REPRODUCTIVE AND JUVENILE ECOLOGY OF MOUNTAIN WHITEFISH IN THE UPPER GREEN RIVER, WYOMING

by

Colter Davis Brown

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Fish and Wildlife Management

MONTANA STATE UNIVERSITY
Bozeman, Montana

January 2022

ACKNOWLEDGEMENTS

I would first like to extend my thanks to the Wyoming Game and Fish Department for providing funding, without which this research would not have been possible. I thank Mark Smith and my committee members Tom McMahon and Molly Webb for their assistance on study design and thesis writing. Special thanks to Molly Webb for her additional aid in histological sample processing and assessment. I express my appreciation to Christopher Guy for his consistent support, guidance, and patience with me throughout this process. His perceptive feedback and the example he provided encouraged me to improve my skills and produce higher-quality research. I also extend my gratitude to the numerous Wyoming Game and Fish Department biologists and technicians, and my fellow students in the Montana Cooperative Fishery Research Unit. Your contributions to this project were invaluable, and I will always be grateful for your assistance on this research. I thank Darren Rhea for this help and guidance throughout the project planning and implementation. I also thank Russell Wilson and Maxwell Majinska for their hard work and positive attitudes while tracking fish, often in harsh conditions. They made the fieldwork for this project both successful and enjoyable. In addition, thanks to Luke Shultz and Arthur Tolley for their personal assistance, which added data to the study and made fieldwork much more feasible.

I express my deepest thanks to my family for their constant support and help during the project and throughout my life. Without your encouragement I would not be in the position I am today. Lastly and most importantly, I thank my wife, Alysia, for her unwavering love, support, and patience through this process.

TABLE OF CONTENTS

1. REPRODUCTIVE AND JUVENILE ECOLOGY OF MOUNTAIN WHITEFISH IN THE UPPER GREEN RIVER, WYOMING 1

Introduction 1
Methods 3
Study Area 3
Habitat Characterization 5
Fish Sampling 6
Age and Growth 6
Reproductive Development 7
Fecundity 8
Radio Transmitter Allocation and Implantation 8
Radio Tracking 10
Spawning Locations and Timing 11
Movement and Spawning Analysis 12
Age-0 Habitat Use and Distribution 13
Population Comparisons 14
Results 15
Length, Weight, Age, and Growth 15
Reproductive Development 16
Fecundity 17
Spawn Timing, Movement, and Locations 18
Age-0 Habitat use and Distribution 20
Discussion 21
Management and Research Needs 29
Tables 31
Figures 36

REFERENCES CITED 47

APPENDIX 56

LIST OF TABLES

Table Page

1. Descriptions of sex-specific reproductive phases and stages of gonadal development used to describe the population reproductive structure of the Mountain Whitefish in the Green River modified from Brown-Peterson et al. (2011) in Crossman et al. (In Review). Abbreviations of reproductive phases and stages are provided in parentheses. Reproductive condition suggests which stages and phases have spawning potential (active) or not (inactive), within that reproductive cycle 31

2. Age (years) and total length (mm) at 50% and 90% first maturity in the Green River, Wyoming and the Madison River, Montana predicted using binomial logistic regression (Boyer et al. 2017a). Values in parentheses are 90% confidence intervals 34

3. Habitat characteristics of the Green River, and the percentage of radio-tagged Mountain Whitefish in each reach during the prespawn and spawning periods 35

LIST OF FIGURES

Figure Page

1. Map of the study area on the Green River, Wyoming. Labels delineate reaches (reach boundaries are indicated by black lines); Lower Green River Lake and Warren Bridge bound the study area 36

2. Age-length (total) relationship with von Bertalanffy growth models by sex for Mountain Whitefish sampled in the Green River (2019) and Madison River (2012–2013). The end of each line indicates the oldest Mountain Whitefish sampled in each river by sex 37

3. Horizontal histograms of the relative frequency by age in years of Mountain Whitefish sampled in the Green River in 2019 (*n* = 80; left), and the Madison River in 2012 (*n* = 146; right). The center y-axis shows the age in years determined from otolith cross sections 38

4. Photomicrographs of testicular tissue containing primary oocytes (PO) in Mountain Whitefish in the Green River, Wyoming. The Bateman ranking system (Bateman et al. 2004) modified by Blazer et al. (2007) was used to assign a severity index based on the distribution pattern of PO only. A) Severity index 1 with focal distribution with a single PO within the microscopic field (10x objective); B) severity index 2 with diffuse distribution of more than one PO in a field of view and no association with neighboring oocytes; and C) severity index 3 with a cluster distribution of more than one but less than five closely associated PO.SG=spermatogonia; SC=spermatocytes; ST=spermatids; and SZ=spermatozoa. Tissue was stained with Periodic Acid Schiff reagent 39

5. Mountain Whitefish fecundity–weight relationship for the Green River population, Madison River population, and other populations (Sigler 1951; Brown 1952; Northcote and Ennis 1994; Wydoski 2001). Solid line is the linear model for the Green River and the dashed line is the linear model for the Madison River 40

6. Reproductive stage of female Mountain Whitefish sampled angling in the Green River, Wyoming from September 1 to November 5 in 2019 and 2020. Angling data were pooled weekly with day one being September 1 each year...........41

LIST OF FIGURES CONTINUED

Figure Page

7. Maximum, mean, and minimum daily water temperature in the Green River for 2019 and 2020 (left panels), and the Madison River for 2014 and 2020 (right panels [top right panel; recreated from Boyer et al. 2017a]). Vertical solid lines indicate the estimated spawning period, and vertical dashed lines indicate the spawning period based on prior estimates (Boyer et al. 2017a). Red horizontal lines indicate the maximum (9°C) and upper optimal (6°C) water temperature for Mountain Whitefish embryo development (Rajagopal 1979; Brinkman et al. 2013) 42

8. Frequency histograms for total distance (top panel) and net distance (bottom panel) moved of radio-tagged Mountain Whitefish in 2019 and 2020 pooled in the Green River. Negative net movement indicates downstream movement and positive indicates is upstream movement. Movement distances are the sum of all movements during the tracking season 43

9. Net movement and total movement by week of radio-tagged Mountain Whitefish in 2019 and 2020 pooled in the Green River (left panels), and in 2012, 2013, and 2014 pooled in the Madison River (right panels; recreated from Boyer et al. 2017a). Net movement downstream is considered negative and upstream is considered positive. The bold line delineates the median, box ends are the 25th and 75th quartiles, and the whiskers are 1.5 times the interquartile range 44

10. Kernel-density estimate maps for Moutain Whitefish locations in the Green River during the prespawn and spawning periods for 2019 and 2020 pooled (top panels). Maps in the lower panels indicate where embryos were sampled in the Green River in the autumn of 2019 and 2020 (lower left panel) and presence of age-0 Mountain Whitefish seined in May 2021 in the Green River (lower right panel). Reach boundaries are indicated by black lines (see Figure 1) and the study area is delineated by Lower Green River Lake and Warren Bridge 45

11. Catch per unit effort (CPUE; number per m^2) of age-0 Mountain Whitefish from seining in slow-water habitats in the spring of 2021 in the Green River, Wyoming. The top left panel shows the longitudinal distribution of CPUE at sample locations beginning at Lower Green River Lake. In the lower panels and top right panel, the bold line delineates the median, box ends are Q1 and Q3, whiskers are 1.5 times the interquartile range, and open circles are CPUE values from each site. Dashed lines highlight break in the *y*-axis 46

ABSTRACT

Mountain Whitefish *Prosopium williamsoni* are a salmonid native to the northern Rocky Mountains that has experienced declines in population abundance in rivers throughout Idaho, Colorado, Wyoming, and Montana. Problems with recruitment are suspected, but often the specific mechanisms causing population declines are unknown. Our approach to better understand the mechanisms that influence Mountain Whitefish population dynamics was to compare population characteristics between the Green River, Wyoming and the Madison River, Montana populations. Boyer et al. (2017a) conducted an extensive study on the movement and reproductive ecology of Mountain Whitefish in the Madison River, and we used this study as a template to make direct comparisons between the populations. Our primary research questions were 1) what is the age and length at first maturity, spawning periodicity, fecundity, and age structure of Mountain Whitefish, 2) what is the spatial and temporal distribution of Mountain Whitefish through their spawning period, and what influence do abiotic factors have on spawning and movement, and 3) what is the spatial distribution and habitat use of age-0 Mountain Whitefish? We collected otoliths and gonadal samples from 127 Mountain Whitefish in the Green River, implanted 100 fish with radio transmitters and tracked them from September 1 to early November in 2019 and 2020, determined spawning period and locations using egg mats, kick netting, and angling, and sampled age-0 Mountain Whitefish using a beach seine in slow-water habitats. The geographic separation and difference in hydrogeomorphic conditions between the systems allowed us to form generalizations about Mountain Whitefish in the Intermountain West. We found Mountain Whitefish in both systems mature between ages 2 and 4, primarily spawn annually, have a similar relative fecundity, spawning movements vary, males begin movement prior to females, and age-0 fish drift downstream of spawning locations and use slow-water silt-laden habitats after hatching. The main disparities between systems were that in the Green River water temperature was more suitable for embryo development, and age structure was more uniform and older. This research enhanced our understanding of Mountain Whitefish reproductive and juvenile ecology and provided evidence for factors that may influence recruitment of Mountain Whitefish.

REPRODUCTIVE AND JUVENILE ECOLOGY OF MOUNTAIN WHITEFISH IN THE UPPER GREEN RIVER, WYOMING

Introduction

Mountain Whitefish *Prosopium williamsoni* are a salmonid native to the northern Rocky Mountains and have experienced declines in population abundance in rivers throughout Idaho, Colorado, Wyoming, and Montana (Paragamian 2002; Kennedy 2009; Schisler 2010; Edwards 2014, Boyer 2017a). Habitat fragmentation, habitat degradation, disease, and increasing water temperature are hypothesized as mechanisms for the observed declines (Paragamian 2002; Kennedy 2009; Schisler 2010; Pierce et al. 2012; Brinkman et al. 2013). Although several mechanisms have been hypothesized, the causes of decline in specific Mountain Whitefish populations remain largely unknown.

Research on Mountain Whitefish has been limited because of their lack of popularity as a sportfish species, yet there is evidence that Mountain Whitefish have an important role in lotic ecosystems. Mountain Whitefish are often the only remaining native salmonid species in lotic ecosystems that contain popular nonnative trout species, and Mountain Whitefish are often a large percentage of the total biomass of fishes (Paragamian 2002; Lance and Baxter 2011; Pierce et al. 2012). Mountain Whitefish are important in terrestrial food webs and the terrestrial-aquatic exchange of nutrients because they can be an important part of predator diets for species such as river otters *Lontra canadensis*, osprey *Pandion haliaetus*, and bald eagles *Haliaeetus leucocephalus* (Van Daele and Van Daele 1982; Melquist and Hornocker 1983; Northcote and Ennis 1994). Furthermore, Mountain Whitefish are a good indicator of ecosystem health because they are sensitive to increasing water temperature, degraded habitat, and degraded water quality

(Paragamian 2002; Brinkman et al. 2013). Although Mountain Whitefish are sensitive to environmental change and have reduced abundances in portions of their native range, robust populations still occur in some ecosystems (Lance and Baxter 2011; Edwards 2014). One example is the Mountain Whitefish population in the upper Green River, Wyoming, which had the highest abundance of 11 rivers in Wyoming (1,478 fish per km; [Edwards 2014]).

Our approach to better understanding the mechanisms that influence Mountain Whitefish population dynamics was to compare the reproductive ecology and early life-history characteristics between divergent populations. We accomplished this by comparing population characteristics between the robust Mountain Whitefish population in the upper Green River, Wyoming to the Mountain Whitefish population in the Madison River, Montana. The Mountain Whitefish population in the Madison River, Montana has declined in abundance since the 1990s according to angler reports, and these reports were corroborated by declines in Mountain Whitefish catch per unit effort (CPUE) in Hebgen Lake (Boyer et al. 2017a; Clancey and Lohrenz 2013). Boyer et al. (2017a) conducted an extensive study on the movement, reproductive ecology, and juvenile distribution of Mountain Whitefish in the Madison River. Using the Boyer et al. (2017a) study as a template, we studied the upper Green River Mountain Whitefish population, which enabled us to establish generalizations and identify differences between the Mountain Whitefish populations while limiting bias caused by different study designs (Nakagawa and Parker 2015).

Our focus was on identifying the similarities and differences between the upper Green River, Wyoming and Madison River, Montana Mountain Whitefish populations to help discern specific mechanisms that cause Mountain Whitefish population declines. Additionally, our research provides baseline knowledge of the reproductive ecology of Mountain Whitefish in Wyoming and is the first extensive study on the reproductive ecology of a robust Mountain Whitefish population. Our primary research questions were 1) what is the age and length at first maturity, spawning periodicity, fecundity, and age structure of the upper Green River Mountain Whitefish population, 2) what is the spatial and temporal distribution of Mountain Whitefish through their spawning period in the upper Green River, and what influence do abiotic factors have on Mountain Whitefish spawning and migratory behavior, and 3) what is the spatial distribution and habitat use of age-0 Mountain Whitefish in the upper Green River in the spring? In addition to addressing each question for the upper Green River population, comparisons were made for each metric between the upper Green River and the Madison River populations. Increasing our knowledge on the ecology of Mountain Whitefish and the specific mechanisms leading to population declines in the Madison River will help inform Mountain Whitefish restoration efforts and ensure persistence of Mountain Whitefish populations throughout the Intermountain West.

Methods

Study Area

The Green River is a tributary of the Colorado River that flows through Wyoming, Colorado, and Utah. The study was conducted in the upper Green River from Lower Green River Lake downstream 85.2 km to Warren Bridge (Figure 1). The upstream and downstream boundaries of the study area were selected based on the need to better understand the ecology of Mountain Whitefish in this section of the Green River and logistic constraints (i.e., limitations on tracking intervals for individual fish [see below]). The upper Green River is a relatively unaltered high-elevation (2428–2280 m) river in northwestern Wyoming that originates in the Bridger Wilderness, Wind River Mountains. River conditions vary in the upper Green River with 46 km of moderate to high gradient habitat with coarse substrates (e.g., gravel, cobble, boulder) in a relatively confined valley, and 39 km of high-sinuosity, low-gradient habitat with primarily fine substrates in a broad valley. The Green River from Lower Green River Lake downstream 30.1 km is in the Bridger-Teton National Forest, and the lower 51 km is private, State of Wyoming, and Bureau of Land Management property that is used for grass-hay production and cattle grazing. Mountain Whitefish can move upstream of the study area into Lower Green River Lake or downstream 101 km before reaching Fontenelle Reservoir. Mean peak discharge was 80 m^3/s, and mean minimum discharge was 3 m^3/s from 1998 to 2017 at Warren Bridge (USGS 2020a).

The upper Green River has a popular trout fishery, and the fish assemblage includes: Speckled Dace *Rhinichthys osculus*, Redside Shiner *Richardsonius balteatus*, White Sucker *Catostomus commersonii*, Mountain Sucker *Catostomus platyrhynchus*, Cutthroat Trout *Oncorhynchus clarkii*, Rainbow Trout *Oncorhynchus mykiss*, Mountain Whitefish *Prosopium williamsoni*, Brown Trout *Salmo trutta*, Brook Trout *Salvelinus fontinalis*, Lake Trout *Salvelinus namaycush*, and Mottled Sculpin *Cottus bairdii* (Baxter and Stone 1995). The parasite *Myxobolus cerebralis*, which causes whirling disease, is also present in the Green River. The current fishing regulation for Mountain Whitefish harvest is six fish per day and in possession, but little Mountain Whitefish harvest occurs in the upper Green River (D. Rhea, Wyoming Game and Fish Department, unpublished data).

Habitat Characterization

The study area was divided into seven macroscale habitat characterization reaches (5-22 km in length; Figure 1) to assess broad scale spawning habitat selection, assist in radio transmitter allocation, and define habitat in the study area. Reach divisions were based on changes in bedrock type, tributaries, elevation changes, or a combination of these metrics (Frissell et al. 1986). Aerial imagery with QGIS was used to calculate gradient, braiding index, sinuosity, channel width, and floodplain width for each reach (QGIS Development Team 2019). Gradient was calculated by dividing elevation change by segment length. Braiding index was calculated by dividing the total length of all channels (width $\geq$ 6 m) by main channel length (Friend and Sinha 1993). Sinuosity was calculated by dividing segment length by the straight-line length of the valley (Fisher et al. 2012). Channel width and floodplain width were measured at the upstream end and every 500-m downstream for each reach, and the mean was used to characterize channel width and floodplain width. Floodplain width was estimated based on an elevation change of about 1.5 m and vegetation consisting primarily of willows (*Salix* spp.) because a floodplain map of the Green River was not available.

Water temperature data were obtained from temperature data loggers (HOBO UA-001-64 Pendant Data Logger) located in reaches 1, 4, and 7 (Figure 1). Temperature loggers were placed in the Green River in August and retrieved in November and recorded water temperature every 15 minutes. An additional temperature logger (HOBO U20-001-0x Water Level Logger) was placed in reach 4 in the autumn and retrieved in the spring to record winter water temperature. Discharge data were obtained from the USGS gauging station near Warren Bridge (USGS 09188500).

Fish Sampling

Mountain Whitefish were sampled in reaches 2, 4, and 6 by throwable anode electrofishing or angling from September 7 to October 14 to assess reproductive development, fecundity, and age and growth. Reaches 2, 4, and 6 were sampled to spatially distribute sampling while considering logistic constraints. When electrofishing, the variable voltage pulsator (VVP) was set at 20 pulses per second (frequency), 20% pulse width (duty cycle), and voltage was initially set at 250 volts (Edwards 2014). When necessary, voltage was increased until electrotaxis was observed in Mountain Whitefish. When angling, one or two flies were fished with fly-fishing or spinning tackle. Fish were landed as quickly as possible in a rubber mesh landing net, and the hook was removed immediately. Once captured, Mountain Whitefish were transferred to a small holding tank (15 L), anesthetized using an AQUI-S 20E solution (15–30 mg/L), measured to the nearest millimeter total length (TL), and weighed to the nearest gram.

Six Mountain Whitefish per 10-mm length class were euthanized using an AQUI-S 20E solution (500 mg/L) for collection of otoliths and gonads (n = 127). Of the 127 fish euthanized, otoliths and gonadal tissue from all fish were used to estimate age and length at first maturity. Whole mature ovaries were used to estimate fecundity (n = 29), and otoliths from the first 80 fish sampled were used for age-structure analysis. Gonadal tissue was preserved in 10% phosphate buffered formalin, and whole ovaries were preserved in 70% ethanol.

Age and Growth

Sagittal otoliths were mounted in epoxy and cross sectioned using a low-speed saw (Buehler Isomet 11-1280-160). Two readers counted annuli on the otolith cross sections using a compound microscope to determine age. If estimated age differed between readers, both readers viewed the otolith cross section again and an estimated age was determined. Age and length at 50% and 90% first maturity were estimated for male and female Mountain Whitefish using binomial logistic regression. All statistical tests were completed using R software (R Core Team 2021; version 3.6.2) at an alpha level of 0.1 to reduce the probability of a type II error.

Growth was described using the von Bertalanffy growth model. Models were fit for males and females in the Green and Madison rivers to compare growth rates and asymptotic mean length between sexes and populations. Males with primary oocytes in the testicular tissue were functionally male and included in the male growth model. Models were compared by fitting nested models and using ANOVA to determine the best fit model (Ogle 2013).

Reproductive Development

One tissue cross section (1 cm^3) of each ovary and testis was preserved in 10% phosphate buffered formalin for histological analysis. Gonad tissue was embedded in paraffin, sectioned at 5 μm, and stained using Periodic Acid Schiff stain (Luna 1968). One to two histologic sections from the cross-sectioned tissue were examined under a compound microscope (40-400x), and predominant stage of maturation was identified based on Brown-Peterson et al. (2011) modified by Crossman et al. (In Review; Table 1). When assessing age and length at first maturity, maturity is defined as spawning capable (Table 1).

The presence of primary oocytes in testicular tissue was evident during microscopic examination. Hence, the Bateman ranking system (Bateman et al. 2004) modified by Blazer et al. (2007) was used to assign a severity index. Similar to Smallmouth Bass *Micropterus dolomieu*, generally only previtellogenic oocytes were observed, therefore the severity index was based only on the distribution pattern (Blazer et al. 2007). The whole gonad section was scanned for the presence of testicular oocytes, and the severity index was scored by focusing on the central area of the section. A score 1 had focal distribution with a single oocyte within the microscopic field (10x objective), and a score 2 had diffuse distribution with more than one oocyte in a field of view (no association with neighboring oocytes). Score 3 had a cluster distribution with more than one but less than five closely associated oocytes. Score 4 had zonal distribution with more than five closely associated oocytes or numerous clusters in a field of view.

Fecundity

Ovaries from 29 spawning capable females (262 mm to 435 mm TL; body weight of 163 g to 753 g) were collected to estimate fecundity. Absolute fecundity was estimated using the equation:

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

where O_i was the subsample ovarian follicle count, W_i was the subsample weight, n was the number of subsamples, and $W_{ovaries}$ was the combined weight of both ovaries. Relative fecundity was then estimated by dividing absolute fecundity by total body weight (g) (Nikolsky 1963; Bagenal 1978). Mean relative fecundity was compared between the Green River and Madison River populations using a two-sample *t*-test. In addition, linear models were fit for the Green River and Madison River fecundity–weight relationships.

Radio Transmitter Allocation and Implantation

One hundred Mountain Whitefish were selected for radio transmitter implantation—61 females and 39 males. Allocation of radio transmitters implanted in Mountain Whitefish was distributed among reaches with seven in reach 1, four in reach 2, four in reach 3, 35 in reach 4, zero in reach 5, 25 in reach 6, and 25 in reach 7. Sampling was attempted in reach 5, but no fish of sufficient size to tag were captured. Using the same methods described in fish sampling (see above), boat-mounted electrofishing equipment and angling were used to sample fish for radio tagging. Additionally, one fish in reach 1 was sampled with a trammel net 27.4-m long by 1.8-m deep, with 15.2-cm outer bar mesh and 2.5-cm inner bar mesh that was drifted downstream. Fish were sampled for radio tagging on May 2 and from July 10 to 17 in 2019, and from July 1 to 10 in 2020. All sampling was conducted when water temperature was < 15°C to reduce stress (Deters et al. 2010).

Advanced Telemetry Systems (ATS) model F1210 radio transmitters (weight = 11 g) with an internal-coiled antenna were used in 2019, and ATS model F1170 radio transmitters (weight = 4 g) with an internal-coiled antenna were used in 2020 (Advanced Telemetry Systems, Isanti, Minnesota 2020). A body weight threshold of < 2.5% of body weight was used to select Mountain Whitefish for tagging (Hildebrand 2014). Transmitter model was changed between years to reduce transmitter weight; thus, a larger proportion of the Mountain Whitefish population could be tagged in 2020.

Mountain Whitefish were placed in a cradle ventral side up for radio-transmitter implantation. A battery-operated liquid transfer pump with a pressure-control valve was used to irrigate their gills with water during the surgery. A 2-cm incision was made anterior to the pelvic fins on the ventral side of the fish, several millimeters off the midline (Wagner et al. 2011). Gonads were viewed through the incision with an otoscope to determine sex and stage of maturity, and spawning capable fish were implanted with a radio transmitter. The incision was closed with 2–3 simple interrupted sutures (Ethicon, 3-0 PDS-II violet monofilament with CP-2

26 mm reverse cutting needle) (Wagner et al. 2000; Boyer et al. 2017a). After surgery, fish were placed in a live-cage until they regained equilibrium (usually within 3 min) then released within 2 km of the location they were sampled.

Radio Tracking

Tagged Mountain Whitefish were located using an ATS Challenger R2000 or Lotek SRX 400A (Lotek Wireless, Inc., Newmarket, ON, Canada) radio receiver and a three-element Yagi antenna. Tracking was conducted from a vehicle, canoe, raft, or on foot depending on river and weather conditions. A fixed-station receiver (Lotek SRX 400A) with a four-element Yagi antenna was located at the outlet of Lower Green River Lake to detect Mountain Whitefish moving upstream of the study area (Figure 1). However, the fixed station was not operational the entire tracking period in 2019.

Tagged Mountain Whitefish were located at least once per week beginning September 1. Tracking was scheduled to minimize days between detections throughout the study area. Tagged fish were located by triangulation. When tagged fish were located, a waypoint was recorded in Universal Transverse Mercator (UTM) coordinates. Fish status was also recorded (alive, dead, or unknown) based on movement. If tagged fish did not move after two relocations, an attempt was made to slightly startle the fish to determine if the fish was dead or had shed the tag. To test tracking accuracy, blind tests were conducted (n = 20) by placing a radio transmitter in the river at a known location and comparing the distance between the estimated location and the true location. The mean difference between estimated and true locations was 2 m (SD = 1) and the maximum difference was 6 m.

Spawning Locations and Timing

Spawning locations were estimated based on locations of tagged Mountain Whitefish, while egg mats and kick nets were used to confirm spawning locations. Egg mats (0.91-m x 0.54-m rebar frame with natural-fiber furnace filter attached inside the frame) anchored with a cinderblock were placed near suspected spawning locations. Egg mats were checked weekly, and embryos were counted and removed, if present. In 2020, kick nets were also used at suspected spawning locations if embryos were not collected on egg mats. A 1-m^2 area was kick netted near the tagged fish in the nearest riffle upstream and in the nearest riffle downstream. If present, embryos were counted at each location. Other autumn spawning species are present in the Green River, but Mountain Whitefish embryos (1.94 – 3.70 mm) can be differentiated from Brook Trout (4.12 – 5.22 mm) and Brown Trout (4.08 – 5.85 mm) embryos by size (Sigler 1951; Brown 1952; Rajagopal 1979; Hutchings 1991; Bartel et al. 2005).

Angling for Mountain Whitefish occurred throughout the study area to define the spawning period (see above for methods). When a spawning capable male Mountain Whitefish was sampled, we attempted to sample three or more female Mountain Whitefish. The spawning stage of females was determined as spawning capable (distended abdominal cavity and visible tubercles), spawning (eggs released with gentle pressure applied to the abdominal cavity), or spent (flaccid abdominal cavity). Embryo counts on egg mats were also used to confirm spawning but were not used to define the end of the spawning period because the river began to freeze before the end of the spawning period in 2019 and 2020. Thus, the beginning of the spawning period was defined as the date when the first spawning female Mountain Whitefish was sampled, and the end of the spawning period was defined as the date when all mature female Mountain Whitefish sampled were spent.

Movement and Spawning Analysis

River kilometer (rkm) at a Mountain Whitefish location was calculated using QGIS and R software, and net-daily and total-daily movement distances were calculated for each Mountain Whitefish. Net-daily movement was calculated as the difference in river kilometer between relocations divided by the number of days between relocations; thus, distance traveled upstream was positive movement, and distance traveled downstream was negative movement. Total-daily movement was calculated by dividing the change in river kilometer between relocations by the number of days between relocations (Rogers and White 2007). Movement rates were visually compared to water temperature and discharge data to assess their potential as spawning cues. Kruskal–Wallis (KW) tests were used to compare net-daily and total-daily movement rates among spawning periods (prespawn, spawning, postspawn), between sexes, and between years. Movement data were analyzed using non-parametric tests because the data were over-dispersed, zero-inflated, and had extreme outliers. In addition, the first quartile (Q1) and third quartile (Q3) of movement rates were calculated and reported to describe the variability in movement among tagged fish.

Kernel density estimate (KDE) maps were constructed for the prespawn and spawning periods to display fish locations and movement through the spawning season. If a tagged fish was located more than once per week, only one randomly selected relocation point was used in the KDE to standardize the data. Relocations were pooled from 2019 and 2020 to increase total number of relocations for the KDE map. Maps were made using the heatmap tool in QGIS with a bandwidth of 1 km, which was selected based on study area size and net-daily movement rates. In addition to the KDE maps, a map was made in QGIS delineating locations where embryos were collected on egg mats or from kick netting in 2019 and 2020.

Age-0 Habitat Use and Distribution

Age-0 Mountain Whitefish were sampled downstream of each of the four spawning areas, which were identified by high relative density on the spawning period KDE map and confirmed with embryo collection. Slow-water habitats were identified from 0-2 km, 4-6 km, 8-10 km, 12-14 km, and 16-18 km downstream of each spawning area to assess downstream dispersal. When spawning areas were less than 20-km apart, sampling ended where the next spawning area began. To illustrate age-0 distribution, a map was made in QGIS indicating age-0 presence or absence at sampling locations throughout the study area and downstream of Warren Bridge.

Slow-water habitat was identified using aerial imagery and defined as scour pool (eddy, mid-channel, convergence, lateral), backwater, or abandoned channel (Hawkins et al. 1993). One scour pool, backwater, and abandoned channel was selected as a sampling location in each 2-km reach downstream of the spawning areas (e.g., 0-2 km, 4-6 km). When more than one scour pool habitat, backwater, or abandoned channel was identified in a 2-km reach, one was randomly selected as the sampling location. If the sampling location selected did not match the habitat type identified using arial imagery, the nearest slow-water habitat of the same type (i.e., scour pool, backwater, or abandoned channel) was sampled.

Age-0 Mountain Whitefish were seined at each sampling location (3-m x 1.5-m beach seine, 1.6-mm bar mesh), length and width of the seined area were measured to calculate area sampled (m^2), and primary substate type was visually estimated (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). Entire sampling locations were seined if 50-m long, and if greater than 50 m only the 50 m furthest upstream and nearest the river channel was seined. Three seine hauls were conducted in each location unless an additional seine haul was necessary to seine all habitat in the sample location. For example, in a 50-m long sampling location each of the three seine hauls were conducted for about 16 m parallel to the shoreline. Age-0 Mountain Whitefish were measured to the nearest millimeter TL and CPUE (number per m^2) was used to evaluate age-0 habitat use and distribution.

Differences in CPUE of age-0 Mountain Whitefish among distance downstream of spawning areas, habitat types, and primary substrate types were assessed to characterize dispersal and habitat use. To evaluate longitudinal distribution, sample locations were indexed to river kilometer, and CPUE was plotted by river kilometer. A KW test was used to evaluate differences in CPUE. The KW test was selected because the data were over-dispersed, zero-inflated, and contained extreme outliers. When differences in CPUE were evident using the KW test, the Dunn test was used for multiple comparisons. Boulder and bedrock were not evaluated for primary substrate preference because they were not the primary substrate at any sites sampled.

Population Comparisons

Most of the data from the Madison River was collected during the Boyer et al. (2017a) study in the Madison River from Hebgen Dam downstream to Ennis Dam. One exception is that water temperature data in the Madison River from September 1 to November 10, 2020, was obtained from the USGS gauging station at Kirby Ranch near Cameron Montana (USGS

06038800). To make analyses comparable, methods for data collection in the Madison River (see Boyer et al. 2017a) and Green River (see above) were nearly identical. However, all data from the Madison River were collected from 2012 through 2014 and data from the Green River were collected from 2019 through 2021.

Results

Length, Weight, Age, and Growth

Median length of Mountain Whitefish in the Green River was 323 mm (Q1 = 289, Q3 = 352) and varied from 93 to 435 mm. Weight varied from 9 to 753 g and median weight was 281 g (Q1 = 204, Q3 = 367). At all ages sampled, median length was shorter and median weight was lighter in the Green River than the Madison River. For example, median length of age-6 Mountain Whitefish was 100 mm shorter and median weight was 551 g lighter in the Green River than the Madison River.

Age varied from 0 to 21 years in the Green River (Figure 2) with relatively uniform age structure (Figure 3). Mountain Whitefish generally lived longer in the Green River than the Madison River (Figure 3) where 28.8% of the fish sampled in the Green River were ≥ age 10 and only 8.2% were ≥ age 10 in the Madison River. The age distribution of Mountain Whitefish in the Madison River was highly skewed toward young fish with most less than age 4 (Figure 3).

Growth models were similar between sexes for Mountain Whitefish in the Green River ([F = 0.279, df = 3, P = 0.841] females: L_{∞} = 370 mm, K = 0.305, t_0 = -1.215; males: L_{∞} = 370 mm, K = 0.284, t_0 = -1.378) and in the Madison River ([F = 1.785, df = 3, P = 0.152] females: L_{∞} = 472 mm, K = 0.313, t_0 = -1.206; males: L_{∞} = 453 mm, K = 0.328, t_0 = -1.205), thus a model for each river where sex was pooled was used to compare populations. Growth coefficients (K) were similar between the Green River and Madison River populations (*F* = 0.983, df = 1, *P* = 0.322) (Figure 2); however, asymptotic length (L_∞) was shorter in the Green River than the Madison River (*F* = 647.750, df = 1, *P* < 0.001) (Figure 2).

Reproductive Development

Female and male Mountain Whitefish in the Green River matured at similar ages and lengths (Table 2). For example, the estimated age at 50% first maturity varied by 0.1 years and the estimated length at 50% first maturity varied by 7 mm—the confidence intervals for age and length for 50% and 90% first maturity overlapped (Table 2). Female Mountain Whitefish matured at a similar age between the Green River and Madison River; however, length differed considerably with females smaller at first maturity in the Green River (Table 2). Males matured later and were smaller in the Green River compared to the Madison River (Table 2). Length at 50% first maturity was 59 mm shorter for females and 23 mm shorter for males in the Green River than in the Madison River (Table 2). As the percent of mature fish increased (i.e., 50% to 90%) so did the difference between populations, where length at 90% maturity was 94 mm shorter for females and 62 mm shorter for males in the Green River than the Madison River (Table 2).

Most reproductively active female Mountain Whitefish in the Green River were in the developing or spawning capable phase of maturity when sampled in the autumn (Table 1). Females in the cortical alveolar (Table 1; *n* = 1) and primary vitellogenic (Table 1; *n* = 6) reproductive stages could not spawn that autumn because sampling was done less than one month prior to the spawning period—these female Mountain Whitefish (224-276 mm in TL) were developing oocytes/ovarian follicles to spawn for the first time in the next season, not experiencing resting skip spawning (Rideout and Tomkiewicz 2011). In addition, three females were in the regressing stage (Table 1) and had undergone follicular atresia (skip spawning; Rideout and Tomkiewicz 2011). The regressing females comprised 6% of reproductively active females and represent reabsorbing skip spawning, which is characterized by females beginning oocyte development but reabsorbing all oocytes before they are fully developed (Rideout and Tomkiewicz 2011). No regressing females were sampled in the autumn in the Madison River, thus there was no evidence of skip spawning.

Reproductively active male Mountain Whitefish sampled in the autumn were spawning capable; five males (9%) were intersex fish with primary oocytes interspersed within the testicular cysts (Figure 4). Two intersex fish had a severity score of 1 according to Bateman et al. (2004) modified by Blazer et al. (2007), one had a score of 2, and two had a score of 3 (Figure 4). All mature male Mountain Whitefish sampled in autumn in the Madison River were spawning capable, and no intersex males were identified (Boyer et al. 2017a).

Fecundity

Absolute fecundity of Mountain Whitefish in the Green River varied from 2,282 to 16,156 eggs (mean = 5,123 eggs) and was highly correlated with body weight (Figure 5; r^2 = 0.82, df = 27, $P < 0.001$; $ß_0$ = -698, $ß_1$ = 17). Body weight of gravid female Mountain Whitefish varied from 163 g to 753 g, which resulted in a mean relative fecundity of 15 eggs/g (90% CI, 11–18 eggs/g). Body weight of gravid female Mountain Whitefish in the Madison River varied from 291 g to 1,254 g (mean = 747 g), which resulted in higher absolute fecundity (Figure 5; mean = 13,732 eggs) than for Mountain Whitefish in the Green River. Fecundity was highly correlated with body weight in the Madison River (Figure 5; r^2 = 0.91, df = 26, $P < 0.001$; $ß_0$ =

466, $ß_1$ = 18), and the relative fecundity was 18 egg/g (90% CI, 15–22 eggs/g). Relative fecundity was lower in the Green River than in the Madison River (t = -5.54, df = 55, $P < 0.001$).

Spawn Timing, Movement, and Locations

The first spawning female Mountain Whitefish was sampled October 10 in 2019 (mean water temperature = 3.2°C) and October 13 in 2020 (mean water temperature = 5.7°C) in the Green River (Figure 6). Embryos were first collected on egg mats October 23, 2019, and October 15, 2020. All females sampled were spent on October 27, 2019 (mean water temperature = 1.8°C) and November 5, 2020 (mean water temperature = 4.0°C). Therefore, the spawning period was defined from October 10 to October 27 in 2019, and October 13 to November 5 in 2020. Spawn timing differed by six days between years in the Green River and two days between years in the Madison River, and mean spawning period length was 20 days in the Green River and 21 days in the Madison River. Mountain Whitefish spawned one week earlier on average in the Green River than in the Madison River.

Although Mountain Whitefish spawned earlier in the Green River, mean-daily water temperature was lower during the spawning period in the Green River than in the Madison River (t = 7.48, df = 80.24, $P < 0.001$) (Figure 7). In the Green River, mean maximum-daily water temperature during the spawning period was 5.2°C in 2019 (October 10 to October 27) and 6.1°C in 2020 (October 13 to November 5), and mean mean-daily water temperature was 3.2°C in 2019 and 3.9°C in 2020. In the Madison River, mean maximum-daily water temperature during the spawning period was 10.9°C, and mean mean-daily water temperature was 8.2°C in 2014 (October 16 to November 4). During the estimated spawning period in 2020 (October 18 to November 7), mean maximum-daily water temperature was 8.6°C, and mean mean-daily water temperature was 6.6°C in the Madison River. Water temperature was colder in the Green River (mean = 0.3°C, reach 4) than in the Madison River (mean = 1.6°C, reaches 4–7; [USGS 2020b]) during the winter embryo development period from December 3 to March 7.

Seventy-four percent of Mountain Whitefish moved less than 4 km during the tracking season in the Green River, and 58% of net movements were less than 1 km upstream or downstream (Figure 8). Total-daily movement was minimal during the prespawn period and increased during the spawning period (KW: $\chi^2 = 48.082$, df = 2, $P < 0.001$). Male Mountain Whitefish became slightly more active one week prior to females as indicated by total movement increasing during the week of October 6 (mean water temperature = 5.3°C) for males and October 13 (mean water temperature = 3.8°C) for females (Figure 9). Net-daily movement did not differ between sexes ($\chi^2 = 0.626$, df = 1, $P = 0.429$), between years of tracking ($\chi^2 = 0.108$, df = 1, $P = 0.743$), or among spawning stages ($\chi^2 = 3.217$, df = 2, $P = 0.200$) in the Green River. Median net-daily movement was 0 km/day (Q1 = -0.01, Q3 = 0) in the Green River. Although total-daily movement increased during the spawning period, differences in net-daily movement between spawning stages were undetectable because movement direction, upstream or downstream, was similar among individual Mountain Whitefish in the Green River (Figure 9)—indicating no clear pattern in migration. Conversely, a migration pattern was evident in the Madison River, where most Mountain Whitefish moved downstream in the prespawn and spawning periods, spawned in the same area, and tended to move upstream late in the spawning period and during the postspawn period (Figure 9; Boyer et al. 2017a). Similar to the Green River, male movement increased, albeit at a greater magnitude, during the week of October 6 (mean water temperature = 9.7°C) and female movement increased the week of October 13 (mean water temperature = 8.0°C) in the Madison River (Figure 9).

In general, Mountain Whitefish were concentrated in four areas during the prespawn period (Figure 10). Given that Mountain Whitefish had limited movement during the spawning period, the spawning locations, which were all confirmed by the collection of Mountain Whitefish embryos, were identical to the prespawn locations (Figure 10). However, 8% of tagged Mountain Whitefish did move to spawn in a different area than where they were located during the prespawn period.

Broad habitat characteristics of each reach indicated that adult Mountain Whitefish used areas with high gradient (> 0.21 m/km) and avoided areas with low gradient (0.21 m/km) to spawn (Table 3; Figure 10). During the spawning period, Mountain Whitefish primarily remained in one location in reach 1, whereas fish in reaches 4, 6, and 7 were more evenly distributed throughout the reach (Figure 10). Nearly all Mountain Whitefish located in reaches 2 and 3 were in the downstream 1 km of reach 2 and the upstream 1 km of reach 3, which is a transition area between high gradient in reach 2 and low gradient in reach 3 (Table 3; Figure 10). In addition, reach 5 had a low gradient (0.21 m/km) and was generally unused by Mountain Whitefish (Table 3; Figure 10).

Age-0 Habitat use and Distribution

Median CPUE for age-0 Mountain Whitefish was 0.15 (Q1 = 0.01, Q3 = 0.34) per m^2. Catch per unit effort was highly right skewed, in part because two sites had CPUE values about 30 times the median CPUE value (Figure 11; CPUE = 5.10, 4.42). Total length of age-0 Mountain Whitefish varied from 12 mm to 33 mm, and the median was 21 mm. Mean total length of age-0 Mountain Whitefish sampled from May 16 to May 25 was 9 mm shorter (95% CI, 9 – 10) in the Green River than in the Madison River (t = -35.457, df = 485.750, $P < 0.001$) (Boyer et al. 2017b).

Sample locations with the highest CPUE values were between river kilometer 34 and 46 (Figure 11), which is immediately downstream of the spawning area in reach 4 (Figure 10). In addition, CPUE was relatively high between river kilometer 7 and 16, which is downstream of the spawning area in reach 2, and between river kilometer 80 and 85, which is downstream of the spawning area in reaches 6 and 7 (Figures 10 and 11). Catch per unit effort was similar at 0–2 km, 4–6 km, 8–10 km, 12–14 km, and 16–18 km downstream of spawning areas (Figure 11; KW: χ^2 = 1.012, df = 4, P = 0.908). The uniform distribution of age-0 Mountain Whitefish CPUE downstream of spawning areas indicates dispersal of Mountain Whitefish is variable—that is, some age-0 fish moved 0-2 km and others moved 16-18 km (Figure 11).

Catch-per-unit-effort was similar among abandoned channels, backwaters, and scour pools (Figure 11; KW: χ^2 = 0.241, df = 2, P = 0.887), although the two sites with highest CPUE values were from scour-pool habitat (Figure 11). Catch per unit effort differed among primary substrate type (Figure 11; KW: χ^2 = 6.543, df = 3, P = 0.088) and was higher at sites with silt (median = 8.5) than cobble (median = 0.0) (Dunn test: Z = -2.466 P = 0.082). No other differences among primary substrate types were evident, but CPUE was relatively high at sites with sand as a primary substrate (median = 0.25) and low at sites with gravel (median = 0.05) or cobble (median = 0.0).

Discussion

Understanding variation in the reproductive ecology and early life-history for a species is central to fully understanding a species response to varying abiotic and biotic conditions throughout its range. Thus, a species response to perturbations such as climate change, habitat alteration, or harvest could be better predicted by having a more complete understanding of the species life history. Here, we had the unique opportunity to replicate research on the reproductive ecology, spawning behavior, and early-life history of Mountain Whitefish in two rivers in the Intermountain West, which are geographically (200 km) and hydrologically (Colombia and Colorado river basins) separated, and have varied hydrogeomorphic conditions and angling pressure. Replication is the cornerstone of scientific inquiry, and by using identical methodology, we were able to further the understanding of the life-history variation of Mountain Whitefish.

We summarize the similarities and differences between Mountain Whitefish populations in the Green River and Madison River. We found variation in length at first maturity, which was a result of the variation in growth of Mountain Whitefish between the Green River and Madison River. Spawning periodicity was similar between populations with both sexes generally spawning on an annual cycle. However, a low incidence of skip spawning was observed in female Mountain Whitefish in the Green River. In addition, a low incidence of intersex was observed in male Mountain Whitefish in the Green River. Relative fecundity was similar between populations, but absolute fecundity varied with differences in size structure. Spawning movement varied between populations, with the Green River population moving relatively little and having no clear movement pattern and Mountain Whitefish in the Madison River exhibiting distinct spawning migrations, mostly downstream. Mountain Whitefish spawned earlier in the Green River and at cooler water temperatures than in the Madison River. In the following spring, age-0 Mountain Whitefish in the Green River were commonly located 0 to 18 km downstream of spawning locations in slow-water habitat with fine substrate, similar to the Madison River Mountain Whitefish population. In general, Mountain Whitefish mature between ages 2 and 4, are annual spawners, males begin spawning movement prior to females, can have varying length of spawning migrations, spawn for about 3 weeks, and age-0 fish use slow-water silt-laden habitats 0–18 km below spawning locations. The generalities described here for the Green River and Madison River populations likely apply to other Mountain Whitefish populations in the Intermountain West.

Variation observed in reproductive traits and growth rates among populations can be a function of fish density and system productivity (Michaletz 1998; Bohlin et al. 2002). The differences in growth can be expressed in reproductive output, such as larger female fish are more fecund than smaller fish of the same age (Beacham 1982; Thorpe et al. 1984). Thus, when large differences in growth are observed there can be large differences in absolute fecundity, which is what we observed between the Green River and Madison River. For example, the Green River had no female Mountain Whitefish sampled that were >800 g and the highest absolute fecundity estimate was 16,000, whereas the Madison River had female Mountain Whitefish as large as 1250 g with an estimated absolute fecundity of 25,000. However, relative fecundity is somewhat similar among populations, varying from 11 to 21 eggs/g (Sigler 1951; Brown 1952; Northcote and Ennis 1994; Wydoski 2001) with the Green River (15 eggs/g) and Madison River (18 eggs/g) populations differing by 3 eggs/g. Interestingly, despite differences in growth between Mountain Whitefish in the Green River and Madison River, age at first maturity was similar and comparable to most other populations (Sigler 1951; Thompson and Davies 1976;

Meyer et al. 2009) apart from the population in the West Fork of the Blacks Fork River, Utah, which matured at a greater age (Wydoski 2001). Thus, age at first maturity is relatively consistent among populations with most Mountain Whitefish maturing between ages 2 and 4 (Sigler 1951; Thompson and Davies 1976; Meyer et al. 2009).

Skip spawning occurs in fishes and is a reproductive strategy to increase lifetime reproduction by increasing survival and the likelihood of spawning in the future (Bull and Shine 1979; Rideout et al. 2005). We observed skip spawning in female Mountain Whitefish in the Green River, albeit at low levels. The observation of skip spawning in this study is the first to show evidence of skip spawning in Mountain Whitefish, though it is common in other Coregoninae species (Kennedy 1953; Savereide and Huang 2016). Skip spawning is often associated with low system productivity and poor diet (Rideout et al. 2005; Rideout and Tomkiewicz 2011), thus skip spawning observed in the Green River may be a result of low system productivity (Sublette County Conservation District 2014).

The observation of primary oocytes in male fishes (intersex) is becoming more common throughout the world (Jobling et al. 1998; Hecker et al. 2002; Hinck et al. 2009). In many cases the high incidence of intersex is the result of environmental pollution (Jobling et al. 1998; Hecker et al. 2002). Thus, the finding of intersex male Mountain Whitefish in the Green River was surprising given the upper Green River is considered a relatively pristine ecosystem (Sublette County Conservation District 2014). Nine percent of male Mountain Whitefish from the Green River had the presence of primary oocytes embedded in their testicular tissue, which is higher than background levels described in gonochoristic fish species (e.g., 4% in Roach *Rutilus rutilus*, Jobling et al. 1998; 1% in Atlantic Sturgeon *Acipenser oxyrinchus*, Van Eenennaam &

Doroshov, 1998; 0.5% in Bream *Abramis brama*, Hecker 2002; 2.6% in Spottail Shiners *Notropis hudsonius*, Aravindakshan et al. 2003). The probability of detecting intersex with the severity score of 1 in one section of gonadal tissue examined was about 0.6 in Smallmouth Bass (Blazer et al. 2007), thus the incidence of intersex may have been missed in some Mountain Whitefish sampled in the Green River. Intersex in gonochoristic fish species can be increased by cattle grazing near the river and tributaries (Kolodziej and Sedlak 2007), atmospheric deposition of contaminants (Landers et al. 2010; Pritz et al. 2014), or human inputs (Depiereux et al. 2014). However, the upper Green River watershed is relatively undeveloped, and there are no water-quality concerns (Sublette County Conservation District 2014). Thus, the incidence of intersex fish and the mechanism(s) that cause intersex Mountain Whitefish in the Green River should be further examined.

Mountain Whitefish are one of several species in the Intermountain West (e.g., Brook Trout, Brown Trout, Bull Trout *Salvelinus confluentus*) that spawn in the autumn. Mountain Whitefish spawning behavior occurs from mid-October through November when water temperatures decline to 4–10°C (Thompson and Davies 1976; Northcote and Ennis 1994; Pierce et al. 2012). Movement prior to spawning and during spawning are often thought to be linked to water temperature and discharge (Brenkman et al. 2001; Hildebrand et al. 2014; Tornabene et al. 2020). However, in the Green River and Madison River, Mountain Whitefish spawned at similar dates despite variation in water temperature and discharge. There are many physiological factors that can influence when a fish spawns, but we suspect predictable factors influence spawn timing because spawning date was consistent annually in the Green and Madison rivers. Photoperiod has been found to effect spawn timing (Bon et al. 1999; Bromage et al. 2001; Hess et al. 2016;

Quinn et al. 2016) and may more strongly influence spawn date than water temperature and discharge for Mountain Whitefish.

Mountain Whitefish movement during prespawn, spawning, and postspawn periods is highly variable among populations throughout the species range. For example, most Mountain Whitefish in the Blackfoot River, Montana moved less than 3.2 km to spawn (Pierce et al. 2012), which is similar to what was observed in this study. Conversely, Mountain Whitefish can move great distances during the prespawn period such as in the North Fork Clearwater River, Idaho where Mountain Whitefish moved 82 km upstream (Pettit and Wallace 1975) and in the Madison River where they moved 25.5 km downstream (Boyer et al. 2017a). Mountain Whitefish have been observed moving into lentic habitat or low-velocity lotic habitat in the mainstem after spawning to overwinter (Davies and Thompson 1976; Benjamin et al. 2014; Boyer et al. 2017a). Despite lentic habitat available upstream of the spawning locations in the Green River, none of the Mountain Whitefish in our study moved into Lower Green River Lake; however, 12% of the Mountain Whitefish did move downstream to a low-gradient lotic reach.

Dispersal by larval fishes can be beneficial by reducing crowding, exposing fish to preferred habitats, and reducing predation (Jonsson 1991; Copp et al. 2002; Humphries 2005). Furthermore, juvenile fish often use different habitat than adults because of ontogenetic shifts in diet (Lechner et al. 2016). Dispersal to slow-habitat by juvenile Mountain Whitefish results in habitat partitioning between juvenile (age-0) and adult Mountain Whitefish and was observed in the Green River and Madison River where juvenile fish occupied slow-water habitat with fine substrate, downstream of spawning areas. Ontogenetic shifts in habitat use by Mountain Whitefish has also been observed in the Sheep River, Alberta (Davies and Thompson 1976). The use of slow-water habitat is likely of function of juvenile Mountain Whitefish consuming chironomids (Stalnaker and Gresswell 1974), which are common in slow-water habitat (Ruse 1994; Syrovatka et al. 2009) and avoiding high-velocity areas until they develop the body mass to negotiate increased velocity and switch prey (Thompson and Davies 1976). Unfortunately, use of habitat with fine substrate increases exposure of age-0 Mountain Whitefish to whirling disease (Zendt and Bergersen 2000), which is present in the Green and Madison rivers and can cause high mortality in Mountain Whitefish (Schisler 2010). However, timing of peak *Myxobolus cerebralis* triactinomyxon release, which causes whirling disease, does not coincide with age-0 Mountain Whitefish when they are susceptible to whirling disease (Downing et al. 2002; Schisler 2010; Pierce et al. 2012) unless the system is groundwater influenced (Pierce et al. 2012).

Our comparison between Mountain Whitefish populations in the Green River and Madison River identified two differences most likely contributing to the apparent decline in the Madison River. First, water temperature was lower during embryo development in the Green River than in the Madison River. Mountain Whitefish embryos require water temperatures below 8.4°C during the development period for successful recruitment, which is colder than most native and introduced salmonids in the Intermountain West require (Rajagopal 1979; USEPA 1986; Elliott and Elliott 2010; Brinkman and Vieira 2011; Brinkman et al. 2013). In the Madison River, water temperatures were often above the upper optimal or maximum temperature for embryo development whereas water temperature during the spawning and early development period was generally suitable for embryo development in the Green River. Consequently, it is probable that high water temperature in autumn is increasing embryo mortality in the Madison River. High water temperature during embryo development is a growing concern in fisheries and has been implicated for recruitment failure in other fish species (Burbot *Lota lota*, Stapanian et al. 2010; Vendace *Coregonus Albula*, Kangur et al. 2020). Second, the age structure of the Green River Mountain Whitefish population was more uniform and older than the population in the Madison River. Mountain Whitefish spatial distribution can change among life stages (Davies and Thompson 1976), which could bias age structure assessment. However, most Mountain Whitefish mature by age 2 in the Madison River and age 3 in the Green River, thus most fish sampled were mature and evidence does not suggest that spatial distribution of mature Mountain Whitefish differs based on age (Northcote and Ennis 1994). In addition, fish were sampled in multiple locations in the Green River and Madison River, further reducing any bias caused by differences in spatial distribution among ages. The age structure in the Green River represented an unexploited population (Kocovsky and Carline 2001) in the climax stage, which is dominated by older individuals (Johnson 1983). The age structure in the Madison River was skewed toward more younger fish, which is often a characteristic of an overfished population (Hsieh et al. 2010). Angling pressure in the Green River has not been quantified but is probably well below the Madison River, which received an estimated 180,000 angler days in 2016 (Montana FWP 2018; D. Rhea, Wyoming Game and Fish Department, unpublished data). Additionally, in the Madison River catch rates are relatively high (0.24 Mountain Whitefish caught per hour) and angling pressure is highest during the summer when Mountain Whitefish can have a high catch and release mortality rate (28%) due to high water temperatures (>23°C) (Montana FWP 2018; Boyd et al. 2010). Differences in age structure between the Green River and Madison River populations resemble the change in age structure of European Whitefish *Coregonus lavaretus* in Lake Imandra, Russia (Lukin et al. 2006) and Lake Whitefish *Coregonus clupeaformis* in Lake

Winnipeg, Manitoba (Davidoff et al. 1973) with increased fishing pressure. In Lake Imandra and Lake Winnipeg whitefish populations prior to high fishing pressure the age structure was more uniform and older, resembling the Green River population, and with increased harvest the age structure became less uniform and younger, resembling the Madison River population (Davidoff et al. 1973; Lukin et al. 2006).

Generalizations drawn from comparing Mountain Whitefish populations in the Green River and Madison River could apply throughout in the Intermountain West given the large geographic and hydrologic separation, variation in hydrogeomorphic conditions, and differences in angling pressure between systems. By comparing the populations, we identified two factors to assess in populations that have declined—autumn water temperature for its effect on embryo mortality and population age structure if harvest or angling pressure are high. Our study builds on a relatively small body of knowledge on Mountain Whitefish reproductive and juvenile ecology and is especially important given the increasing frequency of reports suggesting declines in the abundance of Mountain Whitefish throughout the species range.

Management and Research Needs

- Conduct outreach to improve public perception of Mountain Whitefish. Increasing angler appreciation for Mountain Whitefish may reduce catch-and-release mortality by improving fish handing practices and increase support for future management actions that may be necessary to maintain the Green River Mountain Whitefish population.
- Set a temperature logger in the Green River in a central location (e.g., Warren Bridge) to monitor summer water temperature and water temperature during embryo development.

Collect temperature data yearly with emphasis on ensuring data is collected in the summer and autumn.

- Conduct creel surveys and use trail cameras to quantify angling pressure in the Green River from Lower Green River Lake downstream to Fontenelle Reservoir.
- Estimate Mountain Whitefish abundance in a section of the Green River (e.g., Warren Bridge to 40 Rod boat launch) at the same time of year every five years using methods outlined by Edwards (2014) to assess population trends and detect changes in abundance.
- Conduct a stock assessment and develop an age-structured model to assess the population dynamics of the Mountain Whitefish population in the upper Green River. Use the model to assess perturbations to the population such as increased mortality from catch-and-release angling.
- Investigate the cause of high Mountain Whitefish intersex levels in the upper Green River by testing the water multiple times during the year for endocrine-disrupting compounds. In addition, collect blood samples from male Mountain Whitefish in multiple locations and quantify their plasma vitellogenin concentrations.

Tables

Table 1. Descriptions of sex-specific reproductive phases and stages of gonadal development used to describe the population reproductive structure of the Mountain Whitefish in the Green River modified from Brown-Peterson et al. (2011) in Crossman et al. (In Review). Abbreviations of reproductive phases and stages are provided in parentheses. Reproductive condition suggests which stages and phases have spawning potential (active) or not (inactive), within that reproductive cycle.

Sex	Phase	Reproductive Stage	Condition	Histological and Macroscopic Features
Female				
	Immature (IMM)	Oogonial Proliferation (OP)	Inactive	Clusters of oogonia; no atresia
	Immature (IMM)	Primary Growth (PG)	Inactive	Primary growth oocytes and oogonia; no atresia
	Early Developing (DEV)	Cortical Alveolar (CA)	Inactive*	Primary growth oocytes with cortical alveoli on periphery of the oocyte or distributed throughout the ooplasm; follicular layer formed; thin zona radiata; may be no atresia or < 20% atresia from the past cycle
	Developing (DEV)	Primary Vitellogenic (PV)	Inactive*	Yolk granules accumulating in periphery of the oocyte; cortical alveoli appear in a central position and migrate toward the periphery of oocyte; zona radiata thickening
	Developing (DEV)	Secondary Vitellogenic (SV)	Active	Yolk globules accumulating toward center or may be present throughout the oocytes; cortical alveoli and lipid droplets move toward the periphery of oocyte; zona radiata thickening
	Spawning Capable (SPC)	Tertiary Vitellogenic (TV)	Active	Yolk fusing into larger globules throughout the oocytes; zona radiata development complete

Table 1 Continued

	Spawning Capable (SPC)	Oocyte Maturation (OM)	Active	Yolk coalesced; offset germinal vesicle or germinal vesicle may be broken down
	Regressing (REG)	Regressing (RG)	Inactive	Ovaries contain numerous postovulatory follicles and the next generation of oocytes (cortical alveolar and/or vitellogenic) or > 50% atretic oocytes or follicles from any stage may be present
	Regenerating (RGN)	Regenerating (RN)	Inactive	Oogonia and primary growth oocytes; degenerating postovulatory follicles may be present; atretic ovarian follicles may be present
Male	Immature (IMM)	Spermatogonial Proliferation (SP)	Inactive	Spermatogonia undergoing mitosis; no lumen in lobules; small testes
	Developing (DEV)	Early spermatogene sis (ES)	Active	Cysts may contain spermatogonia, spermatocytes, spermatids, and/or spermatozoa; spermatozoa not present in lumen of lobules or in sperm ducts; germinal epithelium continuous throughout
	Spawning Capable (SPC)	Mid to late-spermatogenesis (ML)	Active	Cysts contain few spermatogonia and spermatocytes, spermatids, and spermatozoa; spermatozoa present in lumen of lobules and/or sperm ducts; germinal epithelium continuous or discontinuous
	Spawning Capable (SPC)	Ripe (RI)	Active	Only spermatozoa visible; spermatozoa present in lumen of lobules and/or sperm ducts; germinal epithelium discontinuous

Table 1 Continued

Regressing (REG)	Post-spermiation (RG)	Inactive	Residual spermatozoa in lumen of lobules and sperm ducts; cysts near periphery contain spermatogonia, spermatocytes, spermatids, and/or spermatozoa; regeneration of germinal epithelium
Regenerating (RGN)	Regenerating (RN)	Inactive	Little residual spermatozoa in lumen of lobules and sperm ducts; proliferation of spermatogonia throughout testes; germinal epithelium continuous

*Fish in these phases did not have spawning potential because sampling occurred approximately one-month prior to the spawning season. If sampling occurred in the winter or spring, they could potentially spawn the following season.

Table 2. Age (years) and total length (mm) at 50% and 90% first maturity in the Green River, Wyoming and the Madison River, Montana predicted using binomial logistic regression (Boyer et al. 2017a). Values in parentheses are 90% confidence intervals.

Sex	Metric	Percent first mature	Green River	Madison River
Female				
	Age	50	2.9 (2.5–3.0)	2.6 (2.1–3.1)
		90	3.0 (2.6–3.1)	3.7 (2.2–5.0)
	Length	50	270 (260–279)	329 (314–343)
		90	284 (267–289)	378 (346–404)
Male				
	Age	50	3.0 (2.5–3.0)	2.0 (2.0–2.1)
		90	3.1 (2.6–3.1)	2.1 (2.1–2.2)
	Length	50	277 (269–277)	300 (282–316)
		90	278 (271–279)	340 (317–356)

Table 3. Habitat characteristics of the Green River, and the percentage of radio-tagged adult Mountain Whitefish in each reach during the prespawn and spawning periods.

								Percent of fish in reach	
Reach	River kilometer	Length (km)	Braiding index	Gradient (m/km)	Sinuosity index	Channel width (m)	Floodplain width (m)	Prespawn	Spawning
1	0-9.3	9.4	1.32	0.72	1.07	54.4	142.0	11.4	13.0
2	9.3-14.6	5.2	1.25	8.38	1.16	32.7	109.3	14.6	15.0
3	14.6-32.0	17.4	1.15	0.21	1.52	44.0	390.9	4.1	6.0
4	32.0-45.0	12.9	1.35	3.82	1.38	43.4	240.2	34.8	34.0
5	45.0-66.6	21.7	1.09	0.21	1.77	45.1	400.4	0	0
6	66.6-77.7	11.1	1.11	1.52	1.32	60.6	86.4	23.4	17.0
7	77.7-85.2	7.5	1.13	3.19	1.09	50.9	81.9	11.7	15

Figures

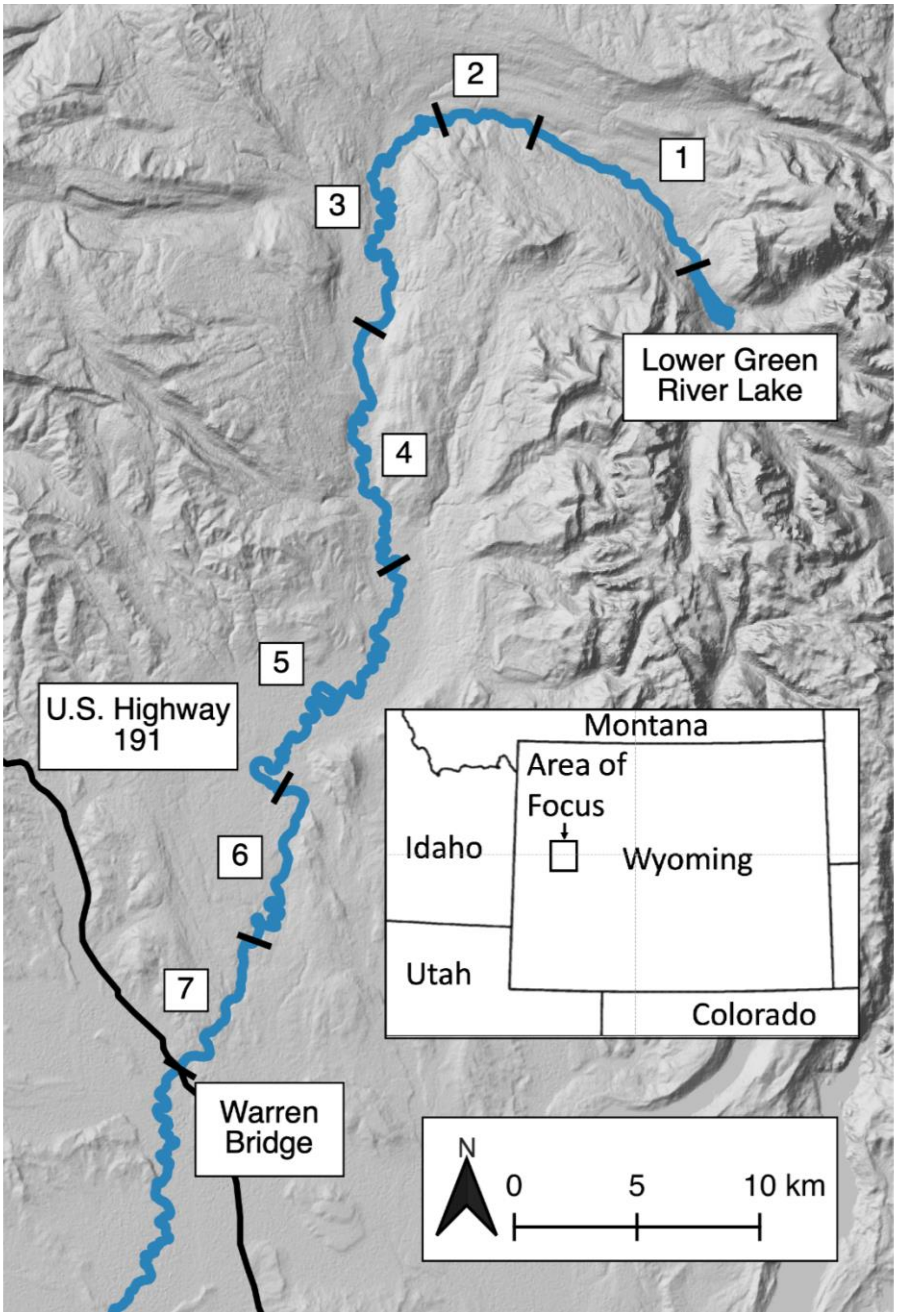

Figure 1. Map of the study area on the Green River, Wyoming. Labels delineate reaches (reach boundaries are indicated by black lines); Lower Green River Lake and Warren Bridge bound the study area.

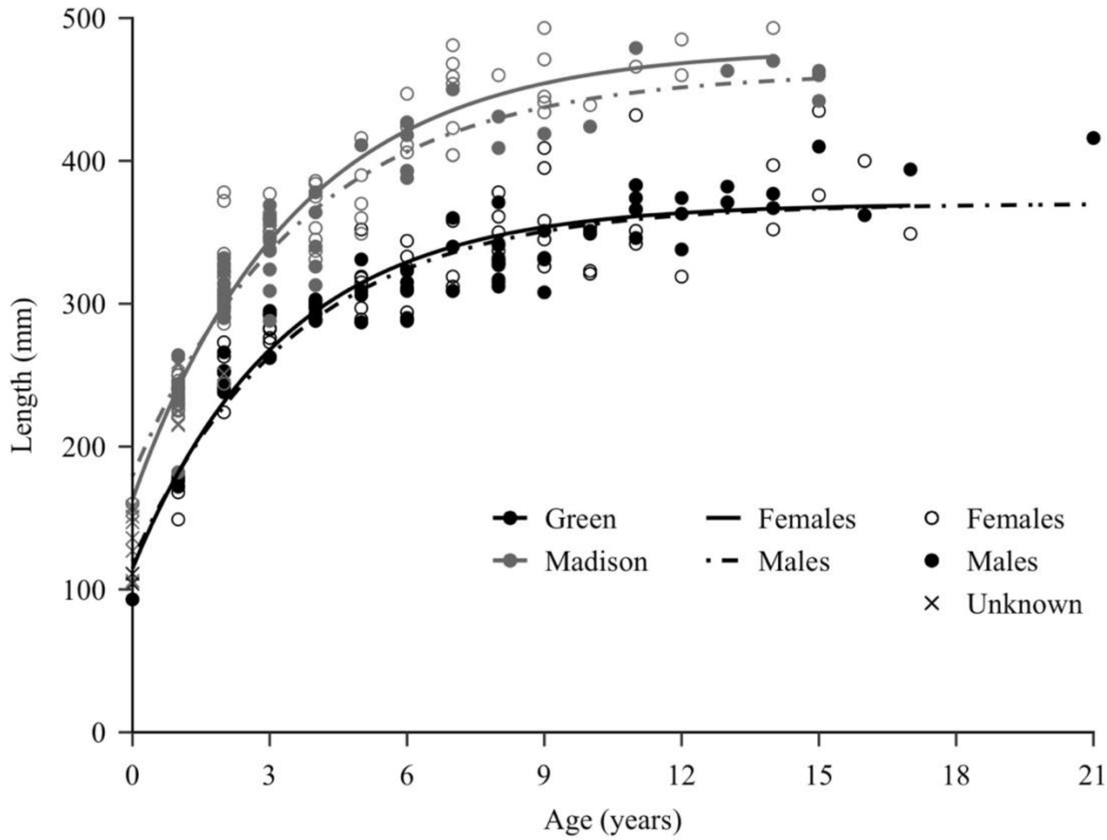

Figure 2. Age-length (total) relationship with von Bertalanffy growth models by sex for Mountain Whitefish sampled in the Green River (2019) and Madison River (2012–2013). The end of each line indicates the oldest Mountain Whitefish sampled in each river by sex.

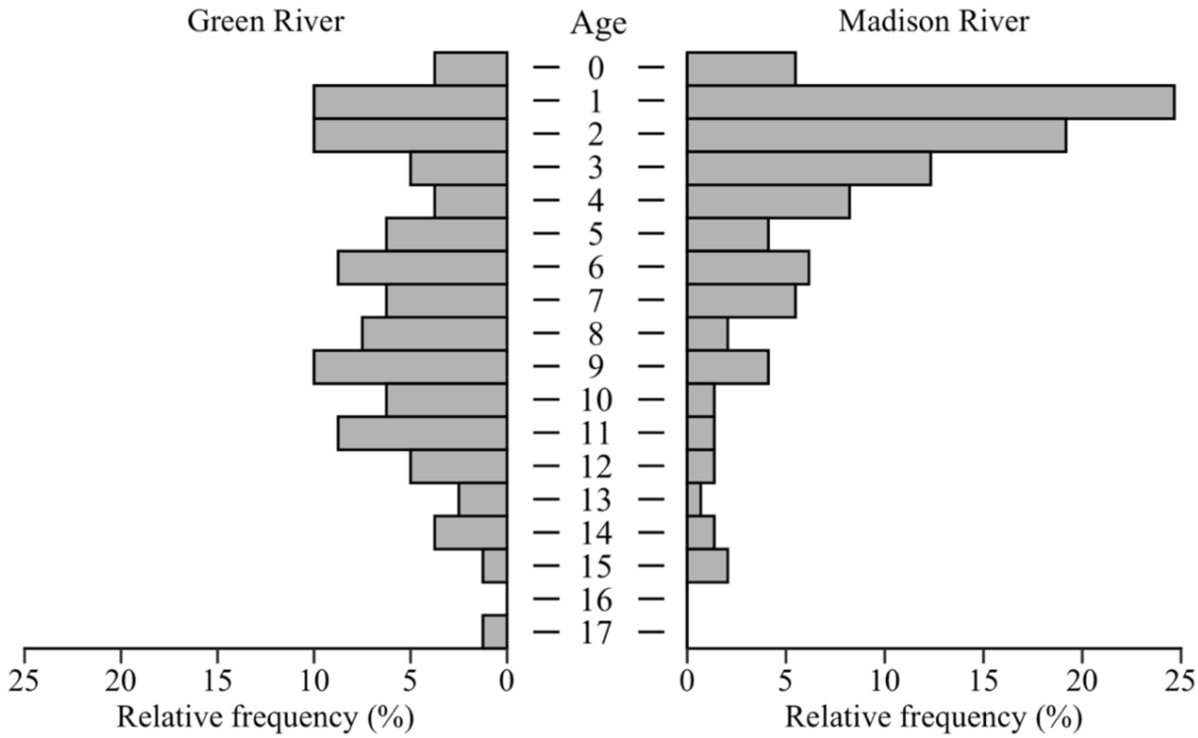

Figure 3. Horizontal histograms of the relative frequency by age in years of Mountain Whitefish sampled in the Green River in 2019 (n = 80; left), and the Madison River in 2012 (n = 146; right). The center y-axis shows the age in years determined from otolith cross sections.

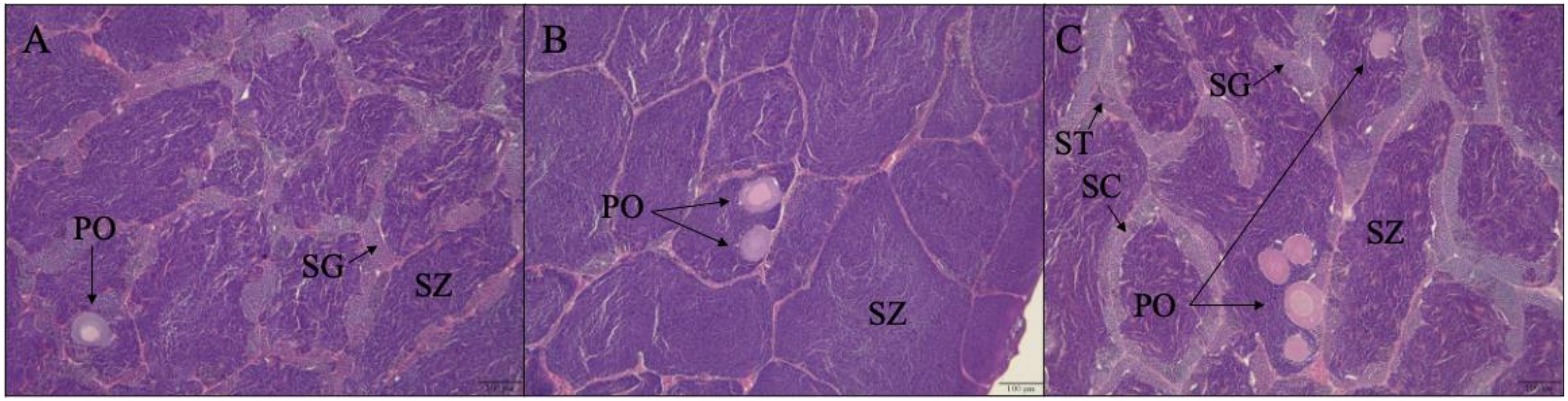

Figure 4. Photomicrographs of testicular tissue containing primary oocytes (PO) in Mountain Whitefish in the Green River, Wyoming. The Bateman ranking system (Bateman et al. 2004) modified by Blazer et al. (2007) was used to assign a severity index based on the distribution pattern of PO only. A) Severity index 1 with focal distribution with a single PO within the microscopic field (10x objective); B) severity index 2 with diffuse distribution of more than one PO in a field of view and no association with neighboring oocytes; and C) severity index 3 with a cluster distribution of more than one but less than five closely associated PO. SG=spermatogonia; SC=spermatocytes; ST=spermatids; and SZ=spermatozoa. Tissue was stained with Periodic Acid Schiff reagent.

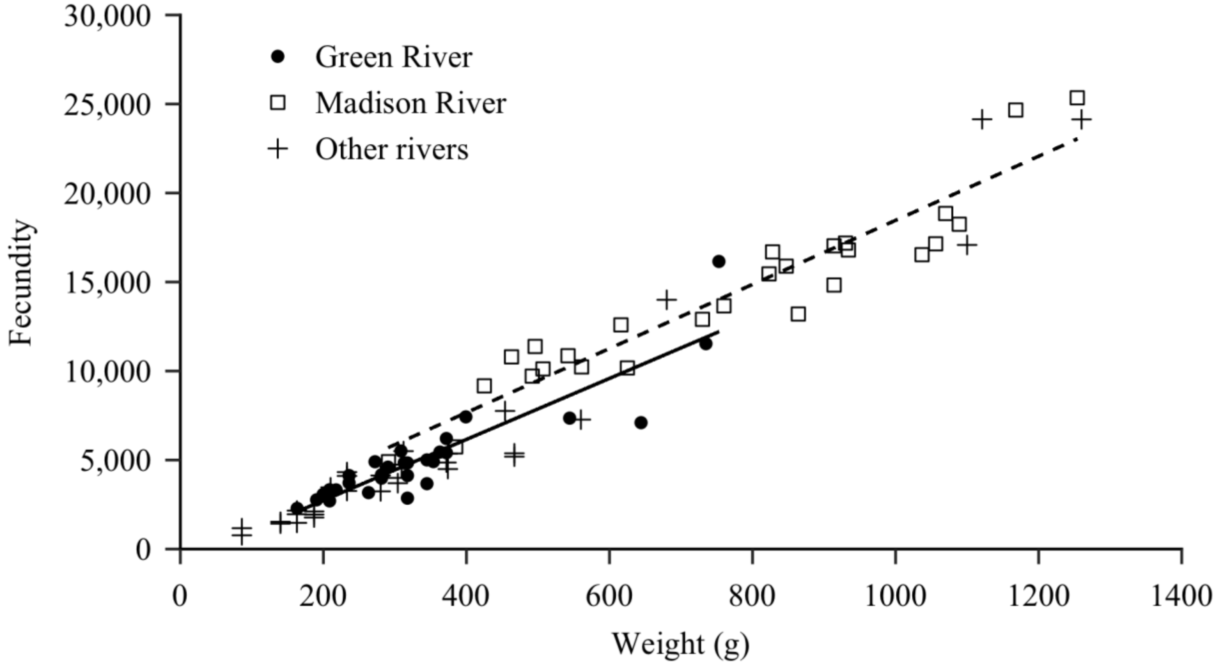

Figure 5. Mountain Whitefish fecundity–weight relationship for the Green River population, Madison River population, and other populations (Sigler 1951; Brown 1952; Northcote and Ennis 1994; Wydoski 2001). Solid line is the linear model for the Green River and the dashed line is the linear model for the Madison River.

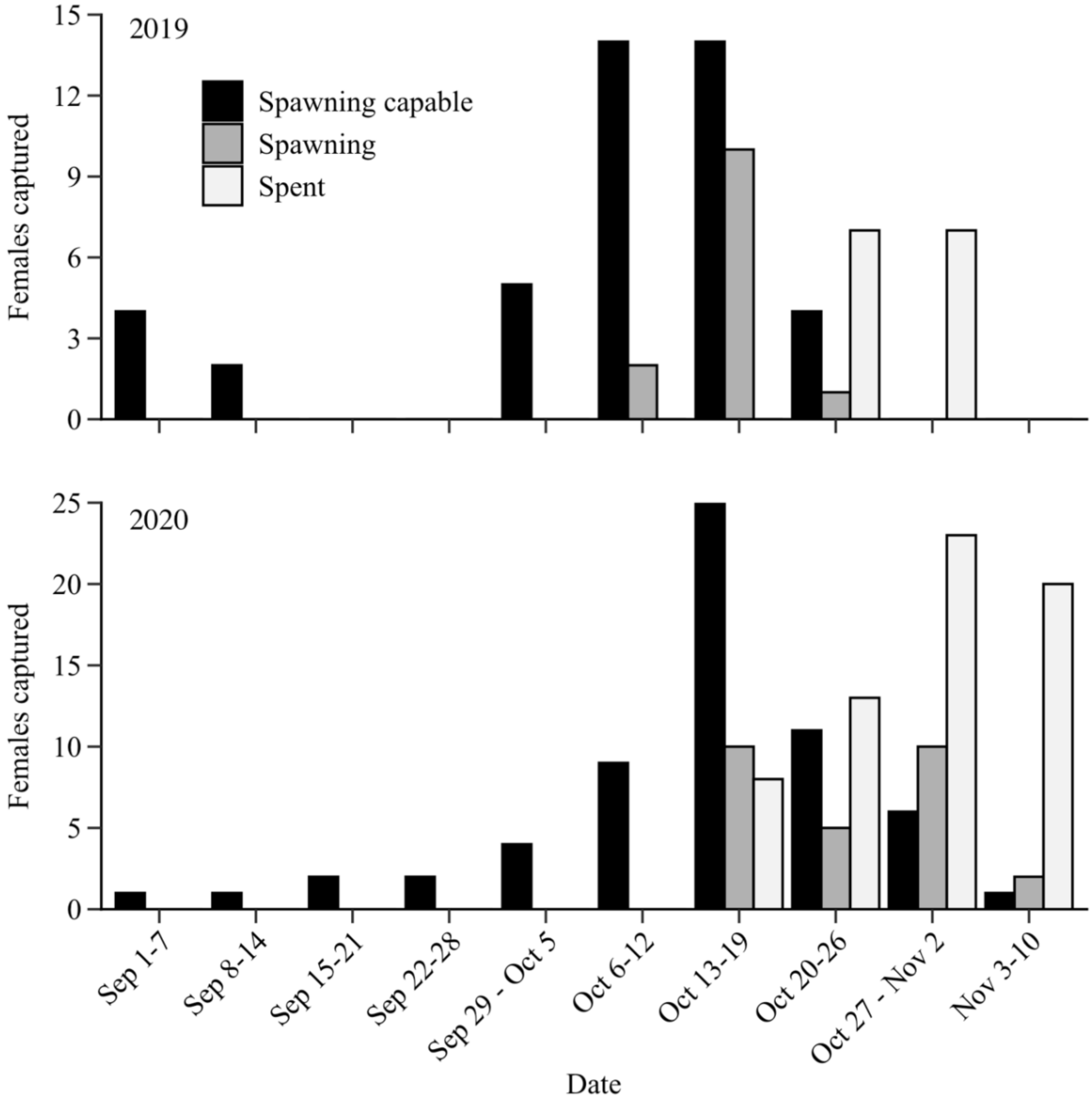

Figure 6. Reproductive stage of female Mountain Whitefish sampled angling in the Green River, Wyoming from September 1 to November 5 in 2019 and 2020. Angling data were pooled weekly with day one being September 1 each year.

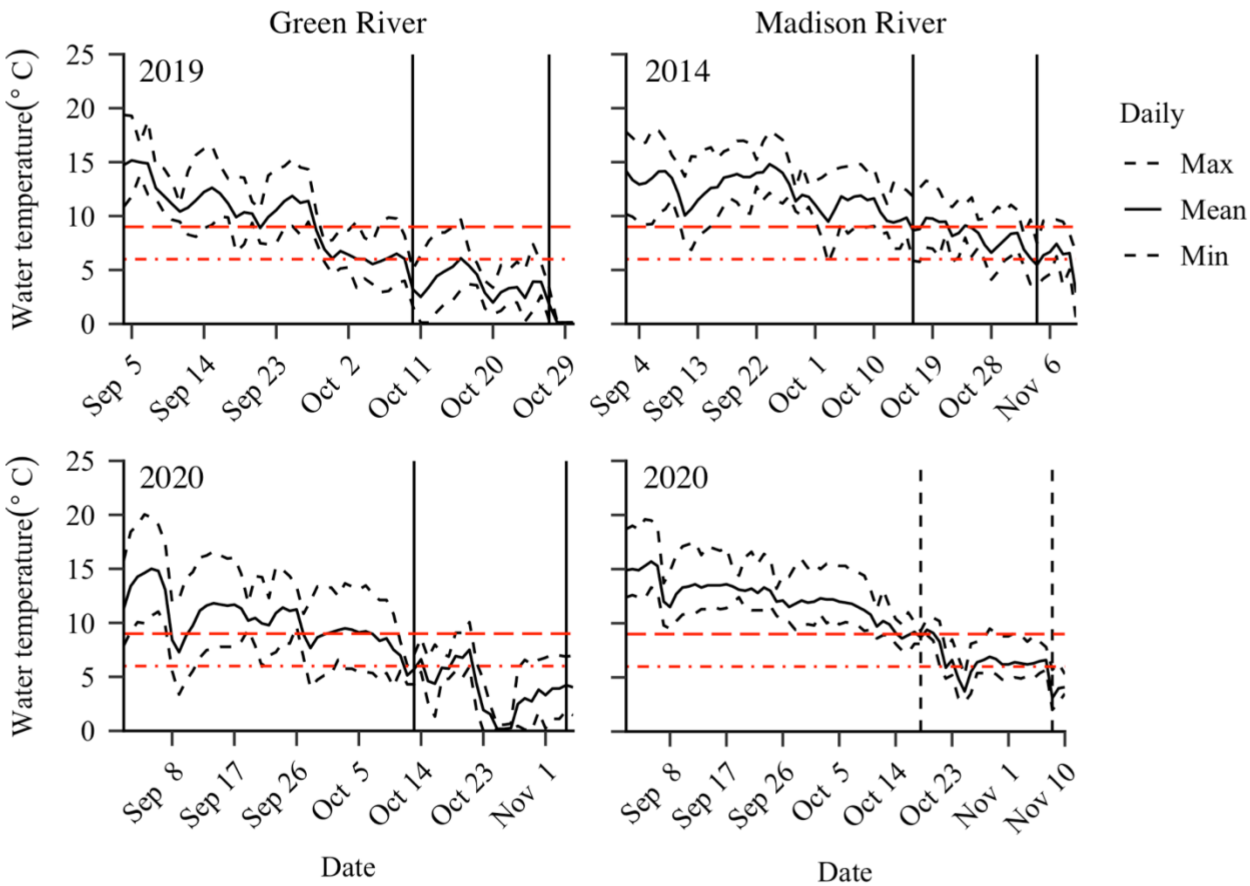

Figure 7. Maximum, mean, and minimum daily water temperature in the Green River for 2019 and 2020 (left panels), and the Madison River for 2014 and 2020 (right panels [top right panel; recreated from Boyer et al. 2017a]). Vertical solid lines indicate the estimated spawning period, and vertical dashed lines indicate the spawning period based on prior estimates (Boyer et al. 2017a). Red horizontal lines indicate the maximum (9°C) and upper optimal (6°C) water temperature for Mountain Whitefish embryo development (Rajagopal 1979; Brinkman et al. 2013).

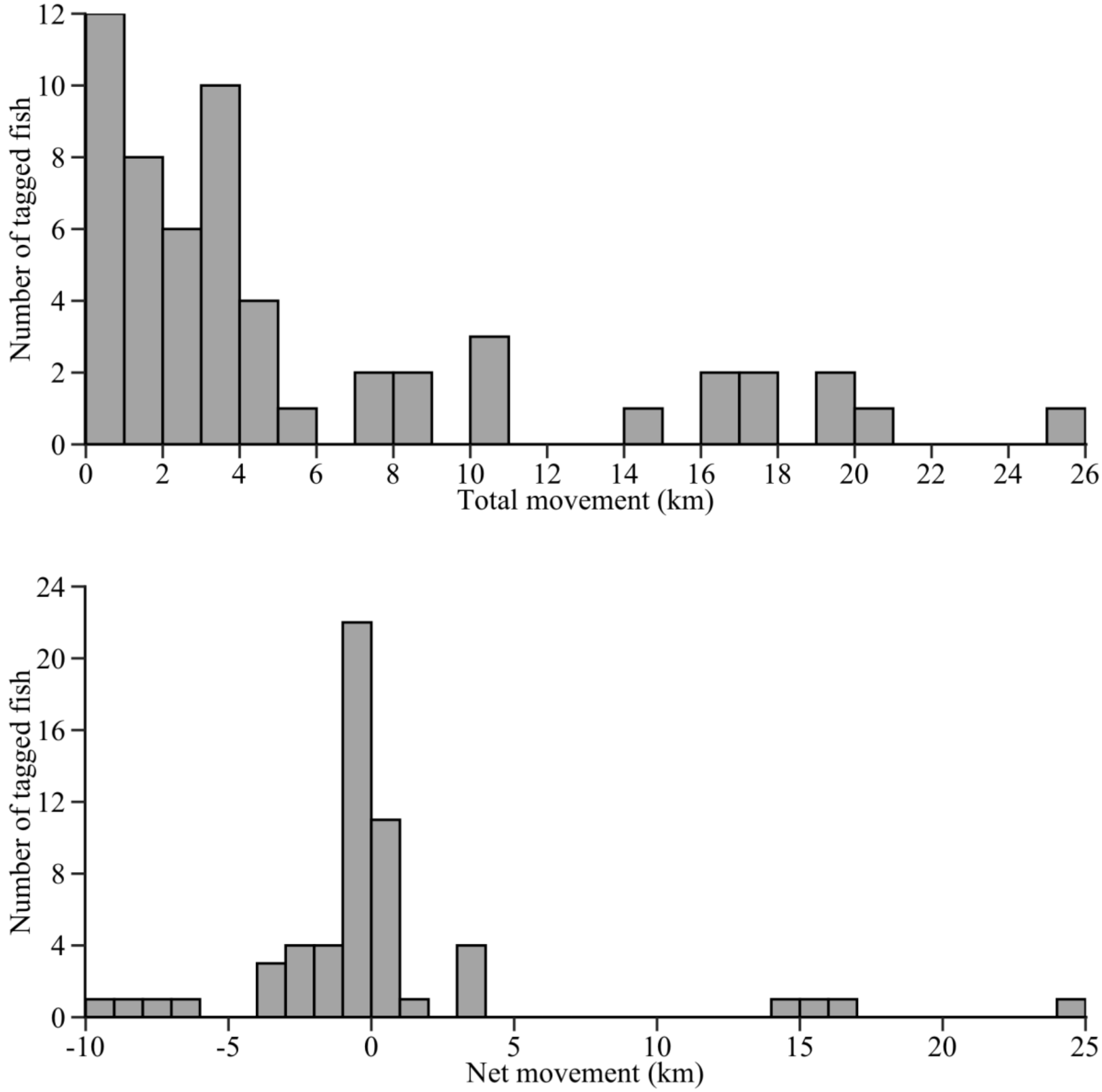

Figure 8. Frequency histograms for total distance (top panel) and net distance (bottom panel) moved by radio-tagged Mountain Whitefish in 2019 and 2020 pooled in the Green River. Negative net movement indicates downstream movement and positive indicates is upstream movement. Movement distances are the sum of all movements during the tracking season.

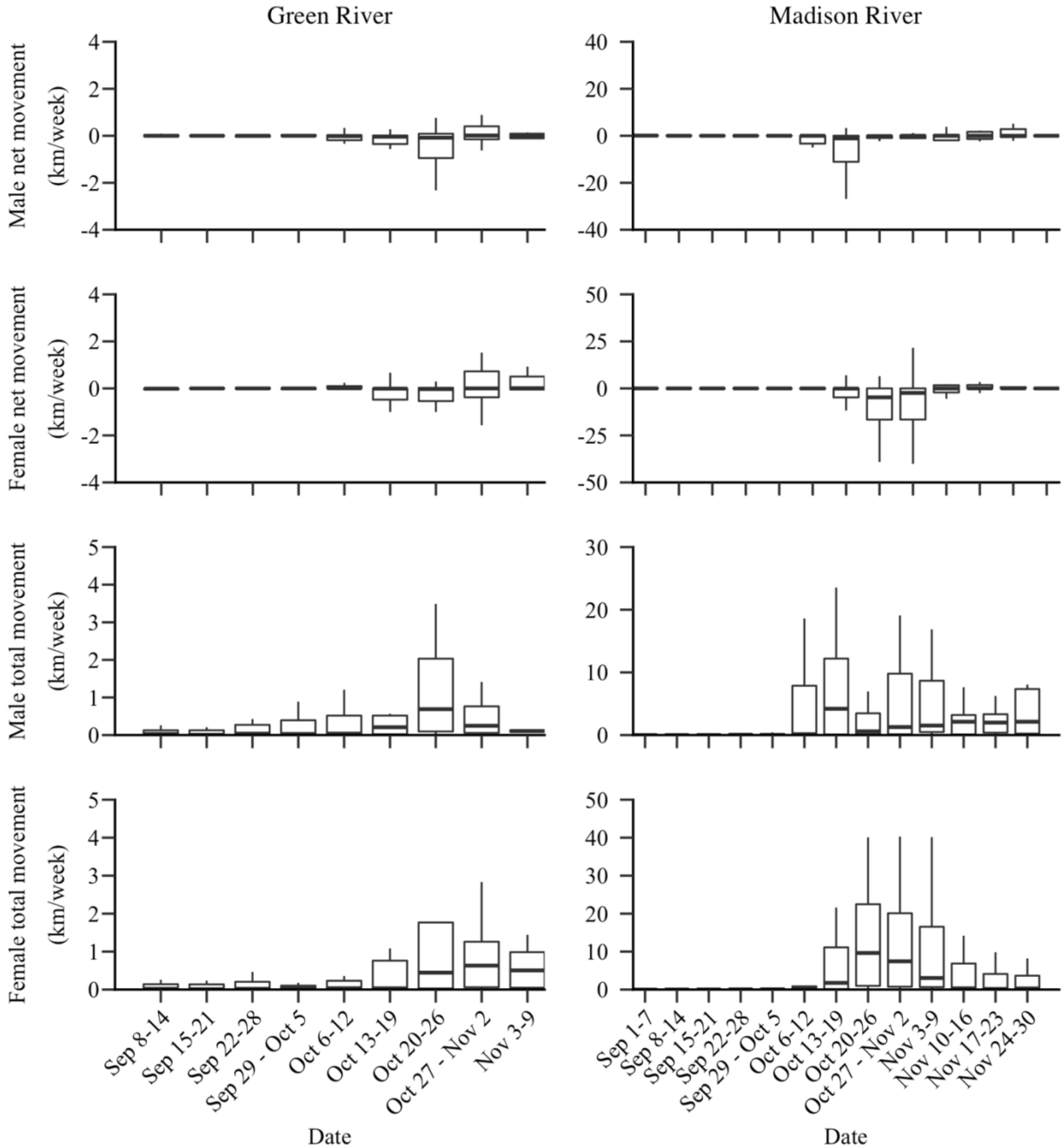

Figure 9. Net movement and total movement by week of radio-tagged Mountain Whitefish in 2019 and 2020 pooled in the Green River (left panels), and in 2012, 2013, and 2014 pooled in the Madison River (right panels; recreated from Boyer et al. 2017a). Net movement downstream is considered negative and upstream is considered positive. The bold line delineates the median, box ends are the 25th and 75th quartiles, and the whiskers are 1.5 times the interquartile range.

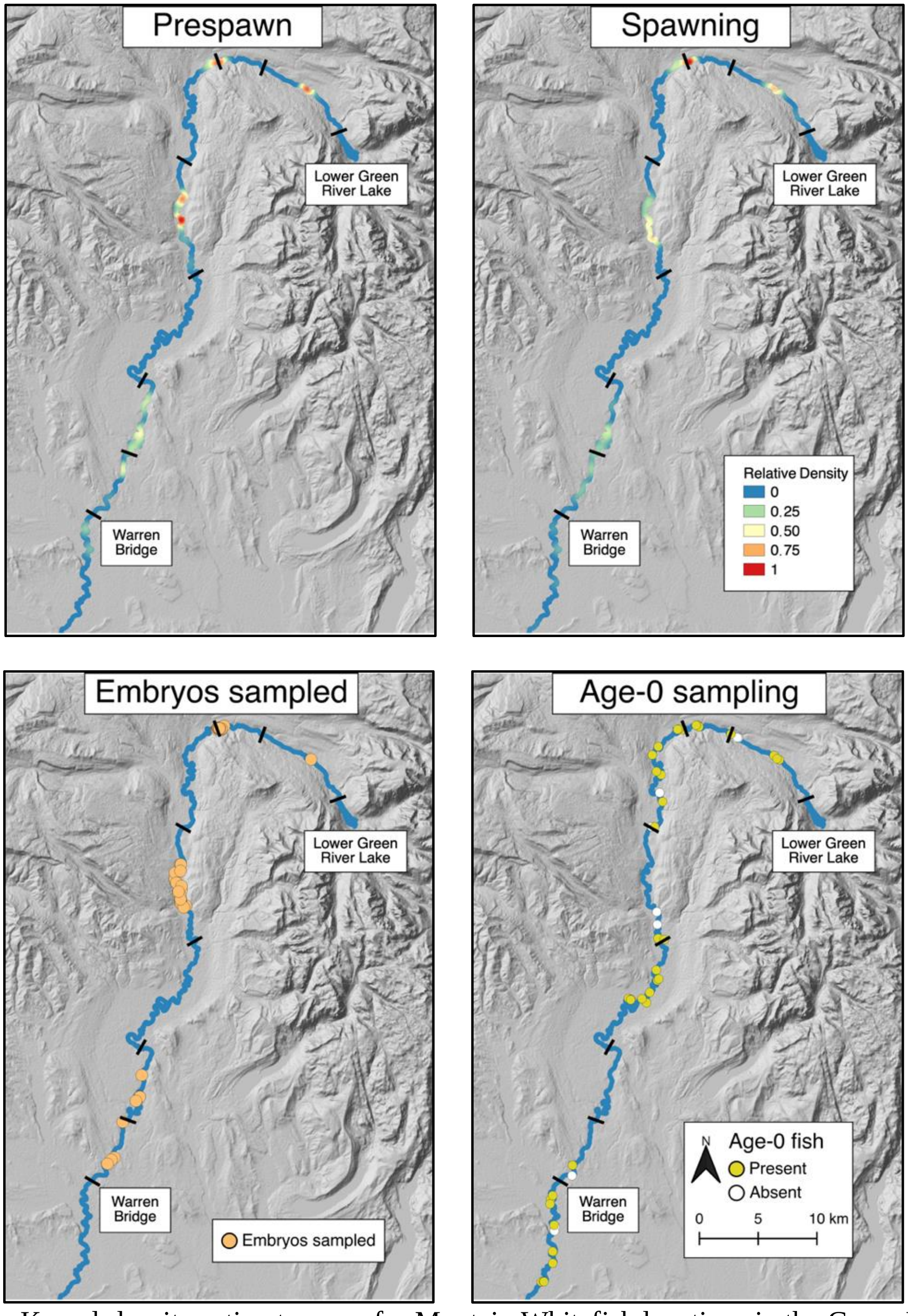

Figure 10. Kernel-density estimate maps for Moutain Whitefish locations in the Green River during the prespawn and spawning periods for 2019 and 2020 pooled (top panels). Maps in the lower panels indicate where embryos were sampled in the Green River in the autumn of 2019 and 2020 (lower left panel) and presence of age-0 Mountain Whitefish seined in May 2021 in the Green River (lower right panel). Reach boundaries are indicated by black lines (see Figure 1) and the study area is delineated by Lower Green River Lake and Warren Bridge.

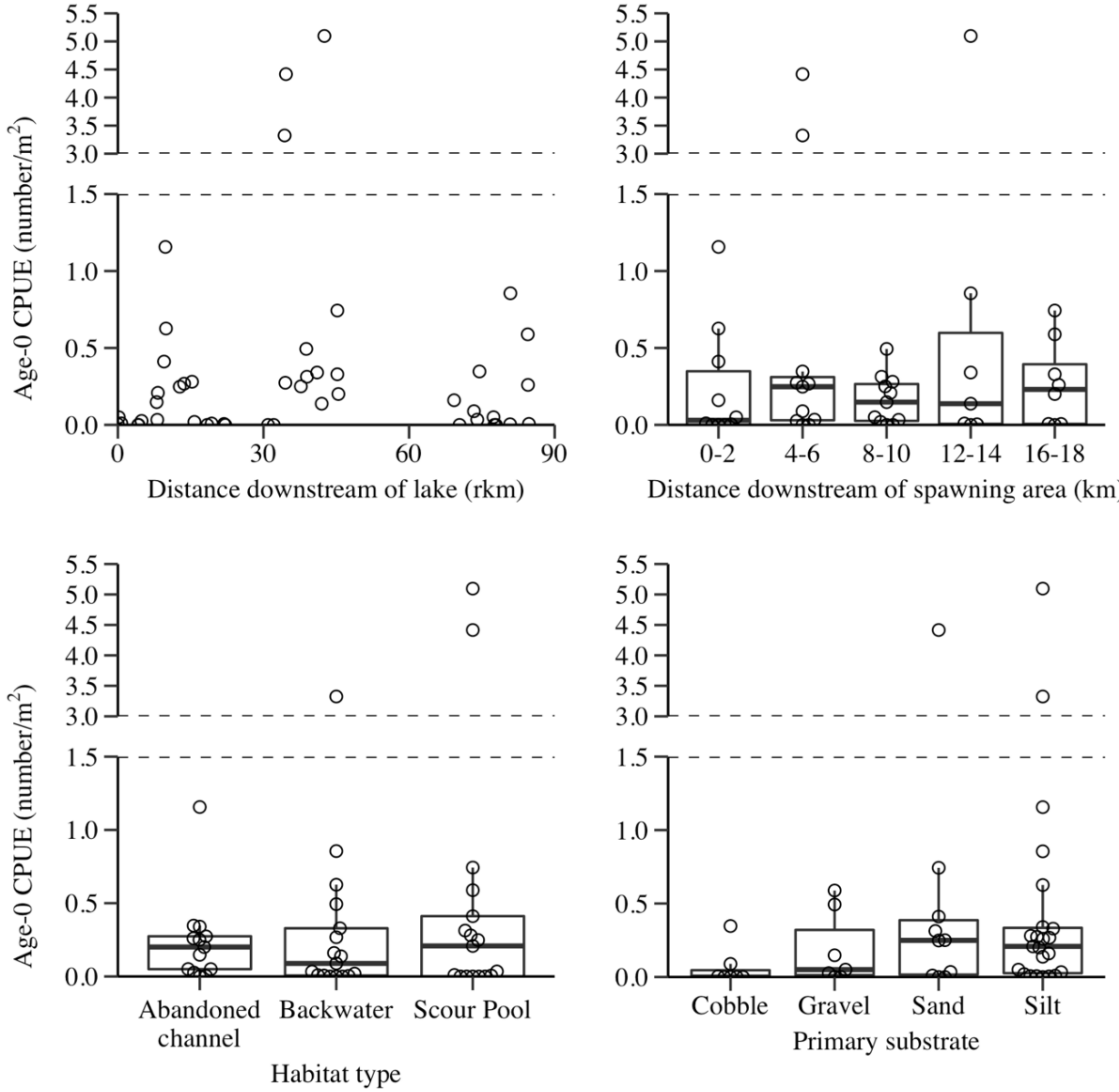

Figure 11. Catch per unit effort (CPUE; number per m^2) of age-0 Mountain Whitefish from seining in slow-water habitats in the spring of 2021 in the Green River, Wyoming. The top left panel shows the longitudinal distribution of CPUE at sample locations beginning at Lower Green River Lake. In the lower panels and top right panel, the bold line delineates the median, box ends are Q1 and Q3, whiskers are 1.5 times the interquartile range, and open circles are CPUE values from each site. Dashed lines highlight break in the *y*-axis.

REFERENCES CITED

Aravindakshan, J., V. Paquet, M. Gregory, J. Dufresne, M. Fournier, D. J. Macrogliese, and D. G. Cyr. 2004. Consequences of xenoestrogen exposure on male reproductive function in Spottail Shiners (*Notropis hudsonius*). Toxicological Sciences 78:156–165.

Bagenal T. B. 1978. Aspects of fish fecundity. Pages 75–101 *in* S. D. Gerking, editor. The ecology of freshwater fish production. Blackwell Scientific Publications, London.

Bartel, R., B. Falowska, K. Bieniarz, and P. Epler. 2005. Dependence of egg diameter on the size and age of cultivated female Lake Trout (*Salmo trutta* M. *lacustris* L.). Archives of Polish Fisheries 13:121–126.

Bateman, K. S., G. D. Stentiford, and S. W. Feist. 2004. A ranking system for the evaluation of intersex condition in European Flounder (*Platichthys flesus*). Environmental Toxicology and Chemistry 23:2831–2836.

Baxter, G. T., and M. D. Stone. 1995. Fishes of Wyoming. Wyoming Game and Fish Department, Cheyenne, Wyoming.

Beacham, T. D. 1982. Fecundity of Coho Salmon (*Oncorhynchus kisutch*) and Chum Salmon (*O. keta*) in the northeast Pacific Ocean. Canadian Journal of Zoology 60:1463–1469.

Benjamin, J. R., L. A. Wetzel, K. D. Martens, K. Larsen, P. J. Connolly, and B. Gillanders. 2014. Spatio-temporal variability in movement, age, and growth of Mountain Whitefish (*Prosopium williamsoni*) in a river network based upon PIT tagging and otolith chemistry. Canadian Journal of Fisheries and Aquatic Sciences 71:131–140.

Blazer, V. S., L. R. Iwanowicz, and D. D. Iwanowicz. 2007. Intersex (testicular oocytes) in Smallmouth Bass from the Potomac River and selected nearby drainages. Journal of Aquatic Animal Health 19:242–253.

Bohlin, T., L. F. Sundstrom, J. I. Johnsson, J. Hojesjo, and J. Pettersson. 2002. Density-dependent growth in brown trout: effects of introducing wild and hatchery fish. Journal of Animal Ecology 71:683–692.

Bon, E., G. Corraze, S. Kaushik, and F. Le Menn. 1999. Effects of accelerated photoperiod regimes on the reproductive cycle of the female Rainbow Trout: II seasonal variations of plasma gonadotropins (GTH I and GTH II) levels correlated with ovarian follicle growth and egg size. Fish Physiology and Biochemistry 20:143–154.

Boyd, J. W., C. S. Guy, T. B. Horton, and S. A. Leathe. 2010. Effects of catch-and-release angling on salmonids at elevated water temperatures. North American Journal of Fisheries Management 30:898–907.

Boyer, J. K., C. S. Guy, M. A. H. Webb, T. B. Horton, and T. E. McMahon. 2017a. Reproductive ecology, spawning behavior, and juvenile distribution of Mountain Whitefish in the Madison River, Montana. Transactions of the American Fisheries Society 146:939–954.

Boyer, J. K., C. S. Guy, M. A. H. Webb, T. B. Horton, and T. E. McMahon. 2017b. Gear comparison for sampling age-0 Mountain Whitefish in the Madison River, Montana. North American Journal of Fisheries Management 37:189–195.

Brenkman, S. J., G. L. Larson, and R. E. Gresswell. 2001. Spawning migration of lacustrine-adfluvial Bull Trout in a natural area. Transactions of the American Fisheries Society 130:981–987.

Brinkman, S. F., H. J. Crockett, and K. B. Rogers. 2013. Upper thermal tolerance of Mountain Whitefish eggs and fry. Transactions of the American Fisheries Society 142:824–831.

Brinkman, S. F., and N. M. K. Vieira. 2011. Effect of temperature on hatch, survival, and growth of Rio Grande Cutthroat Trout (*Oncorhynchus clarki virginalis*). Colorado Division of Wildlife, Federal Aid in Fish and Wildlife Restoration, Progress Report F-243R-16, Fort Collins, Colorado.

Bromage, N., M. Porter, and C. Randall. 2001. The environmental regulation of maturation in farmed finfish with special reference to the role of photoperiod and melatonin. Aquaculture 197:63–98.

Brown, C. J. D. 1952. Spawning habits and early development of the Mountain Whitefish, *Prosopium williamsoni*, in Montana. Copeia 1952:109–113.

Brown-Peterson, N. J., D. M. Wyanski, F. Saborido-Rey, B. J. Macewicz, and S. K. Lowerre Barbieri. 2011. A standardized terminology for describing reproductive development in fishes. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 3:52–70.

Bull, J. J., and R. Shine. 1979. Iteroparous animals that skip opportunities for reproduction. The American Naturalist 114:296–303.

Clancey, P., and T. Lohrenz. 2013. Madison River drainage fisheries and Madison River Westslope Cutthroat Trout conservation and restoration program. 2012 Annual Report to PPL (Pennsylvania Power and Light) Billings, Montana.

Copp, G. H., H. Faulkner, S. Doherty, M. S. Watkins, and J. Majecki. 2002. Diel drift behaviour of fish eggs and larvae, in particular Barbel, *Barbus barbus* (L.), in an English chalk stream. Fisheries Management and Ecology 9:95–103.

Davidoff, E. B., R. W. Rybicki, and K. H. Doan. 1973. Changes in the population of Lake Whitefish (*Coregonus clupeaformis*) in Lake Winnipeg from 1944 to 1969. Journal Fisheries Research Board of Canada 30:1667–1682.

Davies, R. W., and G. W. Thompson. 1976. Movements of Mountain Whitefish (*Prosopium williamsoni*) in the Sheep River watershed, Alberta. Journal of the Fisheries Research Board of Canada 33:2395–2401.

Depiereux S., M. Liagre, L. Danis, B. De Meulder, E. Depiereux, H. Segner, and P. Kestemont. 2014. Intersex occurrence in Rainbow Trout (*Oncorhynchus mykiss*) male fry chronically exposed to ethynylestradiol. PLOS ONE 9:98531. DOI: 10.1371/journal.pone.0098531

Deters, K. A., R. S. Brown, K. M. Carter, J. W. Boyd, M. B. Eppard, and A. G. Seaburg. 2010. Performance assessment of suture type, water temperature, and surgeon skill in juvenile Chinook Salmon surgically implanted with acoustic transmitters. Transactions of the American Fisheries Society 139:888–899.

Downing, D. C, T. E. McMahon, and B. L. Kerans. 2002. Relation of spawning and rearing life history of Rainbow Trout and susceptibility to *Myxobolus cerebralis* infection in the Madison River, Montana. Journal of Aquatic Animal Health 14:191–203.

Edwards, G. 2014. Mountain Whitefish sampling techniques and population assessment in Wyoming's major rivers. Wyoming Game and Fish Department Fish Division, Administrative Report 1–24, Casper, Wyoming.

Elliott, J. M., and J. A. Elliott. 2010. Temperature requirements of Atlantic Salmon *Salmo salar*, Brown Trout *Salmo trutta*, and Arctic Charr *Salvelinus alpinus*: predicting the effects of climate change. Journal of Fish Biology 77:1793–1817.

Fisher, W. L., M. A. Bozek, J. C. Vokoun, and R. B. Jacobson. 2012. Freshwater aquatic habitat measurements. Pages 101-150 *in* A. V. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland.

Friend, P. F., and R. Sinha. 1993. Braiding and meandering parameters. Geological Society of London Publications 75:105–111.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199–214.

Hawkins, C. P., J. L. Kershner, P. A. Bisson, M. D. Bryant, L. M. Decker, S. V. Gregory, D. A. McCullough, C. K. Overton, G. H. Reeves, R. J. Steedman and M. K. Young. 1993. A hierarchical approach to classifying stream habitat features. Fisheries 18:3–12.

Hecker, M., C. R. Tyler, M. Hoffmann, S. Maddix, and L. Karbe. 2002. Plasma biomarkers in fish provide evidence for endocrine modulation in the Elbe River, Germany. Environmental Science and Technology 36:2311–2321.

Hess, J. E., J. S. Zendt, A. R. Matala, and S. R. Narum. 2016. Genetic basis of adult migration timing in anadromous steelhead discovered through multivariate association testing. Proceedings of the Royal Society B: Biological Sciences 283:20153064. DOI: 10.1098/rspb.2015.3064

Hildebrand, B., 2014. Lower Columbia River whitefish life history and egg mat monitoring program: Year 5 interpretive report. BC Hydro, Golder Report No. 11-1492-0111F: 102p, Castlegar, BC.

Hinck, J. E., V. S. Blazer, C. J. Schmitt, D. M. Papoulias, and D. E. Tillitt. 2009. Widespread occurrence of intersex in black basses (*Micropterus* spp.) from U.S. rivers, 1995–2004. Aquatic Toxicology 95:60–70.

Hsieh, C. H., A. Yamauchi, T. Nakazawa, and W. F. Wang. 2010. Fishing effects on age and spatial structures undermine population stability of fishes. Aquatic Sciences 72:165–178.

Humphries, P. 2005. Spawning time and early life history of Murray Cod, *Maccullochella peelii* (Mitchell) in an Australian river. Environmental Biology of Fishes 72:393–407.

Hutchings, J. A. 1991. Fitness consequences of variation in egg size and food abundance in Brook Trout *Salvelinus fontinalis*. Evolution 45:1162–1168.

Jobling, S., M. Nolan, C. R. Tyler, G. Brighty, and J. P. Sumpter. 1998. Widespread sexual disruption in wild fish. Environmental Science and Technology 32:2498–2506.

Johnson, L., 1983. Homeostatic characteristics of single species fish stocks in arctic lakes. Canadian Journal of Fisheries and Aquatic Sciences 40:987–1024.

Jonsson, N. 1991. Influence of water flow, water temperature and light on fish migration in rivers. Nordic Journal of Freshwater Research 66:20–35.

Kangur, K., K. Ginter, A. Kangur, P. Kangur, and T. Mols. 2020. How did the late 1980s climate regime affect temperature-sensitive fish population dynamics: case study of Vendace (*Coregonus albula*) in a large north-temperate lake. Water 12:2694. DOI: 10.3390/w12102694

Kennedy, W. A. 1953. Growth, maturity, fecundity, and mortality in the relatively unexploited whitefish, *Coregonus clupeaformis*, of Great Slave Lake. Journal of the Fisheries Research Board of Canada 10:413–441.

Kennedy, P. A. 2009. The effect of irrigation diversions on the Mountain Whitefish population (*Prosopium williamsoni*) in the Big Lost River. Master's thesis. Utah State University, Logan, Utah.

Kocovsky, P. M., and R. F. Carline. Dynamics of the unexploited Walleye population of Pymatuning Sanctuary, Pennsylvania, 1997–1998. North American Journal of Fisheries Management 21:178–187.

Kolodziej, E. P., and D. L. Sedlak. 2007. Rangeland grazing as a source of steroid hormones to surface waters. Environmental Science and Technology 41:3514–3520.

Lance, M. J., and C. V. Baxter. 2011. Abundance, production, and tissue composition of Mountain Whitefish (*Prosopium williamsoni*) in a central Idaho wilderness stream. Northwest Science 85:445–454.

Landers, D. H., S. M. Simonich, D. Jaffe, L. Geiser, D. H. Campbell, A. Schwindt, C. Schreck, M. Kent, W. Hafner, H. E. Taylor, K, Hageman, S. Usenko, L. Akerman, J. Schrlau, N. Rose, T. Blett, and M. M. Erway. 2010. The western airborne contaminant assessment project (WACAP): An interdisciplinary evaluation of the impacts of airborne contaminants in western U.S. national parks. Environmental Science and Technology 44:855-859.

Lechner, A., H. Keckeis, and P. Humphries. 2016. Patterns and processes in the drift of early developmental stages of fish in rivers: a review. Reviews in Fish Biology and Fisheries 26:471–489.

Lukin, A. A., Y. N. Sharova, and B. F. Prishchepa. 2006. The impact of fishery on the state of populations of European Whitefish *Coregonus lavaretus* in Lake Prishchepa. Journal of Ichthyology 46:383–390.

Luna, L. G. 1968. Manual of histologic staining methods of the Armed Forces Institute of Pathology, 3rd edition. McGraw-Hill, New York.

Melquist, W. E., and M. G. Hornocker. 1983. Ecology of River Otters in west central Idaho. Wildlife Monographs 83:6–57.

Meyer, K. A., F. S. Elle, and J. A. Lamansky. 2009. Environmental factors related to the distribution, abundance, and life history characteristics of Mountain Whitefish in Idaho. North American Journal of Fisheries Management 29:753–767.

Michaletz, P. H. 1998. Population characteristics of Gizzard Shad in Missouri reservoirs and their relation to reservoir productivity, mean depth, and sport fish growth. North American Journal of Fisheries Management 18:114–123.

Montana FWP (Fish Wildlife and Parks). 2018. Angler satisfaction, demographics, and creel surveys – Upper Madison River, 2015–2017. Montana FWP, Report to NorthWestern Energy, Helena, Montana.

Nakagawa, S., and T. H. Parker. 2015. Replicating research in ecology and evolution: feasibility, incentives, and the cost-benefit conundrum. BMC Biology 13:1–6.

Nikolsky, G. V. 1963. The ecology of fishes. Academic Press, London.

Northcote, T. G., and G. L. Ennis. 1994. Mountain Whitefish biology and habitat use in relation to compensation and improvement possibilities. Reviews in Fisheries Science 2:347–371.

Ogle, D. H. 2013. FishR Vignette-von Bertalanffy growth models. Northland College. Ashland, Michigan. Available: http://derekogle.com/fishR/examples/oldFishRVignettes/VonBertalanffy.pdf. (September 2021).

Paragamian, V. L. 2002. Changes in the species composition of the fish community in a reach of the Kootenai River, Idaho, after construction of Libby Dam. Journal of Freshwater Ecology 17:375–383.

Pierce, R., M. Davidson, and C. Podner. 2012. Spawning behavior of Mountain Whitefish and co-occurrence of *Myxobolus cerebralis* in the Blackfoot River basin, Montana. Transactions of the American Fisheries Society 141:720–730.

Platts, W. S., W. F. Megahan, and G. W. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions. U.S. Forest Service General Technical Report INT-138.

Pritz, C. M. F., J. E. Schrlau, S. L. M. Simonich, and T. F. Blett. 2014. Contaminants of emerging concern in fish from western US and Alaskan national parks—spatial distribution and health thresholds. Journal of the American Water Resources Association 50:309–323.

Quinn, T. P., M. J. Unwin, and M. T. Kinnison. 2016. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced Chinook Salmon populations. Society for the Study of Evolution. 54:1372–1385.

Rajagopal, P. K. 1979. The embryonic development and the thermal effects on the development of the Mountain Whitefish, *Prosopium williamsoni* (Girard). Journal of Fish Biology 15:153–158.

Rideout, R. M., G. A. Rose, and M. P. M. Burton. 2005. Skipped spawning in female iteroparous fishes. Fish and Fisheries 6:50–72.

Rideout, R. M., and J. Tomkiewicz. 2011. Skipped spawning in fishes: more common than you might think. Marine and Coastal Fisheries 3:176–189.

Rogers, K. B., and G. C. White. 2007. Analysis of movement and habitat use from telemetry data. Pages 625–676 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Ruse, L. P. 1994. Chironomid microdistribution in gravel of an English chalk river. Freshwater Biology 32:533–551.

Savereide, J. W., and J. Huang. 2016. Spawning location, run timing, and spawning frequency of Kobuk River Sheefish, 2008–2014. Alaska Department of Fish and Game. Fishery Data Report No. 16-31. Anchorage, Alaska.

Schisler, G. J. 2010. Effects of whirling disease (*Myxobolus cerebralis*) exposure on juvenile Mountain Whitefish (*Prosopium williamsoni*). Report to Colorado Division of Wildlife, Aquatic Research Section, Fort Collins, Colorado.

Sigler, W. F. 1951. The life history and management of the Mountain Whitefish *Prosopium williamsoni* (Girard) in Logan River Utah. UAES Bulletins 347:1–21.

Stalnaker, C. B., and R. E. Gresswell. 1974. Early life history and feeding of young Mountain Whitefish. USEPA Report 660/3-73-019. Washington, D.C.

Stapanian M. A., L. D. Witzel, and A. Cook. 2010. Recruitment of Burbot (*Lota lota* L.) in Lake Erie: an empirical modelling approach. Ecology of Freshwater Fish 19:326–337.

Sublette County Conservation District. 2014. Upper Green River watershed study level 1. Sublette County Conservation District, Pinedale, Wyoming.

Syrovatka, V., J. Schenkova, and K. Brabec. 2009. The distribution of chironomid larvae and oligochaetes within a stony-bottomed river stretch: the role of substrate and hydraulic characteristics. Fundamental and Applied Limnology 174:43–62.

Thompson, G. E., and R. W. Davies. 1976. Observations on the age, growth, reproduction, and feeding of Mountain Whitefish (*Prosopium williamsoni*) in the Sheep River, Alberta. Transactions of the American Fisheries Society 105:208–219.

Thorpe, J. E., M. S. Miles, and D. S. Keay. 1984. Developmental rate, fecundity and egg size in Atlantic Salmon, *Salmo salar* L. Aquaculture 43:289–305.

Tornabene, B. J., T. W. Smith, A. E. Tews, R. P. Beattie, W. M. Gardner, and L. A. Eby. 2020. Trends in river discharge and water temperature cue spawning movements of Blue Sucker, *Cycleptus elongatus*, in an impounded Great Plains river. Copeia 108:151–162.

USEPA (U.S. Environmental Protection Agency). 1986. Quality criteria for water—1986. USEPA, Office of Water, EPA 440/5-86-001, Washington, D.C.

USGS (U. S. Geological Survey). 2020a. Real-time data for Wyoming. Available: http://nwis.waterdata.usgs.gov/wy/nwis/rt. (June 2020)

USGS (U. S. Geological Survey). 2020b. Real-time data for Montana. Available: http://nwis.waterdata.usgs.gov/mt/nwis/rt. (June 2020)

Van Daele, L. J., and H. A. Van Daele. 1982. Factors affecting the productivity of Ospreys nesting in west-central Idaho. The Condor 84:292–299.

Van Eenennaam, J. P., and S. I. Doroshov. 1998. Effects of age and body size on gonadal development of Atlantic Sturgeon. Journal of Fish Biology 53:624–637.

Wagner, G. N., S. J. Cooke, R. S. Brown, and K. A. Deters. 2011. Surgical implantation techniques for electronic tags in fish. Reviews in Fish Biology and Fisheries 21:71–81.

Wagner, G. N., E. D. Stevens, and P. Byrne. 2000. Effects of suture type and patterns on surgical wound healing in Rainbow Trout. Transactions of the American Fisheries Society 129:1196–1205.

Wydoski, R. S. 2001. Life history and fecundity of Mountain Whitefish from Utah streams. Transactions of the American Fisheries Society 130:692–698.

Zendt, J. S., and E. P. Bergersen. 2000. Distribution and abundance of the aquatic oligochaete host *Tubifex tubifex* for the salmonid whirling disease parasite *Myxobolus cerebralis* in the upper Colorado River basin. North American Journal of Fisheries Management 20:502–512.

APPENDIX A

MOVEMENT DOWNSTREAM OF WARREN BRIDGE AND ADDITIONAL TABLES

Six tagged Mountain Whitefish (11%) moved downstream of Warren Bridge in 2019 and 2020, thus tracking continued downstream of the study area an additional 40.6 km. Tracking methods were the same used in the study area (see above), except tracking was less consistent due to time constraints.

Four of the Mountain Whitefish moved long distances downstream (9.7 km – 23.0 km) and we suspect they continued greater distances because we were unable to locate the tagged fish in subsequent tracking up to 40.6 km downstream of Warren Bridge. Of the remaining two tagged fish, one was only located once but likely continued further downstream based on prior movements and the other moved relatively little and returned to reach 7 for the majority of the spawning period. Therefore, we know that a portion of the Mountain Whitefish population upstream of Warren Bridge spawn downstream of the bridge, but the location of spawning areas is currently unknown. We recommend future efforts to locate spawning areas downstream of Warren Bridge to Fontenelle Reservoir.

Table A.1. Mountain Whitefish spawning locations in the Green River confirmed with embryo collection (see methods above). Embryos were collected in areas of clean gravel or cobble with moderate to high water velocity and in water depths of about 0.2 to 1.5 m. Locations were recorded in UTM coodinates using North American Datum 1983 (NAD83) and all locations were in Zone 12.

Embryos collected	Sampling method	Northing	Easting
6	Kick net	4790371	0579441
24	Kick net	4789827	0579410
15	Kick net	4788806	0579084
12	Kick net	4788800	0579087
54	Kick net	4788191	0579519
117	Kick net	4788049	0579266
118	Kick net	4787938	0579239
50	Kick net	4787683	0579419
18	Kick net	4786834	0579894
2	Kick net	4799319	0590545
8	Kick net	4768404	0574513
51	Kick net	4765372	0573801
18	Kick net	4789136	0578960
147	Kick net	4787149	0579457
94	Kick net	4787065	0579419
5	Kick net	4770573	0575948
4	Kick net	4765182	0573553
9	Kick net	4789656	0578965
76	Kick net	4787328	0579472
195	Kick net	4787146	0579454
60	Kick net	4786714	0579709
25	Kick net	4787389	0579438
0	Kick net	4801872	0582910
10	Kick net	4801912	0582929
13	Kick net	4801930	0582926
11	Kick net	4802015	0582935
5	Kick net	4802049	0583021
19	Kick net	4802107	0583058
800	Kick net	4801938	0582776
1	Kick net	4801876	0582520
1	Kick net	4801973	0582572

Table A.1 Continued

65	Kick net	4802008	0582597
21	Kick net	4802009	0582640
290	Kick net	4801980	0582712
900	Kick net	4801886	0582800
350	Kick net	4801858	0582841
47	Kick net	4802164	0583152
4	Egg mat	4801929	0582926
460	Egg mat	4801939	0582776
300	Egg mat	4801965	0582737
2	Egg mat	4790366	0579456
2	Egg mat	4789807	0579428
1	Egg mat	4788523	0579514
12	Egg mat	4788050	0579266
7	Egg mat	4770573	0575949
15	Egg mat	4770573	0575949
13	Egg mat	4770547	0575970
23	Egg mat	4770547	0575970
7	Egg mat	4764839	0573215
1	Egg mat	4772397	0576137
8	Egg mat	4770198	0575646

Table A.2. Summary of radio-tagged Mountain Whitefish in the Green River. Spawning reach was estimated based on fish location during the spawning period. Tagged fish that were located alive but have an unknown spawning reach (UNK) moved downstream of the study area before the spawning period.

Located alive	Length (mm)	Weight (g)	Sex	Reach tagged	Spawning reach
Yes					
	302	207	Female	1	1
	311	263	Female	1	1
	336	345	Male	1	1
	319	313	Male	1	1
	327	304	Female	3	1
	325	404	Female	4	1
	317	290	Female	1	2
	295	231	Male	2	2
	321	240	Male	2	2
	293	245	Male	2	2
	298	222	Male	2	2
	381	454	Female	3	2
	395	522	Female	3	2
	308	268	Female	3	2
	346	426	Female	4	2
	336	322	Female	4	2
	312	313	Female	4	2
	378	499	Male	4	2
	317	327	Male	4	2
	382	467	Female	4	2
	368	499	Female	4	4
	360	454	Female	4	4
	394	458	Female	4	4
	350	408	Female	4	4
	351	404	Female	4	4
	326	354	Female	4	4
	332	340	Female	4	4
	325	331	Female	4	4
	398	572	Female	4	4
	415	771	Male	4	4
	387	499	Male	4	4
	350	476	Male	4	4

Table A.2 Continued

	366	426	Male	4	4
	383	517	Male	4	4
	327	336	Male	4	4
	340	399	Male	4	4
	370	472	Male	6	4
	413	680	Female	6	6
	410	572	Female	6	6
	438	848	Female	6	6
	417	594	Female	6	6
	304	281	Female	6	6
	324	376	Female	6	6
	373	454	Female	7	6
	321	313	Female	7	6
	303	249	Female	7	6
	380	454	Male	6	7
	358	408	Male	6	7
	323	340	Male	6	7
	413	544	Female	7	7
	326	308	Female	7	7
	350	426	Female	7	7
	325	318	Female	7	7
	375	463	Male	6	UNK
	305	277	Male	6	UNK
	371	458	Male	7	UNK
	388	567	Female	7	UNK
	394	558	Female	7	UNK
	373	454	Male	7	UNK
No					
	353	417	Female	1	
	315	286	Female	1	
	381	458	Female	4	
	380	544	Female	4	
	368	499	Female	4	
	334	390	Female	4	
	347	408	Female	4	
	366	472	Male	4	
	381	499	Male	4	
	366	435	Male	4	

Table A.2 Continued

353	408	Male	4
315	299	Male	4
396	522	Male	4
457	835	Male	4
367	454	Female	6
365	454	Female	6
402	562	Female	6
397	544	Female	6
305	299	Female	6
326	295	Female	6
334	358	Female	6
375	458	Female	6
417	730	Female	6
304	272	Male	6
306	249	Male	6
317	308	Male	6
322	318	Male	6
367	494	Female	7
380	585	Female	7
305	308	Female	7
351	417	Female	7
350	376	Female	7
346	395	Female	7
353	404	Female	7
366	454	Male	7
350	454	Male	7
379	463	Male	7
365	499	Male	7
373	508	Male	7
372	476	Female	7
366	581	Female	7