

FEATURED PAPER

Temperature—Not Flow—Predicts Native Fish Reproduction with Implications for Climate Change

Gregory S. Fraser*¹

Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, 1484 Campus Delivery, Fort Collins, Colorado 80523, USA

Kevin R. Bestgen 

Larval Fish Laboratory, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, 1474 Campus Delivery, Fort Collins, Colorado 80523, USA

Dana L. Winkelman 

U.S. Geological Survey, Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, 1484 Campus Delivery, Fort Collins, Colorado 80523, USA

Kevin G. Thompson

Colorado Division of Parks and Wildlife, 2300 South Townsend Avenue, Montrose, Colorado 81401, USA

Abstract

Habitat alterations and introduction of nonnative fishes reduced the distributions of the Flannelmouth Sucker *Catostomus latipinnis*, Bluehead Sucker *C. discobolus*, and Roundtail Chub *Gila robusta* to less than 50% of their historical ranges. Climate change models generally predict decreased streamflows and increased water temperatures that may further affect these species. Understanding the effects of flow and water temperature on their life histories should lead to better assessments of climate change impacts on extant populations and more informed management for species conservation. Basinwide larval fish sampling and hatch dates derived from otolith daily increment counts showed that water temperature was the dominant environmental factor cueing reproduction in the upper White River basin, Colorado. Reproduction for all three species began in spring, occurring first at warmer, lower-elevation, downstream locations and progressing upriver to higher elevations as water temperatures increased. Warmer water temperatures in tributaries initiated earlier reproductive activity compared to adjacent cooler main-stem habitat. Presence of larvae in samples and estimated hatch dates demonstrated a distinct, predictable upstream progression of reproduction associated with warming water and clear upstream limits to reproduction for all three species. Larval presence and hatching dates revealed earlier reproductive activity in 2012 than in 2013, driven by lower flow and earlier stream warming. A regression model predicted stream temperature during fish spawning seasons under different climate change scenarios and showed expanded upstream limits of thermally suitable reproductive habitat and earlier reproduction for our study species. The long-term implications of climate change are unknown, but managers should strive to perpetuate the valuable and relatively pristine native fish community in the upper White River drainage as a vestige of those that formerly existed throughout the Colorado River basin.

*Corresponding author: gregory_fraser@fws.gov

¹Present address: U.S. Fish and Wildlife Service, Mid-Columbia Fish and Wildlife Conservation Office, 7501 Icicle Drive, Leavenworth, Washington 98826, USA.

Received August 3, 2018; accepted January 10, 2019

In river ecosystems, flow and water temperature are key factors regulating life histories of aquatic organisms (Coutant 1987; Poff et al. 1997; Olden and Naiman 2010). Flow alters turbidity, channel geomorphology, and spawning habitat suitability and may signal migration or spawning events (Collier et al. 1996; Poff et al. 2007). Water temperature is comparable in value to other ecological resources, such as food and habitat, and fish exhibit niche partitioning based on thermal conditions (Magnuson et al. 1979; Coutant 1987). Furthermore, thermal conditions may limit species distributions (Brett 1971; Magnuson et al. 1979; Coutant 1987; Armour 1991). For example, the distribution of native trout species throughout the Rocky Mountains has been drastically reduced due to increased water temperature in downstream reaches (Selong et al. 2001; Rieman et al. 2007; Isaak et al. 2012; Roberts et al. 2013). Additionally, suitable water temperature may influence reproduction by initiating development of gonads and cueing spawning events when water temperature thresholds are reached (Coutant 1987; Armour 1991; Olden and Naiman 2010).

Water temperature and flow are closely associated with the life histories of some Colorado River basin fishes. For example, endangered Colorado Pikeminnow *Ptychocheilus lucius* migrate up to 400 km in one direction, presumably based on flow cues (Tyus 1990; Irving and Modde 2000; Osmundson 2011). Although flow may cue spawning migrations, the upstream limits of Colorado Pikeminnow habitat may be dictated by thermal constraints (Osmundson 2011). Spawning migration cues for Razorback Suckers *Xyrauchen texanus* may include both flow and water temperature (Tyus and Karp 1990; Modde and Irving 1998; Bestgen et al. 2011). In snowmelt-driven streams of the Colorado River basin, high seasonal variation and correlation between changes in flow and water temperature often confound the understanding of which factor is most influential for reproduction by native fish. In addition, anthropogenic alterations of water temperature and flow further complicate the understanding of the relationship between the environment and life histories of native fish (Moyle and Mount 2007; Poff et al. 2007; Olden and Naiman 2010).

Reproductive patterns and the environmental cues that initiate reproduction for native Colorado River basin fishes, such as the Flannelmouth Sucker *Catostomus latipinnis*, Bluehead Sucker *C. discobolus*, and Roundtail Chub *Gila robusta*, are less understood. For the Flannelmouth Sucker and Bluehead Sucker, spawning begins in early spring to early summer, and the onset of spawning may be cued by water temperature (Chart and Bergersen 1992; Weiss et al. 1998; Bezzerides and Bestgen 2002; Zelasko et al. 2011; Fraser et al. 2017). Roundtail Chub spawning occurs on the descending limb of the hydrograph and is also thought to be initiated by thermal cues (Kaeding

et al. 1990; Brouder et al. 2000; Bezzerides and Bestgen 2002). However, there is uncertainty concerning environmental cues responsible for initiating reproduction, and an evaluation of climate change effects on this relationship has not been attempted.

Flannelmouth Sucker, Bluehead Sucker, and Roundtail Chub are large-bodied, Colorado River native fishes that were once widespread and abundant throughout the upper Colorado River basin. Bezzerides and Bestgen (2002) suggested that each species occupied 50% or less of its historical range by the year 2000, and extant populations were declining in many localities. Declines of these species can be attributed to alterations of habitat and introduction of nonnative fishes (Martinez et al. 1994; Bezzerides and Bestgen 2002; Bestgen et al. 2006). Climate change models for the Colorado River basin predict reduced flows and increased air temperatures (Udall and Overpeck 2017), which will result in increased water temperatures and may influence the three species' life histories. The goal of this study was to evaluate the reproductive patterns of the Flannelmouth Sucker, Bluehead Sucker, and Roundtail Chub in the upper White River basin. We had four objectives. The first was to assess how the timing of reproduction differed among locations and species along a main-stem White River longitudinal gradient. The second was to determine the upstream spawning distribution limits of each species in the White River. The third was to evaluate how the initiation of reproduction related to patterns of water temperature and flow for each species in both main-stem and tributary habitats. The fourth was to develop a predictive stream water temperature model to assess how climate change may impact the distribution and timing of Flannelmouth Sucker, Bluehead Sucker, and Roundtail Chub reproduction within the study area. These findings should enhance the understanding of timing and spatial distribution of reproduction by these species and will allow managers to make better-informed decisions regarding conservation actions for these declining native fishes.

METHODS

Study area.—The White River headwaters are located in the Flat Tops Wilderness in northwestern Colorado. The White River flows west through western Colorado into Utah, draining approximately 13,000 km² until it joins the Green River near Ouray, Utah (Martinez et al. 1994). Taylor Draw Dam, the only main-stem dam on the White River, impounded Kenney Reservoir beginning in October 1984 and is a barrier to upstream fish movement (Figure 1). The White River upstream of Kenney Reservoir to the confluence of the North Fork and South Fork of the White River (hereafter, “North Fork–South Fork confluence”) was chosen as the study site because it is one

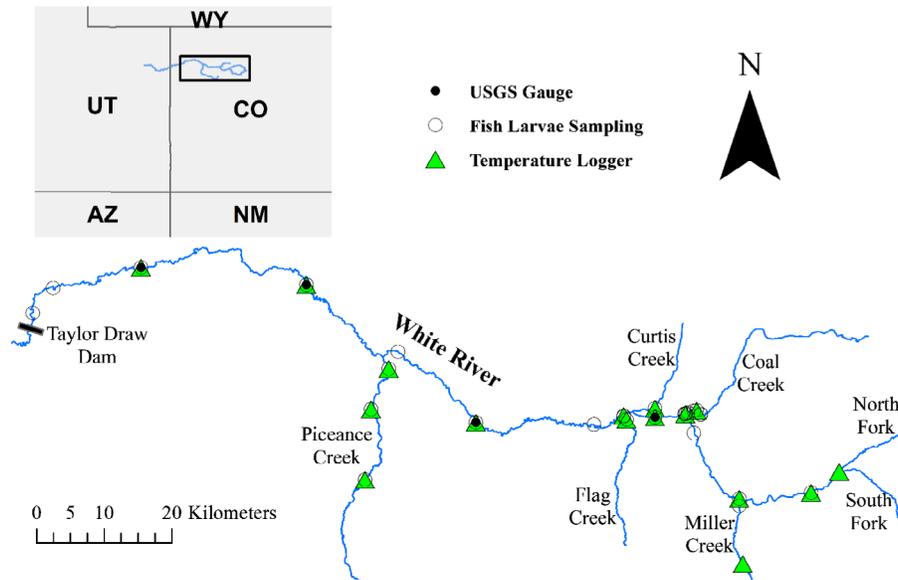


FIGURE 1. Map of the upper White River, Colorado, and selected tributaries, depicting the locations of water temperature loggers, U.S. Geological Survey (USGS) temperature and flow gauges, and larval sampling stations.

of the last large, unobstructed, free-flowing river sections in the upper Colorado River basin and was thought to contain relatively robust native fish populations (Chart and Bergersen 1992). Snowmelt is the dominant water source in the White River, and runoff usually occurs from mid-April through late June. Flow typically peaks in early June, with a mean maximum flow of $91.5 \text{ m}^3/\text{s}$ ($23.7\text{--}186.5 \text{ m}^3/\text{s}$; Figure 2). Base flows (mean = $11.9 \text{ m}^3/\text{s}$) occur in July–March, and summer thunderstorms periodically increase flow and turbidity.

The study area represents a continuum from a coldwater environment upstream to a warmwater one downstream; thus, it is an ideal location in which to study longitudinal effects of water temperature and other factors on timing of fish reproduction. Other studies have used the confluence of the White River with the Green River as river kilometer (rkm) 0 for the White River; this location is 177 rkm downstream from the Kenney Reservoir–White River inflow area (Chart and Bergersen 1992; Martinez et al. 1994). In this study, we designated rkm 0 as the Kenney Reservoir–White River inflow area. The upstream coldwater portion of the study area was delineated approximately by the North Fork–South Fork confluence downstream through Meeker, Colorado (rkm 100–151). The upstream section is typical of other coldwater environments where salmonids predominate (Rahel and Hubert 1991; Griffith 1993). The channel form is pool-riffle-run, with predominantly cobble substrate. Downstream from rkm 100 (near Meeker) to rkm 68, the river is a transition area and supports both warmwater and coldwater species. The downstream portion of the study

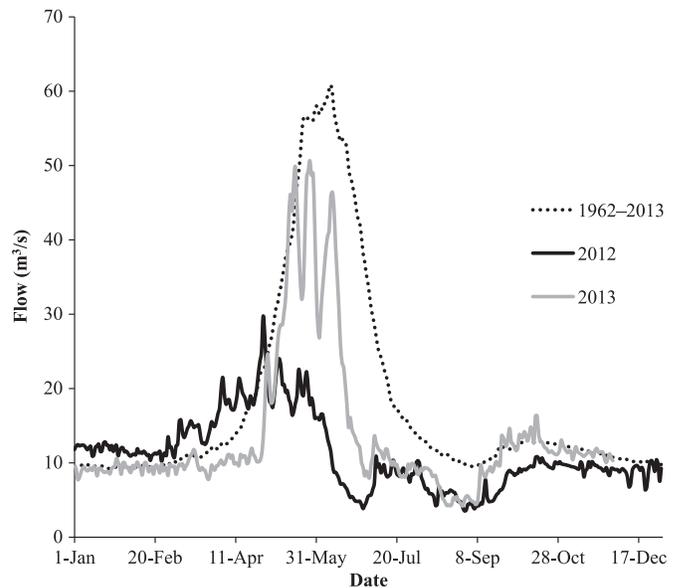


FIGURE 2. Mean daily flow for the White River, Colorado (U.S. Geological Survey gauge 09304800), for the period of record (1962–2013) and the study years 2012 and 2013.

area extends from rkm 0 to rkm 68 and is a warmwater environment where coldwater salmonids are few or non-existent. The channel form in the downstream section is uniform runs, with substrate composed of predominantly sand in low-velocity areas and cobble in higher-velocity locations. The main-stem White River is 30–40 m wide throughout the study area.

In April 2011, surveys revealed seven tributaries potentially used for spawning by the three species. Based on the presence of mostly perennial flows and the presence of Flannelmouth Suckers or Bluehead Suckers, Piceance and Coal creeks were selected for this study. All other streams surveyed were deemed unsuitable due to barriers, low water temperatures, or insufficient spring flows (Hooley-Underwood et al. 2019). The confluence of Piceance Creek and the White River is at an elevation of 1,740 m above sea level (ASL) and is situated 68 rkm upstream from the Kenney Reservoir–White River inflow area (rkm 0). Piceance Creek flows through a landscape dominated by sagebrush *Artemisia* spp., pinyon pine *Pinus edulis*, and Utah juniper *Juniperus osteosperma*. The channel is approximately 3–5 m wide, and the substrate is predominantly sand. The confluence of Coal Creek and the White River is located at 1,935 m ASL and rkm 118. Coal Creek flows through an agricultural valley dominated by irrigated fields. The channel is approximately 5–7 m wide, and the substrate is mixed cobble and sand.

Irrigation practices alter flows in both Piceance and Coal creeks but in different ways. During base flow periods, temporary dams in Piceance Creek divert water into irrigation canals and reduce or eliminate flow in the stream channel. In contrast, flow in Coal Creek is enhanced beginning in spring by agricultural irrigation water that is diverted from the main-stem White River to the Coal Creek drainage. Thus, during the sucker spawning season, flows in Coal Creek are higher than natural flows (Fraser et al. 2017).

Water temperature.—In April 2011, we deployed five water temperature loggers (spaced at about 30-rkm intervals) in the main-stem White River and 15 temperature loggers in various tributaries to evaluate the role of water temperature in reproduction by the three study species on a basinwide scale (Figure 1). However, only temperature data from Coal Creek, Piceance Creek, and the main-stem White River will be discussed further. The loggers recorded water temperature every hour. The temperature logger deployed at rkm 14 on the main stem was never recovered, so no data were available from that location. To replace the lost data, we used data from the U.S. Geological Survey (USGS) gauge at rkm 18.5 (gauge 09306290).

Presence of fish larvae.—We sampled larval fishes at 20 sites throughout the upper White River basin at regularly spaced intervals to assess reproductive patterns and to examine how larval presence changed spatially and temporally. Twelve main-stem White River sites were evenly distributed from the upstream end of Kenney Reservoir (rkm 0) to just downstream of the North Fork–South Fork confluence (rkm 142; Figure 1). We also sampled fish larvae at eight stations in Coal and Piceance creeks, but only the two stations near the respective mouths of those streams produced sufficient larvae for analysis. In 2013, we added

two additional main-stem sampling sites at rkm 118.5 and rkm 121 to bracket the mouth of Coal Creek. Each station was sampled every 5 d from May 14 to July 25, 2012, and from May 17 to July 30, 2013. We concentrated sampling effort in nearshore, low-velocity habitat, where densities of fish larvae are known to be highest (Haines and Tyus 1990; Muth and Snyder 1995). All fish larvae were sampled during daylight hours with either a 1.2- × 1.2-m seine (0.8-mm mesh) or a 0.5-mm-mesh dip net measuring 47 × 28 cm at the mouth and 38 cm in depth. The seine was used in deeper and more complex habitat, whereas the dip net was used in smaller and shallower habitat. We sampled 30 m of nearshore habitat at each location, preserved larval fish in 100% ethanol, and identified specimens in the laboratory by using published keys (Snyder 1981; Snyder and Muth 2004). Identifications were verified by a second investigator; the specimens were then measured to the nearest 0.5 mm TL, counted, and cataloged.

To describe how the onset of reproduction differed spatially and temporally across the study area, we aged early life stages of fish by using otolith daily increments. We used only mesolarvae or earlier life stages (typically just postemergent; Flannelmouth Suckers ≤ 17 mm TL, Bluehead Suckers ≤ 17 mm TL, and Roundtail Chub ≤ 12 mm TL) of each species as an index of reproduction timing (Snyder and Muth 2004; Snyder et al. 2005). The initial presence of larvae based on capture in samples and the hatching dates (below) described the pattern of reproduction spatially and temporally in this study. These metrics were used rather than first spawning because the variability in incubation time for eggs at different water temperatures made the prediction of timing difficult (Gillooly et al. 2002).

Hatch dates.—Hatch dates of larvae were determined by counting daily increments in otoliths extracted from a subsample of larvae obtained at multiple locations. To estimate hatch dates for the remaining unaged larvae, we fit regression equations that estimated *Age* (d) as a function of *TL* (mm) for each location. Validation of aging techniques is important for determining the accuracy and precision of the aging technique (Beamish and McFarlane 1983; Campana 2001). Although no validation study was completed for the study species, otolith daily increment counts as a means to determine hatch dates have been validated for many other fish species (Pannella 1971; Campana and Neilson 1985; Haworth and Bestgen 2016), including the Razorback Sucker and Colorado Pikeminnow, which are native cypriniform fishes of the Colorado River basin (Hoff et al. 1997; Bestgen and Bundy 1998; Bundy and Bestgen 2001; Ellsworth et al. 2010). Therefore, based on previous experience, we felt confident that daily increment counts in otoliths of the sucker larvae we aged could be used to estimate the hatching dates of

larvae. Aging of Roundtail Chub by using counts of daily increments in otoliths was validated in a previous study (Brouder 2005).

Flannemouth Sucker and Bluehead Sucker larvae used for age estimation were selected from two main-stem sampling sites (rkm 47 and rkm 118) where abundant larvae were sampled throughout each season. The sites also represented the potential longitudinal variation in water temperature and flow in the White River, which allowed us to assess the role of these factors in initiating reproduction and hatching. Larvae collected from two tributary sites were also chosen for aging, thus allowing us to determine whether there were differences between tributary and main-stem hatch dates in 2012 and 2013. Two sites in Coal Creek (0.7 rkm and 2.0 rkm upstream from the confluence) were treated as a single site; in Piceance Creek, we used one site (2.8 rkm from the confluence; Figure 1). All suckers used in otolith aging were metalarvae or younger (Flannemouth Suckers ≤ 24 mm TL, Bluehead Suckers ≤ 20 mm TL; Snyder and Muth 2004). Ten fish from each site were aged; the exceptions were the 2012 Bluehead Sucker sample collected at rkm 118 and the 2012 Flannemouth Sucker sample collected at rkm 47, from which only nine fish were available.

Ages were estimated for Roundtail Chub collected from four main-stem White River sites (rkm 4, 18, 47, and 68) in 2012 and 2013. Low numbers of Roundtail Chub larvae at rkm 4 and rkm 18 necessitated combining specimens from these sites. Ten individual Roundtail Chub were selected from each site for each year, and all were metalarvae (≤ 15 mm TL) or younger (Snyder et al. 2005).

Photographs of larvae were taken with a Spot Insight 2 camera (Diagnostic Instruments, Inc., Sterling Heights, Michigan) mounted on an Olympus SZX7 microscope (Olympus America, Center Valley, Pennsylvania). Larvae were measured to the nearest 0.01 mm TL using Image-Pro Express (Media Cybernetics, Inc., Rockville, Maryland), and otoliths were extracted with forceps and a fine probe. Both left and right lapilli were removed, mounted on glass slides, and placed in immersion oil. A single reader counted all daily age increments on a compound microscope at 1,000 \times magnification using transmitted light, followed by an additional count either (1) at least 1 d later or (2) after the increments of 20 other otoliths had been counted. The second count was considered blind because sufficient time had passed so that the reader had no recollection of the initial count. A third blind count was conducted if there was disagreement between the first and second counts. If the third count agreed with either of the previous counts, then the third count was deemed the most accurate. A fourth count was conducted if the third count disagreed with both of the previous counts. If the fourth count agreed with any of the previous counts, then the fourth count was designated the most accurate. There

was never a situation in which all four counts disagreed. Increment counts made by the single reader used in this study were verified by one of us (K.R.B.) throughout the study. Because replicated counts of individual otoliths by both investigators did not usually vary by more than one or two daily increments, the use of a single reader was justified. Hatching date was calculated by subtracting the estimated age (d) from the capture date. This relationship assumes that first otolith increments are formed on the day of hatch, which was verified for Razorback Suckers reared under similar water temperature conditions.

To estimate the hatch dates of the earliest larvae collected at other sites, we created regression equations for fish from a downstream location (rkm 47) and an upstream location (rkm 118) to estimate *Age* (d) as a function of *TL* (mm). We used this technique rather than time-intensive counting of otolith daily increments for all fish from all sites and samples to increase the spatial coverage of sites and the number of aged larvae from samples. We measured fish larvae to the nearest 0.5 mm TL from other sites collected in the same time period and size distribution and then calculated the hatch dates by subtracting the estimated age from the sample date of the individual larvae. Using fish of similar sizes and collection dates for the otolith-aged group and for the group with ages estimated using regression equations ensured that the measured fish were exposed to growing conditions similar to those experienced by otolith-aged fish. We combined fish from the upstream (rkm 118) and downstream (rkm 47) locations to construct a regression equation for the main-stem White River and used this regression to age fish collected at rkm 82, a mid-river sampling location. We did not apply the regression equation to other sampling sites. These three sites selected for aging and regressions were used to describe patterns in the entire White River study area. Tributary regression equations remained separate.

Stream temperature model.—We developed a stream temperature model by using a general linear model to predict water temperature as a function of flow, air temperature, date, and elevation (SAS version 9.4, SAS Institute, Cary, North Carolina; Isaak et al. 2010), which could then be used to predict how stream temperature and patterns of reproduction for Flannemouth Suckers, Bluehead Suckers, and Roundtail Chub might be altered by climate change. We developed several candidate models using different combinations of predictor variables, and we used Akaike's information criterion corrected for small sample size (AIC_c) to select a final model (Burnham and Anderson 2002). We used 6 years of data (2008–2013) for three locations on the White River (USGS gauges 09306290, 09304200, and 09304800). We built our models using data from the period 2008–2012, and we used 2013 data from all three sites and 2014 data from one site to validate the

chosen model. The period 2008–2012 included one of the highest flow years (2011) and one of the lowest flow years (2012) on record, which enhanced variability in flow and water temperatures and strengthened prediction capability. For example, in 2011, the White River recorded a peak flow of 156.3 m³/s and had relatively low water temperatures; in 2012, the peak flow was 32.8 m³/s, and water temperatures were warmer (Figure 2). We restricted the predictive stream temperature model to the period April 1–August 31 (ordinal dates 91–249), which encompassed the spawning period of all three species (Kaeding et al. 1990; Chart and Bergersen 1992; Brouder et al. 2000; Bezzerides and Bestgen 2002; Zelasko et al. 2011). We used mean daily air temperature data from the Meeker Airport in Meeker, Colorado, for all longitudinal river locations in the final model because they represented the nearest regional data available.

We used the stream temperature model to predict the average date and location at which water temperatures associated with the first presence of larvae for each species (16°C for suckers; 20°C for Roundtail Chub) would occur at different main-stem and tributary locations throughout the basin, and we considered this to be the baseline model. We created the baseline model using mean data for all variables from the period 1997–2013. We restricted the baseline model to these years because data describing air temperature, an important predictor variable, were not available for earlier years. The mean daily flow for this time period showed patterns similar to those of the historical record (1901–2013; Fraser 2015).

To evaluate how climate change could alter the timing and spatial distribution of water temperatures associated with reproduction by the three species, we manipulated air temperature and flow in the baseline model to mimic changes in air temperature and streamflow anticipated from climate change scenarios. Climate change models specific to the Colorado River basin predict that flow may decrease by 17% while air temperature may increase 2°C (Christensen et al. 2004; McCabe and Wolock 2007). To mimic these predictions, we modeled a 2°C increase in air temperature with a 20% reduction in flow. We also modeled two more extreme scenarios: a warmer one that modeled a 4°C temperature increase coupled with a 50% flow reduction; and a cooler one that modeled a 2°C air temperature decrease and 20% flow increase.

RESULTS

Temperature and Flow

Water temperatures varied longitudinally in the main-stem White River as well as among seasons and years and were correlated negatively with flow and positively with air temperature (Figure 3). Water temperatures were

similar and cool between years during April but different in May–August. Spring runoff arrived earlier in 2012 than in 2013, when low air temperatures delayed snowmelt and higher flows until May 1. Longitudinal patterns were also evident, as White River water temperatures during late spring and summer were 6–8°C warmer at rkm 18.5 compared to rkm 146 for 2012 and 2013 (Figure 3). The downstream-most locations, rkm 18.5 and rkm 47.5, showed the smallest difference in water temperature between any two locations. Water temperatures upstream (rkm 146) rarely exceeded 16°C. The largest differences in water temperature longitudinally among White River sites occurred during May 9–22, 2012, and May 10–June 6, 2013. A comparison between 2012 and 2013 showed that peak water temperatures at each location were about the same for both years, but sites warmed earlier and more gradually in 2012 than in 2013. As flows decreased in early summer, water temperatures increased, peaking in late June or July during summer base flows.

We observed substantial differences in water temperature among tributaries and main-stem White River sites as well. During the presumptive sucker spawning season in spring, mean daily water temperature in Piceance Creek was warmer than that in the nearby main-stem White River (at rkm 82.5) by 1–4°C in 2012 and by 2–6°C in 2013. The mean daily water temperature in Coal Creek was 1–2°C warmer than the nearby main-stem White River in 2012 and was 4–5°C warmer in 2013. The largest differences in water temperature between Coal Creek and the White River occurred during May 10–26, 2012, and May 10–31, 2013.

Flow varied between years in terms of the timing of runoff and magnitude but spatially varied only slightly across the study area on any specific date (Figure 3) because most of the flow was in the main stem. In 2012, the peak flow reached only 32.8 m³/s on April 27, consistent with warm air temperatures early in the year, while in 2013 the peak flow reached 52.9 m³/s on May 17, consistent with cooler air temperatures later in the year. Flow gradually subsided in 2012 and reached base flow in mid-June. In contrast, there were three peaks in White River flow during 2013, and base flow onset occurred on approximately July 1.

Presence of Fish Larvae

We captured 9,672 early life stage specimens of the three species in 2012 and 2013, many of which were of suitable size for either otolith aging or back-calculation of age based on length (Table 1). Substantial numbers of each taxon were captured in each year, with the exception of Roundtail Chub in 2013, when only 197 individuals were collected.

Earliest reproduction by Flannelmouth Suckers and Bluehead Suckers, as estimated from the dates of first

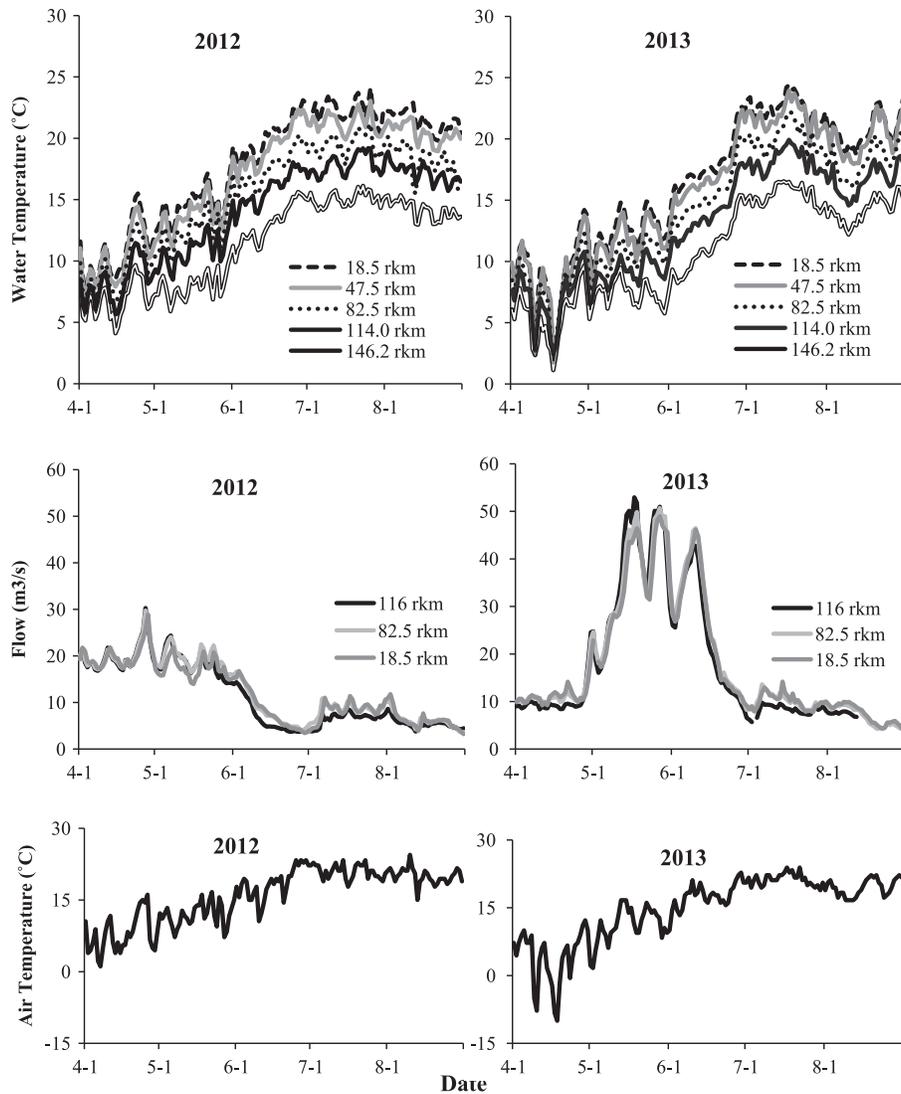


FIGURE 3. Daily average water temperature in the White River, as measured by four temperature loggers (river kilometers [rkm] 47.5–146.2) and one U.S. Geological Survey (USGS) gauge (09306290; located at rkm 18.5), and the mean daily flow measured by three USGS gauges (09306290, 09304200, and 09304800). Air temperature data are from the Meeker Airport Weather Station (Meeker, Colorado).

TABLE 1. Percent composition of Bluehead Suckers, Flannemouth Suckers, Roundtail Chub, and other species (includes introduced as well as native species) captured in seine and dip-net samples in the upper White River drainage, Colorado, from mid-May through late July in 2012 and 2013. The range of TLs (mm) for each taxon is displayed parenthetically below percent composition.

Species	2012% (TL range)	2013% (TL range)
Bluehead Sucker	13.8 (10–58)	23.9 (8–27)
Flannemouth Sucker	13.9 (12–52)	17.6 (9–34)
Roundtail Chub	9.2 (8–40)	1.2 (7–26)
Other	63.2	57.4
Total number of fish captured	10,935	16,410

capture, showed strong longitudinal patterns and was earlier in downstream, warmer locations and later in upstream, cooler locations (Figure 4). First detection of sucker larvae at most White River sampling locations corresponded relatively closely to when water temperatures warmed to about 16°C in both 2012 and 2013.

Similarly, Roundtail Chub larvae were first detected earlier in downstream samples and later in upstream samples during 2012 (Figure 4). In contrast, first detection of Roundtail Chub larvae in 2013 occurred across the study area on July 8 at rkm 4, 18, and 68. The first presence of Roundtail Chub was loosely associated with a mean daily water temperature of 20°C (Figure 4).

In addition to longitudinal differences in timing of the first detection of larvae (presumably because of earlier

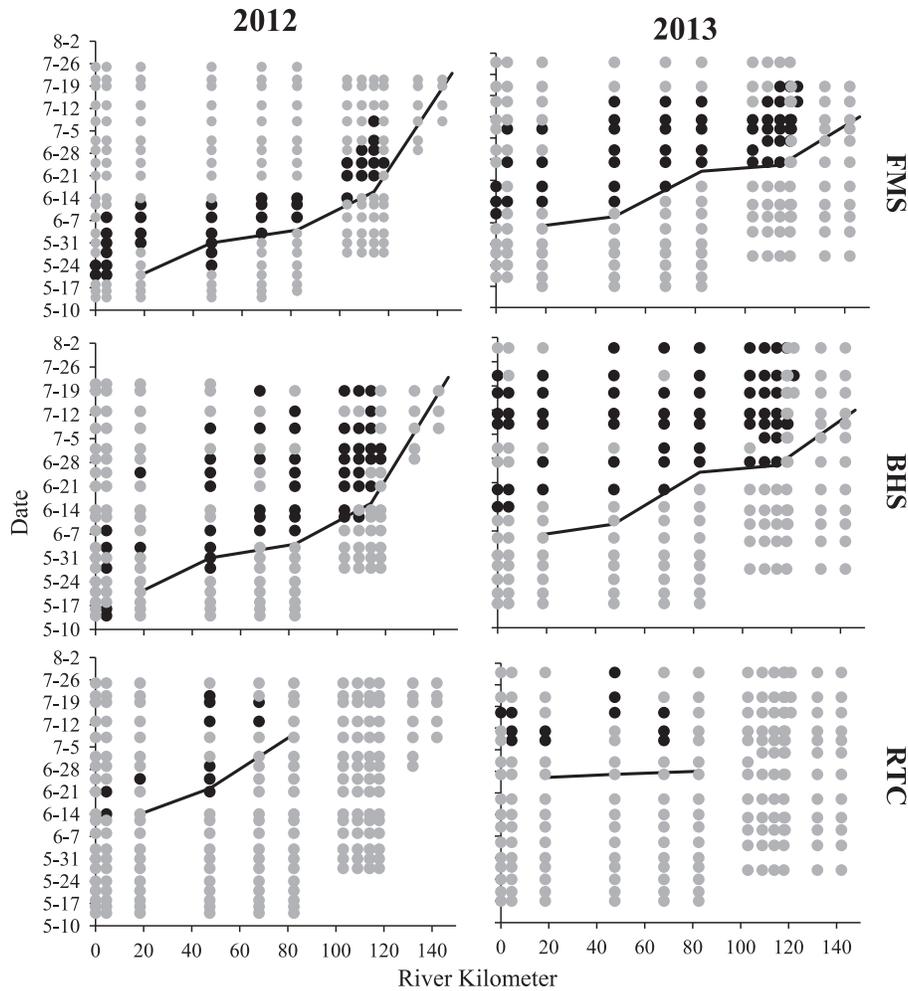


FIGURE 4. Presence (black) and absence (gray) of Flannemouth Sucker (FMS), Bluehead Sucker (BHS), and Roundtail Chub (RTC) mesolarvae in the main-stem upper White River, Colorado, during study years 2012 (12 stations) and 2013 (14 stations; i.e., river kilometer [rkm] 118.5 and rkm 121 were added in 2013). The line depicts the time and location where the temperature was most closely associated with the first detection of larvae (16°C for FMS and BHS; 20°C for RTC).

TABLE 2. Date of the first detection of Flannemouth Sucker (FMS), Bluehead Sucker (BHS), and Roundtail Chub (RTC) larvae at the downstream-most sampling locations (river kilometer [rkm] 0 and rkm 4) in the White River and the difference in timing of first larval detection between the study years 2012 and 2013.

Species	2012	2013	Difference (d)
FMS	May 21	Jun 10	20
BHS	May 14	Jun 10	27
RTC	Jun 12	Jul 11	29

spawning downstream) in the White River, larvae of the three species were detected much earlier in the warmer and lower-flow year, 2012, than in 2013 (Table 2). For example, we detected the first Flannemouth Sucker larvae at rkm 0 on May 21 in 2012 but not until June 10 in

2013. Bluehead Suckers showed a similar pattern, with first presence detected downstream on May 14 in 2012 but 27 d later (on June 10) in 2013. First detection of Roundtail Chub larvae in 2012 was on June 12, whereas the first detection in 2013 was almost 1 month later (on July 8).

Sucker larvae were generally detected earlier in samples collected in Coal Creek than in the adjacent main-stem White River. In 2012, Flannemouth Sucker larvae were detected in Coal Creek 4 d earlier than in the adjacent main-stem habitat; Bluehead Sucker larvae were first detected on the same day in Coal Creek and the main stem. In 2013, larvae of both sucker species were detected in Coal Creek 8 d earlier than in the adjacent main-stem White River site.

Our larval sampling elucidated an upstream limit for reproduction for all three species. In 2012, Flannemouth Sucker and Bluehead Sucker larvae were detected at rkm

118 but not at rkm 132, which suggested an upstream limit for reproduction between those locations. In 2013, we added two sample locations (at rkm 118.5 and rkm 121) to more precisely estimate the upper limit of sucker spawning. Sampling at these locations indicated that suckers spawned as far upstream as rkm 121 in 2013, but larval suckers were never detected at rkm 132 in either year of the study. Therefore, the upper extent of sucker reproduction was between rkm 121 and rkm 132. Roundtail Chub larvae were never detected upstream of rkm 68, indicating that reproduction was limited to downstream sections of the White River study area.

Hatch Dates

We compared the mean TLs (mm) of fish that were aged by counting daily otolith increments to the mean TLs of fish with ages estimated using the age-length regression equations (Table 3), and we found no substantial differences (Fraser 2015). For 2012 samples, the mean TL of otolith-aged fish was only 0.7 mm less than the mean TL of fish whose ages were estimated via regression. For 2013, the difference in mean TLs of otolith-aged fish and the fish with ages estimated using regression was 0.2 mm. Minimal differences in TL between the two groups aged by different methods ensured that length differences did not bias the outcome of age estimations.

For both sucker species in both years, water temperatures were 12–16°C at first hatching regardless of the date or the location in tributary sites or various main-stem White River sites (Figures 5, 6). Main-stem hatching dates showed a clear longitudinal progression, wherein the earliest hatch dates of both sucker species occurred downstream and progressed upstream as spring water temperatures warmed. The earliest sucker hatch dates occurred 13–16 d prior to the first detection of larvae at the same location, with the difference likely due to hatching and emergence times. The peak of Flannemouth Sucker and Bluehead Sucker hatch dates occurred earlier in downstream sample sites than in upstream sample sites during 2012 and 2013.

Tributary spawning occurred earlier than spawning in proximate main-stem White River sampling locations. Piceance Creek (confluent with the White River at rkm 68) had the earliest sucker hatching dates in 2012 for any site: May 5 for Flannemouth Suckers and May 4 for Bluehead Suckers. Hatching dates for suckers in Coal Creek were also earlier than those in the nearest main-stem White River site during both years. Flannemouth Suckers in Coal Creek hatched 6 d earlier than those in the main stem near Coal Creek during 2012 and hatched 15 d earlier during 2013. Bluehead Suckers in Coal Creek hatched 11 d earlier (during 2012) and 6 d earlier (during 2013) than those in the adjacent main-stem habitat. The low number of sucker larvae captured in Piceance Creek during 2013 precluded aging and hatch date estimation.

Hatching of Roundtail Chub occurred later than the hatching of suckers, and when water temperatures were 16–20°C, regardless of White River sample site longitudinal position (Figure 7). Hatching date distributions for Roundtail Chub larvae differed longitudinally among sites and between years. In 2012, the peak hatch date occurred on June 6 at rkm 47 and was 19 d later (June 25) upstream at rkm 68. In 2013, the peak hatch date occurred on June 21 downstream at rkm 4 and was 12 d later (July 3) upstream at rkm 68. Comparing the hatch dates for Roundtail Chub at the same locations between years showed that hatching occurred earlier at all locations in 2012 (a warmer year with low flows) than in 2013. The earliest Roundtail Chub hatch dates in 2012 were 11–20 d earlier than the first detection of larvae in 2013 at the same locations.

Stream Temperature Model

The stream temperature model we chose included air temperature, elevation, ordinal date, and flow; quadratic terms for all variables except air temperature; and a cubic term for discharge. The use of higher-order terms improved model fit. For simplicity, we interpreted only the top model with eight variables (lowest AIC_c value; Table 4) rather than model-averaging the top two models.

TABLE 3. Regression equations to estimate *Age* (d) as function of *TL* (mm) for Flannemouth Suckers (FMS), Bluehead Suckers (BHS), and Roundtail Chub (RTC) in the upper White River basin, as constructed from measured lengths of larval fish that were aged by counting otolith daily growth increments.

Species	Location	2012 equation	2013 equation
FMS	Main-stem White River	$Age = TL \cdot 0.88 + 3.42$	$Age = TL \cdot 1.19 - 5.72$
	Coal Creek	$Age = TL \cdot 0.70 + 7.28$	$Age = TL \cdot 2.73 - 26.05$
	Piceance Creek	$Age = TL \cdot 0.95 + 6.42$	
BHS	Main-stem White River	$Age = TL \cdot 2.87 - 25.70$	$Age = TL \cdot 2.24 - 19.64$
	Coal Creek	$Age = TL \cdot 2.46 - 15.85$	$Age = TL \cdot 1.21 + 0.06$
	Piceance Creek	$Age = TL \cdot 1.57 - 4.20$	
RTC	Main-stem White River	$Age = TL \cdot 1.49 - 0.11$	$Age = TL \cdot 2.33 - 14.11$

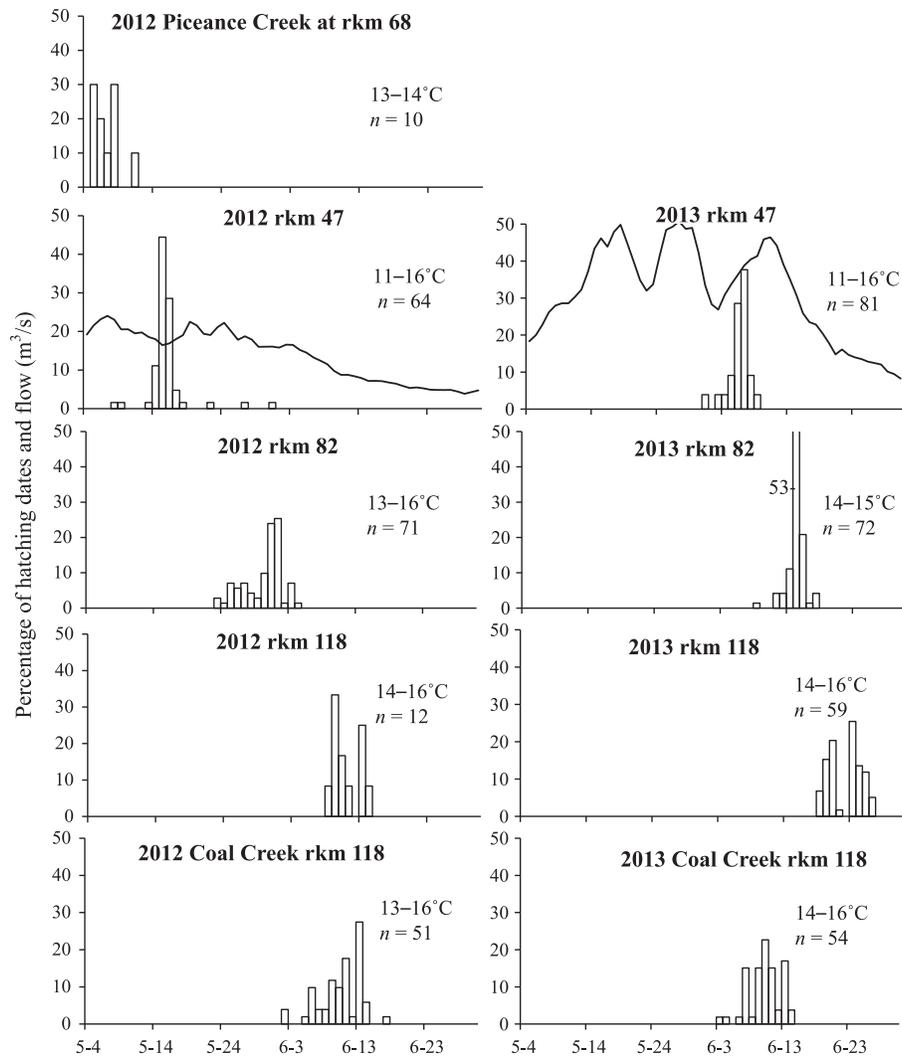


FIGURE 5. Hatching dates (estimated from otolith analyses and age-length regressions) of the earliest Flannemouth Sucker mesolarvae collected at three White River locations (river kilometers [rkm] 47, 82, and 118) and two tributary locations relative to the mean daily flow (line in upper panels; U.S. Geological Survey gauge 09304800) from May 4 to June 30 in 2012 and 2013. Mean daily temperature range is reported for the hatch dates at each site. Larvae were not detected in Piceance Creek during 2013.

We validated stream temperature model predictions against independent water temperature data obtained at three locations in 2013 and at a single location in 2014 (Appendix Figure A.1). Predicted stream temperatures were highly correlated ($R^2 = 0.965$) with observed water temperatures, and 95–97% of the variability in water temperature was accounted for by the predictor variables (Figure A.1; Table 5). Air temperature and ordinal date were positively and importantly related to water temperature, indicating that water temperature increased as air temperatures warmed later in the year. Although air temperature and ordinal date were correlated ($r = 0.82$), we chose to include both variables (1) to account for seasonal and annual changes in air temperature that are not reflected in date alone and (2) because models fitted with

only one or the other variable ranked substantially lower than any other candidate models shown. In contrast to air temperature, water temperature was negatively correlated with elevation and flow, indicating that predicted water temperatures were cooler at higher elevations and during higher flows. Higher-order terms had a mixture of positive and negative effects but were typically less influential than main effects; the exception was the elevation effect, for which the quadratic term was slightly more influential.

We compared timing and location of the first observed stream temperature of 16°C in 2012 and 2013 to the baseline stream temperature model and climate change scenarios to understand what type of scenario these years best represented for sucker reproduction. These predictions vary slightly from those of Fraser (2015) due to slightly

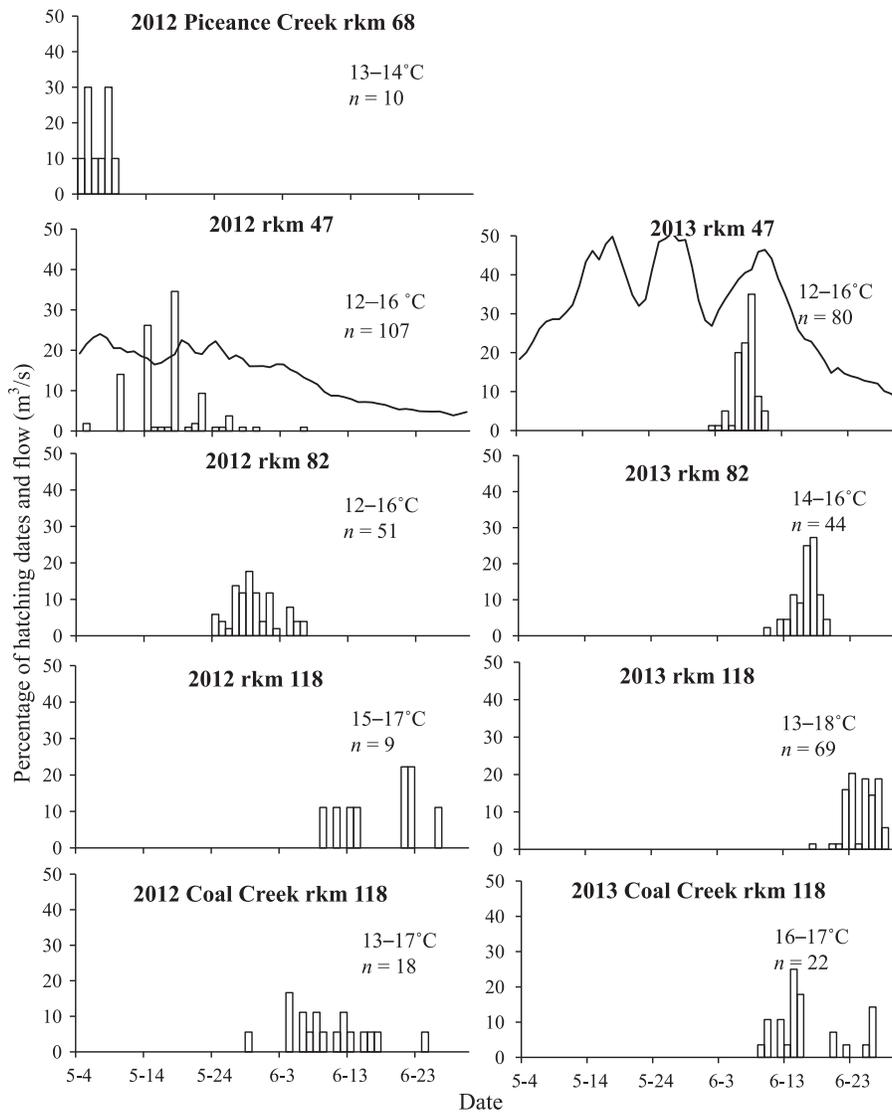


FIGURE 6. Hatching dates (estimated from otolith analysis and age-length regressions) for the earliest Bluehead Sucker mesolarvae collected at three White River locations (river kilometers [rkm] 47, 82, and 118) and two tributary locations relative to the mean daily flow (line in upper panels; U.S. Geological Survey gauge 09304800) from May 4 to June 30 in 2012 and 2013. Mean daily temperature range is reported for the hatch dates at each site. Larvae were not detected in Piceance Creek during 2013.

refined statistical models. In both years, the first observed water temperature of 16°C occurred earlier than predicted by the baseline stream temperature model (Figure 8). For instance, the water temperature at rkm 18 reached 16°C 25 d earlier than predicted in 2012 and 9 d earlier than predicted in 2013. Water temperatures in 2012 closely matched the most extreme climate change scenario that we modeled: a 4°C increase in air temperature and a 50% decrease in flow. Water temperatures in 2013 closely matched the climate change scenario of a 2°C increase in air temperature and a 20% decrease in flow. However, in 2013, water temperature predictions underestimated the actual upstream water temperatures; we recorded 16°C at

rkm 146, whereas the model predicted that 16°C would not occur upstream of rkm 130. The upstream-most location where sucker larvae were found (rkm 121) was also the upstream-most location at which 16°C was predicted to occur in the baseline model.

We also compared the timing and location of the first observed stream temperature of 20°C to understand what type of scenario these years represented for Roundtail Chub reproduction. We used the model to predict when the water temperature would reach 20°C, a level most closely associated with the first detection of Roundtail Chub larvae (Figure 8). In 2012, observed water temperatures reached 20°C earlier than any of the climate change

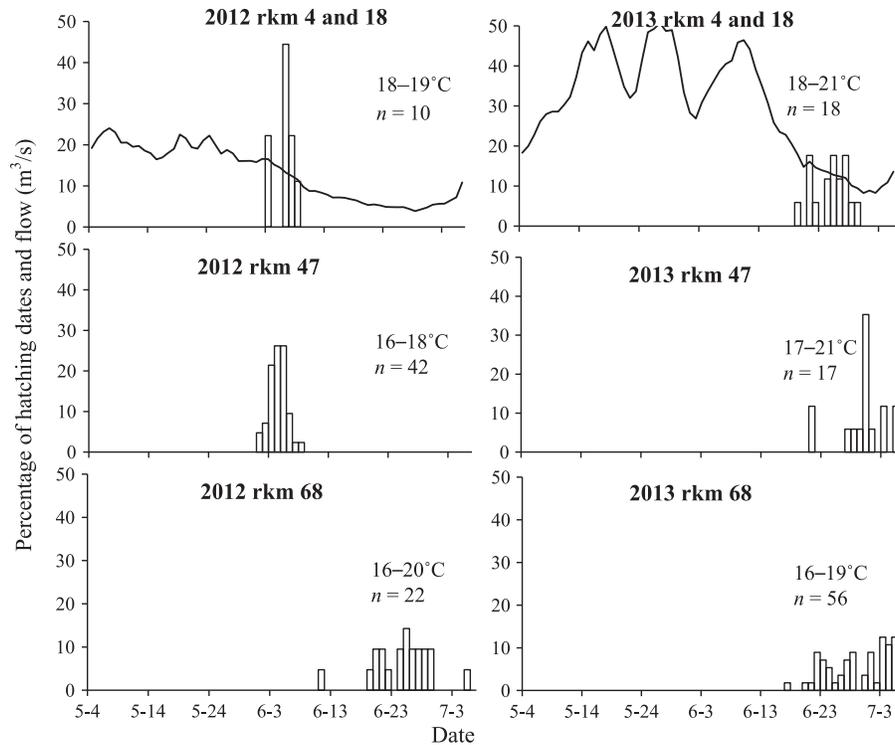


FIGURE 7. Hatching dates (estimated from otolith analysis and age-length regressions) for the earliest Roundtail Chub mesolarvae collected at three White River locations (river kilometers [rkm] 4 and 18 [combined], 47, and 68) in 2012 and 2013 relative to the mean daily flow (line in upper panel; U.S. Geological Survey gauge 09304800) from May 4 to July 6 in 2012 and 2013. The mean daily temperature range is reported for the hatch dates at each site. No Roundtail Chub larvae were detected in tributaries during this study.

TABLE 4. Summary statistics for candidate multiple regression models to predict stream temperature in the upper White River, Colorado (AIC_c = Akaike's information criterion corrected for small sample size; ΔAIC_c = difference in AIC_c value between the given model and the best-performing model; SSE = sum of squared errors). Five years of data (2008–2012) were used to construct these regressions. Model inputs evaluated for model selection included ordinal date (Day; 91–249 [April 1–August 31]), flow (Q ; m^3/s), elevation (Elev; m), air temperature (AirTemp; $^{\circ}C$), and their quadratic or cubic coefficients.

Predictor variables	Number of variables	AIC_c	ΔAIC_c	SSE
Day, Q , Elev, AirTemp, Day ² , Q^2 , Elev ² , Q^3	8	-853.74	0	1,959.78
Day, Q , Elev, AirTemp, Day ² , Q^2 , Elev ² , AirTemp ² , Q^3	9	-851.94	1.80	1,959.63
Day, Q , Elev, AirTemp, Day ² , Q^2 , Elev ²	7	-844.05	9.69	1,968.26
Day, Q , AirTemp, Day ² , Q^2 , Elev ²	6	-829.36	24.38	1,980.45
Day, Q , Elev, AirTemp, Day ² , Q^2	6	-805.35	48.39	1,998.10
Day, Q , Elev, AirTemp, Q^2	5	282.89	1,136.63	2,989.91
Day, Q , Elev, AirTemp	4	491.90	1,345.65	3,232.50

predictions evaluated in this study. The most extreme climate change scenario (4 $^{\circ}C$ increase in air temperature and a 50% decrease in flow) predicted 20 $^{\circ}C$ to occur 5 d later than was observed in 2012 (Figure 8). The 2013 water temperatures most closely resembled the most extreme climate change scenario. This scenario also predicted that water temperatures would reach 20 $^{\circ}C$ up to rkm 96; observed water temperatures in 2012 and 2013 did reach 20 $^{\circ}C$ at rkm 82 but not at rkm 116. We did not measure

water temperatures between rkm 82 and rkm 116 and could not determine the precise upstream limit of 20 $^{\circ}C$. However, this range does encompass the location of the upstream-most model prediction of 20 $^{\circ}C$.

For each of the 16 $^{\circ}C$ and 20 $^{\circ}C$ prediction scenarios, the climate change scenario with cooler water temperatures and higher streamflows delayed reaching the onset of threshold water temperatures for reproduction by 1 week or more relative to the baseline scenario. Cooler water

TABLE 5. Coefficients for the top selected multiple regression model (based on Akaike’s information criterion corrected for small sample size; see Table 4) for predicting April–August water temperature (°C) in the upper White River, Colorado. Data from 2008–2012 were used to build the model, which included a low-flow year (2012) and a high-flow year (2011). Predictor variables were ordinal date (Day; 91–249 [April 1–August 31]), flow (Q ; m^3/s), elevation (Elev; m), air temperature (Air-Temp; °C), and their quadratic or cubic coefficients.

Coefficient for	Estimate	SE	<i>t</i>	<i>P</i>
Intercept	-24.0842	6.7908	-3.55	0.0004
AirTemp	0.3720	0.0056	66.10	<0.0001
Elev	0.0335	0.0076	4.40	<0.0001
Elev ²	-0.00001435	<0.0001	-6.71	<0.0001
Day	0.2202	0.0052	42.59	<0.0001
Day ²	-0.000538	<0.0001	-37.38	<0.0001
Q	-0.1282	0.0051	-24.95	<0.0001
Q^2	0.00083	<0.0001	8.70	<0.0001
Q^3	-0.0000017	<0.0001	-3.42	0.0006

temperatures also resulted in the loss of suitable thermal habitat for reproduction: approximate losses were 25% for suckers and 65% for Roundtail Chub in our study area.

DISCUSSION

Our results indicated that timing of reproduction for Flannemouth Sucker, Bluehead Sucker, and Roundtail Chub in the upper White River, whether based on the presence of larvae in samples or on back-calculated hatching dates, was primarily dictated by water temperature rather than flow. This was evident because reproduction occurred in a narrow but consistent range of water temperatures, beginning in the main-stem White River in warmer downstream locations and proceeding upriver as water temperatures increased. Additionally, reproduction occurred earlier in tributaries than in adjacent main-stem habitats because tributary habitat was warmer. Water temperature predictions under climate change scenarios closely matched observed temperatures in 2012 and 2013, indicating that those low-flow years matched well with potential future warming conditions (Christensen et al. 2004; McCabe and Wolock 2007; Udall and Overpeck 2017). Modeling of climate change projections showed that water temperatures will warm earlier in the year, and this will result in earlier spawning and extend thermally suitable spawning habitat upstream.

Temperature and Flow

Although patterns of water temperature and flow are related, with summer temperatures increasing as flows decline, we found that flow patterns did not directly influence the timing of Flannemouth Sucker, Bluehead Sucker, and Roundtail Chub reproduction. This was because at

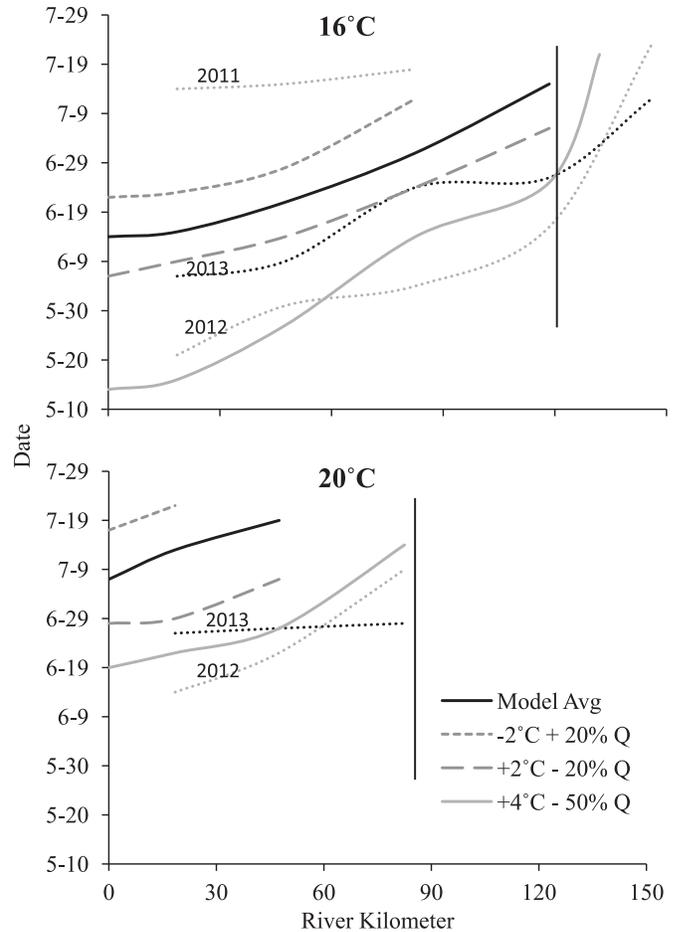


FIGURE 8. Timing of stream temperature model predictions of 16°C and 20°C, the temperatures most associated with the first presence of sucker larvae (Flannemouth Suckers, Bluehead Suckers) and Roundtail Chub larvae, respectively, in the White River. The model used average data from 1997–2013 (black line) and three manipulations (increase [+] or decrease [-] of flow (% Q) and air temperature (°C) to assess climate change scenarios. The date and river kilometer (rkm) at which 16°C and 20°C were first recorded in 2011, 2012, and 2013 (labeled) are also plotted for comparison with the average and climate change scenarios (20°C was not recorded in the study area during 2011). The vertical black lines depict the upstream-most locations (rkm 121 for both sucker species; rkm 86 for Roundtail Chub) at which larvae were detected during this study.

any given time during the study, flow patterns spatially varied only slightly in main-stem White River habitat compared to patterns of water temperature, which warmed progressively in a downstream direction, and certain temperature thresholds were associated with reproduction. If flow played a primary role in the initiation of spawning, we would expect the timing of both the first presence of larvae and hatch dates to have occurred synchronously along the longitudinal extent of the river. This situation is similar to that for reproduction by Razorback Suckers in the main-stem Green River, where water

temperature played a stronger role than flow (Bestgen et al. 2011). Additionally, White River flow patterns in 2012 and 2013 were different, with low-magnitude flows and a single distinct peak in 2012 and moderate-magnitude flows and several peaks evident in 2013. Despite large differences in runoff patterns between years, spawning proceeded longitudinally from downstream to upstream over a duration of 28–46 d for suckers and 0–30 d for Roundtail Chub, indicating that the initiation of spawning was influenced little by flow. Those patterns also prevailed in tributaries, where the sucker species responded predictably to water temperatures. Differences between years in the timing of reproduction, which was earlier in 2012 than in 2013 by as much as 30 d, also suggested that day length was not a primary factor signaling the onset of reproduction; fish could have been responding to increasing day length, which occurred throughout the sucker spawning periods and for Roundtail Chub in 2012. Reproduction by Roundtail Chub in 2013 was later and occurred both before and after the summer solstice, when day length was increasing and decreasing, respectively.

Presence of Fish Larvae

The water temperature most closely related to the first detection of sucker larvae was 16°C, consistent with observations by Carter et al. (1986), who found that the first presence of sucker larvae captured by drift nets in the Colorado River occurred at 16°C. Our White River longitudinal pattern of first larval detection that began downstream and proceeded upstream later in the year, extended over 28–46 d, depending on the year and species. Larvae were detected substantially earlier in 2012 than in 2013 because water temperature was warmer in 2012 due to low runoff. Larval Flannemouth Sucker and Bluehead Sucker hatch dates also indicated that sucker reproduction was cued by water temperature. This was because regardless of location and year, hatch dates across the season occurred at 12–16°C and showed a longitudinal pattern with the earliest hatch dates at downstream locations and later hatch dates upstream. The range of water temperatures associated with hatch dates may be a result of variation in egg incubation periods, which can vary greatly over a small spatial scale at various water temperatures (Gillooly et al. 2002). For example, Haines (1995) reported that times to peak hatching of fertilized Flannemouth Sucker eggs were 16.5, 8.5, and 6 d at water temperatures of 12, 16, and 20°C, respectively. Timing of sucker reproduction, when evaluated by the presence of larvae and hatch dates, showed that reproduction occurred earlier in tributaries than in nearby main-stem habitat. Tributaries had lower flows and were warmer than main-stem habitat, again indicating that reproduction is mainly water temperature dependent.

Presence of Roundtail Chub larvae coincided most closely with a water temperature of 20°C, and larval hatch

dates were consistent with water temperatures of 16–20°C across all locations for both years. Detection of Roundtail Chub larvae from stations sequentially sampled across the basin showed that the larvae were limited to the lowermost 68 rkm of the study area, and water temperatures in this reach generally differed by less than 1°C. The smaller water temperature variation in this reach likely resulted in a weaker relationship with water temperature than was observed with the sucker species, and this was a main reason for less longitudinal variation in the first presence or hatching of Roundtail Chub in the study area. In 2012, there was a clear trend of reproduction beginning in downstream locations and progressing upstream. However, in the higher-flow year, 2013, the presence of larval Roundtail Chub occurred nearly synchronously across locations, perhaps due to more homogeneous water temperatures in that relatively short reach. Similar to suckers, the first presence of Roundtail Chub larvae occurred earlier in 2012 compared to 2013.

Flannemouth Sucker, Bluehead Sucker, and Roundtail Chub each showed clear upstream limits to reproduction based on the absence of larvae in upstream samples. The upstream limit to sucker reproduction occurred between rkm 121 and rkm 132, and reproduction upstream of rkm 121 may be limited by water temperature. Water temperatures of 16°C were recorded above rkm 132 in both years of the study. However, it is likely that water temperatures of 16°C occurred too late in the season (early to mid-July) for these locations to support sucker reproduction. Reproduction may be controlled by prolonged exposure to a given water temperature, which is necessary for successful development of gonads, and upstream locations may not have a sufficient number of days at these water temperatures (Hansen et al. 2001; Gillooly et al. 2002). This would not be true, of course, if the fish resided in warmer water downstream and then moved upstream to spawn, but our data cannot address that hypothesis. Previous monitoring of fish populations in the upper White River showed that no Flannemouth Suckers, Bluehead Suckers, or Roundtail Chub were detected between rkm 142 and rkm 146 (B. Wright, Colorado Parks and Wildlife, personal communication), which supported the idea that the upper limit of sucker reproduction in the upper White River occurred between rkm 121 and rkm 132. Preliminary data collected in the cold, high-flow year, 2011, showed that 16°C was not recorded upstream of rkm 82, demonstrating that water temperature is annually variable and spawning habitat may be limited in upstream reaches during such years. Lower water temperatures will delay the timing of reproduction and potentially delay the development of larvae, possibly reducing the survival rates of larvae or negating reproduction altogether in upstream areas. Fraser et al. (2017) demonstrated that lower water temperatures in 2013 delayed the peak spawning

migrations of suckers into Coal Creek by as much as 7 d compared to 2012, consistent with the temperature control hypothesis. The upper limit of Roundtail Chub larvae based on seine and dip-net sampling was consistent between years, occurring at rkm 68 (with the exception of one sampling event discussed below), and main-stem sampling indicated that Roundtail Chub adults were present at rkm 82, suggesting that successful reproduction was limited to the lowermost reaches of the White River. In 2011, 20°C was not recorded anywhere in the study area, potentially indicating that Roundtail Chub did not spawn, but we have no sampling data to confirm this hypothesis.

Lack of reproduction upstream of apparent distributional limits for the three species does not reflect a lack of suitable spawning habitat, as channel form and substrate types were similar upstream and downstream of the apparent limits. Flannelmouth Sucker and Bluehead Sucker spawn in shallow water on gravel and sand bars (Bezerides and Bestgen 2002), which are present throughout the study area, including upstream of rkm 121. Similarly, Roundtail Chub spawn in gravel found in deep pools and runs, which were observed upstream of rkm 82. Thus, spawning habitat availability does not appear to limit the three species' distributions, and we are not aware of other resource limitations, bioenergetic processes, or biotic interactions that would act as additional constraints to upstream distributions (Lawrence et al. 2015; Rubenson and Olden 2017). However, further research is warranted to investigate other possible constraints to upstream expansion of these species.

Based on the presence of larvae and the hatching dates back-calculated from otolith increments, reproduction by Flannelmouth Suckers and Bluehead Suckers in the White River was not spatially or temporally segregated. Although the peak hatch dates of suckers at the same location did not match precisely, the range of hatching dates overlapped broadly at each location. Additionally, Fraser et al. (2017) showed that the timing of spawning migrations by Flannelmouth Suckers and Bluehead Suckers into Coal Creek occurred nearly synchronously in 2012 and 2013. Others have noted that reproduction by Flannelmouth Suckers and Bluehead Suckers may be spatially and temporally segregated during spawning. Zelasko et al. (2011) estimated that peak spawning of Flannelmouth Suckers occurred 2 weeks earlier than the peak spawning of Bluehead Suckers in the Big Sandy River, Wyoming. Furthermore, spatial separation of these sucker species during reproduction was also noted (Compton et al. 2008; Sweet and Hubert 2010). Differences in the overlap of spawning times for native suckers among various locations in the upper Colorado River basin are not well understood but may be due to differences in habitat, thermal histories of adults, or other factors.

Stream Temperature Model

Water temperature modeling based on anticipated changes in climate (reduced flow and increased warming; Christensen et al. 2004; McCabe and Wolock 2007; Udall and Overpeck 2017) indicated that water temperatures will increase, will likely induce regular, earlier spawning by the three species, and will potentially extend reproduction farther upstream in the White River. However, observed water temperatures in 2012 were similar to those predicted by the most extreme climate change scenario that we modeled, and no shift in reproduction by suckers farther upstream was observed in that year compared to the cooler year, 2013. The lack of sucker reproduction upstream of rkm 121 (based on the presence of larvae) during 2012 suggests that other factors may be limiting at this time. Reproduction in upstream habitat may be controlled by long-term conditions rather than by annual differences in water temperatures, such that if water temperatures were on average warmer upstream, suckers may move upstream over time. However, warmer water temperatures would result in earlier reproduction. Earlier reproduction might have a positive impact on survival of the early life history stages of these fishes because it would enable more growth before the onset of winter, a period of high mortality for age-0 fish (Kaeding and Osmundson 1988; Thompson et al. 1991; Coleman and Fausch 2007; Bennett et al. 2014).

Climate change effects may also extend to downstream reaches via excessive warming of water. However, projected climate trends will likely not impact the presence of the three species at downstream locations, as they were historically found throughout the Colorado River basin in much warmer environments (Brouder 2001; Bezerides and Bestgen 2002; Brouder et al. 2006). No studies of upper thermal tolerances have been performed for Flannelmouth Sucker or Bluehead Sucker, but another Colorado River basin catostomid, the Razorback Sucker, tolerated water temperatures up to 36°C in a laboratory study (Carveth et al. 2006). Carveth et al. (2006) also found that Roundtail Chub tolerated water temperatures up to 36°C. The most extreme climate change scenario modeled in this study—a 4°C increase in air temperature and a 50% decrease in flow—predicted that water temperatures would not reach 23°C at the warmest downstream locations. Therefore, it is unlikely that the three species will be detrimentally impacted by warmer water temperatures under climate change scenarios in the upper White River. However, a factor not considered in the stream temperature model is the increase in water demand from development and irrigation as human populations in the region grow. Increased water usage due to warmer air temperatures and lower precipitation would likely result in lower flows (Udall and Overpeck 2017) and could magnify the effects of climate change on this native fish community.

Baseline stream temperature predictions indicated that rkm 121 would be the upstream-most location to achieve 16°C, which matched well with the observed upstream extent of successful sucker reproduction based on larval presence. The match between the baseline model predictions and the observed upstream extent of larval presence indicated that the long-term average water temperature at first larval presence was a good metric for predicting the upper limits of successful spawning for these sucker species. Using long-term average water temperatures to predict the upstream limits to reproduction for these species in other systems may be a tool for determining the distribution of successful reproduction on a larger spatial scale and could be tested with additional sampling and water temperature monitoring.

The baseline stream temperature model also predicted that the 20°C threshold would occur later than we observed and would not occur upstream of rkm 47. However, Roundtail Chub larvae were repeatedly detected upstream at rkm 68 during both years of the study, and adults were detected even farther upstream. This suggests that even though water temperatures of 20°C were most closely associated with the first presence of Roundtail Chub larvae, 20°C was not strongly associated with first reproduction. Perhaps water temperature at the first presence of larvae was not a good metric with which to determine the upstream limit to successful reproduction by Roundtail Chub. A comparison of the observed water temperatures to the baseline stream temperature model showed that 20°C occurred 1 month earlier in 2012 than was predicted by the model and 3 weeks earlier in 2013 than was predicted. Although no Roundtail Chub larvae were detected at rkm 82 in 36 sampling events over the duration of this study, a few larvae were detected between rkm 82 and rkm 86 during sampling on June 27, 2012. This demonstrated localized Roundtail Chub reproduction slightly upstream of rkm 68 in that year. However, the low number of fish detected indicated that this was an anomalous event in a year characterized by low flow and warm water temperatures. A similar pattern was observed in the John Day River, Oregon, when a warm spring resulted in a 6-rkm upstream shift in the distribution of invasive Smallmouth Bass *Micropterus dolomieu* (Rubenson and Olden 2017).

Understanding the relationship between water temperature and reproduction for the Flannelmouth Sucker, Bluehead Sucker, and Roundtail Chub should help resource managers to make more informed decisions regarding flow requirements and water usage, thereby facilitating the maintenance of native fish populations. Using water temperature to evaluate potential reproductive habitat could be a management tool for identifying barriers to upstream spawning migrations or stream restoration sites. The low flows and higher water temperatures we observed during

our study years serendipitously resembled future climate change scenarios and indicated that all three species could successfully reproduce in those conditions. Reduced habitat size under climate-change-induced flow reductions would certainly reduce population abundance, which may be partially offset by expansion upstream into thermally suitable habitat. However, the long-term implications of climate change are unknown, and managers should strive to perpetuate the valuable and relatively pristine native fish community in the upper White River drainage as a vestige of the native fish communities that formerly existed throughout the Colorado River basin.

ACKNOWLEDGMENTS

Funding for this project was provided by the USGS and Colorado Parks and Wildlife. We thank the Strang and Nelson families of Meeker, Colorado, for granting us access to Coal Creek. We are grateful to E. Kluender, D. E. Snyder, S. Seal, N. Shannon, C. Bryant, E. Pettigrew, J. Smith, and others for contributing to field work, larval fish identification, and other technical assistance. We thank T. Jones and two anonymous reviewers for their valuable revisions that improved the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This study was performed under the auspices of Protocol Number 12-3365A approved by the Institutional Animal Care and Use Committee at Colorado State University. There is no conflict of interest declared in this article.

ORCID

Kevin R. Bestgen  <https://orcid.org/0000-0001-8691-2227>
 Dana L. Winkelman  <https://orcid.org/0000-0002-5247-0114>

REFERENCES

- Armour, C. L. 1991. Guidance for evaluating and recommending temperature regimes to protect fish. U.S. Fish and Wildlife Service Biological Report 90(22).
- Beamish, R. J., and G. A. McFarlane. 1983. The forgotten requirement for age validation in fisheries biology. *Transactions of the American Fisheries Society* 112:735–743.
- Bennett, S., R. Al-Chokhachy, B. B. Roper, and P. Budy. 2014. Annual variation of spawning Cutthroat Trout in a small western USA stream: a case study with implications for the conservation of potamodromous trout life history diversity. *North American Journal of Fisheries Management* 34:1033–1046.
- Bestgen, K. R., D. W. Beyers, J. A. Rice, and G. B. Haines. 2006. Factors affecting recruitment of young Colorado Pikeminnow: synthesis of predation experiments, field studies, and individual-based modeling. *Transactions of the American Fisheries Society* 135:1722–1742.

- Bestgen, K. R., and J. M. Bundy. 1998. Environmental factors affect daily increment deposition and otolith growth in young Colorado Squawfish. *Transactions of the American Fisheries Society* 127:105–117.
- Bestgen, K. R., G. B. Haines, and A. A. Hill. 2011. Synthesis of flood plain wetland information: timing of Razorback Sucker reproduction in the Green River, Utah, related to stream flow, water temperature, and flood plain wetland availability. Colorado State University, Larval Fish Laboratory Contribution 163, Fort Collins.
- Bezzlerides, N., and K. R. Bestgen. 2002. Status review of Roundtail Chub *Gila robusta*, Flannelmouth Sucker *Catostomus latipinnis*, and Bluehead Sucker *Catostomus discobolus* in the Colorado River basin. Colorado State University, Larval Fish Laboratory Contribution 118, Fort Collins.
- Brett, J. R. 1971. Energetic responses of salmon to temperature—study of some thermal relations in physiology and freshwater ecology of Sockeye Salmon (*Oncorhynchus nerka*). *American Zoologist* 11:99–113.
- Brouder, M. J. 2001. Effects of flooding on recruitment of Roundtail Chub, *Gila robusta*, in a southwestern river. *Southwestern Naturalist* 46:302–310.
- Brouder, M. J. 2005. Age and growth of Roundtail Chub in the upper Verde River, Arizona. *Transactions of the American Fisheries Society* 134:866–871.
- Brouder, M. J., D. D. Rogers, and L. D. Avenetti. 2000. Life history and ecology of the Roundtail Chub, *Gila robusta*, from two streams in the Verde River basin. Arizona Game and Fish Department, Technical Guidance Bulletin 3, Phoenix.
- Brouder, M. J., D. D. Rogers, and L. D. Avenetti. 2006. Observations on the reproductive biology of Roundtail Chub, *Gila robusta*, in the upper Verde River, Arizona. *Western North American Naturalist* 66:260–262.
- Bundy, J. M., and K. R. Bestgen. 2001. Confirmation of daily increment deposition in otoliths of young Razorback Suckers. *Southwestern Naturalist* 46:34–40.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.
- Campana, S. E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* 59:197–242.
- Campana, S. E., and J. D. Neilson. 1985. Microstructure of fish otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1014–1032.
- Carter, J. G., V. A. Lamarra, and R. J. Ryel. 1986. Drift of larval fishes in the upper Colorado River. *Journal of Freshwater Ecology* 3:567–577.
- Carveth, C. J., A. M. Widmer, and S. A. Bonar. 2006. Comparison of upper thermal tolerances of native and nonnative fish species in Arizona. *Transactions of the American Fisheries Society* 135:1433–1440.
- Chart, T. E., and E. P. Bergersen. 1992. Impact of mainstream impoundment on the distribution and movements of the resident Flannelmouth Sucker (*Catostomidae: Catostomus latipinnis*) population in the White River, Colorado. *Southwestern Naturalist* 37:9–15.
- Christensen, N. S., A. W. Wood, N. Voisin, D. P. Lettenmaier, and R. N. Palmer. 2004. The effects of climate change on the hydrology and water resources of the Colorado River basin. *Climatic Change* 62:337–363.
- Coleman, M. A., and K. D. Fausch. 2007. Cold summer temperature regimes cause a recruitment bottleneck in age-0 Colorado River Cutthroat Trout reared in laboratory streams. *Transactions of the American Fisheries Society* 136:639–654.
- Collier, M., R. H. Webb, and J. C. Schmidt. 1996. Dams and rivers: primer on the downstream effects of dams. U.S. Geological Survey Circular 1126.
- Compton, R. I., W. A. Hubert, F. J. Rahel, M. C. Quist, and M. R. Bower. 2008. Influences of fragmentation on three species of native warmwater fishes in a Colorado River basin headwater stream system, Wyoming. *North American Journal of Fisheries Management* 28:1733–1743.
- Coutant, C. C. 1987. Thermal preference—when does an asset become a liability? *Environmental Biology of Fishes* 18:161–172.
- Ellsworth, C. M., M. C. Belk, and C. J. Keleher. 2010. Residence time and drift patterns of larval June Sucker *Chasmistes liorus* in the lower Provo River as determined by otolith microstructure. *Journal of Fish Biology* 77:526–537.
- Fraser, G. S. 2015. Movement patterns, reproduction, and potential impacts of climate change on three native fishes in the upper White River drainage, Colorado. Master's thesis. Colorado State University, Fort Collins.
- Fraser, G. S., D. L. Winkelman, K. R. Bestgen, and K. G. Thompson. 2017. Tributary use by imperiled Flannelmouth and Bluehead suckers in the upper Colorado River basin. *Transactions of the American Fisheries Society* 146:858–870.
- Gillooly, J. F., E. L. Charnov, G. B. West, V. M. Savage, and J. H. Brown. 2002. Effects of size and temperature on developmental time. *Nature* 417:70–73.
- Griffith, J. S. 1993. Coldwater streams. Pages 405–425 in C. C. Kohler and W. A. Hubert, editors. *Inland fisheries management in North America*. American Fisheries Society, Bethesda, Maryland.
- Haines, G. B. 1995. Effects of temperature on hatching success and growth of Razorback Sucker and Flannelmouth Sucker. U.S. Fish and Wildlife Service, Vernal, Utah.
- Haines, G. B., and H. M. Tyus. 1990. Fish associations and environmental variables in age-0 Colorado Squawfish habitats, Green River, Utah. *Journal of Freshwater Ecology* 5:427–435.
- Hansen, T., O. Karlsen, G. L. Taranger, G. I. Hemre, J. C. Holm, and O. S. Kjesbu. 2001. Growth, gonadal development and spawning time of Atlantic Cod (*Gadus morhua*) reared under different photoperiods. *Aquaculture* 203:51–67.
- Haworth, M. R., and K. R. Bestgen. 2016. Daily increment validation and effects of streamflow variability and water temperature on growth of age-0 Flathead Chub *Platygobio gracilis*. *North American Journal of Fisheries Management* 36:744–753.
- Hoff, G. R., D. J. Logan, and D. F. Markle. 1997. Otolith morphology and increment validation in young Lost River and Shortnose suckers. *Transactions of the American Fisheries Society* 126:488–494.
- Hooley-Underwood, Z. E., S. B. Stevens, N. R. Salinas, and K. G. Thompson. 2019. An intermittent stream supports extensive spawning of large-river native fishes. *Transactions of the American Fisheries Society* 148:426–441.
- Irving, D. B., and T. Modde. 2000. Home-range fidelity and use of historic habitat by adult Colorado Pikeminnow (*Ptychocheilus lucius*) in the White River, Colorado and Utah. *Western North American Naturalist* 60:16–25.
- Isaak, D. J., C. H. Luce, B. E. Rieman, D. E. Nagel, E. E. Peterson, D. L. Horan, S. Parkes, and G. L. Chandler. 2010. Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecological Applications* 20:1350–1371.
- Isaak, D. J., C. C. Muhlfeld, A. S. Todd, R. Al-Chokhachy, J. J. Roberts, J. L. Kershner, K. D. Fausch, and S. W. Hostetler. 2012. The past as prelude to the future for understanding 21st-century climate effects on Rocky Mountain trout. *Fisheries* 37:542–556.
- Kaeding, L. R., B. D. Burdick, P. A. Schrader, and C. W. McAda. 1990. Temporal and spatial relations between the spawning of Humpback Chub and Roundtail Chub in the upper Colorado River. *Transactions of the American Fisheries Society* 119:135–144.
- Kaeding, L. R., and D. B. Osmundson. 1988. Interaction of slow growth and increased early-life mortality—an hypothesis on the decline of Colorado Squawfish in the upstream regions of its historic range. *Environmental Biology of Fishes* 22:287–298.

- Lawrence, D. J., D. A. Beauchamp, and J. D. Olden. 2015. Life-stage-specific physiology defines invasion extent of a riverine fish. *Journal of Animal Ecology* 84:879–888.
- Magnuson, J. J., L. B. Crowder, and P. A. Medvick. 1979. Temperature as an ecological resource. *American Zoologist* 19:331–343.
- Martinez, P. J., T. E. Chart, M. A. Trammell, J. G. Wullschleger, and E. P. Bergersen. 1994. Fish species composition before and after construction of a main stem reservoir on the White River, Colorado. *Environmental Biology of Fishes* 40:227–239.
- McCabe, G. J., and D. M. Wolock. 2007. Warming may create substantial water supply shortages in the Colorado River basin. *Geophysical Research Letters* 34(22):L22708.
- Modde, T., and D. B. Irving. 1998. Use of multiple spawning sites and seasonal movement by Razorback Suckers in the middle Green River, Utah. *North American Journal of Fisheries Management* 18:318–326.
- Moyle, P. B., and J. F. Mount. 2007. Homogenous rivers, homogenous faunas. *Proceedings of the National Academy of Sciences of the United States of America* 104:5711–5712.
- Muth, R. T., and D. E. Snyder. 1995. Diets of young Colorado Squawfish and other small fish in backwaters of the Green River, Colorado and Utah. *Great Basin Naturalist* 55:95–104.
- Olden, J. D., and R. J. Naiman. 2010. Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. *Freshwater Biology* 55:86–107.
- Osmundson, D. B. 2011. Thermal regime suitability: assessment of upstream range restoration potential for Colorado Pikeminnow, a warmwater endangered fish. *River Research and Applications* 27:706–722.
- Pannella, G. 1971. Fish otoliths: daily growth layers and periodical patterns. *Science* 173:1124–1127.
- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. *BioScience* 47:769–784.
- Poff, N. L., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences of the United States of America* 104:5732–5737.
- Rahel, F. J., and W. A. Hubert. 1991. Fish assemblages and habitat gradients in a Rocky Mountain–Great Plains stream: biotic zonation and additive patterns of community change. *Transactions of the American Fisheries Society* 120:319–332.
- Rieman, B. E., D. J. Isaak, S. B. Adams, D. L. Horan, D. E. Nagel, C. H. Luce, and D. Myers. 2007. Anticipated climate warming effects on Bull Trout habitats and populations across the interior Columbia River basin. *Transactions of the American Fisheries Society* 136:1552–1565.
- Roberts, J. J., K. D. Fausch, D. P. Peterson, and M. B. Hooten. 2013. Fragmentation and thermal risks from climate change interact to affect persistence of native trout in the Colorado River basin. *Global Change Biology* 19:1383–1398.
- Rubenson, E. S., and J. D. Olden. 2017. Dynamism in the upstream invasion edge of a freshwater fish exposes range boundary constraints. *Oecologia* 184:453–467.
- Selong, J. H., T. E. McMahon, A. V. Zale, and F. T. Barrows. 2001. Effect of temperature on growth and survival of Bull Trout, with application of an improved method for determining thermal tolerance in fishes. *Transactions of the American Fisheries Society* 130:1026–1037.
- Snyder, D. E. 1981. Contributions to a guide to the cypriniform fish larvae of the upper Colorado River system in Colorado. U.S. Bureau of Land Management, Biological Sciences Series 3, Denver.
- Snyder, D. E., K. R. Bestgen, and S. C. Seal. 2005. Native cypriniform fish larvae of the Gila River basin—morphological descriptions, comparisons and computer-interactive key. Colorado State University, Larval Fish Laboratory, Fort Collins.
- Snyder, D. E., and R. T. Muth. 2004. Catostomid fish larvae and early juveniles of the upper Colorado River basin—morphological descriptions, comparisons and computer-interactive key. Colorado Division of Wildlife, Technical Publication Number 42, Fort Collins.
- Sweet, D. E., and W. A. Hubert. 2010. Seasonal movements of native and introduced catostomids in the Big Sandy River, Wyoming. *Southwestern Naturalist* 55:382–389.
- Thompson, J. M., E. P. Bergersen, C. A. Carlson, and L. R. Kaeding. 1991. Role of size, condition, and lipid content in the overwinter survival of age-0 Colorado Squawfish. *Transactions of the American Fisheries Society* 120:346–353.
- Tyus, H. M. 1990. Potamodromy and reproduction of Colorado Squawfish in the Green River basin, Colorado and Utah. *Transactions of the American Fisheries Society* 119:1035–1047.
- Tyus, H. M., and C. A. Karp. 1990. Spawning and movements of Razorback Sucker, *Xyrauchen texanus*, in the Green River basin of Colorado and Utah. *Southwestern Naturalist* 35:427–433.
- Udall, B., and J. T. Overpeck. 2017. The twenty-first century Colorado River hot drought and implications for the future. *Water Resources Research* 53:2404–2418.
- Weiss, S. J., E. O. Otis, and O. E. Maughan. 1998. Spawning ecology of Flannelmouth Sucker, *Catostomus latipinnis* (Catostomidae), in two small tributaries of the lower Colorado River. *Environmental Biology of Fishes* 52:419–433.
- Zelasko, K. A., K. R. Bestgen, and K. Hayes. 2011. Drift and retention of Flannelmouth Sucker *Catostomus latipinnis*, Bluehead Sucker *Catostomus discobolus*, and White Sucker *Catostomus commersonii* in the Big Sandy River, Wyoming. Colorado State University, Larval Fish Laboratory Contribution 165, Fort Collins.

Appendix: Additional Data

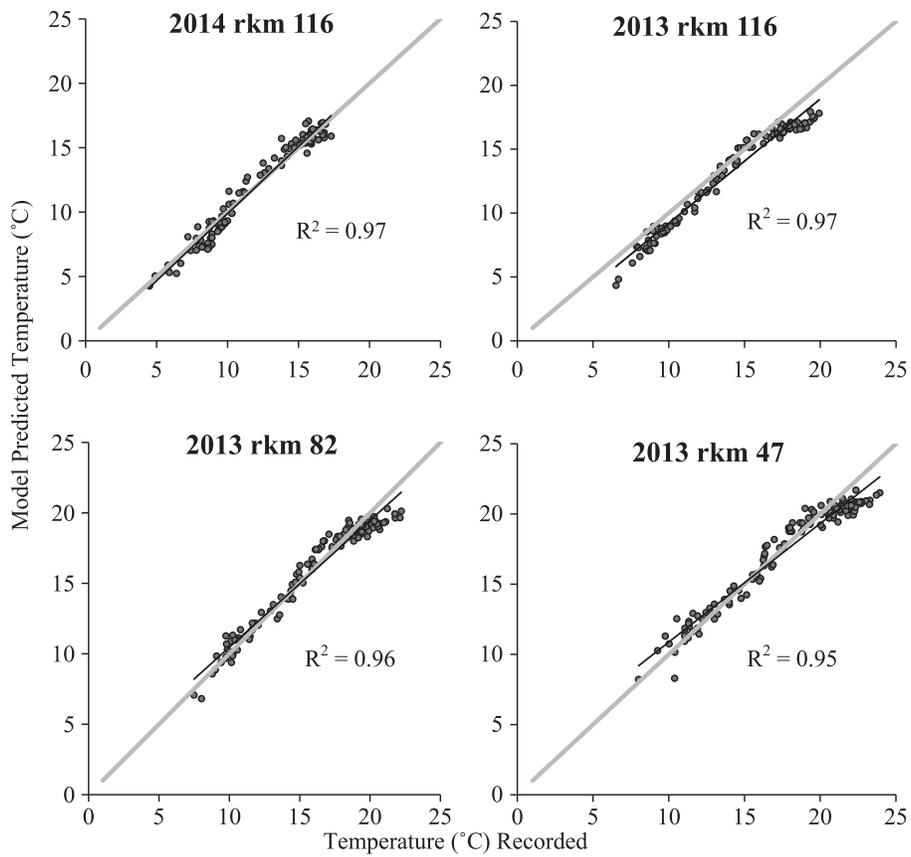


FIGURE A.1. Comparison of water temperature predictions from the stream temperature model developed in this study and main-stem White River temperatures recorded by three temperature loggers (at river kilometers [rkm] 116, 82, and 47) during 2013 and one 2014 record from U.S. Geological Survey gauge 90304200 (at rkm 116). The slope of the regression (black line) and the 1:1 relationship (i.e., slope = 1; gray line) are plotted on each panel for comparison.