Spawning Characteristics of Rainbow Trout and Brown Trout in a Tailwater Fishery Infected with Whirling Disease

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Abstract

We evaluated trout spawning characteristics in the mainstem Missouri River and its tributaries to determine if spawning behavior, spawning locations and changes in the amount of river versus stream spawning could explain the stable trout population after a longstanding infection of whirling disease. Radio telemetry showed trout spawning locations were highly variable form year to year. Rainbow trout spawners were not localized to the half of the study area in which they were tagged (p=0.009), but brown trout showed some disposition to localized spawning in the lower half of the study area (p=0.13). Home site was not a determining factor in where rainbow trout (p=0.39) or brown trout (p=0.28) spawned. Rainbow trout traveled an average of 68.5 km to reach spawning sites and brown trout traveled an average of 26.2 km. Rainbow trout returned to within 6.7 km of previous spawning sites and brown trout returned to within 11.7 km. The mean annual number of redds for rainbow trout was 4,071 in 118 km of stream and for brown trout was 2,016 in 104 km of stream. We estimated 6.6 million rainbow trout and 4.3 million brown trout eggs are spawned each year. After 13 years of monitoring M. cerebralis infection, about 47% of the spawning habitat has no infection or has levels that are survivable to rainbow trout. Comparing our data with past studies showed changes in the number of redds in tributaries and the mainstem Missouri River. The annual variability in trout redds, differences in spawning locations from year to year, and variation in the spatial *M. cerebralis* infection tend to support the theory that a diverse life history strategy is important in maintaining a strong rainbow trout population.

We believe the affect of whirling disease has replaced natural population control factors that historically regulated the trout populations and has resulted in no net loss to the adult trout populations.

Introduction

The Missouri River -Holter Dam tailwater fishery is one of the top trout fisheries in Montana. From 1995 through 2009 the average angler-days spent on this fishery was 97,430 (~75,000-123,000) per year and this section of river consistently ranks in the top four most heavily fished out of 1,200 fisheries the state monitors for angler use statistics (Montana FWP unpublished data). The trout assemblage is roughly 83% rainbow trout (*Oncorhynchus mykiss*) and 17% brown trout (*Salmo trutta*). Stocking brown trout in this area was discontinued in1952 and rainbow trout stocking was discontinued in 1973 when Montana instituted a wild fish management policy in rivers and streams statewide. Since then this trout fishery has sustained by wild reproduction. Since 1980 Montana Fish, Wildlife & Parks conducts yearly mark and recapture population estimates of trout > 25 cm in two sections of this river using boat mounted electrofishing. The median estimates in the 8.9 km-long Craig section are 1,793 (1,096-3,185) rainbow trout and 306 (91-827) brown trout per km (Grisak et al. 2010). In the 6.6 km-long Pelican Point section the median estimates are 885 (389-2,360) rainbow trout and 193 (84-427) brown trout per km (Grisak et al. 2010).

In 1995, *Myxobolus cerebralis*, the parasite that causes whirling disease in salmonids, was discovered in Little Prickly Pear Creek, which is one of the most productive trout spawning tributaries to the Missouri River below Holter Dam. Within three years the clinical signs of whirling disease (blacktail and whirling behavior) were observed in wild age 0 rainbow trout in Little Prickly Pear Creek, and the disease progressed by spreading into the Missouri River and other tributaries (Grisak 1999, Leathe 2001). This development raised great concern among fishery managers because from 1991-94 whirling disease had caused a 90% reduction of rainbow trout in Montana's world famous Madison River (Vincent 1996). Fearing similar population declines in the Missouri River, fishery managers instituted investigations that focused on the relative contribution of spawning tributaries infected with *M. cerebralis* to the overall trout production (Leathe 2001, Munro 2004). This strategy was chosen in part due to the assumption that the mainstem Missouri River contributed little to its overall trout population. In addition, monitoring the infection in the Missouri River and its tributaries began in 1997 to evaluate the progression of the disease and to develop population risk assessments. Montana Fish, Wildlife & Parks adopted a standardized monitoring protocol that involves placing caged fish (60 age 0 rainbow trout) at select sites for 10d during the peak infection periods. A thermograph attached to the cage records the temperature during the exposure period. After exposure, the fish are moved to laboratory facility where the parasite is allowed to incubate for 90 d. Histological analyses of cranial tissue are used rank the severity of infection of the sample (Baldwin et al. 2000). This monitoring has continued for 13 years.

Historically, fishery managers assumed that trout in the Missouri River had highly localized life histories where fish in the upper half of the study area spawned in Little Prickly Pear Creek, and fish in the lower half spawned in the Dearborn River. The high *M. cerebralis* infection in both of these spawning tributaries helped fuel speculation that the adult population would ultimately become recruitment limited resulting in population declines.

Despite 15 years of *M. cerebralis* infection in the most productive tributaries there has been no negative impact to the adult trout population in the Missouri River. Another perplexing question surrounding the influence of the disease in this area is how each year such large numbers of rainbow trout return to spawn in tributaries with high infection levels when one would expect the number of returning spawners to diminish. In an attempt to explain these questions, we sought to (1) describe trout spawning migrations and spawning locations to determine if previous theories of localized spawning behavior had any basis in reality, (2) to determine the relative proportion of spawning in the mainstem Missouri River versus the tributaries, (3) to describe spawning habits (homing, straying) over multiple years, (4) to describe the scale at which repeat spawners returned to previous spawning sites as a measure of spawning site fidelity, and (5) to describe the total amount of spawning occurring each year. We also calculated the fecundity of trout as a measure of the total number produced each year.

Study Area

The study area is located in central Montana and consists of a 41.6-km reach of the Missouri River spanning from Holter Dam downstream to the Pelican Point Fishing Access Site (Figure 1). At this point in its basin, the Missouri River drains 47, 187 km^2 and the river gradient is 0.88m/km. The upper 37 km of river flows in a stable channel surrounded by mountains. It has been highly channelized from past highway, railroad and housing development activities. It is generally considered gravel recruitment limited due to buffered flows from three hydroelectric dams (Canyon Ferry, Hauser, Holter) on the mainstem, immediately upstream. At river-kilometer (rkm) 38, the river exits the Big Belt Mountains and becomes wider and shallower as it enters prairie. There are numerous islands and side channels throughout the study area. The mean annual discharge measured below Holter Dam from 1946-2010 was 151 m^3/s (range 85-241) (USGS unpublished data for station 06066500) and mean annual temperature is 9^oC. The principle tributaries are Little Prickly Pear Creek (which includes Lyons Creek and Wolf Creek), the Dearborn River, and Sheep Creek. Little Prickly Pear Creek originates near the continental divide and flows easterly from the Rocky Mountains for 57 km before entering the Missouri River 3.8 km downstream of Holter Dam. The Little Prickly Pear Creek basin drains 1,026 km^2. Mean annual discharge from 1963-2010 was 2.4 m^3/s (1.25-5.06) (USGS unpublished data for station 6071300) and the mean annual temperature is 7.7^oC. The Dearborn River originates on the east slope of the Rocky Mountain front near the continental divide and flows easterly for 107 km before entering the Missouri River 25.3 km downstream of Holter Dam. The upper 31 km of river is situated in the mountains; it flows across the prairie for 45 km, and then flows through the Big Belt Mountains for 31 km before meeting the Missouri River. This basin drains 1,418 km^2 and the mean annual discharge from 1946-2010 was 5.5 m^3/s (1.65-10.28) (USGS unpublished data for station 6073500). The mean annual temperature is generally near 7.7°C. The North and South forks of Sheep Creek originate in the Big Belt Mountains and each flows for approximately 10 km before forming Sheep Creek. Sheep Creek flows westerly for 3.3 km before entering the Missouri River 37.8 km downstream of Holter Dam. The Sheep Creek basin drains 96 km^2.

Methods

Radio Telemetry

We used radio telemetry to 1) monitor and characterize trout spawning migrations over multiple years, 2) to identify spawning locations including similarities (homing) and changes in locations (straying) between years, 3) to evaluate spawning site fidelity between years. We divided the Missouri River portion of the study area into five 8.3-km sections and dedicated an equal proportion of radios for each section. By proportioning the number of radios throughout the Missouri River we were able to test the theory that fish from the upper half of the study area were prone to spawning in the upper half and similarly with fish from the lower half. Also, this design provided a finer scale by which to compare spawning site fidelity in repeat spawners. Fish were captured from each section using fixed boom boat electrofishing (smooth DC, 300 V, 4 A) then held in a live well for several minutes before the surgery. Fish were randomly selected from the capture lots between 40 and 60 cm long to ensure they were sexually mature, young enough to spawn in the next two seasons, and large enough to carry the radio transmitter without negatively affecting their behavior (Brown et al. 1999). We surgically implanted radio transmitters (Lotek model MCFT-3A, 148 MHz) in the abdomen of six trout from each species in each section in a manner similar to the external antennae procedure described by Cooke and Bunt (2001). Transmitters were implanted in each species approximately six months before their respective spawning seasons (April-May for rainbow, October-November for brown) to allow the fish to acclimate to the transmitter implant. We implanted transmitters in 22 female and 8 male rainbow trout. Mean length was 46.7 (42.4-51.1) cm and mean weight was 1,012 (717-1,374) grams. Mean surgery time was 3:09 (2:25-4:34). Mean body weight loading of the transmitters in rainbow trout was 1.65% (1.05-2.23). We implanted transmitters in 9 male and 21 female brown trout. Mean length was 48.5 (43.4-57.6) cm and mean weight was 1,157 (807-1,597) grams. Mean surgery time for brown trout was 3:21 (2:28-4:46). Mean body weight loading of the transmitters in brown trout was 1.48% (0.76-1.98).

We used a truck, jet boat, airplane and stationary receivers to locate radioed fish in the study area. In the truck, boat and airplane we used a Lotek SRX 400 W5XG frequency/code scanning receiver. The airplane was a Piper PA-18 Supercub fitted with a four element Yagi antenna on the wing strut. We fitted the truck with a four element Yagi antenna that could be set at 90^{o} positions to receive signals from the front, back, left and right side of the truck. Approximately 70% of the study area was accessible by road and provided a reasonable opportunity for tracking fish by truck. We stationed Lotek SRX 400 W7AS code logging receivers at the mouth of Sheep Creek, Dearborn River and Little Prickly Pear Creek to monitor radioed fish moving into each tributary or moving in the Missouri River past each tributary mouth (Figure 1). Another stationary receiver was located at the town of Craig to monitor radioed fish movements in a long span of river between tributaries. The W7AS software monitors up to 200 codes for each radio frequency, which optimizes the detection of many radios in large study areas such as ours. The stationary receivers were powered by two 89 amp-hour lead acid batteries wired in parallel. The batteries were charged by a 30 W solar panel. A Morning Star Sun Saver 10L solar controller was used to automatically switch the power source from solar to battery during times of low sun light, during nighttime hours, or after the batteries were recharged. Each stationary receiver had two four-element 148-151 MHz Yagi antennae. The receiver, batteries, antennae switch box and solar controller were housed in an insulated steel box.

Surveillance was increased during the respective spawning periods of both trout species in order to accurately determine spawning sites. A spawning site was determined by documenting a fish's furthest movement during the spawning season and assuming it spawned in that area (Grisak 1999, Burrell et al. 2000, Hendersen et al. 2000). Brown trout were monitored from 2007-09 and rainbow trout were monitored from 2008-10.

Throughout the study three of the radioed fish were captured and released by anglers. Radios from five brown trout were recovered from osprey (*Pandion haliaetus*) or bald eagle (*Helietus leucocephalus*) nesting sites and re-implanted in new fish. Radios from seven rainbow trout were tracked to osprey, bald eagle and great blue heron (*Ardea herodias*) nesting sites, and we were able to recover and re-implant four of them. All calculations and analyses were corrected for these losses and additions.

Redd Counts

To determine the total amount of spawning conducted each year and the relative proportion of spawning that occurred in the mainstem Missouri River versus the tributaries, we counted spawning redds. We conducted weekly redd counts in index section of the tributaries starting on March 15 for rainbow trout and October 15 for brown trout. At the point when few or no new redds were found in the index sections, we assumed that the peak of the spawn had occurred, and then we conducted an expanded basin-wide count within one week. We counted redds in the Missouri and Dearborn rivers using a Bell OH-58 helicopter flying ~75 meters above the water surface. We positioned two observers wearing polarizing eyeglasses in the back seat of the helicopter with the doors removed. At this flight altitude each observer was able to clearly view redds on their respective side of the helicopter. Two-way communication between the observers reduced the likelihood of double counting redds in the center of the rivers, and allowed for instructing the pilot to hover or circle high use areas for recounts to increase precision. We conducted flights in May and November 2007 to evaluate the spatial distribution of trout spawning areas in the Missouri River, and used the same protocol in 2008, 2009 and 2010 to count redds in the Missouri and Dearborn rivers. We used GPS to identify the sites for mapping purposes. We counted redds in the rivers within one week of the stream surveys.

Fecundity

We used fixed boom boat electrofishing (smooth DC, 300 V, 4 A) to collect 60 trout from both species from the Missouri River for fecundity analyses. Fish were euthanized with a lethal dose of denatured clove oil while in the field. Ovaries were removed in the laboratory within 12 h, stored in a plastic bag, inventoried and frozen until the eggs were counted. The fish were categorized by 25 mm length group and the mean number and range of eggs were reported for each group.

Fish spawning locations in the rivers and streams, landmarks and prominent habitat features, were related to a rkm reference system that has longstanding use in this reach of river where Holter Dam is located at rkm 0.0 and continues downstream 141.5 km to Black Eagle Dam. All locations were recorded to the nearest 0.1 km.

Data Analysis

The telemetry data were categorized by collection method. Data from the stationary receivers were summarized on 30 minute intervals using a software feature available on the Lotek W7AS receiver. This software condenses multiple records of each frequency and code to prevent storage problems with large amounts of repetitive data. For instance, if a radioed fish stayed within the reception range of a receiver, and the receiver recorded the code every 26 s, the receiver condensed the number of records and reported a single entry over a 30 min period rather than reporting an entry every 26 seconds. As such, our data include a large number of records that have been condensed by the radio receivers.

When evaluating the movements of each fish we used the 8.3 km-long section of the Missouri River where it was implanted with a radio transmitter as its home site for the first year and for each successive year we used rainbow trout location on 1 January and brown trout location on 1 July as the home site. We also used fish movements to evaluate site fidelity for both home site and spawning location. We expected all fish to spawn within their home site in the Missouri River, or in the closest tributary within their home site, based solely on the abundance of spawning habitat. However, each fish had an equal probability of using spawning habitat within their home site, or moving outside of their home site to spawn. To evaluate this dichotomy we used chi-square goodness-of-fit tests (α-0.05) to calculate whether the predicted and observed number of fish that spawned within their home site was significantly different. Such tests help to determine if a fish's location in the Missouri River, as determined by home site, is any indication of where they would spawn. We used the same test to evaluate whether the number of fish spawning in the upper half and lower half of the study area was significantly different.

We assigned group numbers to corresponding river sections where the fish were implanted with radios and assumed that the mean distance traveled to spawning sites would be similar among the groups. Movement data from each group were evaluated using single factor analysis of variance (ANOVA) (α-0.05) to determine whether magnitudes of movements were significantly different between the five sections.

Linear regression was used to determine if total fecundity was dependant on fish length or weight. The data were $\log_{10}$ transformed and plotted to test for skewing.

Results

Throughout the study, we made 1,577 relocations of radioed fish. Passive monitoring by stationary receivers accounted for 49% of the relocations followed by 33% by truck, 17% by airplane and 2% by boat.

Rainbow trout spawners were not localized to the half of the study area in which they were tagged (p=0.009) but brown trout showed some disposition to localized spawning in the lower half of the study area (p=0.13).

The Missouri River home site locations of rainbow trout were not a determining factor in where they spawned. Fish were just as likely to spawn outside of their home site as within (p=0.39). The distance rainbow trout migrated to spawning locations was significantly different between sections (p =0.03). The data showed fish from the uppermost section (1) of the Missouri River moved the greatest average distance (33.7 km) to spawning locations. On average males moved slightly greater distance (16.9 km) than females (15.8 km) to reach spawning sites. Fish from each section entered the

Dearborn River to spawn, and 36% (*n* = 4) of the Dearborn spawners came from section 1.

In 2008, 88% of the radioed rainbow trout displayed movements consistent with spawning. Of those, 74% spawned in the Missouri River and 33% (*n* = 7) spawned in the Dearborn River. Spawners migrated an average of 18.9 (range 4.0-56.6) km to reach spawning sites. In 2009, the number of radioed spawners decreased to 81%, and only 20% of those moved outside of their home site to spawn, but the mean distance fish traveled to spawning sites increased to 36.4 (range 11.7-77.4) km. Only one fish from each section traveled outside of their respective sections to spawn in 2009. Fish from sections 2 and 4 moved the greatest distance to spawning sites (77.3 km and 56.2 km, respectively). By 2010 only 50% of the radios were active and only 20% of the fish with active radios moved outside of their home site to spawn. The mean distance traveled to spawning sites was 40.6 km, but this number is skewed because one fish left the study area in late 2009 and resided near the town of Great Falls over the winter. In early 2010 it traveled 116.8 km from its home site to spawn in the Dearborn River for the second time in three years.

Overall, radio tagged rainbow trout spawned over a 79 d period from 3 March to 5 May. However, we observed some rainbow trout spawning in the Missouri River as early as 18 February. Over the three year period, 69% of rainbow trout spawned only in the Missouri River, 31% spawned in a tributary at least one time, 12 % spawned in tributaries multiple times, 73% spawned in consecutive years, 27% spawned only once and, 15%

of the spawners strayed to a new stream/river. After spawning 21% of the rainbow trout returned to within 1.6 km of their pre-spawn location, and the remaining fish moved to decidedly new locations after spawning. Only 8% of the spawners displayed repeat tributary spawning in successive. The mean distance between spawning locations for repeat tributary spawners was 6.7 kilometers. Missouri River mainstem spawners accounted for over half (58%) of the sample based on positive movements during the spawning seasons and the fact that these fish did not enter a tributary during the spawning season. Mean distance between spawning locations for repeat mainstem spawners was 6.1 kilometers. The average total distance rainbow trout traveled over the three year period was 68.5 km (range 1.9-520.5). Only 11% traveled more than 160 km in any one calendar year. Radioed rainbow trout spawned in each of the five sections in the Missouri River and in the lower 52.8 km of Dearborn River. None of the radioed fish entered the Little Prickly Pear drainage (Little Prickly Pear Creek, Lyons Creek, Wolf Creek) or Sheep Creek during the study. Over half (52%) of rainbow trout traveled downstream to reach spawning locations (Figure 2).

As with rainbow trout, brown trout were just as likely to spawn within their home sites as they were to spawn in a different section (p=0.28). The distance that brown trout migrated to spawning sites was not significantly different between river sections (p=0.38). The data showed fish from section 4 traveled the greatest average distance (32.6 km) to reach spawning locations. Mean distance traveled to spawning sites for all brown trout was 11.0 (0.5-32.5) kilometers. Only 13% of the radio tagged brown trout entered a tributary to spawn.

In 2007, 81% of the radioed brown trout spawned and 50% of the spawners moved outside of their home site to spawn. The average distance fish traveled to spawning sites was 10.6 km for females and 8.5 km for males. In 2008, 63% of the radioed brown trout spawned and 40% traveled outside of their home site to spawn. Females traveled an average of 12.9 km and no males traveled outside of their home site to spawn. The greatest number of fish that traveled outside of their home site to spawn in 2008 came from section 4. The greatest distance traveled was 32.5 km by a female brown trout from section 4. In 2009 only one brown trout radio was active, which was a female that traveled 13.4 km outside of its home site to spawn.

Radio tagged brown trout spawned over a 20 d period between 19 October and 7 November. We observed brown trout on redds in the Missouri River as early as 7 October and in both Little Prickly Pear Creek and Wolf Creek as late as 4 December. The average total distance traveled for all brown trout over the three year period was 26.2 km and the furthest distance traveled by any one fish during this time period was 136.3 kilometers. Only 12% of the brown trout traveled more than 64 km in any one year. Over the three year period 6% of radioed brown trout spawned in a tributary, none of the radioed fish displayed repeat spawning in tributaries, 44% spawned in consecutive years, 31% spawned only once, and 8% strayed to a different river/stream. The average distance between spawning locations for repeat Missouri River spawners was 11.7 km. Overall, 17% of the brown trout returned to within 1.6 km of their pre-spawn location, and the remaining fish went to new locations after spawning. Missouri River mainstem spawners accounted for 94% of the sample based on positive movements during the spawning season and the fact that these fish did not enter a tributary during the spawning season. Radio tagged brown trout spawned in each of the 5 sections of the Missouri River and in Sheep Creek. Most of the brown trout (71%) traveled upstream to reach spawning locations (Figure 3). Ice and low water flows in November and December were the factors limiting brown trout to move further upstream in tributaries.

Redd Counts

In April 2007 we identified 21 sites in the Missouri River where rainbow trout spawned and the average distance between these sites was 1.89 (0.38-4.48) kilometers. Discharge of the Missouri River below Holter Dam was 105 m^3/s on the day of the flight. In November 2007 we identified 37 different sites where brown trout spawned and the average distance between brown trout spawning sites was 1.06 (0.27-2.32) kilometers. Discharge of the Missouri River during the survey was 91 m^3/s. These findings indicated there was ample spawning habitat in the Missouri River, and there were no apparent concentrations of redds, such as near tributary mouths or specific island complexes.

In 2008 and 2009 high flows (>142 m^3/s) or poor weather in late April and early May caused unfavorable conditions for counting rainbow trout redds in the mainstem Missouri River. However, in November 2008 flows (119 m^3/s) were suitable for an aerial survey and we counted 644 brown trout redds in the mainstem. We observed what we called “deep water” (> 2 m deep) brown trout redds at rkm 5.3, rkm 14.1 and rkm 14.4. In 2009, with similar flows (113 m^3/s) we counted 1,202 brown trout redds in the mainstem (Table 1). In the spring of 2010 the flow conditions (122 m^3/s) were ideal for counting rainbow trout redds in the mainstem and we counted 1,644 redds, which was 38% of the redds counted in 2010. We observed deep water rainbow trout redds at six locations; three of which were located near deep water brown trout redds. The greatest number of deep water rainbow trout redds was 47 which occurred at rkm 3.5, followed by 24 redds at rkm 4.9, 11 redds at rkm 14.2, 2 redds at rkm 16.9, 2 redds at rkm 18.4 and 6 redds at rkm 22.7. Rainbow trout spawning redds were observed in 122 km of river and stream habitat annually. The mean annual number of rainbow trout redds for the entire system was 4,071 (Table 2). On average Little Prickly Pear Creek had 44-47% of the total annual redds, the highest number of redds (n = 1,793), and the highest average density (92/km) of redds. The Dearborn River had the lowest average density at 21/km (Table 2).

The mean annual number of brown trout redds for the entire system was 2,016 (Table 1). Similar to rainbow trout, Little Prickly Pear Creek had the highest average number of brown trout redds at 1,025 which represented 51% of the total redds counted. Wolf Creek had the highest average density of redds at 63 per km and the Dearborn River had the lowest average number of redds per km at 5 (Table 1). Brown trout spawning occurred over a minimum of 105 km of stream annually. The Little Prickly Pear drainage comprised 29% of the available brown trout spawning habitat. Despite none of the radioed fish entering it, from 2007-2009 the Little Prickly Pear drainage (Little Prickly

Pear, Lyons and Wolf creeks) accounted for 36-65% of the brown trout redds. We consistently observed noticeably smaller sized brown trout on redds in Lyons Creek.

Fecundity

The mean number of eggs per fish was 1,627 (974-2,392) for rainbow trout and 2,145 (1,356-2,936) for brown trout (Table 3). Fish length or weight were not correlated with total fecundity for either species (R^2=0.16, R^2 =0.12 respectively, for rainbow trout, R^2 =0.49, R^2 =0.53 respectively, for brown trout). The data indicate that the longest rainbow trout fish had the most number of eggs, but there was not a predictable trend of diminishing egg numbers as length decreased (Table 3). For brown trout, the longest fish did not have the greatest number of eggs (Table 3).

The average number of rainbow trout eggs spawned each year was 6.6 (3.2-10.8) million based on average annual redds we counted and mean number of eggs per female. For brown trout, the average number of eggs spawned each year was 4.3 (2.2-8.0) million.

Discussion

Trout spawning in the mainstem Missouri River is much more prevalent than we expected or than had ever been measured. We predicted radio tagged fish would spawn within or very close to their home site section based on the availability of suitable habitat, but clearly the two were not related. Rainbow trout spawning was not localized to either half of the study area as previous theories suggested, and brown trout did show some affinity for localized spawning in the lower half of the study area. It is not understood why both species traveled such long distances to spawning sites given the amount of suitable habitat in their home sites and the amount of spawning habitat they traveled through to reach spawning destinations. Such behavior suggests a determination to reach a certain area for spawning, but our data showed fish used different spawning areas each year. For both species, tributary spawning accounted for more than half of the total spawning. This life history strategy is in contrast to rainbow trout in the Madison River system, in which spawning occurs almost exclusively in the mainstem and is highly concentrated in the upper reaches where the majority of emerging young are susceptible to high infections of *M. cerebralis* (Downing et al. 2001).

Although the telemetry data showed a high percentage of the brown trout spawned in the Missouri River, it accounted for less than half of the available brown trout spawning habitat and about half of the average annual redds counted. The average distance that brown trout migrated to spawning sites was less than rainbow trout, but substantially more than that reported by other researchers (2.1-7.4 km) (Burrell et al. 2000).

Straying to new spawning sites by both species further demonstrates a diverse life history for Missouri River fish. This valuable component of salmonid life history helps to colonize new habitats or avoid unfavorable habitats (Quinn 1995) and can range from 10-77% for hatchery origin fish (Grant 1997) and 0-9% in wild fish (Vernon 1957, Bakke 1995).

We defined homing as adult trout returning to the same spawning areas in successive years. The concept of homing in salmon relates to adult spawners returning to their natal streams to spawn a single time before dying (Bams 1976). Other studies have shown that wild sockeye salmon (*Oncorhynchus nerka*) are capable of exceptionally fine-scale homing by differentiating natal creek mouths separated by only 1.5 km (Quinn 1995, Quinn et al. 2006). Once in their natal stream, chinook salmon (*Oncorhynchus tshawytscha*) spawning site fidelity can range from 13 to 41 km (Dittman et al. 2010), which is relatively close considering spawning migrations reach several hundred kilometers. The low site fidelity in our study area, and the broad scale at which fish returned are two characteristics that allow them to avoid unfavorable habitat conditions. After spawning, the majority of fish reestablished themselves in home sites different than their pre-spawn locations. By contrast, the majority (76%) of radio tagged spawners in the Blackfoot River, Montana returned to their starting locations after they spawned (Pierce et al. 2009)

The low numbers ($\bar{x}$ =153) of brown trout redds we measured in the Dearborn River raised questions about the factors limiting brown trout production. In November the Dearborn River is at base flow (2.5 m^3/s). It is a wide shallow river that offers little cover to large brown trout that are dependent on deep water (> 90 cm), instream structures or overhanging cover for concealment (Shuler et al. 1994, Dieterman et al. 2006). Brown trout spawning coincides with mountain whitefish (*Prosopium williamsoni*) spawning and each year during aerial surveys we observed tens of thousands of mountain whitefish schooling in the deep water zones of the Dearborn River. We concluded that mountain whitefish displace brown trout from the only available cover in the Dearborn River (deep water), which helps explain why more brown trout do not use it for spawning. We considered the lack of groundwater inputs in the Dearborn River as a factor that limits brown trout spawning. Although this habitat feature is important for other fall spawning salmonids, it is not as important to brown trout. Other research has shown that brown trout are just as likely to spawn in areas without groundwater inputs as they are to spawn in areas with groundwater inputs (Hansen 1975, Witzel and MacCrimmon 1983, Essington et al. 1998).

Unlike some rivers, trout spawning in the Missouri River was not associated with any particular habitat feature such as side channels or edge of river (Henderson et al. 2000, Downing et al. 2001). We observed both species spawning on shallow riffles in mid channel, in side channels, along river banks and in deep water zones. Total fecundity of Missouri River rainbow trout and brown trout was highly variable compared to other fisheries (Hao and Chen 2009, Serezli et al. 2010). Pender and Kwak (2002) suggest many factors such as food, water flows and water quality [metals] add to variability in trout fecundity in a tailwater fishery. However, their study area was dependant on supplemental stocking to maintain desirable population levels. Our study area has not been stocked since 1973 and 1952, respectively (MFWP, unpublished data) and sustains relatively high populations of rainbow trout and brown trout from wild spawning fish.

Rainbow trout were able to survive three years with a radio transmitter implant and most showed positive movements during spawning periods each year. The fact that some fish spawned only once during the study raised questions about the possibility of alternate year spawning by a low percentage of trout in the Missouri River system.

A number of previous spawning evaluations and *M. cerebralis* monitoring programs in the study area provided a basis by which to compare our results. Past studies of rainbow trout spawning in the Dearborn River reported a high number (5,797) of redds in the lower 67 km (Leathe et al. 1988). The lower 32 km-long section of that survey had 2,652 redds and corresponds roughly to the 30.4 km-long section we evaluated in 2010 in which we counted 632 redds. Three radioed rainbow trout traveled as far as 31.2, 43.2, and 52.8 km up the Dearborn River to spawn, so we are confident rainbow trout use much more of the Dearborn River than we measured during the 2010 redd count. During previous redd surveys by helicopter in the Missouri River, from Holter Dam to the town of Cascade (54.5 km), fishery managers estimated 600 rainbow trout redds which they characterized as a probable "overestimate" (Leathe et al. 1988). In 2010 we counted 1,644 rainbow trout redds in the 41.6 km reach between Holter Dam and Pelican Point Fishing Access Site. In 1998, there were 7,311 rainbow trout redds counted in 44.5 km of the Little Prickly Pear Creek drainage (Little Prickly Pear, Lyons and Wolf creeks) (Grisak 1999). The highest number of redds in the Little Prickly Pear Creek drainage was 4,261 which occurred in 2007. Nevertheless, the 2007 count was 37% less than in 1998. In 2010, the number of redds in Wolf Creek (1,451) was considered high, but it was still 27% less than in 1998 (1,981). Comparing our results with past studies (Leathe et al.

1988, Grisak 1999) suggests rainbow trout in the Missouri River-Holter Dam tailwater system have had some change in spawning to include more use of the mainstem Missouri River, which has lower levels of *M. cerebralis* than its two major tributaries, the Little Prickly Pear drainage and Dearborn River.

The *M. cerebralis* monitoring data has shown some interesting aspects in the spread of the infection. Little Prickly Pear Creek has the most severe infection in the study area and has maintained lethal infections for 11 of 13 years (Table 4). Lyons Creek remains the lone standout of all the sample sites and has shown no infection in 8 samples over an 11 year period. About 53% of the habitat used by rainbow trout for spawning has very high infections of *M. cerebralis*, 38% has survivable infections ranging from very low to none, and 9% has never been infected. The adult trout population in the Missouri River remains near the long term median during the past 13 years despite high infections (>2.75) of *M. cerebralis* in over half (53%) of the available spawning habitat (Table 4). The annual variability in trout redds, differences in spawning locations from year to year, and variation in the spatial *M. cerebralis* infection tend to support the theory that a diverse life history strategy helps to maintain this population.

Brown trout life history provides an advantage for survival to *M. cerebralis* infection because the young emerge from their spawning redd much earlier than rainbow trout and during the time when water temperature is lower and the infectious stage of the parasite (Triactinomyxon, TAM) is not prevalent. In addition, brown trout co-evolved with the parasite and are therefore more resistant than rainbow trout (Hedrick et al. 1999, Baldwin et al. 2000). Shortly after discovering *M. cerebralis* in our study area, whirling behavior and black tail were observed in wild age 0 rainbow trout in Little Prickly Pear Creek (Grisak 1999, Leathe 2001) indicating a severe infection from high (100-1000/fish) TAM loading (Hedrick et al. 1999). Other clinical signs of infection such as jaw deformity, dolphin head, spinal deformity (Vincent 2002) persist and are observed at low levels in adult rainbow trout sampled during annual population estimates in the Missouri River (authors personal observations).

There is some evidence that salmonids can survive an *M. cerebralis* infection with no impacts to the population (Sandell et al. 2001). Prior to discovering *M. cerebralis* in our study area, we believe this system consistently over-produced high numbers of young rainbow trout. Similar to other salmonids, juvenile trout in our study area likely displayed a population regulatory mechanism known as “self thinning” (Elliott, 1993, Pender and Kwak 2002, Keeley 2003) in which populations decline in abundance from intraspecific density dependent mortality and growth as mean body size increases. Some research has shown that such competition for food and space can result in behavioral changes in fish (McMahon and Tash 1988, Dunham et al. 2000). We submit that in the Missouri River-Holter Dam tailwater area, the factors historically responsible for self thinning have been replaced by the affects of *M. cerebralis,* resulting in no net loss to the adult population. The rainbow trout spawning characteristics we describe and changes in spawning are likely contributors to the stable populations in the Missouri River, even after 15 years of *M. cerebralis* infection.

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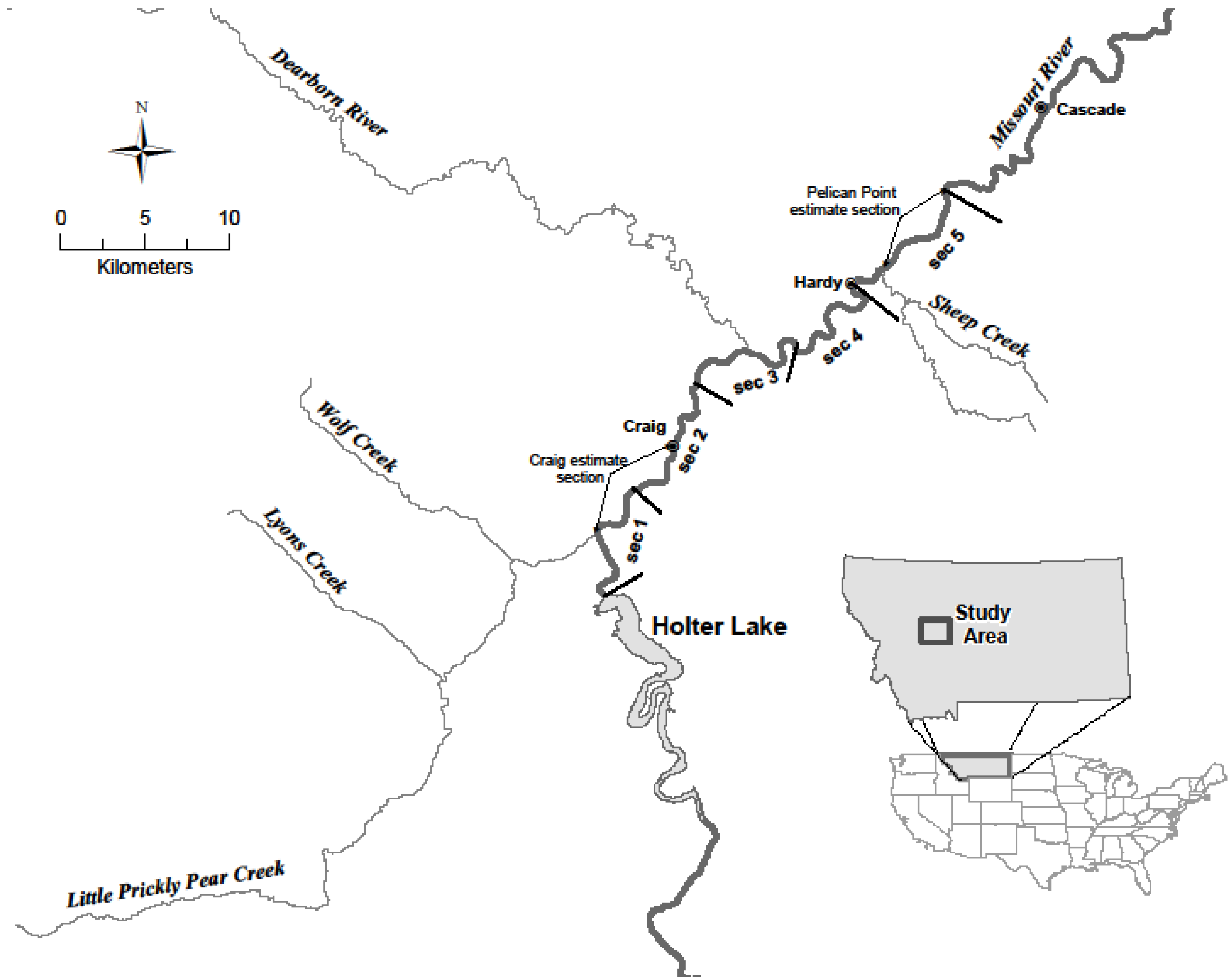
Dearborn River
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0 5 10
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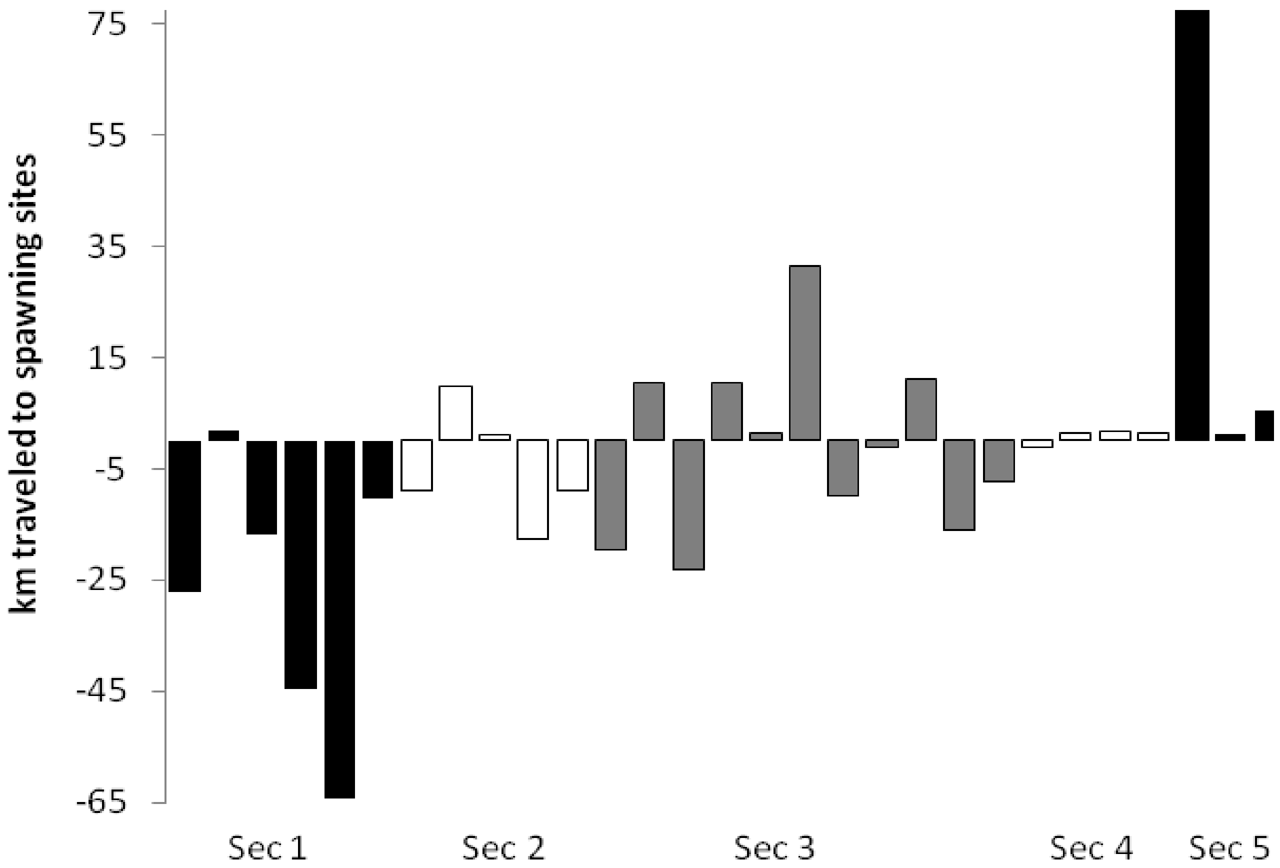
Hardy
Sheep Creek
sec 4
sec 3
Craig
sec 2
Craig estimate
section
Wolf Creek
sec 1
Lyons Creek
Holter Lake
Study
Area
Little Prickly Pear Creek

Figure 1. Missouri River-Holter Dam tailwater study area.



km traveled to spawning sites
75
55
35
15
-5
-25
-45
-65
Sec 1
Sec 2
Sec 3
Sec 4
Sec 5

Figure 2. Spawning distances and direction (+) upstream or (-) downstream traveled to spawning sites for rainbow trout by section, Missouri River, Montana.

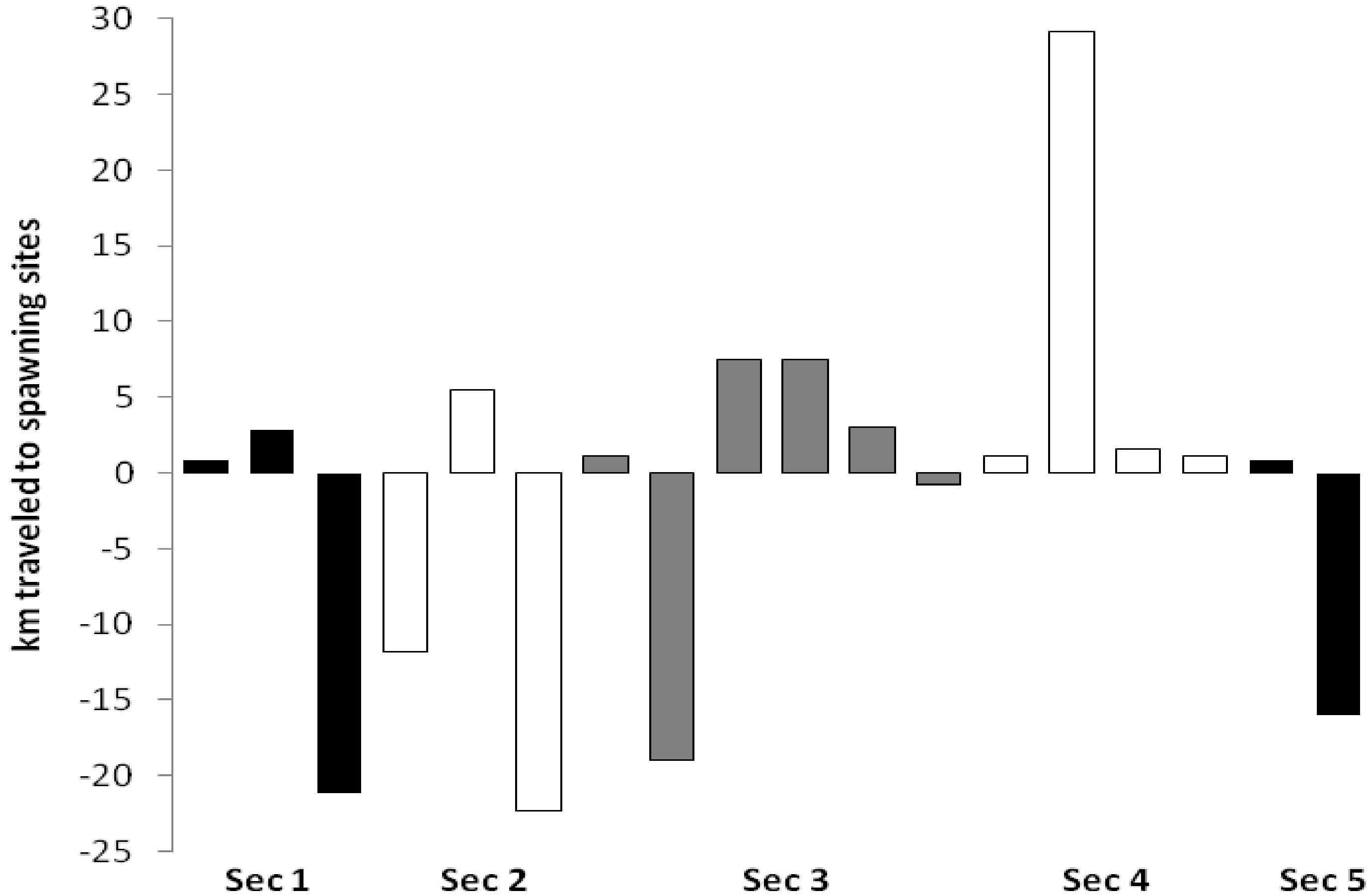

30
25
20
15
10
5
0
-5
-10
-15
-20
-25
km traveled to spawning sites
Sec 1
Sec 2
Sec 3
Sec 4
Sec 5

Figure 3. Spawning distances and direction (+) upstream or (-) downstream traveled to spawning sites for brown trout by section, Missouri River, Montana.

Table 1. Brown trout redds counted during the basin wide surveys and redd density (redds/km) for the Missouri River and tributaries, Montana 2007-09.

stream	Dist (km)	2007	2008	2009	Mean	Rel%
		Number of redds (redds per km)				
Missouri River	41.6	---	644 (15)	1202 (29)	923 (22)	46
Dearborn River	30.4	---	137 (5)	169 (6)	153 (6)	8
Little Prickly Pear Creek	19.5	1111 (57)	973 (50)	990 (51)	1025 (53)	51
Lyons Creek	4.8	81 (17)	249 (52)	a	165 (35)	8
Wolf Creek	5.4	390 (72)	269 (50)	362 (67)	340 (63)	17
Sheep Creek	3.2	114 (36)	129 (40)	a	122 (38)	6
total		1696	1620	2732	2016	

a- ice precluded counting redds

Table 2. Rainbow trout redds counted during the basin wide surveys and redd density (redds/km) for the Missouri River and tributaries, Montana 2007-10.

stream	Dist (Km)	2007	2008	2009	2010	Mean	Rel %
			Number of redds (redds per km)				
Missouri River	41.6	---	b	b	1644 (40)	1644 (40)	40
Dearborn River	30.4	---	b	b	632 (21)	632 (21)	16
Little Prickly Pear Creek	19.5	2125 (109)	1461 (75)	b	b	1793 (92)	44
Lyons Creek	11.2	847 (76)	897 (80)	b	386 (34)	710 (63)	17
Wolf Creek	12.5	1289 (103)	678 (54)	b	1451 (116)	1139 (91)	28
Sheep Creek	3.2	282 (88)	286 (89)	b	234 (73)	267 (83)	7
total		4543	3322		4347	4071	

b- high turbid flows precluded counting redds

Table 3. Fecundity statistics for rainbow trout and brown trout from the Missouri River, Montana, 2010.

	Rainbow trout			Brown trout		
Length group (mm)	Mean eggs	Range	N	Mean eggs	Range	N
381-405	1724	1279-2168	2	1431	---	1
406-431	1724	1531-1929	3	1562	1452-1671	2
432-456	1422	974-1581	11	---	---	---
457-482	1682	1282-2464	10	1841	1356-2251	4
483-508	2246	2100-2392	2	2456	2025-2936	5
509-533	---	---	---	2427	2104-2852	5

Table 4. Mean cranial lesion histopathology scores (0-5) of *M. cerebralis* from sentinel rainbow trout exposed at select sites in the Missouri River below Holter Dam and its tributaries. Values represent the highest mean infection measured for any 10 d period for each year. Scores >2.75 generally cause population declines (Vincent 2002). Hedrick et al. (1999) and Baldwin et al. (2000) describe the 0-4 scale, which was revised in 1999 adding level 5 in order to be more descriptive of very severe lesions (Vincent 2002) such as those commonly measured in sentinel fish from Little Prickly Pear Creek, and infrequently from Wolf Creek and Dearborn River.

	Year												
Stream -site	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
Little Prickly Pear Creek - Wirth div	2.94	4.00	4.66	4.76	4.43	4.96	4.92	4.87	4.97	0.11	4.72	1.96	4.70
Lyons Creek - mouth	---	0.00	---	0.00	0.00	0.00	0.00	0.00	0.00	---	---	0.00	---
Wolf Creek - mouth	---	---	0.20	0.78	4.47	3.96	3.98	4.80	4.42	0.15	4.58	2.70	3.94
Missouri River - Holter Dam	0.00	0.00	0.28	0.14	0.00	0.20	0.00	---	---	---	---	0.00	0.00
Missouri River - Craig	0.66	1.83	2.35	2.82	3.47	2.22	1.76	3.33	3.78	0.15	2.02	4.02	0.85
Missouri River - Mid Canon	---	---	---	---	1.60	0.19	0.34	2.00	3.00	0.13	1.96	---	1.44
Missouri River - Pelican Point	---	---	---	---	---	0.10	0.12	0.97	1.66	0.00	1.80	0.04	1.56
Dearborn River - Hwy 287	---	---	0.00	0.00	0.07	1.18	2.58	4.59	4.72	4.13	---	4.27	4.13
Sheep Creek - mouth	0.00	0.11	0.00	0.00	0.00	0.00	0.00	---	0.08	---	---	---	---