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Reproductive Ecology, Spawning Behavior, and Juvenile Distribution of Mountain Whitefish in the Madison River, Montana

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Abstract

Mountain Whitefish *Prosopium williamsoni* were historically common throughout much of the U.S. Intermountain West. However, within the last decade Mountain Whitefish have exhibited population-level declines in some rivers. In the Madison River, Montana, anecdotal evidence indicates Mountain Whitefish abundance has declined and the population is skewed toward larger individuals, which is typically symptomatic of recruitment problems. Describing reproductive development, spawning behavior, and juvenile distribution will form a foundation for investigating mechanisms influencing recruitment. We collected otoliths and gonadal samples from fish of all size-classes to characterize fecundity, age at maturity, and spawning periodicity. We implanted radio tags in mature Mountain Whitefish and relocated tagged fish in autumn 2012–2014. Timing of spawning was determined from spawning status of captured females and from density of eggs collected on egg mats. In spring 2014, we seined backwater and channel sites to describe age-0 whitefish distribution. Mountain Whitefish were highly fecund (18,454 eggs/kg body weight) annual spawners, and age at 50% maturity was 2.0 years for males and 2.6 years for females. In 2013 and 2014, spawning occurred between the third week of October and first week of November. During spawning, spawning adults and collected embryos were concentrated in the downstream 26 km of the study site, a reach characterized by a complex, braided channel. This reach had the highest CPUE of age-0 Mountain Whitefish, and the percentage of spawning adults in the 25 km upstream from a sampling site was positively associated with juvenile CPUE. Within this reach, age-0 Mountain Whitefish were associated with silt-laden backwater and eddy habitats. Future investigations on mechanisms influencing recruitment should be focused on the embryological phase and age-0 fish.

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The Madison River is home to a world-renowned recreational fishery (Gates et al. 2009) and one of the most heavily fished rivers in Montana (MFWP 2011), and as such this fishery provides a major economic contribution to southwest Montana (Grau et al. 2014; Lewis and King 2014). Anglers fishing in the Madison River primarily target Brown Trout *Salmo trutta* and Rainbow Trout *Oncorhynchus mykiss*, but Mountain Whitefish *Prosopium williamsoni* are also a part of the recreational fishery. However, in the last decade anglers reported declining catches of Mountain Whitefish (P. Clancey, Montana Fish Wildlife and Parks, personal communication). No population trend data exists to corroborate the angler reports. However, Mountain Whitefish CPUE declined in the late 1990s through the early 2000s and has stabilized at relatively low levels in Hebgen Lake, an impoundment on the upper Madison River (Clancey and Lohrenz 2013), suggesting that recent observations made by anglers are plausible.

Declines in abundance of Mountain Whitefish are not confined to the Madison River. For example, declines have been reported in the Yampa River, Colorado (K. Rogers, Colorado Wildlife and Parks, personal communication); Big Lost and Kootenai rivers, Idaho (Paragamian 2002; IDFG 2007); and several Wyoming lakes (G. Edwards, Wyoming Fish and Game, personal communication). The exact mechanisms for declines are often unknown. Studies have documented mechanisms of Mountain Whitefish mortality including whirling disease (Schisler 2010; Pierce et al. 2012), high temperatures (Boyd 2008; Brinkman et al. 2013), pollutants (Brinkman et al. 2008; Quinn et al. 2010), decreased discharge, and entrainment (Kennedy 2009). However, little is known about the effects of these stressors on populations (but see IDFG 2007; Kennedy 2009).

Investigations into the mechanisms for declines are difficult because of limited information on factors influencing recruitment for Mountain Whitefish. Recruitment is typically highly variable in fish populations and can limit population growth (Bradford and Cabana 1997; Myers 2002), so describing factors that influence the abundance and distribution of juvenile Mountain Whitefish could provide a foundation for investigating limiting factors.

Our research focused on describing the reproductive ecology and juvenile habitat use of Mountain Whitefish in the Madison River to provide a foundation for investigating mechanisms regulating the population. The specific objectives of this study were to (1) describe fecundity, age at maturity, and spawning periodicity; (2) describe migration and spawning and identify environmental factors that may influence the timing and location of spawning; and (3) describe the distribution of age-0 Mountain Whitefish at the macroscale (throughout the study site) and mesoscale (among habitat types). Addressing these objectives in combination strengthened our understanding of Mountain Whitefish ecology by allowing us to examine linkages among life stages.

METHODS

Study area.—The Madison River is a sixth-order headwater tributary of the Missouri River. The study area is between Hebgen Dam and Madison Dam, a distance of 101 km (Figure 1). Both dams lack fish passage structures and are barriers to upstream movement. Hebgen Dam, which was constructed in 1914, regulates discharge in this section. Discharge peaks near 48 m³/s during spring runoff and is 25–30 m³/s during base flow (USGS 2015a). Hebgen Dam releases hypolimnetic and surface water, and water temperatures remain cold for approximately 50 km downstream throughout the summer (Clancey and Lohrenz 2013). From Hebgen Lake to Varney Bridge the river is primarily a single channel (Figure 1). Below Varney Bridge, the river is braided, with numerous side channels and backwaters. Throughout the study site, the river is characterized by a high gradient (>4 m/km), predominately cobble substrate, and shallow mean depths (0.5–0.6 m). Two main-stem lakes are present: Earthquake Lake (58 m depth) and Ennis Lake (7 m depth).

The fish assemblage comprises Mountain Whitefish, Rainbow Trout, Brown Trout, Arctic Grayling *Thymallus arcticus* (present

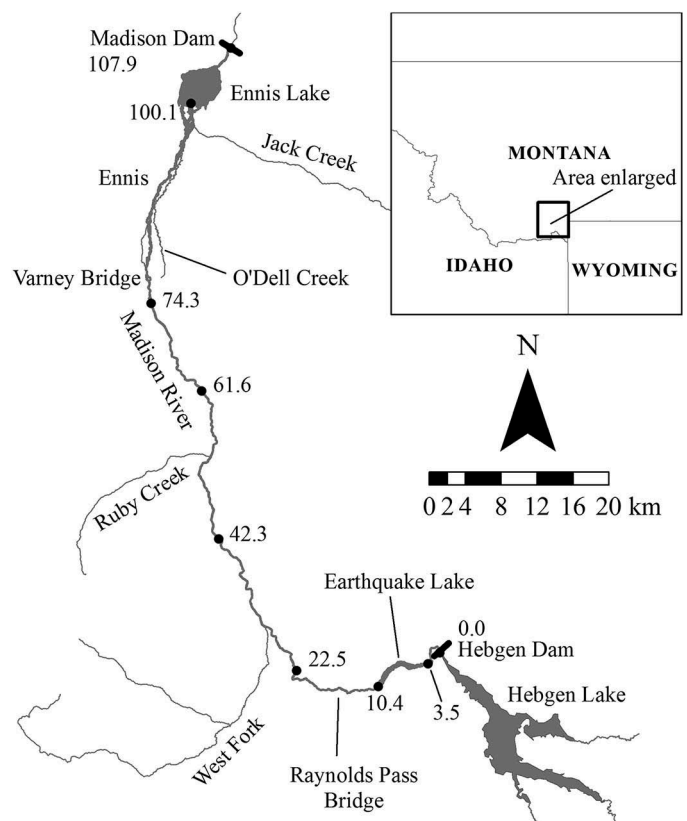


FIGURE 1. Study site on the Madison River, Montana. Solid circles labeled with river kilometer (Hebgen Dam = 0.0) show boundaries of river reaches used for sampling stratification and macroscale habitat descriptions. Only tributaries sampled for age-0 Mountain Whitefish in spring 2014 are shown.

at low abundance near Ennis Lake), Mountain Sucker *Catostomus platyrhynchus*, Longnose Sucker *C. catostomus*, White Sucker *C. commersonii*, Longnose Dace *Rhinichthys cataractae*, Utah Chub *Gila atraria*, and Mottled Sculpin *Cottus bairdi* (Brown 1971; Vincent 1987). In 2011, estimated angler pressure within the study site was $88,252 \pm 4,325$ angler-days (mean \pm SE) (MFWP 2011). Harvest regulations on Mountain Whitefish are 20 fish daily and 40 in possession, but few anglers harvest Mountain Whitefish (Clancey, personal communication).

Reproductive development.—Gonadal tissue was collected from Mountain Whitefish sampled by means of boat-mounted boom electrofishing (Smith Root VVP 15 B; 125–500 V, 2–3 A) or angling in May and October 2012 before spawning and in late October and November 2013 during the spawning period. Length (TL, ± 1 mm) and weight (± 1 g) were measured on all fish sampled. In October 2012, six fish per 10-mm length class were sacrificed for gonadal tissue and sagittal otoliths ($n = 147$). Fish were classified in the field as immature, mature and reproductive, or mature and nonreproductive based on examination of ovaries or testes (Strange 1996). Reproductive females were defined as fish that were midvitellogenic, late vitellogenic, or postvitellogenic in autumn, and males were considered reproductive if testicular stage was midspERMatogenic or ripe in autumn (Table 1). A 1-cm³ section of ovary or testes was collected and stored in 10% phosphate-buffered formalin (1:10 tissue : fixative) from all fish, except for 28 mature females whose entire ovaries were collected to estimate fecundity. Histological analysis of gonadal tissue was used to confirm the accuracy of field identification of sex and stage of maturity.

Gonadal tissue was processed histologically by embedding the tissue in paraffin, sectioning at 5 μ m, and staining with periodic acid Schiff stain (Luna 1968). Slides were examined under a compound microscope (5–100 \times ; Leica DM2000), and germ cells were scored for stage of maturation according to a protocol modified from Blazer (2002) and Goetz et al. (2011) (Table 1).

Fecundity of individual females was estimated gravimetrically. Each ovary was weighed whole (± 0.01 g). Three subsamples containing 50–100 ovarian follicles were dissected from the anterior, middle, and posterior sections of each ovary, weighed, and counted. Fecundity (F) was estimated for each female using the equation,

$$F = \frac{[\sum_i \frac{O_i}{W_i}]}{n} (W_{\text{ovaries}}),$$

where O_i was the subsample ovarian follicle count, W_i was the subsample weight, n was number of subsamples, and W_{ovaries} was the combined weight of both ovaries. All weights were wet weights. Linear regression was used to evaluate the relationships among fecundity, length, and weight. Fecundity and weight data from Mountain Whitefish in other rivers were obtained from the

literature (Brown 1952; Northcote and Ennis 1994; Wydoski 2001; Meyer et al. 2009).

Age in years was determined from sagittal otoliths. Otoliths were set in epoxy, sectioned with a low speed saw (Buehler Isomet 11-1280-160), and viewed under a microscope. Annuli were counted by two readers to determine age. If readers disagreed, both readers viewed the otolith and annuli together and determined an age by consensus. Age and length at 50% and 90% maturity were estimated using binomial logistic regression. Separate values were estimated for males and females.

Fish capture and radio-tagging.—Mountain Whitefish were sampled throughout the study site using boat-mounted electrofishing and angling in the spring when water temperatures were $< 15^\circ\text{C}$ to minimize stress and limit the risk of infection (Deters et al. 2010). Fish were anaesthetized, weighed (± 1 g), and measured (TL, ± 1 mm). Fish greater than 450 g (9-g tag $< 2\%$ of body weight: Cooke et al. 2012) were selected for tagging. Radio transmitters

TABLE 1. Stages of reproductive development used to assign stages to Mountain Whitefish gonad samples (modified from Blazer 2002; Goetz et al. 2011). Stages marked with an asterisk (*) were not observed in fish sampled histologically from the Madison River.

Reproductive stage	Description
Females	
Previtellogenic	Oocytes in cortical alveolus stage.
Early vitellogenic	Cortical alveoli present and small yolk granules present in periphery.
Midvitellogenic	Cortical alveoli pushed to edge of oocyte, yolk globules fill center of oocyte, nucleus central.
Late vitellogenic	Yolk globules and lipid droplets coalescing to nearly fully fused, nucleus off center.
Postvitellogenic*	Yolk globules and lipid droplets fused, nucleus has migrated to animal pole but remains intact.
Spawning	Entirely fused yolk, nucleus broken down, ovulated ova.
Spent	Postovulatory follicles and previtellogenic oocytes present.
Males	
Prespermatogenic*	Only spermatogonia present.
Early spermatogenic	Spermatogonia, spermatocytes, and spermatids may be present.
Midspermatogenic*	Spermatocytes, spermatids, and spermatozoa present in approximately equal proportions.
Ripe	Greater than 50% spermatozoa.
Spawning	Primarily spermatozoa, cysts beginning to empty, actively spermiating.
Spent	Cysts mostly empty, although residual spermatozoa may be present.

(ATS, model F1205 body-implant internal antenna) were implanted in 53 mature females and 17 mature males in 2012, and in 53 mature females and 13 mature males in 2013, using methods modified from Cooke and Bunt (2001) and Wagner et al. (2011). Sex was determined by using an otoscope to view gonads before radio transmitter insertion.

Radio tracking.—Radio tags transmitted for 24 h per day from September 1 through November 30 for 2 years. Radio-tagged fish were relocated from September through November in 2012, 2013, and 2014. Radio-tracking was primarily conducted from a drift boat or raft using an omni-directional whip antenna, a handheld three-element Yagi antenna, and an ATS Challenger R2000 receiver. Additional tracking was conducted from vehicles and on foot. Waypoints for fish locations were obtained by a combination of triangulation and floating directly over fish. Location accuracy was 6 ± 7 m (mean \pm SD) in blind tests ($n = 12$) using transmitters placed in the river and never exceeded 20 m. Status of each relocated fish (alive, dead, or unknown) was determined based on movement. In early autumn (water temperature $> 8^\circ\text{C}$), fish were located once weekly. Once the water temperature reached 8°C , we attempted to locate fish twice weekly. Two continuous-recording fixed stations (Lotek Wireless, SRX-400A) were deployed at the Ennis Lake inlets (river kilometer [rkm] 100.1) from October 19 to November 30, 2013, and October 30 to November 17, 2014. Mobile-tracking and fixed-recording stations recorded 1,437 relocations. We located 40 fish alive in autumn 2012, 58 in 2013, and 41 in 2014 (1–47 relocations per fish). Fish located alive six times or more were included in movement analyses and location maps.

Timing of spawning.—Embryo collection and examination of mature females was used to confirm spawning and determine timing of spawning. Embryos were collected using egg mats constructed of a 0.91×0.54 -m rectangle of natural fiber furnace filter in a $\frac{1}{2}$ -in (13-mm) rebar frame attached to a cinderblock anchor. From October 10 through November 27, 2013, and from October 9 through November 20, 2014, 18 egg

mats were deployed near suspected spawning areas. Egg mats were examined twice a week, and Mountain Whitefish embryos were counted and removed.

Angling and boat-mounted boom electrofishing were used to capture mature female Mountain Whitefish and assess spawning status (2013: $n = 49$, 2014: $n = 50$) from late September through mid-November. Sex and spawning stage (reproductive, spawning, spent, or immature) were determined externally based on expressed gametes, tubercles, and body shape. Three reproductive females and three spent females were sacrificed to verify spawning status histologically.

Habitat characterization.—To characterize habitat at the macroscale (Frissell et al. 1986), the study site was divided into eight reaches (3.5–25.8 km in length) using boundary features including tributary junctions, lakes, and major elevation changes (Table 2; Figure 1). Boundary elevations, thalweg length, side channel (>6 m width) lengths, and valley length were measured for all river reaches, and channel width and width between scarps nearest each riverbank were measured at 500-m intervals in ArcMap 10.1 (ESRI, Redlands, California) using aerial photos, digital elevation models, and topographical maps (Montana State Library 2015; USGS 2015b). Reach gradient was measured by dividing the elevation change by thalweg length. Sinuosity was calculated by dividing thalweg length by valley length (McMahon et al. 1996). Braiding index was calculated by dividing total length of all channels by thalweg length (Friend and Sinha 1993). Mean channel and scarp widths were calculated for each reach.

At a smaller scale (sampling sites 200–400 m in length) depth, substrate, and velocity were measured at availability and use (spawning) sites in autumn 2013 and 2014 during base flow. Availability sites characterized river habitat between Reynolds Pass Bridge and Ennis Lake (Figure 1). Random sampling, stratified by reach, was used to select 30 availability sampling sites, spaced > 400 m apart. Use sampling sites were

TABLE 2. Macroscale habitat measurements and Mountain Whitefish locations by period for reaches in the Madison River. Reaches 2 and 8 are lakes.

Reach	Start point	Start rkm	Gradient (m/km)	Sinuosity index	Braiding index	Mean channel width (m)	Mean width between scarps (m)	Percent of fish in reach	
								During prespawning	During spawning
1	Hebgen Dam	0.0	7.7	1.9	1.9	50	114	2.5	2.8
2	Earthquake inlet	3.5						0.0	0.0
3	Earthquake outlet	10.4	10.5	1.3	1.5	42	369	14.9	7.8
4	Gradient change	22.5	4.6	1.2	1.4	59	358	23.1	9.6
5	Wolf Creek	42.3	4.6	1.2	1.1	66	675	29.9	14.6
6	Story Ditch	61.6	4.9	1.1	1.1	70	1,888	4.6	23.0
7	Wigwam Creek	74.3	4.3	1.1	3.6	58	2,601	24.9	36.3
8	Ennis inlet	100.1						0.0	5.9

at confirmed spawning sites (2013: $n = 5$, 2014: $n = 8$) where embryos were collected on egg mats. At each availability site, four diagonal downstream transects were followed by rowing a boat (sampled length, 250–350 m), and at each spawning site, two diagonal downstream transects were rowed. At each transect, depth and substrate were measured at five points evenly spaced across the channel. Depth was measured to the nearest 0.1 m using a measuring rod. The dominant and secondary substrate types (e.g., bedrock, boulder, cobble, gravel, sand, silt; Platts et al. 1983) within a 1-m radius of the depth measurement were visually estimated. A video camera (Contour) attached to the measuring rod allowed us to observe substrate in deep areas. At the downstream end of the final rowed transect, three velocity measurements, spaced evenly across the channel width, were made by using the orange float method (Gordon et al. 1997). If sites contained side channels, substrate and depth measurements ($n = 3$ per transect) were made along waded diagonal transects in each side channel.

Water temperature was measured from May 5 through November 30 each year at four locations (rkm 29.0, 42.0, 57.7, and 91.1) using temperature loggers (Onset HOBO Pendant UA-001-64). Mean, maximum, and minimum daily temperatures were calculated using temperature records from all temperature loggers. Temperature loggers were deployed during the 2014–2015 incubation period from December 3, 2014, through March 7, 2015, to compare winter water temperatures between randomly selected availability sites stratified by reach ($n = 18$) and confirmed spawning sites ($n = 8$). Discharge data were obtained from three U.S. Geological Survey gauging stations.

Analysis of spawning and movement.—Spawning dates were determined based on embryo density from egg mats and reproductive stage of captured females. Mean daily embryo density ($\text{embryos} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) was calculated for all egg mats combined. In 2013 and 2014, we defined the start of the spawning period as the first day when either a spawning female was captured or we collected at least one embryo on an egg mat. The start of the postspawning period was defined as the day when we captured only spent females and did not catch reproductive or spawning females on future sampling days, or the day when daily embryo densities declined to <10% of the maximum density. Movement rates were similar among years (see Results), and females were reproductive in early October each year. Thus, the spawning period in 2012 was defined (for movement mixed-effects models) by calculating mean start and end dates of spawning periods from 2013 and 2014.

All fish locations were indexed to river kilometer (± 0.1 km) using ArcMap 10.1 (ESRI). Minimum daily total and net distances moved were calculated for each fish (Rogers and White 2007). Total movement rate was calculated by dividing distance (rkm) between successive relocations by number of days elapsed between relocations. Net movement rate was

calculated by dividing the difference in river kilometers between subsequent relocations by number of days elapsed; thus, upstream movement yielded positive net movement rates and downstream movement yielded negative net movement rates. All movement rates represented minimum movement rates. Water temperature and discharge (USGS 2015a) were graphically compared with weekly movement rates to assess relationships. Linear mixed-effects models (Zuur et al. 2009) were fit using the R package nlme (Pinheiro et al. 2015) to test for differences in net and total movement rates between males and females, among years, and among periods (prespawning, spawning, and postspawning). Mixed-effects models included categorical fixed effects for sex, period, year, and an interaction between sex and period, and a random effect that accounted for repeated measures on individual fish by nesting period within year and fish (Pinheiro and Bates 2000; Zuur et al. 2009). Individual radio-tagged fish were the experimental units for all comparisons.

Kernel density maps were used to illustrate locations of Mountain Whitefish during the prespawning, spawning, and postspawning periods and to identify congregation areas. Frequency of relocations was standardized to one relocation per fish per week by randomly selecting one relocation on weeks a fish was located multiple times. We pooled sex and years on maps because movement analyses showed no differences in movement rates between sexes or among years (see Results). Kernel density maps were constructed for each period using the kernel density function in ArcMap (ESRI) and a search radius of 2 km.

Binomial logistic regression models were fit to habitat data from 2013 and 2014 separately to determine whether mean water velocity, mean depth, proportions of gravel, and proportions of cobble were associated with the odds of a site being used for spawning. Proportions of silt and sand were not included in the analysis because these substrate types were rare; for example, of 1,579 dominant substrate observations, silt was observed 16 times and sand 14 times. The proportion of boulder was not included because the small sample size of spawning sites (2013: $n = 5$, 2014: $n = 8$) limited the number of explanatory variables we could use in the logistic regression models.

Mean daily temperatures and daily temperature change, pooled by reach and type (availability or spawning), were calculated for temperature loggers deployed during winter 2014 through 2015. Simple linear regression was used to determine whether mean daily water temperature and temperature range at spawning and availability sites within the same reach exhibited a 1:1 relationship.

Age-0 fish distribution.—In spring 2014, seining (3×1.5 -m beach seine, 1.6-mm bar mesh) in backwaters, channels, and four tributaries (Figure 1) was used to describe the distribution of age-0 Mountain Whitefish (defined as hatch date to December 31 of same year, age < 1.0). In 2013, age-0 Mountain Whitefish were patchily distributed and present at

relatively low numbers in the Madison River (Boyer et al. 2017), so we restricted 2014 sampling to habitats likely to have age-0 Mountain Whitefish present. Aerial maps were used to delineate backwaters, 200-m channel lengths (channel > 6 m wide), and 50-m tributary lengths (within 500 m of confluence with Madison River). In each reach (Table 2), random stratified sampling (strata were backwaters or large channel) was used to select sampling sites ($n = 207$). In tributaries, random sampling was used to select sites ($n = 15$). In the field, wadeable sampling sites 50 m in length (that included at least 2 m² of slow velocity habitat) were identified in preselected large channel sites. Sample sizes were determined from a power analysis using 2013 seining data (Boyer et al. 2017).

All wadeable habitat within each selected site was seined (minimum of three seine hauls). Total length (± 1 mm) was measured for all Mountain Whitefish. Water temperature ($\pm 0.1^\circ\text{C}$), maximum depth (± 0.1 m), and channel width (± 0.5 m) were measured at each sampled site. Length and width (± 0.5 m) were measured for each backwater. Primary and secondary substrate, turbidity, and water velocity were visually estimated in each sampled site. Additionally, numbers of spawning adults upstream from each sample site were quantified using 2013 telemetry data (Table 3).

Maps and logistic regression were used to relate age-0 Mountain Whitefish catch data to spawning adult locations, habitat types (channel, backwater, tributary), and habitat characteristics. Data from reach 1 were limited; thus this reach was not included in the logistic regression. Age-0 Mountain Whitefish CPUE (number per seine haul) was calculated for each sampled site. A point map of age-0 Mountain Whitefish presence or absence and a kernel density map of age-0 CPUE were created with ArcMap 10.1 (ESRI). No age-0 Mountain Whitefish were captured at 140 of 221 sites; subsequently CPUE data were overdispersed. Poisson distributions are not

suitable for modeling count data with zero-inflation and overdispersion, so zero-altered negative-binomial models (ZANB) (Mullahy 1986; Zuur et al. 2009) were used to evaluate relationships between CPUE and habitat characteristics.

All habitat variables (Table 3) and CPUE were plotted to evaluate relationships. Examination of plots suggested relationships between CPUE and habitat type, dominant substrate, channel width, water velocity, and percentage of spawning adults within 25 km (Table 3). These variables were fit to a rich ZANB model using the R package *pscl* (Zeileis et al. 2008), and backwards maximum likelihood selection was used to select the most parsimonious model. All statistical analysis was performed in R (R Core Development Team) using $\alpha = 0.05$ unless noted otherwise.

RESULTS

Reproductive Development

Fecundity estimates varied from 4,369 to 25,349 for females weighing from 291 to 1,254 g (309–493 mm TL, ages 2–14 years). Fecundity was significantly correlated with weight ($R^2 = 0.91$, $df = 26$, $P < 0.0001$; Figure 2) and length ($R^2 = 0.82$, $df = 26$, $P < 0.0001$) and was similar to populations in other water bodies throughout the species range (Figure 2).

Histological examination of a subset of gonadal samples ($n = 120$) corroborated the field determinations of maturity and developmental stage (Figures 3, 4). Ninety-seven percent of the females age 3 and older were reproductive, and all males age 3 and older were reproductive. Ovaries collected from reproductive females contained ovarian follicles at one of two stages (midvitellogenic or late vitellogenic). Oocytes in ovarian samples exhibited group synchronous maturation. Females showed varying levels of yolk and lipid coalescence and centered or off-center nuclei

TABLE 3. Habitat variables measured at seining sampling sites in the Madison River in May and June 2014. All variables were compared graphically with age-0 Mountain Whitefish CPUE data, but only variables marked with an asterisk (*) were included in rich, zero-inflated, negative-binomial models fit to age-0 fish CPUE data.

Variable	Explanation
Habitat type*	Backwater, channel, or tributary.
Dominant substrate*	Visual estimate of dominant substrate in sampled area.
Secondary substrate	Visual estimate of second most common substrate in sampled area.
Width*	Channel width ± 0.5 m.
Velocity*	Visual estimate: fast (>1.0 m/s), moderate (0.6–1.0 m/s), slow (<0.6 m/s).
Temperature	Water temperature ($\pm 0.1^\circ\text{C}$) at sampled site.
Maximum depth	Maximum depth (± 0.1 m) sampled.
Discharge	m ³ /s (daily mean for day of sampling), obtained from nearest U.S. Geological Survey gauge.
Spawners within 1, 5, 10, 15, 20, or 25* km upstream	Percent of tagged adult relocations during the 2013 spawning window (October 19 to November 10, 2013, standardized to one location per fish per week) within 1, 5, 10, 15, 20, or 25 km upstream from the sampling unit, respectively.

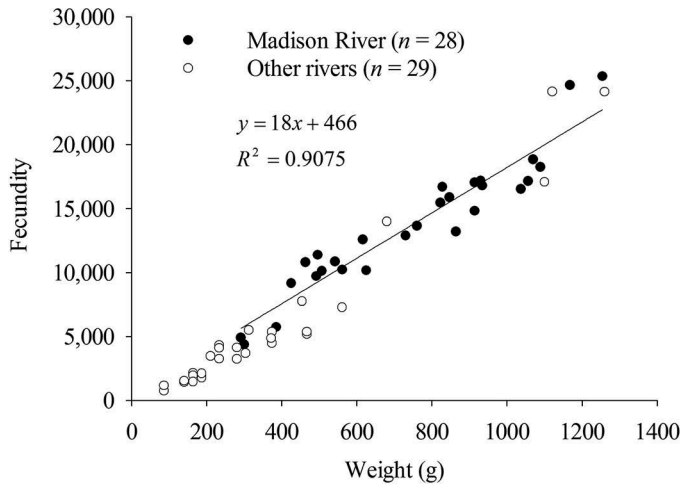


FIGURE 2. Weight–fecundity relationship for Mountain Whitefish captured by means of boat electrofishing in the Madison River, Montana, during October 10–12, 2012, and in other watersheds (Sigler 1951; Brown 1952; Northcote and Ennis 1994; Wydoski 2001). The regression line includes only Mountain Whitefish from the Madison River.

(Figure 3). Examination of vitellogenic ovaries revealed primarily intact ovarian follicles, and spent ovaries had primarily postovulatory follicles. Follicular atresia of developing ovarian follicles was limited (<10%) in both vitellogenic and spent ovarian samples (Figure 3).

Female Mountain Whitefish matured at slightly older ages and larger sizes than males (Figure 5). Fifty percent of female Mountain Whitefish were sexually mature at age 2.6 (95% CI, 2.1–3.3), and 90% were mature at age 3.7 (95% CI, 2.2–5.6). Males were 50% mature at age 2.0 (95% CI, 2.0–2.1) and 90% mature at age 2.1 (95% CI, 2.1–2.2). For females, length at 50% maturity was 329 mm (95% CI, 313–346) and at 90% maturity was 378 mm (95% CI, 339–411). Males were 50% mature at 300 mm (95% CI, 279–318) and 90% mature at 340 mm (95% CI, 314–361). Age at first maturity was 2 years for females and males.

Timing of Spawning

In 2013, the first evidence of spawning was an ovulating female captured on October 19. The last spawning female was captured on November 10. On November 11, the density of embryos collected on egg mats declined to 0.3 embryos/m², 7% of the maximum embryo density (4.27 embryos/m²; Figure 6). Based on the above observations, we defined the 2013 spawning period as October 19 to November 10. In 2014, embryos were first collected on October 16. All females (n = 19) captured by electrofishing on November 5 were spent (Figure 6). The spawning period was determined to be from October 16 to November 4 in 2014.

Movement

Mean total movement greater than 1 km/d was first observed during the first week in October in all years (Figure 7). In general,

mean total movement for both sexes was greatest during the spawning period. Total movement rates varied between the pre-spawning, spawning, and postspawning periods, and were higher for females than males during the spawning period but higher for males in the pre-spawning and postspawning periods ($F = 5.89$, $df = 180$, $P = 0.0033$; Figure 7). We did not detect differences in mean total movement rates among years ($F = 2.61$, $df = 49$, $P = 0.084$).

Most tagged fish moved downstream (negative net movement values; Figure 7) during the pre-spawning and spawning seasons (n = 24, 37, and 16 in 2012, 2013, and 2014, respectively), although some tagged fish moved short distances upstream (n = 1, 5, and 6 in 2012, 2013, and 2014, respectively), and others remained within 1 rkm for the entire tracking period (n = 7, 14, and 9 in 2012, 2013, and 2014, respectively). The mean distance (farthest downstream location – farthest upstream location) of spawning movements was 25.5 km (SD = 21.7 km). The longest distance an individual fish moved was 68.1 km downstream, and the shortest distance was 0.1 km. Fish that moved downstream typically moved rapidly enough to reach spawning areas within hours or days; for example, a fish relocated five times in less than 2 h moved at 4.2 km/h, and total movement rates calculated from biweekly relocations of individual fish sometimes exceeded 10 km/d. Mean net movement varied between the pre-spawning, spawning, and postspawning periods, and these variations depended on the sex of the fish; there was a significant interaction between sex and period ($F = 4.11$, $df = 180$, $P = 0.018$). Male movement was more downstream during the pre-spawning period and female movement was more downstream during the spawning season (Figure 7). There were no differences in mean net movement among years ($F = 1.04$, $df = 49$, $P = 0.37$). Direction of movement was variable, but trended upstream during the last week of the spawning period and the postspawning period.

Spawning Locations

Fish relocations and embryo collection suggested most spawning occurred downstream from rkm 73. Each year during the pre-spawning period, tagged fish were evenly distributed throughout the study site (Table 2; Figure 8A). Mountain Whitefish were relocated throughout the entire study site (from 0.9 km downstream from Hebgen Dam to the Ennis Lake inlet) during the spawning period, but a disproportionate number of fish were observed downstream from rkm 56, with the highest numbers relocated between rkm 73 and 78 (Table 2; Figure 8B). Collection of embryos on egg mats confirmed spawning at rkm 73.2, 74.7, 76.8, 77.2, 82.9, 85.2, 85.4, and 90.5 (Figure 8).

During the postspawning period, fish were relocated throughout the river and in Ennis and Earthquake lakes (Figure 8C). In 2013, 60% of the fish (33 of 55) remained in the river after spawning, while 40% of the fish entered the

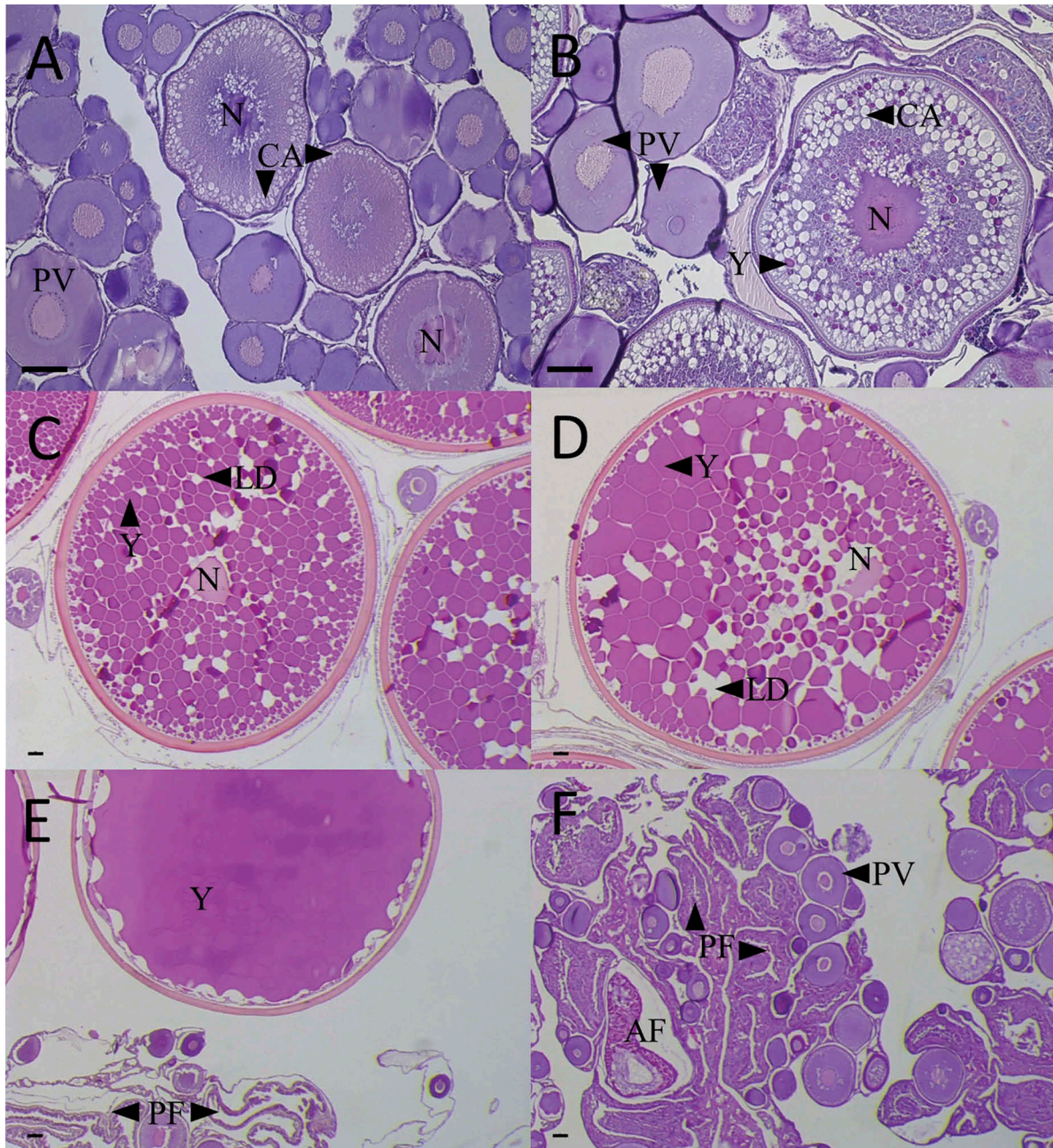


FIGURE 3. Ovarian development of Mountain Whitefish (periodic acid Schiff stain, bar = 100 μ m). Stages shown are: (A) previtellogenic, with cortical alveoli present; (B) early vitellogenic, with cortical alveoli and small yolk droplets present; (C) midvitellogenic, ovarian follicles with coalescing yolk globules and lipid droplets, and nucleus centered; (D) late vitellogenic, yolk globules and lipid droplets coalescing to nearly fused, and nucleus off center; (E) spawning, with ovulated ova showing fully fused yolk and nearby postovulatory follicles; and (F) spent, with postovulatory follicles, one atretic ovarian follicle, and previtellogenic oocytes. Abbreviations are as follows: AF = atretic follicle, CA = cortical alveoli, LD = lipid droplet, N = nucleus, PF = postovulatory follicle, PV = previtellogenic oocyte, and Y = yolk.

lakes between October 24 and November 24. More fish entered Ennis Lake (35%, 19 of 55) than Earthquake Lake (5%, 3 of 55). We were unable to accurately determine numbers of fish in the lakes in 2012 and 2014 because fixed stations were not operational during the entire movement period.

Spawning Habitat

Spawning was concentrated in reach 7 (rkm 74.3–100.1), which had the highest braiding index value and mean width between scarps (Table 2). Fish were most frequently located in reaches 6 (rkm 61.6–74.3) and 7 during the spawning period, but fish located in reach 6 were typically moving through this

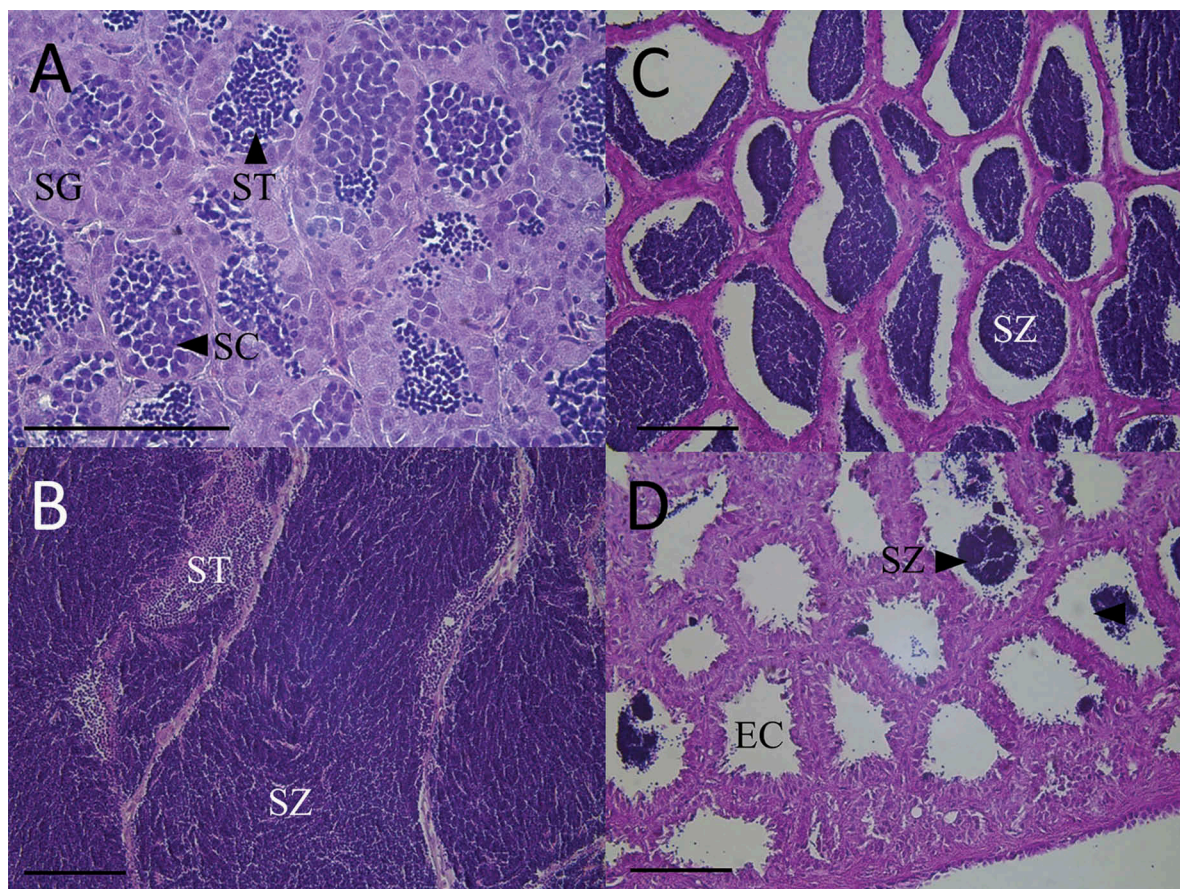


FIGURE 4. Testicular development of Mountain Whitefish (periodic acid Schiff stain, bar = 100 μ m). Stages shown are: (A) early spermatogenic, containing only spermatogonia, spermatocytes, and spermatids; (B) ripe, primarily spermatozoa with small numbers of spermatids (C) spawning or spermiating, only spermatozoa present and cysts beginning to empty, and (D) spent, as seen by residual spermatozoa present but mostly empty cysts. Abbreviations are as follows: EC = empty cyst, SC = spermatocytes, SG = spermatogonia, ST = spermatids, and SZ = spermatozoa.

reach (i.e., the next relocation was >5 rkm upstream or downstream). Spawning sites confirmed with embryo collection were in reach 7 ($n = 7$) or 1.1 km upstream from the reach 7 boundary in reach 6 ($n = 1$).

At the mesoscale, we found little evidence for selection of specific depth, water velocity, or substrate at spawning sites. There was no evidence that depth (2013: $Z = 1.044$, $df = 29$, $P = 0.296$; 2014: $Z = 0.891$, $df = 33$, $P = 0.373$), water velocity (2013: $Z = -1.842$, $df = 29$, $P = 0.066$; 2014: $Z = -0.744$, $df = 33$, $P = 0.457$), or proportion of gravel (2013: $Z = -0.254$, $df = 29$, $P = 0.799$; 2014: $Z = 1.319$, $df = 33$, $P = 0.187$) were associated with the odds of a site being used for spawning. There was no evidence that proportion of cobble was associated with spawning use in 2013 ($Z = 1.235$, $df = 29$, $P = 0.217$), but in 2014 the proportion of cobble was positively associated with odds of spawning use ($Z = 2.230$, $df = 33$, $P = 0.029$). Because this association was weak, and was not detected in 2013, this result may not be biologically meaningful.

Water temperatures during the winter incubation period were relatively warm (mean = 2.3°C) and stable (mean daily temperature change = 0.7°C) at sites near Hebgen Dam (reach 1) and Earthquake Lake (reach 3) between December 3, 2014, and March 7, 2015. Sites > 20 km downstream from a lake (reaches 4–7) had colder (mean temperature = 1.6°C) and more variable (mean daily temperature change = 1.6°C) water temperatures during the same time period. We did not detect differences in mean daily water temperature or mean daily water temperature change between spawning sites and availability sites within the same reach; differences in temperature between spawning and availability sites were smaller than the accuracy ($\pm 0.53^\circ\text{C}$) of the temperature loggers.

Age-0 Fish Distribution

A total of 1,449 age-0 Mountain Whitefish were sampled between May 13 and June 12, 2014. Age-0 Mountain Whitefish were captured at 82 sampled sites and not detected at 139 sites (Figure 8D). At sites with age-0

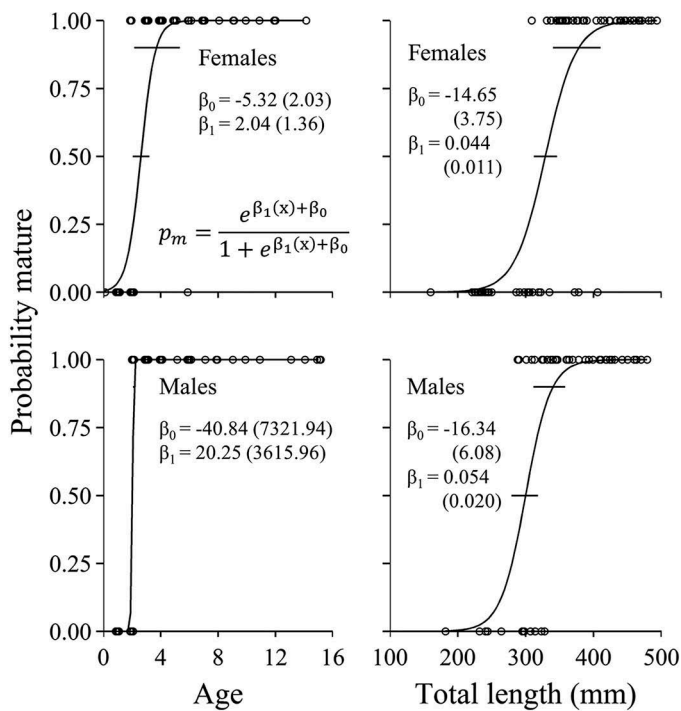


FIGURE 5. Logistic-regression models used to predict age and length at 50% and 90% maturity for Mountain Whitefish in the Madison River, Montana. Points are jittered on the age x -axis to show numbers of fish in year-classes where multiple individuals were aged. Model parameter estimates are shown with SE in parentheses (large SE values for male age-parameter estimates is a result of quasi-complete separation).

Mountain Whitefish present, CPUE varied from 0.1 to 17 fish per seine haul.

At the macroscale, age-0 Mountain Whitefish catch was highest downstream from rkm 73.0. For example, 90% of age-0 Mountain Whitefish were sampled downstream from rkm 73.0, although this reach accounted for only 29% of study-site length and 39% of sites sampled (Figure 8E). The Mountain Whitefish caught in the reach between Hebgen Dam and Earthquake Lake (3.5 km, 3% of sites sampled) represented 8% of the total catch. Only 2% of age-0 Mountain Whitefish were captured between Earthquake Lake and rkm 73.0 (67% of study site length and 58% of sites sampled). Spawning was also concentrated downstream from rkm 73.0 (Figure 8B), and age-0 fish presence ($Z = 5.77$, $df = 15$, $P < 0.0001$) and CPUE ($Z = 2.91$, $df = 15$, $P = 0.004$) were positively associated with numbers of adults within the 25 km upstream from a sampling site (Table 4). There were no correlations between log CPUE and percentage of adults at 1, 5, 10, or 15 km upstream from a site ($r^2 = 2.2 \times 10^{-5}$ to 0.09, $df = 220$, $P < 0.0001$ to 0.94), but log CPUE was correlated with the number of adults within 20 km ($r^2 = 0.19$, $df = 220$, $P < 0.0001$) and 25 km ($r^2 = 0.31$, $df = 220$, $P < 0.0001$) upstream from a site.

Age-0 Mountain Whitefish were present in 27% of the channel sites (34 of 123), 55% of the backwater sites (47 of 84), and 7% of the tributary sites (1 of 15). We did not find evidence that the odds of Mountain Whitefish presence differed between backwaters and channels ($Z = -0.206$, $df = 15$, $P = 0.837$), but Mountain Whitefish were less likely to be present in tributaries ($Z = -2.003$, $df = 15$, $P = 0.045$; Table 4) than in channels. Dominant substrate was the best predictor of age-0 Mountain Whitefish presence. The odds of age-0 Mountain Whitefish presence were higher at sites where silt was the dominant substrate ($Z = 3.075$, $df = 15$, $P = 0.002$; Table 4; Figure 9). Silt-laden sites where age-0 Mountain Whitefish were captured included backwaters, eddies, beaver ponds, and slow-velocity areas immediately downstream from islands and rock bars.

At sites with age-0 Mountain Whitefish present, CPUE was variable and difficult to predict using mesoscale habitat variables. Models predicted that at sites where age-0 Mountain Whitefish were present, CPUE was higher at sites with cobble ($Z = 2.353$, $df = 15$, $P = 0.019$), gravel ($Z = 2.222$, $df = 15$, $P = 0.026$), and silt ($Z = 2.811$, $df = 15$, $P = 0.005$) as the dominant substrates than at those with boulders (Table 4).

DISCUSSION

We investigated multiple life stages for Mountain Whitefish in the Madison River—a world-renowned fishery and an important watershed in the Greater Yellowstone ecosystem—with the understanding that we would begin to clarify the mechanisms limiting Mountain Whitefish abundance. Similarities in fecundity and age at maturity between Mountain Whitefish in the Madison River and other rivers at similar latitude and elevation suggest that low fecundity or infrequent spawning are not plausible limiting factors. In the Madison River, Mountain Whitefish fecundity relative to weight was comparable with values reported for fish in Utah, Wyoming, and other Montana rivers (Sigler 1951; Brown 1952; Hagen 1970; Wydoski 2001). Age at maturity of Mountain Whitefish in the Madison River was similar to that in the Snake River Basin, Idaho, where age at 50% maturity was 2.7 years for females and 2.0 years for males (Meyer et al. 2009), and in the Logan River, Utah, where 70% of fish were mature at age 3 (Sigler 1951). Annual spawning was also reported for populations in the Snake River basin (Meyer et al. 2009). Lower fecundity and delayed maturation have been reported at higher latitudes and altitudes (Thompson and Davies 1976; Wydoski 2001), where low temperatures presumably limit growth and reproductive development.

Histological examination of gonadal tissue also suggested that the Mountain Whitefish population in the Madison River is not limited by reproductive development. Evidence of environmental stressors, which decrease fecundity or increase the length of spawning cycles, can be observed in ovarian tissue as widespread follicular atresia or accumulations of pigments

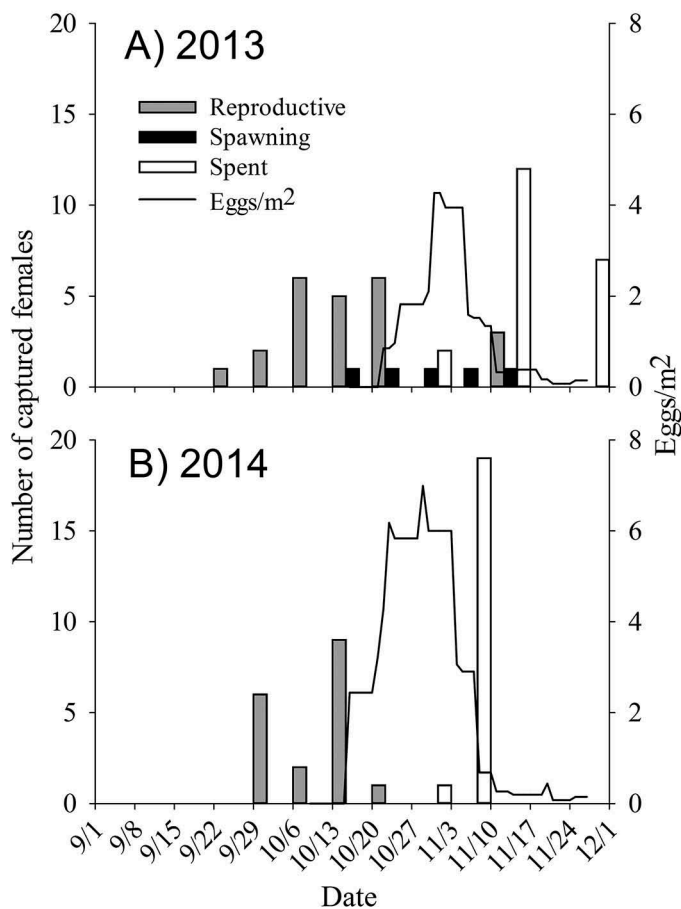


FIGURE 6. Status of captured female Mountain Whitefish (grouped by week) and daily densities of Mountain Whitefish embryos collected on egg mats in the Madison River, Montana, during autumn in (A) 2013 and (B) 2014. Egg mats that did not collect any embryos were excluded from density calculations. Dates are given as month/day.

and macrophages (Blazer 2002). We did not observe those symptoms. All males and females of age 3 (with the exception of one) and older were reproductive, indicating that annual spawning is typical at a population level.

After 3 years of studying the movement of Mountain Whitefish in the Madison River, clear patterns emerged. Spawning-related movement began in early October, when males moved first to spawning sites followed by females, and spawning occurred during the last 2 weeks of October and first week of November. Water temperatures varied between 13.3°C and 0.0°C during spawning periods, and movement patterns were similar among years with varying water temperature schedules, suggesting that factors other than declining water temperature provide movement and spawning cues. Spawning sites were concentrated in the lower portion of the study site where the river starts to become braided and valley bottom width is widest. In May and June, age-0 Mountain Whitefish were most common in braided reaches, and age-0 fish presence was associated with protected, silt-laden habitat. After

spawning, most adult Mountain Whitefish returned to river habitats, but some fish moved into Ennis and Earthquake lakes, presumably to overwinter.

Prespawning movements in the Madison River were similar in distance and speed to Mountain Whitefish movements reported in other rivers (Liebelt 1970; Pettit and Wallace 1975; Pierce et al. 2012; Benjamin et al. 2014), but net direction of movements differed. Most Mountain Whitefish in the Madison River moved varying distances (1.0–68.1 km) downstream during the prespawning and spawning periods, and longer movements were observed for fish moving downstream than for fish moving upstream. Mountain Whitefish moved similar distances (<1–80 km) in other rivers (Pettit and Wallace 1975; Pierce et al. 2012; Benjamin et al. 2014). However, migratory Mountain Whitefish typically moved upstream to main-stem or tributary sites before spawning in the Methow River, Washington (Benjamin et al. 2014), Yellowstone River, Montana (Liebelt 1970), Blackfoot River, Montana (Pierce et al. 2012), and Clearwater River, Idaho (Pettit and Wallace 1975).

Females and males moved similar distances throughout the tracking period, but timing of movement varied, and males moved earlier. Males will move to spawning sites before females because early arrival at breeding sites maximizes male reproductive opportunities (Morbey 2000). This reproductive strategy has been described for a variety of vertebrate taxa (Morbey and Ydenberg 2001), including fishes such as Pacific salmon *Oncorhynchus* spp. (Morbey 2000; Quinn 2005), Redhorse *Moxostoma* spp. (Reid 2006), and Rainbow Smelt *Osmerus mordax* (Lischka and Magnuson 2006).

Timing of spawning movements in the Madison River was not correlated with water temperature, although declining water temperature is believed to be an important cue for migration and spawning of autumn-spawning fish (Swanberg 1997; Brenkman et al. 2001; Riedel and Peter 2013). In the Madison River, the timing of Mountain Whitefish migration and spawning was similar over 3 years despite wide variability in temperatures and rates of temperature decline. Thus, either water temperature cues are more complex than we can resolve given our data or additional factors act as cues for movement and spawning. In addition to unpredictable environmental factors such as temperature, fish reproductive cycles can also be influenced by predictable environmental factors including photoperiod (Vlaming 1972; Bromage et al. 2001) and by genetic factors (Quinn et al. 2000). Water temperatures earlier in the year can also affect timing of spawning (Bromage et al. 2001; Warren et al. 2012). The similarities in timing of movement and spawning we observed among years with varying water temperature schedules suggest that factors such as genetics or photoperiod, which are relatively constant among years, could be important spawning cues.

Net downstream movement during the prespawning and early spawning periods led to a concentration of spawning activity downstream from rkm 73.0. Interestingly, the Madison River changes near rkm 73.0, transitioning from a single channel confined between high scarps to a braided channel with a wider

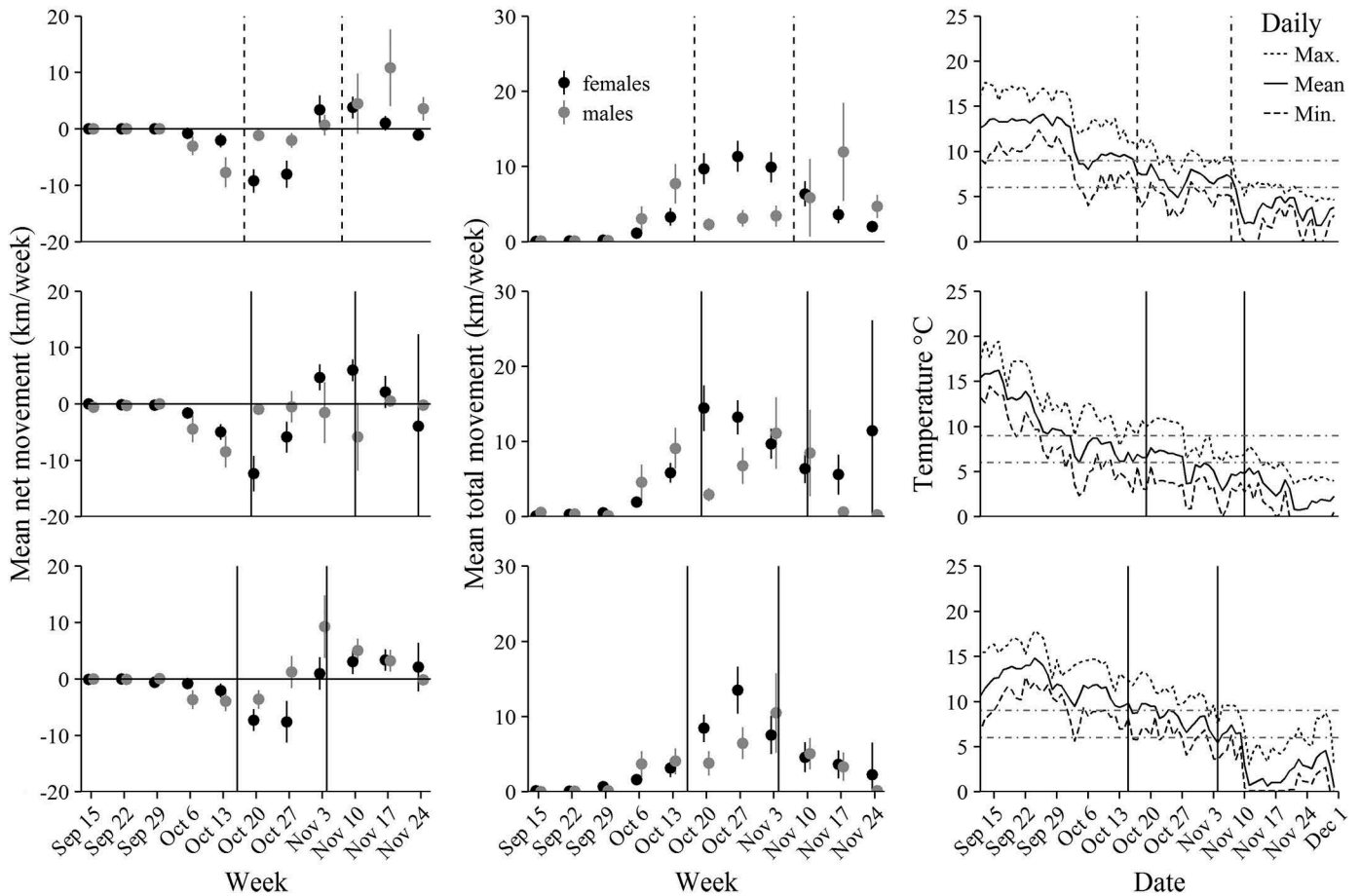


FIGURE 7. Total and net weekly movement rates (mean \pm 95% CI) of radio-tagged Mountain Whitefish and daily mean, maximum, and minimum water temperatures in the Madison River, Montana, during autumn in 2012, 2013, and 2014. Vertical lines indicate the spawning period (solid = determined from embryo collection and female spawning status, dashed = estimated from other years). Weekly movement rates for females and males are offset and are for the week starting with the date labeled on the axis. On temperature plots, horizontal lines indicate thermal thresholds for successful embryo development (9°C = maximum, 6°C = upper optimal; Rajagopal 1979; Brinkman et al. 2013).

floodplain. Macroscale habitat features (e.g., braiding and valley width) appear to be the best explanation for spawning site locations, because we did not find evidence of adult selection for mesoscale habitat features (e.g., depth, substrate, water velocity) or any relationship between spawning sites and winter water temperatures. We are not aware of other studies that have statistically tested spawning habitat selection, but observations of Mountain Whitefish spawning in a wide variety of depths, substrates, and velocities (Brown 1952; Stalnaker and Gresswell 1974; Thompson and Davies 1976; Pierce et al. 2012) suggest that spawning Mountain Whitefish do not show strong selection for mesoscale habitat features in other rivers. Age-0 Mountain Whitefish were associated with slow-velocity, silt-laden habitats (e.g., backwaters, eddies, beaver ponds), and these habitats were most common in braided reaches of the Madison River. Recently hatched (<4 months posthatch) Mountain Whitefish occupy protected areas in many rivers (Brown 1952; Pettit and Wallace

1975; Davies and Thompson 1976), likely because these areas provide velocity refuges. In the Madison River, age-0 fish were concentrated in a relatively small area because of their association with uncommon silt-laden habitat and the clustered nature of spawning locations. Thus, if present in incubation or rearing areas, even localized stressors could have population level influences on Mountain Whitefish recruitment or abundance. Future studies on spatial and temporal overlap between Mountain Whitefish embryos and juveniles and mortality factors could identify limiting factors and guide management, and our description of age-0 Mountain Whitefish spatial distribution can inform future research.

Fluvial Mountain Whitefish typically overwinter in lotic habitats; for example, fish in the Methow and Columbia rivers, Washington, (Benjamin et al. 2014) and the Sheep River, Alberta, (Davies and Thompson 1976) moved downstream to lotic wintering habitats with deep water. Conversely, in the

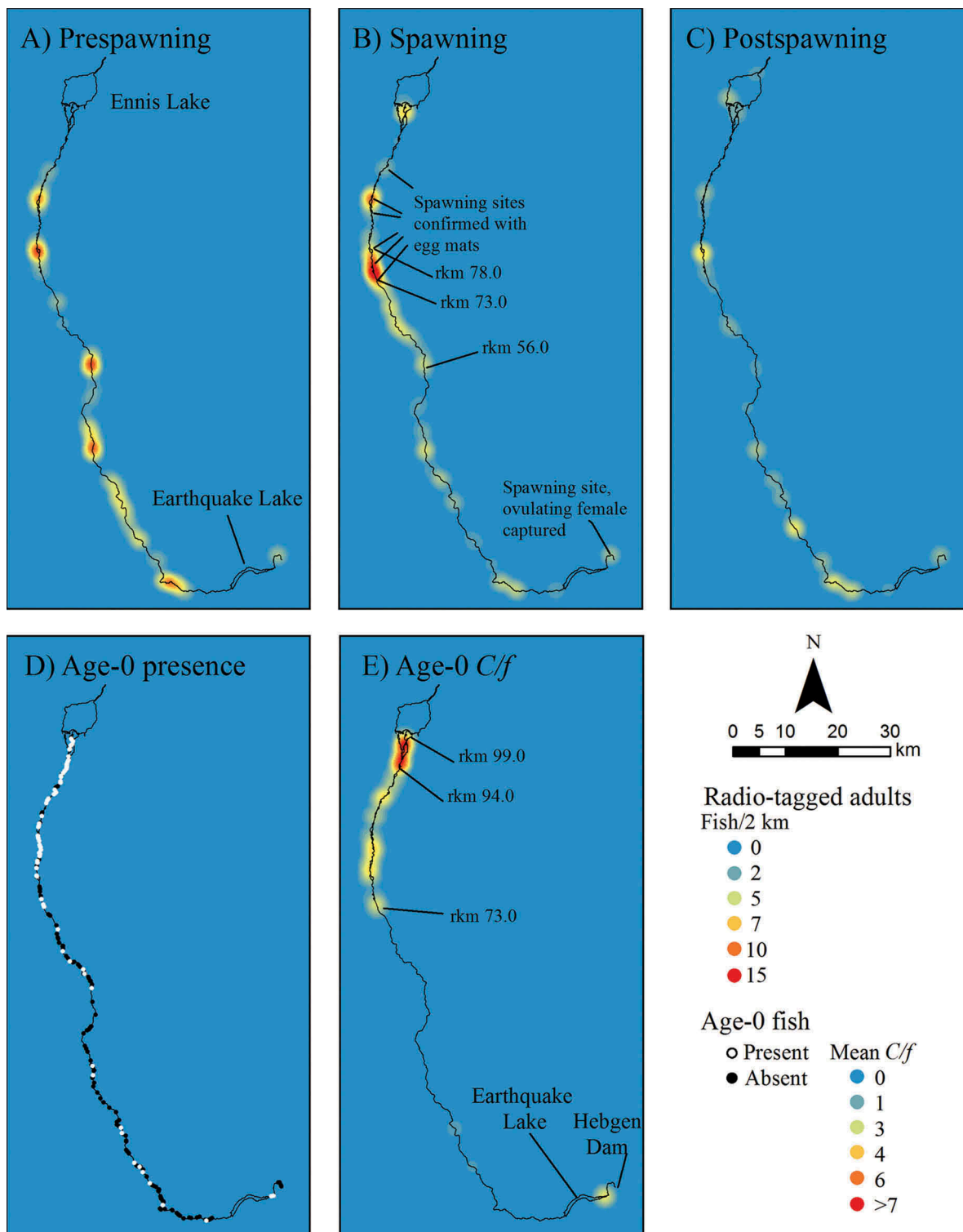


FIGURE 8. Locations of radio-tagged mature Mountain Whitefish during the (A) prespawning, (B) spawning, and (C) postspawning periods in 2012–2014 (all years pooled); and (D) presence and (E) CPUE (C/f) of age-0 Mountain Whitefish sampled by seining in May and June 2014 from the Madison River, Montana.

Madison River drainage Mountain Whitefish used both lotic and lentic habitats for overwintering. In coldwater systems, fish typically select overwintering habitat to minimize energy

expenditure or escape adverse environmental conditions such as ice blockages, frazil ice, and low dissolved oxygen (Cunjak 1996; Huusko et al. 2007). Lentic habitat can meet both

TABLE 4. Coefficient estimates and measures of variation for explanatory variables from zero-altered negative binomial model of age-0 Mountain Whitefish presence and CPUE (i.e., only locations where one or more age-0 Mountain Whitefish were sampled) in the Madison River, Montana, during May–June 2013.

Model parameter	Coefficient estimate	SE	95% CI limits for coefficient estimate	Z-value	P-value	Odds ratio estimate	95% CI limits for odds ratio estimate
Presence model (binomial)							
Intercept	-3.90	0.61	-5.09, -2.70	-6.388	<0.0001		
Spawners25	0.09	0.01	0.06, 0.12	5.773	<0.0001	1.090	1.06, 1.12
Habitat type (reference = channel)							
Backwater	-0.11	0.53	-1.14, 0.92	-0.206	0.837	0.900	0.32, 2.51
Tributary	-2.34	1.17	-4.64, -0.05	-2.003	0.045	0.100	0.01, 0.95
Primary substrate (reference = boulder)							
Cobble	-0.40	1.03	-2.43, 1.62	-0.391	0.696	0.670	0.09, 5.06
Gravel	1.07	0.67	-0.25, 2.39	1.584	0.113	2.910	0.78, 10.93
Sand	0.55	0.97	-1.35, 2.44	0.567	0.571	1.730	0.26, 11.50
Silt	2.19	0.71	0.79, 3.59	3.075	0.002	8.940	2.21, 36.09
CPUE model (negative binomial)							
Intercept	-5.03	1.43	-7.83, -2.23	-3.526	<0.001		
Spawners25	0.06	0.02	0.02, 0.11	2.907	0.004		
Primary substrate (reference = boulder)							
Cobble	3.98	1.69	0.66, 7.30	2.353	0.019		
Gravel	2.98	1.34	0.35, 5.60	2.222	0.026		
Sand	2.79	1.48	-0.12, 5.70	1.880	0.060		
Silt	3.61	1.28	1.09, 6.12	2.811	0.005		

criteria; for example, Atlantic Salmon *Salmo salar* parr in the Stoney River, Newfoundland, entered small lakes during winter to maintain body condition prior to spawning or smolting (Robertson et al. 2003), and Arctic Grayling in the Kuparuk

River, Alaska, migrated to a headwaters lake to escape river ice (Buzby and Deegan 2004).

Mountain Whitefish provide angling opportunities and ecological services in watersheds throughout western North America (Northcote and Ennis 1994; Lance and Baxter 2011; Bellmore et al. 2013), but limited information makes it difficult to understand and effectively manage Mountain Whitefish populations. Our study complements work in other watersheds to characterize the ecology of a widespread, but relatively little studied salmonid. We provided the first histological description of gametogenesis for Mountain Whitefish, and our fecundity, age-at-maturity, and spawning-periodicity values augment a relatively scarce knowledge base.

In the Madison River, our study comprehensively described the reproductive ecology and juvenile habitat use of a Mountain Whitefish population for which little empirical data existed and provides a foundation for studying mechanisms regulating this population. Our fecundity and maturity descriptions are a first step towards understanding the dynamics of this population and show that this population is unlikely to be limited by reproductive development. Our results suggest that investigations into possible factors limiting the Mountain Whitefish population should focus on the embryological and juvenile life stages, and our descriptions of spawning timing and locations and age-0 fish distribution can inform studies investigating these life stages.

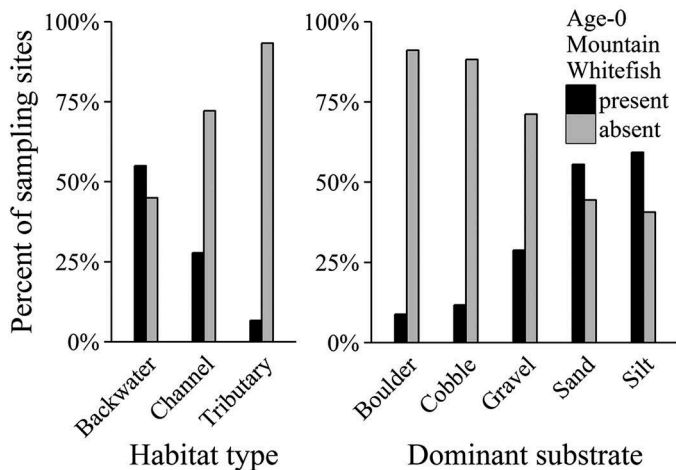


FIGURE 9. Habitat variables associated with the probability of detecting age-0 Mountain Whitefish by means of seines in the Madison River, Montana, in May–June 2014.

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