RIVER REGULATION AFFECTS REPRODUCTION, EARLY GROWTH, AND SUPPRESSION STRATEGIES FOR INVASIVE SMALLMOUTH BASS IN THE UPPER COLORADO RIVER BASIN

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EXECUTIVE SUMMARY

Understanding the reproductive ecology and phenology of organisms enables prediction of effects of environmental factors that may control population growth. Otolith microstructure analysis was used to estimate hatching dates and growth rates of early life stages of invasive smallmouth bass *Micropterus dolomieu* collected in the free-flowing Yampa River, and regulated or partially regulated reaches of the Green River, Colorado and Utah, from 2003-2011. Smallmouth bass first hatching in the unregulated Yampa River was initiated in June through mid-July just after a threshold water temperature of 16°C was achieved. First hatching of smallmouth bass in the regulated portion of the Green River occurred several days after water temperature reached the 16°C threshold but was closely linked to flows, as first hatching occurred within 21-23 days of peak flow cessation and within 0-7 days of onset of baseflow releases. In the partially regulated reach of the Green River, first spawning occurred nearly two weeks after onset of 16°C mean daily water temperature and flows were variable and relatively high. In dam-regulated and partially regulated Green River reaches, spawning may have been inhibited by lack of habitat at higher flows. A general linear model (GLM) to predict first hatching of smallmouth bass in the Yampa River and both reaches of the Green River (model R^2 = 0.98) indicated a metric of flow magnitude and duration, onset of the threshold 16°C mean daily water temperature, and number of days and water warming rates post peak flow, affected date of smallmouth bass first hatching. In all reaches, smallmouth bass hatched later in the year when flows were higher and cooler and earlier when flows were lower and warmer. A second GLM (model R^2 = 0.85) predicted smallmouth bass first hatching in each reach as a function of a single variable, April-July total runoff. Those predictions can be used to model hydrologic scenarios for the Green River, and specifically, understand effects of flow release spikes to disadvantage spawning success of smallmouth bass on Flaming Gorge Reservoir storage elevations. Mean number of days from first hatching to peak hatching of smallmouth bass was 13 and 12 d in the unregulated Yampa River and the partially regulated Green River reach, respectively, but was shorter (7 d) in the regulated Green River reach. Distributions of hatching dates were usually bell-shaped and the peak was sometimes in the earliest third of the hatching dates (Cohort 1), but was usually in the middle third (Cohort 2). Peak hatching was never in the final third (Cohort 3) of the hatching dates within a year. In both the Yampa and Green rivers, smallmouth bass mean hatching season duration each year in the 2004-2011 period was about 4 weeks. The range of annual first hatching dates was widest in the regulated Green River reach (64 d) and nearly twice that for the unregulated Yampa River (35 d). In the partially regulated Green River reach, first hatching date range was intermediate (54 d), and those data collectively suggested that streamflow regulation had a large effect on when spawning and hatching occurred compared to an unregulated system. Earlier baseflow onset or warmer temperatures of releases from Flaming Gorge Dam may induce earlier first hatching of smallmouth bass and enhance reproductive success in the Green River without additional suppression actions. Predicted total length (TL) of age-0 smallmouth bass in mid-September and summer growth rates were strongly influenced by timing of hatching (cohort), summer water temperature, and first hatching date, with minor reach effects. We used TL in mid-September as an endpoint for predictions because that was typically when smallmouth bass growth slowed or ceased due to declining water temperatures. Early hatched smallmouth bass in warm years with long growing seasons were the largest and fastest growing (e.g., Cohort 1 in 2007) and late-hatched bass in cool years with shorter growing seasons were the smallest and slowest growing (e.g., Cohort 3 in 2011). Contrary to some published literature, TL was longest and growth was fastest for earliest hatched smallmouth bass in a year, because bass had longer to grow and water temperatures were warmest. Growth rates calculated over fixed periods averages over the substantial variation during smallmouth bass early life, slowest just after hatching, and increasing over time, so caution is urged when interpreting growth rates calculated in that manner. Enhanced understanding of smallmouth bass ecology in the upper Green River basin should guide efforts to disrupt spawning and hatching and reduce recruitment of this invasive predaceous species. Management actions such as abrupt flow increases (managed floods or flow spikes), reduced water temperatures, or physical disturbances directed at spawning smallmouth bass may reduce reproductive success but those actions need to consider effects on other native and non-native fishes as well as water availability tradeoffs. We offer recommendations for flow management or other disturbances relative to timing within a

year for smallmouth bass disturbance flows, as well as how other flow management activities could be temporally staggered within a single year to benefit native fishes. Increased use of flow and water temperature regimes from dams to reduce negative effects of non-native fishes, and to increase growth and survival of native fishes, is advocated as a viable use of reservoir water storage and may offer management agencies another tool to achieve a more naturally functioning river ecosystem and enhance recovery of native biota.

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KEY WORDS

Invasive species, river regulation, Yampa River, Green River, Flaming Gorge Dam, otolith analysis, aging, hatching date distributions, population control, smallmouth bass

INTRODUCTION

Humans have facilitated introduction and establishment of many invasive species, sometimes via well-intentioned and purposeful actions. However, such introductions often result in a subsequent need to reduce negative effects of invasive biota on native taxa (Kolar and Lodge 2002; Lodge et al. 2006; Vander Zanden and Olden 2008). One such species is predaceous smallmouth bass *Micropterus dolomieu*, which has been introduced across much of the globe primarily for recreational fisheries. A note published in 1970 presented useful information on reproduction and growth of smallmouth bass (Turner and MacCrimmon 1970), and suggested a justification for the study as follows: "Because of worldwide interest in extending the world distribution of smallmouth bass (*Micropterus dolomieu*) to provide sports fisheries, documentation of the biology of a self-sustaining population of the species….. should prove useful for persons considering introductions….". Indeed. Forty-three years later, Loppnow et al. (2013) reported widespread smallmouth bass populations established throughout most of North America, including Mexico, as well as in Europe, Africa, and portions of Southeast Asia and Japan, summarized the negative impacts to native ecosystems, and reported the history of mostly ineffectual control techniques. They emphasized that management agencies have been mostly unsuccessful controlling invasive populations, that eradication has not been successful even when expensive and intensive techniques were used, and that an important part of control should emphasize efforts to "prevent *M. dolomieu* (re)introduction". Similar to Turner and MacCrimmon (1970), we also report on smallmouth bass reproduction and growth, but with the purpose of understanding effects of various degrees of river flow regulation on smallmouth bass hatching and early growth. This information may be useful to identify opportunities to effect control of smallmouth bass via disadvantaging the reproductive success of this invasive taxon in the endangered-species-rich upper Colorado River basin.

Describing patterns of reproduction of fishes and their early life stage ecology is useful to understand population dynamics of juveniles and adults, because the strength of reproduction in a year often drives abundance of subsequent life stages (Thorson 1950; Shepherd and Cushing 1980; Roughgarden et al. 1988; Bestgen et al. 2006a; 2007a). This may be particularly true when attempting to disadvantage populations of invasive species that are having an undesirable effect on native taxa. Such approaches are needed in rivers of the western US where introduction and establishment of non-native fishes is a major threat to conservation of native fish assemblages (Minckley and Deacon 1968; Moyle et al. 1986; Carlson and Muth 1989; Minckley and Deacon 1991; Muth et al. 2000; Olden et al. 2006; Lawrence et al. 2014; Lawrence et al. 2015). In the Colorado River basin, non-native fish invasions began over 100 years ago, with introduction of channel catfish *Ictalurus punctatus*, common carp *Cyprinus carpio*, salmonids, and continued more recently with introductions of small-bodied species such as red shiner (Vanicek et al. 1970; Holden and Stalnaker 1975a and 1975b), each with documented negative effects on native fishes (Dill 1944; Minckley 1983; Haines and Tyus 1990; Dunsmoor 1993; Ruppert et al. 1993; Muth and Snyder 1995; Bestgen et al. 2006a, Markle and Dunsmoor 2007; Yard et al. 2011). Non-native piscivores such as smallmouth bass and northern pike *Esox lucius* have also established in the upper Colorado River basin and are now common in certain reaches, including the lower Yampa River, the upper and middle Green River basins, and the upper Colorado River (Wick et al. 1985; Bestgen et al. 2006b; Johnson et al. 2008; Breton et al. 2013; Breton et al. 2014; Breton et al. 2015; Zelasko et al. 2015; 2016 in press).

The predatory threat of invasive and large-bodied piscivorous taxa such as northern pike and smallmouth bass in the upper Colorado River basin is substantial. For example, based on results of a bioenergetics model, Johnson et al. (2008) ranked smallmouth bass as the most problematic invasive species because of their high abundance, habitat use that overlaps with most native fishes, and ability to consume a wide variety of life stages of native fishes (Bestgen et al. 2008). Expanded populations of piscivores such as smallmouth bass are a major impediment to conservation actions aimed at recovery efforts for the four endangered fishes in the upper Colorado River basin: Colorado pikeminnow *Ptychocheilus lucius*, razorback sucker *Xyrauchen texanus*, humpback chub *Gila cypha*, and bonytail *Gila elegans* (U.S. Fish and Wildlife Service 2002a, b, c, d). In response to the predatory threat posed by non-native smallmouth bass, the Upper Colorado River Endangered Fish Recovery Program (Recovery Program) initiated efforts to control them via mechanical removal in affected stream reaches. Results to date show a downward trajectory of smallmouth bass density due to removal, as well as environmental factors that reduce reproduction and abundance (Breton et al. 2014). However, additional means of control are needed because effects of mechanical removal are short-term, limited in geographic area, and relatively expensive, and even single years of favorable environmental conditions for reproduction and recruitment – low and early spring snowmelt runoff and long summers with warm water temperatures – can negate several years of control efforts (Loppnow et al. 2013; 2014; Breton et al. 2014; Breton et al. 2015).

It is well-established that increased flows during or shortly after smallmouth bass spawning and hatching reduce their reproductive success in streams (Larimore 1952; 1975; Pflieger 1966; 1975; Reynolds 1990; Reynolds and O'Bara 1991; Lukas and Orth 1995; Peterson and Kwak 1999). Flow disturbances alter spawning and guarding behavior of adult smallmouth bass, physically sweep eggs and weak-swimming larvae from nests (Winemiller and Taylor 1982, Orth and Newcomb 2002), and associated increased turbidity reduces feeding success of young (Larimore 1975, O'Brien and Showalter 1993). Thus, one means to reduce smallmouth bass abundance in the upper Colorado River basin may be to disrupt reproductive success of smallmouth bass. Using a simulation model parameterized with smallmouth bass early life history information that was similar to Loppnow and Venturelli (2014), Breton et al. (2015) found that disrupting the earliest hatching cohorts of smallmouth bass was among the most effective means to reduce their abundance in the Yampa River. Specifically, physical nest disturbance via removal of guarding males may be effective to reduce survival of newly deposited eggs or just-hatched larvae (Winemiller and Taylor 1982). Flow disturbance may be another means to disrupt reproduction on a larger scale with fewer person-hours and could be implemented by releases of short-term flow spikes in flow-regulated river reaches such as the Green River downstream of Flaming Gorge Dam where smallmouth bass now exist. However, a better understanding of smallmouth bass early life history, including predictions of timing and duration of reproduction, and patterns of growth and survival of young, would be useful to implement well-timed management actions to reduce reproductive success and recruitment of smallmouth bass (Winemiller and Taylor 1982; Graham and Orth 1986; Ridgway and Friesen 1992; Jager et al. 1993; Knoteck and Orth 1998; Smith et al. 2005; Loppnow et al. 2013; Breton et al. 2014).

Here, we describe timing and patterns of hatching of smallmouth bass in the free-flowing Yampa River, as well as fully dam-regulated and partially regulated sections of the Green River, in the upper Colorado River basin, particularly related to flow and water temperature regimes.

Those river reaches are geographically proximal and thus, act as a natural laboratory to observe effects of various environmental variables within a year on smallmouth bass reproduction and growth. We further describe length and growth patterns of age-0 smallmouth bass across years with different hydrologic and water temperature conditions. This information may be useful to managers who seek to reduce distribution and abundance of smallmouth bass, which may aid recovery efforts for native and endangered fishes in the upper Colorado River basin.

STUDY AREA

The Yampa River drains mountainous and high desert portions of south-central Wyoming and northwestern Colorado and is the largest tributary of the Green River (Figure 1). The mainstem Yampa River flows west from near Steamboat Springs, CO, downstream to the Green River confluence in Dinosaur National Monument. The main study reach was in the vicinity of Little Yampa Canyon (LYC), just downstream of Craig, Colorado (Reach 1). In the late summer and autumn low-flow sampling season, habitat consists mostly of low-velocity runs or pools separated by shallow, higher-velocity riffles. Substrate is typically a mix of boulder, cobble, gravel, and sand in low velocity areas, and cobble and gravel in riffles. Backwaters and isolated pools of varying depths are created mostly by cutoff high-flow side channels and contain cobble, gravel, and fine-grained substrate.

The Green River basin drains mountainous and high desert portions of southwestern Wyoming, eastern Utah, and northwestern Colorado (Figure 1) and is the largest tributary of the Colorado River. The study area encompassed two reaches of the Green River in Dinosaur National Monument and one reach of the Yampa River that has its confluence between the two Green River reaches. The Lodore Canyon reach of the Green River upstream of the Yampa River (Reach 2) is completely regulated by upstream Flaming Gorge Dam, while regulation effects in the reach downstream in Whirlpool Canyon and Island-Rainbow parks (Reach 3) are partially attenuated by contributions from the free-flowing Yampa River (Sabo et al. 2012). The Green River downstream of Flaming Gorge Dam flows for 22 km through Red Canyon, enters the 48-km-long, low-gradient Browns Park valley, and then flows for 32 km through high-gradient Lodore Canyon before entering Echo Park at the Yampa River confluence. In Lodore and Whirlpool canyons, the Green River is generally confined to a mostly single, relatively narrow channel with occasional low velocity side channels. Canyon river reaches constricted by debris fans form riffles and rapids with cobble and boulder substrate. These river reaches generally have higher current velocities and deeper runs and pools than lower gradient areas without debris fans; low velocity habitat typically consists of cutoff secondary channels associated with sand bars that sometimes serve as smallmouth bass spawning areas.

Flows and water temperatures during the study period were generally low but variable, with the lowest flow and warmest water temperatures in 2007 and 2012 and the highest flow and coolest water temperatures in 2011, the second highest peak flow on record since 1904 for the Yampa River (USGS gauge # 09251000). Annual days of flow during spring runoff > 8,000 ft^3/sec range from 0 (2007) to 62 (2011) in the Yampa River. During the study period, the relatively unregulated Yampa River exhibited greater spring peaks but lower summer baseflows than the Green River upstream of the Yampa River (Figure 2). During the period 1963 to 2014, the maximum mean daily flow in the Yampa River was 33,200 ft^3/sec (1984), but baseflows were often < 500 ft^3/sec and sometimes < 50 ft^3/sec in late summer (U. S. Geological Survey Gauge 09251000 Maybell, CO). Water temperatures in the Yampa River from April-September were typically lowest in spring due to cool ambient air temperatures but by summer were warmer than the regulated portion of the Green River, sometimes by as much as 3°C, during a main portion of the smallmouth bass summer growing season.

Green River flows upstream of the Yampa River are almost wholly controlled by releases from Flaming Gorge Dam, and are higher in spring due to releases made for downstream floodplain inundation to benefit native fishes (Muth et al. 2000; Bestgen et al. 2011) and channel maintenance (Figure 2). Annual peak flows from Flaming Gorge Dam in the study period ranged from about 4,300-8,600 ft^3/sec but since they were timed differently and were usually of relatively short duration, flow peaks in the Green River downstream of the Yampa River are smoothed out in the hydrograph. Green River summer baseflow releases from Flaming Gorge Dam were lower than spring peaks but much higher than baseflows in the Yampa River. Water temperatures in the Green River upstream of the Yampa River were warm in spring relative to the unregulated Yampa River, but were cooler than the Yampa River in summer because releases were relatively high and did not warm quickly and water temperatures were controlled at the dam by water intake elevation and generally limited to about 13-15°C (Figure 2).

The Green River downstream of the Yampa River exhibited traits of both regulated and unregulated regimes but at different times. This was because flows of the Yampa River dominated downstream Green River flows in spring, but in later summer until the subsequent spring, baseflows from Flaming Gorge Dam accounted for most of the flow, thus, the partially regulated nature of that reach. Water temperatures in the Green River downstream of the Yampa River were warmest of any reach in spring and early summer due to the downstream location, lower elevation, and warmer air temperatures. However, by mid-summer after peak flows declined and releases from Flaming Gorge Dam made up most of the flow, water temperatures there were cooler than the Yampa River due to the preponderance of cooler regulated reach Green River water. Thus, during the smallmouth bass summer growing season, the Yampa River was the warmest reach, followed by the Green River downstream of the Yampa River, and the coolest reach was the Green River upstream of the Yampa River.

The fish assemblage of the Yampa River was historically composed of 12 native species and today, four of those are federally listed as endangered and another two are listed as species of special concern by the State of Colorado (Bestgen 2015). The downstream-most 80-km reach of the Yampa River is designated as critical habitat for all four of the endangered fishes, and Colorado pikeminnow critical habitat extends upstream to about RK 225 near Craig, CO (Figure 1). Many nonnative fishes have been introduced and several provide recreational fisheries. Channel catfish were introduced into the basin in 1892 and have been abundant in the Yampa River for decades (Holden and Stalnaker 1975b; Tyus and Nikirk 1990). Northern pike were first stocked in the Yampa River basin in 1977 (Hawkins et al. 2005) and were widespread in the main-stem Yampa River beginning in the mid-1980s (Tyus and Beard 1990). Smallmouth bass were introduced into the basin in the late 1970s, when they were stocked into Elkhead Reservoir (on Elkhead Creek, a Yampa River tributary; P.J.M., unpublished data). Smallmouth bass were rarely found in the Yampa River until the early 1990s (Tyus et al. 1982; Nesler 1995), when a rapid drawdown of Elkhead Reservoir in the winter of 1991–1992 introduced many into the river (Martinez 2003). Several subsequent years of low river flows, which were probably favorable for recruitment, were thought to have increased the primarily downstream distribution and abundance of smallmouth bass. By 2003, smallmouth bass were detected near the confluence of the Green and Yampa rivers, and bass have subsequently spread upstream and downstream of there, and are considered abundant in most Green River reaches except the lowest 193 RK or so. As a result of widespread establishment in the Yampa and Green rivers, intensive, multi-agency mechanical removal efforts are conducted annually to remove non-native piscivores including northern pike and smallmouth bass from the upper Green River basin, including in the Yampa River (Breton et al. 2014; Zelasko et al. 2015; in press). Removal efforts are partially effective in terms of achieving relatively high annual removals, but recruitment and dispersal from other areas limits the long-term efficacy of control programs at this time. Other studies that focus on means to reduce recruitment and source populations are ongoing. Additional information about the introduction of smallmouth bass to the Yampa River and their subsequent dispersal in the Green River basin is found in Johnson et al. (2008), and Breton et al. (2013; 2014; 2015).

METHODS

Yampa River.—Small-bodied age-0 smallmouth bass were captured during electric seine sampling in Little Yampa Canyon, a 38 river km (RK) reach that has an associated long-standing smallmouth bass removal sampling effort (Bestgen et al. 2006b; Hawkins et al. 2009; Breton et al. 2013 and 2014). Smallmouth bass removal sampling occurred from 2003-2011 in the 19 RK treatment reach; there was also an adjoining 19 RK upstream control reach where no bass were removed. Age-0 smallmouth bass were sampled from a mix of habitat types including backwaters, eddies, pools, riffles, runs, pools isolated from the main channel (not used in analyses), and low velocity shorelines of pools and runs, the most common habitat. The number of channel area types sampled was about proportional to their availability.

Green River.—Low-velocity channel margin habitat in the Green River in Browns Park and Lodore Canyon (upstream of the Yampa River) and Whirlpool Canyon and Island-Rainbow parks (downstream of the Yampa River) were sampled with seines (1.3 and 4.6 m length, 1.6 and 4.7-mm mesh size, respectively). Seine sampling was conducted in summer and autumn each year from 2003 to 2011 (Bestgen et al. 2006b; Bestgen et al. 2007b; Bestgen et al. 2008). Habitat types sampled were mostly backwaters, but channel margin eddies, low velocity runs and pools, and a few riffles were also sampled. More effort was expended in larger habitat areas and less in smaller ones so that the proportion of each habitat type sampled was approximately equal. Smallmouth bass from all habitat types and reaches were preserved separately in samples in 95% ethanol to maintain otolith integrity, and processed at the Larval Fish Laboratory, Colorado State University.

Age-0 smallmouth bass hatching, age, and growth.—To obtain more information about smallmouth bass ecology in the study area, we undertook studies of otolith micro-increment structure (Hill and Bestgen 2014). Ten or more small bass were randomly selected from the series of ethanol-preserved samples collected throughout summer and early autumn from the Yampa River; we also selected the largest and smallest bass specimens from samples in an attempt to bracket the earliest (typically the largest fish) and latest (smallest fish) portions of the spawning season. Most small bass captured from the Green River were used in this analysis because small bass were mostly only available from the Green River upstream and downstream of the Yampa River from two week-long sampling trips, one in summer (mid to late July) and one in autumn (mid to late September). We chose more specimens of smallmouth bass from the largest collections, to represent the highest abundances of the season, and attempted to age 100 or more bass from each of the three reaches in each year. Variable-sized cohorts, or recently established populations (e.g., Green River 2003-2004), sometimes prevented us from obtaining 100 bass samples.

We measured each fish with electronic calipers to the nearest 0.01 mm TL. Both left and right sagittal otoliths were extracted and mounted on separate microscope slides (Stevenson and Campana 1992). Otoliths were fixed to the slide with cyanoacrylate glue that bonded to glass and were then ground and polished using lapping film (0.3-12 micron grit size). A compound microscope fitted with a calibrated ocular micrometer was used to measure maximum diameter of each sagittae, typically from the tip of rostrum to the post-rostrum (Stevenson and Campana 1992). Core diameter was measured at 320x magnification, and was the maximum diameter of the first distinct and dark band surrounding the primordia. Counts of otolith microincrements were at 320x; immersion oil placed on the otolith increased increment clarity and otolith readability. Increments were counted in the sagittal plane of each otolith with one increment consisting of one light band and one dark band (the L-zone and D-zone, after Kalish et al. 1995), using modifications for increment counts suggested by Hill and Bestgen (2014). Increment counts were verified with a second reader. In general, otolith increments were obvious and easy to read and were counted with high accuracy and precision, based on known-age laboratory reared fish.

Smallmouth bass hatching dates were derived by subtracting estimated age in days from the date of capture. Hill and Bestgen (2014) verified that the first daily increment was deposited at hatching, and that a 1:1 relationship existed between age in days and otolith microincrement count. Thus, increment counts directly correspond to age in days post-hatching.

Fish growth rate was estimated by subtracting length at hatching (mean of 5.5 mm TL, see Hill and Bestgen 2014) from length at capture, and dividing by age in days. Importantly, this growth rate is the average rate for the entire period of time from hatching until capture. In other words, growth rates simply reflect the average change in length rather than growth specific to early or late periods. Time-period-specific growth rates, such as immediately after hatching, would require measurement of increment widths near the otolith core, and also assumptions about proportional relationships of increment width to growth, which is often unreliable (Bestgen and Bundy 1998). Regardless, smallmouth bass samples collected in earlier, relatively warm portions of the growing season such as August would reflect growth in a mostly warm period; the relatively slow growth of early hatching fish in cooler water would be factored into that growth rate. Growth of smallmouth bass collected later in the season (September) would reflect all seasonal changes in water temperature and potentially growth, including the warm summer as well as cooler early autumn temperatures. We avoided using fish from samples collected after mid-September because water temperatures were cooler and reduced fish growth, and would not accurately represent growth rates calculated in the manner we used. Even though otolith increments were visible and relatively easily counted even when water temperatures cooled (< 15°C or so), fish growth was minimized. Thus, minimal changes in length of a fish living in relatively cold water that continued to add days in age resulted in reductions in growth rates when calculated in this manner. Choosing a standard endpoint of mid-September (13 to 23 September across years) when water temperatures were still relatively warm reduced effects of cooler water temperatures in later autumn, when otolith increments of bass were closely spaced and more difficult to observe. Smallmouth bass otolith increments were very difficult to discern when mean daily water temperatures dropped below 10°C.

A main goal of this project was to be able to predict timing of smallmouth bass hatching under variable environmental conditions so that management actions to reduce reproductive success could be implemented. To accomplish this, we plotted hatching dates of smallmouth bass as a function of flow and water temperature patterns, and looked for univariate patterns in those relationships. We also fit general linear models (GLMs) to predict date of first smallmouth bass hatching in each reach and year (2005-2011, with addition of year 2004 in the Green River downstream of the Yampa River) as a function of various flow, water temperature, and timing variables (Appendix I). First hatching date for smallmouth bass in a reach was determined as above and adjusted as the number of days since 1 January (Julian date). For example, first smallmouth bass hatching on 15 June would translate to a first hatching Julian date of 166 days. The 29 February day in leap years was ignored for consistency. We used River Reach (Yampa River, Green River upstream of the Yampa, and Green River downstream of the Yampa River) in GLMs to understand variation in first hatching as a function of reach effects independent of environmental factors, and assumed those first hatching dates were independent among reaches. They were in fact not independent because timing of hatching was often affected by the same variables across reaches. For example, smallmouth bass in all reaches hatched late in the high flow and cold year 2011 and earlier in the low flow and warm year 2007. However, we assumed independence because we wanted to understand differences among effects on first hatching date among reaches that may be a function of partial or full flow regulation (e.g., Green River reaches) compared to an unregulated setting (Yampa River), and whether those differences were important. Additional covariates included: maximum mean daily spring peak discharge (Maybell, Colorado gauge for the Yampa River, Greendale, Utah gauge for the Green River upstream of the Yampa River, and the Jensen gauge for the Green River downstream of the Yampa River), mean discharge (same gauges as above) and water temperature (Yampa River at Juniper Springs, Green River just upstream of the Yampa River, and Green River in Mitten Park, U. S. Fish and Wildlife Service gauges, http://www.fws.gov/mountain-prairie/riverdata/temperatures.html) for the 5-day period centered on first hatching date, and Julian day when mean daily water temperature in the post-peak flow period first exceeded 16°C (prior to first hatching in all but one year). Degree-day metrics included annual degrees days and post-peak degree days, which were calculated as the sum of mean daily water temperatures beginning either 1 January, or the day after the annual spring peak flow (same gauges as above) until the first hatching day, respectively. We also used a reach-specific high flow days metric, which likely reflected both flow magnitude and duration. We used days of flow > 8000 ft^3/sec during the spring snowmelt runoff period for the Yampa River, because that flow value was well above the typical mean spring runoff flow level, and the high flow day values ranged from 0 in the low flow year 2007 to 62 days in the high flow year 2011. Flow day metrics based on 6,000 or 10,000 ft^3/sec flow levels often had an excess of 0 days (the 10,000 ft^3/sec metric) or an extremely wide range of values (6,000 ft^3/sec). That 8,000 ft^3/sec metric, based on data presented here, was also used to successfully predict first spawning of smallmouth bass in the Yampa River and to parameterize a bass population dynamics model (Breton et al. 2015). In the regulated reach of the Green River upstream of the Yampa River, which had lower peak flows because of storage of some spring runoff in Flaming Gorge Reservoir, a reasonable metric was the number of days when peak power plant flow releases exceeded 4,300 ft^3/sec, an approximate maximum release commonly made in lower flow years and historically (4,300-4,600 ft^3/sec). The high flow days metric for the Green River downstream of the Yampa River was 12,300 ft^3/sec, the sum of the flows from the two upstream reaches. The number of days post-peak was directly calculated for the Yampa River and the Green River downstream of the Yampa River as the number of days following maximum mean daily peak flow in a given year to the day of first smallmouth bass hatching. The number of days post peak flow in the regulated Green River required different treatment because high flow releases of the same magnitude were often made for many and often, consecutive days. In that situation, the last day of the obvious spring peak flow release period (a flat, relatively high, and steady flow rate) was used as the beginning of the period to calculate the days post-peak metric. Minor variations in flow releases during the peak flow period (200-300 ft^3/sec) were ignored when determining the beginning of the post-peak flow period for the regulated Green River reach. In at least one year (2011), peak releases of about 9,000 ft^3/sec declined to a lower power plant level and remained there for several days; the date when flow declined from the higher peak was used. A final covariate calculated to predict smallmouth bass hatching dates was the April-July flow volume, a value used by river flow forecasters and modelers, to predict dam operations and water yields for runoff periods. Daily flow volume was calculated for the Yampa River and the Green River upstream of the Yampa River (same gauges already detailed) by multiplying the mean daily flow for each day in the April to July period by 1.9835, and summing those daily values over the 122 d period, to yield volume in acre-feet. Flow volume for the Green River downstream of the Yampa River was simply the sum of the two values for that day. We fit a separate GLM for first hatching date of smallmouth bass as a function of April-July flow volume, which was specifically for use by managers interested in modeling effects of flow spikes to disadvantage smallmouth bass, and how those releases may affect reservoir water supplies. We did not fit a year effect in GLMs, even though hatching dates (and growth and length) varied among years, because we were interested mainly in assessing effects of environmental variables on first hatching, total length, and growth, independent of year. We used Akaike's Information Criterion (AIC) to guide selection for GLM models in this report, where we focused on predictor variables that were known prior to first hatching of smallmouth bass (spring peak flow metrics) or could be approximated when predictions were needed (post peak flow but prior to first hatching, to guide management of disturbance event timing), based on trends in temperatures (days post-peak flow, or degree days post peak). We chose not to use spring peak runoff because of the regulated nature of the upstream Green River reach, instead using the number of high flow days metric as a variable to portray magnitude and duration of flows.

We also fit GLMs to understand effects of date of first smallmouth bass hatching in a reach (Jdays), length of growing season (days), hatching cohort (Cohort 1= early third of season, Cohort 2= middle third of season, Cohort 3 = late third of season), river reach (Yampa River, Little Yampa Canyon; Green River in Lodore Canyon upstream of the Yampa River; Green River in Whirlpool Canyon and Island-Rainbow parks downstream of the Yampa River), average water temperature experienced by that cohort, and mean water temperature from 1 July to 15 August (Julytemp; same for each cohort, and thought a surrogate for water temperature conditions that year) on TL of smallmouth bass collected in mid-September in all three reaches, 2005-2011. A similar analysis was conducted to predict growth rates of smallmouth bass (TL change post-hatching until mid-September/number of days = growth/day in mm), but only for the Yampa River where such an analysis was useful for other modeling and where data was available for fish from every cohort. Water temperature data for the Yampa River were from near Maybell, CO, and for the Green River were from Lodore Canyon (just upstream of Yampa River) and Mitten Park (just downstream of the Yampa River; all water temperature monitoring sites were within the study areas for each river so represent well thermal regimes and all data were from http://www.fws.gov/mountain-prairie/riverdata/temperatures.html).

The three cohorts of age-0 smallmouth bass for each year were derived by dividing the distribution of hatching dates for each year and river reach into equal thirds through time, and calculating the mean TL and mean growth rate of fish in each. Cohort 1 contained the earliest hatching fish, Cohort 2 contained fish hatched in the middle of the season, and Cohort 3 fish that hatched latest in the year. We used the cohort approach to simplify growth rate calculations, rather than calculate and predict bass growth for every day of the hatching season. We also found the cohort concept useful to streamline analysis and discussions about how management actions might affect smallmouth bass survival. In other words, it was easier to convey for example, that a flow spike might affect certain cohorts (qualitatively early or late) of smallmouth bass rather than bass hatched on a certain range of dates, especially when those dates change among years contingent on river regimes in that year. We used mid- to late-September samples only for TL and growth rate analyses because we typically had samples available at that time and because water temperatures were declining, such that most annual growth would be realized by then. Use of only mid- to late-September samples standardized the end dates of samples so that summer effects of various growth environments would be estimated consistently.

RESULTS

A total of 3,253 age-0 smallmouth bass were aged using otolith daily increments from 2003-2011 (Table 1). Sample size for early years of Green River smallmouth bass collections was small owing to recent colonization by bass (2002 or 2003, unpublished data, KRB) and restricted early distribution and abundance in that system. Samples were larger in the Yampa River than the Green River, and nearly 2/3 of all smallmouth bass aged in this study were from the former. In general, sample sizes reflected abundance of smallmouth bass in each river and year. Thus, because fewer smallmouth bass were available from the Green River, we analyzed most of those specimens for age and growth information. In contrast, subsampling was needed for the more abundant Yampa River smallmouth bass population, as many hundreds or even thousands of smallmouth bass were collected each year.

Distributions of hatching dates, Yampa River.—First hatching of smallmouth bass in the Yampa River was closely associated with warming water temperatures following spring runoff flows that were declining from peak (Table 2, Figure 3). First hatching dates among years varied widely from 12 June (2007) to 16 July (2011), with a mean of 27 June and a relatively narrow range of 35 d (Table 3). First hatching dates were closely linked with the first day that mean daily water temperature exceeded 16°C each year (Table 4, Figure 4); the mean number of days after water temperatures first reached 16°C that smallmouth bass first hatched was 4 (-1 to 10 days after) and in most years first hatching was the day after that threshold temperature level was reached. First hatching dates for Yampa and Green River smallmouth bass were also closely related to annual or post-peak degree day metrics of water temperature. First spawning dates would be 4-5 d before first hatching dates, based on observations of hatching times of eggs (Hill and Bestgen 2014).

Flow level each year was also linked with hatching date in the Yampa River; mean flow at first hatching for smallmouth bass in the period 2005-2011 was 3907 ft^3/sec (2990-5350 ft^3/sec), with lower flows in warm and early runoff years (2007) and higher flows in cooler and later runoff years (2011). First hatching date for smallmouth bass in the Yampa River was positively associated with number of high flow days > 8000 ft^3/sec in the Yampa River spring runoff season in the period 2005-2011 (Figure 4). For example, in 2007 when there were no runoff days > 8,000 ft^3/sec, first hatching date for smallmouth bass in the Yampa River was 12 June. Conversely, in 2011 when there were 60 days of flow > 8,000 ft^3/sec and water temperatures were colder, first hatching was 35 days later on 16 July. Date of first hatching of smallmouth bass in the Yampa River, and both reaches of the Green River, were only weakly and inconsistently correlated with water temperature during the hatching season (Appendix II).

The distribution of hatching dates of smallmouth bass in the Yampa River was typified by a few early fish, increased until hatching peaked in mid-season, and ended with a few fish, resulting in mostly bell-shaped distributions (Figure 3, upper panels). Mean time from first hatching until peak hatching was 13 d (7-19 d). Flow levels of the Yampa River typically declined to < 1,500 ft^3/sec by the time Cohort 1 bass finished hatching, a key flow level below which boat navigation and sampling was increasingly difficult in the Yampa River.

Hatching season durations for smallmouth bass in the Yampa River and both reaches of the Green River were variable at 19-39 days (Appendix III). Hatching typically ended by mid-July to early August, although in 2011, hatching ended in mid-August. Hatching season duration was only weakly (always slightly negative) related to hatching onset date. Similarly, the duration of the hatching season for smallmouth bass in the Yampa River and both reaches of the Green River was only weakly and inconsistently related to mean water temperature during the hatching season (Appendix IV).

Distributions of hatching dates, regulated Green River.—First hatching detected for smallmouth bass in the regulated Green River upstream of the Yampa River was always after Flaming Gorge Dam releases had declined to the stable summer baseflow and water temperatures were above the mean daily 16°C threshold level for several days (Figure 3, Table 4). Mean first hatching date over the study period was 27 June, identical to the Yampa River, and 2 days later than in the Green River downstream of the Yampa River. First hatching dates for regulated reach Green River smallmouth bass averaged 8 days (4-14 days) after the first day that mean daily water temperature exceeded 16°C (Figure 4). First hatching occurred after baseflows began regardless of timing of baseflow onset. Post-baseflow hatching began as early as 9 June (2007) and as late as 2 August (2011), a wide range of 64 days, and nearly twice that of the Yampa River in 2011 (Table 3). Late spawning in 2011 indicated the role that high flow can have on delaying spawning, because water temperatures had warmed well above 16°C earlier in the year but hatching (spawning) did not occur until baseflow was achieved.

First hatching date for smallmouth bass in the regulated Green River reach was positively associated with number of high flow days > 4300 ft^3/sec in the spring runoff season in the period 2005-2011 (Figure 4). Notably, in all but one year, first hatching date was in a narrow range of 21-23 days after peak flows began to decline. Only in 2009 was it different at 42 days.

First hatching of smallmouth bass in the Green River upstream of the Yampa River also occurred over a relatively narrow flow range; mean flow level at first hatching was 1663 ft^3/sec (1040-2490 ft^3/sec), with lower flows in warmer and earlier runoff years (2006, 2007) and higher flows in cooler and later runoff years (2011).

Similar to the Yampa River, distributions of hatching dates of smallmouth bass in the Green River upstream (and downstream) of the Yampa River typically began with a few fish, peaked in mid-season, and ended with a few fish. However, the fewer Green River samples collected over relatively short sampling periods often resulted in gaps or multiple peaks in the distributions of hatching dates. Mean time from first hatching to peak hatching was 7 days (0-20) in the regulated reach of the Green River.

Distributions of hatching dates, partially regulated Green River.—First hatching detected for smallmouth bass in the partially regulated Green River downstream of the Yampa River occurred at much higher flows but more moderate water temperature levels compared to the two other upstream reaches (Figure 3, Table 4), and averaged two days earlier (mean = 25 June, range = 4 June-28 July). The range of first hatching dates across years was 54 d, intermediate between the shorter period for the unregulated Yampa River and the longer period for the regulated Green River reach. Water temperatures were higher at first hatching as well, and were warmer than the upstream regulated Green River at this time of year (Figure 2); water temperatures in the Green River downstream of the Yampa River were typically cooler than the Yampa River later in summer but warmer than in the regulated Green River reach upstream of the Yampa River.

First hatching dates for smallmouth bass in the Green River downstream of the Yampa River averaged 12 d (6-24 d) after mean daily water temperature exceeded 16°C, which was 4 d later than the mean for the upstream Green River reach and 8 d later than the Yampa River. Thus, successful first hatching was relatively late given the warm early water temperatures and suggested other factors may have inhibited early successful spawning and hatching. The pattern of progressively earlier attainment of the 16°C threshold for the Yampa, the regulated Green River reach, and the partially regulated Green River reach can be viewed in the hatch date distributions for each year. In comparison, first hatching in the distributions of hatching dates began on relatively similar dates, with the downstream-most site, the partially regulated Green River, being only slightly earlier in most years than the upstream-most Yampa River. This portrays the relatively stronger influence of the 16°C threshold upstream than downstream.

In contrast to the low and stable baseflows of the Green River upstream of the Yampa River at first hatching, flows in the downstream Green River were high and variable. There, first hatching of smallmouth bass occurred at mean flow of 8,294 ft^3/sec (4,790-10,900 ft^3/sec). Regardless, first hatching date for smallmouth bass in the partially regulated reach of the Green River was positively associated with number of high flow days > 12,300 ft^3/sec in the period 2004-2011 (Figure 4). Similar to other reaches, we do not know if smallmouth bass spawned earlier in the downstream portion of the Green River and none of those offspring survived, or if documented first hatching indicated first reproduction in that year. Higher flow levels in the Green River may inhibit successful reproduction by eliminating low velocity spawning habitat.

General linear models to predict smallmouth bass hatching.—We fit several GLMs using a variety of environmental variables, to predict timing of first smallmouth bass reproduction among the three reaches. The top model indicated by AIC had five variables and included flow magnitude the day of first hatching, a variable that would be difficult to determine accurately if predictions were needed prior to hatching occurring. That model was only marginally better (< 1 AIC point) than the second-ranked model ($p < 0.00001$, $R^2 = 0.98$), which had four environmental covariates: days of high flow during the runoff period; # days post-peak flow, onset of the first day that mean daily water temperatures exceeded 16°C, and number of degree days post peak, with only the flow magnitude at hatching variable as different. Because this model was more easily used and interpreted, we chose it as our top model (Tables 5 and 6).

All four individual covariates were positively correlated with hatching date and indicated that hatching (and spawning) occurred later in higher or extended flow years, and was closely associated with reaching the threshold 16°C water temperature. The positive association of hatching date with number of days post peak flow and degree days post-peak also indicated that as time extended from the peak period and as water warmed, hatching was more likely to occur. The negative coefficient for the number of days post-peak variable in the GLM likely was a result of the positive associations being accounted for in model variation by the other three variables. Predictions would thus be adjusted backwards as the number of days post-peak extended further into the summer season.

The GLM to predict hatching date as a function of April-July volume was fit with an interaction term for river reach. Thus, predictions can be tailored for each study area. Model fit remained substantially high ($df = 3, 18$; $F = 33.58$; $p < 0.00001$, $R^2 = 0.85$, Table 7) with just the single predictor variable, albeit slightly lower than for the four-variable model.

Smallmouth bass TL and growth.—In a typical water temperature year such as 2008 (albeit a slightly shorter than average growing season) or warmer years, smallmouth bass in the Yampa River grew quickly in summer. This was particularly true in July and early August (5-12 August samples), when 20-35 day-old fish were 23-51 mm TL (Figure 5) and grew 1.0-1.7 mm TL/day. The slightly higher slope for the age-length relationship in early August also suggested faster growth then compared to later periods. Fish continued to grow quickly through August and early September, but by mid-September (17-23 Sept. samples) and later, mean lengths and ranges of lengths of age-0 smallmouth bass were largely unchanged, indicating growth had stopped. Mean daily water temperature for the period just prior to growth cessation (13-17 September, 2008) was 16.6°C, and suggested a minimum threshold temperature for growth (see also Shuter et al. 1980, their Figure 7).

Size range of age-0 smallmouth bass varied widely in individual samples throughout the summer and early autumn. For example, in samples collected from 3-9 September 2008, the largest bass were nearly three times longer than the shortest bass. In general though, smallmouth bass grew at a relatively consistent rate, given that lengths of fish in samples collected at regular but relatively closely-spaced intervals, belonged to largely identifiable groups through time. In other words, there was little overlap of bass lengths from samples, which one would not expect if bass growth was highly variable.

The model to predict smallmouth bass TL in mid-September by reach (R^2 = 0.92) included effects for Cohort, Julytemp, Julytemp^2, Jdays, and Reach (Table 8):

$$\text{TL (mm)} = 353.4 - 0.79 * \text{Jdays} - \text{Julytemp} * 19.1 + \text{Julytemp}^2 * 0.52 + \text{Cohort (1, 2, or 3)}, + \text{Reach (1, 2, 3)}, \quad (1)$$

where Jdays was number of days from Jan. 1 to the first day of smallmouth bass hatching for the year in each Reach, Julytemp was the mean water temperature of the Reach from 1 July to 15 August, Cohort 1 = 27.8, Cohort 2 = 13.7, and Cohort 3 = 0, and Reach 1 = 1.6 (Yampa River), Reach 2 = -3.5 (Green River upstream of the Yampa River), and Reach 3 = 0 (Green River downstream of the Yampa River). The 1 July to 15 August period was used because that reflected the time when most or all smallmouth bass cohorts had hatched and was also the warmest and most important portion of the growing season.

Mean TL of smallmouth bass varied substantially across cohorts within a year, and among reaches across years (Figure 6). Data and TL model effects showed that Cohort 1 fish were longer than Cohort 2 fish, which were longer than Cohort 3 fish, within a year and reach; the magnitude of the cohort effect reflected the importance of timing of hatching within a year and was by far the largest effect (see sums of squares and *F*-values) in the growth model to predict age-0 smallmouth bass TL. Year would have had a major effect on age-0 smallmouth bass growth or length in statistical models, but was excluded to allow predictions of only environmental factors on growth, irrespective of year. It was reasonable that earlier hatching age-0 bass were larger, because they had a longer time to grow and when water temperatures were, on average, warmer, over the summer than later hatching cohorts. Hypothetically, an earlier hatching cohort that experienced 40 d of growth at 20°C in summer and subsequently experienced 10 d of autumn water temperatures that cooled to 15°C by mid-September, would accumulate 950 total degree days (40d*20°C + 10d*15°C = 950 degree days). Comparatively, a later hatching cohort that experienced only 25 d of growth at 20°C in summer and subsequently experienced the same 10 d of autumn water temperatures that cooled to 15°C by mid-September, would accumulate 32% fewer degree days (25d*20°C + 10d*15°C = 650 degree days).

The negative effect for Jdays was also reasonable because it was a surrogate for duration of growing season, where higher (later) Jdays dictated a shorter growing season and shorter bass in mid-September. The $Julytemp^2$ quadratic coefficient importantly affected bass growth in a positive and non-linear fashion, suggesting larger and older smallmouth bass grew more quickly per day than smaller and younger ones (see growth rate discussion below). This likely reflected more efficient transfer of food energy to somatic tissue in those larger fish compared to smaller ones. Reach effects showed slight differences, with Yampa River fish growing fastest, Green River fish upstream of the Yampa growing slowest, and Green River downstream of Yampa River fish exhibiting intermediate growth. The Reach effect was also mostly accounted for in the TL model because of water temperature and hatching date differences among years.

Smallmouth bass in the Green River upstream of the Yampa River were the shortest by mid-September of any of the three study reaches, and showed within year cohort patterns similar to those for the Yampa River, where Cohort 1 fish were longest and Cohort 3 fish were shortest. In the regulated Green River reach, mean TL of Cohort 3 fish was shorter than 50 mm, a possible threshold for bass to survive winter (e.g., Shuter et al. 1980; Breton et al. 2015). Similar TL patterns were observed in the Green River downstream of the Yampa River, although smallmouth bass TL was greater than in the upstream Green River reach.

Among all reaches, smallmouth bass TL in mid-September was greatest for Cohort 1 fish in warm years and least for Cohort 3 fish in cold years. Warmest and highest growth years were in 2006 and 2007, when Cohort 1 age-0 bass approached or exceeded 100 mm mean TL by mid-September in all reaches except the Green River upstream of the Yampa River. Alternatively, Cohort 3 smallmouth bass in all reaches in the high flow and cold year 2011 had mean TL of < 20 mm (Figure 6)

Mean TL of all cohorts of smallmouth bass collected in mid-September in the Yampa River was well predicted by a quadratic relationship using mean water temperature in summer (Figure 7, $R^2 = 0.98$). For example, in the warmest year (2007), mean smallmouth bass length in mid-September was 84.3 mm TL when summer water temperatures averaged 23.7°C. In contrast, in the coldest study year (2011), mean bass length in mid-September was only about half that, 45.8 mm TL, when mean summer water temperature was 18.3°C. This analysis was not conducted for Green River reaches due to small samples sizes of bass captured in mid-September.

Daily growth rates for smallmouth bass in the Yampa River and regulated and partially regulated reaches of the Green River showed that within a year, Cohort 1 fish grew faster than Cohort 2 fish, and Cohort 2 fish grew faster than Cohort 3 fish (Figure 8). Similar to patterns for TL, smallmouth bass growth rates were highest in the Yampa River, followed by those in the partially regulated Green River reach, and were lowest in the regulated Green River reach. In some years, the fewer data available for the Green River limited comparisons with growth rates of smallmouth bass in the Yampa River, where sample sizes were larger.

Overall, smallmouth bass growth was greatest for Cohort 1 fish in warm years but approached or exceeded 0.9 mm/d in all years. Warmest and highest growth rate years were in 2006 and 2007, but there was considerable variation by year and cohort. Alternatively, years 2005 and 2011 were the slowest growth rate years, particularly for Cohort 3 in 2011, when mean smallmouth bass growth rate was only 0.52 mm/d. Differences in the relationship of TL and growth rate among years for cohorts of age-0 smallmouth bass were due to differences in the length of the growing season. For example, growth rates of bass in all cohorts were similar in 2007 and 2008, but bass TL in each 2008 cohort was less than the corresponding one in 2007 because the growing season was shorter.

A GLM model to predict age-0 smallmouth bass summer growth rate (ending in mid-September) in the Yampa River (too few data in some years to model the Green River reaches) included effects for cohort and Julian days prior to first hatching (Table 9) and was:

$$\text{Growth rate (mm/day)} = 1.70 - 0.0052*\text{Jdays} + \text{Cohort (1, 2, or 3)}, \qquad (2)$$

where Jdays is number of days from Jan. 1 to the first day of smallmouth bass hatching for the year, and where Cohort 1 = 0.26, Cohort 2 = 0.16, and Cohort 3 = 0. Also, Jdays and its inverse, length of the growing season, had a negative effect on growth, whereby, fish that hatched later in a given year had a shorter and relatively cooler growing season and grew more slowly until mid-September than fish in years that were exposed to a longer growing season.

We further investigated early season growth of age-0 smallmouth bass specifically because other literature indicated slower growth of smallmouth bass hatched early in the year (Figure 9). We focused finely on the early growth patterns for the abundant Yampa River smallmouth bass, with samples collected early in the summer in a warm, low flow year (2007), a moderate temperature and moderately high flow year (2008), and a high flow and cool year (2011), where bass hatched early, mid-season, and late in summer, respectively. We found a pattern opposite that reported in the literature because early growth rates were high, and the fastest in those samples when bass growth should have been maximized, but declined even over these relatively short durations (2-3 weeks). In each case, water temperatures in the same period when smallmouth bass were hatching were increasing as well.

Additional evidence for slower early growth rates of young smallmouth bass is from the 22 August 2011 sample (n = 20) of smallmouth bass (Figure 9) which averaged 22 d-old (hatched from 29 July-1 August; mean TL = 19.3 mm), and had a mean growth rate of 0.62 mm/d (0.50-0.77 mm/d). In comparison, smallmouth bass from the later 6-8 September sample (mean age = 38 d, mean TL = 46.5 mm), but that hatched in the same 29 July to 1 August interval (n = 17), had average growth rates of 1.08 mm/d (0.87-1.18), or a 71% higher growth rate than for bass collected on 22 August. Water temperatures were an identical 21.2°C over the growth intervals for fish in each sample. To achieve that mean change in length of 27.2 mm over the 16-d interval between samples, meant that average growth rates increased to 1.7 mm/d. Those patterns were not observed in 2007 and 2008.

DISCUSSION

Graphical patterns and GLM analyses indicated spring streamflow magnitude and duration, and time in d from post-peak, post-peak warming, and flow level each influenced timing of reproduction by smallmouth bass in unregulated and regulated stream reaches of the upper Green River drainage. However, the influence of each varied depending on the degree of regulation, with water temperature being a first threshold factor for all reaches (e.g., days to first mean daily water temperature of 16°C) but more important in the unregulated Yampa River. In contrast, streamflow level, likely a surrogate for spawning habitat availability, water temperature, and other factors were both important in regulated and partially regulated reaches of the Green River. Length of the growing season and water temperatures in summer, which were inversely related to spring peak streamflow magnitude, had strong effects on smallmouth bass length in autumn, an important driver of overwinter survival (Shuter et al. 1980; Breton et al. 2015). Thus, the degree of stream regulation – unregulated to fully regulated – and associated water temperatures affected predictions of timing of first reproduction and growth. Understanding those factors and their variation across reaches and seasons importantly affects predictions of spawning times, which are key to determine correct timing of flow or temperature disturbances from upstream dams, or mechanical disruptions via nest disturbance or removal of adults, which may assist with disadvantaging reproduction and growth of invasive smallmouth bass.

Distributions and GLM predictions of hatching dates and timing of reproduction.— Reproduction patterns for smallmouth bass in lotic systems were poorly known compared to lentic systems, so we provide here the first comprehensive examination of effects of water temperature and streamflow on smallmouth bass reproduction in large streams along a continuum of streamflow regulation. Distributions of hatching dates for smallmouth bass in the unregulated Yampa River indicated that first reproduction typically occurred 1-4 days after mean daily water temperature reached 16°C and at flows less than about 5,000 ft^3/sec. The Yampa River alluvial valley geomorphic setting was less constrained than the other two reaches, which may have allowed for more nearshore, low-velocity habitat availability under a variety of flow levels.

Patterns of reproduction in regulated or partially regulated Green River reaches were in contrast with the Yampa River, where smallmouth bass reproduction occurred at a similar time but sometimes was well after water temperatures reached the threshold 16°C. In the regulated reach of the Green River, successful hatching did not occur until relatively low and stable baseflow levels were reached, noting that high streamflow in 2011 delayed hatching. We postulated that stable baseflows were required for smallmouth bass so spawning habitat was available and suitable for successful reproduction; spawning at higher flows may have been attempted but we have no way to ascertain that.

The finding that smallmouth bass in the regulated Green River reach first hatched in a narrow range of post-peak time window in most years, 21-23 d, is a potentially valuable metric to institute management actions. That threshold suggested a confluence of environmental events, where a critical temperature was achieved and when spawning habitat was available, so that smallmouth bass could reproduce. The time threshold was much more variable in the other reaches.

Observations of smallmouth bass spawning locations in the regulated reach during field surveys suggested that most were in side channels that were isolated from main channel inflow only at relatively low flow levels. Spawning in such places at higher flows likely would not occur because water velocities were too high, and few other locations were available in the reach for spawning (Lukas and Orth 1995). Similarly, in the partially regulated Green River reach, side channels that ceased flowing formed embayments as flows receded, and in several of those locations we noted presence of male smallmouth bass in reproductive condition (pers. obs, K. Bestgen, T. Jones, USFWS, Vernal, Utah). The relatively high flows in that reach that occurred in later spring and early summer limited the availability of those habitats and bass reproduction, even though water temperatures had warmed to 16°C on average nearly two weeks earlier. Thus, smallmouth bass initiated spawning and hatching at about the same time in all three reaches, even though water temperatures suitable for spawning occurred relatively late in the year in the upstream and unregulated Yampa River, at an intermediate time in the regulated Green River reach, and were available earliest in the most downstream, partially regulated Green River reach.

Across all years and reaches, timing of first reproduction was inversely related to magnitude and duration of spring peak flows (high flow days metric in GLM analyses) and associated cooler water temperatures (Julian days to first mean daily water temperature of 16°C), such that bass spawned later in high flow and relatively cold years and earlier in low flow and warmer years (Figure 4). The GLM analysis also showed that days since peak flow and warming after peak flow cessation also affected smallmouth bass first hatching. For example, this resulted in the close association of number of higher flow days in the Yampa River and date of hatching, a relationship that was used to cue flow-dependent reproduction in a smallmouth bass population dynamics model (Breton et al. 2015). The effects of low and early flow years such as 2006-07 on reproduction and abundance of smallmouth bass was evident because large year-classes of fast-growing smallmouth bass were produced basinwide (Breton et al. 2014). In those years, the number of Yampa River spring peak flow days > 8,000 ft^3/sec was low or zero. Because age-0 bass hatched early in summer were large in autumn, they had high overwinter survival and the year-class was strongly evident in field samples for 2-3 years after reproduction (Breton et al. 2014); modeling results were consistent with those observations (Breton et al. 2015). The abundant smallmouth bass populations were subsequently more difficult to control via mechanical removal, requiring up to three years to reduce populations to abundance levels prior to years of high reproduction (Breton et al. 2014).

The close link between smallmouth bass reproduction, production of large year classes of young fish, and magnitude of spring flows strongly suggested that reductions to spring flow would increase bass abundance. Streamflow reductions in the mostly free-flowing Yampa River (Bestgen 2015), as well as in the Green River, could occur as a result of off-channel storage, transbasin transfers of water, or climate change, and would increase the negative effects of smallmouth bass predation and competition with native and endangered fishes (Bestgen et al. 2007c, Johnson et al. 2008; Project 140 annual reports). Higher smallmouth bass abundance would also increase the need for more intensive, short-term mechanical removal to reduce negative effects of competition and predation. Similarly, reduced streamflows that increased water temperatures, especially in the baseflow period when flows were already depleted on average by 37% over historical regimes (Bestgen 2015), may enhance the growth and size of invasive smallmouth bass, again increasing negative effects on native biota.

Hatching season duration for smallmouth bass in each of the three study area river reaches was relatively similar, about 4 weeks, with only the season in the regulated Green River reach being slightly shorter (not the range of first hatching days, e.g., Table 3, which has a different pattern). The duration of hatching seasons in each reach declined slightly when first reproduction was later in the summer (Appendix III). This was perhaps predictable as water temperatures begin to cool even in August in many years, such that the potential scope for reproductive season length was compressed between starting in June or later and onset of cooler water temperatures in late summer.

Hatching season duration was also only loosely associated with water temperature during the hatching season in each of the three river reaches studied. For example, Yampa River water temperatures were highest during hatching and showed the most negative trend with hatching season duration.

Sample size of smallmouth bass captured in each reach could play a role in the inferences made regarding first hatching dates. This was true because detection of the few early spawned fish may have influenced relationships of first reproduction to environmental variables, and other relationships. We assumed that the reproductive season timing and durations were accurately portrayed by our sampling in the absence of other information. Relative consistency of hatching season durations across most reaches and years suggested that if hatching season duration was being controlled by environmental factors, those were operating over a broad geographic area.

The wide range of first hatching dates across years in the regulated reach of the Green River was not expected, but in retrospect, was predictable perhaps because of the strong link of bass hatching to water temperatures and low flows, and the near complete control that Flaming Gorge Dam releases had on those variables. This suggested that baseflows achieved earlier in the year would result in earlier hatching, and longer growing seasons with warmer water (e.g., 2007). Subsequent flow spikes or reduced water temperatures from Flaming Gorge Dam during the approximately 4-week spawning or hatching season could then be used to disadvantage reproduction by smallmouth bass.

Conversely, higher flows in later spring or early summer will reduce smallmouth bass reproduction (e.g., 2011) in the regulated reach of the Green River, and perhaps, in the partially regulated downstream Green River reach. This is true because water temperatures will be cooler and delay reproduction and higher flows may reduce or eliminate available spawning habitat present at lower flow levels. Flow and water temperature levels of the Yampa River would need to be factored into those relationships, because higher Yampa River flows may negate efforts to control bass reproduction in the partially regulated reach even if releases were low from Flaming Gorge Dam.

Smaller populations of smallmouth bass in the Green River (Breton et al. 2014) likely reflected more recent colonization, cooler water temperatures, and fewer locations with shallow near-shore and low velocity nursery habitat for age-0 fish. Catch rates for adult and subadult smallmouth bass in the recently colonized, cool, and fully regulated Green River in Lodore Canyon in the post-invasion period 2003-2007 were about 2.7 fish per h electrofishing (2.5 in the entire 2003-2014 period). In the same time periods, smallmouth bass capture rates in the partially regulated and warmer Green River in Whirlpool Canyon were 2-4 X higher, between 5.5 and 10.5 fish per h electrofishing. In contrast, in the warm Yampa River where smallmouth bass colonized in the early 1990's, smallmouth bass capture rates in a comparable period (2004-2007) in Little Yampa Canyon were 30.9 fish per h electrofishing, and 9.9 fish per h in Lily Park (Breton et al. 2015). Although we cannot predict the long-term trajectory of abundance for smallmouth bass in any of these river reaches, recent data suggested Green River abundance patterns were dynamic, declining in years with higher flows and low reproductive success and increasing following low flow years with higher reproductive success (Breton et al. 2014, Bestgen, Project 115 Annual Report, Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado).

Smallmouth bass TL and growth.—Smallmouth bass growth was relatively fast, especially in the relatively warm Yampa River, compared to the moderate growth rates in the partially regulated Green River reach and slowest rates in the cooler regulated reach. Throughout the study area, warmer water temperatures, as well as longer growing seasons, resulted in larger smallmouth bass. Larger bass are not only more piscivorous on a larger size range of native fishes, but are also more capable of overwinter survival and resultant increased abundance of year classes into the future (Shuter et al. 1980; Shuter et al. 1990; Curry et al. 2005; Breton et al. 2015). Growing season length, illustrated by Yampa River bass in the average water temperature year 2008, was relatively short because of late runoff but also showed that bass growth was essentially finished for the year by mid-September. Any flow reductions or warming due to climate change that increase summer water temperatures or extend the growing season will result in increased size and abundance of smallmouth bass in subsequent years.

The statistical model to predict smallmouth bass length (or growth) was fit to variables linked to the environment rather than specific years in order to increase utility of those relationships in smallmouth bass abundance dynamics modeling. Such models have already been developed (Breton et al. 2015), and have been used to predict bass lengths and overwinter survival rates in various reaches in a meta-population sense. This allows for greater understanding of spatial dynamics of smallmouth bass, and may allow for greater focus of control efforts in the most appropriate reaches.

Cohort had the largest effect on growth of smallmouth bass to mid-September and indicated that the early hatched and largest fish were the most likely future recruits. We used cohorts to group fish into general seasonal times rather than specific hatch dates because those vary across years. Use of the cohort approach also facilitated communication with managers who wished to know in general (early, middle, late) which seasons were best for bass hatching and growth and which of those to target for management actions. Increased growing season length for early vs late-hatched cohorts was the likely reason for the large effect, because mean water temperatures that fish in cohorts experienced differed only slightly. Thus, early season cohorts (cohorts 1 and 2) of smallmouth bass should be targeted in control efforts, if managers wish to reduce smallmouth bass populations, a sentiment echoed by others (Loppnow et al. 2013; Breton et al. 2014). Breton et al. (2015), using a comprehensive smallmouth bass population dynamics model, found that implementing early season reductions in reproductive success was one of the most effective ways to reduce overwinter survival of age-0 bass and eventual reductions in adult populations in the Yampa River. The Jdays parameter was the second largest effect in the growth model to predict bass TL in September, which was intuitive because that factor was a proxy for the length of the summer growing season. Thus, any flow factors that increased growing season length would have predictable and positive effects on age-0 bass lengths in autumn. This may be especially true for reducing Yampa River flows via diversion to off-channel reservoirs or climate change related flow reductions, because baseflows are already low.

July water temperature also had a positive effect on smallmouth bass TL and growth rates. The importance of the squared term also suggested that bass growth was not linear, but rather that larger bass grew faster than small bass. This again supported the notion that if reduced bass abundance was a goal, efforts should be made to maintain (rather than increase via reduced flows) water temperatures in occupied reaches. The idea that bass growth rates change (increase) through ontogeny during the first summer of life is also discussed below. Finally, reach had a relatively small effect on bass lengths. This was likely because bass growth and length was driven mainly by reach differences in water temperatures as well as timing of first reproduction, so most reach effects were accounted for by other variables. Reach was maintained in the model for completeness even though the effect was small, and to illustrate the direction of effects for the reader.

Early life stage smallmouth bass growth rates documented in this study were similar to those observed elsewhere (Phelps et al. 2008). For example, age-0 smallmouth bass in two South Dakota lakes ranged from 0.56-1.56 mm/d, although growth rates were biased because of likely incorrect estimation of age (Hill and Bestgen 2014). The few other daily growth rate data available for other locations, and potential biases of those, was discussed by Hill and Bestgen (2014).

Counter to the literature (Sabo and Orth 1995), we found early hatching smallmouth bass in each of a low, moderate, and high flow year had consistently higher rather than lower growth rates. This was in spite of choosing years when flows and water temperature varied among years and bass hatching was relatively early (2007), mid-summer (2008), and late in the year (2011). It is possible that density dependence caused reduced growth rates of the fish that hatched later in those samples. However, because it was early in the year and smallmouth bass densities were relatively low, density-dependent reductions in growth rates may be difficult to invoke.

We discovered a likely flaw underlying the aging technique that others have historically used to age small smallmouth bass (Graham and Orth 1986; but see Hill and Bestgen 2014). The technique of Graham and Orth (1986) likely underestimated the number of early otolith increments, and where the growth zone and first increment deposition occurs. Their experimental setup may have been partly to blame because water temperatures were variable and may have induced difficult to interpret increment deposition patterns or sub-daily increment deposition. Hill and Bestgen (2014) describe this more fully and the likely consequences of using their technique for aging and growth studies. At least in our conditions, we feel confident of our aging techniques, and the growth calculations that follow from them.

We went to some lengths to investigate patterns of early growth of smallmouth bass (e.g., Figure 9). Reductions in growth rates of our smallmouth bass even in samples collected early and over short durations could be due to different growth rates of bass of different ages in samples, such that the younger bass hatched relatively nearer the sampling date grew more slowly. Our method of estimating growth would average over periods of relatively slow or fast growth such that differences among younger or older bass would be obscured. However, laboratory observations of slower growth of very young smallmouth bass supports this case (from Hill and Bestgen 2014). For example, 5-d-old smallmouth bass reared at 20°C, a temperature consistent with early season hatching bass in the Yampa River, averaged only 7.45 mm TL and results in a post-hatching growth rate of 0.39 mm/d (larvae were 5.5 mm TL at hatching), considerably lower than our field-captured and older fish. Because those laboratory fish were likely just transitioning fully to exogenous feeding after the yolk was exhausted, those growth rates likely represents growth of very young bass in the wild. Thus, a young and relatively slow growing smallmouth bass would have to increase growth rate greatly to achieve the average 1 mm/d or greater rates we observed (Figure 9).

Further evidence for slower early growth rates of young smallmouth bass was from comparison of growth rates of smallmouth bass collected in late August and early September 2011 (Figure 9). Water temperature conditions were essentially identical in terms of mean daily values so that is discounted as a reason for differences. It is possible that differential selection for faster growing fish was exerted in that short time period, but it is unlikely that factor accounted for a large difference, given that the fastest growing smallmouth bass in the August sample had a slower growth rate (0.77 mm/d) than the slowest growing bass in the September sample (0.87). We conclude that growth rates of smallmouth bass changed substantially through early ontogeny, and those differences need to be considered when interpreting mean growth rates calculated over long time intervals such as we did in our study.

All these environmental data, including cohort hatching dates, stream flow, water temperature, were used to mechanistically model their effects on smallmouth bass population dynamics (Breton et al. 2015). The flexible model structure used also allowed for exploration of scenarios to alter bass growth and abundance, either via disturbances, altered thermal or flow regimes induced by water availability, or climate change. Thus, effects of those factors on bass growth and abundance, and potential recovery for native fishes, can be predicted.

Comparison of post-hatching growth rates of invasive smallmouth bass in the upper Green River system and several native fishes showed bass with a large advantage. For example, minimum growth rates of smallmouth bass were 2-4x that for any native taxa (Table 10, Bestgen et al. 2006a; Bestgen 2008; unpublished data for other species), and maximum growth rates were similarly disparate. Based on similar growth and water temperature conditions, and assuming 1 July hatching dates, a smallmouth bass larva growing 1 mm/d was large enough to consume a Colorado pikeminnow larva only 13 days later. This occurred even though pikeminnow were larger than smallmouth bass at hatching, 6.5 vs 5.5 mm TL, respectively, and assumed bass can swallow prey items 2/3 their length. Native suckers hatch earlier in the year (May-early June) than smallmouth bass (late June-July), and are larger at hatching, typically 9 -12 mm TL, but may grow slowly during cold, post-hatching periods. High smallmouth bass growth rates may allow predation on native suckers by the end of the first growing season. Because native fishes are relatively slow growing compared to smallmouth bass, and because smallmouth bass are very abundant in many stream reaches, environmental changes that enhance growth or length of smallmouth bass may further reduce survival of native taxa (Breton et al. 2014; Bestgen and Hill 2016).

Management to disadvantage smallmouth bass, Yampa River.—The negative effects of flow disturbances, as well as water temperature reductions, on smallmouth bass hatching and recruitment are well known in the literature (Larimore 1952; 1975; Pflieger 1966; 1975; Reynolds 1990; Reynolds and O’Bara 1991; Lukas and Orth 1995; Peterson and Kwak 1999).

Those factors, combined with the predictable hatching season of smallmouth bass in the Green and Yampa rivers, indicated that management to disadvantage reproductive success may be useful. This was true because hatching of smallmouth bass in the Yampa and Green rivers was nearly always associated with declining or stable baseflows in spite of variable flow magnitude and increasing water temperatures, and occurred sometime after achieving a mean daily water temperature threshold of about 16°C. Hatching seasons also spanned relatively short time periods, and suggested that infrequent disturbances, perhaps just 1 or 2 per season, may have a substantial negative impact on survival of bass early life stages. Efforts to suppress reproduction and abundance of age-0 bass should focus on early hatching cohorts because those fish were the largest ones in autumn and were most likely to survive the winter in the Yampa and Green rivers, assertions supported by modeling efforts (Breton et al. 2015). Such experiments should be evaluated carefully though, as removal of early hatching smallmouth bass could result in an ecological release for later hatching bass, which may increase their growth and TL in autumn. Timing of reproduction and growth information should assist with understanding population dynamics of smallmouth bass in large western rivers including the Yampa and Green, and inform actions that may reduce their abundance and impacts on native fauna.

Flows in the Yampa River may limit ability of managers to effect control actions such as mechanical removal on smallmouth bass in that system. That is because the Yampa River becomes less navigable at flows less than about 1,500 ft^3/sec by large boats that are efficient at fish removal, although boating is possible at lower flows (e.g., 1,000 ft^3/sec) with experienced operators. That was typically about the time that Cohort 1 fish were finished hatching in the Yampa River (see distributions of hatching dates, Figure 3). Thus, mechanical removal and nest disruption activities were possible mostly only prior to then. Although removal of Cohort 1 fish was desirable, some of the substantial numbers of smallmouth bass remaining in Cohort 2 would also likely be large enough to survive the winter, so additional midsummer control efforts (e.g., the “Surge”, smallmouth bass removal focused during the early portion of the reproductive season so adult fish could be more easily captured, with associated higher nest failure from removal of the guarding males) should be directed at those fish. Cohort 3 fish may be less problematic in higher flow years, because our modeling and the literature suggested that they will likely be too small to survive the winter (Breton et al. 2015). These were essentially the recommendations of previous works (Breton et al. 2014) which supported Surge efforts.

Additional removal efforts might include targeted angling or electrofishing to capture aggressive males defending nests, with emphasis on extending this later into the summer to help remove males that protect young fish produced in later cohorts. Direct disruption of nests may also be effective (Loppnow et al. 2013). It is also possible that flow manipulations from Elkhead Reservoir could be used to disrupt nesting success. Such a practice would necessarily have to occur when Yampa River flows were quite low, perhaps 500 ft^3/sec or less, and only if relatively high flow releases could be arranged, perhaps up to the outlet maximum of about 500 ft^3/sec. This is because supplemented flows would likely have to be high to increase flow velocities substantially in the main channel Yampa River, a main factor in disrupting spawning and hatching success (Smith et al. 2005). The flow rating curve data for the Maybell USGS gauge (#09251000) showed water stages at flow levels of 250, 500, 750, and 1000 ft^3/sec were 1.85, 2.37, 2.76, and 3.08 feet respectively. Thus, a baseflow of 250 ft^3/sec in the Yampa River increased to 500 ft^3/sec, would result in a stage change of 0.52 ft., with unknown changes in velocity. A baseflow of 500 ft^3/sec increased by that same flow to 1000 ft^3/sec would result in a stage change of 0.71 feet. Because low flow years typically produce large year classes of larger fish, undertaking a flow disturbance in a low flow year would be especially timely and would allow the disturbance flow to be large relative to baseflow. A flow increase may alter conditions in spawning areas to the point that eggs and weak-swimming larvae are swept away, or may encourage adults to abandon nests. Attempting a flow disturbance at higher baseflow levels would not be likely to succeed because river stage and velocity changes possible with a 500 ft^3/sec increase, when baseflows are at 1,000 ft^3/sec or higher, would not likely be substantial enough to alter habitat or flows in a meaningful way.

Understanding effects of flow disturbances would likely require an assessment of physical effects of increased flows, in addition to a biological investigation, regardless of the reach involved. Physical habitat changes during flow increases should focus on those characteristics that may disrupt nesting success (increased velocity over the nest, reconnection of a side channel). A physical effects analysis may involve finding and marking active nests, taking measurements of velocity and depth characteristics around the nest area before and during the flow disruption, and describing macro-habitat features of the site, including whether the nest was located in the downstream end of a secondary channel. Flows would have to be sustained for a long-enough period, perhaps 2-3 days, to have an effect in the desired reach, and allow investigators to measure effects over broad reaches.

Biological measures of effects of flow or temperature disruptions might include assessments of pre- and post-disturbance egg or larvae presence in nests, marking of male-guarded nests, and observations of male behavior on nests. This approach could also be used to evaluate effects of disturbance from sampling during the Surge, where removal or displacement of adults might result in reduced nest success. Observations might also include abundance of newly dispersed smallmouth bass larvae that occupy low velocity areas, in both pre- and post-disturbance periods. A longer-term assessment would also include estimates of abundance of various life stages (Project 125), and abundance of age-0 fish in autumn (Project 140 results), in locations such as Little Yampa Canyon. That reach has a long history of sampling, both for smallmouth bass as well as for native and other small-bodied fishes that might respond to bass removal, and should be included in an assessment of disturbance effects designed to reduce smallmouth bass reproductive success.

Management to disadvantage smallmouth bass, Green River.—Similar assessment approaches just described for the Yampa River could be used in the regulated and perhaps the partially regulated sections of the Green River. Disturbance flows there may have a much larger effect since higher releases are possible from Flaming Gorge Dam, recognizing that higher baseflows would also be present. Care must be taken to implement disturbance actions at specific times, because flow releases that occurred too early would be prior to most bass spawning or hatching, while disturbances too late in the year may occur after early hatching bass have grown to a size where they are less or not affected by disturbances. In the regulated Green River reach upstream in Lodore Canyon, a few locations are known where smallmouth bass have regularly spawned in the past, based on capture of adults, or larvae, or both. These include mainly side channel backwaters or eddies, including ones just upstream of Hells Half Mile rapid (about RK 556.7, river right), just downstream of Wild Mountain campground (Screaming Jay backwater, about RK 562.4, river left), and near the Green River confluence with the Yampa River (river left). As for the Yampa River, physical as well as biological measures would need to be assessed in the Green River. Physical factors include assessing the flow levels needed to make connections of side channels that provide spawning habitat for smallmouth bass, and determining what flow levels might accomplish those connections to achieve a relatively high flow velocity (e.g., > 30 cm/sec) in the desired habitat. This is needed because smallmouth bass 20-25 mm TL were displaced in laboratory studies in current velocities of about 15-22 cm/sec in water temperatures of about 15-20°C (Larimore and Duever 1968). Thus, understanding various flow level effects would require assessing flow conditions in side channels during various levels of inundation.

Biological investigations would include measuring presence and abundance of larvae with seine samples at specific locations pre- and post-flow disturbance, to assess if increased flow removed or dispersed early life stages of smallmouth bass. Placement of marked smallmouth bass early life stages in key backwaters could also be conducted to assure presence of larvae in specific locations, prior to flow manipulations, so disturbance effects could be measured more unambiguously. If spawning nests can be found, investigators could also make observations of those in pre- and post-disturbance time periods.

Drift nets may also be effective to capture early life stages of smallmouth bass during flow disruption events. We have captured early life stages of smallmouth bass in the Green River just upstream of the Yampa River during higher flow and turbidity events caused by upstream rain events in 2003 and 2004 (Bestgen et al. 2006b). Thus, we know bass larvae were dispersed (mean TL = 18.1 mm [8.8-28.1 mm]; mean age = 24 days [10-36 days old]) and we were capable of capturing them in drift nets. Such sampling should be timed to coincide with the rising and maximum portion of the flow pulse to ensure that bass are detected. Seine sampling is also conducted in the Green River in regulated and partially regulated reaches in summer and autumn. Density of smallmouth bass in backwaters in summer and autumn, between which flow disturbances might happen, could be compared to determine effects on a larger, river scale. Abundance of young bass could also be assessed in autumn, and compared to previous years when no flow disturbance events occurred.

Samples of bass collected in autumn could be aged via otolith microstructure to determine if any smallmouth bass survived from the time period prior to flow pulses. This would be similar to constructing the hatch date distributions already shown. A main difference is we would know that bass actually spawned based on observations and sampling conducted pre-disturbance. In other words, if all bass captured in autumn were produced post-disturbance, and we know bass were spawned in a pre-disturbance time period, we would know the disturbance was effective.

Those same assessments could be made in the partially regulated reach of the Green River. Locations of bass nesting are known, including the lower ends of cutoff, low flow channels, or large backwaters in Whirlpool Canyon and Island Park. A key to success is flows large enough to create a disturbance. This may require moderate to low Yampa River flows, and a relatively large flow pulse from Flaming Gorge Dam, so flow and stage levels are substantially increased. It would seem reasonable to increase flow during disturbances to powerplant level (e.g. 4,500 ft^3/sec) to have a large enough increase over baseflows to effect flow-through conditions in key spawning and nursery habitat locations, both in the regulated reach of Lodore Canyon, and in the partially regulated Green River downstream of the Yampa River.

It may be also worth discussing the option of lowering baseflows to very low levels, which would naturally warm water temperatures, to induce smallmouth bass reproduction early in the post-peak flow period. This is important because baseflow levels established early and at low levels to induce warm water temperatures and smallmouth bass reproduction could be used in concert with subsequent higher baseflows or colder water temperatures (or both) to disrupt spawning or hatching. Subsequent higher flows would then have a larger effect in terms of increased stage as well as in reduced water temperatures, and may create more certainty that most smallmouth bass will be attempting to spawn in the reach of interest when the disturbance is attempted. These flows would not necessarily represent the natural flow paradigm (Poff et al. 1997), but in an experimental program, are justified, especially if effective to reduce bass abundance. This flow regime should perhaps be considered only after the efficacy of the technique of flow spikes to reduce smallmouth bass reproductive success has been demonstrated. This is needed because production of large year classes of large smallmouth bass would be counterproductive if flow spike control was not effective.

Reducing flows early in the season in the regulated reach of the Green River upstream of the Yampa River may have additional benefits for non-native fish control (Zelasko et al. 2015). That is because northern pike, which spawn during high flow releases in the Browns Park area of the upper Green River, may be negatively impacted by early season flow reductions because of reduced survival of young. This may occur because pike are attracted to spawn in areas of shallow submerged vegetation in the flood plain or the channel margin during higher flows in May and early June. If flows are reduced when sensitive eggs or larvae are present in the shallow floodplain or the channel margin, those life stages may be stranded or flushed to the river, resulting in lower survival.

Timing of releases for disruption of reproduction should be predicted with the smallmouth bass hatching date distributions and GLMs described above and verified with observations. However, the precise timing to conduct such an experiment is not well established, even if it is known that bass spawning is underway. Certainly, disturbance flows would be post-spawning and post-hatching, but whether to target cohort 1 or 2 is not certain (Figure 10). It seems as though disturbance flows could target both simultaneously, given the short time between initiation of hatching and the peak in the distributions of hatching dates. Targeting the peak time of hatching would follow production of Cohort 1 fish, typically the largest fish produced in any year, and also the first portion of Cohort 2, which is typically the one with most bass produced in any year. For example, if one assumed bass hatching commenced on 4 June as in 2007, and hatching season duration was about 40 days, at average water temperatures in the Green River most larvae would be < 2 weeks old and barely have achieved swim-up, a vulnerable life stage when maximum swimming speeds are likely < 15 cm/sec (Larimore and Duever 1968). Additionally, most or all Cohort 2 eggs would have been deposited by 25 June and early Cohort 2 fish would be hatching already. Thus, a flow disturbance by 25 June would target most life stages of the first and second cohorts of bass when they are relatively small. We know the flow and turbidity disturbance documented during Green River drift net sampling in 2004 displaced many early life stages of smallmouth bass from 8.8-28.1 mm TL. The flow stage was increased 7-8 cm and turbidity was very high based on observations. However, absolute flow magnitude change was not known because the flood flow input from Vermillion Creek was downstream of the gauge at Flaming Gorge Dam, but far enough upstream of the gauge at Jensen, Utah, that only a small mean daily flow increase was recorded from 16 to 17 July (1,610 to 1,660 ft^3/sec, respectively). Thus, turbidity was likely a major displacement factor in addition to slightly increased flow.

Targeting the early bass hatching period would also reduce the chance that flow disruptions would affect spawning by native fishes. This is true because such a flow disturbance would occur after reproduction by most native suckers, but just prior to spawning by chubs and Colorado pikeminnow in the Green and Yampa rivers. Flow disturbances would likely also affect native fish eggs less than smallmouth bass eggs. This is true because smallmouth bass lay eggs, which are at least somewhat adhesive, on the top of substrates in nests constructed in low velocity habitat, which would likely be swept away with small increases in flow velocity near the benthos. In contrast, native fish reproduction occurs in high velocity runs and riffles, where adhesive eggs are deposited in the deeper interstitial spaces of large cobble and gravel. Thus, eggs are attached and placed below the surface of the substrate and would be less affected by flow increases in habitat that is already relatively swift. Similar to smallmouth bass, densities of native fishes captured in autumn after flow disturbances (Project FR115) could be compared to those in previous years to assess if there were effects from flow disturbances.

Focusing on the early portion of the smallmouth bass reproductive effort would also reduce overlap with Colorado pikeminnow larvae that drift from the lower Yampa River into the Green River (Bestgen et al. 2006a; Bestgen 2015). Relatively lower Green River flows and water velocities ensures that larvae will not be swept from nursery habitat present in downstream Middle Green River reaches. In the example shown, first 2007 Colorado pikeminnow drift into the Green River was on 26 June and the first substantial pulse of larvae was on 7 July. Thus, the end of the smallmouth bass hatching period typically barely overlaps with that of the first larger pulse of Colorado pikeminnow larvae of the year, so earlier flow spikes should not affect pikeminnow drift patterns. This pattern occurs in most years.

Smallmouth bass are known to renest following disturbances that destroy nests in lentic systems (Winemiller and Taylor 1982), but we do not know if bass would renest in lotic habitat in the upper Green River system. Even if they did, the relatively late hatching fish that remained may experience lower overwinter survival because of small body size during winter (Shuter et al. 1980, Breton et al. 2015). In other words, the short time window for reproduction in this system, combined with the removal of early cohorts, may be effective enough to create a large and negative effect on smallmouth bass recruitment. Managers could also entertain the idea that two flow disturbance events could occur in a single reproductive season, perhaps one during each of cohorts 1 and 2.

In addition to timing of disturbance events, duration of high flows also needs to be considered. A higher flow event sustained for 3 days may be sufficient for flows to reach Island-Rainbow Park and have the desired disturbance effect. This time period would also be sufficient to allow investigators to traverse the downstream, mostly canyon-bound reach in inflatable rafts and assess effects of the disturbance at various locations.

Overlap of flow releases for fish management, Green River.—Multiple requests for flow releases from Flaming Gorge Dam for various purposes creates a need to visualize the temporal schedule of these events to ensure that detrimental overlap of desired flows does not occur. Experimental flow releases already occur in spring during the peak or just post-peak of the Yampa River snowmelt flows (Figure 11). This experimental program, the Larval Trigger Study Plan (LTSP, LaGory et al. 2012), involves releases of water in spring to connect floodplain wetlands at a time when razorback sucker larvae are present, and allows early life stages to rear in relatively warm and food-rich environments. Fast growth of larvae in summer increases the likelihood that young razorback suckers will survive and perhaps recruit to adult life stages, a rare event in the wild (Bestgen 2008; Bestgen et al. 2011; Webber et al. 2013). The flows implemented under the LTSP have been successful entraining larvae into floodplain wetlands each year from 2012-2015, and in 2013 and 2014, over 1,500 juveniles (42-168 mm TL) were produced from a single experimental wetland, Stewart Lake (Skorupski 2014, Schelley 2015, Recovery Program annual reports, Project FR-165). That number of juveniles far exceeds the number known from all previous upper Colorado River basin studies since the early 1960's and thus, is considered a provisional success, pending recruitment of some juveniles to adult life stage.

Another proposed but yet only partially unimplemented flow release would be to benefit young Colorado pikeminnow growth and survival in backwaters of the Green River downstream of the Yampa River (Bestgen and Hill 2016). Higher baseflows in a range of about 1,700-3,000 ft^3/sec were consistent with higher levels of age-0 pikeminnow juveniles in autumn in the Green River since 1979 as well as presence of more important backwater habitat (Bestgen and Hill 2016). Increased baseflows were thought especially important since about 2000, when extended drought reduced flows. Reduced recruitment of age-0 Colorado pikeminnow is consistent with reduced abundance of adults in the Green River basin, and more robust year-classes are needed to stabilize those populations, the largest that remain in the wild (Bestgen et al. 2007a; Bestgen et al. 2010).

The newest proposed flow release from Flaming Gorge Dam is the one described in this report, and the only one designed to disadvantage non-native fishes such as smallmouth bass. This managed flow event is well positioned in the middle of the temporal time frame of other flow release actions, and thus, would interfere only minimally with those effects if all were implemented in a single year. Effective flow disturbance events would be very valuable because smallmouth bass are thought the most problematic invasive species in the upper Green River basin, based on their high abundance, ability to prey on many life stages of native fishes, and their broad habitat overlap with many native fishes of most life stages (Johnson et al. 2008). Although mechanical removal of smallmouth bass is somewhat effective for a short time (Breton et al. 2014), flow treatments such as the one described offer the distinct advantage, if successful, to reduce entire year classes over large river reaches. If reduced abundance of smallmouth bass can be effected by flow disturbances, and higher abundance of native fishes can be recruited with increased spring peak and summer baseflows, a double benefit could be realized, and funds normally reserved for non-native fish removal could be used for other recovery activities. Broader-scale control of non-native fishes is needed because increased recruitment of early life stages of both Colorado pikeminnow and razorback sucker, as well as other native and endangered fishes, is the key factor in stabilizing these populations.

An important consideration for implementing flow management actions is to identify if sufficient water is available to conduct all three fish management releases in a single flow year, and if not, which action(s) have the highest priority for implementation. A key part of that determination is the hydrologic conditions present in the upper Green River basin in a given flow year. For example, floodplain inundation is achievable and important, but more difficult, in low magnitude flow years. Conversely, smallmouth bass flow disruptions may work best in low flow years, given that such are the ones best suited for bass recruitment and because those flow management events are short-term and relatively low volume releases. Pikeminnow recruitment via enhanced summer baseflows is best effected in lower to moderate flow years. The duration and magnitude of various flow prescriptions, the amount of water available in Flaming Gorge Reservoir, reservoir inflow forecasts, drought and storage trends, status or abundance on non-native fish, and the many other competing uses for that water need to be considered as well. An advantage, though, is that Flaming Gorge Reservoir has a relatively large storage volume, downstream uses are relatively low, and the amount of flow required may be modest relative to the overall storage capacity and inflows into the system. These actions should be considered as part of the continued operational thinking and benefits of reservoirs: that their releases can be used to positively influence native and endangered wildlife and ecosystems.

CONCLUSIONS

- Smallmouth bass are now reproducing and relatively abundant in the unregulated Yampa River, the regulated reach of the Green River upstream of the Yampa River, and the partially regulated reach of the Green River downstream of the Yampa River. River regulation is from Flaming Gorge Dam operation located on the Green River 65 river miles upstream of the Yampa River.
- Studies of smallmouth bass otolith microstructure were useful to understand early life ecology of smallmouth bass and factors that may reduce their negative effects.
- Degree of streamflow regulation had many and varied effects on reproductive ecology and early life stages of invasive smallmouth bass.
- First hatching of smallmouth bass occurred on average, at about the same time each year in the Yampa River and both reaches of the Green River, but under different environmental conditions.
- First hatching of smallmouth bass each year in the unregulated Yampa River was associated with onset of mean daily water temperatures of 16°C, occurred over a range of flows, and similar to other reaches, was also influenced by time since peak flow cessation and warming in the post-peak period. First hatching there was also positively related to high flow magnitude and duration, with first hatching occurring later in summer in years with higher flow peaks. Flow level each year was also linked with hatching date in the Yampa River; mean flow at first hatching for smallmouth bass in the period 2005-2011

was 3907 ft^3/sec (2990-5350 ft^3/sec), with lower flows in warm and early runoff years (2007) and higher flows in cooler and later runoff years (2011).

- First hatching of smallmouth bass each year in the regulated reach of the Green River occurred several days after the 16°C water temperature threshold was reached and occurred over a narrow range of lower flows that were associated with formation of limited and cutoff side channel habitat. First hatching also occurred in a narrow time window of 21-23 days in 6 of 7 years. The side-channel habitat was likely used by spawning smallmouth bass so higher flows may limit smallmouth bass reproduction. First hatching of smallmouth bass in the Green River upstream of the Yampa River occurred over a relatively narrow flow range; mean flow level at first hatching was 1663 ft^3/sec (1040-2490 ft^3/sec), with lower flows in warmer and earlier runoff years (2006, 2007) and higher flows in cooler and later runoff years (2011).
- First hatching of smallmouth bass each year in the partially regulated Green River reach occurred nearly two weeks after the 16°C water temperature threshold was reached and over a wide range of flows, but those flow levels may also be associated with formation of limited and cutoff side channel habitat. That habitat was likely used by spawning smallmouth bass so higher flows may limit smallmouth bass reproduction. In contrast to the low and stable baseflows of the Green River upstream of the Yampa River during first hatching, flows in the downstream Green River were high and variable. There, first hatching of smallmouth bass occurred at mean flow of 8,294 ft^3/sec (4,790-10,900 ft^3/sec). Similar to the reach upstream of the Yampa River, we do not know if smallmouth bass spawned earlier in the downstream portion of the Green River and none of those offspring survived, or if documented first hatching indicated first reproduction in that year.
- First hatching of smallmouth bass in all reaches of the study area occurred later in the year when flows were cold and high (e.g., 2008, 2011) and earlier when flows were warm and low (2006-2007).
- A general linear model (GLM) was constructed to predict timing of first hatching as a function of number of high spring flow days, onset of mean daily water temperature of 16°C, and number of days and accumulated degree days between spring peak flow and

first hatching. A second GLM predicted first hatching as a function of April-July flow volume, which may be useful for flow modelers and managers.

- Mean time from first hatching to peak hatching was less than two weeks in each reach, and the entire hatching period was generally about 4 weeks long.
- The range of first hatching dates was widest in the regulated Green River reach, shortest in the unregulated Yampa River, and intermediate in the partially regulated reach of the Green River.
- Total length of smallmouth bass at the end of the growing season (mid-September) was affected primarily by hatching cohort, summer water temperature, and timing of first hatching. Early hatched fish in warm years with long growing seasons were the largest and fastest growing (e.g., Cohort 1 in 2007) and late hatched fish in cool years with shorter growing seasons were the smallest and slowest growing (e.g., Cohort 3 in 2011).
- Management actions such as abrupt flow increases (managed floods), reduced water temperatures, or physical disturbances directed at spawning and hatching smallmouth bass may reduce reproductive success of smallmouth bass, and is facilitated by understanding their timing of hatching and early life ecology.
- Flow and other disturbances to disadvantage smallmouth bass reproductive success needs to consider effects on other native and non-native fishes as well as water availability tradeoffs.
- Recommendations for flow management or other disturbances relative to disadvantaging smallmouth bass, as well as other flow management actions implemented to benefit native fishes, can be conducted within a single year without conflicting overlaps.
- Increased use of flow and water temperature regimes from dams to reduce negative effects of non-native fishes, and to increase growth and survival of native kinds, is advocated as a viable use of reservoir water storage and may offer management agencies another tool to achieve a more naturally functioning river ecosystem and enhance recovery of native biota.

RECOMMENDATIONS

- Continue to develop information on early life ecology of smallmouth bass to assist with general ecological understanding and enhance efforts to reduce abundance of this invasive species.
- Develop a detailed study plan to investigate effects of disturbances, whether from flow alterations, temperature shifts, or physical disturbances, on smallmouth bass reproductive success in the Yampa and Green rivers.
- Continue studies that support efforts to evaluate smallmouth bass reproductive success in the Yampa and Green rivers (projects 22f, 125, FR 115, 140) as integral parts of an overall evaluation plan.
- Investigate operational flexibility at Flaming Gorge Dam and Elkhead Reservoir to accomplish flow or water temperature (Flaming Gorge only) management activities to disadvantage smallmouth bass.
- Implement disturbance regimes and conduct field studies to understand their effects to disadvantage smallmouth bass reproductive success and further recovery of native and endangered fishes.

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Table 1. Number of age-0 smallmouth bass that were captured and aged by counting otolith daily increments, Yampa River, Green River upstream of the Yampa River (Lodore Canyon), Colorado, and Green River downstream of the Yampa River (Whirlpool Canyon), Colorado and Utah, 2003-2011.

	Yampa	Green River	
Year	River	Lodore	Whirlpool
2003			6
2004		7	75
2005	147	58	15
2006	140	76	28
2007	176	45	154
2008	376	151	74
2009	458	116	81
2010	488	158	52
2011	296	37	39
Total	2081	648	524

Table 2. Mean water temperature (range) during smallmouth bass hatching each year in the unregulated Yampa River, the regulated Green River reach upstream of the Yampa River (Lodore Canyon), Colorado, and the partially regulated Green River reach downstream of the Yampa River (Whirlpool Canyon), Colorado and Utah, 2003-2011.

	Yampa River °C (range)		Green River, °C (range)			
			Lodore Canyon		Whirlpool Canyon	
2004					18.6	(14.9-20.2)
2005	21.1	(17.3-23.7)	18.5	(15.8-22.0)	20.9	(17.7-24.7)
2006	20.5	(14.5-24.3)	20.0	(15.8-22.7)	19.5	(16.5-22.9)
2007	20.8	(16.3-24.5)	19.8	(15.0-22.7)	20.6	(13.9-23.8)
2008	21.2	(17.9-23.7)	17.4	(16.5-18.3)	18.1	(17.4-19.3)
2009	21.0	(17.0-23.5)	18.5	(17.2-20.2)	19.3	(18.0-21.8)
2010	21.0	(15.8-25.7)	18.6	(16.2-20.3)	18.2	(16.1-20.3)
2011	19.9	(16.3-22.5)	18.5	(17.6-19.3)	20.9	(19.4-20.3)
Mean	20.8		18.8		19.6	

Table 3. Flows and dates at first hatching of smallmouth bass in three reaches of the upper Green River basin, 2005-2011. LD = Lodore Canyon, the regulated Green River reach upstream of the Yampa River; WP = Whirlpool Canyon, the partially regulated Green River reach downstream of the Yampa River. The range below each date column represents the spread of days over the study period that first reproduction occurred.

	Yampa River		Green River, LD		Green River, WP	
	Flow	Date	Flow	Date	Flow	Date
2005	2990	3-Jul	2030	22-Jun	8380	29-Jun
2006	3950	15-Jun	1040	13-Jun	9310	11-Jun
2007	2270	12-Jun	1170	9-Jun	4790	4-Jun
2008	4280	3-Jul	1660	28-Jun	10900	27-Jun
2009	4790	28-Jun	1710	2-Jul	8110	29-Jun
2010	3720	23-Jun	1540	26-Jun	8450	21-Jun
2011	5350	16-Jul	2490	2-Aug	8120	28-Jul
mean	3907	27-Jun	1663	27-Jun	8294	25-Jun
range		35 d		64 d		54 d

Table 4. Summary statistics of flow, water temperature, and timing variables in the unregulated Yampa River, and fully regulated and partially regulated reaches of the Green River, 2004-2011, used in general linear model predictions of first hatching date of smallmouth bass.

	Yampa River			Green River, Lodore Canyon			Green River, Whirlpool Canyon		
	Mean	Range	STD	Mean	Range	STD	Mean	Range	STD
First SMB hatching	178.1	163 - 197	11.7	178.7	160 - 215	6.8	174.8	155 - 209	16.7
Maximum spring flow	12561	6330 - 19600	4365.4	5730.9	4336 - 9190	685.8	19313	11400 - 31300	6231.1
Mean flow at hatching	3881.1	2442 - 5542	989.1	1662.9	1040 - 2482	186.6	7694.8	4830 - 10880	2008.2
Mean temperature at hatching	16.7	15.3 - 17.9	1.0	17.4	14.9 - 18.9	0.5	18	16 - 20.8	1.5
Number of high flow days	23.1	0 - 62	20.1	25.1	6 - 91	11.3	25.1	0 -76	23.9
Number of days post peak	30.6	14 - 41	9.8	24.7	21 - 42	2.9	26.9	11 - 47	12.2
Julian day of first 16°C	174.3	155 - 196	12.7	171.4	153 - 201	5.9	163.5	148 - 185	12.8
Days 16°C and hatching different	3.9	-1 - 10	4.0	7.3	4 - 14	1.2	11.3	0 - 24	6.9
Annual degree days	989.7	852 - 1232	146.6	1217.3	1073 - 1392	48.1	1218.9	994 - 1652	213.3
Post-peak degree days	405.9	192 - 527	126.2	354	273 - 597	42.5	418.1	159 - 780	203.3
Spring volume	1576	736 - 2903	682.1	552	318 - 1327	131.9	1986	991 - 4229	1014.0

First SMB hatching = first smallmouth bass hatching in the year and reach, adjusted as days since 1 January
River reach, 1 = Yampa River, 2 = Green River upstream of Yampa River, 3 = Green River downstream of Yampa River
Maximum flow = spring peak flow in the river and reach, in ft^3/sec
Mean flow and temp, hatching = mean flow and water temperature in the five-d period centered around first hatching day
Number of high flow days = number of days > 8,000, 4,300, and 12,300 ft^3/sec for reaches 1, 2, and 3 respectively. See text for details.
Number of days post-peak = number of days after spring flows peak until first hatching of smallmouth bass in the reach
Julian day first 16°C = the first day in the reach and year when mean daily water temperature is 16ºC or greater, adjusted to 1 January (Julian day)
Days 16°C and hatching different is the number of days between when 16ºC was achieved and first smallmouth bass hatching
Degree d annual and post-peak is the sum of the mean daily water temperatures for each respective reach beginning 1 January or post-peak, respectively
April-July flow = volume of water in the respective reach, in 1000s of ac-feet, see text for details

Table 5. Covariates used in the statistical model (Type III statistics) to predict first hatching date of smallmouth bass in the Yampa River, and the Green River upstream and downstream of the Yampa River, 2005-2011. Final model statistics were: DF = 4, 17; $F = 213.26$; $p < 0.0001$; model fit was $R^2 = 0.98$.

Source	DF	Type III SS	*F*-Value	Pr > *F*
# high flow days	1	35.20	6.40	0.0216
Julian day, 16°C	1	340.83	61.94	< 0.0001
# d post-peak	1	51.98	9.45	0.0069
Degree d post-peak	1	104.56	19.00	0.0004

Table 6. Parameter estimates to predict first hatching date of smallmouth bass in the Yampa River (Reach 1), and the Green River upstream (Reach 2) and downstream (Reach 3) of the Yampa River, 2005-2011.

Parameter	Estimate	SE	T-value	Pr > T
Intercept	44.872	13.76	3.26	0.0046
# high flow days	0.141	0.0558	2.53	0.0216
Julian day, 16°C	0.709	0.0900	7.87	< 0.0001
# d post-peak	- 0.864	0.2812	- 3.07	0.0069
Degree d post-peak	0.082	0.0188	4.36	0.0004

Table 7. Parameter estimates to predict first hatching date of smallmouth bass in the Yampa River (Reach 1), and the Green River upstream (Reach 2) and downstream (Reach 3) of the Yampa River, 2005-2011, as a function of April-July flow volume (Volume below).

Parameter	Estimate	SE	*T*-value	Pr > *T*
Intercept	149.68	3.08	48.55	< 0.0001
Volume (Reach 1)	0.018	0.0022	8.05	< 0.0001
Volume (Reach 2)	0.051	0.0056	9.12	< 0.0001
Volume (Reach 3)	0.013	0.0016	8.14	<0.0001

Table 8. Covariates used in the statistical model (Type III statistics) to predict TL of age-0 smallmouth bass in the Yampa River (Reach 1), and the Green River upstream (Reach 2) and downstream (Reach 3) of the Yampa River, 2005-2011. Final model statistics were: DF = 7, 49; $F = 82.67$; $p < 0.0001$; model fit was $R^2 = 0.92$. The predictive equation was: TL (mm) = 353.4 - 0.79*Jdays - Julytemp*19.11 + Julytemp^2*0.52 + Cohort (1, 2, or 3), + Reach (1, 2, 3), where Jdays was number of days from Jan. 1 to the first day of smallmouth bass hatching for the year in the Reach, Julytemp was the mean water temperature of the Reach from 1 July to 15 August, where Cohort 1 = 27.8, Cohort 2 = 13.7, and Cohort 3 = 0, and Reach 1 = 1.6, Reach 2 = -3.5, and Reach 3 = 0.

Source	DF	Type III SS	Mean Square	F-Value	Pr > F
cohort	2	7291.57	3645.79	105.11	<0.0001
Jdays	1	1793.52	1793.52	51.71	<0.0001
Jultemp	1	219.48	219.44	6.33	0.0152
Jultemp^2	1	286.95	286.95	8.27	0.0059
Reach	2	111.59	55.80	1.61	0.2105

Table 9. Covariates used in the final statistical model (Type III statistics, DF = degrees of freedom) to predict growth rate of age-0 smallmouth bass in the Yampa River, 2005-2011. Final model statistics were: $df = 3, 20$; $F = 13.44$; $p < 0.0001$; model fit was $R^2 = 0.70$. The predictive equation was: Growth rate (mm/day) = 1.70 - 0.0052*Jdays + cohort (1, 2, or 3), where Jdays was number of days from Jan. 1 to the first day of smallmouth bass hatching for the year, and where cohort 1 = 0.26, cohort 2 = 0.16, and cohort 3 = 0.

Source	DF	Type III SS	Mean Square	F-Value	Pr > F
cohort	2	0.236	0.118	14.89	0.0002
Jdays	1	0.084	0.084	10.54	0.0047

Table 10. Comparison of spring and summer growth rates of early life stages of invasive smallmouth bass and four native fishes in the upper Colorado River basin. Growth rate data are from published and unpublished sources (this study; Muth et al. 2000; Bestgen et al. 2006; Bestgen 2008; Bestgen et al. 2011; Zelasko et al. 2011).

Species	Growth rate (mm TL/d)
smallmouth bass	0.36-1.66
Colorado pikeminnow	0.15-0.65
flannelmouth sucker	0.18-0.67
bluehead sucker	0.15-0.58
razorback sucker	0.08-0.53

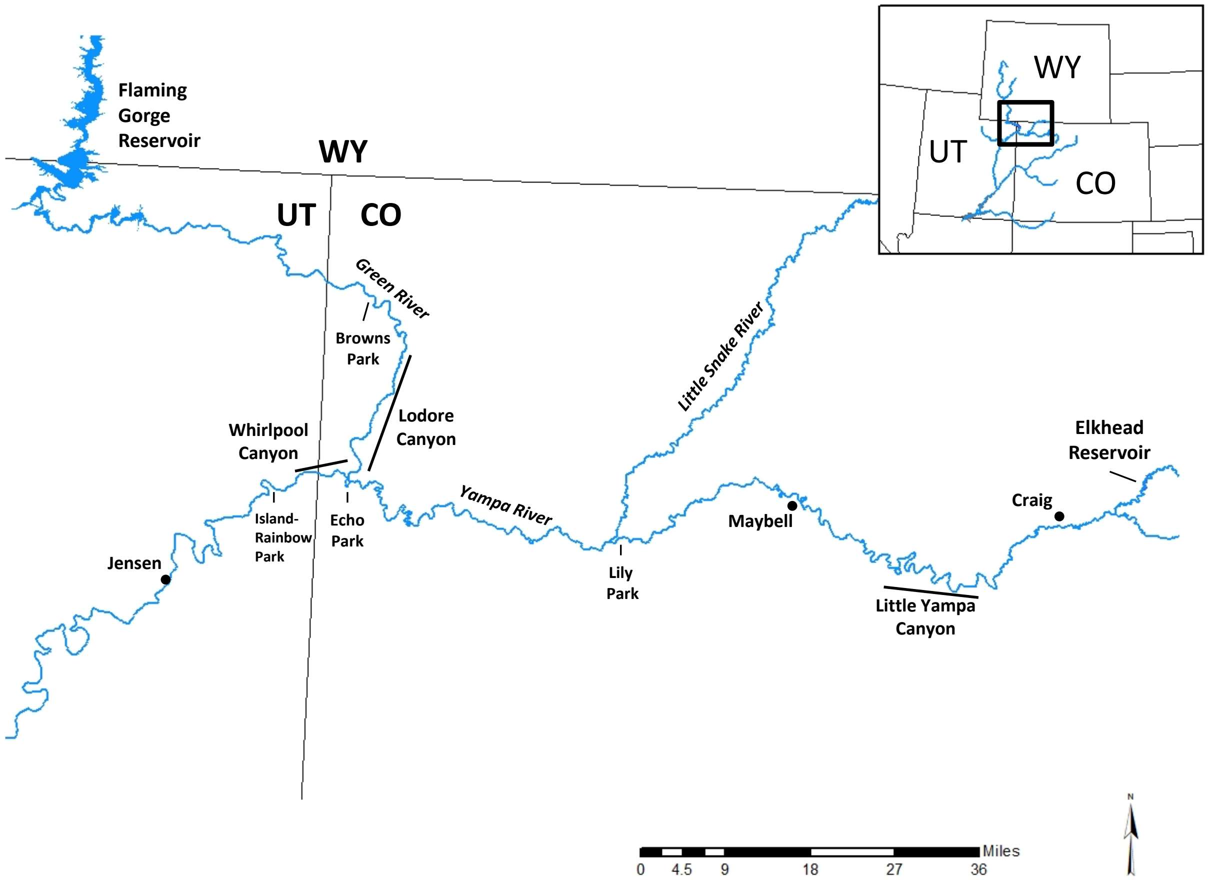


Figure 1. The Yampa River subbasin and the upper Green River basin including the Yampa River-Green River confluence at Echo Park in Dinosaur National Monument. Main study areas are Lodore Canyon and Whirlpool Canyon in the Green River and Little Yampa Canyon in the Yampa River.

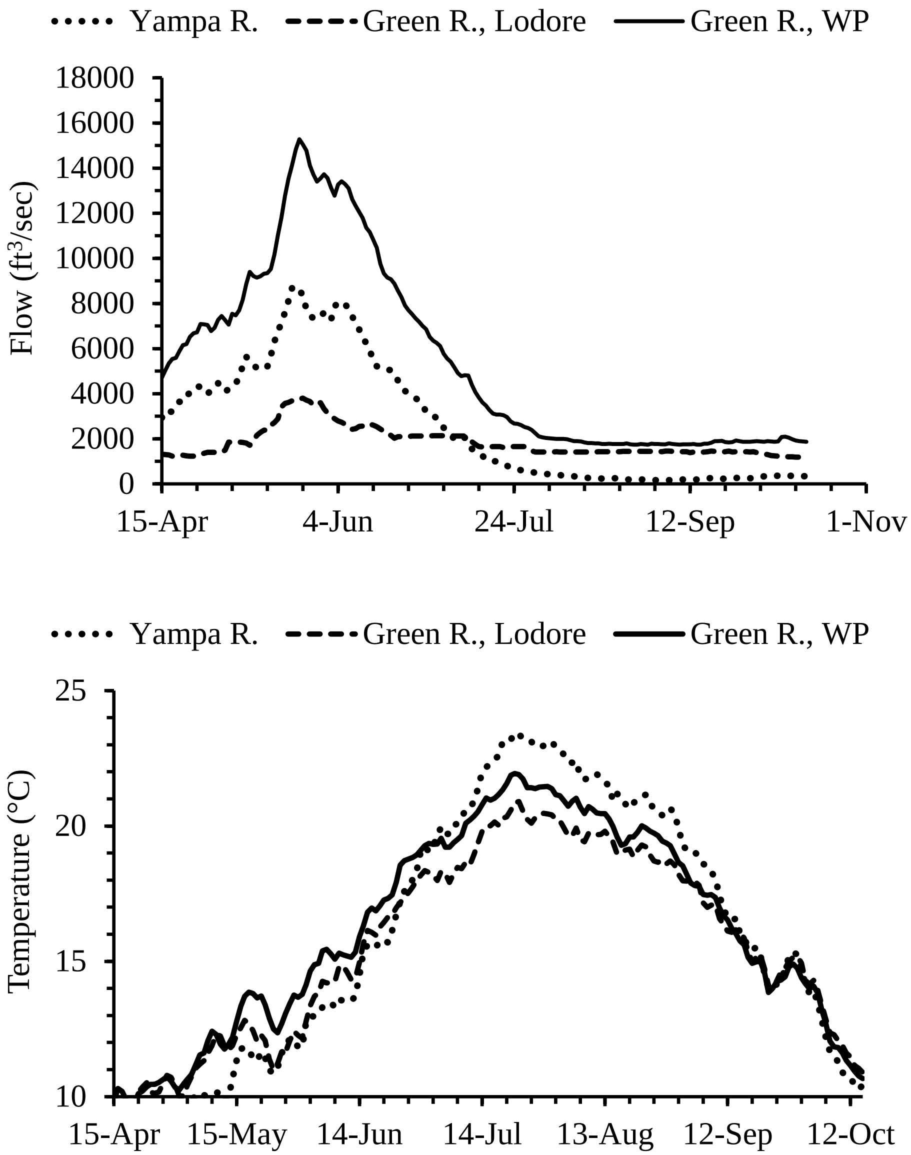
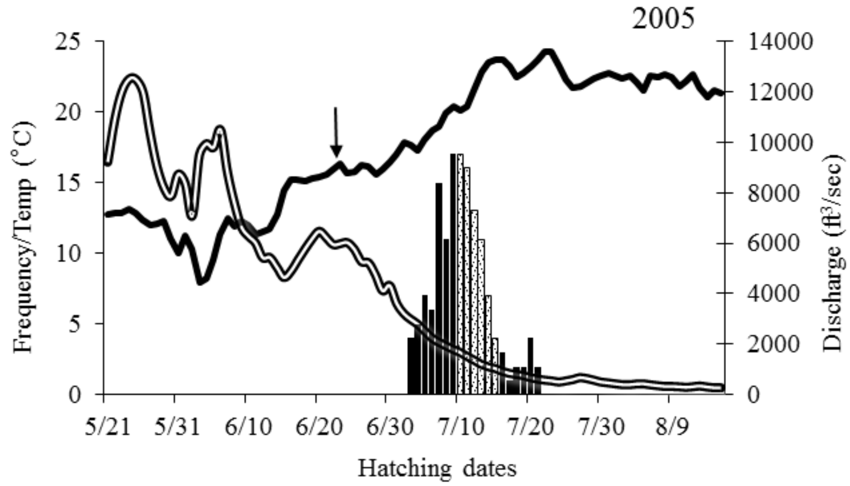
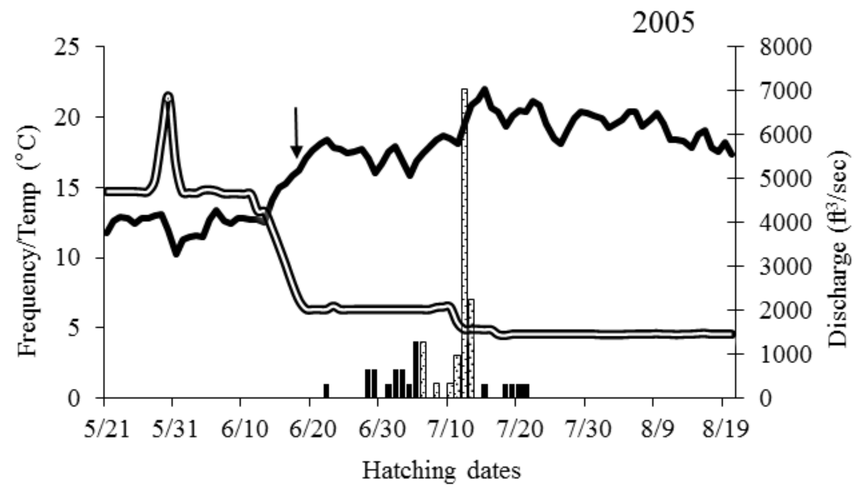
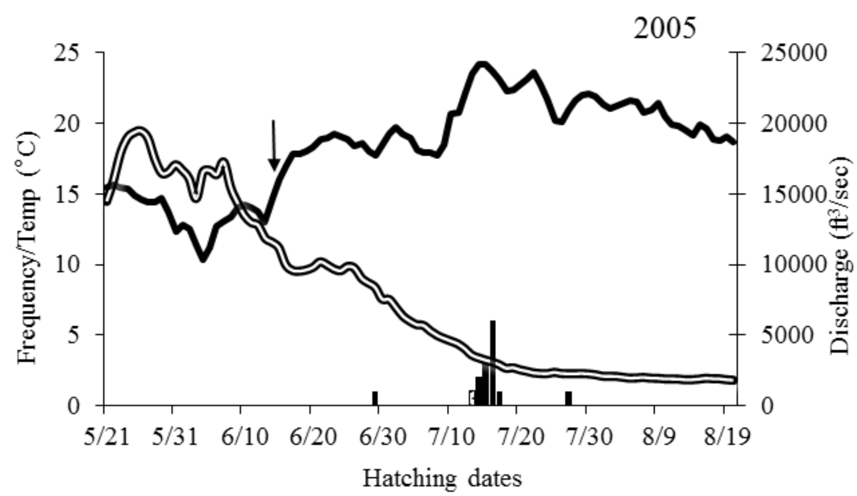


Figure 2. Mean daily flow of the Yampa River (Maybell gauge 09251000; does not include Little Snake River flows), the Green River upstream of the Yampa River (Lodore; Greendale gauge, 09234500), and the Green River downstream of the Yampa River (WP; Jensen gauge, 09261000), 2005-2011. Mean daily water temperatures for the Yampa River were from a site near Maybell, CO (Juniper Springs), those for the Green River at the lower end of Lodore Canyon, and those for the Green River downstream of the Yampa River were from near Mitten Park (all three sites; http://www.fws.gov/mountain-prairie/riverdata/index.html).







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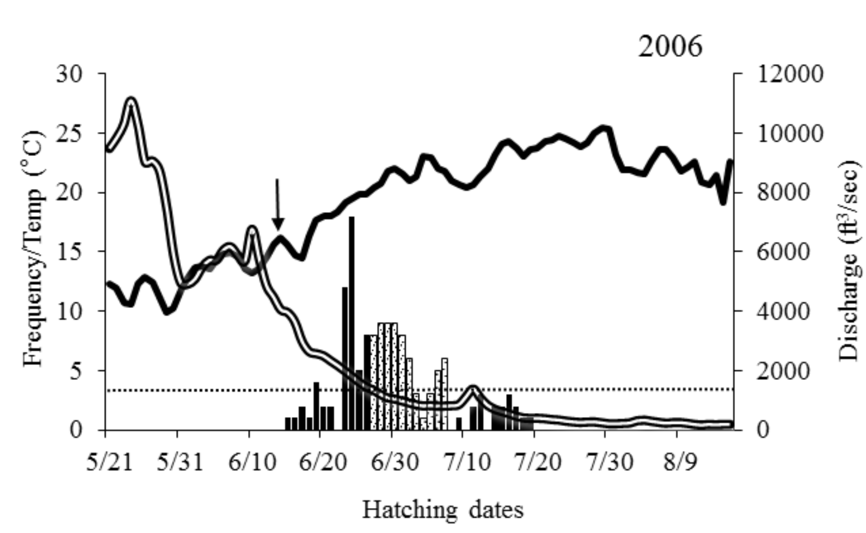

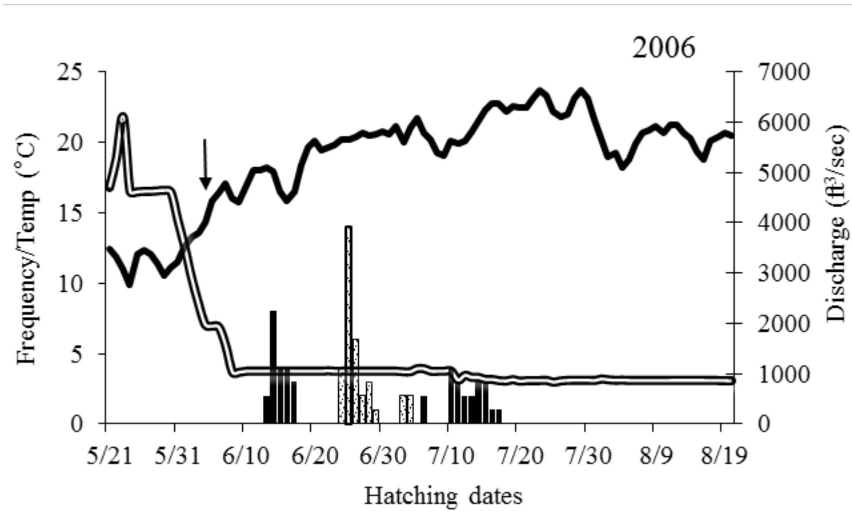

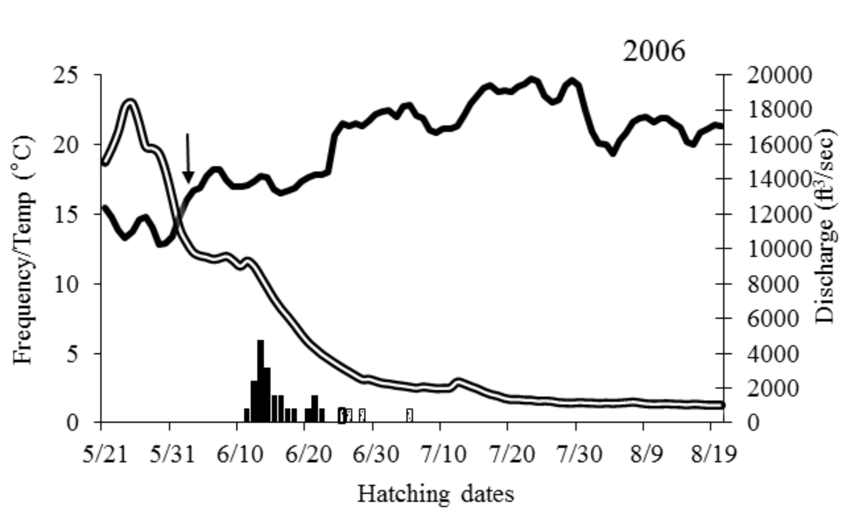

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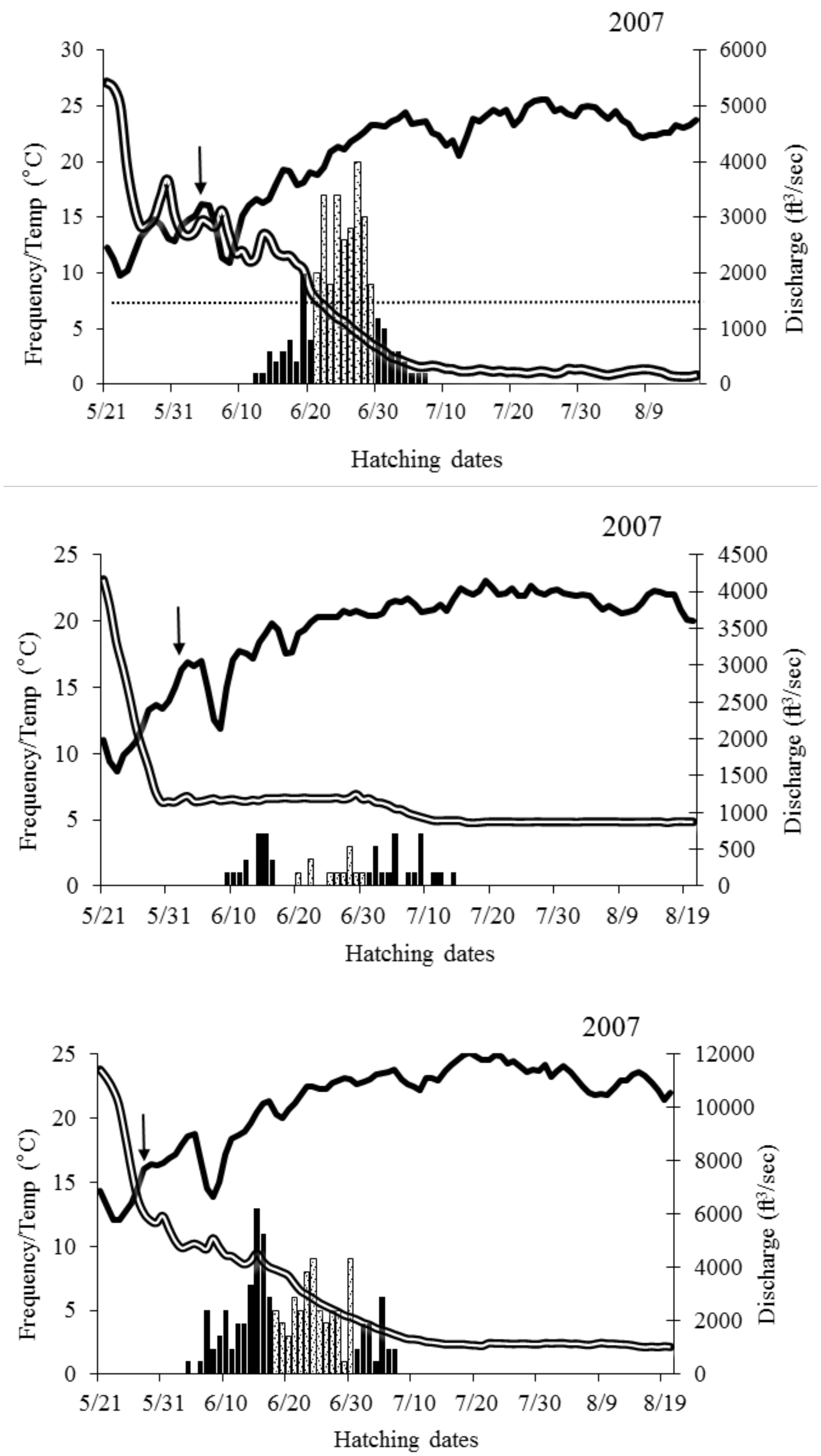

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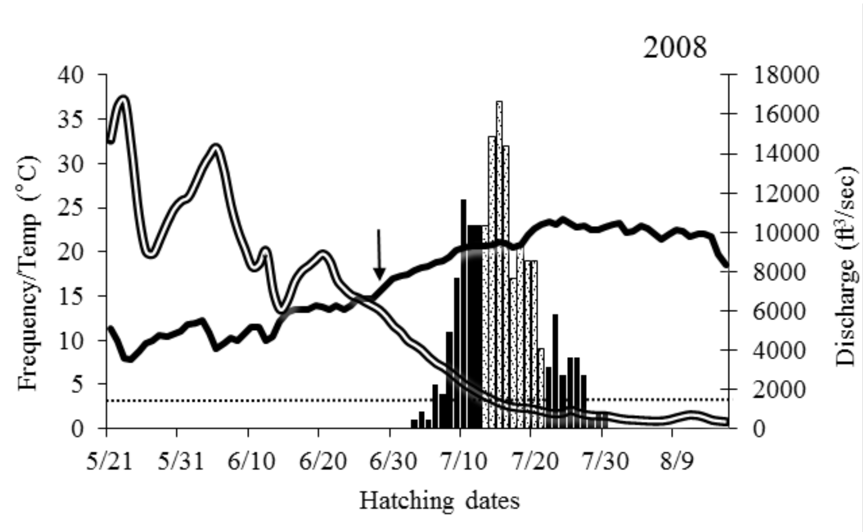

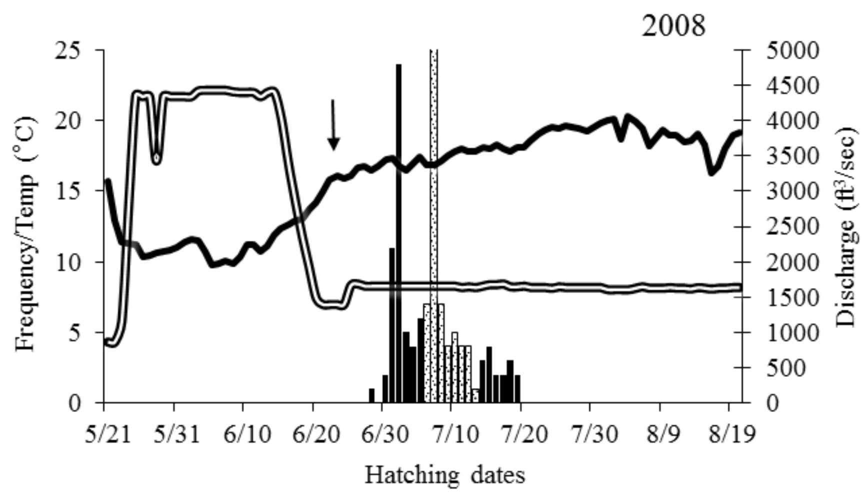

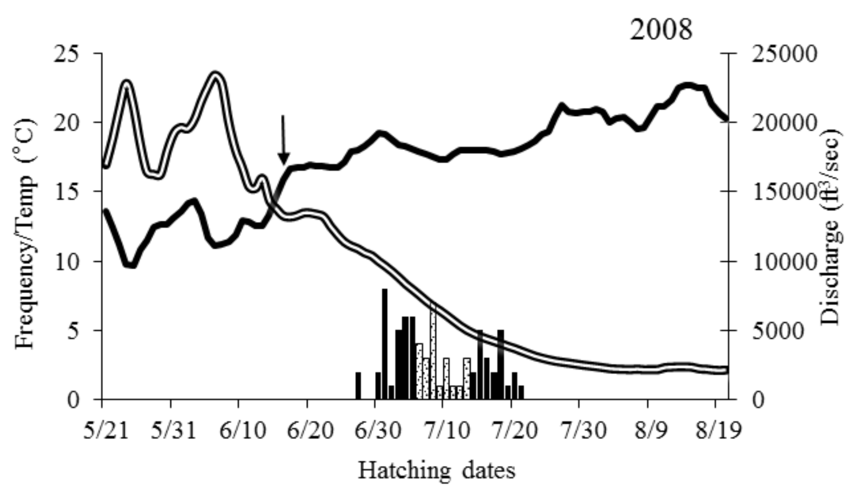

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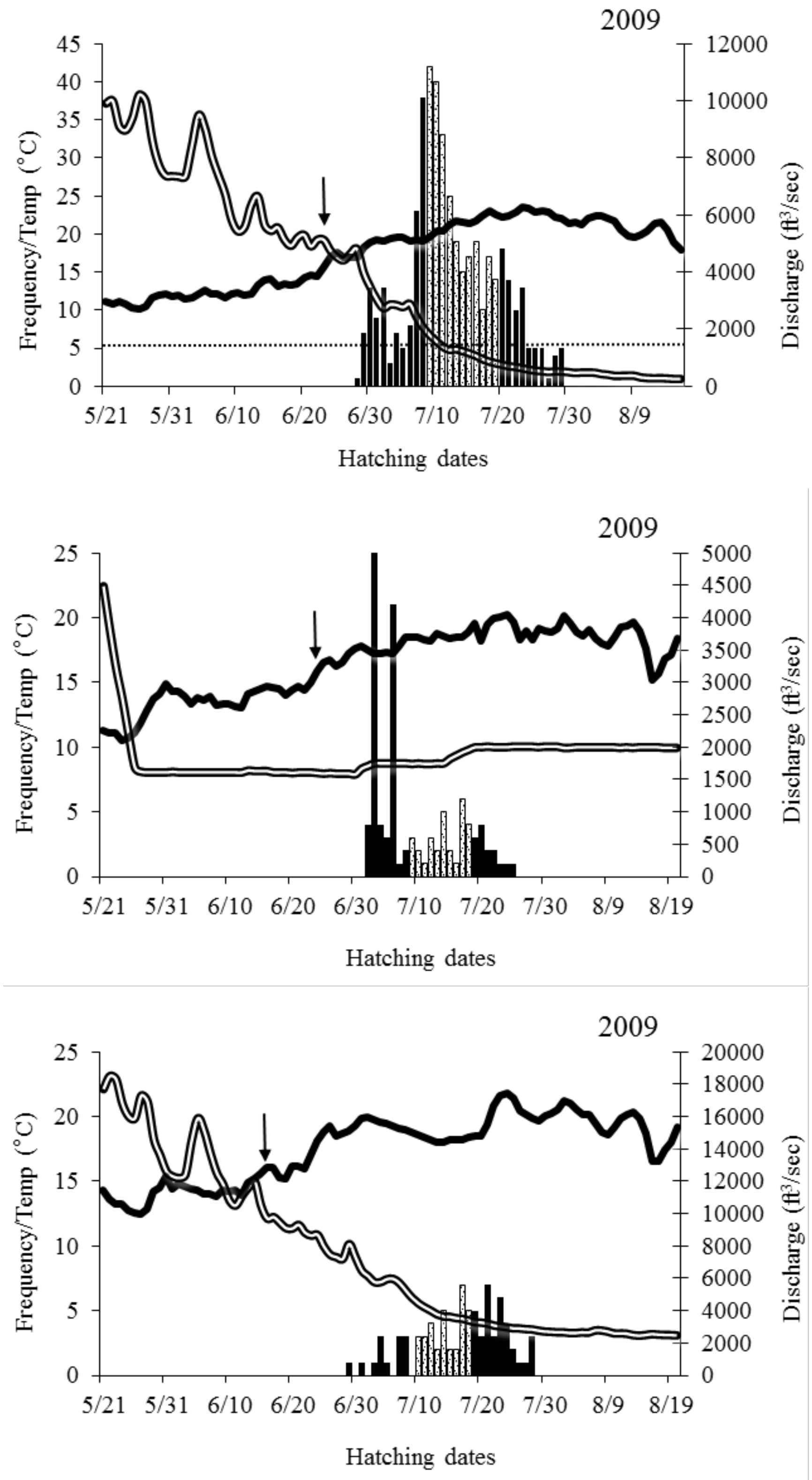

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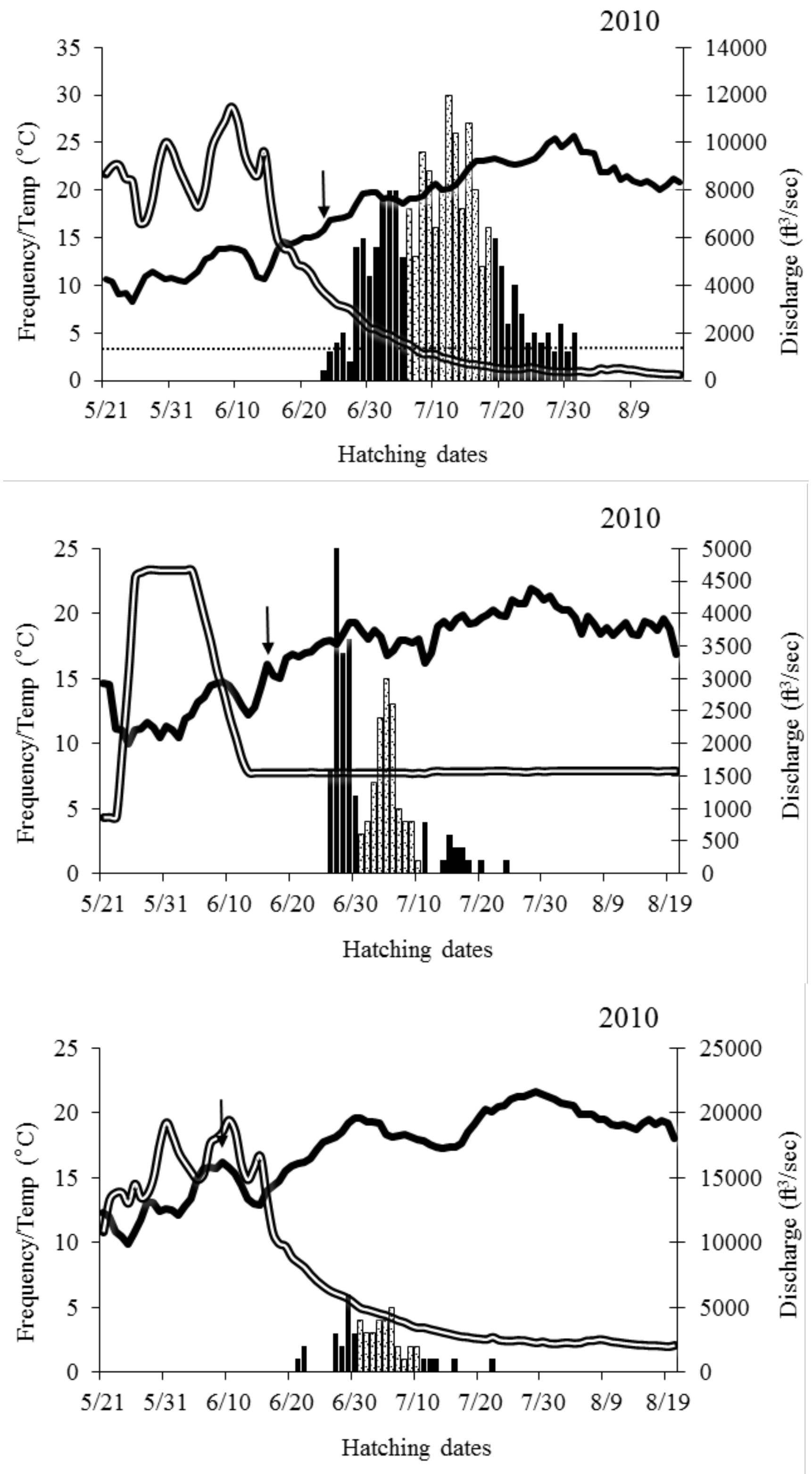

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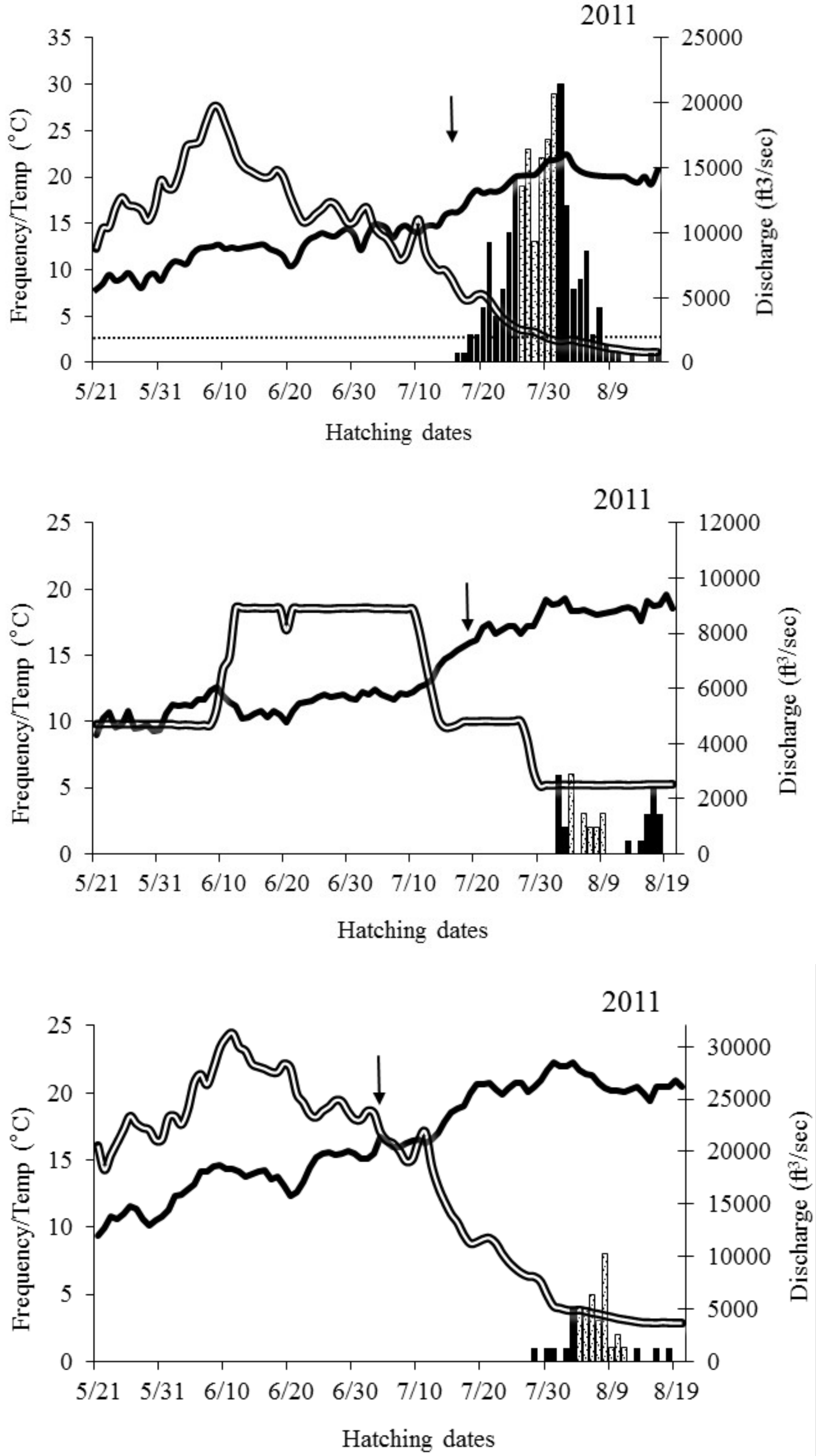


Figure 3. Frequency distributions of hatching dates for age-0 smallmouth bass captured in the Yampa River (upper panel), the regulated Green River upstream of the Yampa River (middle

panel), and the partially regulated Green River downstream of the Yampa River, Colorado and Utah (lower panel), for years 2005-2011. Water temperatures (solid line) for the Yampa River were from a site near Maybell, CO, those for the Green River in Lodore Canyon were from just upstream of the Yampa River, and those for the Green River downstream of the Yampa River were from near Mitten Park (http://www.fws.gov/mountain-prairie/riverdata/index.html). Discharge data (double lines) for the Yampa River were from Maybell, CO (U. S. Geological Survey gauge, 09251000), those for the Green River, Lodore Canyon from the Greendale, Utah gauge (U. S. Geological Survey Gauge 09234500), and for the Green River downstream of the Yampa River were from the Jensen, Utah gauge (U. S. Geological Survey Gauge 09261000). The vertical arrow represents the first day when mean daily water temperature exceeded 16°C. The three cohorts of age-0 smallmouth bass in histograms were derived by dividing the distribution into approximately equal thirds through time, and are indicated by filled (Cohort 1), open dotted (Cohort 2), and filled (Cohort 3) bars proceeding from left to right.

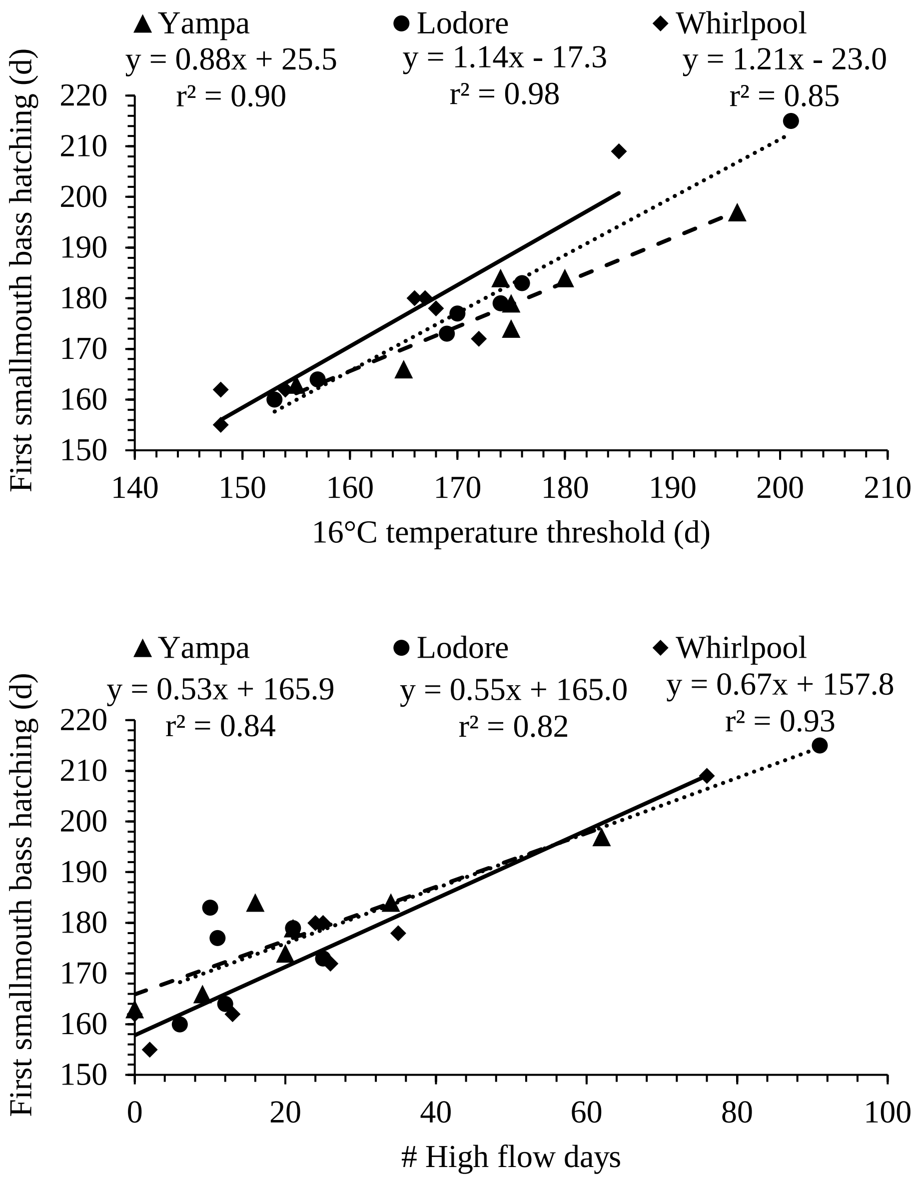


Figure 4. First hatching date of smallmouth bass in the Yampa River (solid line), the Green River upstream of the Yampa River (Lodore, dotted line) and the Green River downstream of the Yampa River (Whirlpool, dashed line) from 2005-2011 (2004 included for Whirlpool reach) as a function of Julian day that mean daily water temperature exceeded a 16°C threshold, and first hatching date as a function of high flow days in each reach in the spring of that year (lower panel). Hatching dates were estimated by counting otolith daily increments in young bass; first hatching date and the 16°C water temperature threshold was calculated as the number of days beginning 1 January (30 June is 181 days in a non-leap year).

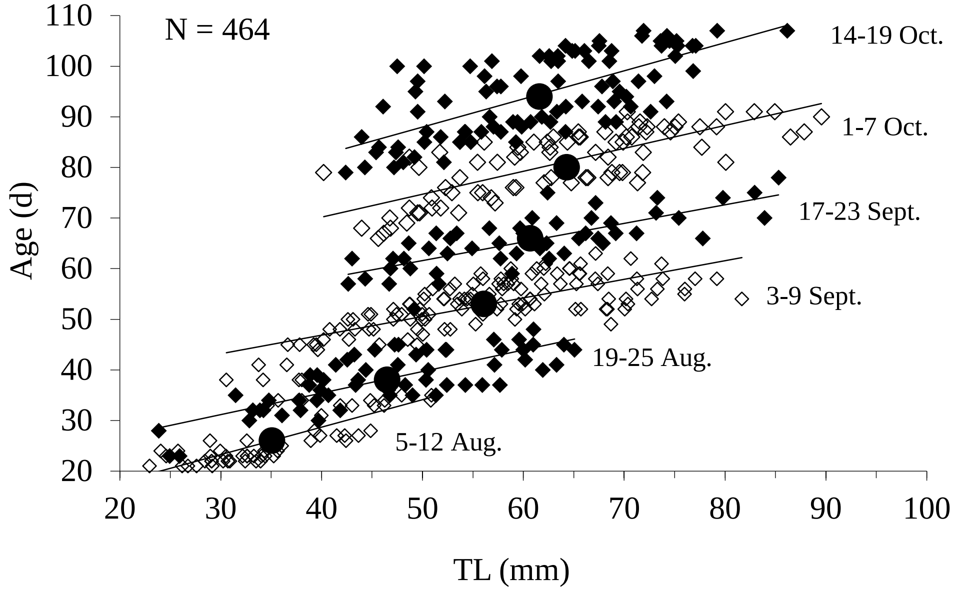
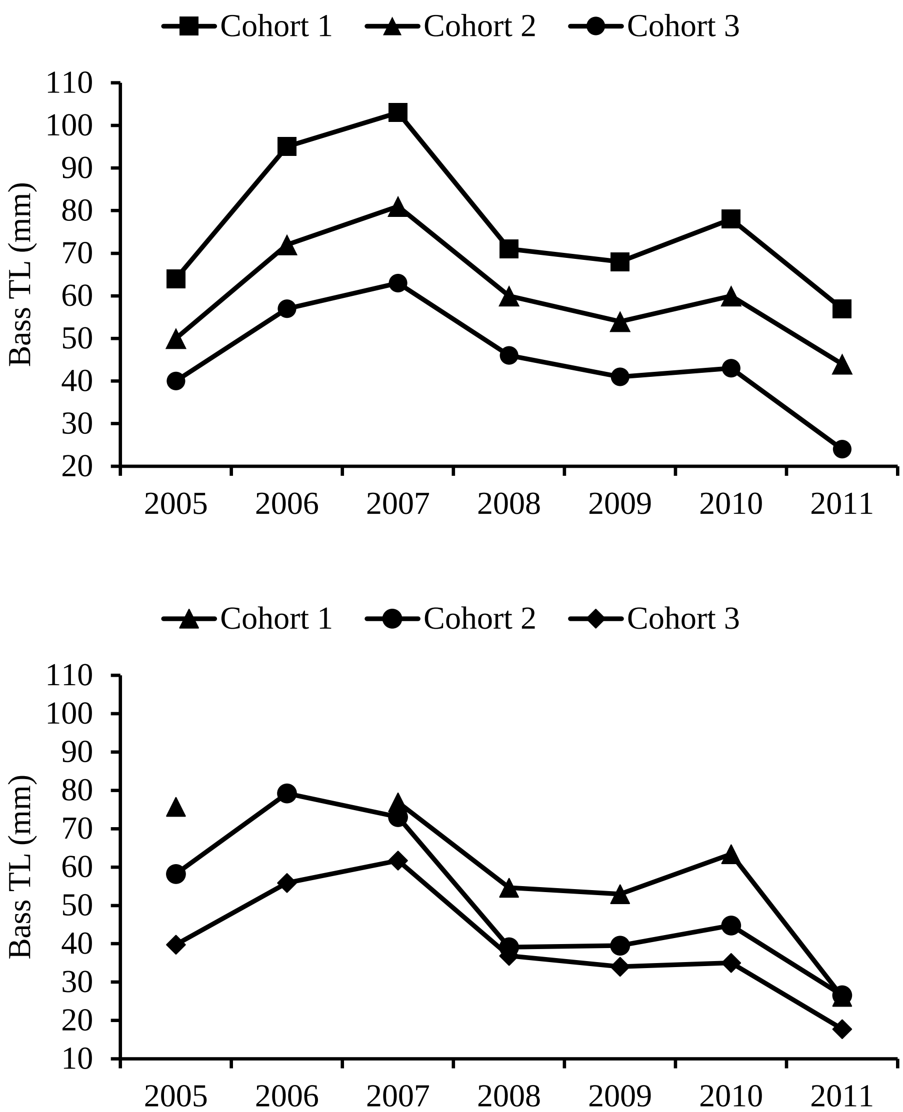


Figure 5. Age as a function TL of age-0 smallmouth bass collected from the Yampa River, Little Yampa Canyon, near Maybell, CO, 2008. Sampling dates are indicated for proximal groups of age and length data indicated by open and filled diamonds. Regression lines indicate slopes of age as a function of length relationships, and large filled circles indicate mean age and mean TL of age-0 smallmouth bass in samples from each period.



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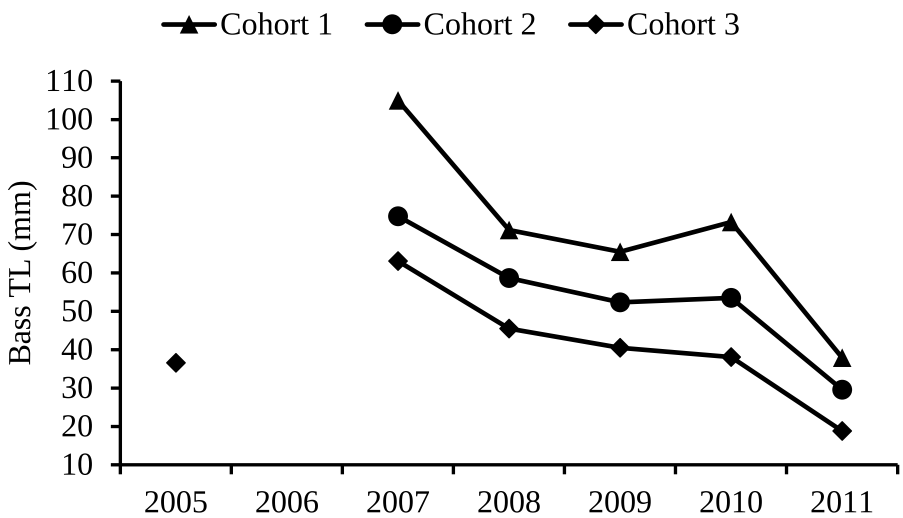


Figure 6. Mean TL of age-0 smallmouth bass in Cohorts 1-3 collected in mid-September from the Yampa River, Little Yampa Canyon, near Maybell, CO (upper panel), the Green River upstream of the Yampa River (Lodore Canyon), Colorado (middle panel; no data for Cohort 1, 2006), and the Green River downstream of the Yampa River (Whirlpool Canyon), Colorado and Utah (lower panel; no data for all of 2005-2006 except Cohort 3, 2005), 2005-2011. The three cohorts of age-0 smallmouth bass were derived by dividing the distribution of hatching dates for each year into approximately equal thirds through time, and calculating the mean TL of fish in each. Cohort 1 contained the earliest hatching fish, cohort 2 contained fish hatched in the middle of the season, and cohort 3 fish hatched latest in the year.

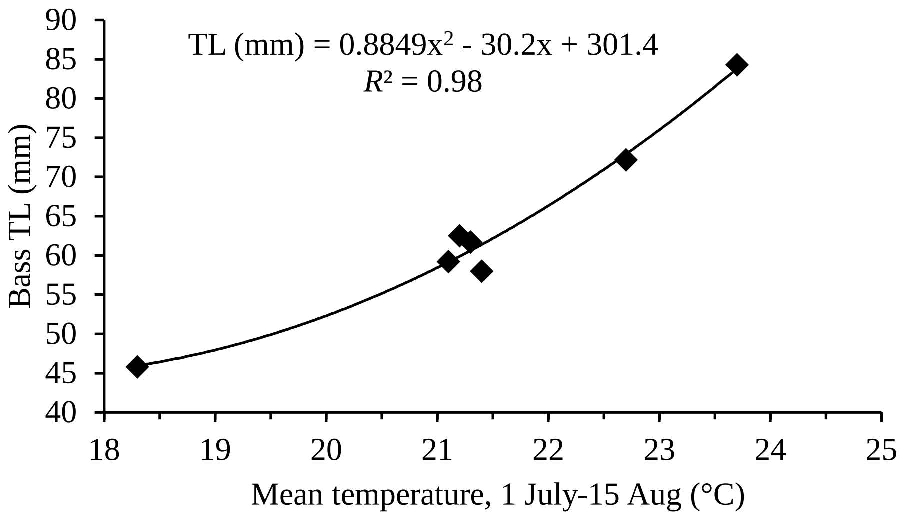
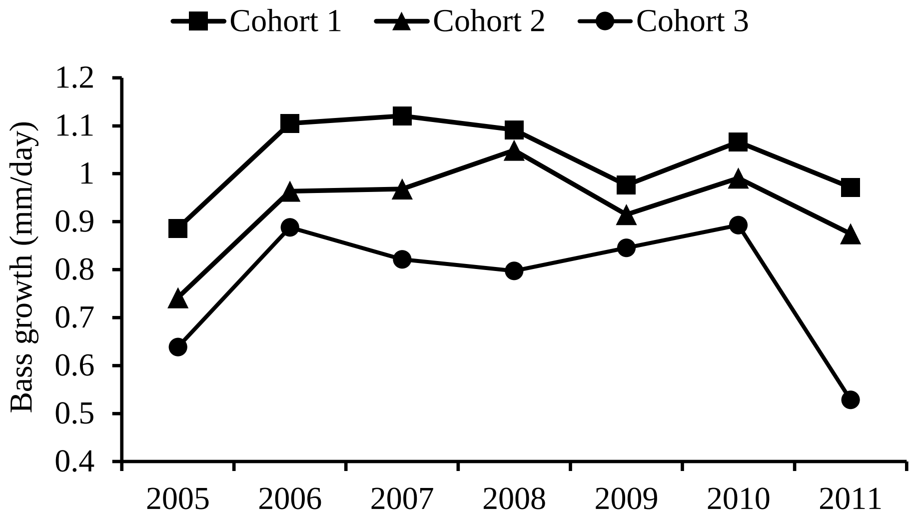
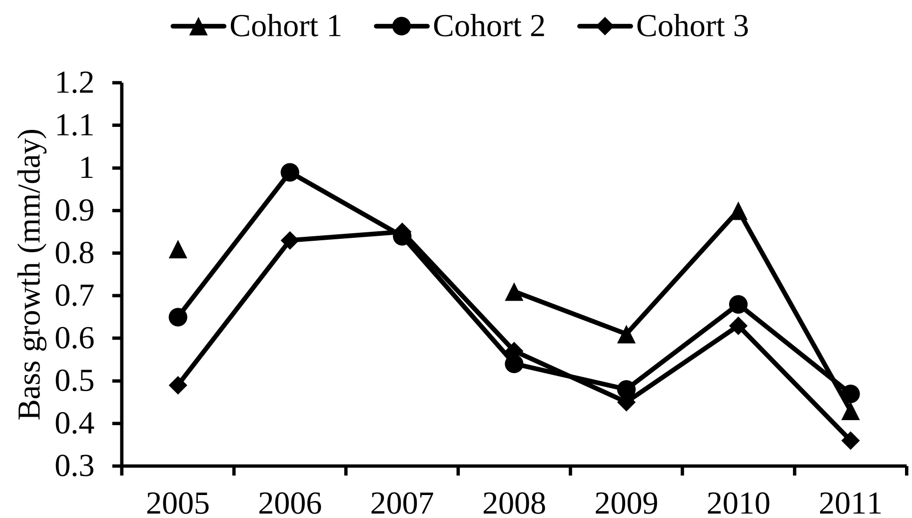


Figure 7. Mean annual age-0 smallmouth bass TL from samples collected in mid-September as a function of mean daily summer water temperature from 1 July-15 August in the Yampa River, Little Yampa Canyon, near Maybell, CO, 2005-2011. The lowest water temperature and TL datum is year 2011, and the highest is 2007.


Cohort 1
Cohort 2
Cohort 3
Bass growth (mm/day)
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
2005
2006
2007
2008
2009
2010
2011


Cohort 1
Cohort 2
Cohort 3
Bass growth (mm/day)
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
2005
2006
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2008
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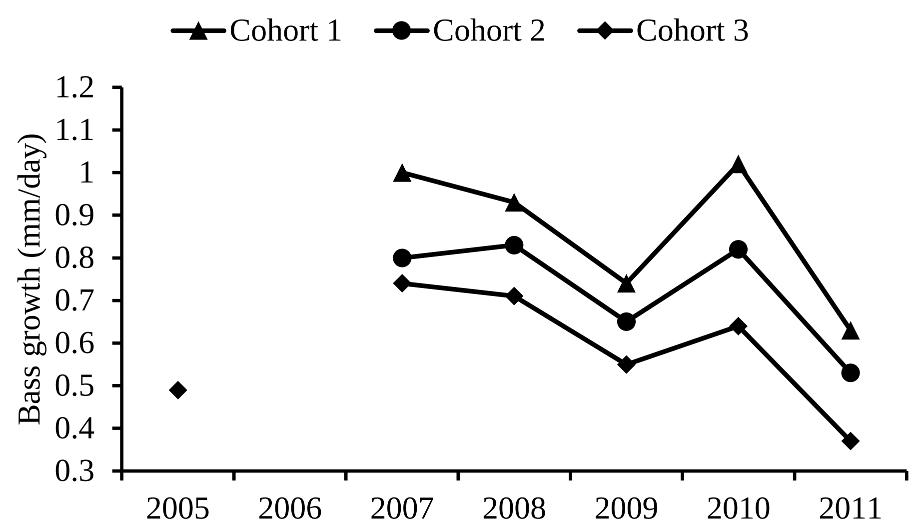
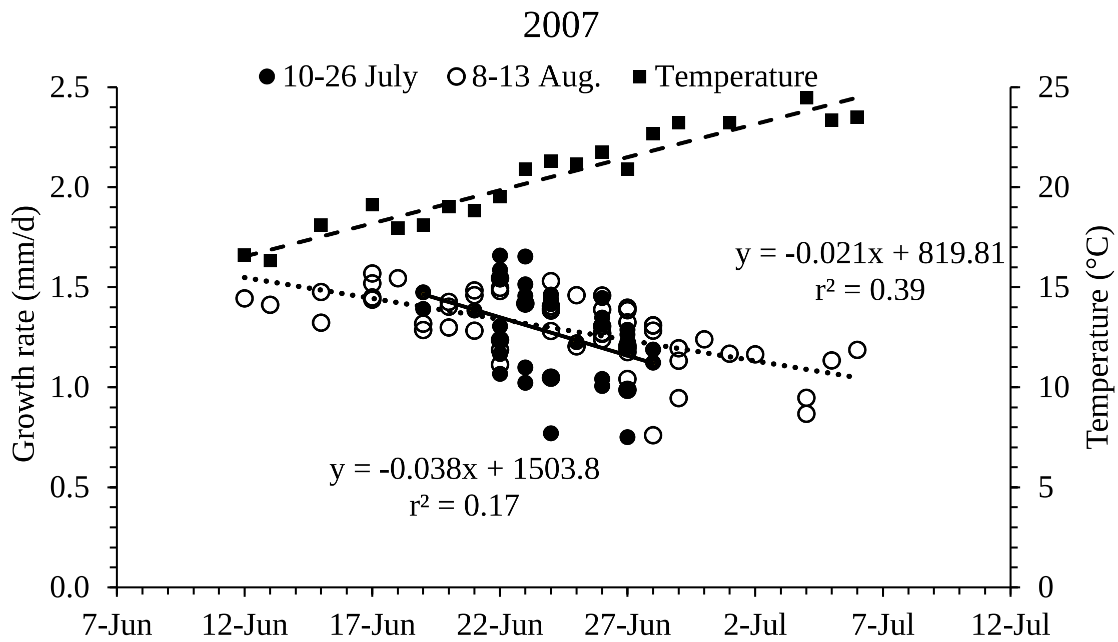
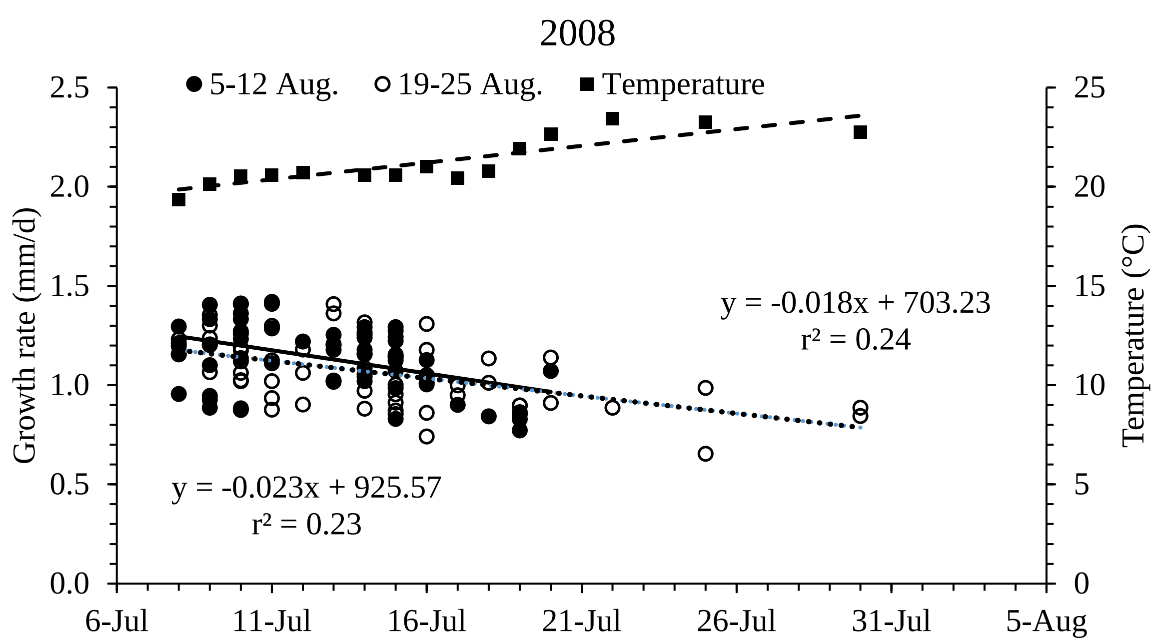

Cohort 1
Cohort 2
Cohort 3
Bass growth (mm/day)
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
2005
2006
2007
2008
2009
2010
2011

Figure 8. Mean daily growth rate (mm) of age-0 smallmouth bass in Cohorts 1-3 collected in mid-September from the Yampa River, Little Yampa Canyon, near Maybell, CO (upper panel), the Green River upstream of the Yampa River (Lodore Canyon), Colorado (middle panel; no data for Cohort 1, 2006), and the Green River downstream of the Yampa River (Whirlpool Canyon), Colorado and Utah (lower panel; no data for all of 2005-2006 except Cohort 3, 2005), 2005-2011. The three cohorts of age-0 smallmouth bass were derived by dividing the distribution of hatching dates for each year into approximately equal thirds through time, and calculating the mean TL of fish in each. Cohort 1 contained the earliest hatching fish, cohort 2 contained fish hatched in the middle of the season, and cohort 3 fish hatched latest in the year.





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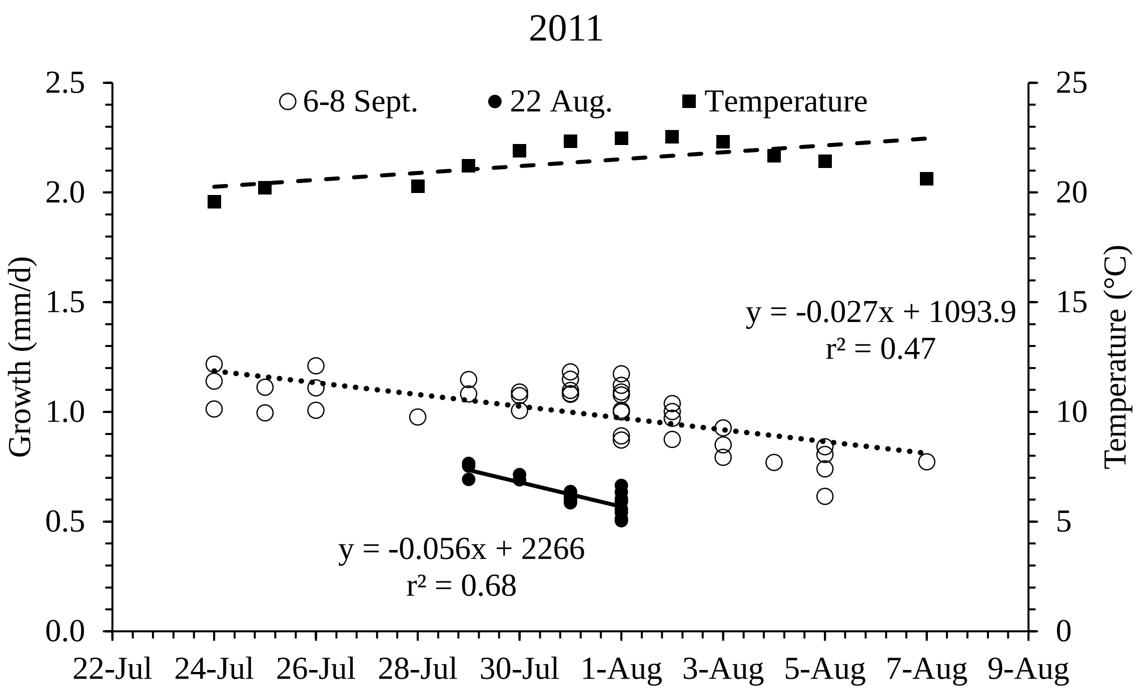


Figure 9. Growth (mm/d) of age-0 smallmouth bass in the Yampa River in a low flow, warm year (2007), a moderate temperature and moderately high flow year (2008), and a cool and high flow year (2011) when bass hatched relatively early, mid-season, and late, respectively. Smallmouth bass samples were mainly from Little Yampa Canyon (a few from Lily Park in 2008) and were from the first two sampling occasions each year when water temperatures were typically the warmest achieved for the year.

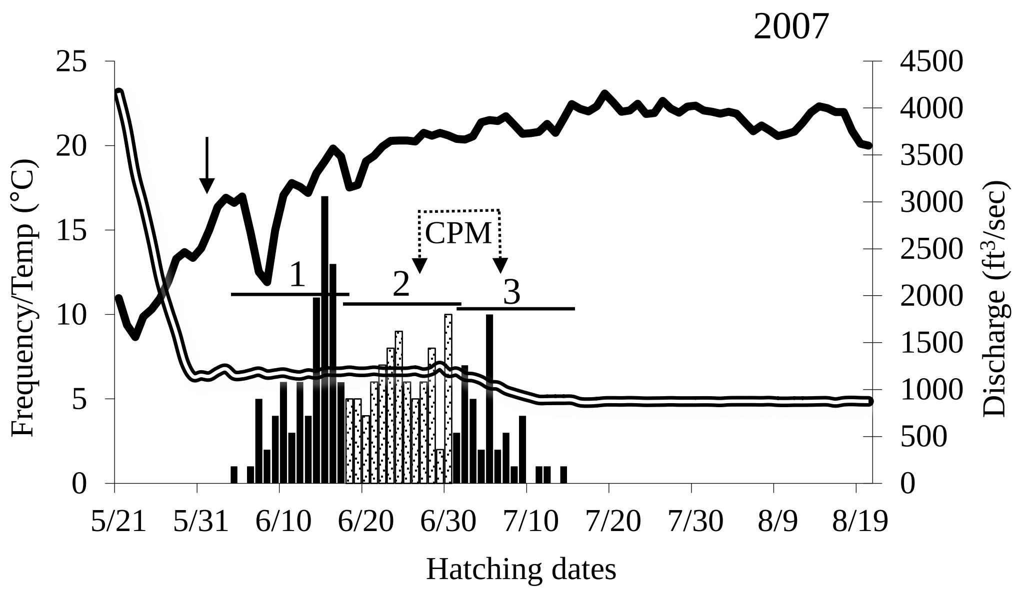


Figure 10. Hatch date distribution for smallmouth bass combined for the regulated and partially regulated sections of the Green River, Colorado and Utah, 2007, to show the range of dates for hatching; flow and water temperature regimes are from the regulated upstream section. Solid vertical arrow indicates onset of 16°C water temperature in the upstream regulated reach, the over-numbered horizontal solid lines indicate temporal extent of 1st, 2nd, and 3rd hatching cohorts, and the dotted vertical arrows indicate dates of first capture of drifting Colorado pikeminnow (CPM) larvae hatched in the Yampa River and the first drift peak entering the Green River.

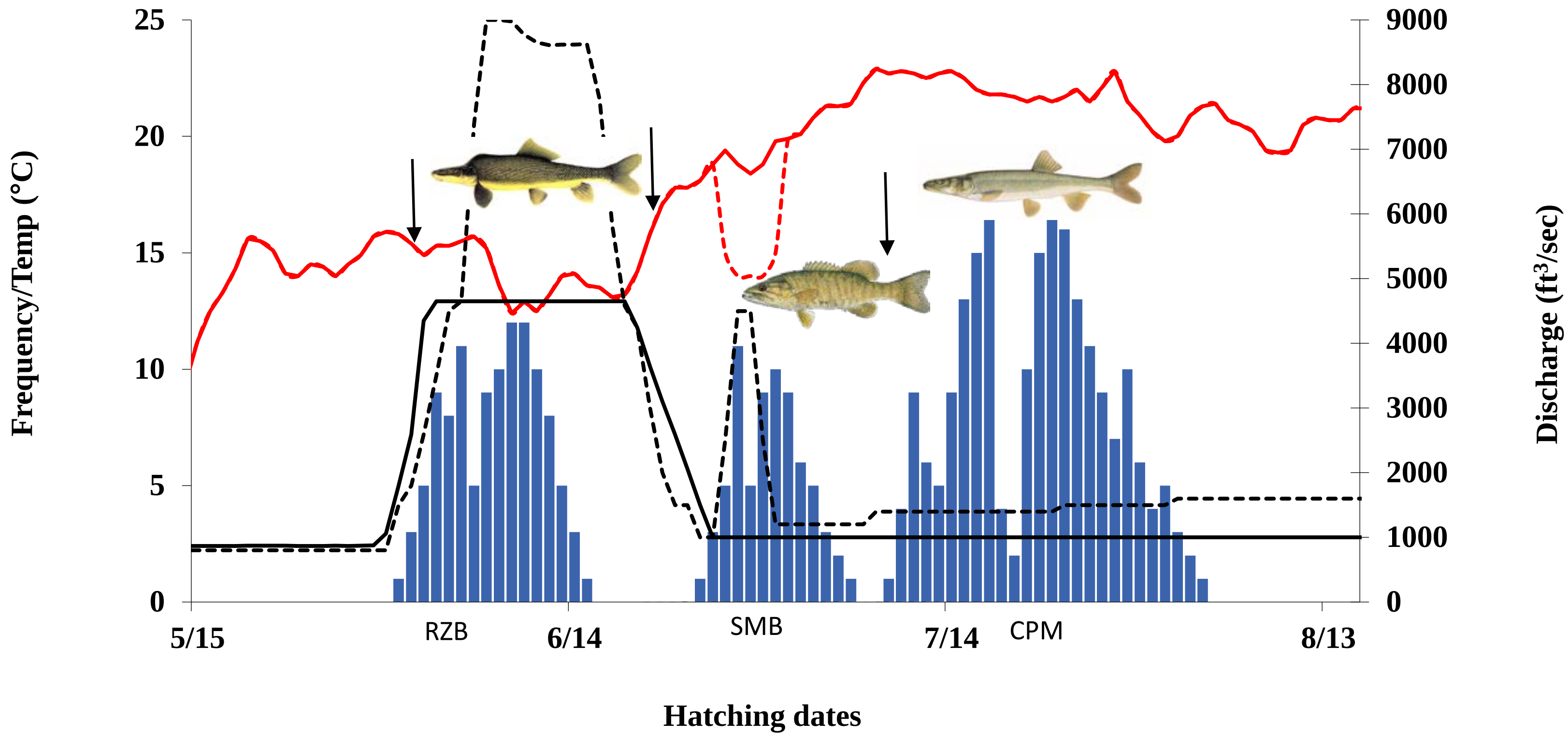


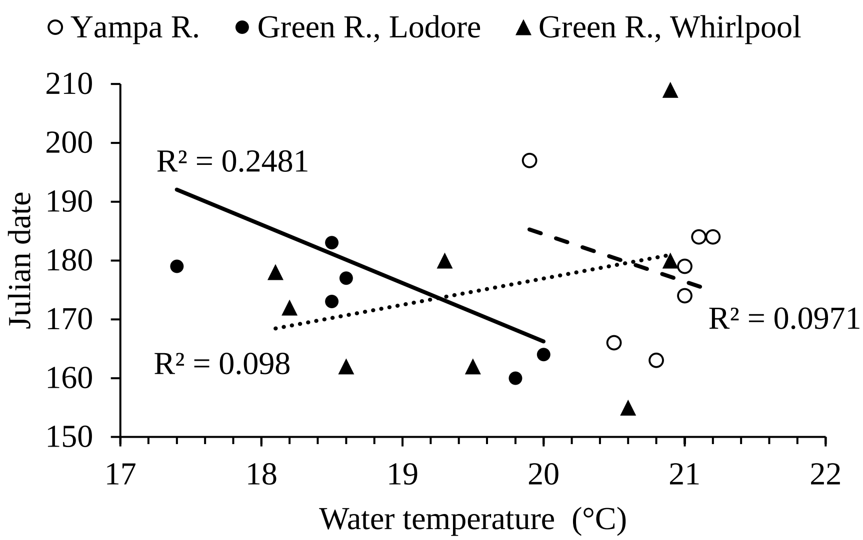
Figure 11. Conceptual diagram showing temporal sequencing of flow and water temperature regimes to benefit native razorback sucker and Colorado pikeminnow and disadvantage invasive smallmouth bass in the Green River, downstream of Flaming Gorge Dam. Hatching dates for each species (indicated by arrows) are well-known and used to trigger flow management actions at appropriate times. Solid black line indicates a standard flow release from Flaming Gorge Dam under the 2006 Record of Decision. The dashed line indicates proposed (and presently implemented) higher magnitude flows for razorback sucker in spring under the Larval Trigger Study Plan to promote floodplain connection with the Green River, the flow spike in late June is designed to disadvantage the early portion of smallmouth bass reproduction, and increased baseflows in summer are designed to benefit age-0 Colorado pikeminnow in Green River nursery backwaters. The water temperature decline associated with the late June flow during

smallmouth bass hatching could be effected either by reduced water warming as higher flows proceed downstream more quickly, or by releasing colder water from the variable elevation penstocks at Flaming Gorge Dam.

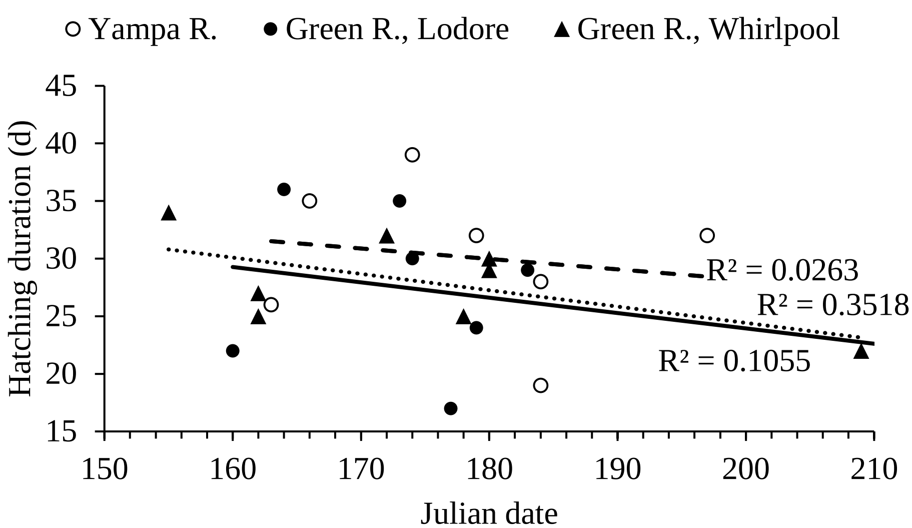
Appendix I. Parameters used to estimate first hatching date for smallmouth bass in the Yampa River (River reach 1), and the Green River upstream (reach 2) and downstream (reach 3) of the Yampa River, 2004-2011. The bottom row of numbers is the Pearson correlation coefficient of the number of days to first smallmouth bass hatching and the variable at the top of the column.

First SMB hatching	River Reach	Year	Maximum Flow	Mean flow, hatching	Mean temp, hatching	# high flow days	# days post-peak	Julian day first 16°C	Diff 16°C and hatching	Degree d annual	Degree d post-peak	April-July flow (K ac-feet)
184	1	2005	12500	3028	17.5	16	39	174	10	1232	527	1332
166	1	2006	11100	3816	15.3	9	22	165	1	856	295	1202
163	1	2007	6330	2442	16.2	0	28	155	8	893	372	736
184	1	2008	16700	4286	17.9	34	41	180	4	923	513	1847
179	1	2009	10200	4252	17.6	21	33	175	4	1064	441	1654
174	1	2010	11500	3802	16	20	14	175	-1	852	192	1359
197	1	2011	19600	5542	16.7	62	37	196	1	1108	501	2903
173	2	2005	6890	2046	18	25	23	169	4	1312	318	555
164	2	2006	6110	1040	17.7	12	21	157	7	1091	297	412
160	2	2007	4440	1172	14.9	6	21	153	7	1073	273	318
179	2	2008	4336	1666	16.8	21	21	174	5	1100	284	447
183	2	2009	4490	1692	17.5	10	42	176	7	1392	597	414
177	2	2010	4660	1542	17.8	11	22	170	7	1276	335	390
215	2	2011	9190	2482	18.9	91	23	201	14	1277	374	1327
162	3	2004	11400	5050	16.4	0	29	148	14	1189	447	991
180	3	2005	19500	8244	18.4	25	34	166	14	1341	523	1887
162	3	2006	18400	9006	17.2	13	17	154	8	1094	269	1615
155	3	2007	12500	4830	17.8	2	18	148	7	994	272	1053
178	3	2008	23500	10880	18	35	21	168	10	1060	317	2293
180	3	2009	18500	7276	19	24	38	167	13	1319	578	2068
172	3	2010	19400	8522	16	26	11	172	0	1102	159	1749
209	3	2011	31300	7750	20.8	76	47	185	24	1652	780	4229
		0.64	0.38	0.09	0.62	0.92	0.53	0.92	0.40	0.56	0.59	0.58

Appendix II. First hatching date of smallmouth bass (Julian date, number of days since January 1) as a function of mean water temperature during the hatching season in the unregulated Yampa River, the regulated Green River upstream of the Yampa River (Lodore), and the partially regulated Green River downstream of the Yampa River (Whirlpool), 2005-2011. Solid line is Green River, Lodore reach, dotted line is Green River, Whirlpool reach, and dashed line is Yampa River.



Appendix III. Duration of the smallmouth bass hatching season as a function of first hatching date (Julian date, number of days since January 1) in the unregulated Yampa River, the regulated Green River upstream of the Yampa River (Lodore), and the partially regulated Green River downstream of the Yampa River (Whirlpool), 2005-2011. Solid line is Green River, Lodore reach, dotted line is Green River, Whirlpool reach, and dashed line is Yampa River.



Appendix IV. Duration of the smallmouth bass hatching season as a function of mean water temperature during the same period in the unregulated Yampa River, the regulated Green River upstream of the Yampa River (Lodore), and the partially regulated Green River downstream of the Yampa River (Whirlpool), 2005-2011. Solid line is Green River, Lodore reach, dotted line is Green River, Whirlpool reach, and dashed line is Yampa River.