



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

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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.

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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 km², 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 m³/s. Minimum and maximum flows at Kirby Ranch, 28 km downstream from Hebgen Dam, are 17 and 99 m³/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.

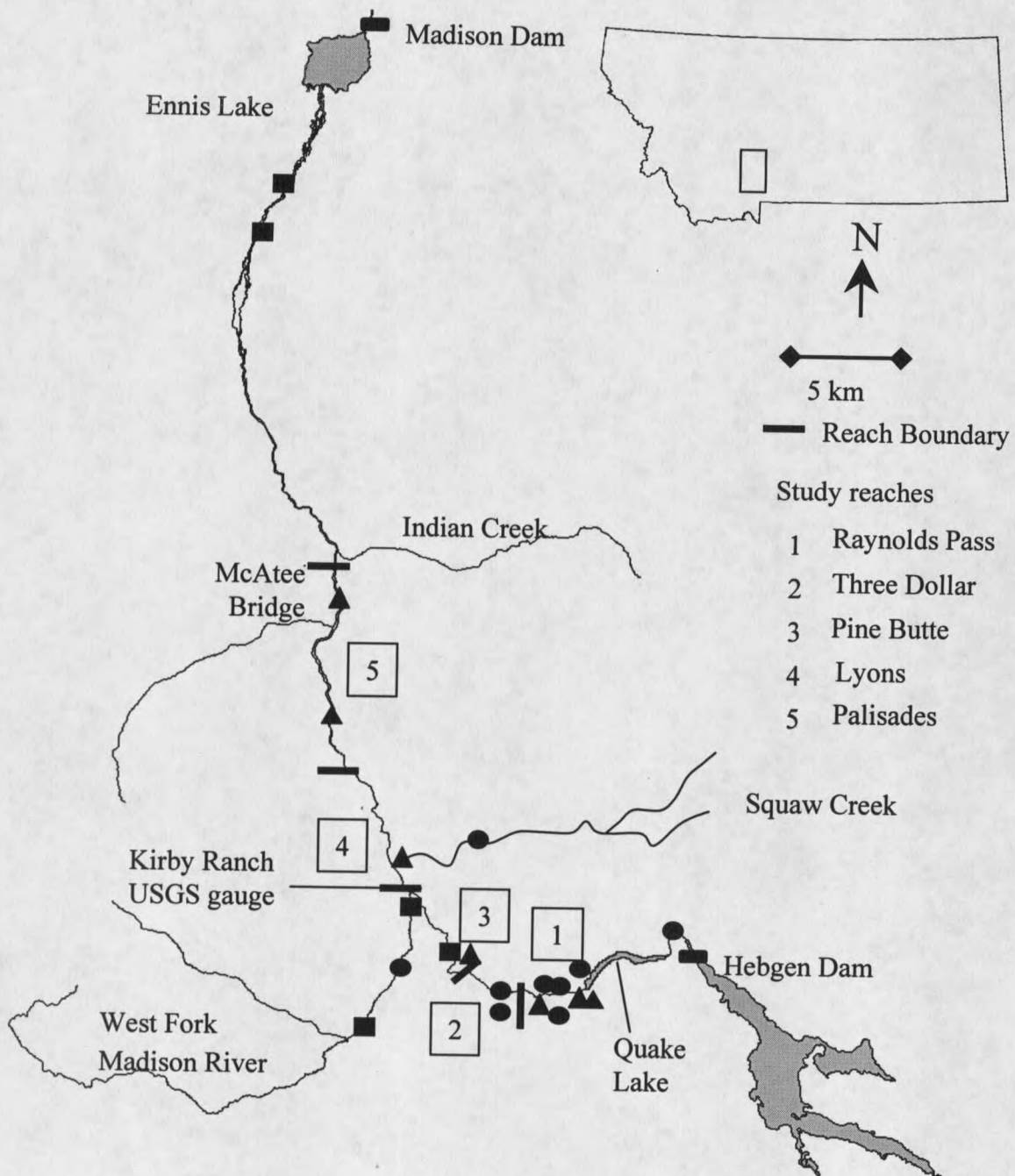


Figure 1. Study reaches and radiotagged rainbow trout spawning locations in the upper Madison River, Montana. Spawning locations are shown for fish tagged upstream from West Fork Madison River (WF) (●), between Indian Creek and WF (▲), and downstream from Indian Creek (■). Study reach boundaries are 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 *Catostomus commersoni*, longnose sucker *C. catostomus*, 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.

Emergence

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 ($^{\circ}\text{C}$) 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 m² sampling section using three-pass depletion ($CPUE = 3.30 + 0.114 \text{ density}$, $r^2 = 0.72$, $P < 0.001$, $n = 119$), 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 $25 \text{ m}^3/\text{s}$ and $37 \text{ m}^3/\text{s}$, 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 Reynolds 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.

Variable	Mainstem			Tributary			P value
	N	Mean	Range	N	Mean	Range	
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 Reynolds 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

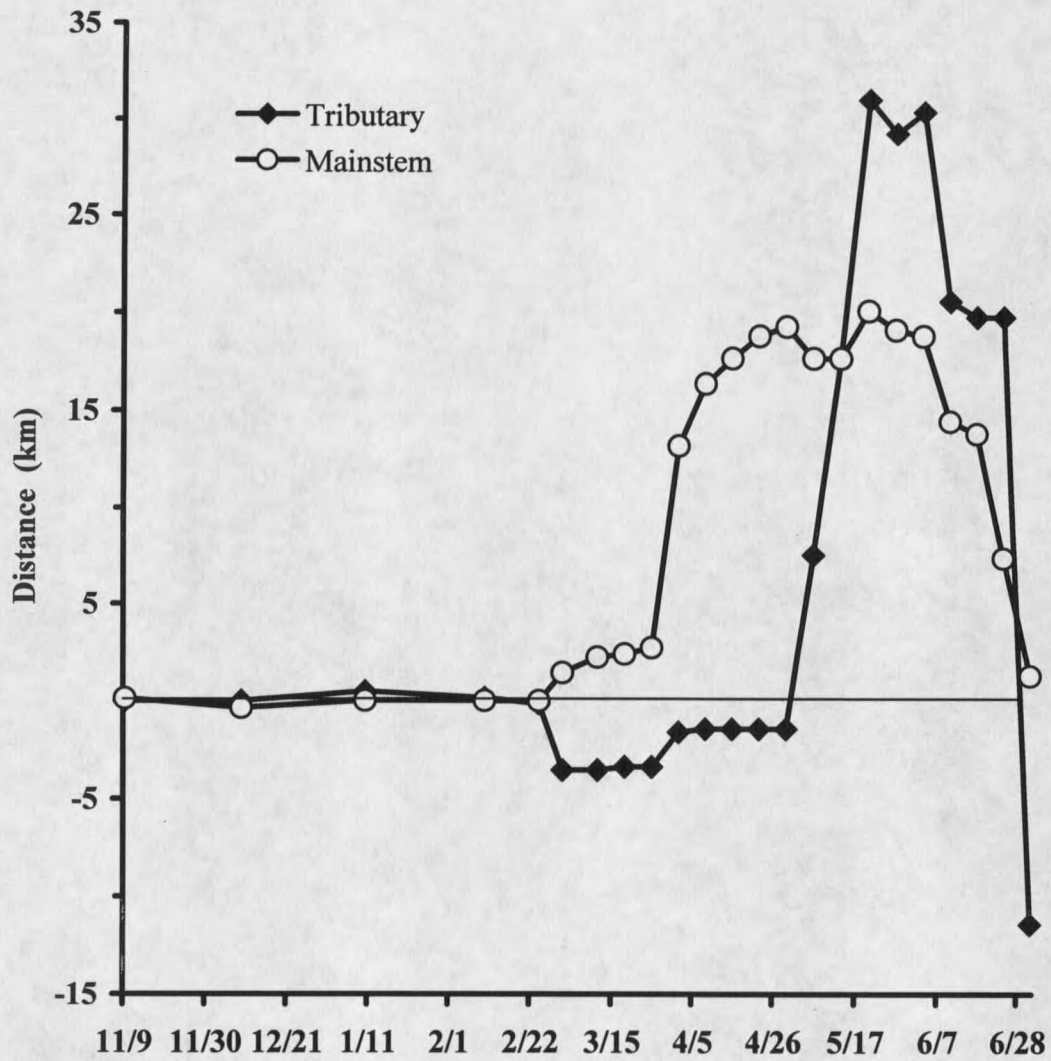


Figure 2. The cumulative mean weekly movement for radiotagged rainbow trout spawning in tributaries or the mainstem Madison River, Montana, 1999 relative to the initial tagging location (horizontal line).

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 m³/s but about 48 m³/s in 1999, a 29% increase.

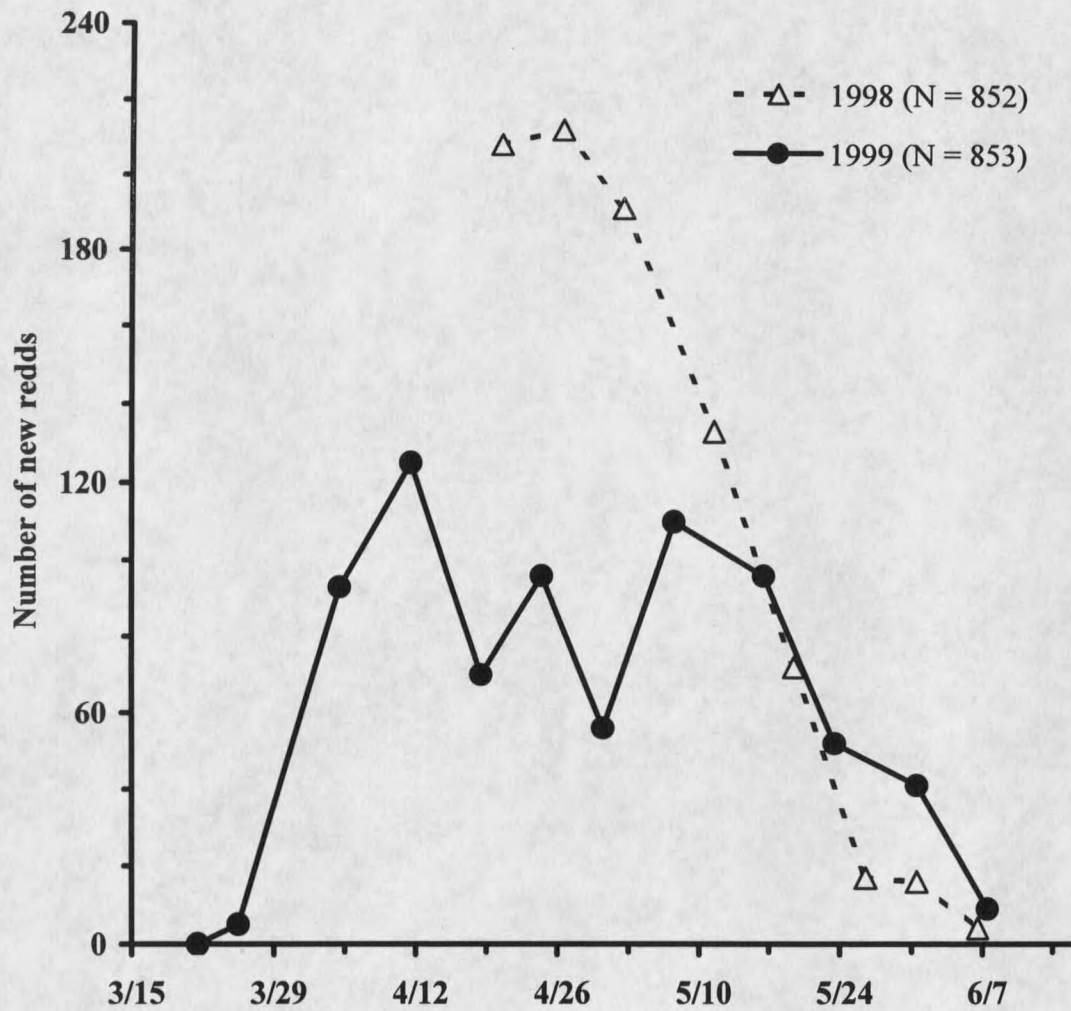


Figure 3. Number of new rainbow trout redds observed each survey period on the Madison River, Montana, during the 1998 and 1999 spawning seasons.

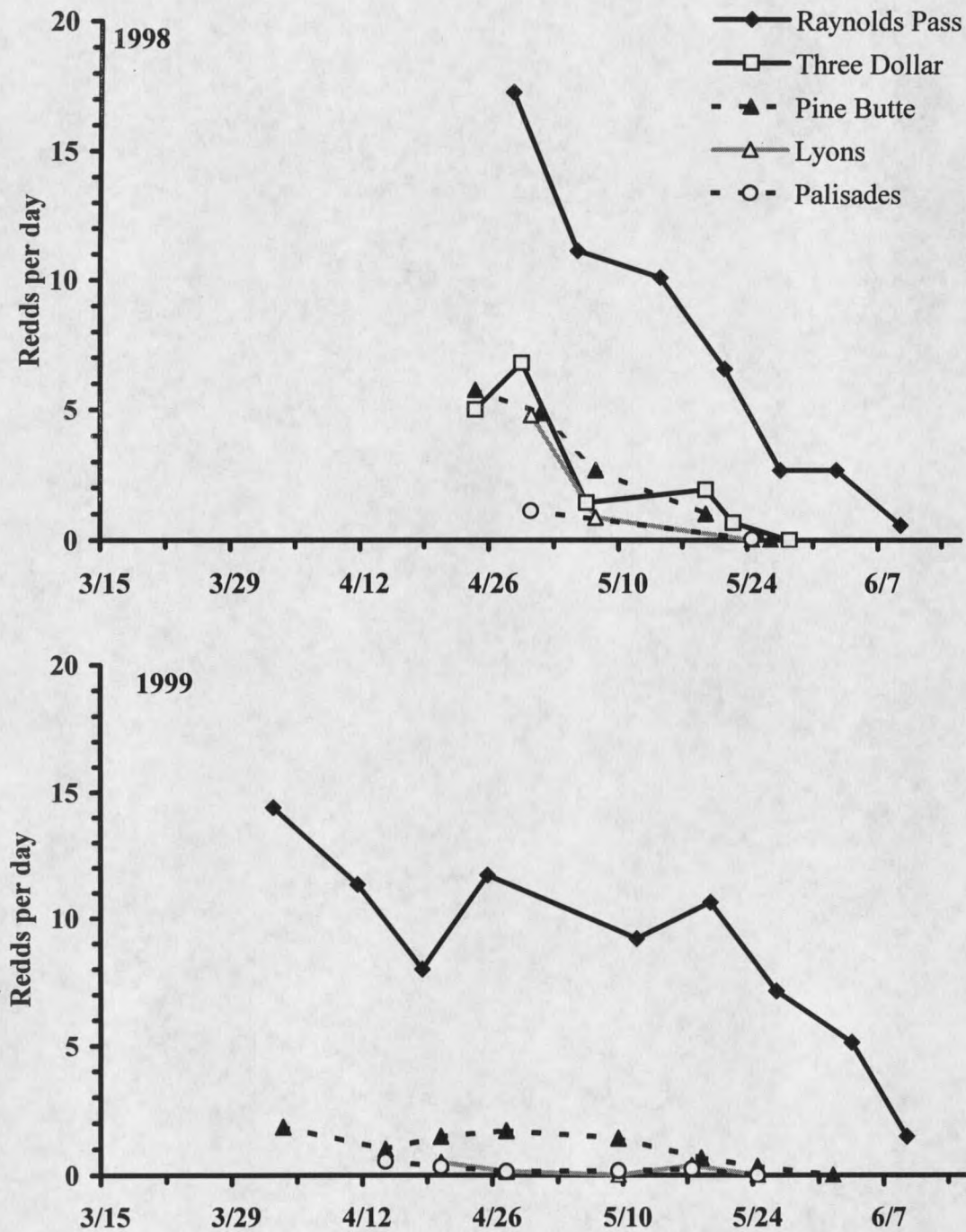


Figure 4. Number of new rainbow trout redds observed per day since the previous survey for each study reach in the Madison River, Montana for the 1998 and 1999 spawning seasons. The highest values indicate peak spawning periods for each reach. Data was not available for the Three Dollar study reach in 1999.

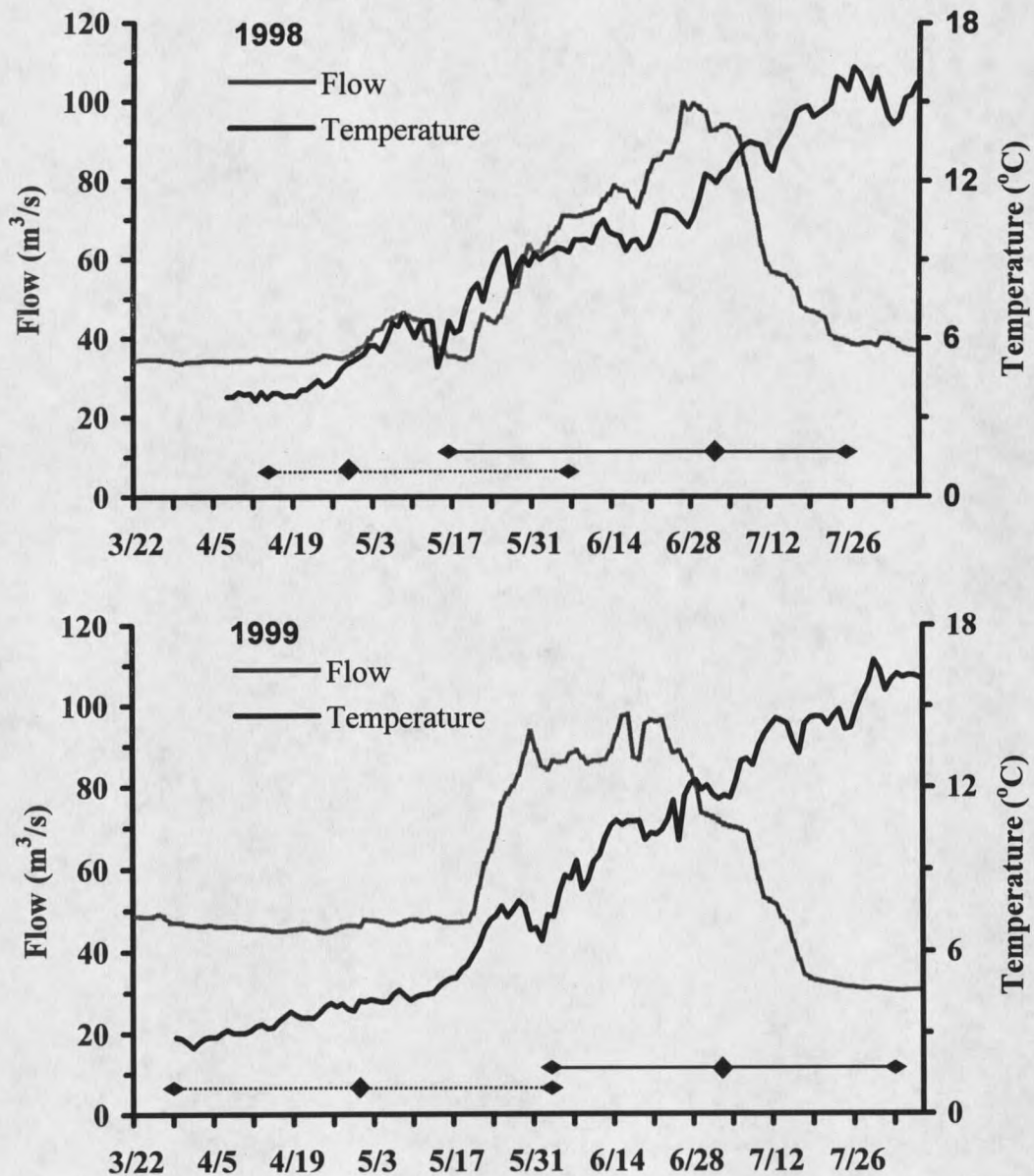


Figure 5. Flow and mean daily temperature data for the Madison River, Montana during the 1998 and 1999 spawning and emergence periods. Flows were measured at the Kirby Bridge USGS gauging station and mean daily water temperatures at Reynolds Pass Bridge. Temperature data are unavailable prior to April 7, 1998 and March 28, 1999. Range and peak of rainbow trout spawning (dashed) and emergence (solid) are shown near the bottom of each chart.

Table 2. Study reach and rainbow trout spawning attributes for 1998 and 1999 in the Madison River, Montana. The length, total side channel (SC) area, and number of redds observed are reported for each study reach. Redd densities are the mean number of redds observed per hectare of side channel surveyed for each study reach. The estimated total number of redds and proportion of total spawning are calculated by multiplying the mean redd density and total SC area available for each study reach.

Study reach	Length (km)	Total SC area (ha)	Redds		SC area surveyed (ha)		Redd density (#/ha)		Estimated total redds		Proportion of total spawning (%)	
			1998	1999	1998	1999	1998	1999	1998	1999	1998	1999
Raynolds Pass	5.3	5.3	495	649	4.7	4.7	106	138	564	734	58	59
Three Dollar	5.3	3.1	141	77	3.0	1.3	47	61	144	187	15	15
Pine Butte	7.6	6.5	126	89	5.4	2.8	23	32	149	207	15	17
Lyons	12.9	2.4	53	16	2.4	0.5	22	33	54	81	5	6
Palisades	15.1	3.1	38	21	1.7	1.5	22	14	69	44	7	3
Total	46.2	20.4	853	852	17.2	10.8	50	79	980	1253	100	100

Most spawning occurred in the upper study reaches, with redd density declining sharply as distance downstream increased (Table 2; Figure 4). Redd density of the uppermost study reach, Reynolds Pass, was over 4 times higher than in the three study reaches furthest downstream (Pine Butte, Lyons, and Palisades) and 1.25 times higher than in the Three Dollar study reach in both years. Combined, the two uppermost study reaches, comprising 10.6 km or 23% of the total river km surveyed, were estimated to contain nearly 75% of the redds throughout the entire study area.

Despite nearly identical total observed redds in each year (853 in 1998 and 852 in 1999), redd density increased in all but the lowest study reach from 1998 to 1999. The estimated total number of redds increased 28% from 1998 to 1999, but the proportion of total estimated spawning within each reach was very similar between years. The Reynolds Pass study reach was estimated to contain 58% (564 of 980) of the total redds in 1998 and 59% (734 of 1253) of the redds in 1999 (Table 2).

An estimated 95% of redds occurred in side channels. Redd density and side channel area were not significantly correlated ($r^2 = 0.48$, $P = 0.19$ in 1998 and $r^2 = 0.53$, $P = 0.17$ in 1999; Figure 6) when all study reaches were compared. However, when the Pine Butte study reach was removed from the regression analysis, the two attributes were highly positively correlated ($r^2 = 0.96$, $P = 0.02$ in 1998 and $r^2 = 0.95$, $P = 0.03$ in 1999), suggesting that redd density in the Pine Butte study reach was lower than expected.

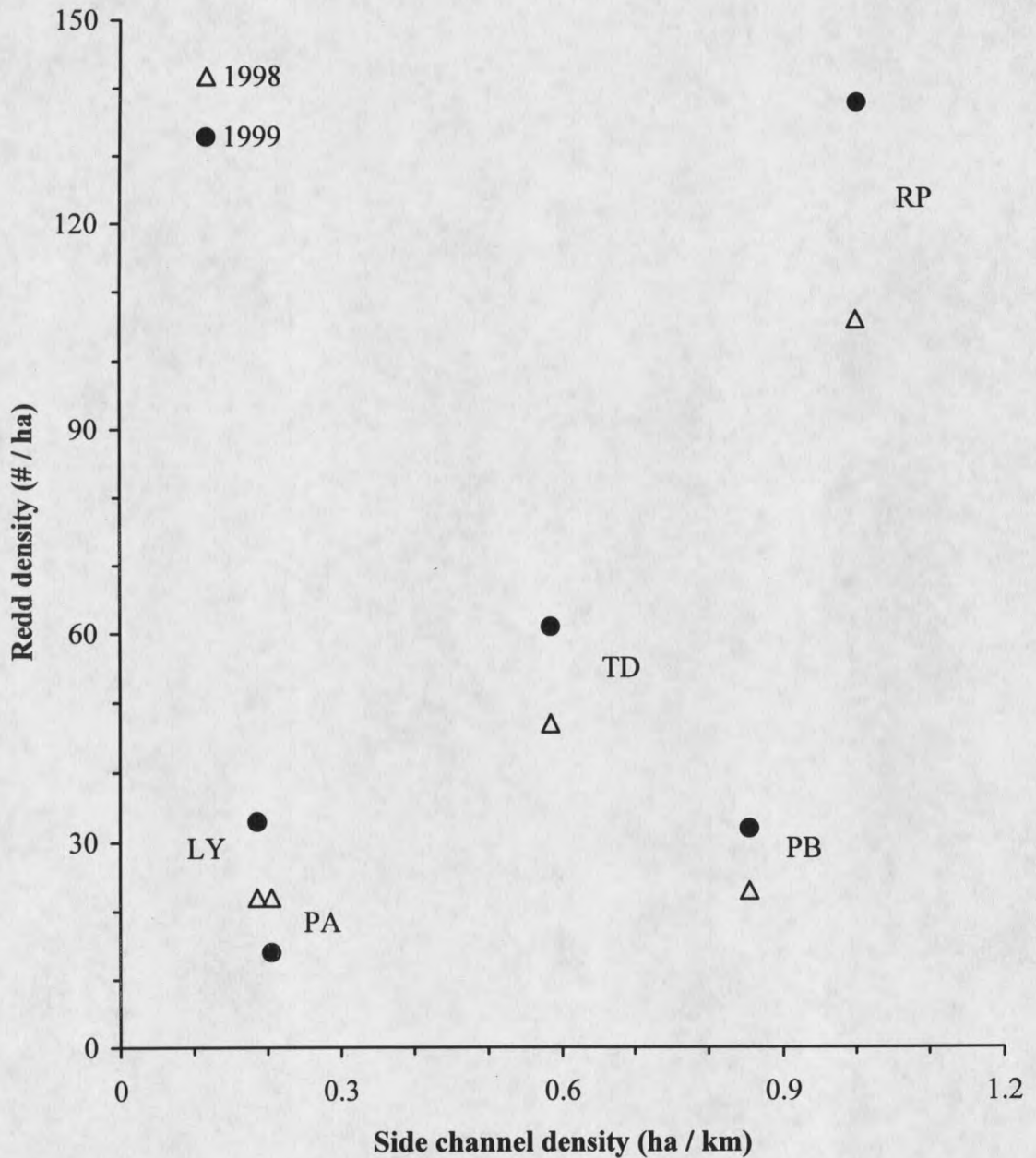


Figure 6. Association of rainbow trout redd density and side channel density for each study reach in the Madison River, Montana during 1998 and 1999. Redd density was calculated as the total number of redds observed per ha of side channel area surveyed. Side channel density was calculated as total ha of side channel per km of each study reach. Data for each study reach abbreviated: Raynolds Pass (RP), Three Dollar (TD), Pine Butte (PB), Lyons (LY), and Palisades (PA).

Emergence

Despite a wide variation in spawning timing (2 months), most rainbow trout emergence occurred within a relatively narrow 3 week window from late June to early July (Figure 7). I collected emergent fry from 12 of 20 (60%) capped redds in 1998 and 31 of 45 (69%) capped redds in 1999. The median emergence date in 1998 was July 2 (range May 19 to July 21) and July 6 (range June 3 to August 3) in 1999. Emergence peaked during the falling limb of the hydrograph in both 1998 and 1999 (Figure 5). Water temperature at the time of emergence averaged 11.8 °C (range 7.5 to 13.7 °C) in 1998 and 12.5 °C (range 7.1 to 15.5 °C) in 1999. The mean number of thermal units from redd formation to emergence was similar between years ($P = 0.15$; Figure 8) and among reaches ($P = 0.38$), averaging 523 (SD = 193) thermal units in 1998 and 614 (SD = 115) in 1999. In 1999, the water column temperature averaged 0.74 °C ($N = 31$; SD = 1.3; Appendix B) higher than the intragravel temperature. The influence of upwelling was highly variable among individual redds within reaches, and no significant differences were found among reaches ($P = 0.19$).

Rearing

The relative abundance of age-0 rainbow trout varied widely among mainstem study reaches, and was greatest in the two uppermost study reaches where the majority of redds were located. In 1999, fry density in September and redd density were positively correlated ($r^2 = 0.91$, $P = 0.01$). In general, age-0 rainbow trout abundance decreased with distance downstream from Quake Lake. In both years and throughout the sampling periods, age-0 rainbow trout abundances in the two upper reaches (Raynolds Pass and

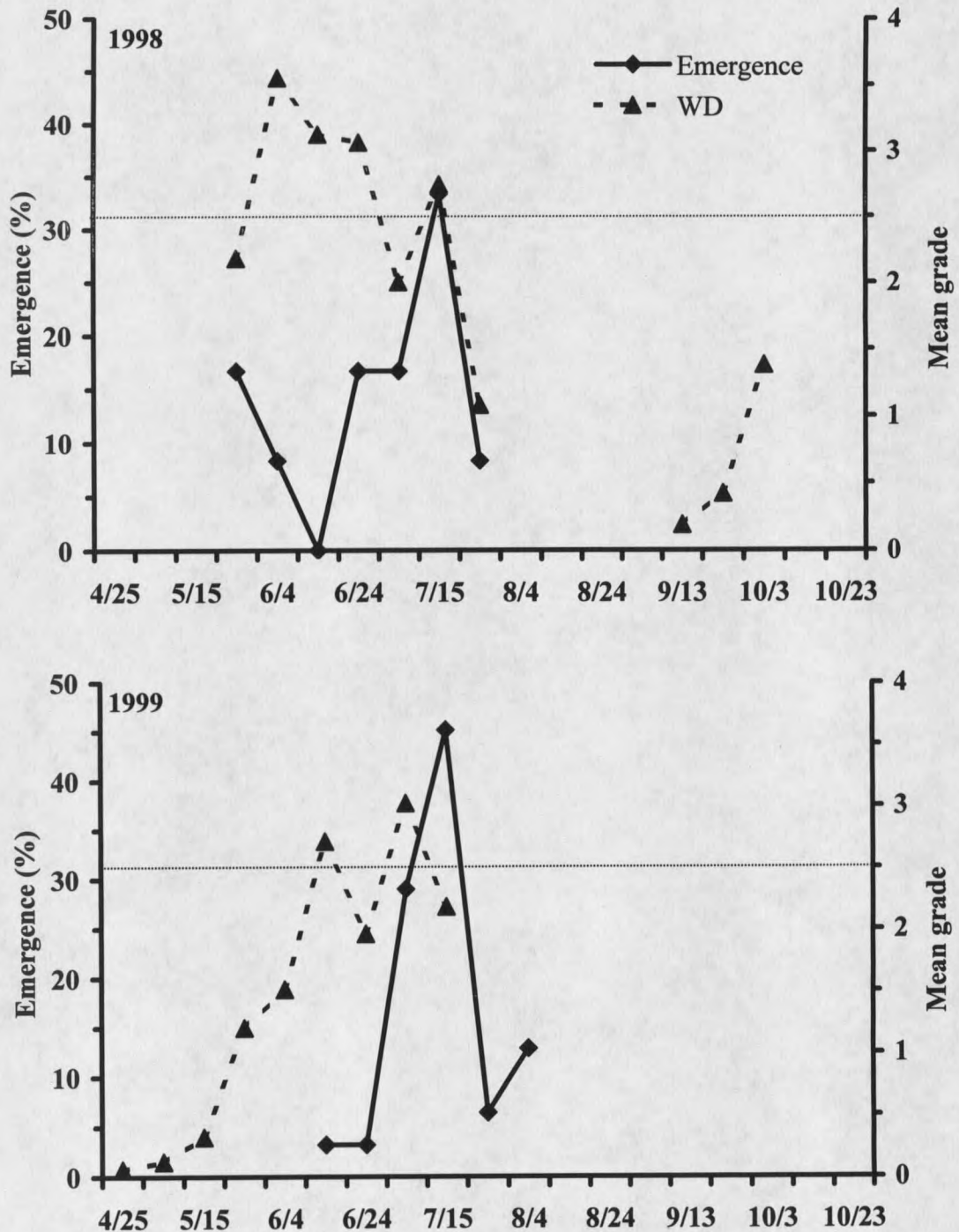


Figure 7. Mean whirling disease infection grade in relation to timing of rainbow trout emergence of 12 redds during 1998 and 31 redds during 1999 in the Madison River, Montana. Whirling disease infection grades are means of sentinel cage rainbow trout for the Kirby Bridge time sequence sampling. The dashed line indicates the critical mean whirling disease infection grade of 2.5 (Vincent 2000).

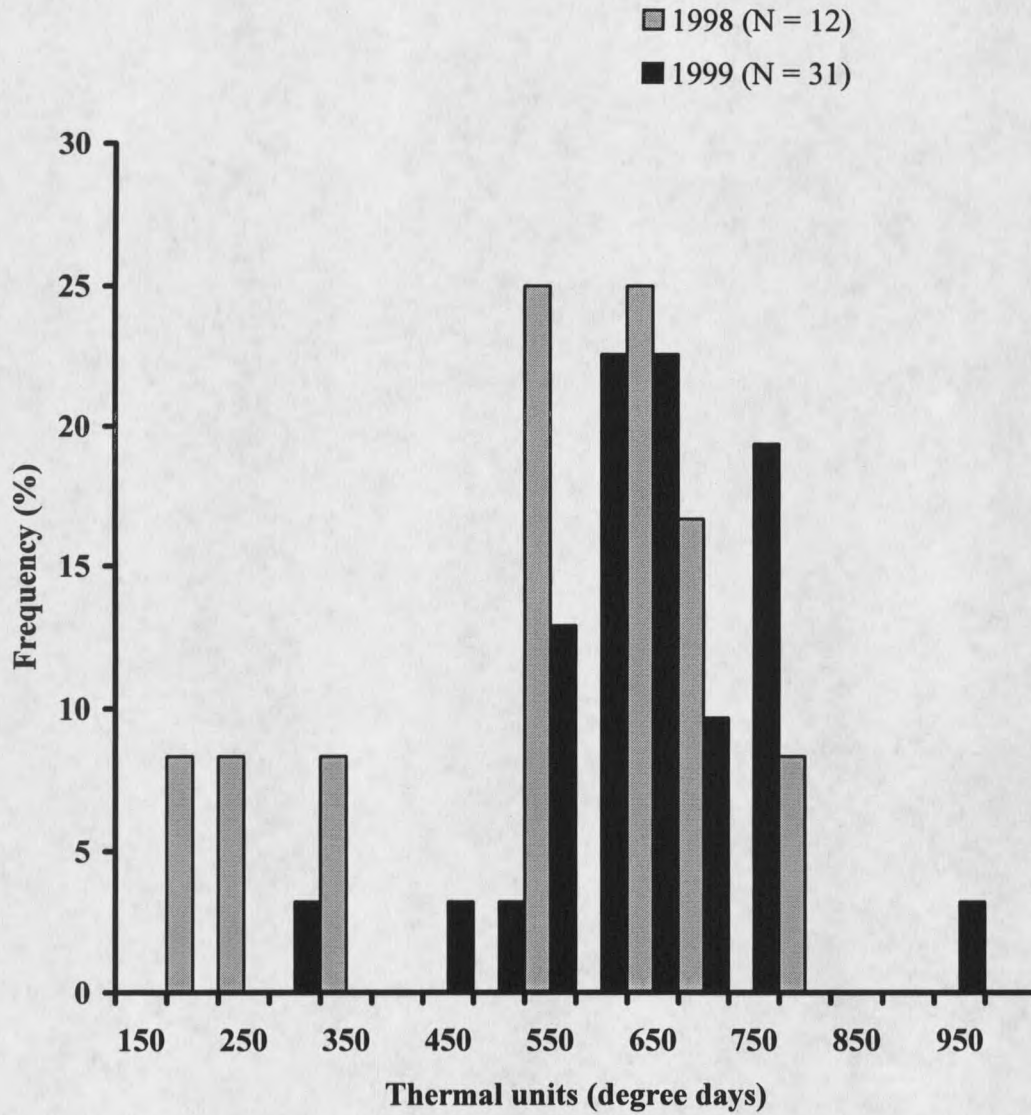


Figure 8. The relative frequency of thermal units from redd formation to emergence for rainbow trout redds in the Madison River, Montana, during 1998 and 1999.

Three Dollar) were greater than those of the three lower study reaches (Pine Butte, Lyons, and Palisades; Figure 9). The upper two study reaches comprised 78% (range 74–84%) of the total age-0 rainbow trout densities for all study reaches combined during each sampling period in 1999. On average, 62% and 78% of the age-0 fish were sampled in the upper two study reaches compared to 73% and 74% of total estimated spawning in 1998 and 1999, respectively (Table 2).

The July sampling period in 1998 likely occurred before emergence was completed as abundances during the August sampling period increased in all study reaches. In 1999, age-0 rainbow trout abundances generally declined over time and by distance downstream from Quake Lake (Figure 9). There was no evidence for a shift in abundance to downstream study reaches over time, indicative of movement of age-0 fish to downstream reaches (Figure 9).

Habitat Characteristics

There was little evidence of significant scouring or filling of spawning areas. There was no significant difference between mean scour depth in 1998 (33 mm, SD = 37.7 mm, N = 4) and 1999 (54 mm, SD = 39.0 mm, N = 12, $P = 0.37$, Table 3); peak discharge was similar in both years (Figure 5). The average amount of fill material deposited was also similar between years ($P = 0.48$), 100 mm (SD = 63.2 mm) in 1998 and 73 mm (SD = 52.3 mm) in 1999. Scour and fill were not significantly different among reaches ($P = 0.59$ and $P = 0.32$ respectively) comparing combined 1998 and 1999 data.

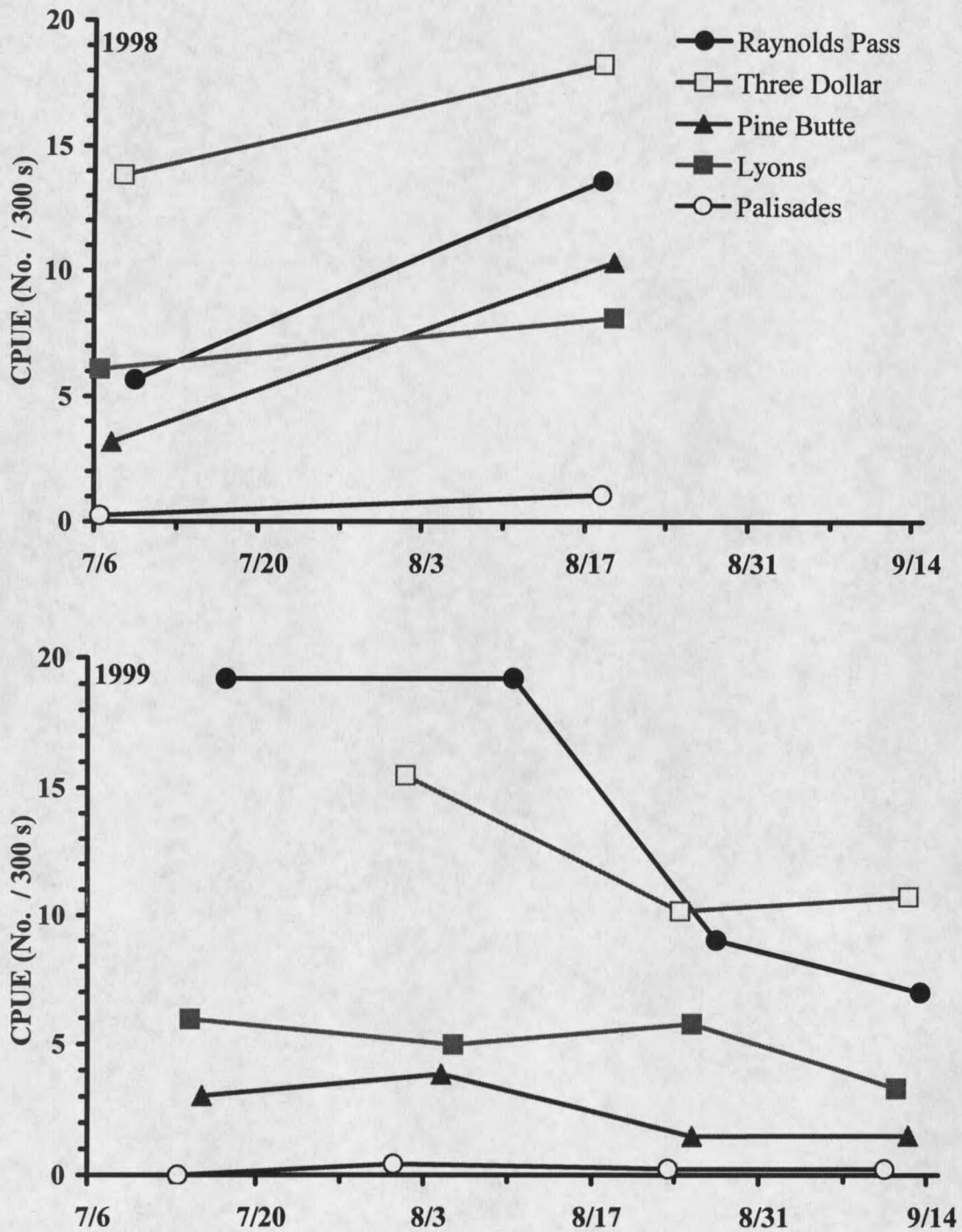


Figure 9. Abundance of age-0 rainbow trout for each study reach and sampling period during 1998 and 1999 on the Madison River, Montana. Abundances were expressed as number of fish caught per 300 s of electrofishing.

Table 3. Scour and fill data for each study reach in the Madison River, Montana. Data for 1998 and 1999 were combined.

		Raynolds Pass	Three Dollar	Pine Butte	Lyons	Palisades
Scour (mm)	Mean	50	-	38	75	34
	SD	45	-	45	19	34
	N	6	0	4	3	3
Fill (mm)	Mean	73	-	65	60	133
	SD	57	-	44	60	45
	N	6	0	4	3	3

Response to changes in main channel discharge varied widely among side channels. (Table 4). One of the side channels within the Raynolds Pass study reach showed a decrease in proportion of wetted width to bankfull width by 3% while the other increased by 16% in response to increased discharge. The two side channels from the Pine Butte study reach showed similar disparity as one increased 9% while the other which was dry during the lower flow showed a 41% increase. The remaining side channel showed no change in wetted width. Despite the dewatered cross section in the Eagle Nest side channel, the lower discharge did not appear to limit side channel rearing habitat availability. The proportion of wetted width to bankfull width was > 60% in most side channels during the lower discharge. Historic (1980-1999) mean daily discharges between July 1 and September 30 were lower than 25 m³/s 19% of the time, and higher than 37 m³/s 22% of the time, thus the two discharges sampled were near the lower and upper limits of summer discharge (Figure 10).

Table 4. Bankfull width, wetted width proportion of bankfull width (%), and change in wetted width percentage of selected side channels of the Madison River, Montana, at two discharges recorded at Hebgen Dam during 1999. Bankfull width was estimated for the Kirby side channel.

Side channel	Study reach	Bankfull width (m)	Wetted width to bankfull width (%) during discharges of:		Change in wetted width (%)
			25 m ³ /s	37 m ³ /s	
S. Slide	Raynolds Pass	9.7	66	63	-3
N. Slide	Raynolds Pass	13.6	60	76	16
Eagle Nest	Pine Butte	10.4	0	41	41
Kirby	Pine Butte	14.0	67	76	9
Lyons	Lyons	6.9	93	93	0

Whirling disease severity

Considerable spatial variability among and within study reaches was found in the severity of whirling disease infection (Figure 11). Peak severity values ranged from 0 to 3.55 among sites in 1998 and 0.15 to 3.90 in 1999, and varied greatly even over short distances (Appendix C). For example mean severity index values of two sentinel cages located in the Raynolds Pass study reach in side channels on opposite banks about 100 m apart were 0.11 and 3.48 during the same sampling period in 1998 (Appendix C).

Similarly, two cages in the Pine Butte study reach on the same bank and 2.4 km apart showed mean disease severity values of 0.91 and 3.85. The percentage infected with whirling disease also varied widely, ranging from 0 to 94% in 1998 and 0 to 98% in 1999. Despite wide spatial variation; however, in 1998, 36% (4 of 11) of the sites showed high infection with peak severity values greater than 2.5, a level considered to

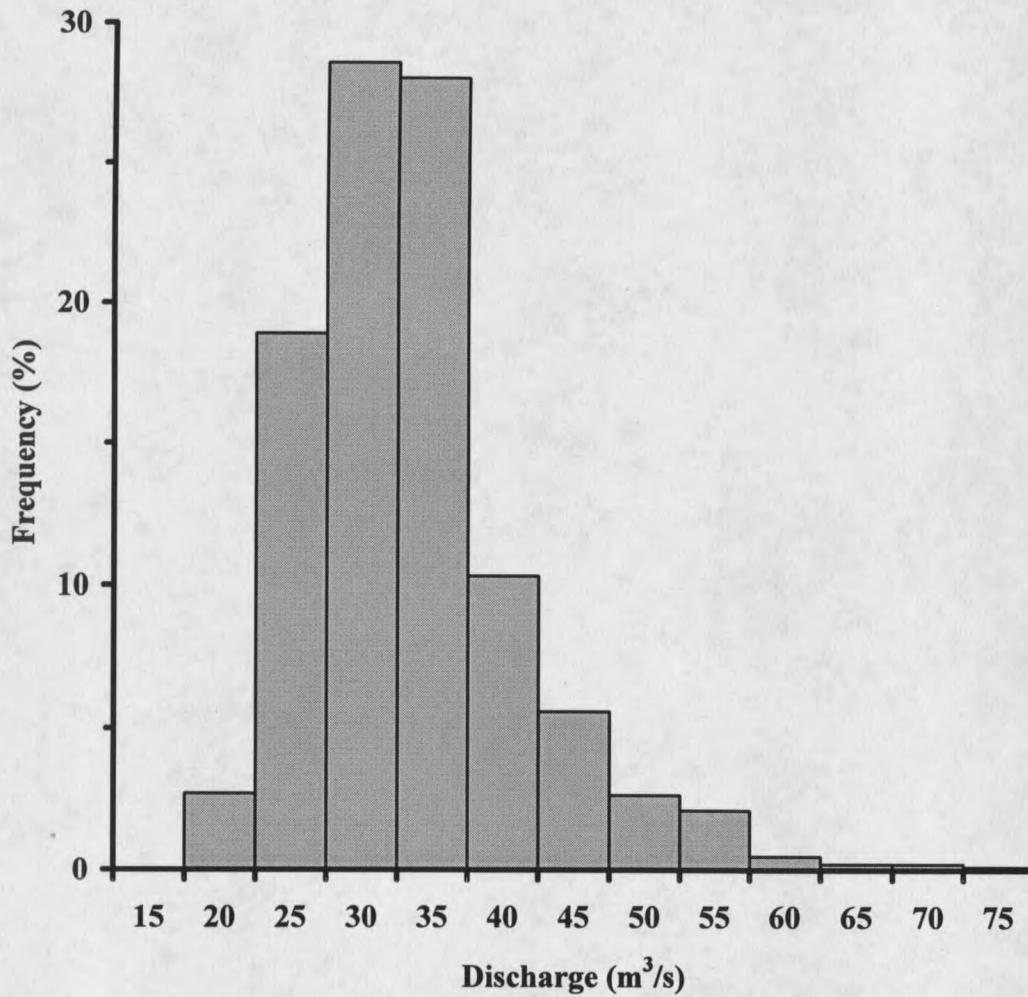


Figure 10. The relative frequency of historical (1980 to 1999) mean daily discharge at Hebgen Dam on the Madison River, Montana, between the days July 1 to September 30. The discharges examined in this study were 25 m³/s and 37 m³/s.

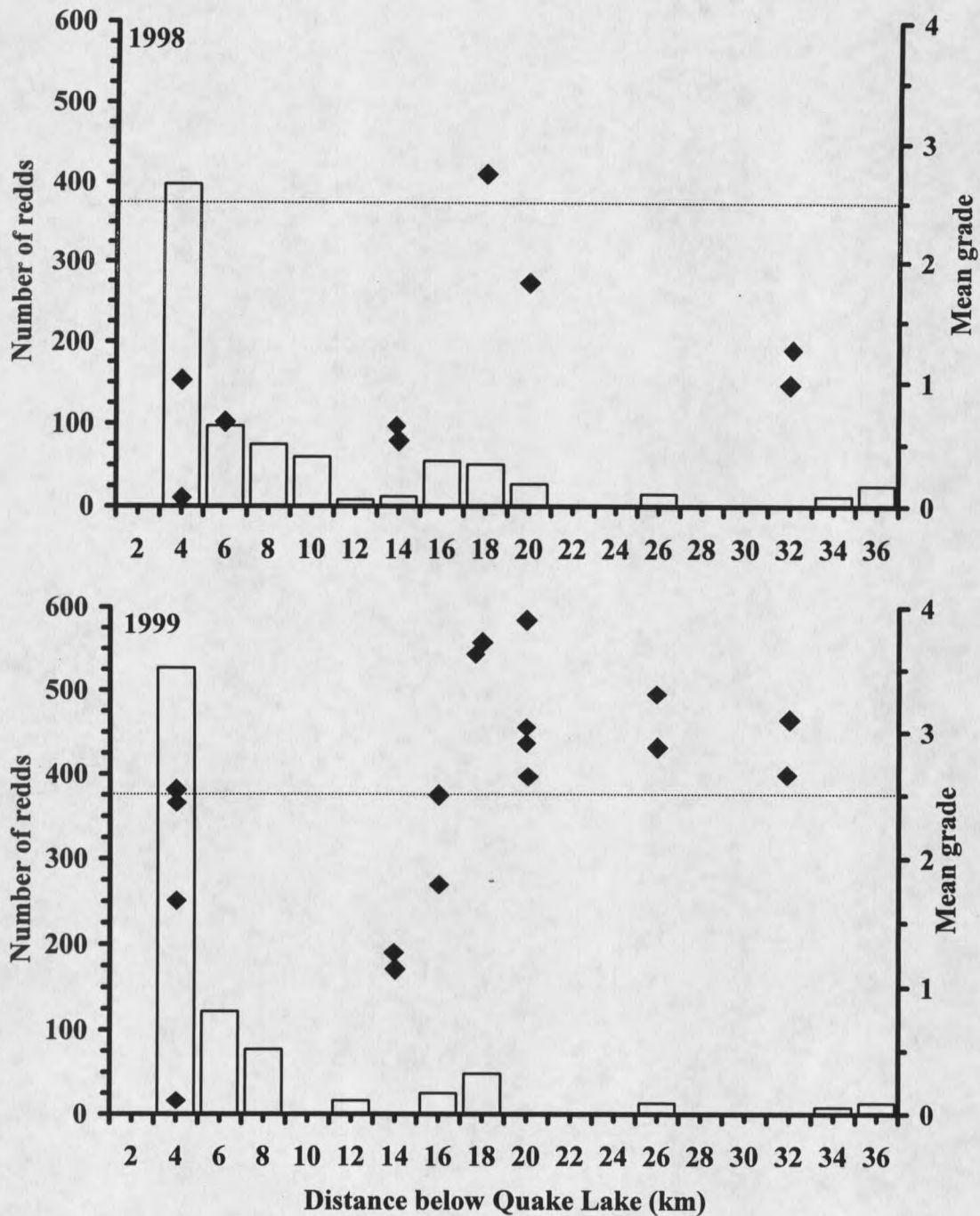


Figure 11. Mean whirling disease infection grade from sentinel cages (diamonds) and total redds observed in 2 km sections (bars) displayed as distance downstream from Quake Lake outlet in the Madison River, Montana. The whirling disease data are based on the July 8 to 18, 1998 and June 24 to July 5, 1999 sampling periods which best represent the timing of peak emergence. The dashed line indicates the critical mean whirling disease infection grade of 2.5 (Vincent 2000).

result in significant levels of mortality in wild salmonid populations (Vincent 2000). In 1999, 72% (13 of 18) of the sites exhibited peak severity values of 2.5 or greater. In general, sites which showed the highest disease severity were located in the lower study reaches, but upper study reaches also had localized sites of high infection (Figure 11). No data on infection risk was available from a 9.3 km section of river including the Three Dollar study reach. Whirling disease severity was very low in tributaries, averaging < 1 in Squaw Creek and West Fork Madison River. No infection was recorded in the section of river between Hebgen Dam and Quake Lake, where one radiotagged rainbow trout spawned.

Considerable temporal variation in whirling disease severity also was observed (Figure 7). In 1998 at the time-sequence site at Kirby Bridge, severity ranged between 0.19 and 3.55 from May 15 to October 18 with peak severity occurring during the May 25 to June 4 sampling period, about 5 weeks prior to peak emergence. Infection severity indices were > 2.5 for four consecutive 10 d sampling periods from May 25 to June 24, 1998. The lowest severity occurred during the September 16 to 26 sampling period (Figure 7). In 1999, the highest disease severity occurred during the June 24 to July 5 sampling period, which was coincident with the peak rainbow trout emergence period (Figure 7), but about 1 month later than the peak infection period in 1998.

Discussion

The purpose of this study was to determine how rainbow trout spawning and rearing timing and location related to the degree of exposure and hence potential population response to whirling disease infection. Spawning and rearing life histories

were the focus as they likely have the greatest influence on the infection risk of the vulnerable young fish.

Redd surveys and radio telemetry results indicated that rainbow trout migrated long distances (up to 55 km) to spawn primarily in a relatively small portion of the upper Madison River. The majority (81%, 17 of 21) of radiotagged rainbow trout migrated upstream and spawned in side channels of the mainstem river. Similarly, nearly 75% of observed redds were found in the upper 11 km of this 46 km section of river. In contrast, only four (19%) radiotagged fish spawned in tributaries, migrating up to 65 km. After spawning, fish from both groups returned to near their original prespawning location. Similar post spawning site fidelity has been observed for bull trout in the Blackfoot River, Montana (Swanberg 1996) and for cutthroat trout in the South Fork of the Snake River, Idaho (Henderson 1999).

Salmonids inhabiting large rivers typically exhibit a fluvial-adfluvial life history, migrating to small tributaries to spawn (Northcote 1997). In contrast, I found the predominant strategy of fluvial-adfluvial Madison River rainbow trout was mainstem spawning. Mainstem and tributary spawning cutthroat trout also were found within the North Ram River, Alberta (Brown and Mackay 1995). In that study, 56% of the radiotagged trout spawned in the mainstem, and the rest spawned in tributaries. Similarly, 69% (33 of 48) radiotagged rainbow trout, cutthroat trout, and rainbow x cutthroat hybrid trout spawned in the mainstem of the South Fork Snake River (Henderson 1999).

Within mainstem rivers, side channels are commonly used for spawning. In this study, nearly all (estimated > 95%) mainstem spawning occurred in side channels.

Similarly, 85% (28 of 33) mainstem spawning fish used side channels in the South Fork Snake River (Henderson 1999). Eiler et al. (1992) reported 55% of mainstem sockeye salmon *O. nerka* spawning occurred in side channels in the Taku River, Alaska.

Rainbow trout in the San Juan River, New Mexico were reported to use side channel habitat in response to increased spring flow (Gido et al. 2000). Refuge from increased velocity and availability of spawning habitat were postulated as explanations for use of side channels. Side channels in the Madison River received little scour or fill suggesting suitable conditions for spawning. The mean scour measure for both years combined was < 5 cm, while DeVries (1997) reported rainbow trout egg pocket depths of 15 and 20 cm. Because of lesser discharge compared to the main channel, side channels are typically areas of deposit for spawning sized substrates, which are often limited downstream from a reservoir (Allan 1995).

In contrast to the concentration of spawning locations, the duration of the spawning period for mainstem spawners was protracted. Both redd surveys and radiotelemetry data indicated that mainstem spawning occurred over an 8 week period from April to May. The apparent peak in 1998 redds (Figure 3) is probably misleading and more likely reflects the late start to redd surveys rather than actual spawning timing. The large number of redds found during the initial survey likely represents redds formed from late March through mid April as suggested by the 1999 data. The duration of mainstem spawning was longer than most reported for spring spawning salmonids. In general, duration of the spawning season extends from 1 to 5 weeks in unregulated rivers (Brown and Mackay 1995; Magee et al. 1996; Knapp et al. 1998). Regulated rivers such

as the Madison River may allow more protracted period of spawning because of greater flow and water temperature stability compared to unregulated tributaries.

Duration and timing of spawning also differed between mainstem and tributary spawners. Tributary spawning occurred over a two week period in late May, nearly a month later than the mainstem spawning. It should be noted, however, that the sample size of tributary spawning fish in this study was very small ($N = 4$), which limited the ability to fully assess the extent of the spawning period. Similar differences were found with cutthroat trout in the South Fork Snake River, Idaho as tributary spawners spawned an average of 18 d later than mainstem spawning fish (Henderson 1999). In contrast, Brown and Mackay (1995) noted no difference between timing of mainstem and tributary spawning cutthroat trout in the North Ram River, Alberta.

Despite the protracted period of the mainstem spawning, most age-0 rainbow trout in the mainstem emerged during a 3 weeks in late June and early July. The average number of thermal units from redd formation to emergence was 589 for redds from both years. The number of thermal units was about 25% lower than that reported for hatchery steelhead trout (791; Chandler and Bjornn 1988). Knight (1963) reported a duration of 23 d to hatching and 39 d to "voracious free feeding" at a constant temperature of 12.2 °C (476 thermal units) for rainbow trout in standard hatchery troughs. Differences in the thermal units of incubation and rate of development likely reflect differences in temperatures during incubation (Embody 1934; Kwain 1975; Piper et al. 1982). It is well documented that stream temperatures often differ from redd substrate temperature (Acornley 1999). In this study, the difference in temperature was highly variable among individual redds (Appendix B). This temperature difference combined with wide

variation in spawning timing may have interacted to result in the observed convergence of emergence timing. Temperature of individual redds should be monitored to provide an accurate measure of thermal units to emergence.

As a consequence of rainbow trout spawning location, age-0 fish were initially concentrated in the side channels of the upper study reaches. Age-0 trout abundance decreased over time in all study reaches. The decline in abundance could be due to mortality (Knight et al. 1999) or a shift into deeper, swifter water as fish grew (Chandler and Bjornn 1988; Baltz et al. 1991). Though age-0 trout are known to undergo long distance movements during their first summer after emergence (Rosenau 1991; Hayes 1995; Knight et al. 1999), I found no evidence of large scale downstream movement. Age-0 rainbow trout densities were positively correlated with redd densities in September suggesting a lack of distribution shifts among study reaches during the vulnerable period of age-0 rainbow trout. Similar correlation between age-0 trout and spawning areas have been reported for brown trout (Beard and Carline 1991; Mesick 1995), golden trout *O. m. aguabonita* (Knapp et al. 1998), cutthroat trout (Bozek and Rahel 1991; Magee et al. 1996), and steelhead (House and Boehne 1985). These studies suggest that trout may not disperse widely from natal areas and that proximity of spawning habitat appears to be a primary determinant influencing age-0 trout distributions.

The importance of side channels as rearing habitat for age-0 trout has been reported in previous studies (Berg 1981; House and Boehne 1985). Dewatering of side channels would be deleterious to age-0 fish because of the resulting loss of rearing habitat. I found that only one side channel monitored was completely dewatered at the lower flow level (25 m³/s). In comparison to historic (1980 to 1999) mean daily flows

during the summer rearing period (July 1 to September 30), mean daily flows less 25 m³/s were experienced only 19% of the time. This indicates side channel dewatering likely occurs relatively infrequently. The influence of changing flows had diverse effects on side channel wetted width, and further study is needed to more completely describe the effects of flow on side channel rearing habitat availability, especially during winter low flows.

Unlike spawning and rearing distribution, whirling disease infection risk was highly spatially variable throughout the mainstem. Areas with high whirling disease infection severity were interspersed with areas of low whirling disease infection severity among and within study reaches, thus providing high variation in infection risk. For example, two side channels directly across from one another differed greatly in whirling disease severity grade (0.11 and 3.48). Such high variation of whirling disease infection risk throughout the river was greater than other river systems where similar data are available. For example, in Little Prickly Pear Creek, Montana, all eight sites sampled within a 30 km section of stream consistently exceed the critical whirling disease severity grade (2.5) during peak severity periods (Vincent 2000). In addition, sampling of upper Madison River tributaries, though limited, indicated that tributaries have low incidence of infection. Such variability of infection risk in the Madison River may result from variability in spore load (Zendt and Bergersen 2000) or availability of suitable habitat for *T. tubifex*, the alternate host of the parasite (Hedrick et al. 1999). Such high variability in disease severity within river systems has not been well documented, but could greatly influence the degree of exposure to whirling disease in trout populations.

Considerable temporal variation in whirling disease infection risk was also observed. For example, the whirling disease severity grade dropped from 3.48 to 0.02 over a 6 week period in the South Slide Lower site in 1998 (Appendix C). Similar seasonal variation in the magnitude and duration of peak whirling disease severity within sites has also been found in other rivers (Vincent 2000). Considerable interannual variation in infection risk has also been found. In 1998, whirling disease severity peaked in early June and generally declined through July, whereas in 1999, whirling disease severity was higher and did not reach peak values until early July. Such interannual differences in infection risk may be related to flow or thermal regime differences between the two years or recruitment and turnover in the *T. tubifex* population (Zendt and Bergersen 2000). Water temperature regimes were similar between the two sampling years; however, differences in the flow regime were apparent. In 1999, the magnitude of peak flow was similar to that in 1998, but base flow was nearly 25% greater and peak discharge was earlier and more sustained (Figure 5). Zendt and Bergersen (2000) suggest flushing flows likely affect *T. tubifex* densities, hence the rate of increase from base to peak discharge may influence whirling disease severity indirectly. Vincent (2000) hypothesized that dilution of the waterborne infective stage of the parasite may be a possible mechanism for reduced whirling disease severity at higher flows.

High spatial and temporal variation in infection severity suggests that future whirling disease related investigations should consider seasonal changes in discharge, temperature, and *T. tubifex* population dynamics as well as the spatial scale most appropriate for a particular river system. In the Madison River, an ongoing companion study by R. Krueger and B. Kerans (Montana State University, Bozeman) is investigating

the spatial distribution of *T. tubifex* and potential spore loading in relation to infection risk. The spatial scale used in my study, although appropriate for determining the spawning and rearing distribution, may have been too broad for effective investigation of whirling disease infection risk given the high spatial variation in infection risk observed at even relatively small scales. Future investigations also need to incorporate time sequence studies similar to those used in this study to determine the magnitude and duration of peak whirling disease infection risk. Also, whirling disease severity should be monitored at times that are biologically significant. Most effort should be expended to determine infection risk at times when age-0 fish are vulnerable to the disease. For example, studies of whirling disease severity during March or October may not accurately represent conditions for fish whose vulnerable period occurs from June to August. Thus, the temporal and spatial scales for whirling disease investigation need to be appropriate for the river system and life history traits of the fish of concern.

Spawning location, as it relates to whirling disease infection risk, is important because it directly influences the initial location of rainbow trout fry during their vulnerable period. Consequently, the variability in life history strategies would likely have equally diverse implications on vulnerability to whirling disease within a river system. On the broadest scale, high levels of spawning and whirling disease severity were observed in the mainstem while low levels of each were observed in tributaries (especially in the West Fork Madison River). Several differences in whirling disease infection risk exist between mainstem and tributary spawned fish. Most tributary spawning occurred in late May, nearly a month later than mainstem spawning. This could have important ramifications depending on when age-0 fish from tributaries

emerge and subsequently enter the mainstem. Although little spawning data and no emergence and rearing data were collected for tributary spawned fish, it is likely that since spawning occurred later in tributaries, emergence in tributaries would also occur later than in the mainstem (Chandler and Bjornn 1988). Tributary spawned rainbow trout fry in the Madison River system should experience low exposure to whirling disease and may have higher survival rates for two reasons. First, the whirling disease severity in West Fork Madison River is very low (Vincent 2000), allowing fish to rear with minimal exposure to whirling disease. Second, since the onset of whirling disease within the Madison River, competition and predation have been reduced in the mainstem due to decreased numbers of juvenile and adult trout. Prior to the presence of whirling disease, tributary reared fish were likely selected against due to later emergence, resulting in competition with large numbers of larger mainstem cohorts (Hayes 1995) and increased predation by large numbers of mainstem adults. Analogous situations exist in spawning tributaries to New Zealand lakes where fry emigrate from inlet tributaries at differing periods in their lives (Rosenau 1991, Hayes 1995). Some fry migrate immediately after emergence from the tributaries to the lake, and others rear in the tributary stream until a minimum size is reached and then migrate to the lake. Fish migrating to the lake immediately suffer high mortality rates due to predation and from competition with other species in the lake that are more efficient plankton feeders. Similar selection may take place in the Madison River with the presence of whirling disease in the mainstem. For instance, fish migrating from the tributaries to the mainstem immediately after emergence would be exposed to whirling disease during their vulnerable period, whereas fish rearing in tributaries until their vulnerable period has passed would avoid exposure to the disease.

Spawning habitat in Madison River tributaries is thought to be limited, although it has not been quantitatively measured in sections of streams accessible to Madison River rainbow trout (P. Clancey, FWP Ennis, personal communication), and habitat enhancement, therefore, could enhance recruitment.

Within the mainstem, vulnerability to whirling disease is also variable. Spawning and rearing are spatially concentrated. If we assume fish home to spawn in natal areas (Banks 1969; Taylor 1991; Northcote 1997), then spawning concentrations reflect successful recruitment areas experienced by returning adults from 3 to 5 years prior to current spawning. Based on this, successful reproduction is limited to the side channels of the upper two study reaches and localized recruitment to the populations of the lower three study reaches may be limited due to the high spatial overlap between spawning areas and high infection risk areas (Figure 11).

I believe whirling disease led to the decline in the Madison River rainbow trout population by one of two ways. First, if the pre-whirling disease spawning distribution was similar to the present distribution, the high exposure risk to whirling disease further downstream would have strongly selected against those age-0 fish dispersing downstream after emergence. The location of the uppermost source of whirling disease would mark the downstream limit that vulnerable fish could safely disperse to, thus limiting the amount of low infection risk rearing habitat. In this scenario, recruitment to the entire study area would be limited by the amount of low infection risk rearing habitat available in the upper reach. The alternative explanation assumes the pre-whirling disease spawning distribution had similar spawning densities in side channel habitat throughout the study area and that rainbow trout fry reared close to areas in which they were

spawned. In this case, the presence of high whirling disease infection severity in the lower reaches would have caused poor survival and recruitment of rainbow trout juveniles spawned in this area, thereby resulting in lower than expected spawning and rearing densities, as observed in the Pine Butte study reach. Which of these two explanations is correct is unclear because pre-whirling disease spawning distribution is unknown.

Despite the large decline in rainbow trout populations in the Pine Butte and Lyons study reaches, the population has stabilized near 25% of its historic abundance (Vincent 1996). Several possible reasons for this exist. First, the spatial overlap of high infection risk areas over spawning and rearing areas was incomplete and some spawning occurred in low infection risk areas, such as in the Reynolds Pass study reach. Similarly, some fish spawned in the low infection risk tributaries. Finally, at least one fish radiotagged in each study reach migrated to and spawned in side channels of the upper study reach implying that at least some downstream dispersal from Reynolds Pass occurs. Thus, the combination of several sources of limited recruitment could be contributing to the present population.

Temporal variation in the timing of whirling disease infection severity and emergence is also likely to play an important role. In this study, there was high overlap in both the duration and peak of infection and fry emergence in 1999. In 1998, however, the peak infection period occurred prior to the peak in emergence. The difference in timing between peak disease severity and peak emergence may have contributed to an increase in the yearling cohort population estimate in 1999 (Clancey 2000; D. Vincent, FWP Bozeman, personal communication). Preliminary data shows the 1999 yearling

cohort abundance to be over 5 times greater than the mean post-whirling disease (1991 to 1998) yearling abundance.

These results suggest that the relation of life history traits of rainbow trout to spatial and temporal variation in whirling disease infection risk provides insight useful to managing whirling disease positive waters. Potential management considerations in systems with such variability in whirling disease infection risk could take advantage of areas or periods of low infection risk. Increasing spawning and rearing habitat quality in areas of low infection risk, or introduction of stocks that differ in timing of key life history events could boost production within those areas and compensate for severe population declines.

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APPENDICES

APPENDIX A

PHYSICAL CHARACTERISTICS, TAGGING INFORMATION, AND DATES OF
SPAWNING RELATED MOVEMENTS OF ALL RADIOTAGGED RAINBOW
TROUT

Physical characteristics, tagging information, and dates of spawning related movements of all radiotagged rainbow trout in the Madison River, Montana during 1998 and 1999. Abbreviations for spawning status are as follows: mainstem (MS), tributary (TR), pre-spawning mortality (PSM), transmitter malfunction (TM), and unknown (U). Spawning locations are river km downstream from Quake Lake outlet, and a negative value indicates upstream from Quake Lake outlet. Spawning locations in tributaries are abbreviated as follows: Freezeout Creek (FC), Gazelle Creek (GC), Squaw Creek (SC), and West Fork Madison River (WF) with distance (km) upstream from the mouth of the tributary in parentheses.

Total length (mm)	Weight (g)	Tagging Date	Number of relocations	Tagging location (km)	Spawning status	Spawning location (km)	Initial migration date	Spawn date	Return date
399	680	9/27/1998	41	9.7	MS	-9.5	5/4	5/23	6/22
394	771	9/27/1998	42	2.1	MS	1.6	4/8	4/11	4/15
394	635	9/27/1998	43	5.3	MS	1.6	5/18	6/1	6/10
460	916	3/27/1999	16	2.4	MS	2.4	-	3/30	MORT
414	807	10/22/1998	44	20.4	MS	2.6	3/2	5/27	6/27
450	880	10/22/1998	27	24.0	MS	2.9	3/2	4/20	MORT
368	508	10/24/1998	34	49.9	MS	4.2	3/26	5/10	6/7
368	544	9/27/1998	43	5.3	MS	5.3	-	-	-
343	408	9/27/1998	37	8.2	MS	7.9	-	-	-
389	680	9/27/1998	35	9.7	MS	9.0	-	-	-
445	953	10/24/1998	28	49.9	MS	11.7	2/26	4/19	N/A
427	780	9/24/1998	31	68.1	MS	13.0	3/23	5/28	6/20
358	608	10/22/1998	45	20.4	MS	20.4	-	-	-
366	454	10/22/1998	49	29.0	MS	29.1	-	-	-
348	454	10/24/1998	30	49.9	MS	45.2	2/24	4/4	5/9
457	998	10/1/1998	14	79.3	MS	67.3	2/11	3/12	4/22
363	558	9/24/1998	25	66.0	MS	72.6	4/19	5/27	6/22
356	522	9/27/1998	6	8.2	PSM	-	-	-	-
389	594	3/27/1999	2	17.4	PSM	-	-	-	-
406	726	9/27/1998	9	14.5	PSM	-	-	-	-
366	417	10/24/1998	10	48.4	PSM	-	-	-	-
429	794	3/21/1999	15	13.7	PSM	-	-	-	-
396	644	10/22/1998	23	24.0	PSM	-	4/19	-	-
371	490	10/22/1998	6	48.4	PSM	-	-	-	-
409	662	10/1/1998	10	80.9	PSM	-	-	-	-
432	762	10/1/1998	15	79.3	PSM	-	-	-	-
419	699	10/22/1998	8	20.4	TM	-	-	-	-
399	594	3/27/1999	28	17.4	TR	WF (9.1)	5/18	5/29	MORT
432	776	9/27/1998	44	13.0	TR	SC (4.2)	5/18	5/31	6/14
384	617	9/24/1998	21	68.1	TR	FC (3.4)	4/30	5/30	6/20
406	798	9/24/1998	20	68.1	TR	GC (0.5)	5/1	5/21	6/14
384	653	9/24/1998	17	66.0	U	-	4/10	-	7/1

APPENDIX B

THERMAL UNITS FROM REDD FORMATION TO EMERGENCE

Thermal units (TU) from redd formation (Formed) to emergence (Emerged), temperature differences between the water column (T_w) and redd substrate (T_s), and adjusted thermal units for 31 rainbow trout redds capped in the Madison River, Montana, during the 1999 spawning season.

Formed	Emerged	Days	TU ($^{\circ}\text{C d}$)	$T_w - T_s$ ($^{\circ}\text{C}$)	TU diff ($^{\circ}\text{C d}$)	Adjusted TU ($^{\circ}\text{C d}$)
3/27	7/3	98	593	1.8	172	421
3/30	6/22	84	476	0.0	0	476
3/30	7/2	94	590	-0.1	-5	596
3/30	7/5	97	625	0.1	10	616
3/30	7/11	103	704	0.4	45	659
4/4	6/29	86	541	0.1	4	537
4/4	7/11	98	690	0.0	0	690
4/7	6/3	57	267	-0.3	-19	286
4/7	7/3	87	580	0.1	13	567
4/7	7/3	87	580	1.2	105	475
4/7	8/3	118	946	1.3	150	796
4/9	7/3	85	608	1.3	114	493
4/9	7/3	85	608	0.6	51	557
4/9	7/6	88	644	1.4	126	518
4/9	7/11	93	675	-0.2	-22	698
4/14	7/5	82	581	-0.1	-7	588
4/14	7/5	82	569	0.0	0	569
4/14	7/11	88	644	0.9	80	563
4/14	7/11	88	660	4.1	361	299
4/17	6/29	73	543	1.2	85	458
4/17	7/6	80	614	-0.2	-16	630
4/21	7/3	73	533	0.1	10	523
4/21	7/11	81	620	-1.9	-152	771
4/24	7/16	83	723	1.1	94	630
4/28	7/6	69	542	1.2	81	461
4/28	7/9	72	581	0.0	0	581
5/3	7/20	78	738	5.5	429	309
5/15	7/27	73	714	1.1	80	634
5/22	7/27	66	727	0.7	45	682
5/23	7/6	44	413	0.3	15	398
5/30	8/3	65	705	1.1	69	636
Mean	7/8	82	614	0.7	62	552
SD	12	14	115	1.3	109	127
Minimum	6/3	44	267	-1.9	-152	286
Maximum	8/3	118	946	5.5	429	796

APPENDIX C

WHIRLING DISEASE SEVERITY GRADE AND PERCENT INFECTED FOR
SENTINEL CAGES DURING 1998 AND 1999. DATA SUMMARIZED FROM
VINCENT (2000).

Whirling disease severity grade and percent infected (in parentheses) in 1998 and 1999 in the Upper Madison River.
 Location is distance downstream from Quake Lake outlet, a negative value indicates location upstream from Quake Lake outlet.
 Dates are the initial date of the 10-d exposure period. Data are from Vincent 2000.

Mainstem	Location (km)	Bank	5/1	5/15	5/26	6/4	6/14	1998 6/24	7/8	7/15	8/3	9/16	9/28	10/8
Hebgen-Quake	-9.49	R			0.00 (0)				0.00 (0)				0.00 (0)	
North Slide Upper	2.41	R												
North Slide Lower	2.57	R			0.11 (11)				1.02 (64)				0.17 (13)	
High S.Slide	2.57	L												
South Slide Upper	2.65	L												
South Slide Lower	2.90	L			3.48 (90)				0.02 (2)				0.02 (2)	
Raynolds Pass Bridge	5.31	R			1.20 (56)				0.68 (42)				0.11 (11)	
Pine Butte Upper	14.64	R			0.59 (22)	1.30 (50)	1.00 (44)		0.53 (36)				0.10 (6)	
Pine Butte Lower	14.80	R			1.18 (47)	1.40 (62)	0.64 (27)		0.59 (36)				0.17 (10)	
Eagle Nest Upper	14.98	L												
Eagle Nest Lower	15.04	L												
Grizzly Upper	17.06	R												
Grizzly Lower	17.22	R												
Kirby Upper	17.86	L												
Kirby Lower	17.97	L	1.69	2.18 (77)	3.55 (93)	3.12 (86)	3.06 (88)	2 (84)	2.74 (84)	1.08 (60)		0.19 (15)	0.42 (32)	1.38 (56)
Lyons Bridge	19.68	L			1.58 (72)				1.82 (74)				0.64 (33)	
Lyons side channel Upper	20.35	L												
Lyons side channel Lower	20.43	L												
Sun West Upper	25.62	R												
Sun West Lower	25.71	R												
Palisades Upper	32.10	R			3.07 (93)	3.16 (94)	2.20 (77)		0.98 (57)				0.04 (4)	
Palisades Lower	32.18	R			2.88 (88)	3.43	2.76		1.27 (57)				0.20 (10)	
McAtee Bridge	46.18	L			1.68 (70)				0.96 (49)				0.10 (4)	
Varney Bridge	65.49	R			2.76 (93)				1.78 (76)				0.10 (7)	
Tributaries														
Squaw Creek											0.00 (0)			
Upper West Fork							0.00 (0)		0.24 (10)			0.12 (8)		
Lower West Fork							0.00 (0)		0.98 (54)			0.00 (0)		

1999

[illegible]

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10/1/79