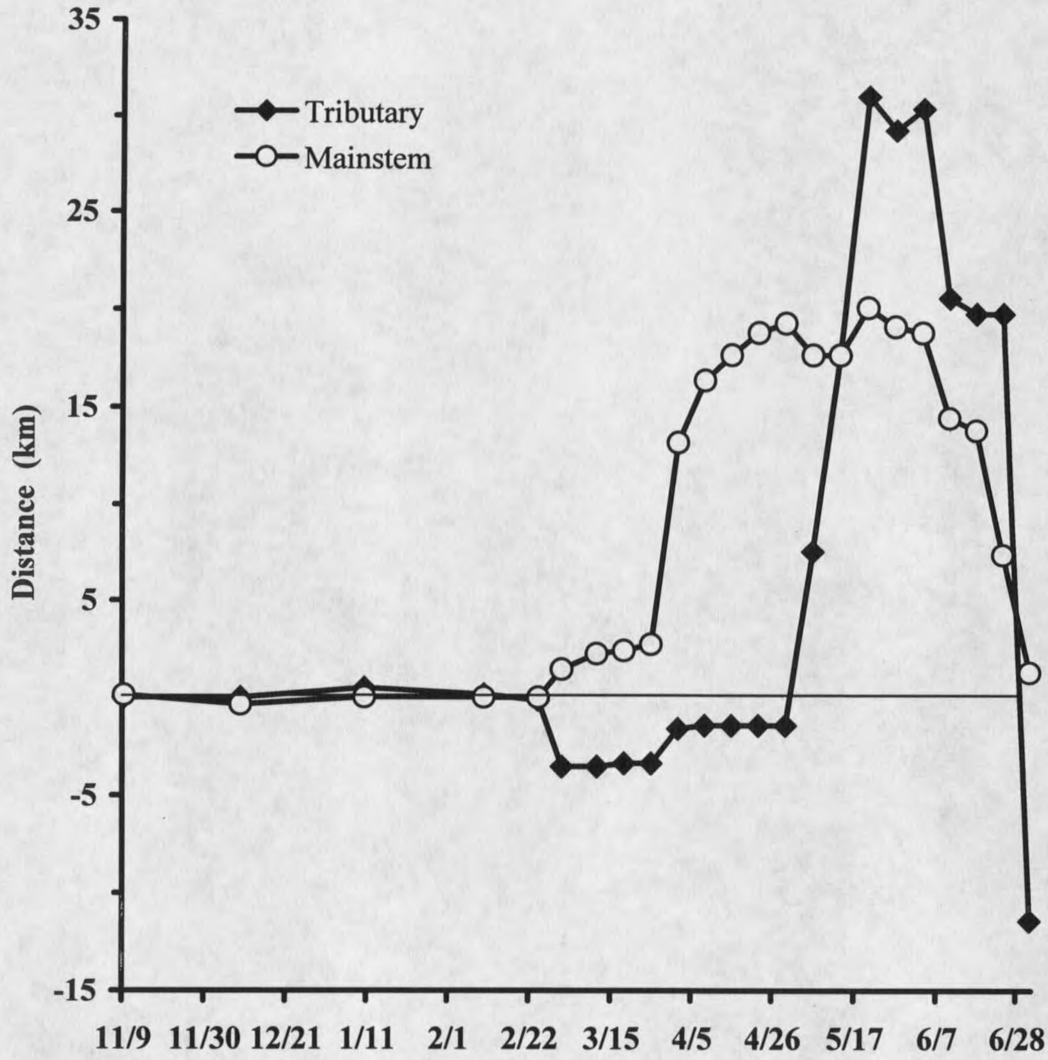

Figure 2. The cumulative mean weekly movement for radiotagged rainbow trout spawning in tributaries or the mainstem Madison River, Montana, 1999 relative to the initial tagging location (horizontal line).

top of one another, was very low as only 9 and 15 observations were recorded in 1998 and 1999, respectively. Ova or sac fry were present in 86% (68 of 79) of the partially excavated redds in 1998 and 100% (77 of 77) in 1999, thus the proportion of false redds was also low. Ten of the 11 redds with no ova or sac fry were excavated after June 10, 1998 suggesting that fry may have already emerged.

Rainbow trout exhibited extended spawning periods (about 2 months) in both 1998 and 1999. In 1998, 208 redds were found during the first week of redd surveys, suggesting spawning had begun before this period (Figure 3). Peak spawning was estimated to have occurred on April 30, but redds were found as late as June 9. In 1999, surveys were conducted earlier than in 1998 to better characterize the initiation of spawning. Spawning was observed from late March to early June, but most spawning occurred from April through late May when spawning activity noticeably decreased, similar to the observed pattern in 1998 (Figure 3). Spawning timing was also similar among the study reaches (Figure 4).

Mean daily water temperature at Raynolds Pass Bridge was similar during peak spawning (median spawning dates) both years (Figure 5). Mean daily water temperature during the median spawning dates in 1998 (April 30) and in 1999 (May 1) was 4 °C and 5 °C, respectively. Mean daily water temperature ranged from 5 to 10 °C during the spawning period in 1998 and from 4 to 9 °C in 1999. Most spawning occurred during the relatively stable flow prior to the spring peak in the hydrograph (Figure 5). Discharge at the Kirby Bridge gauging station during this period was much higher during 1999 than 1998. In 1998, average discharge during the majority of spawning was 37 m^3/s but about 48 m^3/s in 1999, a 29% increase.