SPAWNING AND EARLY LIFE HISTORY OF MOUNTAIN WHITEFISH IN THE MADISON RIVER, MONTANA

by

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ABSTRACT

Mountain Whitefish were historically common throughout much of the 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. Recruitment is influenced by factors including reproductive development, spawning behavior, and juvenile distribution. Describing these factors and identifying efficient methods for sampling age-0 fish would form a foundation for investigating mechanisms influencing recruitment. I collected otoliths and gonad samples (n = 147) to characterize fecundity, age-at-maturity, and spawning periodicity. I implanted radio tags in mature Mountain Whitefish (n = 138) and relocated tagged fish in autumn 2012 - 2014. Timing of spawning was determined from spawning status of captured females (n = 85) and from density of eggs collected on egg mats. In spring 2013, I evaluated backpack electrofishing, seining, minnow traps, and lighted minnow traps at sampling sites downstream of Varney Bridge (n = 92). In spring 2014, I seined backwater and channel sites (n = 221) to describe age-0 distribution. Mountain Whitefish in the Madison River were highly fecund (18,450 eggs/kg body weight) annual spawners, and age at 50% maturity was 2.0 for males and 2.6 for females. In 2013 and 2014, spawning occurred between the third week of October and first week of November. Movement varied as a function of spawning behavior, and prespawning movements trended downstream. 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. Of the gears tested, seines were most efficient at sampling age-0 Mountain Whitefish. The downstream reach had the highest catch-per-unit effort of age-0 Mountain Whitefish. Within this reach, age-0 fish were associated with silt-laden backwater and eddy habitats. Maturation and fecundity were similar to other populations, and reproductive development appeared normal, thus factors influencing recruitment probably occur post spawning. Spawning and age-0 rearing sites were concentrated in a small area, thus future work should investigate stressors present in incubation and rearing areas.

CHAPTER ONE

INTRODUCTION TO THESIS

Mountain Whitefish are a relatively common salmonid found throughout western North America (Scott and Crossman 1973). The range of Mountain Whitefish extends from Colorado to the Yukon Territory and from the Pacific Ocean to the Rocky Mountain Front (Brown 1971; Scott and Crossman 1973). Within this range, Mountain Whitefish are most common in mountain lakes and 4th – 7th order streams (Scott and Crossman 1973; Meyer et al. 2009). In the upper Missouri River Basin, Montana, Mountain Whitefish are present in the Missouri River upstream of Missouri River Breaks National Monument and in large (≥ 4th order) tributaries including the Madison, Gallatin, Jefferson, Smith, and Sun rivers. Mountain Whitefish are generally absent from small tributaries (< 4th order) and are not found in warmwater streams where water temperature frequently exceeds 23°C (Brown 1971; Eaton and Scheller 1996).

Mountain Whitefish are often at high abundance in areas where they are present, and are ecologically and economically important. For example, Mountain Whitefish can represent the highest biomass within a fish assemblage (Northcote and Ennis 1994; Paragamian 2002; Meyer et al. 2009); in the Kootenai River, Idaho, Mountain Whitefish represented 70% of catch and 42% of fish biomass, and in the Snake River Basin, Idaho, the highest Mountain Whitefish abundance was 1,257/100 m (Paragamian 2002; Meyer et al. 2009). Thus, Mountain Whitefish probably play an important role in ecosystem dynamics (Lance and Baxter 2011; Bellmore et al. 2013). Mountain Whitefish consume a variety of aquatic invertebrates including Ephemeroptera, Diptera, Trichoptera, and Plecoptera (Laakso 1951; Pontius and Parker 1973) and are consumed by aquatic predators including trout. Mountain Whitefish are also linked to terrestrial food webs through predation by river otters *Lontra canadensis* (Melquist and Hornrocker 1983), osprey *Pandion haliaetus,* and bald eagles *Haliaeetus leucocephalus* (Van Daele and Van Daele 1982). Additionally, Mountain Whitefish are important for human recreation and local economies. Recreational fishing provides a major economic contribution to many Western states and provinces (Bailey and Sumaila 2012, CTC 2012, USFWS 2011). Finally, Mountain Whitefish are the only native salmonid in many of the larger rivers in the Intermountain West (Brown 1971; Scott and Crossman 1973).

In the past decade, population-level declines of Mountain Whitefish have been reported in the southern portion of their range. Declines in abundance have been reported in the Yampa River, Colorado (K. Rogers, Colorado Wildlife and Parks, personal communication), the Big Lost and Kootenai rivers, Idaho (IDFG 2007, Paragamian 2002), and several Wyoming lakes (G. Edwards, Wyoming Fish and Game, personal communication). Anecdotal information suggests Mountain Whitefish abundance may be declining in additional watersheds. In the Madison River, Montana, anglers have reported declining catches of Mountain Whitefish throughout the last decade (P. Clancey, Montana Fish Wildlife and Parks, personal communication). No population trend data on Mountain Whitefish in the Madison River exists to corroborate the angler supposition. However, Mountain Whitefish catch-per-unit-effort (*C/f*) 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 observations made by anglers are plausible.

The reported declines in the Madison River are a cause for concern because Mountain Whitefish are part of a world-renowned recreational fishery. The Madison River supports more angler days than any other river in Montana (MFWP 2008 - 2012), and 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 are also a part of the recreational fishery, and historically provided additional angling opportunities when angling for Brown Trout and Rainbow Trout proved difficult. However, given their current abundance, Mountain Whitefish are more difficult to catch.

The exact mechanisms for reported Mountain Whitefish declines in the Madison River are unknown. Investigations into mechanisms are difficult because of limited ecological information on Mountain Whitefish, relative to other salmonids. Additionally, efficient sampling techniques have not been described for all Mountain Whitefish life stages. A review of Mountain Whitefish biology and habitat use by Northcote and Ennis (1994) located only 112 relevant references published prior to 1994, including grey literature. I located only 22 peer-reviewed papers published since 1994 that addressed Mountain Whitefish ecology (EBSCO Fish, Fisheries & Aquatic Biodiversity database search for “Mountain Whitefish” in abstract). Given the lack of scientific studies and little empirical data for Mountain Whitefish in the Madison River, our research questions focused on understanding female reproductive characteristics, spawning habits, and distribution of juvenile Mountain Whitefish. Fish populations are often limited by recruitment (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.

My objectives in chapter two were to: 1) describe fecundity, age-at-maturity, and spawning periodicity, 2) describe migration, 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 a macroscale (i.e., throughout the study site) and mesoscale (i.e., among habitat types). My objectives in chapter three were to determine which sampling gear had the highest *C/f* of age-0 Mountain Whitefish, and describe habitat characteristics associated with age-0 Mountain Whitefish *C/f*. A lack of information on Mountain Whitefish ecology and habitat requirements has made it difficult to identify mechanisms for declines in abundance reported in the Madison River and throughout the western United States. My findings from chapter two provide the first detailed description of Mountain Whitefish behavior and distribution in the Madison River, and suggest that future studies on mechanisms for decline should focus on juvenile survival and recruitment. My sampling recommendations from chapter three can be used to design efficient standardized sampling protocols for age-0 Mountain Whitefish in the Madison River and likely throughout their range.

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CHAPTER TWO

SPAWNING BEHAVIOR AND JUVENILE DISTRIBUTION OF MOUNTAIN WHITEFISH IN THE MADISON RIVER, MONTANA

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Contributions: Helped conceive study design, implemented study, collected and analyzed data, and authored manuscript.

Co-Author: Christopher Guy

Contributions: Helped conceive study design, provided technical insights, provided guidance on data analysis, and edited manuscript.

Co-Author: Molly Webb

Contributions: Helped conceive study design, provided technical insights, provided guidance on data analysis, and edited manuscript.

Co-Author: Travis Horton

Contributions: Helped conceive study design, coordinated funding and logistics to support data collection.

Co-Author: Thomas McMahon

Contributions: Helped conceive study design, provided technical insights, and reviewed manuscript.

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Abstract

Mountain Whitefish were historically common throughout much of the 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 (n = 147) to characterize fecundity, age-at-maturity, and spawning periodicity. We implanted radio tags in mature Mountain Whitefish (n = 138) and relocated tagged fish in autumn 2012 - 2014. Timing of spawning was determined from spawning status of captured females (n = 85) and from density of eggs collected on egg mats. In spring 2014, we seined backwater and channel sites (n = 221) to describe age-0 distribution. Mountain Whitefish were highly fecund (18,454 eggs/kg body weight) annual spawners, and age at 50% maturity was 2.0 for males and 2.6 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 *C/f* of age-0 Mountain Whitefish, and the percentage of spawning adults in the 25 km upstream of a sampling site was positively associated with juvenile *C/f*. 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.

Introduction

The Madison River is a world-renowned recreational fishery (Gates et al. 2009), supporting more angler days than any other river in Montana (MFWP 2006 - 2012), and 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. Other than Arctic Grayling *Thymallus arcticus* (present at low abundance), Mountain Whitefish are the only native species available to anglers in the Madison River between Hebgen and Ennis lakes (Brown 1971), and historically provided additional angling opportunities when angling for Brown Trout and Rainbow Trout proved difficult. However, in the last decade anglers have reported declining catches of Mountain Whitefish (P. Clancey, Montana Fish Wildlife and Parks, personal communication). No population trend data on Mountain Whitefish in the Madison River exists to corroborate the angler supposition. However, Mountain Whitefish catch-per-unit-effort (*C/f*) 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 observations made by anglers are plausible.

Declines in abundance of Mountain Whitefish are not confined to the Madison River, Montana. Throughout the southern portion of the range of Mountain Whitefish, there are reports of population-level declines; 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 (IDFG 2007; Paragamian 2002); and several Wyoming lakes (G. Edwards, Wyoming Fish and Game, personal communication). Although numerous declines have been reported, the exact mechanisms for declines are often unknown. Some studies have documented mechanisms of Mountain Whitefish mortality including whirling disease (Schisler 2010; Pierce et al. 2012), entrainment (Kennedy 2009), high temperatures (Boyd 2008; Brinkman et al. 2013), decreased discharge (Kennedy 2009), and pollutants (Brinkman et al. 2008; Quinn et al. 2010). However, little is known about the above stressors effect on populations (but see IDFG 2007; Kennedy 2009).

Investigations into mechanisms for declines are difficult because of limited ecological information on Mountain Whitefish, relative to other salmonids. A review of Mountain Whitefish biology and habitat use by Northcote and Ennis (1994) located only 112 relevant references published prior to 1994, including grey literature. We located only 22 peer-reviewed papers published since 1994 that addressed Mountain Whitefish ecology (EBSCO Fish, Fisheries & Aquatic Biodiversity database search for “Mountain Whitefish” in abstract). Given the lack of scientific studies and little empirical data for Mountain Whitefish in the Madison River, our research questions focused on understanding female reproductive characteristics, spawning habits, and distribution of juvenile Mountain Whitefish. Recruitment is typically highly variable in fish populations and can limit population growth (Bradford and Cabana 1997; Myers 2002), so describing factors which influence the abundance and distribution of juvenile Mountain Whitefish could provide a foundation for investigating limiting factors.

A better understanding of the above factors is necessary because Mountain Whitefish are an important part of recreational fisheries and river ecosystems. Mountain Whitefish provide angling opportunities throughout their range. In addition, Mountain Whitefish are the only native salmonid in many of the larger rivers in the Intermountain West and can represent the largest proportion of fish biomass (Goodnight and Bjornn 1971; Paragamian 2002; Lance and Baxter 2011), thus they serve an important role in food webs and nutrient cycling (Bellmore et al. 2013). Mountain Whitefish can also act as indicator species for environmental stresses. For example, Mountain Whitefish have a lower thermal tolerance than Rainbow Trout and Brown Trout (Eaton and Scheller 1996; Boyd 2008; Brinkman et al. 2013) and may be an early indicator of ecological responses to increases in water temperature from climate change.

Describing the reproductive ecology and juvenile habitat use of Mountain Whitefish in the Madison River will provide a foundation for investigating the mechanisms regulating population. The specific objectives of this study were to: 1) describe fecundity, age-at-maturity, and spawning periodicity; 2) describe migration, 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). Here we used a variety of techniques including aging, fecundity estimates, telemetry of spawning adults, and seining of age-0 fish to address the objectives above. Addressing the objectives in combination strengthened our understanding of Mountain Whitefish ecology by allowing us to examine how reproductive development affected timing of spawning and how spawning locations affected juvenile distribution.

Methods

Study Area

The Madison River is formed at the confluence of the Firehole and Gibbon rivers in Yellowstone National Park, Wyoming, and flows north 195 km to Three Forks, Montana, where its confluence with the Gallatin and Jefferson rivers forms the Missouri River. The study area is between Hebgen Dam and Madison Dam, a distance of 101 km (Figure 2.1). Both dams lack fish passage structures and are barriers to upstream movement, but downstream passage is possible. Hebgen Dam, which was constructed in 1914, regulates discharge in this section and functions primarily to store and release water for downstream hydropower plants on the Madison and Missouri rivers. Discharge peaks near 48 m^3/s during spring runoff and is 25 - 30 m^3/s during base flow (10 year daily averages, 2000-2010; 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). Within the last 10 years, pollutants have not exceeded recommended Environmental Protection Agency (EPA) levels, and cadmium, zinc, and copper are below levels toxic to juvenile Mountain Whitefish (Brinkman et al. 2008; PBS&J 2011).

From Hebgen Lake to Varney Bridge the river is primarily a single channel (Figure 2.1). 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 mainstem lakes are present within the study site: Earthquake Lake, a deep (58 m) lake formed by a landslide in 1959, and Ennis Lake, a shallow (7 m) impoundment created by the construction of Madison Dam in 1906. The largest tributaries are the West Fork of the Madison, which enters the mainstem 19 km downstream of Earthquake Lake, and O'Dell Creek, a spring creek that enters the mainstem near Ennis Lake.

The native fish assemblage is comprised of Mountain Whitefish, Arctic Grayling (present at extremely low abundance near Ennis Lake), Mountain Sucker *Catostomus platyrhynchus*, Longnose Sucker *Catostomus catostomus*, White Sucker *Catostomus commersonii*, Longnose Dace *Rhinichthys cataractae*, and Mottled Sculpin *Cottus bairdi*. Non-native species present are Rainbow Trout, Brown Trout, and Utah Chub *Gila atraria* (Brown 1971; Vincent 1987). The parasite *Myxobolus cerebralis*, the causative agent of whirling disease, was first detected in the Madison in 1994, and was responsible for declines in Rainbow Trout (Vincent 1996; Baldwin et al. 1998). However, Rainbow Trout population abundance has rebounded and stabilized at approximately 85% of pre-whirling disease (1951–1990) estimates (Clancey and Lohrenz 2013).

The majority of land in the Madison River Basin is federally owned; the headwaters are within Yellowstone National Park and most of the mountainous terrain surrounding the Madison Valley is owned by the U.S. Forest Service. Lower elevation land adjacent to the study site is primarily privately owned, with small parcels of state and federal land. Public lands are managed for recreation, wilderness, timber, and grazing. The primary land use in the valley is grazing, with irrigated agriculture near Ennis, Montana. In 2011, estimated angler pressure within the study site was 88,252 ± 4,325 angler days (MFWP 2012). Fishing effort in the Madison River is high relative to other lotic systems in Montana. From 2005 through 2010 the study site had the highest use (in angler days) of any river section in Montana (MFWP 2006 - 2010). Harvest regulations on Mountain Whitefish are 20 daily and 40 in possession, but few anglers harvest Mountain Whitefish (P. Clancey, personal communication).

Reproductive Development

Gonadal tissue was collected from Mountain Whitefish sampled with boat-mounted electrofishing (Smith Root VVP 15 B, 200 - 300 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). In October 2012, females were classified in the field as immature or non-reproductive if ovaries contained oocytes ≤ 1.5 mm in diameter, and reproductive if they contained ovarian follicles > 1.5 mm diameter. Males were classified as immature or non-reproductive if testes were pink and threadlike and reproductive if they were large, white, and milty (Strange 1996). Reproductive females were defined as fish which were mid-vitellogenic, late-vitellogenic, or post vitellogenic in autumn, and males were considered reproductive if testicular stage was mid spermatogenic or ripe in autumn (Table 2.1). A section of ovary or testes (1 cm^3) was collected and stored in 10% phosphate buffered formalin (1:10 tissue:fixative) from all fish, except 28 mature females whose entire ovaries were collected to estimate fecundity. Histological analysis of gonadal tissue was used to confirm the accuracy of macroscopic identification of sex and stage of maturity in the field.

Gonadal tissue was processed histologically by embedding in paraffin, sectioning at 5 µm, and staining by Periodic Acid Schiff stain (PAS; Luna 1968). Slides were examined under a compound scope (5-100x, Leica DM2000), and the germ cells were scored for stage of maturation according to a protocol modified from Blazer (2002) and Goetz et al. (2011) (Table 2.1).

Fecundity of individual females was estimated gravimetrically. Each ovary was weighed whole (±0.01 g). A subsample containing 50-100 ovarian follicles was dissected from the anterior, middle, and posterior sections of each ovary. Weight and ovarian follicle count were recorded for each subsample. Fecundity (F) was estimated for each female using the equation:

$$F = \frac{[\sum_i \frac{Oi}{Wi}]}{n} (W_{ovaries}),$$

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.

Simple linear regression was used to evaluate the relationships among fecundity, length, and weight. Fecundity and weight data from other rivers were obtained from the literature (Brown 1952; Northcote and Ennis 1994; Wydoski 2001; Meyer et al. 2009) and compared graphically to fecundity of Mountain Whitefish from the Madison River.

Age 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 binocular microscope. Annuli were counted by two readers to determine age. Age and length at 50% and 90% maturity was estimated using binomial logistic regression in R (R Core Development Team). Separate values were estimated for males and females, because males typically mature at smaller sizes (Wydoski 2001; Meyer et al. 2009).

<u>Fish Capture and Radio-tagging</u>

Mountain Whitefish were sampled throughout the study site using boat mounted electrofishing (boom or mobile anode, Smith Root VVP 15 B, 500 V, 2 - 3 A) and angling in the spring, when water temperatures were < 15°C to minimize stress during surgery and limit risk of infection (Deters et al. 2010). Fish were anaesthetized, weighed to the nearest gram, and measured to the nearest millimeter TL. Fish greater than 450 g (9 g tag was less than 2% of body weight; Cooke et al. 2012) were selected for tagging. Radio transmitters (ATS, model F1205 body implant with internal coil 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 using an otoscope to view gonads before radio transmitter insertion.

Radio Tracking

Radio tags transmitted 24-h per day from 1 September through 30 November for two 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, handheld three-element yagi antenna, and an ATS Challenger R2000 receiver. Additional tracking was conducted from vehicles and on foot where access allowed, primarily upstream of rkm 42.3 (Figure 2.1). Fish locations were obtained by a combination of triangulation and floating directly over fish. A waypoint was recorded in UTMs for each fish location. Location accuracy was 6 ± 7 m (mean ± 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°C) fish were located once weekly. Once water temperature reached 8°C, we attempted to locate fish twice weekly. Areas with fewer fish were floated less often to allow for twice weekly tracking in areas with higher abundances of fish. Two continuous recording fixed stations (Lotek Wireless, SRX-400A) were deployed at the Ennis Lake inlets from 19 October to 30 November 2013 and 30 October to 17 November 2014 to detect fish moving between the Madison River and Ennis Lake. 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 greater than or equal to six times 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-m x 0.54-m rectangle of natural fiber furnace filter attached to a ½-in (13 mm) rebar frame attached to a cinderblock anchor. From 10 October through 27 November 2013 and from 9 October through 20 November 2014, 18 egg mats were deployed near suspected spawning areas that were informed by tracking adults. Egg mats were examined twice a week and Mountain Whitefish embryos were counted and removed. We were able to identify embryos because Mountain Whitefish and Brown Trout are the only fall spawners in the Madison River, and Mountain Whitefish embryos are smaller (~3 mm; Sigler 1951; Brown 1952) than Brown Trout embryos (5-6 mm; Scott and Crossman 1973).

Angling and boat mounted boom electrofishing (Smith Root VVP 15 B, 125 - 300 V, 2 - 3 A) were used to capture mature female Mountain Whitefish and assess spawning status (2013: n = 49, 2014: n = 50) from 27 September through 15 November 2013 and from 29 September through 5 November 2014. For all captured Mountain Whitefish, length, sex, and spawning stage (reproductive, spawning, spent, or immature) were recorded. Sex and spawning stage were determined externally based on observed gametes, tubercles, and body shape. Three reproductive females and three spent females, as determined from external characteristics, were sacrificed to verify spawning status histologically.

<u>Habitat Characterization</u>

The study site was divided into eight reaches (varying from 3.5 to 25.8 km) to characterize habitat at the macroscale (Frissell et al. 1986). Aerial photographs, geological maps, and topographical maps were used to delineate reaches based on boundary features including bedrock types, tributary junctions, lakes, and major elevation changes (Table 2.2; Figure 2.1). 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 river bank were measured at 500-m intervals in ArcMap 10.1 (ESRI) using aerial photos, digital elevation models, and topographical maps (Montana State Library 2015; USGS 2015b). Reach gradient was measured by dividing 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 sites in autumn 2013 and 2014 during base flow. Availability sites characterized river habitat between Raynolds Pass Bridge and Ennis Lake. Random sampling, stratified by reach, was used to select 30 availability sampling sites, spaced > 400-m apart to avoid overlap. Use sampling sites were at confirmed spawning sites (2013: n = 5, 2014: n = 8) where embryos were collected on egg mats. At each spawning site two diagonal downstream transects were followed by rowing a boat, and at each availability site, four diagonal downstream transects were rowed (sampled length 250 - 350 m). At each transect, depth and substrate were measured at five points evenly spaced across the channel width. 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 waterproof video camera (Contour; Roam) attached to the measuring rod at 0.6 m above the substrate was used to estimate dominant and secondary substrate in areas too deep for field observations. Three velocity measurements, spaced evenly across the channel width and level with our landing point at the downstream end of the final rowed transect, were made using the orange float method (Gordon et al. 1997). If sites contained side channels, substrate and depth measurements were made along waded diagonal transects in each side channel, with three measurements per transect.

Water temperature was measured every 5 minutes from 5 May through 30 November each year at four locations (rkm 29.0, 42.0, 57.7, 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 3 December 2014 through 7 March 2015, to compare winter water temperatures between randomly selected availability sites stratified by reach (n = 21) and confirmed spawning sites (n = 7). Discharge data was obtained from three U. S. Geological Survey stations within the study site.

Analysis of Spawning and Movement Data

Spawning dates were determined based on embryo density from egg mats and reproductive stage of captured females. Embryo densities (embryos/m^2/day) were calculated for individual egg mats. Mean daily embryo density was calculated for all egg mats combined. In 2013 and 2014, we defined the start date of the spawning period as the first day when either a spawning female was captured or we collected ≥ 1 embryo on an egg mat. The start of the postspawning period was defined as the day when we captured only spent females or 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, in 2012, the spawning period 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 rkm (± 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 rkm distance between successive relocations by number of days elapsed between relocations. Net movement rate was calculated by dividing the difference in rkm 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 to weekly movement rates to assess relationships. Linear mixed effects models (Zuur et al. 2009) were fit using the R package 'nlme' (Pinheiro et al. 2013) to test for differences in net and total movement rates between males and females, among years, and among periods (prespawning, spawning, and postspawning). Periods were defined as described above. 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). Therefore, 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. This scale was appropriate for comparing fish densities among reaches (3.5 km to 25.8 km in length), and accounted for observed movement rates and the possibility that spawning sites may be several kilometers from telemetry relocations. This function calculates a value for each pixel in the map, with higher values indicating more relocations of tagged fish nearby. The value is dependent on the number of locations within 2 km and the distance to relocations, such that closer locations are weighted more heavily than relocations at the edge of the search radius.

Binomial logistic regression models were fit to habitat data from 2013 and 2014 separately, to determine if mean water velocity, mean depth, proportions of gravel, and proportions of boulder were associated with the odds of a site being used for spawning. At each site, mean water velocity and depth were calculated, and substrate was converted to a set of continuous variables by calculating the proportion of primary substrate observations for each substrate type. 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. Proportion of cobble was not included because it was collinear with proportions of gravel and boulder and 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 if mean daily water temperature and temperature range at spawning and availability sites within the same reach exhibited a 1:1 relationship.

Age-0 Distribution

In spring 2014, seining (3-m x 1.5-m beach seine, 1.6-mm bar mesh) was used to describe age-0 Mountain Whitefish distribution. Sampling in 2013 (Chapter 3) demonstrated that age-0 Mountain Whitefish were rarely present in small channels (≤ 6 m wide) and were only common in large channels when slow velocity areas (≥ 2 m^2) were present. Age-0 Mountain Whitefish were patchily distributed and present at relatively low numbers in the Madison River (Chapter 3), so in order to describe distribution throughout the study site we restricted 2014 sampling to habitats likely to have age-0 Mountain Whitefish present. Thus, we sampled backwaters, channels > 6 m wide (restricted to sites with ≥ 2 m^2 of slow velocity habitat), and four tributaries (O'Dell Creek, Jack Creek, Ruby Creek, and the West Fork; Figure 2.1). 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 2.2), random stratified sampling (strata were backwaters or large channel) was used to select sampling sites (n = 221). In tributaries, random sampling was used to select sites (n = 16). In the field, wadeable sampling sites 50 m in length (that included ≥ 2 m^2 of slow velocity habitat) were identified in pre-selected large channel sites. Sample sizes were estimated from a power analysis using 2013 seining data (see Chapter 3).

Number of seine hauls varied depending on area of wadeable habitat at a site and presence of obstructions (e.g., submerged logs, boulders), but a minimum of three seine hauls were conducted at each site. Total length (TL) was measured for all Mountain Whitefish (± 1 mm). At each sampled site, water temperature (± 0.1 ºC), maximum depth (± 0.1 m), and channel width (± 0.5 m) were measured. Length and width (± 0.5 m) was measured for each backwater. Primary and secondary substrate, turbidity, and water velocity were visually estimated in each sampled site (Table 2.3).

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 *C/f* (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 *C/f* were created with ArcMap 10.1 (ESRI). No age-0 Mountain Whitefish were captured at a large proportion of sites (140 of 221 sites), subsequently *C/f* 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 *C/f* and habitat characteristics.

All habitat variables (Table 2.3) and *C/f* were plotted to evaluate relationships. In addition to graphs, simple linear regression was used to explore possible correlations between log *C/f* of age-0 fish and percentages of spawners within 1, 5, 10, 15, 20, or 25 km upstream. Examination of plots suggested relationships between *C/f* and habitat type, dominant substrate, channel width, water velocity, and percentage of spawning adults within 25 km (Table 2.3). The above 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 using $\alpha = 0.05$ unless noted otherwise.

Results

Reproductive Development

Fecundity estimates varied from 4,369 to 25,349 for females from 291 to 1254 g (309 to 493 mm TL, ages 2 – 14). Fecundity was significantly correlated with weight (R^2

= 0.91, *df* = 26, $P < 0.0001$; Figure 2.2) and length ($R^2 = 0.82$, *df* = 26, $P < 0.0001$) and was similar to other water bodies throughout the species range (Figure 2.2).

Histological examination of a subset of gonadal samples ($n = 120$) corroborated the field determinations of maturity and developmental stage (Figures 2.3 and 2.4). 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 (mid vitellogenic or late vitellogenic). Females showed varying levels of yolk and lipid coalescence and centered or off-center nuclei (Figure 2.3). Examination of vitellogenic ovaries revealed primarily intact ovarian follicles, and spent ovaries had primarily post-ovulatory follicles. Follicular atresia of developing oocytes was limited (< 10%) in both vitellogenic and spent ovarian samples (Figure 2.3).

Female Mountain Whitefish matured at slightly older ages and larger sizes than males (Figure 2.5). 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 to 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 19 October. The last spawning female was captured on 10 November. On 11 November density of embryos collected on egg mats declined to 0.3 embryos/m^2, 7% of the maximum embryo density (4.27 embryos/m^2; Figure 2.6). Based on the above observations, we defined the 2013 spawning period as 19 October to 10 November. In 2014, embryos were first collected on 16 October. All females (n = 19) captured by electrofishing on 5 November were spent (Figure 2.6). Given the above information, the spawning period was determined to be from 16 October to 4 November in 2014.

Movement

Mean total movement > 1 km/day was first observed during the first week in October in all years (Figure 2.7). In general, mean total movement for both sexes was greatest during the spawning period. Total movement rates varied between the prespawning, spawning, and postspawning periods, and these variations depended on the sex of fish; there was a significant interaction between sex and period (F = 5.89, df = 180, P = 0.0033). Total movement rates were higher for females than males during the spawning period, but total movement rates were higher for males in the prespawning and postspawning periods (Figure 2.7). We did not detect differences in mean total movement rates among years (F=2.61, df = 49, P = 0.084).

The majority of movement was downstream during the transition between the prespawning and spawning periods (negative net movement values; Figure 2.7). Most tagged fish moved downstream during the prespawning and spawning seasons (n = 24, 37, 16 in 2012, 2013, and 2014, respectively), although some tagged fish moved short distances upstream (n = 1, 5, 6 in 2012, 2013, and 2014, respectively), and others remained within 1 rkm for the entire tracking period (n = 7, 14, 9 in 2012, 2013, and 2014, respectively). The mean distance (furthest downstream location – furthest 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. Mean net movement varied between the prespawning, spawning, and postspawning periods, and these variations depended on the sex of 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 prespawning period and female movement was more downstream during the spawning season (Figure 2.7). 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.

The declining trend in autumn water temperatures varied among years, with a relatively slow decline punctuated by rapid cooling periods in 2012, the steepest decline in 2013, and a relatively slow decline in 2014 (Figure 2.7). For example, in early September water temperature was similar among all years, but during the first two weeks of October mean water temperature was 9.9°C in 2012, 7.8°C in 2013, and 10.9°C in 2014 (Figure 2.7). Water temperature declined more rapidly during the 2013 prespawning period (slope = -1.5°C/wk) compared to 2012 (-1.1°C/wk) and 2014 (-0.8°C/wk). In 2012, a sharp decline in water temperature (12.7 – 8.6°C) was observed between 2 October and 4 October, but in 2013 and 2014 water temperature declined more gradually during the prespawning period (Figure 2.7). One consequence of this variability in temperature during the prespawning season was that spawning related fish movements were observed in water temperatures varying from 2.7°C to 14.8°C (Figure 2.7). During the spawning period, mean water temperature was 5.6°C in 2013 and 8.2°C in 2014 (Figure 2.7). Water temperature during the 2013 spawning period was variable, with mean daily water temperature declining 3.0°C from 27 October to 28 October, and minimum temperatures of < 1°C recorded on 2 days. Conversely, temperature declined gradually throughout the entire 2014 spawning period, and the lowest temperature recorded was 4.1°C (Figure 2.7).

We also examined lunar phase as a possible cue for movement and spawning, but did not find any evidence that certain lunar phases were associated with movement or spawning events. Among 2012, 2013, and 2014, the start of spawning movements, peak movement, and the start of spawning occurred during various lunar phases.

Spawning Locations

Fish relocations and embryo collection suggested most spawning occurred downstream of rkm 73. Each year during the prespawning period, tagged fish were evenly distributed throughout the study site (Table 2.2; Figure 2.8 panel A). Mountain Whitefish were relocated throughout the entire study site (from 0.9 km downstream of Hebgen Dam to the Ennis Lake inlet) during the spawning period, but a disproportionate number of fish were observed downstream of rkm 56, with the highest numbers relocated between rkm 73 and 78 (Table 2.2; Figure 2.8 panel B). 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 2.8).

During the postspawning period, fish were relocated throughout the river and in Ennis and Earthquake lakes (Figure 2.8 panel C). In 2013, 60% of the fish (33 of 55) remained in the river after spawning, 35% (19 of 55) entered Ennis Lake between 24 October and 24 November, and 5% (3 of 55) entered Earthquake Lake. We were unable to accurately determine numbers of fish in lakes in 2012 and 2014 because fixed stations were not operational during the entire movement period.

Spawning Habitat

At the macroscale, mean bench width and braiding were highest where the largest concentration of Mountain Whitefish spawning occurred. Spawning was concentrated in reach 7 (rkm 74.3 – 100.1), which had the highest braiding index value and mean bench width (Table 2.2). Fish were most frequently located in reaches 6 (rkm 57.7 – 74.3) and 7 during the spawning period, but fish located in reach 6 were typically moving through this reach (i.e., 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 of 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 (Figure 2.9). There was no evidence that depth (2013: Z = 1.072, df = 29, P = 0.284, 2014: Z = 0.875, df = 33, P = 0.382), water velocity (2013: Z = -1.870, df = 29, P = 0.062, 2014: Z = -1.136, df = 33, P = 0.256), or proportion of gravel (2013: Z = -0.819, df = 29, P = 0.413, 2014: Z = -1.461, df = 33, P

= 0.144) were associated with the odds of a site being used for spawning. There was no evidence that proportion of boulder was associated with spawning use in 2013 (Z = -1.232, df = 29, P = 0.218), but in 2014 the proportion of boulder was negatively associated with odds of spawning use (Z = -2.093, df = 33, P = 0.036).

Winter water temperatures 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 3 December 2014 and 7 March 2015. Sites > 20 km downstream of a lake (reaches 4 – 7) had colder (mean = 1.6°C) and more variable (mean daily temperature change = 1.6°C) water temperatures during the same time period (Figure 2.10). Mean daily water temperature and mean daily water temperature change were similar between spawning sites and availability sites within the same reach (Figure 0.10; Figure 0.11).

Age-0 Distribution

A total of 1449 age-0 Mountain Whitefish were sampled between 13 May and 12 June 2014. Age-0 Mountain Whitefish were captured at 82 sampled sites and not detected at 139 sites (Figure 2.8 panel D). At sites with age-0 Mountain Whitefish, *C/f* varied from 0.1 to 17.

At the macroscale, age-0 Mountain Whitefish catch was highest downstream of rkm 73.0. For example, 90% of age-0 Mountain Whitefish were sampled downstream of rkm 73.0, although this reach accounted for only 29% of study-site length and 39% of sites sampled (Figure 2.8 panel E). 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 of rkm 73.0 (Figure 2.8 panel B), and age-0 presence (Z = 5.77, df = 15, P = < 0.0001) and C/f (Z = 2.91, df = 15, P = 0.004) were positively associated with numbers of adults within the 25 km upstream of a sampling site (Table 2.4). Correlations between log C/f and percent of adults upstream of a site were weak when adults within 1, 5, 10, and 15 km were considered (r^2 = 2.2 X 10^{-5} - 0.09, df = 220, P = < 0.0001 - 0.94), slightly stronger at 20 km (r^2 = 0.19, df = 220, P = < 0.0001), and the best at 25 km (r^2 = 0.31, df = 220, P = < 0.0001).

Age-0 Mountain Whitefish were present in 27% of 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 2.4) compared to channels. Dominant substrate was the best predictor of age-0 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 2.4; Figure 2.12). Silt-laden sites where age-0 Mountain Whitefish were captured included backwaters, eddies, beaver ponds, and slow velocity areas immediately downstream of islands and rock bars.

At sites with age-0 Mountain Whitefish present, C/f was variable and difficult to predict using mesoscale habitat variables. Models predicted that where age-0 Mountain Whitefish were present, C/f 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) dominant substrates, when compared to boulder (Table 2.4).

Discussion

Our study investigated the reproductive development, spawning behavior, and early-life distribution of Mountain Whitefish in the Madison River—a world-renowned fishery and an important watershed in the Greater Yellowstone Ecosystem. We used a variety of methods to investigate multiple life stages with the understanding that we would begin to clarify the mechanisms causing the decline in Mountain Whitefish abundance. Here, we found that fecundity, age-at-maturity, and spawning periodicity were similar to values reported for other Mountain Whitefish populations studied (Brown 1952; Northcote and Ennis 1994; Meyer et al. 2009). Adult movement patterns were similar among years despite variable water temperature schedules during the spawning season. Spawning activity and age-0 fish were concentrated in the downstream 26 km of the study site, a braided area with complex habitat. Finally, age-0 Mountain Whitefish were sampled near spawning areas and were most often found in slow velocity, silt-laden habitats.

Reproductive Development

Female Mountain Whitefish in the Madison River were highly fecund annual spawners, typically matured by age 3, and oocytes in ovarian samples exhibited group synchronous maturation. Among fish age 3 and older, 97% of females were and all males were reproductive, demonstrating that fish in this population spawn annually once sexual maturity is reached. Mountain Whitefish are group synchronous spawners, but spawning dates of individual females likely vary by several weeks, which matches our observations of a 23-day spawning period in 2013 and a 22-day spawning period in 2014.

Mountain Whitefish fecundity, age-at-maturity, and spawning periodicity were similar between the Madison River and other rivers at similar latitude and elevation. In the Madison River, Mountain Whitefish fecundity relative to weight was comparable to values reported for fish in the Gallatin, Yellowstone, and Missouri rivers, Montana (Brown 1952), the Logan and Blacks Fork rivers, Utah (Sigler 1951; Wydoski 2001), and Phelps Lake, Wyoming (Hagen 1970). Age at 50% maturity in the Madison River was 2.6 years for females and 2.0 years for males. Mountain Whitefish matured at similar ages in in the Snake River Basin, Idaho, where age at 50% maturity was 2.7 for females and 2.0 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 Snake River Basin populations (Meyer et al. 2009). Lower fecundity and delayed maturation have been reported at higher altitudes and latitudes, where low temperatures presumably limit growth and reproductive development. Maturation was delayed in a high elevation stream, the Blacks Fork River in Utah, where males reached maturity by age 4 and females reached maturity at ages 4 – 7 (Wydoski 2001), and in the Sheep River, Alberta, where 90 % of fish were mature at age-4 (Thompson and Davies 1976). There is no evidence to suggest that fecundity, age-at-maturity, and spawning periodicity for the Mountain Whitefish population in the Madison River are atypical when compared to stable or increasing populations. That is, the similarities in fecundity and age at maturity between Mountain Whitefish in the Madison River and other rivers at similar latitude and elevation suggests that low fecundity or infrequent spawning are not plausible limiting factors.

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 and macrophages (Blazer 2002). We did not observe the above symptoms. In vitellogenic females and spent females, we observed primarily normal ovarian follicles or postovulatory follicles and < 10% atresia. The only evidence of limited reproduction was one non-reproductive age-6 female sampled in October 2012. All other females age-3 and older were reproductive, indicating that annual spawning is typical at a population level, and biennial or longer spawning cycles are rare.

Our characterization of reproductive development in the Madison River is useful because information on Mountain Whitefish reproductive development is limited relative to other salmonids. To our knowledge, our study provides the first histological description of gametogenesis in Mountain Whitefish and the second report on spawning periodicity (Meyer et al. 2009). Age-at-maturity and fecundity have been described in several other populations, but our study augments a relatively sparse knowledge base and facilitates comparative studies.

Movement, Spawning, and Age-0 Distribution

After three years of studying the movement of Mountain Whitefish in the Madison River, clear patterns emerged. Spawning related movement began in early October, with males moving first to spawning sites, females following, and spawning occurring during the last two weeks of October and first week of November. Spawning occurred at water temperatures between 13.3°C and 0.0°C, and movement patterns were similar among years with varying water temperature schedules, suggesting that factors other than declining water temperature may 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 fish were most common in braided reaches, and age-0 presence was associated with protected, silt-laden habitat, and possibly with larval drift patterns. 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, 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. 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. Mountain Whitefish moved similar distances in other rivers; for example, movements from < 1 km to 80 km were observed in the Clearwater River, Idaho and Blackfoot River, Montana (Pettit and Wallace 1975; Pierce et al. 2012). However, migratory Mountain Whitefish typically moved upstream to mainstem 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 movements varied between sexes. Total movement rates were higher for males during the prespawning period, and higher for females during the first two weeks of the spawning period. Males likely began spawning movements 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. For example, decreasing water temperatures were correlated with spawning movements of Bull Trout *Salvelinus confluentus* (Swanberg 1997; Brenkman et al. 2001) and Brown Trout (Riedel and Peter 2013). Water temperatures in the Madison River declined during prespawning movements and spawning, but we observed wide variability in temperatures, rates of temperature decline, and dates of rapid decreases in temperature among years. Prespawning movements began during the first week of October in all 3 years, and in 2012 water temperature declined rapidly during this week, in 2013 the rate of temperature decline decreased during this week, and in 2014 temperature declined for several days then warmed. 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. Lunar cycles can also cue spawning (Forsythe et al. 2012), but we did not observe any correlations between lunar phase and spawning in the Madison River. 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), and in the Madison River females began vitellogenesis in May suggesting spring and summer conditions may influence rates of ovarian development. The similarities in timing of spawning and movement 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 of rkm 73.0. Interestingly, the Madison River changes near rkm 73.0, transitioning from a single channel confined between high benches to a braided channel with a wider floodplain. Limited sampling in the moderately braided reach between Hebgen and Earthquake Lakes (rkm 0.0 – 3.5) confirmed that spawning also occurs in this reach (ovulating female captured and evening observations of spawning aggregations). We found little evidence that mesoscale habitat features or winter temperatures were associated with spawning site selection. It is possible that spawning is concentrated in these reaches because adults are returning to rearing areas. Homing to natal areas for spawning is well documented in anadromous salmonid populations (Quinn 2000), and although fewer studies have investigated this behavior in inland salmonids, spawning site fidelity has been documented. For example, genetic analyses on Bull Trout in tributaries of Lake Pend Oreille, Idaho (Spruell et al. 1999), and Arctic char *Salvelinus alpinus* in the Forth catchment, Scotland (Adams et al. 2006) found that spawning site fidelity maintains genetically distinct populations in watersheds with high connectivity. Individual Mountain Whitefish adults have been observed in the same pool or tributary during the spawning period over consecutive years (Pettit and Wallace 1975; Davies and Thompson 1976; Benjamin et al. 2014), suggesting that homing behavior may occur. 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, silt-laden areas in many rivers, likely because these areas provide velocity refugia. Age-0 Mountain Whitefish occupied shallow backwaters in a braided reach of the Sheep River, Alberta (Davies and Thompson 1976), and protected areas including backwaters and pockets behind boulders in the Gallatin and Yellowstone rivers, Montana (Brown 1952), and Clearwater River, Idaho (Pettit and Wallace 1975). Backwaters are important rearing habitat for many warmwater fish species (Scheidigger and Bain 1995; Nannini et al. 2012) and coldwater cyprinids (Gee and Northcote 1963), but age-0 salmonids are more commonly associated with unembedded rocky substrates (Bjornn and Reiser 1991). Many age-0 salmonids use cover such as interstitial spaces or woody debris as refugia from predators and high velocities, but age-0 Mountain Whitefish were captured in open areas with little cover. Silt-laden areas such as backwaters and eddies are selected by Mountain Whitefish; however, the exact reason for the habitat selection is difficult to determine from our study.

We suspect larval drift also influenced age-0 distribution. Larvae of river spawning whitefishes *Coregonus spp.* in Eurasia emerged from the substrate into the water column immediately after hatching (Fabicius and Lindroth 1954; Braum 1964, cited by Naesje et al. 1995), and drift downstream to rearing areas. High discharge during spring floods lead to increased hatching and larval drift distances for whitefishes including Common Whitefish *C. lavaretus*, Broad Whitefish *C. nasus,* and Peled *C. peled* (Naesje et al. 1986; Bogdanov and Bogdanova 2012). Our observations of Mountain Whitefish behavior and distribution suggest similar larval drift occurs. Embryos were collected on egg mats in relatively fast water velocities, thus hatching Mountain Whitefish are likely dispersed by the current. Larval drift is also a logical explanation for two spatial patterns in age-0 *C/f* observed in the Madison River. Age-0 Mountain Whitefish were frequently present in silt-laden backwaters and eddies adjacent to channels with high flow, but absent in similar silt-laden habitats adjacent to side channels with lower flow. Additionally, spawning adult locations were associated with age-0 *C/f* at large scales (25 km) but not at smaller scales (< 15 km). For example, we captured no whitefish when sampling a silt-laden eddy within 10 m of a confirmed spawning site, and recorded our highest *C/f* in a backwater near Ennis Lake, 9 km downstream of the closest confirmed spawning site. We speculate that many age-0 fish were located in habitats distant from spawning sites in May and June because fish drifted to these areas from upstream spawning sites.

Proximity to age-0 rearing habitat appears to be the best explanation for spawning site locations, because we did not find evidence of adult selection for mesoscale habitat features or any relationship between spawning sites and winter conditions. We did not find evidence that spawning adults selected for depth, substrate type, or water velocity. Mountain Whitefish are broadcast spawners, so it is logical that we failed to detect evidence of mesoscale habitat selection. We are not aware of other studies which 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. For example, Mountain Whitefish have been observed spawning in pools and riffles (Stalnaker and Gresswell 1974) at depths from 0.1 m to > 2 m (Brown 1952; Thompson and Davies 1976), in water velocities from slow to fast (Brown 1952; Thompson and Davies 1976; Pierce et al. 2012), and on gravel, cobble, and boulder substrates (Brown 1952; Thompson and Davies 1976; Pierce et al. 2012).

Spawning sites of autumn spawning fish can be associated with stable winter incubation conditions (i.e., stable water temperature, limited ice scour and winter flooding). Winter temperatures and ice formation can affect egg survival (Rajagopal 1979; Baxter and McPhail 1999; Huusko et al. 2007), and changes in water temperatures alter hatching dates and subsequent rearing conditions. Bull Trout and Brook Trout *Salvelinus fontinalis* redds are sometimes associated with groundwater upwelling, where warm, stable temperatures (relative to surface water temperatures) provide favorable incubation conditions (Curry and Noakes 1995; Baxter and McPhail 1999; Baxter and Hauer 2000). However, Mountain Whitefish spawning sites did not appear to be associated with areas that had stable winter water temperatures in the Madison River. Ice scour is most common in the reach where Mountain Whitefish spawning was concentrated. Winter temperatures at spawning sites and nearby availability sites were cold and variable, suggesting that discharge in spawning areas is dominated by surface water rather than groundwater. Temperatures were warmer and less variable in reaches immediately downstream of Hebgen and Earthquake, similar to groundwater upwelling areas in other rivers (Zimmerman and Finn 2012). Fish tagged between Hebgen and Earthquake lakes remained in this reach during the spawning period, but most fish in the reach downstream of Earthquake Lake moved downstream and away from the lake outlet prior to and during spawning. Redds of Brown Trout, another autumn spawner, are most common in upstream reaches of the study site (Montana Fish, Wildlife, and Parks, unpublished data), suggesting that suitable winter incubation conditions exist throughout large portions of the Madison River.

After spawning, many Mountain Whitefish entered lakes to overwinter. In 2013, 40% of the fish entered either Ennis or Earthquake lakes from late October through late November. These fish were captured or relocated in the Madison River in May, July, and early autumn, so fish are likely overwintering in the lakes. Fluvial Mountain Whitefish typically overwinter in lotic habitats; for example fish in the Methow and Columbia Rivers, Washington (Benjamin et al. 2014) and Sheep River, Alberta (Davies and Thompson 1976) moved downstream to lotic wintering habitats with deep water. Conversely, in the Madison drainage Mountain Whitefish used both lotic and lentic habitats for overwintering. In coldwater systems, fish typically select overwintering habitat to minimize energy expenditure (i.e., preferred temperatures or low water velocities) or escape adverse environmental conditions including ice blockages, frazil ice, and low dissolved oxygen (Cunjak 1996; Huusko et al. 2007). Lentic habitat can meet both 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. 2004), and Arctic Grayling in the Kuparuk River, Alaska, migrated to a headwaters lake to escape river ice (Buzby and Deegan 2004).

Future Directions

Future investigations into possible limiting factors for Mountain Whitefish in the Madison River should focus on the embryological and juvenile life stages. Mountain Whitefish were highly fecund and matured at young ages, and histological sections showed normal development of ovarian follicles, thus limited egg production is not a plausible limiting factor. Spawning sites were concentrated in the downstream third of the river, and age-0 Mountain Whitefish were largely restricted to silt-laden habitats within this reach. Thus, if present in incubation or rearing areas, even localized stressors could have population-level influences on recruitment and abundance. Future studies on spatial and temporal overlap between Mountain Whitefish embryos and juveniles and mortality factors could identify limiting factors and guide management.

High water temperatures during spawning may cause embryo mortality, although our temperature loggers deployed in autumn were not placed at spawning sites, and temperatures in spawning areas may have differed from recorded temperatures. Water temperatures throughout most of the winter incubation period were < 6ºC, the upper optimum temperature (Rajagopal 1979) for embryo development. However, temperatures > 9ºC were recorded during spawning. At temperatures > 9 ºC, Mountain Whitefish hatch rates and posthatch survival are reduced, and deformities become more common (Rajagopal 1979; Brinkman et al. 2013). Collecting eggs to investigate embryo mortality and comparing 2012 – 2014 temperatures to historic autumn temperatures could determine if temperature induced embryo mortality is a plausible limiting factor.

Three factors which may influence age-0 growth and survival are whirling disease, drift into lakes, and food availability in rearing habitats. The parasite which causes whirling disease, *M. cerebralis,* is present in the Madison River and has caused Rainbow Trout declines (Vincent 1996; Krueger et al. 2006). Age-0 Mountain Whitefish are susceptible to whirling disease, but mortality rates depend on age at exposure (Schisler 2010), and temporal overlap between vulnerable life stages and peak triactinomyxon (TAM, life stage of *M. Cerebralis* that infects fish) releases typically exists only in river reaches with warm winter temperatures (Pierce et al. 2012). Our results suggest that Mountain Whitefish drift after hatching and may drift into Ennis and Earthquake lakes. We do not know how many age-0 Mountain Whitefish enter lakes or how rearing in lentic systems influences growth or survival. We also know little about conditions in lotic rearing habitat. We did not capture large numbers of other fish species in areas with age-0 Mountain Whitefish, suggesting that predation and interspecific competition are unlikely to be limiting factors. Thus, we suggest evaluating food availability. Determining whether TAM releases overlap temporally with vulnerable Mountain Whitefish, quantifying drift distances, and evaluating food availability in lotic and lentic habitats are logical next steps for investigating factors that affect survival of juvenile Mountain Whitefish in the Madison River.

Tables

TABLE 2.1. Stages of reproductive development used to assign stages to gonad samples (modified from Blazer 2002, Goetz et al. 2011). Stages marked with * 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
Mid vitellogenic	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
Post vitellogenic*	Yolk globules and lipid droplets fused, nucleus has migrated to animal pole but remains intact
Spawning	Entirely fused yolk, oocyte ovulated from follicular layers
Spent	Post-ovulatory follicles and previtellogenic oocytes present
Males	
Pre-spermatogenic*	only spermatogonia present
Early spermatogenic	spermatogonia, spermatocytes, and spermatids may be present
Mid spermatogenic*	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

TABLE 2.2. Macroscale habitat measurements and fish 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 bench width (m)	Percent of fish in reach during	
								Prespawning	Spawning
1	Hebgen Dam	0.0	7.7	1.9	1.9	50	114	2.5	2.8
2	Earthquake Inlet	3.5		Earthquake Lake				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	1888	4.6	23.0
7	Wigwam Creek	74.3	4.3	1.1	3.6	58	2601	24.9	36.3
8	Ennis Inlet	100.1		Ennis Lake				0.0	5.9

TABLE 2.3. Habitat variables measured at seining sampling sites in the Madison River in May and June 2014. All variables were compared graphically to age-0 catch-per-unit effort (*C/f*) data, but only variables marked with * were included in rich zero-inflated-negative-binomial models fit to age-0 *C/f* 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 to 1.0 m/s), slow (< 0.6 m/s)
Temperature	Water temperature (± 0.1°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 USGS gauge
Spawners within 1, 5, 10, 15, 20, or 25* km upstream	Percent of tagged adult relocations during the 2013 spawning window (19 Oct to 10 Nov 2013, standardized to 1 location per fish per week) within 1, 5, 10, 15, 20, or 25 km upstream of the sampling unit, respectively,

TABLE 2.4. Coefficient estimates and measures of variation for explanatory variables from zero-altered negative binomial model of age-0 Mountain Whitefish presence and *C/f* (i.e., only locations where one or more age-0 Mountain Whitefish were sampled) in the Madison River, Montana, from May – June 2013.

	Coefficient estimate	SE	95% CI for coefficient estimate	*Z* value	*P*-value	Odds ratio estimate	95% CI for odds ratio estimate
	Presence model (binomial)						
Intercept	-3.90	0.61	(-5.09, -2.7)	-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, 11.5)
Silt	2.19	0.71	(0.79, 3.59)	3.075	0.002	8.940	(2.21, 36.09)
	***C/f* 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, 7.3)	2.353	0.019		
Gravel	2.98	1.34	(0.35, 5.6)	2.222	0.026		
Sand	2.79	1.48	(-0.12, 5.7)	1.88	0.060		
Silt	3.61	1.28	(1.09, 6.12)	2.811	0.005		

Figures

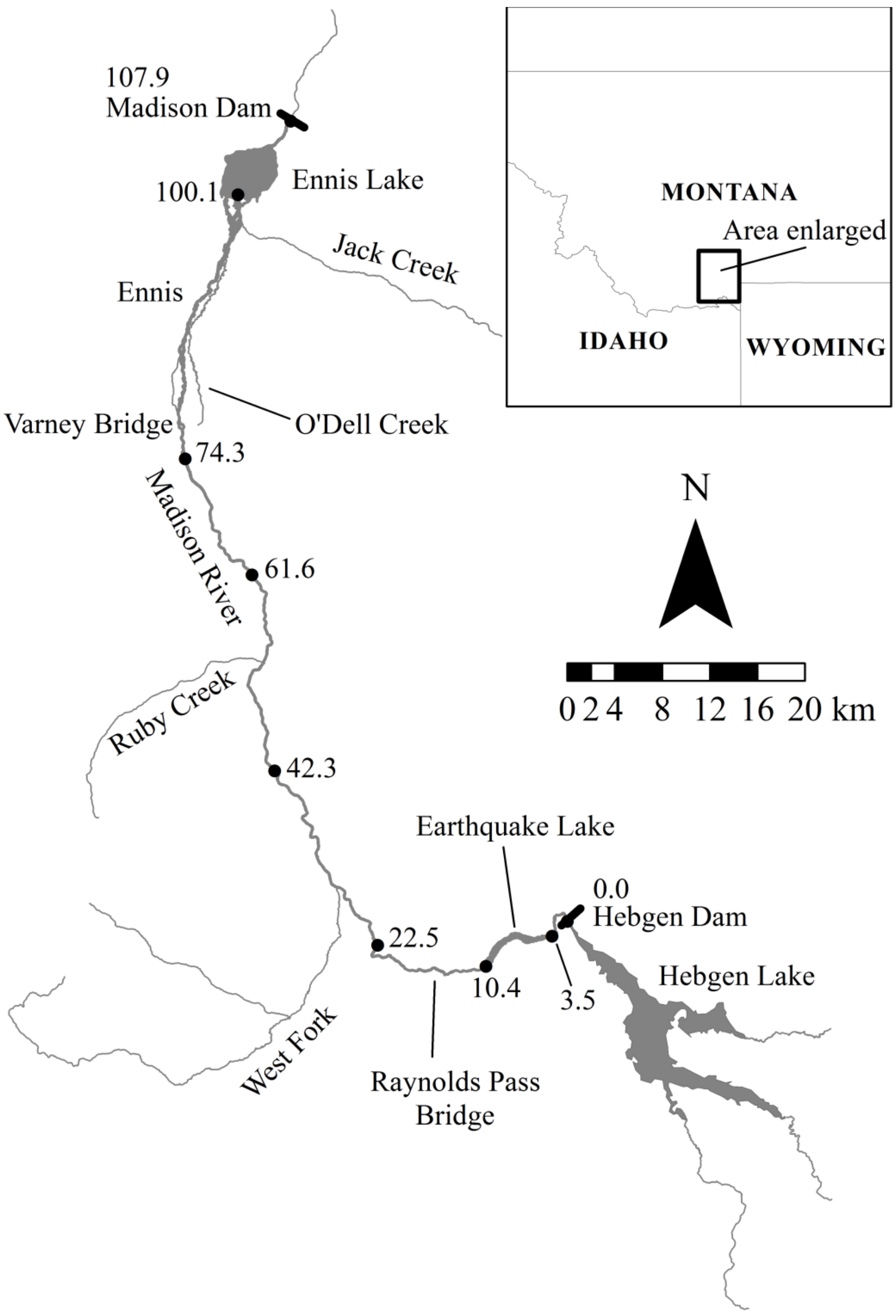

FIGURE 2.1. Map of study site on the Madison River, Montana. Solid circles labeled with river kilometer (Hebgen Dam = 0.0) show boundaries of river reaches used for sampling stratification and macroscale habitat descriptions. Only tributaries sampled for age-0 Mountain Whitefish in spring 2014 are shown.

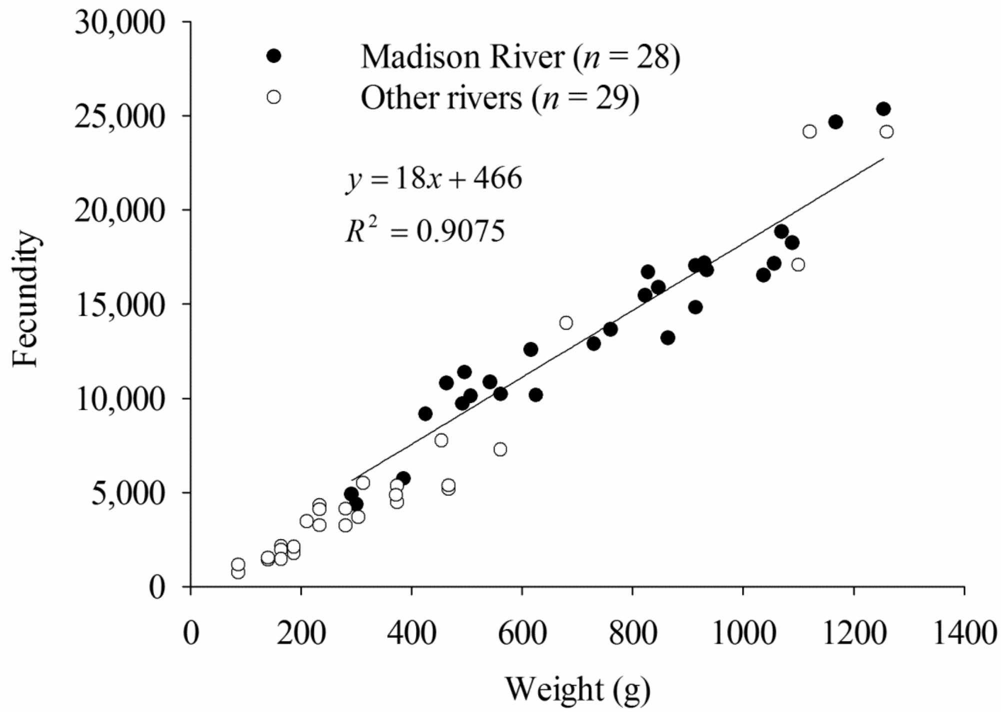

FIGURE 2.2. Weight-fecundity relationship for Mountain Whitefish captured with boat electrofishing in the Madison River, Montana from 10 to 12 October 2012, and in other watersheds (Sigler 1951; Brown 1952; Northcote and Ennis 1994; Wydoski 2001). The regression line includes only Mountain Whitefish from the Madison River.

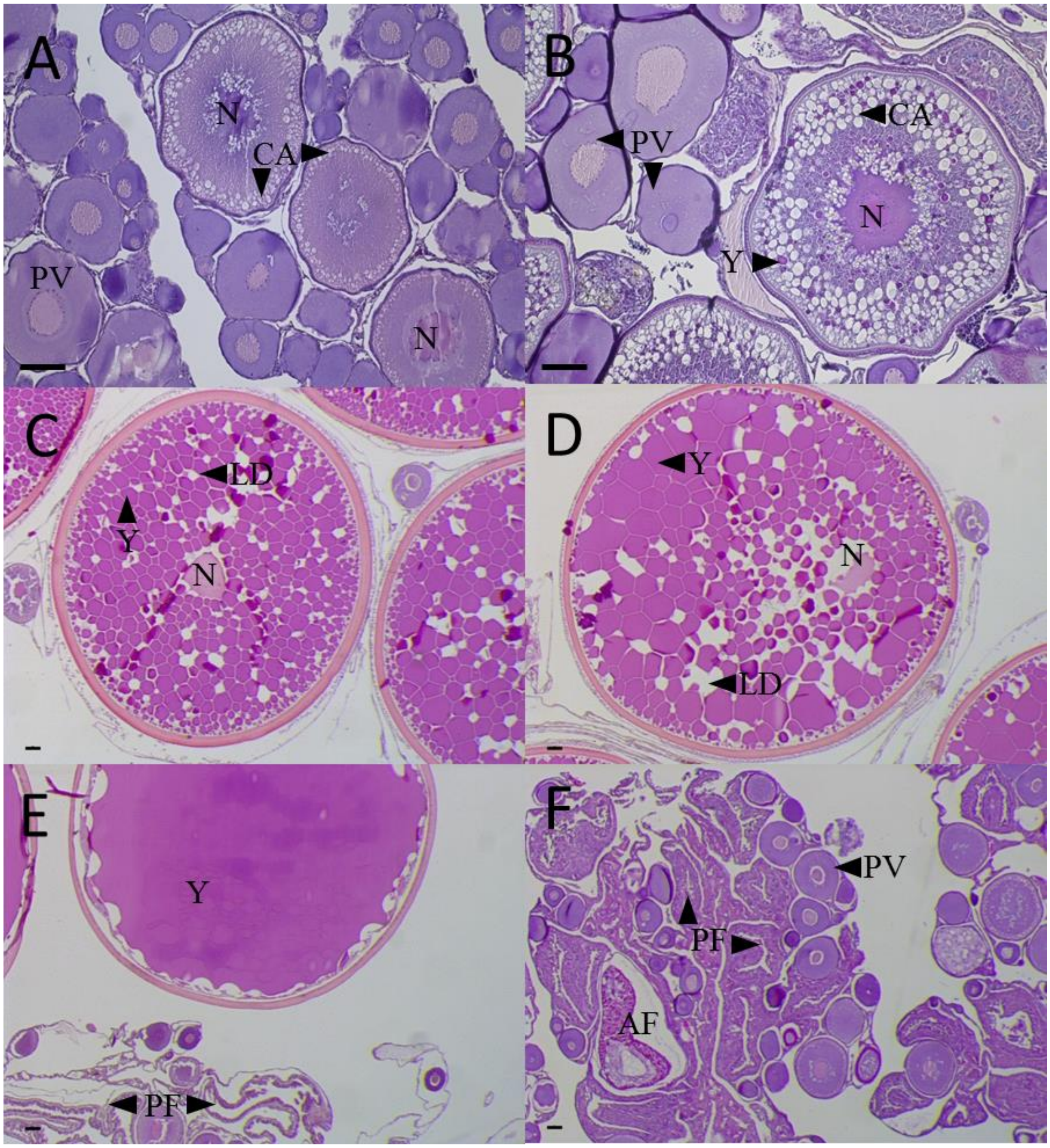

FIGURE 2.3. Ovarian development of Mountain Whitefish, periodic acid schiff stain, bar equals 100 μm. Stages shown are: (A) previtellogenic, with cortical alveoli present; (B) early vitellogenic, with cortical alveoli and small yolk droplets present; (C) mid vitellogenic, ovarian follicles with coalescing 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 post ovulatory follicles; and (F) spent, with post ovulatory 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.

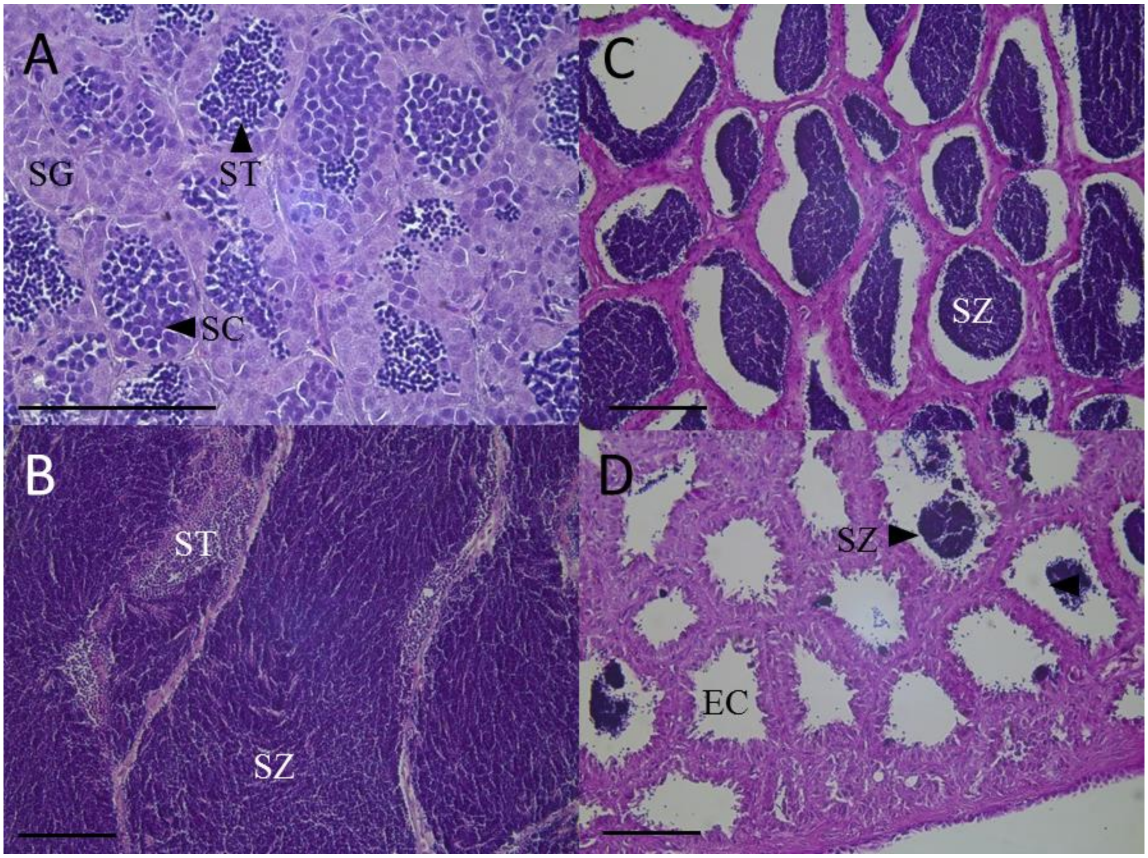

FIGURE 2.4. Testicular development of Mountain Whitefish, periodic acid schiff stain, bar equals 100 µm. Stages shown are: (A) early spermatogenic, containing only spermatogonia, spermatocytes, and spermatids; (B) ripe, primarily spermatozoa with small numbers of spermatids (C) spawning or spermiating, 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.

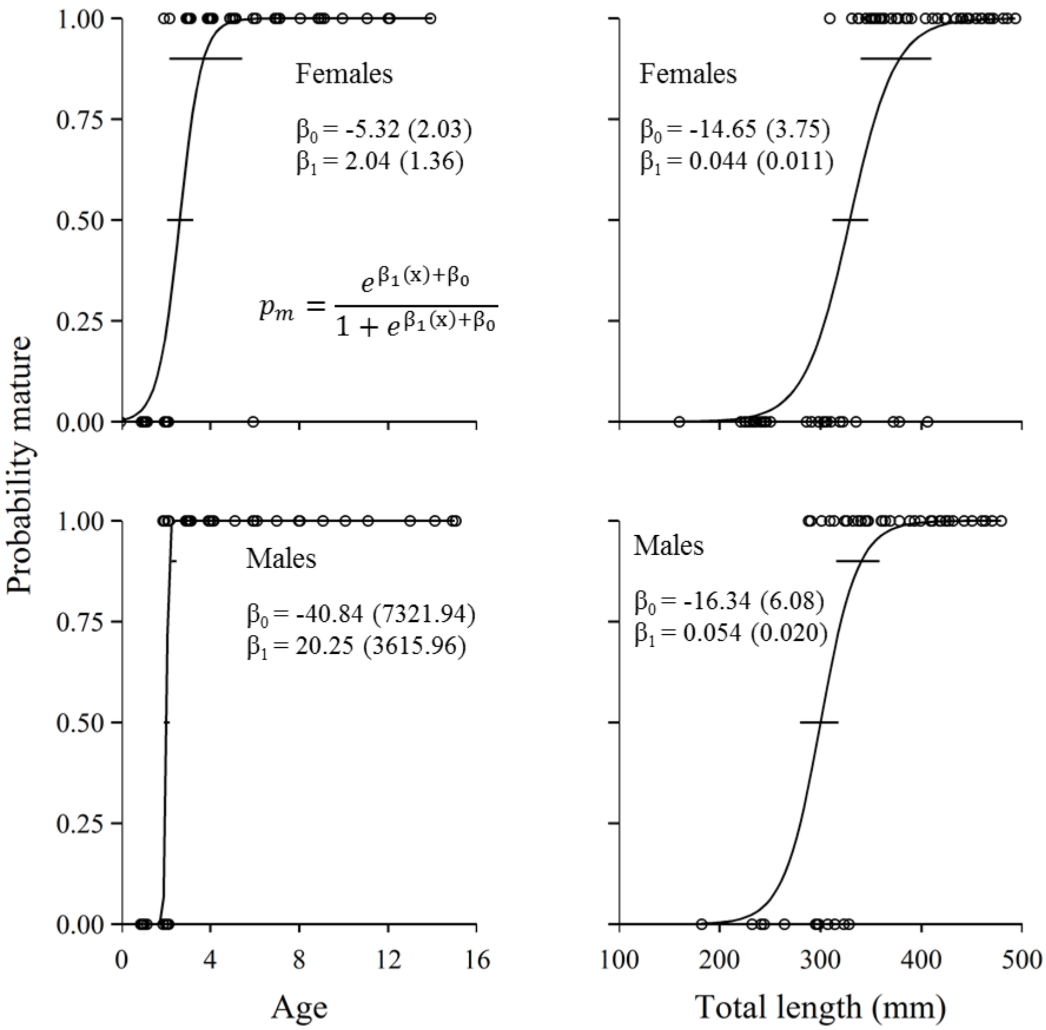

FIGURE 2.5. Logistic-regression models used to predict age and length at 50% and 90% maturity for Mountain Whitefish in the Madison River, Montana. Parameter estimates are shown with SE in parentheses.

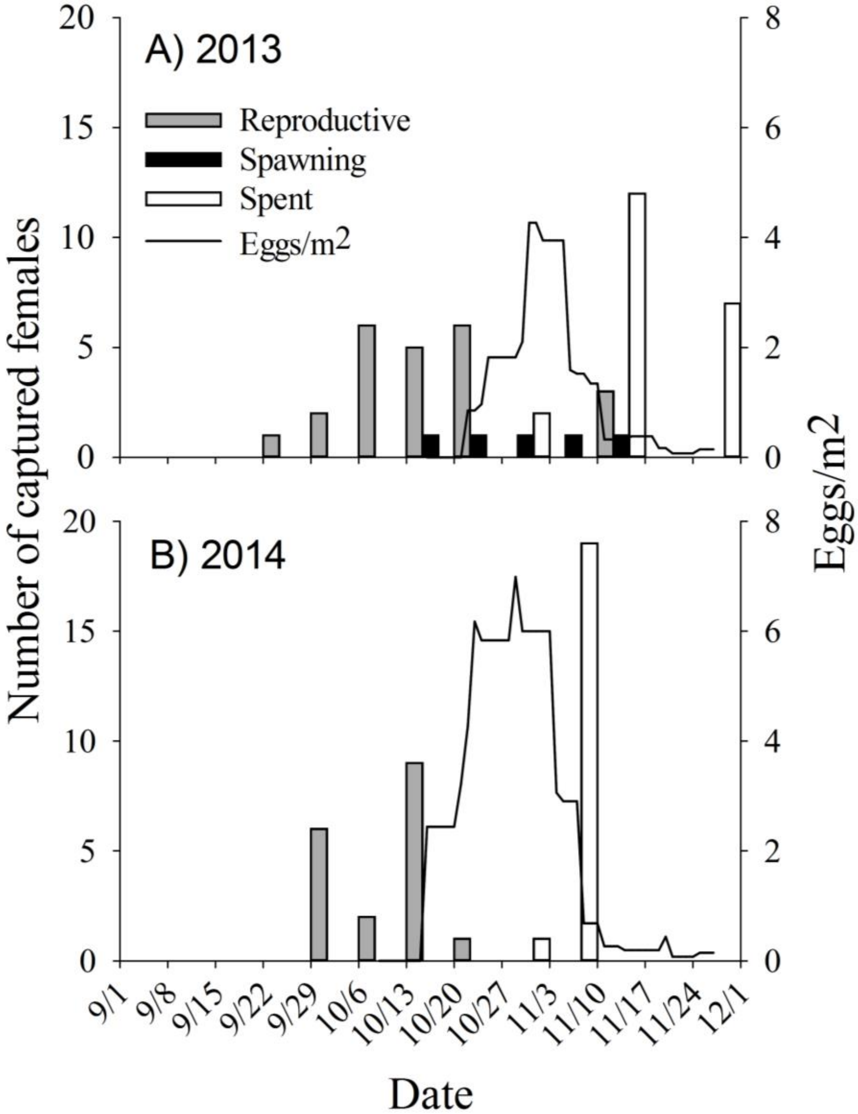

FIGURE 2.6. Status of captured female Mountain Whitefish (grouped by week) and daily densities of Mountain Whitefish embryos collected on egg mats in the Madison River, Montana during autumn **(A)** 2013 and **(B)** 2014. Egg mats that did not collect any embryos were excluded from density calculations.

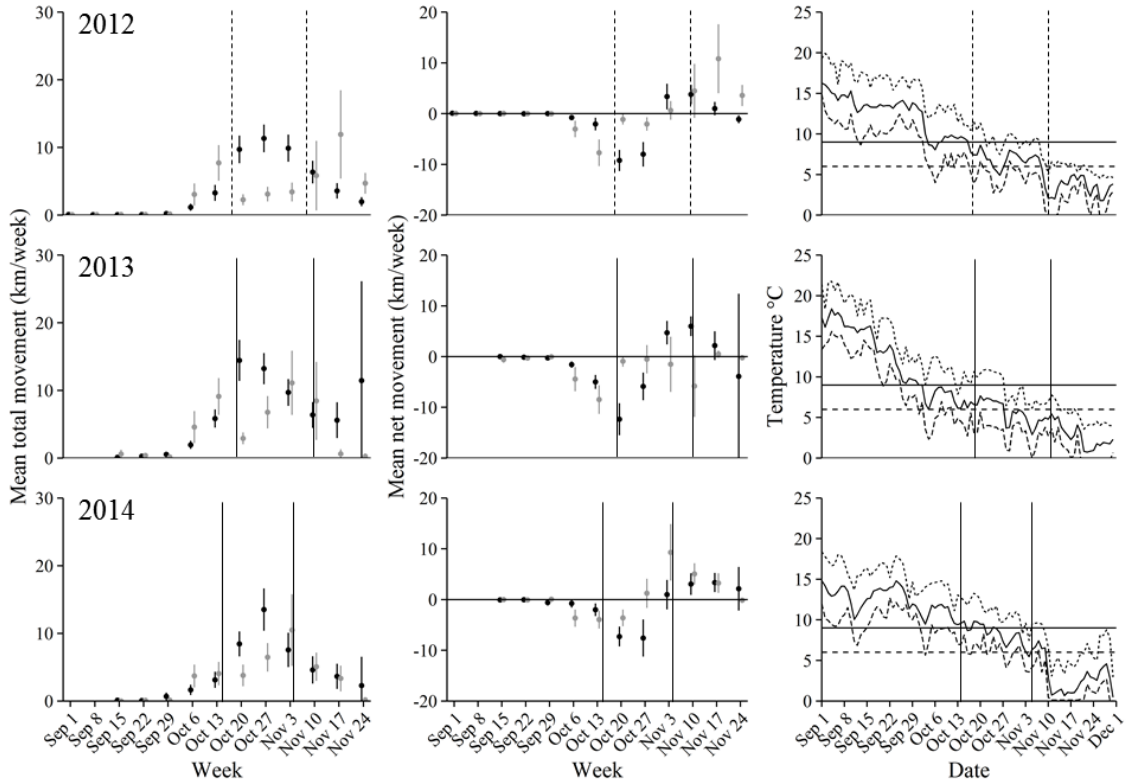

FIGURE 2.7. Mean total and net weekly movement rates (mean ± 95% CI) of radio-tagged Mountain Whitefish and daily mean, maximum, and minimum water temperatures in the Madison River, Montana during autumn 2012, 2013, and 2014. Vertical lines indicate the spawning period (solid = determined from embryo collection and female spawning status, dashed = estimated from other years). On temperature plots, horizontal lines indicate thermal thresholds for successful embryo development (solid = maximum, dashed = upper optimal; Rajagopal 1979; Brinkman et al. 2013). Weekly movement rates for females and males are offset and are for the week starting with the date labelled on the axis.

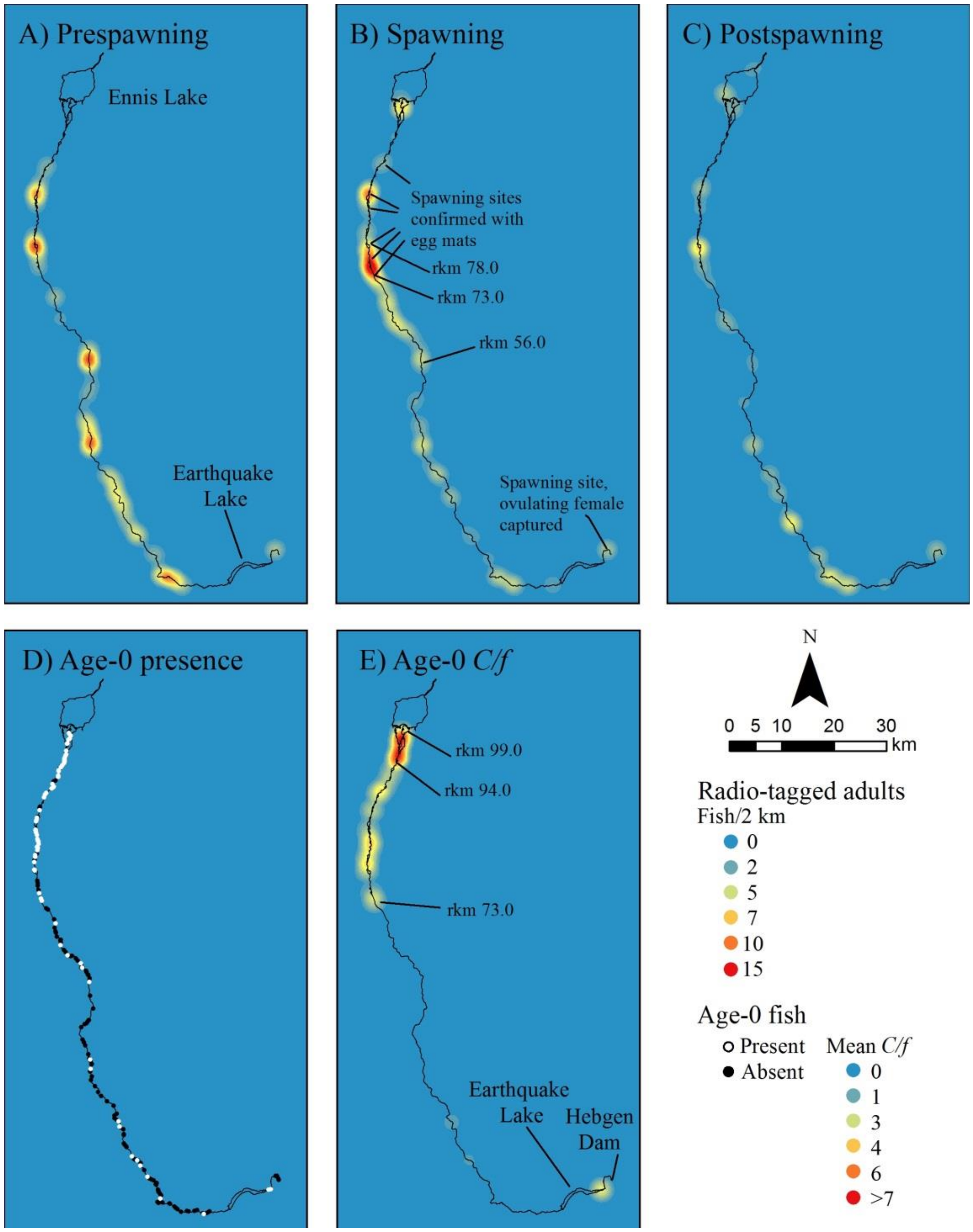

FIGURE 2.8. Maps illustrating locations of radio-tagged mature Mountain Whitefish during the **(A)** prespawning, **(B)** spawning, and **(C)** postspawning periods in 2012 – 2014 (all years pooled); and **(D)** presence and **(E)** *C/f* of age-0 Mountain Whitefish sampled with seining in May and June 2014 from the Madison River, Montana.

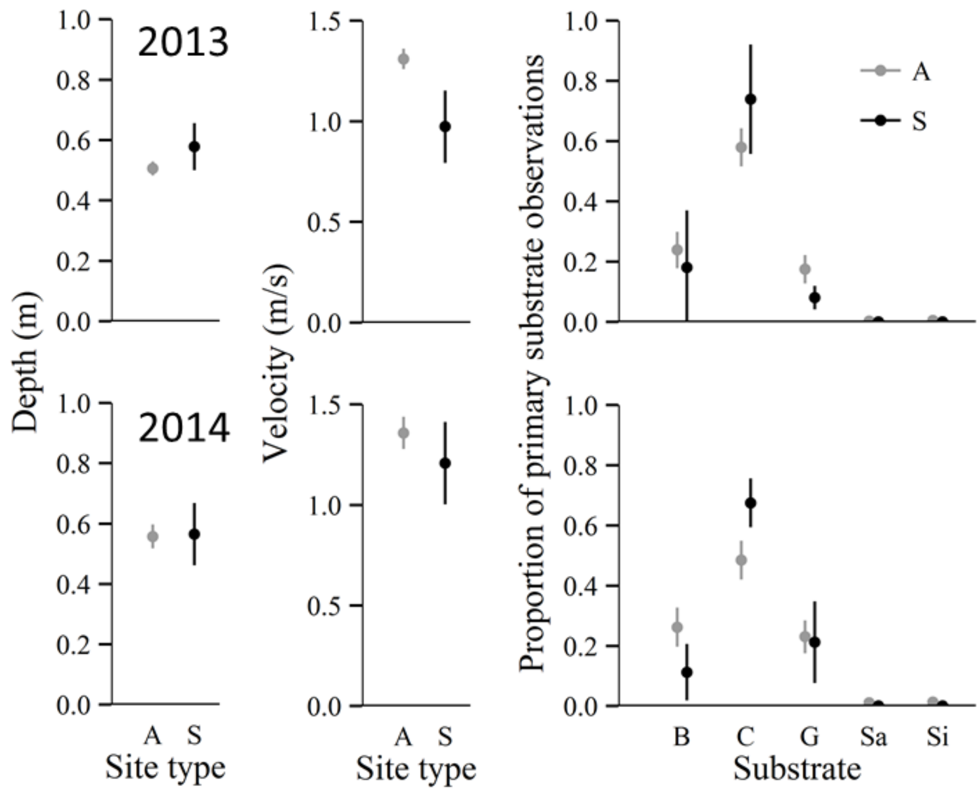

FIGURE 2.9. Depth, water velocity, and substrate type (mean ± 95% CI) in the Madison River, Montana in autumn 2013 and 2014 at randomly selected availability sites (n = 30) and Mountain Whitefish spawning sites (2013: n = 4, 2014: n = 8). Abbreviations are defined as: (A) available, (S) spawning, (B) boulder, (C) cobble, (G) gravel, (Sa) sand, and (Si) silt.

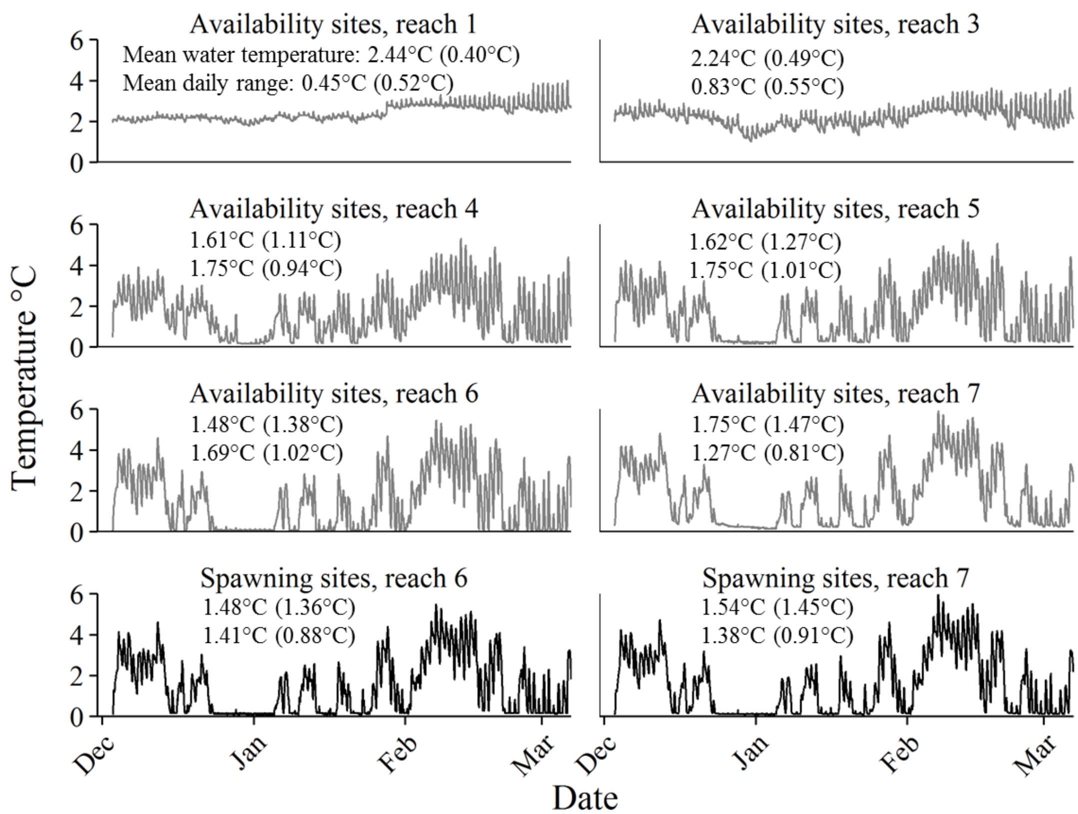

FIGURE 2.10. Winter water temperatures in the Madison River, Montana 2014-2015. Availability sites (*n* = 18) were randomly selected and stratified by reach. Spawning sites (*n* = 8) were locations where embryos were collected on egg mats in Autumn 2014. Mean water temperature (top value) and mean daily water temperature range (bottom value) are shown with SD in parentheses.

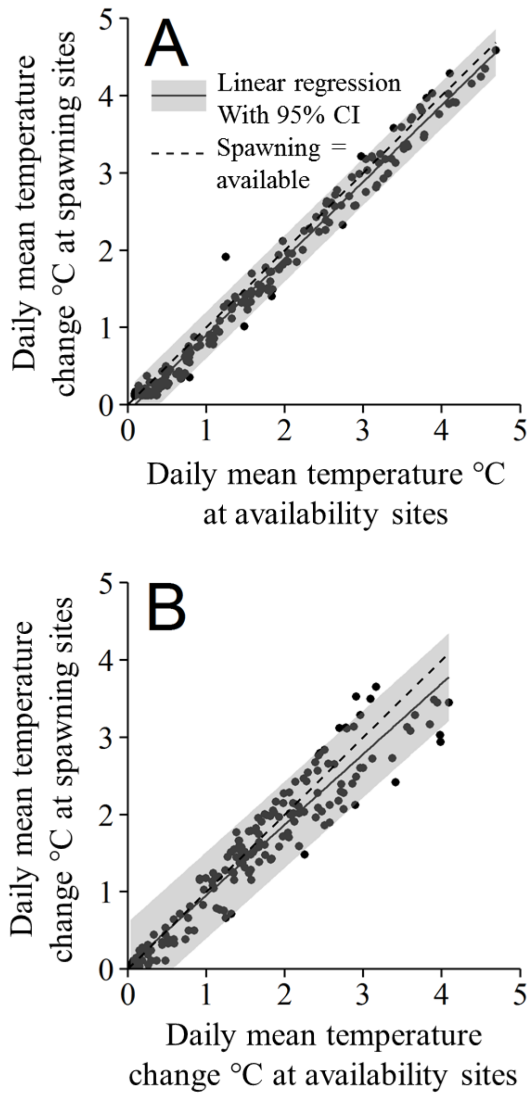

FIGURE 2.11. Daily **(A)** mean water temperatures and **(B)** mean daily water temperature change at spawning sites and availability sites in the same river reach in the Madison River, Montana from 3 December 2014 to 7 March 2015.

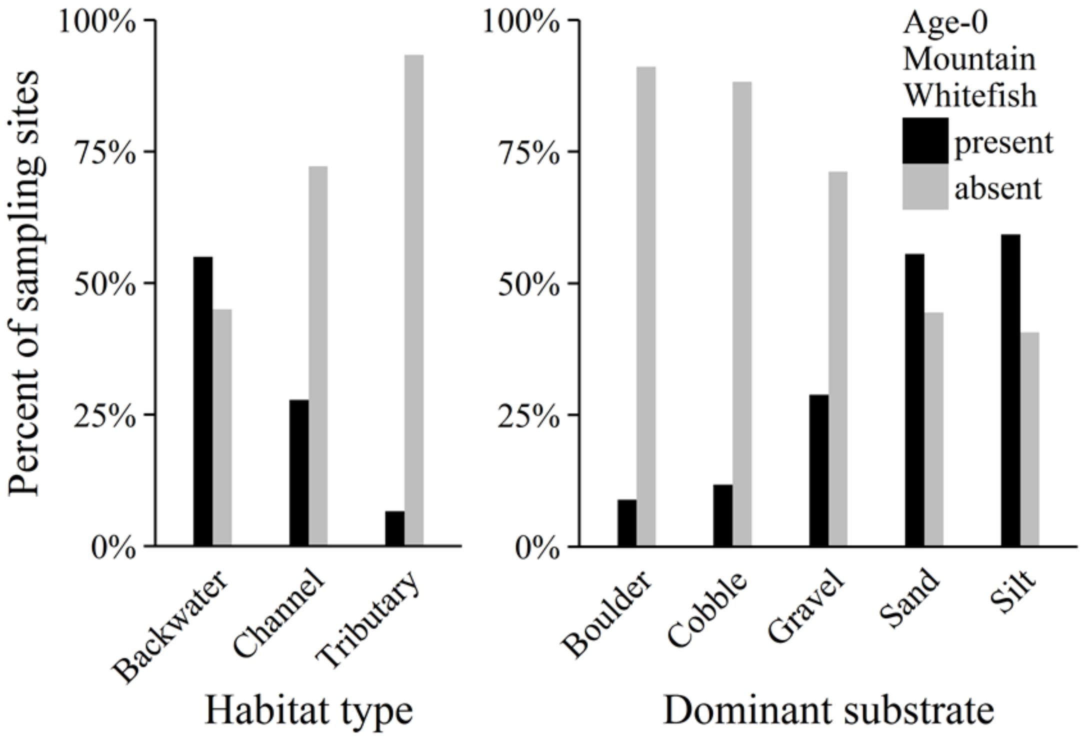

FIGURE 2.12. Habitat variables associated with probability of detecting age-0 Mountain Whitefish using seines in the Madison River, Montana in May – June 2014.

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CHAPTER THREE

GEAR COMPARISON FOR SAMPLING AGE-0 MOUNTAIN WHITEFISH

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Abstract

Sampling gears have not been compared for age-0 Mountain Whitefish *Prosopium williamsoni,* which makes it difficult to investigate recruitment and early life history dynamics for this species. We compared four gears: a seine, a backpack electrofisher, minnow traps, and lighted minnow traps. Gears were tested in backwaters, large channels, and small channels in the Madison River, Montana. No age-0 Mountain Whitefish were captured in minnow traps or lighted minnow traps. Seining had higher age-0 Mountain Whitefish *C/f* (mean, 0.82; SD, 2.19) than electrofishing (mean, 0.04; SD, 0.13), and the coefficient of variation was lower for seining (267) than electrofishing (325). Fish with a greater range of lengths were collected from seining (17 – 41 mm) compared to electrofishing (21 – 36 mm). Age-0 Mountain Whitefish seine catch was highest in backwaters. In channel sites Mountain Whitefish presence was associated with areas of still or slow water ≥ 2 m^2. We recommend seining be used for future sampling of age-0 Mountain Whitefish. Additionally, because Mountain Whitefish *C/f* was higher in slow velocity areas, habitat must be considered when designing sampling protocols.

Introduction

Standardized sampling facilitates comparisons in population metrics across time and space, allowing researchers to investigate trends and compare data to other populations (Bonar and Hubert 2002). Given the importance of standardized sampling, the American Fisheries Society recently published a book that establishes standardized sampling methods throughout North America (Bonar et al. 2009). The sampling recommendations in Bonar et al. (2009) are organized by waterbody type (e.g., wadeable streams, large rivers, ponds, or lakes) and fish assemblage type (e.g., coldwater or warmwater). However, the efficiency of a sampling technique also depends on factors including fish size, behavior, habitat use, and swimming ability, which can vary among species and life stages. Gear comparison studies provide information on efficiency, size selectivity, and ease of deployment of various gears, and assist biologists in selecting appropriate gears for sampling a target species. Gear comparison studies have compared sampling methods for many species, particularly popular sport fish, invasive species, and threatened and endangered species (e.g., Mangan et al. 2005; Phelps et al. 2009; Nett et al. 2012). However, gear comparison studies are nonexistent for many species and life stages.

Sampling gears have not been compared for age-0 Mountain Whitefish *Prosopium williamsoni*, which makes it difficult to investigate recruitment and early life history dynamics for this species. Mountain Whitefish are a salmonid native to coldwater lakes and 4th to 7th order streams throughout large portions of the Western United States and Canada (Brown 1971; Scott and Crossman 1973; Meyer et al. 2009). In the last decade, declines in Mountain Whitefish abundance have been reported in the Madison River, Montana, and in other rivers throughout the Southern portion of their range (IDFG 2007, P. Clancey, Montana Fish, Wildlife and Parks; G. Edwards, Wyoming Fish and Game; K. Rogers, Colorado Wildlife and Parks, personal communications). Studies on Mountain Whitefish ecology are needed to investigate these declines and identify possible limiting factors. Investigating the ecology of juvenile fish is an important component, as fish populations are often limited by bottlenecks occurring early in life (Bradford and Cabana 1997; Myers 2002). Understanding which gear or gears are most efficient (i.e., highest *C/f* and lowest variability in *C/f*) at sampling age-0 Mountain Whitefish is necessary to design cost effective and informative studies. Age-0 Mountain Whitefish have been sampled using seines (Brown 1952), backpack electrofishing (Stalnaker and Gresswell 1974), and dip nets (Pettit and Wallace 1975; Pierce et al. 2012). These methods successfully collected fish for growth, diet, and disease studies, but the relative efficiency of these gears has not been compared.

We compared four gears: a seine, a backpack electrofisher, minnow traps, and lighted minnow traps. These gears were selected based on a literature review of juvenile fish sampling gears, and with the intent of testing a variety of gears with different strengths and limitations. Seines are quick to deploy, thus, using seines would allow for a large number of sites to be sampled. However, seines are less effective in structurally complex habitats and areas with high velocity. Backpack electrofishing is a widely used and effective method for sampling salmonids in wadeable streams (Dunham et al. 2009). However, electrofishing is less efficient at sampling smaller fish, expensive, and time-consuming relative to the other methods. Two passive gears, minnow traps and lighted minnow traps, were also tested. Minnow traps are relatively simple to deploy and can effectively sample small fish; however, efficiency of minnow traps and other passive gears is dependent on activity levels and movement patterns of fish (Kelso and Rutherford 1996). Age-0 Mountain Whitefish are positively phototactic (Liebelt 1970;

Stalnaker and Gresswell 1974; Rajagopal 1979), so lighted minnow traps may attract Mountain Whitefish and increase *C/f*.

Understanding which habitat types are associated with age-0 Mountain Whitefish is also necessary to design cost effective and informative studies. Age-0 Mountain Whitefish have typically been sampled in protected habitats including backwaters and pockets behind boulders (Brown 1952; Davies and Thompson 1976; Pettit and Wallace 1975). However, past age-0 sampling efforts have not randomly selected sampling sites or compared *C/f* among habitat types. We tested gears at randomly selected sites in three habitat strata (backwaters, channels ≥ 18 m wide, and channels ≤ 6 m wide) and recorded habitat measurements (i.e., substrate, water velocity, turbidity) at all sampled sites. This allowed us to compare *C/f* among habitat types and determine which habitat types and characteristics were associated with age-0 Mountain Whitefish.

Our objectives were to determine which gear had the highest *C/f* of age-0 Mountain Whitefish, assess variation in *C/f* among gears, and describe habitat characteristics associated with age-0 Mountain Whitefish *C/f*. We predicted that backpack electrofishing would have higher *C/f* and lower variance for sampling age-0 Mountain Whitefish as compared to seining, minnow traps, or lighted minnow traps. All of the selected gears can effectively sample age-0 fish (Kelso and Rutherford 1996), but electrofishing typically has high salmonid *C/f* in streams with coarse substrate. Finally, we predicted that *C/f* would be higher in small side channels and backwaters with lower water velocity than in main channels because age-0 Mountain Whitefish were found in protected habitats in other river systems (Brown 1952; Pettit and Wallace 1975; Davies and Thompson 1976).

Methods

Study Area

The Madison River is formed at the confluence of the Firehole and Gibbon rivers in Yellowstone National Park, Wyoming, and flows north 195 km to Three Forks, Montana, where its confluence with the Gallatin and Jefferson rivers forms the Missouri River. The study area was between Varney Bridge and Ennis Lake, a distance of 23.5 km (Figure 3.1). This reach was selected because a movement study between Hebgen Dam and Madison Dam, a distance of 101 km, showed that during autumn spawning the highest densities of adult Mountain Whitefish were found near Varney Bridge (see Chapter 2), and thus the reach downstream of Varney Bridge likely held the highest densities of age-0 Mountain Whitefish. Within the study site, the river is braided, with numerous side channels, backwaters, and pools. Hebgen Dam, which was constructed in 1914, regulates discharge in this section and functions primarily to store and release water for downstream hydropower plants on the Madison and Missouri rivers. Mean daily discharge is 24 - 39 m^3/s during base flow and peaks between 60 - 175 m^3/s during spring runoff (2011-2014; USGS 2015). Water quality has been stable within the last 10 years, with no pollutants exceeding recommended Environmental Protection Agency (EPA) levels, and cadmium, zinc, and copper are below levels toxic to juvenile Mountain Whitefish (PBS&J 2011; Brinkman et al. 2013).

The fish assemblage is composed of the native species Mountain Whitefish, Mountain Sucker *Catostomus platyrhynchus*, Longnose Sucker *Catostomus catostomus*, White Sucker *Catostomus commersoni*, Longnose Dace *Rhinichthys cataractae,* and Mottled Sculpin *Cottus bairdi*. Arctic Grayling *Thymallus arcticus* are present at extremely low abundance near Ennis Lake. Non-native species present are Rainbow Trout *Oncorhynchus mykiss,* Brown Trout *Salmo trutta,* and Utah Chub *Gila atraria* (Brown 1971; Vincent 1987). The parasite *Myxobolus cerebralis,* the causative agent of whirling disease, was first detected in the Madison in 1994, and was responsible for declines in Rainbow Trout (Vincent 1996; Baldwin et al. 1998), although since 2000 population estimates have rebounded to approximately 85% of pre-whirling disease (1951–1990) estimates (Clancey and Lohrenz 2013).

The majority of land in the Madison watershed is federally owned; the headwaters are within Yellowstone National Park and most land in the mountains surrounding the Madison Valley is owned by the U.S. Forest Service. Lower elevation land adjacent to the study site is primarily privately owned, with small parcels of state land. Public lands are managed for recreation, wilderness, timber, and grazing. The primary land use in the valley is grazing, with irrigated agriculture near Ennis, Montana.

Gear Comparison

Seining, backpack electrofishing, minnow traps, and lighted minnow traps were tested in wadeable habitat in the Madison River between Varney Bridge and Ennis Lake (Figure 3.1). Prior to field sampling, aerial maps were used to identify three habitat types: backwaters, large channels ($\geq$ 18 m wide), and small channels ($\leq$ 6 m wide)

(Figure 3.2). Channels which were 6 - 18 m wide were excluded from sampling to ensure a clear difference between large and small channel habitat types. Sampling blocks were delineated within each habitat type. Four adjacent backwaters were considered one block because not all sampling gears could be evaluated in a single backwater given the small size of most backwaters (see Figure 3.2 panel A and B). Large channel and small channel blocks were a continuous reach such that large channels were 200 m and small channels were 250 m (Figure 3.2 panel A). Random sampling, stratified by habitat type, was used to select blocks (n = 23) for gear evaluation. We attempted to sample 8 blocks in each habitat strata, but time constraints limited small channel sampling to 7 blocks.

Four sampling sites were delineated in each selected block (Figure 3.2 panel B). As stated above, each backwater site had only one gear used because of the size limitation—in backwaters ≤ 50 m in length the entire backwater was sampled, and in backwaters > 50 m in length the 50 m closest to the channel was sampled. Large channel sites were 50 m in length and were located in wadeable habitat adjacent to one bank. Small channel sites were 50 m in length and included the entire channel width. All adjacent sites where a different gear was used were separated by a buffer ≥ 10 m. Within each block, each of the four gears was randomly assigned to one of the four sites (Figure 3.2 panel B).

All sampling was conducted by the same two-person crew to control for variable sampling efficiency among crews. Seined sites were sampled using a 3-m x 1.5-m beach seine with 1.6-mm bar mesh (Leslie et al. 1983; Rabeni et al. 2009). The seine was used to sample all area in the site that could be effectively seined. The number of seine hauls per site varied depending on area of wadeable habitat in a site and presence of obstructions (e.g., submerged logs, boulders), but there were a minimum of three seine hauls per site. Electrofished sites were sampled using a backpack electrofisher (Halltech HT-2000), and fish were captured in a single pass using dip nets with 1.6-mm bar mesh (Dunham et al. 2009). Voltage and frequency were adjusted based on water conductivity and temperature to standardize power at 300 - 450 W (Burkhardt and Gutreuter 1995; Dunham et al. 2009). We electrofished within 3 m of shore, similar to the area sampled by the seine. Minnow traps and lighted minnow traps were 46 cm x 25 cm x 25 cm (2-mm bar mesh) with two 40-mm entrances. Lighted minnow traps had a 24 h 10-cm x 1-cm chemical glow stick placed inside the trap. Three traps per sampling site were set and removed the following day. All fish captured were identified to species. All Mountain Whitefish were measured to the nearest millimeter total length (TL). For other species, subsamples of 50 fish per site were measured to the nearest millimeter TL. Start and end times of sampling (excluding fish processing) were recorded.

At each site, water temperature (± 0.1 ºC), maximum depth (± 0.1 m), backwater or channel width (± 0.5 m), and site length (± 0.5 m) were measured. Primary and secondary substrate (i.e., bedrock, boulder > 256 mm, cobble 64 - 256 mm, gravel 2 – 63 mm, sand 0.06 – 1.9 mm, silt < 0.06 mm; Platts et al. 1983) and water velocity (i.e., fast: > 1.0 m/s, moderate: 0.6 - 1.0 m/s, slow: < 0.6 m/s) were visually estimated at each sampled site. In blind tests paired with velocity measurements (orange float method; Gordon et al. 1997), 94% of our visual velocity estimates (n = 66) were correct. Presence or absence of slow water areas ≥ 2 m^2 within a site was estimated visually in order to record the presence of small slow water habitats, such as eddies within channel units with predominantly moderate or fast velocity habitat.

Age-0 Mountain Whitefish catch (*C)* was calculated for each site. All statistical comparisons were between seining and electrofishing because no Mountain Whitefish were captured in minnow traps or lighted minnow traps. We calculated catch per unit effort (*C/f*) to standardize catch data between gears using length sampled (m) as a unit of effort. Age-0 *C/f* data were not normally distributed. Log and square root transformations did not normalize the distribution of age-0 *C/f* data. A paired Wilcoxson signed rank test, which is appropriate for non-parametric data, was used to test the null hypothesis that there was no difference in *C/f* between paired (in the same block) seined and electrofished sites. Coefficient of variation ($100 \cdot SD/mean$) for C/*f* was calculated for seined and electrofished sites. Differences in sampling time between paired seined and electrofished sites were normally distributed, thus a paired *t*-test was used to test the null hypothesis that there was no difference in time needed to sample a site between gears. Poisson logistic regression was used to test whether age-0 Mountain Whitefish *C/f* differed among backwaters, large channels, and small channels at seined sites. Relationships between other habitat characteristics and age-0 Mountain Whitefish *C/f* were evaluated graphically, because low sample sizes, along with high collinearity (i.e., silt substrates are associated with slow-water velocity, and both are common in backwaters) limited our ability to conduct statistical tests.

Results

No age-0 Mountain Whitefish were captured in minnow traps or lighted minnow traps. Seining had higher age-0 Mountain Whitefish *C/f* than electrofishing (V = 95, P = 0.008) (Figure 3.3). It was estimated that 0.8 additional age-0 Mountain Whitefish per meter (95% CI, 0.1 - 1.5) were captured with seining compared to electrofishing in the same block. There was a large amount of variation in *C/f* among seined sites (mean, 0.82; SD, 2.19) and among electrofished sites (mean, 0.04; SD, 0.13), but the coefficient of variation was lower for seining (267) than electrofishing (325). Mean TL of age-0 Mountain Whitefish was similar for both gears (seine, 31 mm; electrofishing, 29 mm). Greater variation in length of age-0 Mountain Whitefish was observed in samples from seining (17 – 41 mm) compared to electrofishing (21 – 36 mm; Figure 3.4).

Mean time required for a two-person crew to seine a site was 13 minutes (minimum – maximum, 5 – 28 min), and mean time to electrofish a site was 36 minutes (minimum – maximum, 12 – 63 min). Sampling a site with a seine was 23 minutes faster (95% CI, 17 - 30 minutes) than sampling with a backpack electrofisher (t = -7.56, df = 22, P < 0.0001).

Age-0 Mountain Whitefish seine catch was highest in backwaters, with a mean *C/f* of 2.0 age-0 Mountain Whitefish. Large channels had lower *C/f* (0.16) than both backwaters (Z = 15.020, df = 19, P < 0.0001), and small channels (Z = 2.44, df = 19, P = 0.015), where mean *C/f* was 0.24 (Table 3.1). One high outlier heavily influenced mean *C/f* in small channels. When this outlier was removed, small channels had lower *C/f* (3×10^{-3}) than large channels (Z = -3.871, df = 19, P = 0.0001). Mountain Whitefish presence was associated with areas of still or slow water ≥ 2 m^2 (Table 3.2). All age-0 Mountain Whitefish captured with seining (n = 496) and 92% (46 of 50) of age-0 Mountain Whitefish captured with electrofishing were captured at sites with slow-water habitat. In large and small channels, mean seine *C/f* was 0.24 fish/m at sites with still or slow water, and 0.00 fish/m at sites without still or slow-water pockets. Similarly, electrofishing *C/f* was 0.03 fish/m at sites with still or slow water, and 0.01 fish/m at sites without still or slow water pockets (Table 3.2).

Discussion

We recommend seining be used for future sampling of age-0 Mountain Whitefish. Seines yielded the highest *C/f* with the lowest coefficient of variation of the gears tested, captured the greatest size range of age-0 Mountain Whitefish, and were the fastest sampling gear to deploy. Backpack electrofishing also captured age-0 Mountain Whitefish, but required more time and yielded lower *C/f*. Minnow traps and lighted minnow traps did not capture any Mountain Whitefish.

Seines probably were the most effective gear tested because age-0 Mountain Whitefish inhabited slow velocity, structurally simple areas. Age-0 capture locations, and visual observations, demonstrated that age-0 Mountain Whitefish typically inhabited open habitats with fine substrates, limited cover, and slow water velocities. In addition, Mountain Whitefish were observed schooling in open water. Seines are highly effective at sampling schooling midwater fishes (Lyons 1986; Lapointe et al. 2006) in shallow (< 1 m) areas with limited structural complexity and silt, sand, and gravel substrates (Leslie et al. 1983; Rabeni et al. 2009). Seines are less efficient in areas with cover (e.g., submerged logs, coarse substrate) or fast water velocities (Holland-Bartels and Dewey 1997), but age-0 Mountain Whitefish were rare in these areas. We rarely detected age-0 Mountain Whitefish in the above areas with electrofishing, which is effective at capturing fish in structurally complex or high-velocity habitat (Wiley and Tsai 1983; Dunham et al. 2009). We sampled extensively in high-velocity areas, under woody debris and undercut banks, and over coarse substrate with interstitial spaces. We captured 466 age-0 Brown Trout with electrofishing in the above areas, and four age-0 Mountain Whitefish. At age-0, Brown Trout and Mountain Whitefish have similar body shapes and are similar sizes (Mean TL, 31 mm, both species). Thus, if Mountain Whitefish were common in areas with fast velocity or coarse substrates, we likely would have captured them when electrofishing.

Habitat must be considered when designing sampling protocols because Mountain Whitefish *C/f* was higher in slow velocity areas. If maximizing catch is a study goal (i.e., for growth, diet, or occupancy studies), we recommend selecting slow velocity, silt-laden areas for sampling. Conversely, if estimating abundance or inferring results to reach scales is a study goal, we recommend quantifying total area in a river reach, and the area of slow-water habitat, and using random stratified sampling to select sites, concentrating sampling effort in slow water sites.

In addition to their effectiveness in habitats occupied by age-0 Mountain Whitefish, seines offer several other advantages. Seines are effective in a variety of environmental conditions and are not influenced by water conductivity, a factor that heavily influences electrofishing efficiency (Burkhardt and Gutreuter 1995). Similarly, high turbidity can decrease electrofishing catches, but can increase the efficiency of seines because low light limits net avoidance behavior (Glass and Wardle 1989). This is important because peak discharge in rivers occupied by Mountain Whitefish typically occurs during spring snowmelt, and variable river conditions exist during the early life of Mountain Whitefish (April - June). Seining captured a wider length range of age-0 Mountain Whitefish, including small (16 – 21 mm) fish that were difficult to see and net when electrofishing. Seines are selective for small fish (Wiley and Tsai 1983; Hayes 1989; Van Den Avyle et al. 1995), because larger fish are typically stronger swimmers and can often escape a pulled net. The largest age-0 Mountain Whitefish observed during this study (47 mm TL) were captured with seining, not electrofishing. Thus, seines are an appropriate gear for sampling age-0 Mountain Whitefish up to at least 2 - 3 months post hatch (June), but efficiency would decrease in late summer. Finally, seines were quick to deploy, so a monitoring program based on seining would allow more area to be sampled in a given amount of time, increasing sample sizes.

Our results highlight the importance of investigating appropriate sampling methods for a target species. Prior to this study, we predicted that electrofishing would be the most effective sampling method. Electrofishing is an efficient method for sampling age-0 trout in coldwater streams (Dunham et al. 2009), and we targeted another salmonid with a similar body shape. However, seining was more efficient at capturing age-0 Mountain Whitefish because of different behavior and habitat use. Seining is a standard technique for sampling fishes in warmwater wadeable streams (Rabeni et al.

2009), but standard techniques for small fishes in coldwater streams are typically electrofishing and snorkel surveys (Dunham et al. 2009), methods optimized for sampling trout and salmon. This study illustrates the importance of evaluating sampling methods when little is known about a species and the habitat it occupies.

Tables

TABLE 3.1. Age-0 Mountain Whitefish *C/f* in the Madison River, Montana grouped by habitat type (backwater, large channel, ≥ 18 m width, small channel, ≤ 6 m width) and sampling gear.

	Mean *C/f* (SD)	
Habitat type	Seining	Electrofishing
Backwater	2.05(3.51)	0.08(0.23)
Large Channel	0.16(0.28)	0.04(0.08)
Small Channel	0.24(0.63)	0.01(0.00)

TABLE 3.2. Age-0 Mountain Whitefish *C/f* in channel sites in the Madison River, Montana grouped by presence or absence of areas of slow water ≥ $2m^2$ and sampling gear. Backwater *C/f* data is not included because all backwaters have slow or still water.

Slow water	Mean *C/f* (SD)	
areas ≥ $2m^2$	Seining	Electrofishing
Present	0.24(0.50)	0.04(0.08)
Absent	0.00(0.00)	0.01(0.01)

Figures

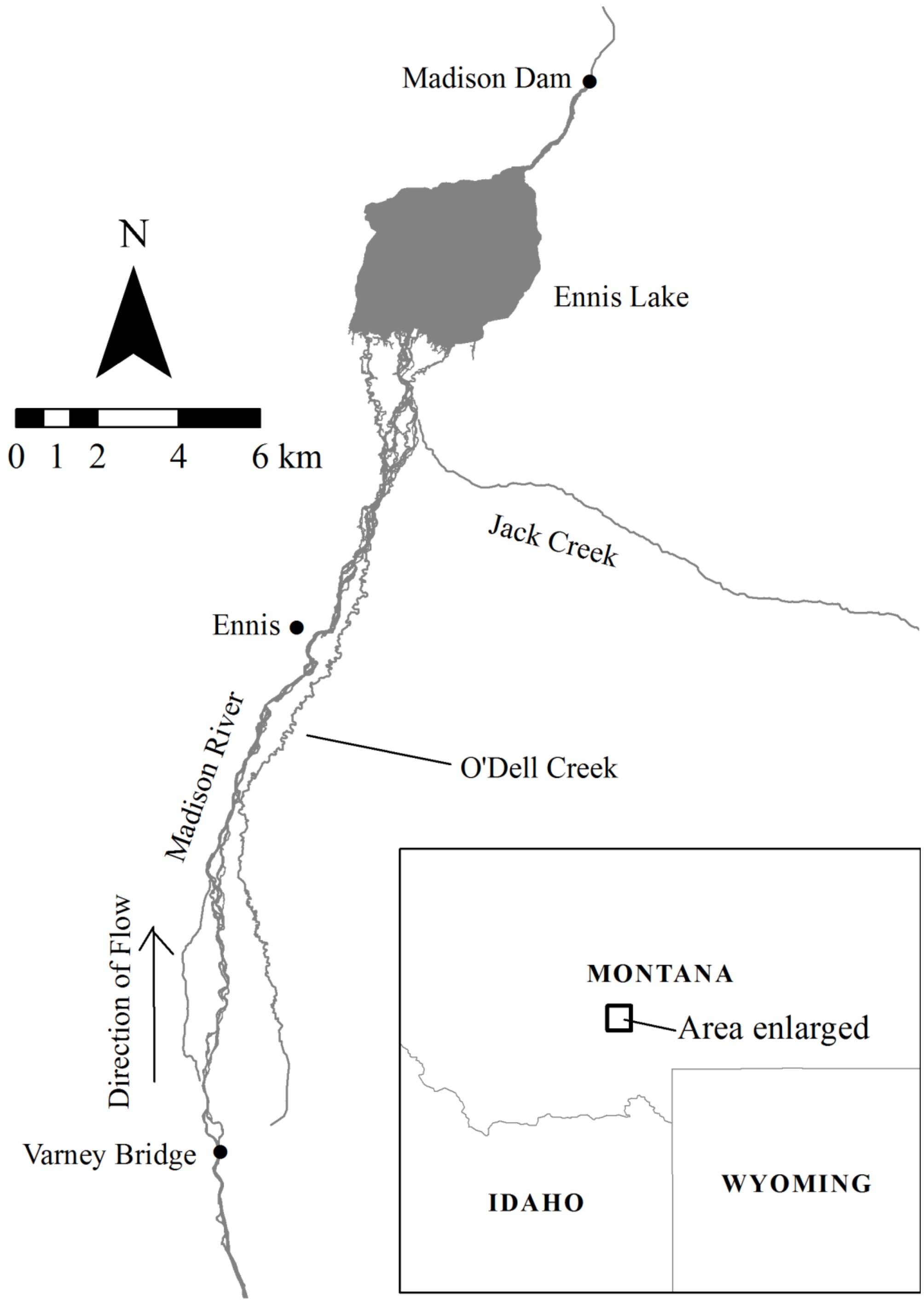

FIGURE 3.1. Map of study site. Sampling was conducted in the Madison River, Montana between Varney Bridge and Ennis Lake, a distance of 23.5 km.

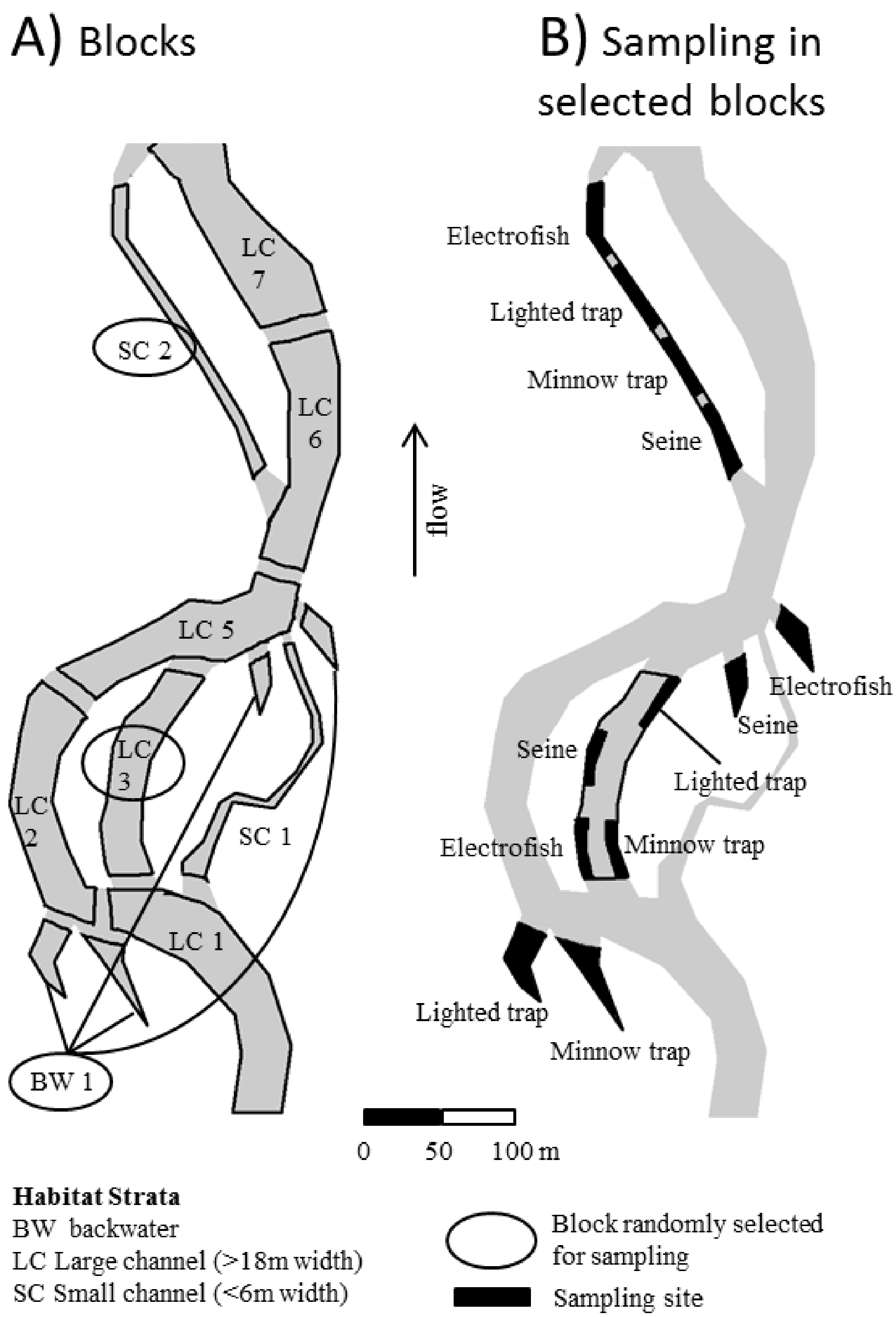

FIGURE 3.2. Schematic illustrating **(A)** delineation of blocks, and **(B)** sampling sites within randomly selected blocks. Blocks were defined as four adjacent backwaters, 200 m reaches in large channels, and 250 m reaches in small channels. Four sampling sites were located in each block, and all four gears were tested in each block, with gear randomly assigned to sampling site.

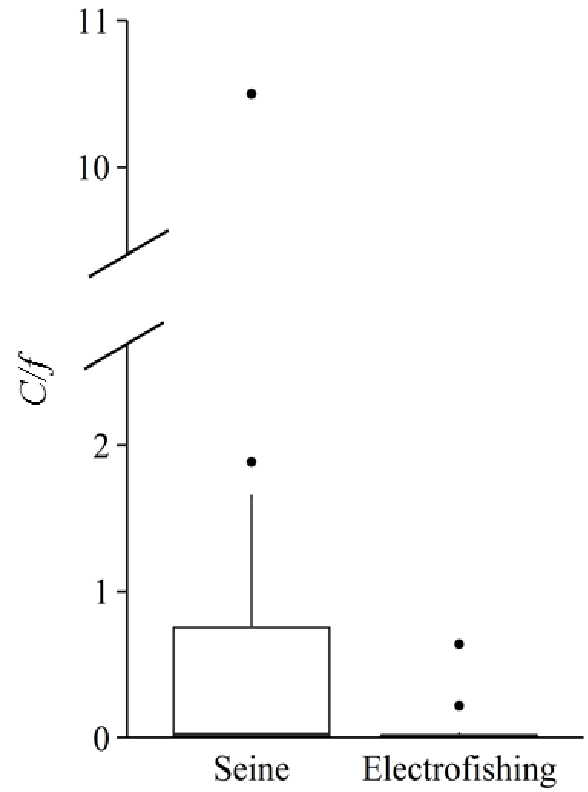

FIGURE 3.3. Catch per unit effort (*C/f* ; number per meter) of age-0 Mountain Whitefish at seined (*n* = 23) and electrofished (*n* = 23) sites in the Madison River, Montana.

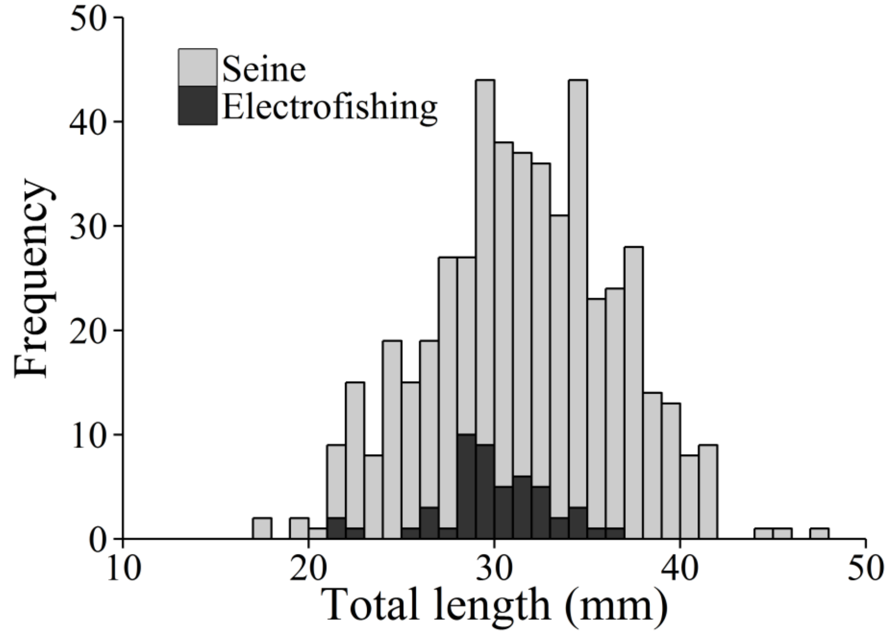

FIGURE 3.4. Length-frequency histogram of age-0 Mountain Whitefish captured with seining and electrofishing in the Madison River, Montana in May and June 2013.

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CHAPTER FOUR

CONCLUSIONS

My objectives were to describe life-history characteristics that could influence recruitment of Mountain Whitefish in the Madison River, Montana, and identify effective sampling methods for age-0 Mountain Whitefish. In chapter two, I used a variety of methods to investigate multiple life stages with the understanding that this research would begin to clarify the mechanisms causing the decline in Mountain Whitefish abundance. I found that fecundity, age-at-maturity, and spawning periodicity were similar to values reported for other Mountain Whitefish populations studied (Brown 1952; Northcote and Ennis 1994; Meyer et al. 2009). Adult movement patterns were similar among years despite variable water temperature schedules during the spawning season. Spawning activity and age-0 fish were concentrated in the downstream 26 km of the study site, a braided area with complex habitat. Finally, age-0 Mountain Whitefish were most often found in low velocity, silt-laden habitats.

In chapter three, I compared seining, backpack electrofishing, minnow traps, and lighted minnow traps, in order to identify an efficient method for sampling age-0 Mountain Whitefish. Seines had the highest age-0 Mountain Whitefish *C/f* with the lowest coefficient of variation of the gears tested, captured the greatest size range of age-0 fish, and were the fastest sampling gear to deploy (Chapter 3). Backpack electrofishing also captured age-0 Mountain Whitefish, but required more time and had lower *C/f*. Minnow traps and lighted minnow traps did not capture any Mountain Whitefish. Therefore, seining should be used for sampling age-0 Mountain Whitefish. Additionally, habitat must be considered when selecting sampling sites. Age-0 Mountain Whitefish *C/f* was highest in backwaters, and among channel sites Mountain Whitefish *C/f* was higher at sites with areas of slow water ≥ 2 m^2 (Chapter 3). If maximizing catch is a study goal (i.e., for growth, diet, or occupancy studies), I recommend selecting protected, low velocity areas for sampling.

These results provide a foundation for investigating possible limiting factors on the Madison River, and suggest that future investigations into limiting factors should focus on juvenile survival, rather than reproductive development of adults. Mountain Whitefish were highly fecund and matured at young ages, and histological sections showed normal development of oocytes, thus limited egg production is not a plausible limiting factor. Age-0 fish were concentrated in silt-laden habitats in the downstream 26 km of the study site, a relatively restricted distribution. Thus, stressors in this reach that reduce growth or survival could have population-level effects. Two potential mortality factors which could be investigated are whirling disease and drift into lakes. The parasite which causes whirling disease, *M. cerebralis*, is present in the Madison River and has caused Rainbow Trout declines (Vincent 1996; Krueger et al. 2006). Age-0 Mountain Whitefish are susceptible to whirling disease, but mortality rates depend on age at exposure (Schisler 2010), and temporal overlap between vulnerable life stages and peak triactinomyxon (TAM, life stage of *M. Cerebralis* that infects fish) releases typically exists only in river reaches with warm winter temperatures (Pierce et al. 2012). Another possible mortality agent is larval drift into lakes. My results suggest that age-0 Mountain Whitefish may drift into Ennis and Earthquake lakes, but I did not investigate how many fish may drift into lakes or determine whether age-0 fish can survive in lentic habitats. Determining whether TAM releases overlap temporally with vulnerable Mountain Whitefish, quantifying drift distances, and evaluating the effects of drifting into lentic habitats are logical next steps for investigating factors that affect survival of juvenile Mountain Whitefish. My gear comparison (Chapter 3) and age-0 distribution (Chapter 2) results can guide future studies in the Madison River that could identify mechanisms responsible for declines in Mountain Whitefish abundance.

Although the scope of inference for this study was limited to the Madison River between Hebgen and Madison dams, the results may help inform Mountain Whitefish studies in other watersheds. I provided the first histological description of Mountain Whitefish reproductive development, the second documentation of annual spawning periodicity, and fecundity and age values which augment a sparse dataset (Chapter 2; Sigler 1951; Pettit and Wallace 1975; Meyer et al. 2009). Estimates of these reproductive parameters form a baseline which can be used for future comparative studies. Similarly, this study augments the information available on seasonal movement and habitat use of Mountain Whitefish. Previous studies have shown that some Mountain Whitefish moved limited distances (< 1 km) during Autumn, but others made large upstream movements (up to 80 km) to mainstem and tributary spawning sites (Pettit and Wallce 1975; Pierce et al. 2012; Benjamin et al. 2014) and moved upstream or downstream to lotic overwintering sites (Davies and Thompson 1976; Baxter 2002; Benjamin et al. 2014). In the Madison River, fish moved similar distances during autumn, but the net direction of prespawning movement was downstream, and fish moved into lotic and lentic habitats to overwinter. Furthermore, comparing age-0 distribution to distribution of spawning adults showed that these two factors were related only at larger scales, suggesting that larval drift may influence age-0 distribution (chapter 2).

My age-0 sampling recommendations (chapter 3) can facilitate efficient sampling in watersheds throughout the the range of the Mountain Whitefish. Seines have been used to capture age-0 Mountain Whitefish in other rivers (Brown 1952; Pettit and Wallace 1975). However, my gear comparison study (Chapter 3) was the first to compare different sampling methods for age-0 Mountain Whitefish, and confirm that seining was the most effective of the gears tested. I also showed that age-0 Mountain Whitefish were most abundant in low velocity, silt-laden habitats (Chapter 2; Chapter 3). Smaller scale descriptive studies in the Yellowstone River, Montana, Clearwater River, Idaho, Sheep River, Alberta, and Logan River, Utah also located age-0 Mountain Whitefish in protected, slow water habitats (Sigler 1951; Brown 1952; Pettit and Wallace 1975; Davies and Thompson 1976), suggesting that the habitat associations I observed in the Madison River persist across large portions of the range of the Mountain Whitefish.

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APPENDIX A

AGE AND GROWTH MODEL

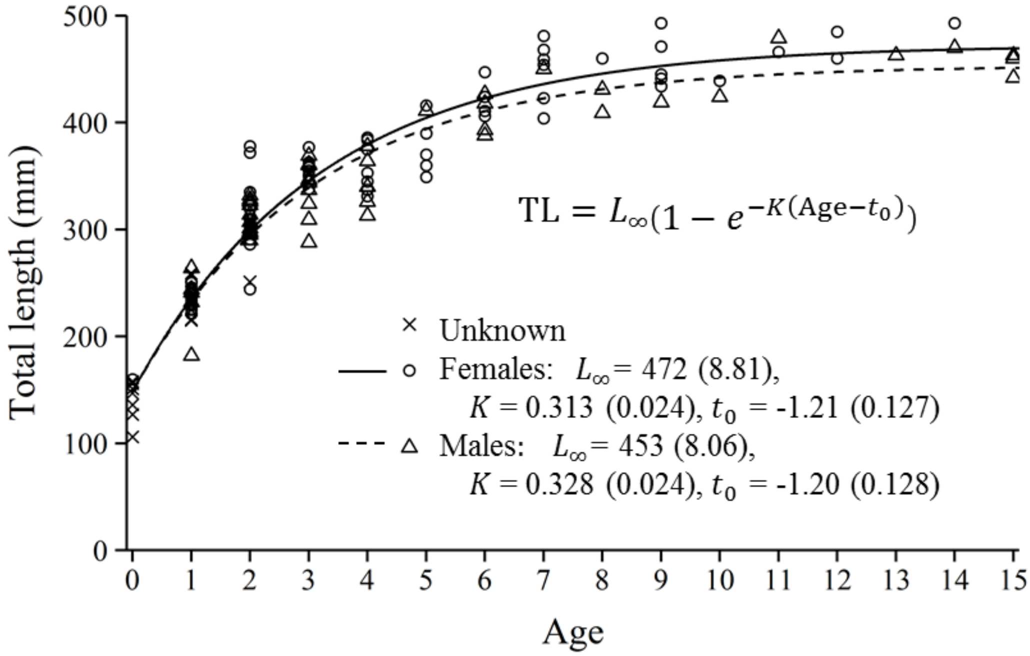

FIGURE A1. Length-at-age and von Bertalanffy growth model for Mountain Whitefish captured with boat electrofishing on 10 to 12 October (n = 146) in the Madison River, Montana. Parameter estimates are shown with SE in parentheses. Young fish (age 0, 1, and 2) of unknown sex were included in the female and male growth models.