

Reproduction, abundance, and recruitment dynamics of young
Colorado pikeminnow in the Green and Yampa rivers,
Utah and Colorado, 1979-2012

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EXECUTIVE SUMMARY

This study was conducted to assess aspects of reproduction, recruitment, and status of early life stages of Colorado pikeminnow *Ptychocheilus lucius* in the Green and Yampa rivers of the Green River subbasin, Utah and Colorado. The first dataset used was from daily drift net sampling of Colorado pikeminnow larvae in summer in the lower Yampa River from 1990-2012 (no sampling in 1997) and the lower Green River from 1991-1996 and 1999. Both sampling sites were within 25 river kilometers downstream of the two main areas of Colorado pikeminnow reproduction in the Green River subbasin. These data enabled estimation of timing of reproduction and a larvae transport abundance index, a flow-corrected metric of annual reproductive effort. A second main dataset was annual (autumn) seine sampling of age-0 Colorado pikeminnow in channel margin backwaters from 1979-2012. That sampling was conducted in middle and lower Green River nursery habitat reaches that were supplied with drifting larvae from upstream spawning areas in the lower Yampa River and the lower Green River, respectively. Because production of age-0 pikeminnow is related to recruitment of adults several years later (adults take 7-9 years to mature), factors that drive abundance of young fish likely affects abundance of adults. Thus, we examined relationships between peak and summer base flow and other environmental factors in each system relative to 1) production of larvae from spawning areas, 2) production of age-0 pikeminnow in backwaters, 3) abundance of larvae relative to age-0 Colorado pikeminnow, and 4) abundance of age-0 to age-1 pikeminnow the next year. We also examined abundance patterns of selected nonnative fishes, including red shiner *Cyprinella lutrensis*, a potential competitor with and predator on native fish larvae including Colorado pikeminnow, other nonnative minnows, and smallmouth bass *Micropterus dolomieu*, relative to the same flow and environmental parameters to better understand potential interactions.

Colorado pikeminnow reproduced each year that sampling occurred in the Green River subbasin at two main localities, the lower Yampa River in Yampa Canyon and the lower Green River in Gray Canyon, from 1979 through 2012. Timing of summer reproduction was positively related to peak spring runoff magnitude, as well as water temperature. Regression models were fit that described timing of reproduction moderately well. Abundance of larvae produced from spawning areas was positively correlated with both spring peak and mean

July-August flow in the downstream portions of the Yampa and Green rivers. In low flow years in the middle Green River, few larvae were produced from spawning areas and transported to nursery habitat reaches in summer (e.g., 1994, 2002, and 2007), so few age-0 pikeminnow were documented, especially in middle Green River backwaters in autumn. In most other years in the middle Green River, production of larvae was sufficient to produce more age-0 fish, but other factors limited their survival and recruitment in autumn. Abundance of larvae produced in the Yampa River was substantially higher than that for the lower Green River in each of seven years, except the low flow year 1994. Relationships between abundance of larvae and age-0 Colorado pikeminnow in the lower Green River were also positive but less certain given the fewer years of data.

Densities of age-0 Colorado pikeminnow captured in backwaters in autumn in the middle and lower Green River declined over the study period, and was a key reason motivating this study. This need was also identified in the Green River Study Plan, a research needs document drafted to address uncertainties in flow and water temperature recommendations implemented for Flaming Gorge Dam operations. Density of age-0 Colorado pikeminnow was higher in the lower than the middle Green River, even though fewer larvae were produced in the lower Green River. We also found that backwater number and area were more limited in the lower than the middle Green River. Thus, higher age-0 Colorado pikeminnow densities in the lower Green River may be a function of less available habitat, rather than real differences in abundance among the reaches; mark-recapture abundance estimation of age-0 Colorado pikeminnow and comparisons among similarly collected catch-per-unit-effort data in the middle and lower Green River supports the idea of similar abundances among reaches. Growth of age-0 Colorado pikeminnow was positively related to length of the summer growing season and summer water temperature. Models with summer base flow magnitude to predict growth also had a good fit but a negative coefficient, which was not surprising given the high and positive correlation between spring peak and summer base flows. Growth of age-0 Colorado pikeminnow was positively related to water temperatures in July-August (the warmest months of the year) and negatively related to August-September base flow levels. Total length of age-0 Colorado pikeminnow was consistently greater in the middle than the lower Green River, but there was no relationship between length and autumn density in backwaters.

Exact mechanisms influencing survival and abundance of age-0 Colorado pikeminnow were not evident, but moderate base flow years were most consistent with higher abundance and lower abundance was noted in low and high base flow years. For example, in the middle Green River, abundance of age-0 Colorado pikeminnow was above average in 63% of years when mean August-September base flow levels were 48-85 m³/sec (1,700-3,000 ft³/sec) but was above average in only 15% of years with lower flows and was never above average in higher flow years. In the lower Green River, a similar relationship was observed with higher abundance of age-0 Colorado pikeminnow when mean August-September base flow levels were 48-108 m³/sec (1,700-3,800 ft³/sec), with the downstream increase in flow due to inputs from the White River and other tributaries. At moderate flow levels, backwater number and area may be optimized thereby providing sufficient habitat to increase survival of early life stages of Colorado pikeminnow. In years with low base flows, the low abundance of age-0 Colorado pikeminnow might be due to sub-optimal habitat conditions or lack of sufficient larvae transported to nursery areas to produce a strong year class. In years when base flows were higher than 85 m³/sec (3,000 ft³/sec, and usually > 2,500 ft³/sec) in the middle Green River and 108 m³/sec (3,800 ft³/sec, and usually > 3,000 ft³/sec) in the lower Green River, abundance of age-0 Colorado pikeminnow in autumn was low, presumably because few low-velocity channel margin nursery habitats developed in such years or larvae never colonized those backwaters. Age-0 Colorado pikeminnow were also shorter in higher flow years, which may invoke length-dependent mortality factors. Regardless, production from both the lower and the middle Green River nursery reaches is needed to produce sufficient numbers of age-0 Colorado pikeminnow to support substantial recruitment and higher abundance of adults in the system.

Base flow levels were also associated with autumn abundance of red shiner in Green River backwaters, but in a manner opposite that for Colorado pikeminnow. Highest red shiner abundance in the middle Green River occurred in years when mean August-September base flows were < 42.5 m³/sec (1,500 ft³/sec); abundance was relatively low when base flows were > 65.1 m³/sec (2,300 ft³/sec). Red shiner abundance was higher in the lower Green River in years when mean August-September base flows were < 56.6 m³/sec (2,000 ft³/sec); abundance was relatively low when base flows were >79.3 m³/sec (2,800 ft³/sec). Higher abundance in low flow years was likely due to extended spawning by that species when water temperatures were elevated. Abundance-flow relationships were potentially important because red shiner and

other nonnative cyprinids (sand shiner *Notropis stramineus*, fathead minnow *Pimephales promelas*) were abundant in backwaters, with mean red shiner densities 20-40 times that of age-0 Colorado pikeminnow. Summer base flows in Green River nursery habitat reaches have declined from the period roughly corresponding to the 1980s to the more recent period from 2001 to 2012, a trend consistent with fewer years with lower Colorado pikeminnow abundance and more abundant red shiner populations; flows were higher from 2006-2012 consistent with production of two above average year classes of age-0 pikeminnow in each reach.

Although relationships between individual environmental variables and Colorado pikeminnow abundance were sometimes inconsistent, a clear signal was that higher summer base flows in drier years in the Green River may favor survival of larger numbers of age-0 Colorado pikeminnow; survival was also low in high base flow years. This was true in the lower Green River, where age-0 Colorado pikeminnow densities were historically higher and more age-1 to age-5 juveniles were produced, as well as in the middle Green River, where age-0 densities have been very low in most years since in 1994. Because the Yampa River contributes Colorado pikeminnow larvae to the middle Green River nursery habitat reach, and supports Green River base flows in summer, peak and base flows of the Yampa River should be protected and enhanced to the extent possible. Releases of water from Flaming Gorge Reservoir to provide biological benefit to endangered fishes in the downstream Green River serve many purposes, including enhancing spring peak flows designed to connect the river to floodplain wetlands, but summer base flows were also identified as a critical need for young Colorado pikeminnow. We discuss historical Flaming Gorge Dam operations and downstream flows of the Green River in nursery habitat reaches so variability in baseflows and age-0 pikeminnow abundance has some context. We also discuss needed changes in flow patterns, including increased base flows during dry to average water years as well as changing timing of onset of base flows in summer, which can be best accomplished using real-time data on timing of drift of Colorado pikeminnow larvae in the lower Green River or the lower Yampa River. Changes in base flow regimes should be implemented as soon as possible to enhance recruitment of age-0 Colorado pikeminnow in the Green River subbasin and bolster populations of adult life stages, which are declining in abundance.

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KEY WORDS

Colorado pikeminnow, reproduction, larvae, drift, transport index, diel variation, otolith analysis, survival, backwater, nursery habitat, predation, stream flow, recruitment, recovery, Flaming Gorge Dam

INTRODUCTION

Understanding the influence of regulated flows, altered thermal regimes, and invasive species on timing and success of reproduction and recruitment is central to conservation of aquatic biota because early life stages often drive recruitment dynamics of older life stages (Roughgarden et al. 1988; Poff et al. 1997; Marchetti and Moyle 2001; Durham and Wilde 2009; Falke et al. 2010; Yarnell et al. 2010). This is true for federally-protected Colorado pikeminnow *Ptychocheilus lucius* in the Green River subbasin of the upper Colorado River basin, because abundance of adults is thought a function of abundance of young produced in previous years (Bestgen et al. 2007a; Bestgen et al. 2010; Bestgen et al. 2016 review draft, abundance estimates 2011-2013). However, the abundance trend of adult pikeminnow in the Green River basin is declining from a peak in year 2000 (Bestgen et al. 2007a; Bestgen et al. 2010; Bestgen et al. 2016 review draft, abundance estimates 2011-2013) to relatively lower levels, and low recruitment of young fish is thought a primary reason for that decline. Thus, the goal of this paper is to better understand factors that affect abundance of young pikeminnow and suggest management actions such as flow alterations from Flaming Gorge Reservoir or nonnative fish management to reverse decline of Colorado pikeminnow abundance in the Green River subbasin.

Mechanisms of recruitment variation in animals, such as fishes, with multi-phase life cycles are particularly difficult to assess because larvae typically disperse, sometimes long distances, away from juveniles and adults and abundances of each life history phase are often constrained by different factors. Moreover, most aquatic organisms with dispersing early life stages have highly variable recruitment because high fecundity, coupled with small variations in recruitment-regulating environmental or biotic processes, can generate large differences in survival of larvae (Hjort 1914; Thorson 1950; Fogarty et al. 1991; Cushing 1995; Bestgen et al. 2006). Thus, factors that regulate distribution, abundance, size-structure, and survival of early life stages are integrated into processes that structure recruitment (Thorson 1950; Gaines et al. 1985; Houde 1987; Miller et al. 1988; Underwood and Fairweather 1989; Johnston et al. 1995).

Life history patterns and populations of Colorado pikeminnow of the Colorado River basin (Figure 1) are consistent with multi-phase life cycle characteristics because each life stage

disperses widely and patterns of survival and recruitment vary within and among years (Tyus 1991; Osmundson and Burnham 1998; Bestgen et al. 2006; Bestgen et al. 2007a; Bestgen et al. 2010; Osmundson and White 2014). In the Green River (Figure 2), where the largest remaining naturally reproducing Colorado pikeminnow population occurs, the two main spawning areas are in the downstream portion of the Yampa River, and the lower Green River in Gray Canyon. Larvae produced from those spawning areas drift downstream often > 100 km to low velocity backwater nursery habitat in the middle and lower Green River. Backwaters are important habitat for early life stages of many fishes including Colorado pikeminnow, where they reside for the first year of life or more. Estimated annual density of age-0 fish in autumn from 1979-2012 ranged from near zero to 75 fish/100 m² of backwater habitat (Haines and Tyus 1990; Tyus and Haines 1991; Bestgen et al. 2010), indicating variable recruitment. However, the relative effects of discharge regime, habitat alterations, invasive fishes, and annual abundance of Colorado pikeminnow larvae on recruitment of age-0 and juvenile life stages remains poorly understood (Bestgen et al. 2006; 2007a; 2010).

Long-term studies to understand early life dynamics of Colorado pikeminnow in the Green River began in 1979 with backwater seining of age-0 fish in autumn. Nursery habitat sampling in the middle and lower Green River yielded estimates of density and annual production by Colorado pikeminnow. Those studies also described habitat use patterns of young Colorado pikeminnow and abundance relative to flow level (Haines and Tyus 1990; Tyus 1991; Tyus and Haines 1991; Bestgen et al. 1998): specifically, in years of flow > 3,500 ft³/sec (100 m³/sec), age-0 Colorado pikeminnow abundance in backwaters was low. Other studies of Colorado pikeminnow in backwaters investigated overwinter survival (Haines et al. 1998; Valdez et al. 1999; Muth et al. 2000). Those studies indicated that year class abundance in spring was positively related to abundance of the same year class in the previous autumn. There was also evidence that overwinter survival of young Colorado pikeminnow in autumn was negatively affected by the combined effect of small fish size in autumn and higher winter flow (Haines et al. 1998; Muth et al. 2000).

Investigations concerning Colorado pikeminnow larvae began after those for age-0 fish in backwaters in the Green River. Drift net sampling of Colorado pikeminnow larvae in summer at the lower Yampa River site began in 1990 and continued through 2012, except in 1997 (administrators decided data analysis should occur for prior years sampling data rather than

conduct concurrent sampling in that year) when no sampling occurred (Bestgen et al. 1998). Sampling in the lower Green River occurred from 1991-1996 and in 1999 (in part, Bestgen et al. 1998). These data sets allowed examination of relationships between abundance of Colorado pikeminnow larvae and their survival to autumn in downstream backwaters. Because pikeminnow larvae drift from the relatively warm Yampa River downstream into the cooler regulated Green River, there is a potential for cold shock (Berry 1985; Muth et al. 2000). Thus, drift net sampling allowed assessment of potential effects of altered flow and water temperature regimes from upstream Flaming Gorge Reservoir when larvae were transported downstream (Bestgen et al. 1998; Muth et al. 2000; U.S. Bureau of Reclamation 2005; Bestgen et al. 2006).

The intent of this study is to identify linkages between timing and abundance of drifting Colorado pikeminnow larvae and subsequent densities of age-0 pikeminnow in backwaters in autumn (Green River study Plan *ad hoc* Committee 2007). This study need was also an outcome of biological uncertainties identified when flow and water temperature recommendations were implemented for Flaming Gorge Dam operations (Muth et al. 2000; Green River Study Plan 2007). The scope of work for this document stated an overall goal to “synthesize physical and biological information to better understand relationships between physical habitat and abundance dynamics of fishes, especially age-0 Colorado pikeminnow”, which was addressed in this report. More in-depth analyses of physical habitat data will be presented by Argonne National Laboratory, the principal entity in a companion study. This overall study also investigated anticipated effects and uncertainties of flow and water temperature recommendations, particularly relative to production and survival of young Colorado pikeminnow in the Green River, as identified in the Green River Study Plan. Those uncertainties (objectives for this study) are identified just below with accompanying descriptions of whether the objective was met as follows:

Task 1: Biological Investigations (this report)

- Gather, review, and summarize information in reports that describe the biological conditions and fish communities in backwaters of the Green River.
- Obtain existing data sets from the authors of past reports that can be used to evaluate biological conditions in backwaters.
- Gather historical hydrology and water temperature data from the USGS gages in the Green River that relate to Interagency Standardized Monitoring Program (ISMP) investigations and other data.

- Describe backwater fish communities (mostly ISMP data) and physical and biological factors that affect communities to understand temporal changes.

Although the main focus was on the middle Green River (Reach 2, in Muth et al. 2000), here we integrated lower Green River data (Reach 3, Muth et al. 2000) to provide a fuller analysis of available data even though there was no complementary backwater habitat topography data analysis for that reach. We also conducted some habitat analysis based in data collected in historical studies in the middle and lower Green River. Task 2 was a comprehensive examination of effects of flow on physical habitat availability, specifically backwater habitat in the middle Green River. Task 3 was an integration effort, designed to synthesize findings outlined in tasks 1 and 2.

Colorado pikeminnow natural history.—This section is mainly background for readers with more limited knowledge of Colorado pikeminnow life history; others may wish to skip this material and move forward to subsequent sections. Specific reasons for reduced distribution and abundance of native or endangered fishes in the upper Colorado River and Green River subbasins are varied and depend in part on the life history of the species. Colorado pikeminnow natural history is relatively well-known, but a description of the life cycle of the species is provided with a conceptual model to illustrate the factors that affect its distribution and abundance.

Colorado pikeminnow is a long-lived (>30 years) species that historically reached nearly 2 m in length, up to 40 kg in weight, and was once abundant throughout the Colorado River basin (Tyus 1991; Quartarone 1995; Osmundson et al. 1997; Osmundson and Burnham 1998; Osmundson et al. 1998; Osmundson 2006; Bestgen et al. 2007a). Lower Colorado River basin populations were extirpated and populations are now restricted to the Green, Colorado, and San Juan River subbasins. Colorado pikeminnow in the Green River subbasin occupy the lower 600 RK of the Green River, extending as far upstream as upper Browns Park, UT and CO, and also reside in the Yampa and White rivers, major Green River tributaries (Bestgen et al. 2007a; 2010; Figure 2). Colorado pikeminnow also intermittently occupy smaller tributaries, including the Duchesne, San Rafael, and Price rivers (Bestgen et al. 2007a; Bottcher et al. 2013) and regularly reside in over 900 RK of habitat in the Green River subbasin.

The numerically largest population of Colorado pikeminnow is in the Green River subbasin, where abundance estimates ranged from over 4,000 adults (> 450 mm total length

[TL]) in 2000 to just over 2000 in 2003. Abundance rebounded somewhat in 2006-2008, but has declined since then (Bestgen et al. 2007a; 2010; unpublished data). Recent capture rates were very low and estimates from 2011-2013 are lower than the 2003 estimate (Bestgen et al. 2007a; 2010; unpublished). This decline is most dramatic for the Yampa River, where the population has declined from over 300 resident adults to fewer than 10 captured in each year during intensive sampling from 2011-2013. The Yampa River is the focus of a nonnative fish control program, where large numbers of predaceous smallmouth bass *Micropterus dolomieu* and northern pike *Esox lucius* have established and walleye *Sander vitreus* are also present (Johnson et al. 2008; Breton et al. 2013; Breton et al. 2014; Martinez et al. 2014).

There are substantial differences in population age- and size structuring among three reaches of the Green River—the middle Green River, Desolation-Gray Canyon, and lower Green River—in up to downstream order, and tributaries the Yampa and White rivers. The lower Green River and the Desolation-Gray Canyon reaches typically support 20-50% of adults (> 450 mm TL) in the Green River subbasin, while middle Green, White, and Yampa River reaches collectively support the remainder of adults (individuals 5-8 or more years old, depending on growth rates; Osmundson 2006). Most juveniles (75-400 mm TL) occur in the lower Green River reach, but the middle Green River was and sometimes still is an important nursery area as well (Bestgen et al. 2007; Bestgen et al. 2010; Recovery Program annual reports, project 138).

Habitat use by adult Colorado pikeminnow is variable and depends on flow conditions. At summer base flows, Colorado pikeminnow use moderate-velocity run or pool habitats (0.2-0.7 m/sec) that are moderately deep (0.7-1.5 m) (Tyus and McAda 1984; Muth et al. 2000). During high flows, typically in spring, large juvenile and adult Colorado pikeminnow occupy the main channel, but prefer low-velocity eddies, pools, flooded tributary mouths, and floodplain wetlands. Such areas support abundant forage fishes and are often warm, factors which may enhance condition of adults in spring prior to spawning in summer (Muth et al. 2000; Bestgen et al. 2006). During winter, adult Colorado pikeminnow occupy runs, embayments, and pools in relatively restricted home ranges under ice-covered rivers (Wick and Hawkins 1989). Occupied areas in winter were typically 0.7-1 m deep, but were sometimes quite shallow, in channel margin backwaters.

Colorado pikeminnow adults migrate in late spring and summer to spawning areas in the upper Colorado River basin when spring flows are declining and water temperatures are

increasing (Tyus 1990, 1991; Bestgen et al. 1998; Irving and Modde 2000; McAda 2003). In the Green River subbasin, Colorado pikeminnow move long distances, sometimes > 800 RK round-trip to two main spawning areas in Gray Canyon of the Green River and Yampa Canyon in Dinosaur National Monument (e.g., Irving and Modde 2000; Figure 3). The Yampa Canyon spawning population has been monitored for many years and production of larvae from that area is variable and low in low flow years, but continues at a high level (Bestgen et al. 1998; this report). Potential other spawning areas have been noted based on congregations of ripe adults (e.g., Lodore Canyon in 2006 and 2010; Green River, lower Mitten Park in the mid to late 2000's [Recovery Program annual reports Projects 115 and 22f]), but these are typically small groups of fish or are ephemeral due to habitat shifts.

The Colorado pikeminnow conceptual life history model (Figure 4, Bestgen et al. 1997; 2006; Bestgen 2015) illustrates possible controlling factors for different life stages. The conceptual model was developed from a synthesis of life history information gleaned from literature, ongoing research, and personal observations summarized in Bestgen et al. (2006), and is a diagrammatic representation of factors that may affect populations as fish progress from egg to adult life stage. Factors controlling life-stage specific abundance and survival are divided into both biotic (e.g., competition and predation) and abiotic (e.g., stream flows, habitat, water temperatures, and pollutants) components to provide focus for management of negative effects. Arrows connecting boxes show the logical development sequence from egg to adult and inter-relationships among life stages. Separate biotic and abiotic limiting factors are presented that affect abundance and survival of each Colorado pikeminnow life stage, recognizing that some of the most important limiting factors likely represent interactions among two or more factors. For example, warm water, an abiotic factor, positively affects growth of a Colorado pikeminnow larva which interacts with predation, a biotic factor, because faster growing larvae are susceptible to predation by other fishes for a shorter duration than slow-growing larvae (Bestgen et al. 2006).

Several compartments in the life-history model detail factors limiting the early life stages of Colorado pikeminnow. This model structure was not intended to imply that early life stages are more important than juveniles or adults. Rather, this was done to underscore the dramatic changes in physical ability that relatively small, weak-swimming, and vulnerable early life stages of fish undergo and to highlight the diversity of habitat needed to support each life stage over a

broad spatial scale. For example, the elapsed time from embryo deposition through hatching, downstream drift, to a larva colonizing a backwater habitat may be less than two weeks, but during that time the 6-9 mm-long organism occupied interstitial spaces in spawning gravel in turbulent and turbid canyon river flows, drifted 10-150 RK or more downstream in swift river currents, and eventually established itself in the shifting channel margin of a large river so it could swim or be entrained into a low-velocity nursery backwater habitat.

In addition, because of their small size and limited energy reserves, early life stages of Colorado pikeminnow are susceptible to a greater variety of harsh conditions and controlling factors than are juveniles and adults. In the conceptual model, later life stages were combined either because they occupy similar habitat or have similar limiting factors (e.g., large juveniles and adults), or because their life history requirements and controlling factors were poorly documented (e.g., age-1 Colorado pikeminnow in winter habitat). The model ends with variable-sized cohorts of adult fish. However, the model should not be viewed as terminating with adults, but instead represent a continuous life history cycle, because abundance of adults may affect the quantity and quality of embryos that begins each annual cycle. The sum of annual production cycles over many years reflects the current distribution, abundance, and status of Colorado pikeminnow, and also portrays the dependence of various fish life history stages on a connected linear river system, including the Yampa and Green rivers (Bestgen 2015).

The life cycle of Colorado pikeminnow consists of five distinct phases, each having a host of biotic and abiotic controlling factors. Colorado pikeminnow reproduce on the descending limb of the hydrograph when water temperatures warm to 16°C or greater (Bestgen and Williams 1994; Bestgen et al. 1998; this report), usually in mid-June to early July. The spawning season typically extends about 3-8 weeks, often into August in the Yampa River. Spawning occurs in clean gravel and cobble riffles in the lower Yampa River, following re-assortment of substrate by elevated spring flows. Eggs are adhesive and deposited into spaces between substrate particles where they adhere to clean rock surfaces. Eggs that do not attach are likely lost downstream and die or are consumed by fishes. Loose gravel-cobble riffles created by high spring flows provide optimal rearing environments for eggs because interstitial spaces allow for through-flow of oxygenated water. Embryos hatch in 4-7 days at water temperatures of 18-30°C, and larvae remain in the substrate for 4-8 days post-hatching. Thus, Colorado pikeminnow embryos require a relatively long incubation period of 8-15 days.

Larvae 5.5-7 mm TL emerge from gravel-cobble spawning riffles and drift downstream 10-150 RK to nursery habitat, which is low-gradient, sand-bedded, and low-velocity channel margin backwaters (Pucherelli et al. 1990; Tyus and Haines 1991; Bestgen and Williams 1994; Bestgen et al. 1998). Higher gradient reaches of the lower Yampa River and the Green River directly downstream of the Yampa River confluence (Whirlpool Canyon, Split Mountain Canyon) offer only limited backwater and channel margin habitat so young pikeminnow are relatively uncommon there.

In the Green River, the two main nursery habitat reaches are each 40-100 RK downstream of spawning areas, one in the middle Green River (near Jensen downstream to just near the White River), and one in the lower Green River (downstream of Green River, Utah; Figure 4). The lower Green River reach is the most productive nursery habitat and recruitment area for young Colorado pikeminnow (Bestgen et al. 2007a; 2010). The middle Green River Colorado pikeminnow nursery habitat reach, which is supplied with larvae from the Yampa River spawning reach, has been less productive of age-0 pikeminnow in recent years. That reach once supported large numbers of age-0 pikeminnow, and declines after about 1994 may be affecting adult abundance in the Green River subbasin. Larvae occupy low-velocity nearshore backwaters through autumn and into the next year and eventually transition to occupy main channel runs and pools when individuals are about 200 mm TL. Juvenile pikeminnow 250-450 mm TL move upstream, apparently in response to greater availability of forage fishes, and eventually establish home ranges in the Green River or tributaries such as the Yampa or White rivers (Osmundson et al. 1998; Bestgen et al. 2007a). It takes at least five and perhaps eight years for a Colorado pikeminnow to grow from a larva to a reproductive adult. Males typically mature before females.

STUDY AREA

The Green River drains portions of southern Wyoming, eastern Utah, and northwestern Colorado (Figure 2) and is the largest tributary of the Colorado River. In the Green River subbasin, Colorado pikeminnow occur in river reaches with varying channel morphologies. Yampa Canyon in the lower Yampa River (river kilometer [RK] 0-74), Whirlpool and Split Mountain canyons (RK 515-555) in the middle Green River, and Desolation and Gray canyons

(RK 211-340) in the lower Green River have high gradient and mixed cobble and sand substrate. The Uintah Basin valley reach in the middle Green River (RK 340-515) and Stillwater and Labyrinth canyons in the lower Green River (RK 0-211) are lower gradient and have substrates dominated by sand and silt with small amounts of cobble; these reaches are where most backwater nursery habitat occurs in the study area and where ISMP sampling took place that generated most autumn abundance data for age-0 Colorado pikeminnow. Discharge in the mainstem Green River upstream of the Yampa River confluence has been regulated since 1963 by Flaming Gorge Dam. During 1964-2014, releases typically ranged from 22.6-130 m³/s (800-4,590 ft³/sec), but were sometimes higher because of bypass or spillway releases in high-water years (e.g. 1983 and 2011) or to connect the Green River with floodplain wetlands (1999, 2012, extending through 2015; Larval Trigger Study Plan; LaGory et al. 2012). Discharge in the Green River downstream of the Yampa River was bolstered by Yampa River flows. In contrast, Green River discharge in late summer, fall, and winter was lower and dominated by releases from Flaming Gorge Reservoir. Discharge in the highly variable Yampa River was occasionally > 566 m³/s (20,000 ft³/sec) in spring but summer flow sometimes declined to < 0.06 m³/s (2 ft³/sec) in drought years (U.S. Geological Survey records, gage 09251000).

METHODS

Drift net sampling.—One sampling site for capturing drifting Colorado pikeminnow larvae was in the Yampa River about 1 km upstream of its confluence with the Green River in Echo Park in Dinosaur National Monument (1990-2012, except 1997), and the second was in the Green River approximately 15-30 km upstream of Green River, Utah (1991-1996, and 1999). Limited data collected from the Green River near Jensen, Utah (1990, 1994, and 1995) were reported elsewhere (Bestgen et al. 1998) and will not be considered herein. Sampling started in mid-June to early-July each year, two to six weeks after spring discharge peaked and when daytime water temperature exceeded about 16°C (Nesler 1986-1987; Nesler et al. 1988; Tyus and Haines 1991; Bestgen et al. 1998). Sampling continued for four to eight weeks after the first Colorado pikeminnow larvae were captured and usually ended when none was captured for three to five consecutive days, usually by mid-August.

Colorado pikeminnow larvae were sampled daily at dawn (ca. 0600 hrs) with conical drift nets (0.15 m² mouth diameter, 4 m long, 560 µm mesh) set near shore and submerged in water 30 to 40 cm deep. Three nets were set on each day for up to 2 hr, but sampling times were less if debris load exceeded 3.8 L/sample. Water depth at which a white object (shoe) disappeared from sight was recorded as a measure of water turbidity. General Oceanics flow meters (model 2030) suspended in each net mouth recorded water velocity during the net set so that flow volume filtered could be estimated.

To evaluate whether dawn near shore samples represented the abundance, age, and size of larvae transported downstream past sampling sites, additional diel and cross-channel sampling was conducted in 1992 (Bestgen et al. 1998; Bestgen et al. 2006). That sampling, and data presented herein, showed that dawn near shore sampling was the least variable of the in-channel locations and times, represented average abundance in non-drought years, and was an accurate metric of daily abundance of larvae transported downstream. Diel sampling was conducted from 1991 to 2012 (2 to 14 times per season, usually 5-6 annually) at the near shore locality to assess effects of time of day on Colorado pikeminnow drift periodicity. In addition to dawn sampling, sampling was conducted at noon (1200 to 1400 hr), dusk (1900 to 2100 hr) and midnight (0000 to 0200 hr), generally for 1-2 hours. All drift net samples were preserved immediately in 100% ethanol and fish were picked from debris within 4 hr and preserved in fresh 100% ethanol. Fish were picked from samples by spreading a small amount of debris in a large volume of water in a sorting tray with good light and removing larvae, which are typically white in preservation. Prompt sample processing prevented fish from being stained by pigments leached from debris, which aided identification and would allow for decisions about future flow management to be made nearly in real time. Our sorting protocol was efficient at recovering fish larvae from the large amounts of debris because 100% of a known number of larvae (range 9-10 fish) were recovered from samples in blind tests.

Laboratory and analytical procedures.—Colorado pikeminnow larvae (< 20 mm TL, 97% < 10 mm TL) captured in drift nets were identified and measured to the nearest 0.1 mm TL. Initiation of spawning was estimated by subtracting the average age of larvae at capture (6 d, Bestgen 1997) and average incubation time of fertilized eggs at 18°C (6 d, Bestgen and Williams 1994) from the date that larvae were first captured in drift nets set in the lower Yampa River and the lower Green River. Date of cessation of reproduction was similarly estimated by

subtracting 12 d from the date of the last capture of larvae. The first peak in reproductive activity was qualitatively determined by subtracting 12 d from the first substantial increase (from 1-2 fish to several to many fish) in capture of larvae in drift nets. Most temperature data for the Yampa River from 1990-2012 were recorded just upstream of the Green River confluence with a continuously recording thermograph (J. Mohrman, pers. comm., U.S. Fish and Wildlife Service, Denver, Colorado, <http://www.fws.gov/mountain-prairie/riverdata/>). Lower Yampa River temperatures were estimated in 1993 and 1994 by adding 2.1°C to temperature measurements from an upstream gauge at Government Bridge upstream of Maybell, Colorado. That value was the average summer-season difference between the two stations in the month of June in 1991, 1992, 1995, and 1996 (Bestgen et al. 1998). Degree-day accumulation in the lower Yampa River was estimated from temperature data collected near Jensen, Utah (U. S. Geological Survey gauge # 09261000), because this was the most geographically proximate gauge with complete seasonal records, including winter. Degree-day accumulation was the mean daily water temperature at the gauge of interest summed from 1 January of the respective year until the day of first reproduction or first peak of reproduction. Lower Green River summer water temperature data were estimated by adding 2.3°C to temperature measurements from an upstream gauge at the Ouray National Wildlife Refuge (see website just above). That value was the average difference between the two stations in summer 1992, the only data that was available at the time of analysis (Bestgen et al. 1998). Temperature data for 1991 and 1995 and degree-day accumulation information for all years prior to 1997 in the lower green River were from instantaneous records collected by the U.S. Geological Survey near the town of Green River, Utah. Temperature values at first reproduction and first peak of reproduction were the average of the 5-d period centered on the estimated date of interest. The 5-d mean temperature best reflected the average water temperature at initiation and first peak of reproduction because of climatic anomalies and uncertainty (± 2.5 d) in estimates of hatch dates of larvae that were aged with otoliths (Bestgen and Bundy 1998). We also calculated number of days that mean daily water temperature exceeded 18°C prior to first reproduction or first peak of reproduction. Maximum spring discharge was the highest mean daily discharge measured at Deerlodge (m^3/sec , USGS gauge # 09260050) for the Yampa River and at Green River, Utah (USGS gauge # 09315000) for the lower Green River. Days post-peak discharge was number of days between highest recorded mean daily discharge during spring runoff and peak reproduction.

Data analyses.—We built regression models (SAS, PROC GLM) to predict time to first reproduction and first peak of reproduction for Yampa River Colorado pikeminnow as a function of flow and water temperature predictor variables. Because data were limited in the lower Green River (n = 7 years), we used the same best-fit models from the Yampa River there as well. Multiple regression models were fit that estimated Julian days (days since 1 January) to first reproduction by Colorado pikeminnow in the Yampa and Green rivers as a function of environmental predictor variables, which were accumulated degree days (DD), spring peak flow (Qpeak) for the Yampa River or Green River, water temperature at first reproduction, and the number of days mean daily water temperature was > 18°C prior to first reproduction.

Colorado pikeminnow larvae annual transport abundance index.—Previous studies calculated number of larvae/volume of water sampled to obtain a density index for Colorado pikeminnow abundance (e.g., Nesler et al. 1988). Although this was adequate for comparing densities of larvae from samples collected at different positions in the stream or diel intervals in a single day (as Nesler et al. 1988 did), comparisons of abundance of larvae produced and transported downstream past the sampling station among years or rivers would be flawed because the percentage of the river sampled by drift nets was inversely correlated with river discharge. Hypothetically, if an identical number of larvae was present in the river at both a high and low discharge, density/sample would be higher at low discharge and lower at high discharge but the actual number transported past the station would be the same. Therefore, the transport abundance index was estimated by dividing the number of larvae captured per hour in dawn drift net samples by the estimated percent of total discharge sampled. This method does not correct for days when no Colorado pikeminnow larvae were captured but some downstream transport may have occurred; there is no correction possible for that scenario such as interpolation between days prior to and after the zero-catch day because it is difficult to predict when few or no larvae were actually in the river. Average daily discharge values for Yampa River transport abundance calculations were from Deerlodge gauge about 75 RK upstream, but were offset one day earlier to account for water travel time. Discharge for lower Green River transport abundance calculations were from the gauge at Green River, Utah 18 RK downstream.

A previous analysis of data collected from 1992-1996 (Bestgen et al. 1998) noted large differences in diel drift densities, particularly at midnight. We have since discovered that differences were due mainly to the type of flow year. In years of very low flow (e.g., Yampa

River mean July-August flow $< 200 \text{ ft}^3/\text{sec}$), capture rates and the transport abundance index for Colorado pikeminnow larvae was very low except at midnight (analysis below). In other years when flows were higher, transport index rates were relatively even across the day. We considered using midnight captures during low flow years, but for a variety of reasons including low variability, used only dawn samples to calculate transport abundance indices. We summed daily transport abundance values for all sampling days, to estimate abundance of larvae transported per hour past each station in the sampling year.

The transport abundance index for Colorado pikeminnow larvae in the lower Yampa River (1990-2012) and the lower Green River spawning areas was plotted as a function of peak flow magnitude and mean July-August daily flow. Mean July-August flow magnitudes were used to better understand flow patterns when Colorado pikeminnow embryos and larvae were developing in the substrate in spawning substrate, dispersing downstream from spawning areas, and colonizing backwaters. Multiple regression models estimated the annual transport abundance index data as a function of environmental predictor variables (spring peak flow, mean July-August flow, days post-peak discharge, and mean daily water temperature in the July-August period in the Green River just downstream of the respective spawning areas). Mean July-August flow levels were inversely related to sampled water volumes because our fixed area nets sampled a greater proportion of the river at lower flow levels.

Autumn abundance of age-0 and juvenile Colorado pikeminnow.—Abundance of age-0 and juvenile Colorado pikeminnow in autumn from 1979-2012 (juvenile data through 2013) was measured using the ISMP protocol (e.g., U. S. Fish and Wildlife Service 1987; Haines and Tyus 1990; Tyus 1991; McAda et al. 1996; Haines et al. 1998). In that protocol, the first two backwaters $\geq 30 \text{ m}^2$ in area and $\geq 30 \text{ cm}$ deep encountered in each 8-km reach (proceeding downriver) of the middle (RK 322-515) and lower (RK 0-193) Green River were sampled with two non-overlapping hauls of a 4.6 m long seine (3.2 mm mesh). Since 2005, data from a third seine haul (middle Green River only) in each sampled backwater, when available, was used to estimate Colorado pikeminnow density. Area seined, number, and TL of Colorado pikeminnow captured was recorded. Densities of Colorado pikeminnow were calculated per backwater sampled by dividing number of Colorado pikeminnow captured by area swept with the seine. We calculated annual density of age-0 ($\leq 75 \text{ mm TL}$) and age-1 juvenile (76-130 mm TL) Colorado pikeminnow separately. Counts of other species were also recorded for the first seine

haul in each primary backwater (the first backwater encountered) in each 8-km reach sampled. Thus, data for species other than Colorado pikeminnow reflect a maximum of about 25% of the sampling effort, assuming that two backwaters were sampled in each reach and two (sometimes more) seine hauls were taken per backwater.

We used regression models to gain understanding of factors that affected mean TL of age-0 Colorado pikeminnow in autumn in each of the middle and lower reaches of the Green River. Independent variables were summer base flow (mean August-September flow, different than for transport abundance analyses but relevant for age-0 fish because that was the time after base flows began, as recognized in flow recommendations, and encompassed most of the growing season) and peak flow (highest peak in spring), age-0 Colorado pikeminnow and red shiner density (#/10 m²), and mean July-August water temperature (the warmest portion of the growing season and most likely to affect growth) in the respective reach. Base flows affect nursery habitat availability (Pucherelli et al. 1990; 2014 Recovery Program annual report, Project 138), and was positively correlated with peak flow magnitude in the same year (e.g., Green River, Jensen, Utah, USGS gauge 09261000, annual peak and mean August-September base flows, Pearson correlation coefficient, $r = 0.83$, $p < 0.0001$). Peak flow may affect backwater formation as well as growing season duration and subsequent fish length, as Colorado pikeminnow spawn later in years with higher peak flows, shortening the growing season. Red shiner density may affect growth of age-0 Colorado pikeminnow through competition for food or may also indicate favorable conditions for shiner reproduction; models with other species were explored but only those for red shiner were reported because it was the most abundant nonnative cyprinid. Breen et al. (2011) also explored relationships of abundance of various species captured during ISMP sampling with environmental variables. Water temperature is known to positively affect growth of young Colorado pikeminnow (Bestgen 1996) and was collected for mainstem habitat as previously described for each the middle and lower Green River reaches; backwater temperatures vary from mainstem habitat but are thought a reasonable surrogate in the absence of other information. Water temperature data were available beginning in 1990 for the middle Green River, and in 1991 for the lower Green River. Thus, if regression models to predict age-0 Colorado pikeminnow length included water temperatures, fish growth information prior to 1990 or 1991 for the middle or lower Green River, respectively, was excluded.

We used regression models to gain an understanding of factors that affected density of age-0 Colorado pikeminnow in autumn in each of the middle and lower reaches of the Green River. As for other models, Colorado pikeminnow density was fit as a function of spring peak and August-September base flows, July-August water temperature, and red shiner density. Abundance of age-0 Colorado pikeminnow in autumn backwater samples for the lower Green River and middle Green River was also plotted as a function of the transport abundance index of larvae for the lower Green River (1991-1996, 1999) and lower Yampa River (1990-2012, except 1997) spawning areas, respectively, to determine if there was a relationship between the number of larvae transported to nursery areas and abundance of age-0 pikeminnow in autumn. Finally, we fit models to describe red shiner density as a function of flow and water temperature variables as described above.

Density of age-0 Colorado pikeminnow and backwater habitat.—We re-analyzed the data provided by Pucherelli et al. (1990), Trammell and Chart (1999), and Day et al. (1999) to re-familiarize the reader with patterns of backwater distribution, number, and area relative to flow levels in the middle and lower Green River. This data was especially valuable to illuminate differences in terms of backwater number and area and how that related to differences in age-0 Colorado pikeminnow density. This was relevant because of the importance of backwaters to early life stages of Colorado pikeminnow and those nursery areas are thought to change with flow level and river reach. Pucherelli et al. (1990) was especially important because that was the only study that examined backwater number and area over spatially extensive reaches. Pucherelli et al. (1990) used remote sensing and geographic information systems analysis to estimate the number and area of backwaters in five reaches of the Green River: from upstream to downstream these were Island Park, Jensen, Ouray, and Sand Wash, all in the middle Green River reach, and near Mineral Bottom in the lower Green River. Reaches ranged in length from about 6-18 river km. Most sites were sampled seven times during spring-summer in 1987 at flow levels that varied from 37-142 m³/sec (1,306-5,013 ft³/sec); Mineral Bottom in the lower Green River was sampled only three times at flows ranging from 79-108 m³/sec (2,789-3,812 ft³/sec).

Backwater habitat number and area was delineated in Pucherelli et al. (1990) by reach, and we calculated area/km (assume this was their “Area”, in Tables 1-5). Even though Pucherelli et al. (1990) measured their study reaches (Island Park = 6 RM, Jensen = 7 RM,

Ouray = 10 RM, Sand Wash = 3 RM, and Mineral Bottom = 6 RM), they did not report the total length of each river section represented by their study areas, which would allow subsequent investigators to assign relative levels of importance to each reach. We assumed that the Jensen and Ouray reaches were the longest in the middle Green River reach, based on geomorphology and personal observations, and Sand Wash and Island Park the shortest. Data were obtained directly from reports (Trammell and Chart 1999) or digitized from graphs (Day et al. 1999).

RESULTS

Timing of reproduction.— Based on capture of recently-hatched larvae in drift nets, Colorado pikeminnow initiated reproduction in the Yampa and Green rivers in early to late June with the exception of the high flow and cold water years 1995 and 2011, when reproduction first occurred in early to mid-July (Table 1). Colorado pikeminnow larvae were first captured in dawn drift net samples collected in the Yampa River in mid-June to mid-July (Figure 5). In the Green River, larvae were captured earlier than in the Yampa River in low or moderate discharge years (Figure 6). However, capture of larvae at the Green River station in 1995 was later than at the Yampa River station, probably because the few early larvae produced were missed by sampling gear in that high water year.

Dates of first reproduction by Colorado pikeminnow in the Yampa River were within a relatively narrow time frame from 8 June to 12 July (mean = 23 June, n = 23 years) and from 9 June to 28 June (mean = 19 June, n = 6 years, 1995 excluded) in the Green River. Reproduction occurred 1 to 16 d earlier in the Green River than in the Yampa River, when dates were compared year by year, excluding 1995. Mean daily water temperatures at initiation of Colorado pikeminnow reproduction in the Yampa River was 18.4°C (16.0 to 20.6°C) if the low flow year 1994 (23.1°C) was excluded. Mean daily water temperature at initiation of reproduction was higher in the Green River at 21.0°C (19.8 to 23.0°C).

The number of days $\geq 18^\circ\text{C}$ prior to first reproduction had a relatively small range in the Yampa River (0 to 15 d), especially if 1994 was excluded (0 to 9 d, mean = 4 d). In years when water temperature had not achieved a mean daily average of 18°C prior to first reproduction, it did so within 2 to 6 d. In contrast, Colorado pikeminnow in the Green River initiated

reproduction after mean daily water temperature exceeded 18°C for 8 to 39 d (mean = 24 d). Total days $\geq 18^\circ\text{C}$ were greater in the Green River than in the Yampa River, mainly because the Green River often warmed to 18°C or greater prior to runoff. Thus, Colorado pikeminnow spawning in the Yampa River occurred with fewer warm days prior to spawning, and lower Green River fish with many more. Variation in thermal regimes prior to reproduction were likely the reason for differences in the signs of regression relationship coefficients for water temperature used to predict reproduction in the Yampa and lower Green River areas (below).

Days post-peak discharge prior to first Colorado pikeminnow reproduction had a wide range in the Yampa River (5 to 51 d, mean = 29 d), but was narrower in the Green River (4 to 32 d, mean = 23 d). If the low-flow year of 1994 was excluded from the lower Green River data, the range of days post-peak discharge was a relatively narrow (12 to 32 d). Mean accumulated degree days at first reproduction were lower in the Yampa River than in the Green River (1312 v 1738), and their ranges barely overlapped. This was again likely a function of pre-runoff warming in the lower elevation and lower latitude Green River.

The first peak in reproduction for Colorado pikeminnow in the Yampa River occurred an average of 5.5 d (range 0 to 20 d) after first reproduction was detected when mean daily water temperatures ranged from 16.3 to 23.1°C (overall mean 19.5°C). Mean daily water temperature at the time of first peak in reproduction exceeded 18°C for 0 to 16 d (mean = 7.4 d). The first peak in reproduction for Colorado pikeminnow in the Green River occurred an average of 3 d (range 0 to 7 d) after first reproduction was detected when mean daily water temperatures ranged from 19.9 to 23°C (overall mean 20.9°C). Mean daily water temperature had exceeded 18°C for 10 to 45 d (mean = 30.6 d) prior to peak discharge.

Spring peak flow magnitude was the individual variable most strongly correlated with timing of first reproduction and first peak of reproduction (Julian dates) by Colorado pikeminnow in the Green River subbasin. In the Yampa and Green rivers, spring peak flow magnitude was positively correlated with both first reproduction (Pearson correlation coefficients $r = 0.77$, $p < 0.001$, $n = 22$ and $r = 0.78$, $p = 0.037$, $n = 7$, respectively) as well as the first peak of reproduction ($r = 0.80$, $p < 0.001$, $n = 22$ and $r = 0.76$, $p = 0.046$, $n = 7$, respectively).

Multiple regression models were fit that described Julian days (days since 1 January) to first reproduction by Colorado pikeminnow in the Yampa River as a function of more than one environmental variable. A good fit was achieved for those relationships ($F = 21.18$, $df = 2, 19$,

$p < 0.0001$, $R^2 = 0.69$) and included accumulated degree days (DD) and spring peak flow (Qpeak, m³/sec) for the Yampa River (First reproduction (Julian d) = $142.1 + 0.0137*DD + 0.037*Qpeak$ (Table 2).

Multiple regression models were also fit that described Julian days to first peak of reproduction by Colorado pikeminnow in the Yampa River as a function of environmental variables. A good fit to the relationship was achieved (overall model $F = 36.52$, $df = 2, 19$, $p < 0.0001$, $R^2 = 0.79$, Table 2) and included number of days mean daily water temperature was $> 18^{\circ}\text{C}$ prior to peak reproduction (D18Peak) and Qpeak (First peak of reproduction = $152.69 + 0.736*D18Peak + 0.055*Qpeak$). Thus, first and peak reproduction in the Yampa River was positively related to both spring flow peak magnitude and a measure of warmer water. The variables were inter-correlated to some degree, but this was partially accounted for by interpreting Type III sums of squares, which allows understanding the predictive capability of each variable as if all the others were absent.

A regression relationship for time to first reproduction by Colorado pikeminnow in the lower Green River had a relatively strong fit for the few data available ($F = 7.36$, $df = 2, 4$, $p = 0.046$, $R^2 = 0.79$), although as noted above, the form of the equation was slightly different than that for the Yampa River as the degree-day coefficient was negative (First reproduction (Julian d) = $172.54 - 0.0114*DD + 0.031*Qpeak$). A relatively strong relationship was also achieved ($F = 13.18$, $df = 2, 4$, $p = 0.02$, $R^2 = 0.87$) that described time to first peak of reproduction by Colorado pikeminnow in the lower Green River (Peak reproduction (Julian d) = $174.25 - 0.277*D18Peak + 0.0128*Qpeak$). Thus, timing of first and peak reproduction (Julian days) in the lower Green River was positively related to spring flow peak magnitude, but negatively related to a measure of water temperature, which was different than for the Yampa River, and likely related to earlier downstream warming.

The reproductive season for Colorado pikeminnow averaged 36 d in length (23 to 52 d) in the Yampa River and was also 36 d (17 to 47 d) in the lower Green River (Table 1).

Colorado pikeminnow reproductive season length was not consistently or strongly related to discharge level in either the Yampa ($r = 0.09$, $n = 22$) or lower Green ($r = -0.48$, $n = 7$) rivers.

Intra-annual abundance patterns of larvae.—Colorado pikeminnow larvae were found each year in dawn drift-net collections from the Yampa River (1990-1996, 1998-2012) and Green River (1991-1996, 1999) sampling stations (Figures 5 and 6). Abundance of Colorado

pikeminnow larvae in drift net samples varied widely within and among years (Figure 7). More than 1,000 larvae were captured in each of years 1990, 2000, and 2012 in the Yampa River, all lower flow years, and only 49 were captured in 1995, a high flow year. Annual captures of larvae in the lower Green River samples varied from 16 to 175; larvae were few compared to Yampa River samples.

Because of differences in number of Colorado pikeminnow larvae within and among years, daily catch rates were adjusted by the percentage of flow sampled to obtain a whole river transport abundance index, here reported as capture of larvae/hr. Intra-annual patterns of Colorado pikeminnow larvae transport abundance were variable in the Yampa River. For example, eight transport abundance peaks exceeded 2,000 larvae/hr in 1990. Spring peak flow (352 m³/sec, 9,960 ft³/sec) and mean July-August flow (11.9 m³/sec; 419 ft³/sec) that year was moderate to low and the spring peak was comparatively late (14 June). Conversely, no peaks in drift abundance of that magnitude were found in most other low flow years 1994, 2001-2003, and 2007, 2012 notwithstanding. The typical number (median) of peaks > 2,000 larvae/hr per year in the lower Yampa River was two. The largest peaks (~11,000 larvae/hr) occurred in 1992, 2010, and 2011. Other large peaks (one per year, ~7,500-10,000 larvae/hr) were found in 1995, 2000, 2005, and 2008. Most peaks in captures of larvae were typically later in the year, from mid to late July.

Daily peaks in transport abundance of Colorado pikeminnow larvae were usually sporadic, and short in duration, typically increasing to peak and declining within 2 d. For example, 64% (835 of 1,306) of Colorado pikeminnow larvae captured at dawn during the high transport year of 1990 were from 5 of 31 sampling days (16%) and most high density periods were only 1-2 d long. Single peaks in drift abundance often constituted a substantial portion (\geq 33%) of the number of larvae transported downstream in any given year, including 1992, 1994, 1995, 2000, 2004, 2005, 2007, 2008, and 2010. Drift abundance patterns in other years were more even or were simply very low.

Similar to the Yampa River, drift patterns for Colorado pikeminnow larvae in the lower Green River were sporadic with a few peaks containing the bulk of reproduction in any given year. However, there were only five peaks > 2,000 larvae/hr in the lower Green River: one in each of 1991, 1996, and 1999, and two in 1992, compared to the Yampa River where there was two or more per year in most years. The largest peak in drift abundance in the lower Green

River (1991, almost 4,000 larvae/hr) was substantially smaller than the largest in the Yampa River.

Diel abundance patterns of larvae.—Samples to describe diel abundance patterns of drifting Colorado pikeminnow larvae were collected on 142 days, 546 time periods (not all periods were sampled on all days), and constituted 1,638 total samples collected (typically 3 net sets per time period) over 22 years of sampling. Abundance of larvae captured during each of dawn, noon, dusk, and midnight periods varied widely across years (Figure 8, Table 3). Midnight samples had the highest abundance of larvae, while the three other time periods were slightly lower but relatively similar. However, drought years had a large influence on diel drift patterns as many of the highest abundances (e.g., 1994, 2000-2002, 2007, 2012) were during midnight sampling and abundance at other times in those same years was consistently very low. For non-drought year data, abundance of larvae in samples was similar across all times, with slightly lower abundance at dusk. Dawn samples had highest mean abundance of larvae captured, with a modest CV. The CV values for diel samples collected in drought years were high at all times of the day.

Colorado pikeminnow larvae annual transport abundance index.—Daily transport abundance index values were summed over the entire reproductive period of Colorado pikeminnow each year to obtain an annual index of production of larvae from Yampa River and lower Green River. Like daily transport values, annual transport abundance indices varied substantially across years (Figure 9). For example, in the Yampa River, transport abundance was very high in 1990 and 2011, one relatively low and one very high flow year, respectively. Production of larvae was very low in relatively dry years of 1994, 2001-2003, 2007, and 2012. In those years mean July-August flows in the Yampa River were 6.1 m³/sec (215 ft³/sec, range 0.8-13.2 m³/sec), compared to 36.1 m³/sec (1,275 ft³/sec, range 7.2-138.8 m³/sec) in other years when production was typically higher. The overall trends at both locations showed a negligible decline in annual production of larvae, which we interpret as temporally stable.

We modeled the relationship of Colorado pikeminnow larvae transport abundance as a function of spring and summer flow levels in the Yampa and Green rivers (Figures 10 and 11). The relationship between Yampa River spring peak flow and Colorado pikeminnow larvae transport abundance was positive, albeit variable, with outliers of high production in at least one relatively modest flow year (1990, peak flow = 282 m³/sec, 9,960 ft³/sec and mean July-August

flow = 11.9 m³/sec; 419 ft³/sec) and low production in a moderate peak flow year (2003, flow = 458.7 m³/sec, 16,200 ft³/sec). In several years including 1994, 2002, and 2007, low peak flow magnitudes (< 283 m³/sec, < 10,000 ft³/sec) resulted in relatively low or near zero production and transport of Colorado pikeminnow larvae, whereas higher peak flow levels typically resulted in higher abundance of Colorado pikeminnow larvae.

The relationship of mean July-August flows for the Yampa River during summer to the Colorado pikeminnow larvae transport abundance index was positive (the relationship with very high 1995, 1997, and 2011 flow peak years excluded [not depicted in Figure 10] was $r^2 = 0.64$). Yampa River mean July-August base flow levels < 14.2 m³/sec (< 500 ft³/sec) often resulted in low production and downstream transport of Colorado pikeminnow larvae. In contrast, mean base flows > 14.2 m³/sec (500 ft³/sec) generally resulted in higher transport abundance of Colorado pikeminnow larvae.

Annual transport abundances for Colorado pikeminnow larvae in the lower Green River were relatively stable up to peak discharges of about 700 m³/sec (24,700 ft³/sec) but declined at flow levels greater than that (Figure 9 and 11). Similarly, transport abundance remained high at summer base flow levels up to about 100 m³/sec (3,530 ft³/sec), but declined at flow levels greater than that; decreasing sampling efficiency in higher flow years may have been an issue.

Abundance and length patterns for age-0 Colorado pikeminnow and other fishes in autumn, Green River.—Seine samples collected in the middle and lower reaches of the Green River annually from 1979-2012 documented distribution and abundance of age-0 Colorado pikeminnow and other fishes in backwaters (Tables 4 to 7). A total of 2,765 backwaters was sampled in both reaches with 5,642 seine hauls, with slightly more effort allocated to the middle Green River reach over the 34 years of study. This was due, in part, to more limited lower Green River backwater habitat, and the smaller effect of addition of a third backwater sample in the middle Green River since 2005. A total of 479,992 fish, representing 26 species (7 native) was collected, with 54.7% of total fish from the middle Green River and the remainder from the lower Green River. Except for Colorado pikeminnow, which were identified and counted on every seine haul in every backwater, identification of all species in samples occurred in only the first of two seine hauls in the first (primary) backwater per reach (2 or more backwaters total per reach), or less than 25% of all seine hauls. That practice reduced the apparent number of total

fish captured in seine sampling, and increased the apparent abundance of Colorado pikeminnow relative to total fish sampled.

Mean size of backwaters sampled each year in the study period was 36% larger in the middle Green River (mean = 1,417 m²; range 656-2247 m²) than in the lower Green River (mean = 1,039 m²; range 360-2,302 m²). We also found that mean backwater size was positively correlated with sampling year in the middle Green River ($r = 0.59$) but not the lower Green River ($r = 0.02$). In addition, mean annual area of backwaters sampled in the lower Green River was weakly negatively correlated with spring peak ($r = -0.27$) and moderately with summer base flow ($r = -0.53$) level. The relationship in the middle Green River for spring peak ($r = 0.27$) and summer base flow ($r = 0.12$) level was slightly positively correlated, which may reflect differences in stream geomorphology in each reach. There was also a weak negative correlation between age-0 Colorado pikeminnow density and mean backwater size each year in each of the middle ($r = -0.28$) and lower ($r = -0.07$) Green River reaches.

Nonnative fishes numerically dominated seine samples in both Green River reaches, both in taxa represented and abundance (Tables 6 and 7). Red shiner, sand shiner *Notropis stramineus*, and fathead minnow *Pimephales promelas* comprised 92.8% of all fish captured in both reaches (Figure 12). Red shiner was the most abundant species and was 67.8% of all fish captured, while fathead minnow and sand shiner were 14.3% and 10.7%, respectively. Abundance of each was highly variable over time in each reach, and sand shiner apparently increased in abundance over time whereas red shiner and fathead minnow abundance was more stable.

A total of 22,469 young Colorado pikeminnow was captured in both the middle and lower Green River from 1979-2012 and 98.7% of those were age-0 individuals (≤ 75 mm TL; Tables 4 and 5). Colorado pikeminnow was the most abundant native fish, and represented 1.6% of all fish captured (Tables 6 and 7). Percent composition of age-0 Colorado pikeminnow in Green River samples may be overstated by about a factor of four because, excluding Colorado pikeminnow, only about 25% of backwater samples of fish were taxonomically identified. The lower Green River reach samples contained nearly three times as many age-0 Colorado pikeminnow than the middle Green River reach (catch-per-unit-effort mean 1979-2012 mean = 1.47 for lower Green River [0.03-9.21], mean = 0.51 for middle Green River [0-2.44]), and

Colorado pikeminnow was more abundant in lower Green River in 25 of 34 years, despite greater effort in the middle Green River in many years.

Colorado pikeminnow occurrence in 8-RK reaches of the middle Green River varied by year and were lowest in the upper end of the middle Green River reach near Split Mountain Boat Ramp (RK 515) and the lower end near Sand Wash (RK 347; Figure 13). In the lower Green River, young Colorado pikeminnow were more evenly distributed.

Length of age-0 Colorado pikeminnow varied over years (Figure 14), likely a consequence of water temperature and length of the growing season. Mean length of Colorado pikeminnow averaged about 10% greater in the middle Green River reach (mean = 42.3 mm TL, range 22.0 to 61.6 mm) than the lower Green River (mean = 38.1 mm TL, range 28.6 to 64.8 mm). In low flow and warm years, such as 1994, 2000, and 2007, age-0 Colorado pikeminnow in the middle Green River were substantially longer than in cooler, higher flow years such as 1986. Similarly, in the low flow year 2002 in the lower Green River (no pikeminnow collected in the middle Green River that year), mean TL of age-0 Colorado pikeminnow (61.6 mm) was the longest recorded during the study. In high flow and cool years 1995, 1999, and 2011, pikeminnow were shorter than average. Middle Green River samples often had low numbers of Colorado pikeminnow, especially in later years (e.g., 2 each in 2003 and 2012, 5 each in 2006 and 2007, 0 in 2002 and 2011), so those mean length data should be interpreted cautiously.

Regression models fit to mean annual length data for age-0 Colorado pikeminnow in the middle and lower Green River reaches had moderately good explanatory power (overall model fits had R^2 of 0.85 and 0.72, respectively) and indicated that flow, water temperature, and red shiner density were important predictor variables (Tables 8 and 9). Spring peak flow was the variable selected and had a negative coefficient, likely because elevated flows lasted longer into summer and resulted in a shorter growing season. Models with summer base flow magnitude also had a good fit but a negative coefficient (see below), which was a consequence of the high and positive correlation between spring peak and summer base flows ($r = 0.83$, $p < 0.0001$). Mean July-August water temperature was positively correlated with age-0 Colorado pikeminnow length in each the middle and lower Green River reaches, and was the first and second-most influential variable in those reaches, respectively. Finally, red shiner density was positively correlated with age-0 Colorado pikeminnow growth, strongly so in the middle Green River, and less so in the lower Green River.

The relationship of mean TL of age-0 Colorado pikeminnow as a function of August-September baseflow was negative for both the middle and lower Green River (Figure 15). The relationship for the middle Green River had a slightly steeper slope, indicating mean TL declined faster as flows increased, than the lower Green River. Mean TL of age-0 Colorado pikeminnow in each reach at flows of 56.6 m³/sec (2,000 ft³/sec) and 85 m³/sec (3,000 ft³/sec) were about 40 mm TL, and 35 mm TL, respectively.

In some years when age-0 Colorado pikeminnow were in low abundance there was a perception among biologists that fish tended to be relatively long and the converse in years of high abundance. However, this perception is not borne out by the data. Pearson correlation coefficients between abundance (# age-0 Colorado pikeminnow/10 m² seined) and mean TL (mm) were weak in the middle Green River for all years (1979-2012, $r = -0.09$), as well as for a set of years when abundances were higher (1979-1994, $r = 0.09$). Similarly, correlation of abundance and mean TL (mm) was weak in the lower Green River for all years (1979-2012, $r = -0.05$).

Age-0 Colorado pikeminnow were moderately abundant in the middle Green River through 1993, but since 1994 had very low abundance, with the exception of 2009 and 2010. In some years of low flows (1994, 2001-2003, 2006-2007, 2012) or high flows (1983-1984, 1997, 1999, 2008, 2011), captures of age-0 Colorado pikeminnow in backwaters in autumn were very low or zero in the middle Green River. The proportion of backwaters where age-0 Colorado pikeminnow were detected also declined with time for both the middle Green River ($r = -0.56$) and the lower Green River ($r = -0.28$).

Age-0 Colorado pikeminnow density was substantially higher in the lower Green River historically than in the middle Green River (Figure 16). Colorado pikeminnow density was also high through 1993, with very large year-classes present in 1980 and 1988. However, after 1994, age-0 Colorado pikeminnow were relatively uncommon, with only 1996, 2000, 2007, and 2009 year-classes being moderately abundant.

Those declining patterns led us to examine environmental factors that may be responsible for abundance of age-0 Colorado pikeminnow in the Green River in autumn. Flows in August-September, when age-0 Colorado pikeminnow occupied backwaters, declined rather dramatically in each the middle and lower Green River reaches over time (Figure 17). For example, by dividing the study period into approximately equal early (1979-1989), middle

(1990-2000) and late (2001-2012) periods, we found mean August-September base flows in the lower Green River, declined progressively from 104.3, to 80.0, to 60.0 m³/sec (3,546, 2,825, and 2,119 ft³/sec, respectively) over the 34-year period. Further, flows in the middle and lower Green rivers were very similar in a given year during low water years (e.g. 2000-2004, 2012), despite tributary contributions to the lower Green River.

We examined the relationship between age-0 Colorado pikeminnow density and summer base flow, which was controlled mainly by Flaming Gorge Dam releases, to determine if certain flow levels consistently produced larger year-classes of fish. In the middle Green River, density of age-0 Colorado pikeminnow was variable but showed a dome-shaped relationship with mean August-September summer baseflow (Figure 18). Densities were highest at intermediate flow levels of 1,700-3,000 ft³/sec, but were much lower at flows < about 1,700 ft³/sec and > about 3,000 ft³/sec; flows > 2,500 ft³/sec produced only a single year with above average age-0 pikeminnow abundance. Dashed lines indicate the intermediate range of flows that encompasses most of the years when densities of age-0 Colorado pikeminnow were highest, recognizing that pikeminnow were not abundant every year. For example, in that intermediate flow range, age-0 Colorado pikeminnow densities were > 0.51 fish/10 m² of habitat seined, the mean density over 34 years of sampling, in 10 of 16 years (63% of the time). In comparison, during lower flow years, pikeminnow densities were that high in only 2 of 13 years (15% of the time), and in the five years when flows were high, pikeminnow density never exceeded the mean level. Thus, the intermediate flow range encompassed by the dashed line included all but two of the years when pikeminnow abundance was greater than the overall mean of 0.51 fish/10 m². The two higher density years in the lower flow range were 1988 and 1990, historical records of importance to be sure, but were from the pre-1994 period when pikeminnow were much more abundant.

Similar to the middle Green River, density of age-0 Colorado pikeminnow in the lower Green River was also variable but showed a similar dome-shaped relationship with mean August-September summer baseflow (Figure 18). Densities were highest at intermediate flow levels of 1,700-3,800 ft³/sec, but were much lower at flows < about 1,700 ft³/sec and > about 3,800 ft³/sec; flows > 3,000 ft³/sec produced only a single year with above average age-0 pikeminnow abundance. Dashed lines indicate the intermediate range of flows that encompassed most years when densities of age-0 Colorado pikeminnow were highest,

recognizing that pikeminnow were not abundant every year. For example, in that intermediate flow range, age-0 Colorado pikeminnow densities were > 1.47 fish/10 m² of habitat seined, the mean density over 34 years of sampling, in 8 of 20 years (40% of the time). In comparison, during lower flow years, pikeminnow densities were that high in only 1 of 7 years (14% of the time), and in the seven years when flows were higher, pikeminnow density never exceeded the mean level. Thus, the intermediate flow range encompassed by the dashed line included all but one of the years when pikeminnow abundance was greater than the overall mean of 1.47 fish/10 m². The single higher density year in the lower flow range was 2007.

The relationship of age-0 Colorado pikeminnow density in backwaters as a function of the larvae transport abundance index in the middle Green River was positive for lower base flow years up to about 3,000 ft³/sec, but the single data point at higher flows resulted in a dome-shaped relationship because no age-0 pikeminnow were sampled that year (2011, the point with the highest estimated transport index, Figure 19). The model for the middle Green River was ($F = 3.04$, $df = 1, 21$, $p = 0.07$, $r^2 = 0.24$; $\ln(\text{density of age-0 Colorado pikeminnow (\#/10 m}^2 \text{ seined)}) = -0.0156 + 0.000018 * \text{transport abundance} - 0.0000000003 * \text{transport abundance}^2$, where \ln is \log_e of pikeminnow density and transport index is the annual estimate of larvae transport abundance as fish/hr-yr). When the transport abundance index for Colorado pikeminnow larvae was $< 15,000$ fish/hr-yr, density of age-0 Colorado pikeminnow exceeded 0.51/10 m² in the middle Green River in 1 (2009) of 9 years. Conversely, when transport abundance was $\geq 15,000$ fish/hr-yr, Colorado pikeminnow density exceeded 0.51/10 m² in 4 of 13 years.

In the lower Green River, we also found the relationship of abundance of age-0 Colorado pikeminnow as a function of transport abundance of larvae was positive, albeit weak, and limited by the few data available ($F = 0.35$, $df = 1, 6$, $p = 0.58$, $r^2 = 0.07$; $\ln(\text{density of age-0 Colorado pikeminnow (\#/10 m}^2 \text{ seined)}) = 0.294 + 0.000029 * \text{transport abundance}$, where \ln is \log_e of pikeminnow density and transport index is the annual estimate of larvae transport abundance as fish/hr-yr). Efforts to model abundance of age-0 Colorado pikeminnow in autumn as a function of multiple other environmental and biological predictor variables, including abundance of select nonnative species other than the one discussed above, were not successful.

A previous analysis (Muth et al. 2000) showed age-1 (75-130 mm TL) Colorado pikeminnow abundance in the lower Green River positively related to abundance of age-0

pikeminnow the year before, particularly for abundance of age-0 pikeminnow > 45 mm TL, as well as age-0 abundance the year the juveniles were captured. Juvenile abundance was also negatively correlated with spring runoff of the same year (overall model fit was $R^2 = 0.80$). We conducted the same analysis with additional years of data from the lower Green River, the only reach with sufficient (non-zero) juvenile density data to conduct such an analysis, and found a much poorer fit ($R^2 = 0.28$) even though the overall model indicated some level of biological importance ($df = 3, 29; F = 3.74; p = 0.02$). That model again showed that age-1 abundance, a measure of overwinter survival, remained a positive function of the abundance of age-0 fish the previous year. Additional models were also run with other base or peak flow variables but none emerged that had an improved fit, likely because of inter-correlated flow variables.

Density patterns of red shiner, a potentially piscivorous and abundant invasive species that occupied the same backwaters as age-0 Colorado pikeminnow, were similar in the lower and middle Green River but increased little or not at all over time (Figure 20). Highest densities have been recorded since the early 1990s, especially in the lower Green River. Red shiner densities were particularly high in low flows years such as 1994, 2000, 2002, 2006, and 2007. We could not examine abundance patterns of only large red shiners, the most piscivorous kinds, related to environmental variables or pikeminnow abundance because size classes of red shiners were not described in the data.

Red shiner density declined in the middle and lower Green River reaches as a function of mean August-September flow, 1979–2012 (Figure 21). In the middle Green River, red shiner abundance was often very high when mean August-September flows were < 65 m³/sec (2,300 ft³/sec) with densities once reaching 323/10 m² (1994, flow = 45.1 m³/sec [1,593 ft³/sec]); densities were lower in high flows years. Similarly, in the lower Green River, red shiner density was often high, once exceeding 150/10 m², at flows < 82.1 m³/sec (2,900 ft³/sec, 2002) and lower at higher flows. Efforts to model abundance of red shiners in autumn as a function of several environmental variables other than summer base flow was not successful.

Density of age-0 Colorado pikeminnow and backwater habitat.—Reanalysis of Pucherelli et al. (1990) showed backwater number/km was highest in Island Park, but was also high in Ouray and Jensen reaches (Figure 22). In general, backwater number declined at the highest flow of 142 m³/sec (5,000 ft³/sec), but within the lower range of flows from 37-71 m³/sec (1,300-2,500 ft³/sec), backwater numbers were essentially stable; only the relatively short Sand

Wash reach showed an increase in backwater number with flow level. The Mineral Bottom reach in the lower Green River had the lowest number of backwaters/km of any Green River reach and that number was essentially stable over the limited range of flows sampled.

In the middle Green River, backwater area was highest in the Ouray reach, followed by Sand Wash, Island Park, and Jensen, over the range of flows that excluded the highest flow measured. Mineral Bottom also had the lowest area of backwater habitat by a substantial margin. In general, backwater area declined at the highest flow level sampled, but at Ouray and Sand Wash, area was stable and high at the lower range of flows (37-71 m³/sec; 1,300-2,500 ft³/sec), and declined over the range of flows sampled at Island Park and Jensen. Backwater area at Mineral Bottom was relatively stable and very low. In general, backwater number and area/km were highest in the Jensen, Ouray, and Sand Wash reaches at flows up to 71 m³/sec (2,500 ft³/sec). Similarly, in the lower Green River, backwater habitat area was stable, over the limited range of flow levels examined.

Backwater habitat number and area was delineated in Pucherelli et al. (1990) by reach, and we calculated area/km (assume this was their "Area", in Tables 1-5). Even though Pucherelli et al. (1990) measured their study reaches (Island Park = 6 RM, Jensen = 7 RM, Ouray = 10 RM, Sand Wash = 3 RM, and Mineral Bottom = 6 RM), they did not report the total length of each river section represented by their study areas, which would allow subsequent investigators to assign relative levels of importance to each reach. We noted that mean backwater size was lowest in the lower Green River, similar to our measured areas for ISMP backwaters, and mean number/km of backwaters in the middle Green River was approximately 2-3 times higher than for the lower Green River. Based on mean number of backwaters and mean area/km, and assuming about equal reach lengths, the middle Green River reach had almost 9X the amount of backwater habitat as the lower Green River.

In general, Day et al. (1999) and Trammell and Chart (1999) found the middle Green River supported many more backwaters in the same length of river than the lower Green River (mean/year = 68 and 25 respectively, Figure 23). Mean backwater number was similar in 1992-1996 in the middle (4.25/RK) and lower Green River (1.6/RK) compared to the number in Pucherelli et al. (1990) in 1987 (compare with Figure 22), but backwater number was much higher in the middle Green River. Similarly, in 1992-1996, total backwater area was on average 4.5 times greater in the middle Green River than the lower Green River, because of

greater backwater number and larger mean area (626 vs 454 m², respectively). However, because age-0 Colorado pikeminnow density in backwaters was higher in the lower Green River than the middle Green River (means = 1.25 vs. 0.25/10 m², respectively), mean estimated pikeminnow abundance for the reach (backwater area x pikeminnow density) was similar in the middle and lower Green River over the 1992-1996 study period (1199 and 1158, respectively, per 16 RK reach per year).

DISCUSSION

Decline in abundance of age-0 juvenile Colorado pikeminnow in the Green River subbasin has been identified as a major factor in the decline of adult life stages (Bestgen et al. 2007a, Bestgen et al. 2010; Bestgen et al. 2016 review draft). Determination of reasons for this decline was a primary impetus for this study and was identified as a critical research need in the Green River Study Plan (Green River Study Plan *ad hoc* Committee, 2007). We found Colorado pikeminnow reproduced in the Green River subbasin at two main localities, the lower Yampa River in Yampa Canyon and the lower Green River in Gray Canyon, each year that sampling occurred from 1979 through 2012. Timing of reproduction in summer was positively related to date of peak spring runoff flow as well as water temperature. Abundance of larvae produced from spawning areas each year was positively correlated with both spring peak and summer base flows in the lower Yampa and lower Green rivers. Densities of age-0 Colorado pikeminnow captured in nursery backwaters in autumn in the middle and lower Green River declined over the study period. We found density of age-0 Colorado pikeminnow in backwaters in each the middle and lower Green River reaches was highest at intermediate summer flow levels, and also positively related to abundance of larvae produced each year, but low when summer flows were low or high. Growth of age-0 Colorado pikeminnow was positively related to July-August water temperatures and negatively related to August-September base flow levels. Abundance of red shiners (a potential predator on and competitor with young Colorado pikeminnow) was negatively associated with base flow magnitude, perhaps due to a shortened summer reproduction period. Mean August-September base flow in the Green River nursery habitat reaches has declined by about 40% from the 1980s to the period from 2001 to 2012, consistent with fewer age-0 Colorado pikeminnow and abundant red shiners. Flows were

higher from 2006-2012, and two larger year classes of age-0 Colorado pikeminnow were observed in the middle Green River.

Age-0 Colorado pikeminnow abundance data did not yield unequivocal relationships, likely a result of high variability in both young pikeminnow abundance and environmental factors, but the data indicate that an increase in August-September base flow in the Green River in lower flow years may be a means to increase survival of age-0 Colorado pikeminnow. This is needed in both the middle and lower Green River. The lower Green River is important because age-0 Colorado pikeminnow densities were historically higher and large numbers of juveniles were present. The middle Green River is also important because it historically produced higher abundances of age-0 pikeminnow in the past when adult abundance in the Green River subbasin was stable or increasing. Because of the contribution of Colorado pikeminnow larvae from the Yampa River to the middle Green River nursery habitat reach, and because Yampa River flows support Green River base flows in summer, peak and base flows of the Yampa River (and other tributaries) should be protected and enhanced to the extent possible. Releases of water from Flaming Gorge Dam serves many purposes, including connecting the river to floodplain wetlands (LaGory et al. 2003; Larval Trigger Study Plan, LaGory et al. 2012). Summer base flows also need to increase in some average and all lower flow years to ensure nursery habitat availability for young Colorado pikeminnow and to support all the other factors that are involved in the annual summer recruitment process including production of larvae at spawning areas, transport of young to backwaters, colonization of backwaters by larvae, flow and water temperature interactions with nonnative fishes that affect pikeminnow survival. The following provide support for these general conclusions and recommendations for future studies that will refine and improve implementation of recommendations.

Timing of reproduction.—Colorado pikeminnow reproduced in early to mid-summer in the Green River subbasin. Dates of initiation of reproduction were earlier, temperatures at first reproduction lower, and days post-peak runoff fewer than reported by other researchers (Hamman 1981; Haynes et al. 1984; Nesler et al. 1988; Tyus 1990; Tyus and Haines 1991). This was probably because capture and aging of larvae was a more accurate estimate of time of reproduction than presence of adults near spawning areas or regression back-calculation of hatching date from total lengths of larvae or juveniles.

Similar to Bestgen et al. (1998), and with an additional 15 years of data from the lower Yampa River, we found that no single variable accurately predicted date of initiation of spawning by Colorado pikeminnow. However, mean date of initiation of spawning (23 June) in the lower Yampa River over the period 1990-2012 was predicted with good accuracy using degree days and spring peak runoff magnitude. The coefficient for degree days was positive and indicated that as temperatures warmed, Colorado pikeminnow were more likely to begin spawning. The coefficient for magnitude of spring peak runoff was also positive, and indicated that Colorado pikeminnow were likely to spawn earlier in years with lower peak flows and later in years when flows were higher, although it is difficult to disentangle associated temperature effects because water temperatures are warmer earlier in lower flow years.

Date of the first peak in Colorado pikeminnow reproduction in the lower Yampa River was typically just a few days after the start of reproduction. In spite of the subjective nature of determining a “first peak”, and differences across years in reproductive patterns (some years when few or no peaks were evident), predictions regarding this metric were about as reliable as that for first reproduction.

Water temperature at initiation of reproduction (mean = 18.4°C) was more variable and lower in the Yampa River than the lower Green River and was lower than previously reported (Hamman 1981; Haynes et al. 1984; Tyus 1990; Tyus and Haines 1991). Those lower temperatures were surprising because it was generally believed that Colorado pikeminnow did not spawn until water temperatures exceeded 18°C (Hamman 1981; Tyus 1990; Tyus and Haines 1991), although reproduction at lower temperatures had been documented (Bestgen et al. 1998). It may be that timing of reproduction is also influenced by day length and a logical result of that would be the observed water temperature differences between the two reaches.

Water temperature was typically 21 °C in the lower Green River when Colorado pikeminnow first reproduced. Also, there were more days when mean water temperature was > 18°C in the lower Green River than in the lower Yampa River, in part, because 18°C was exceeded in some years prior to runoff in the lower Green River. That is also at least part of the reason that total degree days was higher in the lower Green River. Days post-peak runoff before reproduction were typically fewer in the Green River than in the Yampa River because of earlier spawning in the warmer water of the Green River. Additional data collection in the lower Green River, including sampling Colorado pikeminnow larvae with drift nets, would assist

with clarification of the effects of environmental factors on reproduction by Colorado pikeminnow that use that reach.

Lack of a strong correlation between initiation of reproduction by Colorado pikeminnow and environmental variables such as water temperature and days post-peak discharge may be explained by insufficient sampling intensity. For example, estimates of date of initiation of reproduction may be biased in low discharge years because most larvae were captured in just a few midnight samples. Thus, unless diel samples were collected relatively early in the season, the normal dawn-only samples may not detect the first larvae that are transported downstream until relatively late in a season. Sampling during higher discharge years, which results in lower proportions of the river sampled and fewer larvae captured, likely contributed to accurate detection of first reproduction, and because few early fish were available for detection.

The lack of a clear relationship between water temperature and initiation of reproduction by Colorado pikeminnow was surprising with the addition of many more years of data (Bestgen et al. 1998) even though temperature thresholds have been postulated in the past (Hamman 1981; Tyus 1990; Tyus and Haines 1991). It was possible that Colorado pikeminnow responded to thermal cues but perhaps only after peak runoff. A metric of that, the number of days that exceeded 18°C following peak runoff, was nearly as variable as total days that exceeded 18°C, so that hypothesis was dismissed. A main driver of timing of reproduction, spring peak flow level, also had an inter-correlated thermal cue, because higher flows were cooler and occurred later in the year than lower flows, which warmed earlier.

Our results and those of Nesler et al. (1988) confirm that cues for reproduction by Colorado pikeminnow in the variable and fluctuating environment of streams in the Colorado River basin were complex and likely a mixture of interacting factors. During this study, Colorado pikeminnow initiated reproduction within a fairly restricted time frame in both the Yampa and Green rivers despite highly variable discharge and temperature regimes. This suggested that a temporal factor such as photoperiod linked with a circadian rhythm may also serve as a cue, perhaps in conjunction with flow regime, water temperature, and other undetermined factors, to initiate reproduction by Colorado pikeminnow.

Intra-annual abundance patterns of larvae.—Differences in abundance of larvae in samples within and among years is likely the result of numerous factors, including time to attain adulthood and individual condition and number of adult fish at the spawning areas, and

environmental conditions. Even if adult condition and abundance were relatively constant across years and seasons within a year, environmental conditions and flow levels probably affect the survival of eggs and larvae at the spawning area and subsequent abundance in drift samples. Because no data were collected that described the abundance and condition of adults at spawning areas, transport abundance as measured by density of drifting larvae was the best measure of reproductive success. The few high peaks that often constituted a large proportion of transport abundance in any year substantiated the importance of daily sampling to obtain accurate estimates of annual production of larvae. This was true because single transport abundance peaks often constituted 30% or more of annual reproductive effort.

Peaks in larvae transport abundance in the Yampa River from 1991-1996 (Bestgen et al. 1998) were often associated with increased turbidity and discharge, especially in 1991 and 1992. Peaks in abundance of larvae associated with increased turbidity, but not necessarily increased discharge, indicated that elevated turbidity may increase drift. High transport abundance of larvae associated with increased turbidity and discharge has been described for other cypriniform fishes (Lindsey and Northcote 1963; Geen et al. 1966; Gale and Mohr 1978) and might be affected by several factors. Larvae may lose orientation in turbid water and thus become entrained in river currents and be swept downstream. Loss of orientation in the dark may be the reason for higher transport abundance of Colorado pikeminnow at midnight in some years. Transport under such conditions may also reduce susceptibility to predators that are sight feeders or which may be inactive at night (Armstrong and Brown 1983).

Elevated turbidity may also increase sediment deposition in interstitial spaces of the substrate, which may motivate larvae developing in the substrate to emerge and drift. If larvae were simply emerging and losing visual acuity or avoiding predators, more uniform patterns of drift throughout days of high turbidity would be expected. Our data from 1992-1996 did not support this scenario: drift peaked at dawn or noon on most days with increased water turbidity, declined dramatically by dusk, and was very low by midnight and on subsequent days even though water remained turbid. This suggested that larvae ready to emerge were entrained over a short time at the beginning of the event rather than slowly entering the drift over the entire period of elevated turbidity. The turbidity-stress hypothesis was supported by age and length data for larvae captured on six different sample dates throughout the 1992 sampling season; larvae captured during an extreme turbidity event were 1-2 d younger and 1 mm shorter than

larvae captured on other dates when turbidity was lower. During that high turbidity event, a settled volume of Yampa River water was about 50% sediment (pers. obs., KRB). The underdeveloped state of larvae captured when sediment loads were very high but discharge increased only slightly indicated that larvae prematurely emerged from the substrate and drifted to avoid being buried in sediment (Bestgen et al. 1998). In the absence of turbidity, larvae likely emerged from the substrate and entered the drift more uniformly and over a period of days or at times other than when they would be susceptible to sampling at dawn. Effects of turbidity on upper Colorado River basin fishes are understudied but could yield valuable information on ecology and management of these fishes.

Addition of 15 years of data after a previous summary (Bestgen et al. 1998) failed again to detect peaks in reproductive activity associated with increases in discharge above base flow, or “flow spikes”, in the Yampa or the Green rivers (e.g., Nesler et al. 1988). This is further evidence that the flow spike hypothesis was not relevant during our study.

Diel abundance patterns of larvae.— Previous research showed that Colorado pikeminnow larvae in the Yampa River were generally most abundant in dawn drift-net samples and were distributed about equally across the channel (Haynes et al. 1985; Nesler 1986-1987; Bestgen et al. 1998). Addition of 15 years of data since 1996 further supported the notion that diel abundance patterns varied by year, depending on timing of emergence of larvae, the frequency of turbid flow events, water clarity, and flow levels. Diel drift abundance data collected from 1992-2012 revealed two distinct patterns. The first pattern, low abundance at all times except midnight, was associated with low (sometimes very low) and clear flows in summer. The second pattern was more even drift abundance across most times of the day, with highest drift rates at dawn and the lowest at dusk.

When transport abundance was highest at midnight, the combined effects of low stream discharge, low velocity, and clear water likely reduced the tendency of larvae to get entrained except in the dark. Rarity of larvae in downstream samples (Jensen, Utah, Bestgen et al. 1998) indicated that very few larvae were produced or transported downstream in some low flow years. Limited recruitment of juveniles in downstream reaches in low flow years supported the notion that few larvae were produced in the middle Green River nursery habitat reach. Other studies (Gale and Mohr 1978; Armstrong and Brown 1983; Muth and Schmulbach 1984; Corbett and

Powles 1986; Harvey 1991; Johnston et al. 1995) have reported greater densities of drifting larvae of other cyprinid species at midnight than other times of the day.

Colorado pikeminnow larvae annual transport abundance index.—The substantial variation in numbers of larvae captured each year between river reaches was likely largely due to differences in reproductive effort between spawning areas and hatching success. In the Yampa River, we observed relatively high transport abundance of Colorado pikeminnow larvae through 2000. This was followed by a relatively sharp decline during drought years 2001-2003, and relatively low levels of reproduction were documented in most years through 2012. Exceptions were years with comparatively high flows. Overall, transport abundance of Colorado pikeminnow larvae in the lower Yampa and Green rivers indicated a negligible decline over time.

Annual transport abundance metrics for Colorado pikeminnow larvae in the lower Yampa River were positively related spring peak flow and mean July-August summer base flow. This is important because abundance of larvae was positively related to abundance of age-0 pikeminnow in autumn. High peak flows prepare substrate for spawning by mobilizing and transporting fine sediments and elevated base flows maintain clean interstitial spaces, allowing well-oxygenated water to bathe developing embryos. Annual transport abundance for Colorado pikeminnow larvae in the lower Green River plateaued at about 700 m³/sec (24,700 ft³/sec) and declined at flow levels greater than that. Similarly, transport abundance levels remained high at summer base flow levels up to about 100 m³/sec (3,530 ft³/sec), but declined at flow levels greater than that.

Although the lower Green River spawning area does not appear to produce as many larvae, on average, as the lower Yampa River, based on estimates of transport abundance, both reaches are important because nursery habitat is present downstream from each. In fact, recent capture-recapture studies of juvenile (< 400 mm TL), recruit (400-449 mm TL), and adult Colorado pikeminnow showed that most Green River subbasin recruitment occurs in the lower Green River (Bestgen et al. 2007a; Bestgen et al. 2010).

A better understanding of drift abundance and age-0 and juvenile fish abundance dynamics for the lower and middle Green River reaches would add valuable information for management of the system, and for understanding recruitment dynamics of Colorado pikeminnow in the entire Green River basin (Bestgen et al. 2007a; Bestgen et al. 2010).

Likewise, maintaining adult spawning stocks in the lower Yampa River to provide larvae to the middle Green River is a first step toward re-establishing strong year classes of age-0 and older Colorado pikeminnow in the middle Green River. Ensuring strong reproduction from each spawning area is especially vital given recent declines in adult abundance throughout the Green River subbasin (KRB, unpublished data 2011-2013).

Low annual transport abundance during low discharge years might be a consequence of several factors. Years with low transport abundance are likely a consequence of low larvae production, low egg and larvae survival, or both. These hypotheses were difficult to evaluate because reproductive effort and conditions for embryo hatching and survival of larvae in spawning gravel are unknown and adult abundance almost certainly plays a role. Low transport abundance of Colorado pikeminnow larvae during low flow periods might be exacerbated if water quality was reduced as a consequence of diminished flows. However, the effects of presumably diminished water quality were not investigated in this effort. Water temperature is not likely a factor diminishing reproduction because laboratory studies showed that pikeminnow embryos incubate successfully and hatch at relatively high levels in water temperatures of 18-26°C, which is similar to conditions at spawning areas (Bestgen and Williams 1994; Bestgen et al. 1998, this study).

Transport abundance calculated from density estimates of Colorado pikeminnow larvae captured in drift nets has been shown to under-estimate actual abundance; differences in abundance across the stream channel or at different times of the day may be the source of error (Franzin and Harbicht 1992; Johnston et al. 1995). Those sources of error were confirmed in this study because patterns of transport abundance varied temporally and with sampling position and across years. However, sampling date was the single largest source of variation in the GLM models that predicted mean abundance of Colorado pikeminnow larvae (data not shown). Daily sampling ensured that the high amplitude but short duration (most < 2 d) peaks of larvae transported downstream were sampled which reduced the effects of sampling error. Dawn sampling reliably estimated the relative abundance of larvae transported downstream in most years, compared to estimates obtained during other sampling periods. Thus, even though actual abundance of larvae may be underestimated by our sampling protocol, patterns probably reflect trends in actual abundance patterns on intra-annual and inter-annual scales. Transport abundance of Colorado pikeminnow larvae may also be underestimated in high flow years

because larvae may be present but remain undetected during high flow portions of the reproductive season. This is particularly true when larvae are transported but none are captured, a situation for which there are no adjustments. Addition of just a few larvae in a high flow year, especially early in the year when flows are highest, would increase estimates of transport abundance, and perhaps additional nets should be set in those years or sampling time increased.

Strong reproduction, as measured by the transport abundance index, in most years from 1990 through year 2000 was consistent with increasing abundance of adult fish in the same period, as measured by catch-effort sampling from 1990-2000 and abundance estimation from 2000-2003 (Bestgen et al. 2007a; Bestgen et al. 2007b; Bestgen et al. 2010). Abundance of adult Colorado pikeminnow was increasing in the 1990s, but declined by 40% from 2000-2003 (Bestgen et al. 2007a), and that large reduction in abundance of adult fish, many of which presumably spawned in the lower Yampa River, may be partially responsible for reduced transport abundance of larvae from the lower Yampa River after year 2000. Continued low abundance of Yampa River adult Colorado pikeminnow is problematic and population recovery will require recruitment from downstream reaches because no young fish remain resident in the lower river. Bolstering abundance of adult Colorado pikeminnow in the Yampa River may also require continued or increased suppression of northern pike, which are capable of preying on adult Colorado pikeminnow or indirectly causing mortality from bite wounds, and all introduced predators including smallmouth bass, walleye, and northern pike compete for food resources with Colorado pikeminnow (Johnson et al. 2008; McGarvey et al. 2010). The Yampa River population of Colorado pikeminnow is particularly relevant to the spawning population found in the lower river because all resident Yampa River adults are thought to spawn there. In contrast, pikeminnow adults in the White River and perhaps the middle Green River may spawn in either the lower Green River in Gray Canyon or the Yampa River but these also have high spawning site fidelity (Tyus and McAda 1984; Tyus 1990; Irving and Modde 2000; Bestgen et al. 2007a).

Abundance and length patterns for age-0 Colorado pikeminnow and other fishes in autumn, Green River.—Numerical dominance of nonnative fishes is a consistent feature of fish communities in backwaters of the Green River (Haines and Tyus 1990; Tyus 1991, Tyus and Haines 1991; this study). Adults of the abundant nonnative cyprinids and age-0 Colorado pikeminnow (40-70 mm TL) in autumn are about the same size and consume the same

invertebrate prey items (Muth and Snyder 1995) so it is difficult to imagine that negative interactions of some sort are not occurring, given the high abundance of invasive kinds.

Distribution of age-0 Colorado pikeminnow in the middle Green River corresponded approximately to the distribution of backwater habitats and were most abundant in the downstream portions of the Jensen reach, throughout the Ouray reach, and the Sand Wash reach of the middle Green River (Pucherelli et al. 1990; Tyus and Haines 1991). They were also widely distributed and abundant in the lower Green River, albeit slightly more common in downstream reaches, beginning near Mineral Bottom.

Mean annual TL of age-0 Colorado pikeminnow was moderately well-predicted in GLMs as a positive function of summer water temperature and red shiner density and a negative association with spring peak flow level, a surrogate but inverse measure of the length of the growing season. This was consistent with the literature on growth of young Colorado pikeminnow, which indicated warmer water for longer periods of time resulted in larger fish (Tyus and Haines 1991; Bestgen 1996; Bestgen et al. 2006; Breen et al. 2011). Warm water temperatures and long growing seasons occurred in years with lower flows, which resulted in relatively longer age-0 Colorado pikeminnow in autumn. Spring peak flows were an inverse predictor of growing season and thus negatively associated with age-0 pikeminnow length because elevated spring peaks extended later in the year and shortened the growing season. The positive association of age-0 Colorado pikeminnow length and red shiner density was likely a surrogate for length of growing season as well, because long growing seasons promoted early and multiple spawning events by red shiners (Muth and Nesler 1993; Marsh-Matthews et al. 2002; Bestgen et al. 2006). Those same conditions typically do not promote high densities of Colorado pikeminnow in Green River nursery habitat reaches. Because abundance of age-0 Colorado pikeminnow is an important predictor of Age-1 abundance, we assume that abundance is more important a factor in driving abundance trends than is pikeminnow length.

Pikeminnow growth is driven, in part, by water temperature and duration of the growing season so lower base flows earlier in the year that are warmer promote faster growth of age-0 Colorado pikeminnow and potentially higher summer survival (Bestgen 1996; Bestgen et al. 2006). Greater age-0 pikeminnow TL may also promote higher overwinter survival (Haines et al. 1998). In lower flow years in the middle and lower Green River (1,500-2,500 cfs), young

Colorado pikeminnow survival was higher (56-62%) when fish had mean TL of 39-67 mm, but was only 6% in a year when fish were small (mean TL = 28 mm).

Also consistent with previous research, we found larger and sometimes faster-growing age-0 Colorado pikeminnow in the middle than the lower Green River (Tyus and Haines 1991; Bestgen 1997; Bestgen et al. 2006). This was largely inexplicable because lower Green River fish hatched earlier, had a longer growing season, and water was warmer in that downstream reach, all of which should contribute to larger rather than smaller individuals; food availability may also play a role but was not examined. A possible explanation was that some density-dependent factor was operating, where higher densities of pikeminnow in the lower Green River limited growth through competition for resources resulting in shorter fish. It may be that only relatively late-spawned fish survived in the lower Green River, such that those fish had shorter growing seasons. Such differential survival of age-0 Colorado pikeminnow, perhaps due to limited food resources or early season predation by red shiners, was noted in both the lower and middle Green River reaches (Bestgen et al. 2006) and may be stronger in the former reach. Another possible explanation was differences in habitat quality between the two reaches that may affect length, but not density, of age-0 Colorado pikeminnow,

We documented declining abundance of age-0 Colorado pikeminnow in both the middle and lower Green River, each beginning in the early- to mid-1990s. This was consistent with other studies (Bestgen et al. 1998; Muth et al. 2000; Bestgen et al. 2007a; Bestgen et al. 2010; Breen et al. 2011). Lower summer base flow in the middle and lower Green River reaches coincided with declining age-0 Colorado pikeminnow abundance and may indicate a means to halt decline of Colorado pikeminnow in this flow-regulated system.

Analysis of density patterns of age-0 Colorado pikeminnow showed low density at low and high flows, but higher density at intermediate summer baseflow levels in both the middle and lower Green River reaches. Mean August-September flow levels in years that supported higher abundances of age-0 Colorado pikeminnow were $> 48 \text{ m}^3/\text{sec}$ ($1,700 \text{ ft}^3/\text{sec}$) in both the middle Green River and the lower Green River. In spite of variable data, a convincing feature of those patterns was that in nearly all lower flow years, few fish were produced. In only a few of those years was absence of age-0 pikeminnow due to lack of larvae produced at spawning areas (e.g., Figure 19). Also, there were only two instances of high age-0 fish abundance in lower flow years in the middle Green River and one in the lower Green River, and in each of

those middle Green River years, 1988 and 1990, abundance of larvae produced was very high (Nesler unpublished drift net data, 1988; this study). Those low-flow years produced a few relatively large age-0 Colorado pikeminnow; for example, size of fish in the middle Green River in 1994 was the largest on record, with mean TL of nearly 65 mm. In contrast to low flow years, intermediate flow years produced relatively high abundance of age-0 Colorado pikeminnow the majority of the time. Thus, the common pattern was low abundance of age-0 fish in autumn in low base flow years in the middle Green River. Similarly, high summer baseflows do not promote suitable conditions for age-0 Colorado pikeminnow mainly because of a paucity of nursery habitat and, perhaps, short growing seasons. Year-class failure in high flow years is typically not because of lack of larvae. It may be that larvae are unable to find suitable backwater habitat in those higher velocity flows.

More recent sampling in Green River backwaters, some of which is not reported in this report, supports base flows in the recommended ranges. For example, recent above average recruitment years were documented in 2009, 2010, and 2015, and flows were in newly recommended ranges. In other recent years when mean August-September base flows were lower and $< 1700 \text{ ft}^3/\text{sec}$ (2012, 2013), or were higher and $> 3000 \text{ ft}^3/\text{sec}$ (2011) and outside of recommended levels, abundance of age-0 Colorado pikeminnow in the Green River was very low, which is also in support of recommendations reported here. Mean July-Aug flows in 2014 were quite high (2979 cfs) at Jensen and perhaps at the upper end of the suitable range, and produced only modest recruitment; sampling was confounded by large quantities of silt in backwaters, which may have lowered efficiency and biased estimates low.

The positive relationship between abundance of age-0 Colorado pikeminnow produced in backwater habitat as a function of the larvae transport abundance index suggested that higher production of larvae from spawning areas may increase abundance of age-0 Colorado pikeminnow. This is largely an intuitive result, if one assumes that density dependence is not an influence on age-0 Colorado pikeminnow abundance, and that habitat is not limiting. The strength of these relationships is likely affected by sampling variation and other factors associated with a fluctuating, large river environment. For example, transport abundance indices are calculated based on scaling up from a small amount of water sampled with drift nets to entire-river estimates of larvae transport. Also, backwater estimates of abundance of age-0 Colorado pikeminnow based on catch-effort data (our density data) were only modestly (but

positively) correlated with estimates of abundance of fish in larger reaches (Haines et al. 1998), which could be another source of variation. Nonetheless, the general patterns supported by many years of data are convincing.

Analysis of additional juvenile Colorado pikeminnow data since Muth et al. (2000) resulted in a weaker rather than a stronger relationship between age-0 and age-1 juvenile age classes than was previously reported, which was not expected. This weaker model, however, had a modest level of support and suggested that abundance of juveniles was positively related to abundance of age-0 fish the year before, as well as their abundance that same year, plus a negative relationship with spring peak flow. Sparse recent data on juvenile fish may have limited our ability to detect a stronger relationship. Nonetheless, data indicated juvenile abundance was related to positive conditions for young and that those conditions may be required in consecutive years to produce a strong juvenile year-class.

The overwhelming dominance of nonnative cyprinid fishes in backwaters of the middle and lower Green River (Haines and Tyus 1990; Breen et al. 2011; Gido et al. 2013) persists. In our analyses, density of red shiners was weakly correlated with density of Colorado pikeminnow in both the middle ($r = -0.11$) and lower ($r = -0.04$) Green River reaches, which does not support or negate the idea that red shiners may be a serious predator on early life stages of Colorado pikeminnow (Bestgen et al. 2006). We suggest that in most years, the bulk of the red shiners present are relatively small-bodied age-0 fish produced in the same year that sampling occurred and are mostly ineffective predators on early life stages of pikeminnow. Large adult red shiners (\geq age-1) are likely more effective predators on Colorado pikeminnow larvae (Bestgen et al. 2006), but because we could not distinguish size groups due to lack of field measurements or preserved samples, we could make no further inferences about this issue. Highly overlapping diets, demonstrated predation by red shiners on pikeminnow early life stages, and densities of red shiners in the middle and lower Green River reaches that were on average 34.4 (excluded the very high 1994 estimate of 323 red shiners/10 m² seined) and 29.3 times higher than pikeminnow densities in backwaters, respectively, suggested the potential for suppression of pikeminnow density or growth via competition or predation (Haines and Tyus 1990; Muth and Snyder 1995; Bestgen et al. 2006).

Abundance of red shiners was relatively stable over the duration of the study period, but was influenced by flows in a manner opposite that for Colorado pikeminnow because their

abundance declined with increasing base flow level (see also Franssen et al. 2014). Red shiners are fractional spawners and produce clutches of eggs as long as water temperatures are suitable (Gale 1986; Marsh-Matthews et al. 2002). Thus, reduced abundance of red shiner is likely due to a reduction in the duration of the spawning season caused by relatively high flows, which also suppresses water temperature and shortens the spawning season of red shiner. This was demonstrated convincingly for red shiners in the Yampa River by Muth and Nesler (1993). Suppression of red shiner abundance is potentially important because adults are predators on early life stages of fish larvae in the Green River system backwaters, and are predators on Colorado pikeminnow in experimental settings (Ruppert et al. 1993; Bestgen et al. 2006).

We also investigated, but did not find, evidence that other nonnative fishes may be responsible for declining abundance of age-0 Colorado pikeminnow in the Green River that began in 1994, especially the upstream Middle Green River (Breton et al. 2014). Smallmouth bass is an obvious species to assess, as they invaded the system and now occur in the middle Green River reach (Breton et al. 2014). However, abundance declines of age-0 Colorado pikeminnow occurred before smallmouth bass were established in the middle Green River, and smallmouth bass is rare in the lower Green River where Colorado pikeminnow abundance has declined (Recovery Program annual reports; e.g., Projects 123a and 123b, 167). It may be that recently increased populations of smallmouth bass in the middle Green River are suppressing abundance of age-0 Colorado pikeminnow, especially in the middle Green River. Regardless, expanding populations of smallmouth bass will make it more difficult to reestablish the middle Green River as a substantial nursery habitat for young Colorado pikeminnow, and heightens the need to protect the lower Green River from further intrusions of smallmouth bass and associated declines in age-0 pikeminnow abundance. Similar to red shiner, high flow years that are relatively cool are associated with later reproduction by smallmouth bass and lower abundance of small smallmouth bass (Breton et al. 2014, Breton et al. 2015). Also similar is that in low flow years, both red shiner and smallmouth bass spawn early and produce large year-classes of fish that persist for years even with ongoing removal (Breton et al. 2014). Smallmouth bass presence in nursery habitat reaches of age-0 Colorado pikeminnow supports the need to continue non-native fish control.

Much effort has been devoted to collection of backwater samples in the Green River since 1979, and data were collected in a reasonably consistent manner (McAda et al. 1996; Breen

et al. 2011). Sampling issues that could not be controlled in the existing dataset included inconsistencies in identification of fishes, which for Colorado pikeminnow, were hopefully minimal because of relative ease of identification of at least larger individuals of that species. Identification of various nonnative minnows may be less certain. For example, the rise in the number of sand shiners in samples over time in the upper Colorado River basin may be the result of a recent invasion and truly increasing abundance trends, or changes in habitat that favor sand shiner. Alternatively, increased abundance of that species or other changes in fish community composition may be due to investigators' ability to correctly identify species. This was certainly true in the Green River prior to 1987, when all suckers, presumably all native due to absence of introduced white sucker *Catostomus commersonii*, were not identified to species (Haines and Tyus 1990). Effort should be made to reinforce taxonomic identification ability of field workers and to voucher some samples over time to increase the likelihood of high standards for data collection.

The ability of field crew members to identify fishes was likely also variable over time, but is an uncertainty that could be at least partially overcome with training from knowledgeable taxonomists. This seems important if we are to make inferences about the effects of certain nonnative fishes on native species. Another alternative or supplement to identification training is implementation of the historical practice of preservation of large samples of nonnative species, after identifying, measuring, and releasing Colorado pikeminnow and other native fishes in seine hauls. This relieves field personnel from the sometimes difficult task of identifying large numbers of small-bodied fishes in a restricted field session. Individual crews should critically and objectively assess their respective levels of confidence in field identifications of small-bodied fishes and take steps needed to collect the most reliable data possible given the cost and importance of the information generated.

The degree of adherence to sampling protocols by field crews is another issue that is difficult to ascertain when analyzing data collected in a long-term study. Strict training and careful re-reading of protocols is an important feature of consistent monitoring sampling and should be conducted each year, especially when new crew members begin work. Transitions between more experienced field workers to new ones should be buffered with overlapping field sessions to ensure protocols are understood and implemented.

Density of age-0 Colorado pikeminnow and backwater habitat.—Abundance of age-0 Colorado pikeminnow likely changes as a function of the amount of backwater habitat available, size of backwaters changes with flow levels, and those backwater attributes also vary between the two reaches sampled in the Green River (Pucherelli et al. 1990; Day et al. 1999; Trammell and Chart 1999). For example, based on Interagency Standardized Monitoring Protocol (ISMP) data collection, we found differences in the area of backwaters sampled among the middle and lower Green River reaches and those varied with flow, which may be explained by differences in the width of the channels in the middle and lower Green River. Lack of a strong negative relationship between flow and backwater area in the middle Green River noted here and elsewhere (Pucherelli et al. 1990) may be because higher flows in this largely unconstrained reach are able to expand across the wider sand bed channel, and as a result, maintain larger backwater sizes. This is in contrast to the lower Green River, where backwaters may be constrained from expanding laterally by incised banks that are stabilized with extensive growths of woody shrubs, such as invasive tamarisk *Tamarix spp.* or Russian olive *Eleagnus angustifolia*. Thus, as flows increase, backwater size declines because the channel fills with water. The relationship between flow and pikeminnow density (positive) and flow and backwater area (negative) supports this contention. It could also be that a fixed number of Colorado pikeminnow are available to occupy backwaters in any given year, such that as backwater number or area increases, their density declines even though fish abundance in the reach is the same. Haines et al. (1998) found a modest correlation ($r = 0.50$) between density of age-0 Colorado pikeminnow in backwater seine hauls and estimated abundance in the reach, based on tag-recapture data. Minimally, the correlation between the two metrics reflects some positive relationship, and with years of additional data, may indicate trends that are reliable.

Although density of age-0 Colorado pikeminnow in the lower Green River was historically higher, sometimes considerably so, than in the middle Green River, there is evidence to suggest that actual abundances may have been similar in each reach. This is because backwaters are, on average, smaller in the lower Green River, and total area is substantially less, so density estimates may not reflect actual abundance. Fewer and smaller (area) backwaters may have yielded greater density estimates for the lower than the upper Green River simply because the same number of individuals were contained within a smaller area. Also, abundance estimates for age-0 Colorado pikeminnow in non-overlapping years in the early to mid-1990s

also indicated that the middle Green River supported substantially more fish than the lower Green River (Haines et al. 1998). Thus, the perception that the lower Green River historically supported more age-0 Colorado pikeminnow than the middle Green River may be inaccurate. It is likely accurate, however, that juveniles (age-1+) historically were more abundant in the lower than upper Green River (Bestgen et al. 2007a; 2010). Regardless, the importance of the lower Green River in recent times as a nursery area for Colorado pikeminnow is well-supported (Bestgen et al. 2007a, 2010), but also underscores the need to restore populations of young Colorado pikeminnow in the middle Green River.

Most of the conclusions regarding Green River backwater habitat and flow relationships relative to age-0 Colorado pikeminnow abundance were supported by separate investigations in the middle (Day et al. 1999) and lower Green River (Trammell and Chart 1999). In general, Day et al. (1999) and Trammell and Chart (1999) found that total backwater area and volume declined as a function of spring peak flows as well as flows at the time of autumn sampling in the middle and lower Green River. They also found large differences in backwater number and area in each reach, similar to that described for the single year of data presented in Pucherelli et al. (1990). The middle Green River supported many more backwaters in the same length of river than the lower Green River. Mean backwater number was similar in 1992-1996 in the middle (4.25/RK) and lower Green River (1.6/RK) compared to the number in Pucherelli et al. (1990) in 1987 (compare with Figure 22), but backwater number was much higher in the middle Green River. Similarly, in 1992-1996, total backwater area was on average 4.5 times greater in the middle Green River than the lower Green River, because of greater backwater number and larger mean area (626 vs 454 m², respectively). However, because age-0 Colorado pikeminnow density in backwaters was higher in the lower Green River than the middle Green River (means = 1.25 vs. 0.25/10 m², respectively), mean estimated pikeminnow abundance for the reach (backwater area x pikeminnow density) was similar in the middle and lower Green River over the 1992-1996 study period (1199 and 1158, respectively, per 16 RK reach per year). This conclusion was similar to that reported above and Haines et al. (1998), who found similar or higher numbers of age-0 Colorado pikeminnow in the middle Green River compared to the lower Green River, based on abundance estimates generated from recapture of marked fish.

Management implications.—The relationships previously discussed indicate managers need to protect the fundamental drivers that support Colorado pikeminnow populations.

Protecting spawning areas and maintaining their productivity is an important management consideration, given the linkages between abundance of larvae and older fish. Thus, protecting Yampa River and lower Green River flows, both peak and base flows, are important for producing Colorado pikeminnow larvae that supply downstream nursery habitat areas for age-0 fish. Although precise mechanisms of how flows affect fish abundance are lacking, peak flows might affect abundance of Colorado pikeminnow larvae in at least two ways. First, high spring peak flows create high quality spawning substrate for Colorado pikeminnow and other native fishes (Harvey et al. 1993; Wick 1997). This occurs when substrate of spawning areas is redistributed to allow flushing of fine sediment in spaces amongst cobble and gravel, which would otherwise reduce survival of incubating eggs. Also, spawning substrate is scoured of algae and debris when particles are mobilized. This results in clean spawning substrate particles that provide suitable attachment surfaces for eggs. All warmwater native fishes in the upper Colorado River basin have eggs that are adhesive and adhere to clean substrate particles (e.g., Bestgen and Williams 1994).

Second, descending limb peak flows and base flows transport water through interstitial spaces of cobble bars and incubate eggs and provide oxygenated water for larvae after hatch. This is important because larvae develop in the substrate for 4-7 days post-hatching, sometimes in the presence of high turbidity loads. If descending limb flows declined too rapidly portions of the spawning areas for native fishes dehydrate or have reduced interstitial flows, and developing embryos and larvae may be negatively affected. After larvae emerge from spawning areas, they are transported downstream varying distances, depending on flow levels. In the Yampa River, Colorado pikeminnow larvae that emerge from spawning gravel are transported downstream to backwaters in the middle Green River. Descending limb or base flows that are very low either inhibit emergence or are insufficient to carry larvae downstream to suitable nursery habitat, and may result in low year class abundance (Bestgen et al. 1998, Yarnell et al. 2010; this study).

Peak flows in the Yampa and Green rivers are also important because they provide physical habitat maintenance functions including sediment transport from the stream channel, and sand transport and deposition for secondary channel and backwater formation (Pucherelli et al. 1990; Rakowski and Schmidt 1997). Peak flows may also signal fishes to prepare for or begin reproduction; peaks flows may also suppress abundance of red shiner and smallmouth bass. In other relationships, provision of adequate summer base flows is a main supporting

driver for abundance of age-0 Colorado pikeminnow and their backwater habitat. For those processes, Flaming Gorge Reservoir summer releases, as well as contributions from tributaries, are important to sustain habitat and recruitment processes for age-0 Colorado pikeminnow. Elevated peak and base flows are also important to promote high abundance of other native fishes such as bluehead and flannelmouth suckers (*Catostomus discobolus* and *C. latipinnis*, respectively), roundtail chub *Gila robusta*, and speckled dace *Rhinichthys osculus* in some situations; elevated releases from Flaming Gorge Reservoir in summer above levels recommended here, were occasionally responsible for reduced abundance of most fish taxa, native and nonnative, in the mainstem Green River (Haines and Tyus 1990; Tyus and Haines 1991; Muth and Nesler 1993; Breen et al. 2011; Breton et al. 2014; Bestgen 2015). High flows may also reduce abundance of problematic nonnative fishes like red and sand shiner, fathead minnow, and smallmouth bass (Haines and Tyus 1990; Muth and Nesler 1993; Breton et al. 2014; Bestgen 2015).

It is apparent that size and numbers of backwaters, and their relationship with flows and recruitment of age-0 Colorado pikeminnow involves many processes each of which is not completely understood. While backwater habitat quantity or quality is not necessarily considered limiting for age-0 Colorado pikeminnow in this study period in all but the highest base flow years, further channel narrowing and simplification may limit distribution and number of backwaters in the future. Long-term and ongoing channel narrowing and simplification has been documented in the middle and lower Green River since closure of Flaming Gorge Dam and is also coincident with invasion of nonnative tamarisk and other riparian vegetation (Allred and Schmidt 1999; Grams and Schmidt 2002; Friedman et al. 2005; Manners et al. 2014). Flattening of the annual hydrograph (reduced peak flow coupled with elevated base flows) has been associated with vegetation encroachment in the river channel in Grand Canyon (Sankey et al. 2015). It should be noted that abundance of tamarisk has declined in the lower Green River (T. Chart, U. S. Fish and Wildlife Service, Lakewood, CO) and in upstream locations as well, including Dinosaur National Monument (pers. obs., K. R. Bestgen; T. Naumann, botanist, Dinosaur National Monument, Dinosaur, CO) due to introduction of the herbivorous Northern tamarisk beetle (*Diorhabda carinulata*). However, other nonnative vegetation, including Russian olive (*Elaeagnus angustifolia*) is apparently now expanding in areas where tamarisk has declined in the Green River near Jensen, UT (T. Naumann, botanist, Dinosaur National

Monument, Dinosaur, CO) as is native sandbar willow (*Salix exigua*) along the lower Green River in Canyonlands National Park (M. Miller, Ecologist, Canyonlands National Park, Moab, UT). These vegetation dynamics may affect channel morphology and change into the future. The role of altered and increased base flows proposed in this study on shrubby plant distribution and density, channel complexity, and backwater formation in the Green River system should be evaluated with a long-term monitoring program, and will be discussed further in a synthesis of the Green River physical habitat data portion of this larger study (produced by Argonne National Lab) along with the biological data presented here.

Findings presented here indicate that changes in flows of the Green River, particularly summer base flows, are necessary. We first reviewed Green River flow levels in various time periods to provide some historical perspective on magnitude and patterns of flows, especially base flows, and then discussed the types of changes that need to be implemented. These changes are needed as soon as possible to stabilize Colorado pikeminnow populations in the Green River, which are currently in decline, and are time sensitive because year-classes of age-0 fish will not be of adult size for 5-8 years or more.

Summer flows in the middle Green River prior to the installation and operation of Flaming Gorge Dam were driven by natural flow patterns of both the Green and Yampa rivers. Because the Yampa River snowpack melted earlier and had an earlier peak flow than the more northerly Green River headwaters, flows were high and sustained in the Green River main stem well into summer. To examine flow patterns through time, we divided the period of record for gauge measurements into five periods ranging from pre-dam to recent operations (Figure 24), including two short periods in recent years from 2000-2005 and 2006-2012 (post Record of Decision period).

Mean monthly flows from 1947-1962, the pre-dam period of record for the Jensen, Utah gauge, were highest in June, declined through July, and were low (mean = 35.2 m³/sec, 1,243 ft³/sec) and relatively stable from August through March. Post-dam flows in 1964-1980 and 1981-1991 were nearly identical and had lower peak flows and higher base flows in all months, compared to historical patterns. The 1992-1999 period had higher peak flows than those from 1964-1991, in part because of new flow recommendations that featured peak releases each spring from Flaming Gorge Reservoir, because flows in the Yampa and Green rivers were naturally high in several years (e.g., 1993, 1995, 1997, 1999), and because of bypass releases from

Flaming Gorge Reservoir in 1997 and spills and bypass flows in 1999. The 2000-2005 period had the lowest peak flows of the pre-dam or any post-dam period, reflecting drought conditions in most years, and also had the lowest July-February flows for any time except in the pre-dam period. The 2006-2012 period had moderate peak flows and moderate base flows compared to other pre- or post-dam periods, reflecting a few higher flow years including 2008 and 2011. Timing of peak flow in the post-dam era was earlier (May) than in the pre-dam period (June) due to storage of snowmelt flows from the upper Green River basin; any peak flows released from Flaming Gorge Dam during the 1992-1999 period and through 2011 were purposefully released consistent with timing of the Yampa River peak, which historically occurred earlier than Green River peak flows. Recent spring peak releases (includes 2012) were timed to coincide with first appearance of razorback sucker larvae, which was typically slightly after the peak of the Yampa River had passed (Bestgen et al. 2011; Larval Trigger Study Plan, Lagory et al. 2012).

Mean July-August flow magnitudes were analyzed in the same time periods to better understand flow patterns when Colorado pikeminnow larvae are dispersing downstream from spawning areas, colonizing backwaters, and growing in summer. We found that July-August base flows in the pre-dam period were similar to those from 1964-1980 and 1981-1991 (Figures 24 and 25). This was true for that relatively short summer period, but a main difference in longer-term patterns was that in the pre-dam period, base flows continued to decline into September and were low until March, while regulated flows remained higher throughout the year, presumably for hydroelectric generation at Flaming Gorge Dam. Flows from 1992-1999 were lower than the previous periods, including the historical period, in part because releases from Flaming Gorge Reservoir were made to maintain flows in the middle Green River at $> 45\text{-}51\text{ m}^3/\text{sec}$ ($1,600\text{-}1,800\text{ ft}^3/\text{sec}$) even in low flow years such as 1994 to optimize backwater habitat (Pucherelli et al. 1990; Muth et al. 2000). In a typical year in that period, as flow in the Yampa River receded after snowmelt, Flaming Gorge Reservoir releases were regularly adjusted (Bestgen and Crist 2000, figures 12-16; see also Muth et al. 2000). For example, during 1992-1996, Flaming Gorge Reservoir releases were reduced immediately following high spring releases (typically about $127.5\text{ m}^3/\text{sec}$, $4,500\text{ ft}^3/\text{sec}$) to the minimum $22.6\text{ m}^3/\text{sec}$ base flow ($800\text{ ft}^3/\text{sec}$), usually by mid-June. Releases were then increased later in summer as Yampa River flows dropped below levels needed to maintain middle Green River flows at $45\text{ m}^3/\text{sec}$ ($1,600\text{ ft}^3/\text{sec}$) or higher. In a low flow year such as 1994, Flaming Gorge Reservoir releases

constituted nearly all flows in the middle Green River because Yampa River flows were very low. Alternatively, flows during the post-1996 to year 2000 period were higher (about 85 m³/sec, 3,000 ft³/sec 1997-1999) in the middle Green River and near the level where few year classes of pikeminnow recruit. This was also true in the lower Green River, where flows were very high and above recommended levels of 108 m³/sec, (3,800 ft³/sec) for above average recruitment in 1995 and 1997-1999. Average flows in the 2000-2012 period were the lowest of all, but reflect very low flows from 2000-2005, a very dry period, but increased from 2006-2012 in the post Record of Decision period, which had wetter years and included years of the officially implemented recommendations of Muth et al. (2000).

Muth et al. (2000) proposed peak and base flow releases that were proportional to the type of hydrologic year classification, which was based on snowpack amounts in early spring. Thus, peak and base flow levels were divided into wet (0-10% exceedance probability, about 10% of years), moderately wet (10-30% exceedance, 20% of years), average (30-70% exceedance, 40% of years), moderately dry (70-90% exceedance, 20% of years), and dry (90-100% exceedance probability, 10% of years) years, based on snowpack in the spring of that year. This was also done to follow a more natural flow pattern, with lower base flows and higher peaks (Poff et al. 1997), regardless of hydrologic condition. Thus, no accommodation was made for minimum recommended base flows in the middle Green River and summer base flow releases from Flaming Gorge Reservoir were held relatively steady after release levels were set even if Yampa River flows were very low. Specific recommendations were also given for durations of spring peak flows as well as summer water temperature levels for the Green River just downstream and upstream of Yampa River to benefit native fishes (Muth et al. 2000).

Base flows recommended by Muth et al. (2000, Table 5.5; Table 10 of this report) for Reach 2, the Green River downstream of the Yampa River confluence to the confluence with the White River (middle Green River), for the wet thru dry categories were 79-85 m³/sec (2,800-3,000 ft³/sec), 67-79 m³/sec (2,400-2,800 ft³/sec), 43-67 m³/sec (1,500-2,400 ft³/sec), 31-43 m³/sec (1,100-1,500 ft³/sec), and 26-31 m³/sec (900-1,100 ft³/sec), respectively. Onset of each base flow recommendation in summer was staggered to reflect that in wet years, base flows would be reached later than in dry years, when runoff peaked sooner. Thus, in wet years, onset of base flow was 15 August and in dry years 15 June, with other hydrologic classification dates placed evenly between those. Base flow recommendations were also proposed for the lower

Green River (Reach 3, Muth et al. 2000; Table 5.6), and followed those for the middle Green River, essentially reflecting upstream Reach 2 flows and additions from tributaries such as the White River. Thus, the wet thru dry year base flow recommendations for the lower Green River were 92-133 m³/sec (3,200-4,700 ft³/sec), 76-133 m³/sec (2,700-4,700), 52-119 m³/sec (1,800-4,200), 42-95 m³/sec (1,500-3,400), and 38-72 m³/sec (1,300-2,600 ft³/sec), respectively. Dates of onset of base flow periods were identical to those for the middle Green River.

The low base flows observed in the Green River in the 2000-2012 and especially the 2000-2005 period are partially a consequence of drought in the upper Colorado River basin, and lower releases from Flaming Gorge Reservoir, consistent with flow recommendations. For example, mean July-August flow in the middle Green River in 2002 was 24.4 m³/sec (860 ft³/sec), a year when Yampa River flow nearly ceased and Flaming Gorge Reservoir releases were essentially the only water in the Green River downstream of the Yampa River.

Observations made over the 1990-2012 period, and particularly those since 2000, suggest that base flow releases higher than those in the flow recommendations may be needed to enhance survival of age-0 Colorado pikeminnow such that populations of adults in the Green River may eventually be stabilized or increased. As previously indicated, middle Green River mean August-September base flow levels in the range of 48-85 m³/sec (1,700-3,000 ft³/sec) often were associated with the largest year-classes of age-0 Colorado pikeminnow in the middle Green River, and flows from 48-107.7 m³/sec (1,700 to 3,800 ft³/sec) often were associated with the largest year-classes in the lower Green River. Those levels are mostly consistent with flow recommendations made for Colorado pikeminnow in Muth et al. (2000, Table 4.4), particularly in wetter hydrology years.

To gain further insights into flows needed for higher recruitment of Colorado pikeminnow, we also examined flow patterns in good recruitment years rather than just mean July-August flow levels. To accomplish that we plotted July-August mean daily flows as a function of time in years with above average density of age-0 Colorado pikeminnow over the study period (> 0.50 fish/10 m², n = 12 years of 22, 1979-1982, 1986-1988, 1990-1991, 1993, 2009-2010) in the middle Green River to determine if certain flow patterns were responsible for higher recruitment (Figure 26). Flow patterns and magnitudes were widely scattered, especially in 1986, when flow remained very high until late July; a commonality among those flow regimes was that levels were typically well below 100 m³/sec (3,530 ft³/sec) by 1 August. All those

above average recruitment years plotted that fell in the 1990-2012 period, when larvae transport abundance data were available from the Yampa River, showed that larvae abundance was near or above average. Thus, relatively high abundance of larvae and adequate flows were associated with above average densities of Colorado pikeminnow in the middle Green River.

We then plotted the mean of those flow traces for high recruitment years and overlaid that with a set of seven flow traces for years in the middle Green River that had low age-0 pikeminnow density ($\leq 0.10/10 \text{ m}^2$) but had either lower (1996, 2000, 2006) or higher (1998, 1999, 2005, 2008) July-August flows, with the condition that all those years had to have near average or above average values for the larvae transport index (Figure 26). That condition removed the possibility that low age-0 Colorado pikeminnow density in the middle Green River in those years might be due to lack of larvae, but instead might be related to flow level or some other factor(s).

Low recruitment years had flows that were mixed in pattern compared to the mean for good recruitment years. For example, years such as 1996, 2005, and 2008 were similar to the mean flows for years with higher density of age-0 Colorado pikeminnow. On the other hand, years such as 1998 and 1999 or 2002 and 2006 were either substantially higher or lower than the mean. This indicated that factors other than flows were sometimes responsible for low recruitment (e.g., poor habitat quality, low food abundance, many nonnative predators, flooding, and high turbidity, Bestgen et al. 2006). Regardless of what those other factors were, it seemed that one important factor was flow level, which can be manipulated via releases from Flaming Gorge Reservoir.

When recommendations in Muth et al. (2000) were conceived and written, adult Colorado pikeminnow populations were high and rising in abundance and it was thought that a few weaker year-classes of age-0 fish in drier years would not be detrimental to this long-lived species. It was also perceived that because populations of adults were increasing throughout the basin, that the middle Green River nursery habitat, which had declined in productivity around 1994, was less important than the lower Green River. What was not realized was that increasing populations of Colorado pikeminnow require strong or moderately strong year-classes of age-0 and larger juveniles in most years to sustain or increase the adult population (Bestgen et al. 2007a). Our research has also shown how susceptible Colorado pikeminnow populations are to combined effects of weak year-classes of age-0 fish and extended drought. For example,

population abundance of adult Colorado pikeminnow in the Green River subbasin declined about 40% from 2000 to 2003, a drought period. That decline was due to weak year-classes of age-0 fish in both the middle and lower Green River reaches throughout most of the mid- to late-1990s when flows were high and may have precluded age-0 recruitment, especially in the important lower Green River (1995, 1997-1999). Adult Colorado pikeminnow population declines were also consistent with survival rates that declined from 80% in the pre-2000 period to 65% from 2000-2003. Until the time the Muth et al. (2000) flow recommendations were written (1997-1999), few lower flow years had been studied with the exception of 1994, and age-0 fish were previously relatively abundant. This was especially true in the lower Green River, where age-0 fish as well as larger juveniles were relatively abundant and may have suggested that this reach was more important than the middle Green River. This may not be fully accurate, especially with recent evidence of increasing abundance of nonnative species such as walleye, which may be suppressing abundance of age-0 and juvenile pikeminnow in the lower Green River; at least two instances of predation by walleye on relatively large juvenile Colorado pikeminnow was noted in the lower Colorado River, Utah, in 2014 (pers. comm., T. Francis and D. Osmundson, U. S. Fish and Wildlife Service, Grand Junction, CO). Abundance trends of adult Colorado pikeminnow in the Green River subbasin saw an increase in the 2006-2008 period, but have continued to decline through the 2011-2013 period due to continued weak year-classes of young fish in the middle and lower Green River.

To reverse population declines of adults, experimental base flows (minimally July, August, and September) in many average years and all drier conditions should be tested that are higher than those presently implemented. Flow recommendations provided by Muth et al. (2000) are adequate for wet, moderately wet, and wettest portions of average hydrologic conditions, except that the upper ends of those flow ranges may need to be revised downward. This is because flows > about 3,000 and 3,800 ft³/sec, and often even > 2,500, and 3,000 ft³/sec, are not consistent with higher densities of age-0 Colorado pikeminnow in most years in the middle and lower Green River, respectively. Thus, downward revisions of the upper limits of those flow recommendations in wetter years are needed especially for the lower Green River.

We recognize that in some wetter years, higher base flows may exist in unregulated tributaries and that there may be a need to evacuate water from storage in Flaming Gorge Reservoir to create space for the next year, resulting in high Green River flows in Colorado

pikeminnow nursery habitat. However, to the extent possible, high flows should be curtailed, at least in summer (minimally July, August, and warm portions of September), to produce larger year-classes of larger age-0 Colorado pikeminnow when they would not normally be produced; this need has been recognized for many years (Haines and Tyus 1990; Tyus and Haines 1991). Suitable backwater conditions even in higher flow years are needed because larger numbers of larvae are typically produced and if nursery habitat conditions can be made suitable, higher numbers of age-0 pikeminnow may survive. We also recognize that flows likely need to remain lower through winter to promote higher overwinter survival. In lower flow years in the middle and lower Green River (1,500-2,500 ft³/sec), young Colorado pikeminnow survival was relatively higher at 56-62% when mean TL was greater, but only 6% in a year when fish were small and overwinter flows were about 4,000 ft³/sec (Figure 10 in Haines et al. 1998).

In average and lower hydrologic classification years, mean August-September flows should be maintained at > 48 m³/sec (1,700 ft³/sec) in the middle Green River, even in dry years (Table 10 compares these flows with those in Muth et al. 2000). That level is consistent with production of higher densities of age-0 Colorado pikeminnow in the Green River and also supports relatively abundant backwater habitat (Pucherelli et al. 1990, Day et al. 1999; Trammell and Chart 1999). Moderately dry years should target flows of 51-57 m³/sec (1,800-2,000 ft³/sec) and average years should target flows of 57-74 m³/sec (2,000-2,600 ft³/sec). Flows for wetter classifications have lower range limits that overlap with the upper end of the average year ranges to allow managers more flexibility with operations, and those flows are consistent with production of higher age-0 Colorado pikeminnow abundances. The relatively narrow flow magnitude window for summer base flows, compared to that in Muth et al. (2000) is consistent with production of the highest densities of age-0 Colorado pikeminnow in the period 1979-2012 and may offer the best opportunity to produce several consecutive strong year-classes of age-0 Colorado pikeminnow. Lower Green River flows that follow from those in the middle Green River are also proposed, recognizing that those flows depend on upstream flows and tributary inputs.

We recognize that those flow levels may not always produce abundant age-0 Colorado pikeminnow, especially in the middle Green River, because in lower flow years, production of larvae from the Yampa River may be relatively low. Thus, low abundance of larvae may preclude a large middle Green River year-class in spite of provision of conditions in backwaters

suitable for high survival of Colorado pikeminnow. An example of that was 1994, when the few larvae produced in the Yampa River were apparently not sufficient to produce a large year-class of age-0 Colorado pikeminnow (although a few very large fish were present in ISMP samples) even though flow releases from Flaming Gorge Dam maintained middle Green River flows at about 45.1 m³/sec (1,594 ft³/sec) from July-September. This assumes that a relatively low flow year in the upper Green River is usually consistent with a relatively low flow year in the Yampa River, which is reasonable, as drought conditions are typically regional and affect both basins in a similar manner.

Maintaining base flows at higher levels in the middle Green River, even if a large year-class of Colorado pikeminnow is not produced there, has the obvious benefit of transferring water downstream so lower Green River age-0 Colorado pikeminnow can benefit. This is important because larger year-classes of age-0 fish, as well as large juveniles, are typically produced in higher base flow years, similar to the middle Green River, at levels between 48-107.6 m³/sec (1,700-3,800 ft³/sec).

Higher base flow levels would also serve to simultaneously suppress red shiner densities, and perhaps also suppress young smallmouth bass abundance via habitat limitation. Long-term data shows that red shiner density was relatively low, about 20/10 m², when mean August-September base flows were > about 61 m³/sec (2,150 ft³/sec), consistent with recommendations for flows in the range of moderately dry to wetter years. From 1992-1996 (exclusive of 1994 when flows were below average) when Flaming Gorge Reservoir releases were increased in summer to maintain middle Green River flows at about 45-51 m³/sec (1,600-1,800 ft³/sec), mean densities of red shiner were relatively low at 27/10 m². Similarly, red shiner densities were maintained at relatively low densities in the lower Green River when mean August-September base flows were > 80 m³/sec (2,800 ft³/sec). Flows sufficient to reduce red shiner abundance in the lower Green River should be achieved if middle Green River flows are implemented, and importantly, if flows from tributaries such as the White River are maintained.

Timing of onset of the base flow period in the middle Green River is another consideration that may need to be changed. Muth et al. (2000) adjusted the beginning of the base flow period with the hydrologic condition, beginning earlier in low flow years and later in higher flow years. We propose a slight modification to that schedule that uses real-time data in

the form of first captures of Colorado pikeminnow larvae to begin the base flow period. This will require the base flow period to begin earlier in many years, especially those with higher flows, because first Colorado pikeminnow larvae are typically captured in a relatively narrow band of time from late June to mid-July. A supplement to real-time first capture data to trigger onset of base flow conditions could be statistical models (described above) that predict timing of first reproduction based on a suite of environmental variables.

We believe that a different onset of the summer base flow period is needed because of evidence that few larvae produced early in the year from the Yampa and lower Green River spawning areas survive until autumn in backwaters of the Green River. Bestgen et al. (2006) showed this with an analysis of distributions of hatching dates of wild larvae captured in drift nets compared to hatching dates for age-0 Colorado pikeminnow captured in backwaters in the middle and lower Green River in summer and autumn in 1991 and 1992. In all instances, the first of the 3-4 cohorts (portions of a year class) of larvae produced each year were underrepresented as age-0 individuals in autumn, sometimes by a considerable margin.

The issue of underrepresentation of cohorts of larvae in older life stages is problematic because sometimes the early cohorts of larvae are relatively large-bodied, and may contribute substantially to an age-0 cohort in autumn, but often that does not occur. For example, in the middle Green River in 1992, the early and large peak of larvae detected in the Yampa River on 1 July (Figure 5), was barely evident in the hatching date distribution for age-0 autumn-captured fish. Perhaps not coincidentally, density of age-0 Colorado pikeminnow in autumn 1992 was well below average and the 4th lowest in the 14-year period from 1979-1992. The 1992 transport index abundance value was also one of the largest detected in the 22 years of drift net sampling from 1990-2012. It was postulated that early larvae transported downstream to the middle Green River were either eaten by larger red shiners present early in the season or that backwaters and their food base were insufficiently developed at that time to accommodate those fish (Bestgen 1997; Bestgen et al. 2006).

Beginning the onset of the base flow period after larvae have emerged from spawning areas may increase survival of early season fish by ensuring that backwaters are available for occupancy. Early larvae typically have the highest growth rates and are the largest individuals in autumn. A longer growing season would also positively affect growth and length of all

cohorts of age-0 Colorado pikeminnow in Green River nursery habitats, likely increasing their overwinter survival (Bestgen 1997; Haines et al. 1998; Bestgen et al. 2006).

Implementation of real-time monitoring to trigger the base flow period is a relatively simple task given that daily drift net sampling of Colorado pikeminnow larvae occurs in the lower Yampa River (Recovery Program Project 22f). The ongoing implementation of the Larval Trigger Study Plan (LaGory et al. 2012) is an example of how real-time data were effectively used to initiate flow management actions that have benefitted razorback sucker recruitment in wetlands of the middle Green River (Recovery Program annual project reports 164 and 165). The significance of hatching date distribution findings received relatively little attention when they became available, likely because age-0 and adult Colorado pikeminnow were relatively abundant; the loss of larvae from early cohorts was not viewed as significant because the species status was stable or even increasing. The present situation, with declining abundance of Colorado pikeminnow especially in the middle Green River, merits that all available information be fully considered in decisions to produce substantial year-classes of age-0 fish in the Green River subbasin.

Related to the timing of onset of the base flow period, is how appropriate levels for base flows are achieved in the Green River. The present system is operated under a paradigm that natural flow regimes (e.g., Poff et al. 1997) are superior to the type of management implemented in the 1990s, where Flaming Gorge Reservoir flow releases were dropped in June to very low levels and then increased in summer to produce higher flows in the middle Green River. Whether that variable type of flow regime is implemented should be a discussion for managers that includes among other things, the fish community of the Green River upstream of the Yampa River. Native fishes survived the variable flows in the 1990s in places such as Lodore Canyon, and were even more abundant then than now. Those changes could be related to factors other than flows, such as more recent invasions of the area by smallmouth bass, white sucker, and northern pike (Bestgen et al. 2006; 2007c).

Reducing flows early in the season in the Green River upstream of the Yampa River confluence may have additional benefits for nonnative fish control. 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 thereby reducing survival of young. This could occur because northern pike spawn in areas of shallow submerged vegetation in the

flood plain or channel margins during elevated flows in May and early June. If flows are reduced when sensitive eggs or larvae are present in the shallow floodplain or channel margins, those life stages may be stranded or force larvae to less hospitable in-channel habitat, resulting in reduced survival. Smallmouth bass may also be induced to spawn earlier in the Green River upstream of Lodore Canyon if flows are reduced early and water temperatures begin to exceed 16°C, a threshold identified for bass spawning in that reach (Hill and Bestgen 2014; Bestgen and Hill 2015 draft report). This offers an opportunity for subsequent short-term flow releases to disrupt spawning by sending higher flow releases at appropriate times that alter spawning behavior or sweep recently hatched and weak-swimming bass larvae downstream. Earlier disruption allows for abundance reductions of bass hatched early in the year, which is advantageous because those are normally the largest bass produced in a year, and the ones most likely to survive over winter (Breton et al. 2014; Breton et al. 2015). Attempting such treatments early in the year also reduces overlap with native fish spawning and subsequent drift of larvae, including Colorado pikeminnow, in the Green River downstream of the Yampa River confluence. These issues are discussed in detail in Bestgen and Hill (2015 draft report).

The flows proposed above may seem an endorsement to abandon the tenets of the flow recommendations and the Natural Flow Paradigm (Poff et al. 1997). It, however is not, except perhaps in a restricted reach. High flows are endorsed and should perhaps be higher than currently occur. What might be sacrificed in terms of natural flow patterns is the Green River reach upstream of the Yampa River, with cooler flows that result from hypolimnetic releases in spite of variable level penstocks, and relatively few native endangered fishes, for much more spatially extensive downstream reaches with greater conservation value for native fishes. It should also be recognized that the Natural Flow Paradigm is a test of an hypothesis with a goal to return the aquatic community to some more natural state. If portions of the natural flow pattern need to be adjusted to benefit aquatic resources, that should not be viewed as detrimental, but rather, an opportunity to learn more about what drives the dynamics of these communities. This may be especially important when effects of aspects of the natural flow patterns on nonnative fishes are unknown. If nonnative fishes benefit more from natural flows than altered ones, perhaps a reassessment of those patterns is needed, and a re-assessment of the utility of the Natural Flow Paradigm when nonnative fishes are an issue may be in order.

Management of Flaming Gorge Reservoir releases in summer has incorporated efforts to release the warmest water temperatures available in the reservoir, via a variable-level penstock to draw flows, for the benefit of native fishes, and which also maintains the substantial trout fishery downstream of the dam. This effort has minimized the difference between water temperatures of the Green and Yampa rivers at their confluence, which is important to reduce temperature shock to Colorado pikeminnow larvae drifting from the relatively warm Yampa River into the cooler Green River in summer. That effort has been successful because the number of days during the drift period when water temperatures are 5°C or greater between the two rivers is usually zero (personal communication, D. Speas, U.S. Bureau of Reclamation).

Nonnative fishes continue to proliferate in the Upper Colorado River Basin, to the detriment of the native fishes, and efforts to reduce their abundance should continue or increase. This is especially important in Colorado pikeminnow nursery habitats in the middle and lower Green River. Until recently, presence of a highly predaceous and abundant species such as smallmouth bass in backwaters or the main channel of nursery habitat of Colorado pikeminnow has been limited. However, recent sampling indicated that > 50% of middle Green River backwaters contained young smallmouth bass, following successive years (2012 and 2013) with drier hydrology when smallmouth bass reproduction is high (Recovery Program annual reports < Project 138, pers. com., M. Breen, Utah Division of Wildlife Resources, Vernal, Utah). Establishment of species like smallmouth bass in the upper Green River and walleye in the lower Green River is another impediment to survival of young Colorado pikeminnow, especially when adult pikeminnow abundance is relatively low and recruitment is limited. Nursery habitat for age-0 Colorado pikeminnow must be protected if recruitment is to increase as needed.

We recognize that altering flow recommendations a relatively short time after they were approved and implemented may be met with skepticism at best and perhaps disapproval. However, experimental changes in flows reflect an adaptive management approach and advancing knowledge about the ecology of endangered as well as invasive fishes and should be welcomed information that may assist with management and conservation, especially when conducted in an adaptive management framework. Such was the case when spring flow timing and magnitude from Flaming Gorge Reservoir were altered when new information about razorback sucker life history and recruitment became available (Bestgen et al. 2011; LaGory et al. 2012); that experimental plan is yielding important information key to sustaining recruitment

of the species and thereby increasing its recovery prospects. Enhancing natural recruitment of Colorado pikeminnow in the Green River is important and needed immediately to avoid a situation like that in the San Juan River, where stocking is now required in an attempt to re-establish that pikeminnow population (Franssen et al. 2014).

Higher base flow releases to benefit age-0 Colorado pikeminnow may place additional demands on water resources from Flaming Gorge Reservoir when other management actions, such as provision of high spring flows in the middle Green River for the benefit of razorback sucker recruitment (LTSP flows) have already been implemented on an experimental basis. Another competing demand may be spike flows released in early summer (late June or early July) to disadvantage reproductive success of smallmouth bass in the Green River downstream of Flaming Gorge Reservoir. A conceptual model of those competing demands maps out the approximate temporal sequence of flows compared to those under the Record of Decision and may assist visualization of flow releases and overlap with biological processes in a single year (Figure 27). The conceptual flow model is discussed in more detail in Bestgen and Hill (2015 draft report). Competing demands for water for native fishes requires evaluating which species require water resources most and at which time of year and in which years. It may also be that flows at other times of the year need to be altered to accommodate flow increases in spring and summer. Regardless, attempting to enhance pikeminnow recruitment with flow releases, perhaps in several consecutive years, is critical to sustain populations. An experimental plan with strong treatments and adequate monitoring of various life stages, carried out over a sufficiently long period, perhaps many years to decades, is essential to determine effects of altered flow releases on native endangered fishes as well as on invasive species.

Finally, results of this study and other investigations (e.g., Bestgen et al. 2011) reveal that even after many years of data collection and analysis, understanding factors that regulate distribution and abundance of native and nonnative fishes are only partially clear. However, variable data that yields patterns with equivocal relationships is the norm in ecological studies of large river systems in part because of sampling variation, and because controlling factors interact or become more or less important at different flows and water temperatures. Such interactions are further complicated by complex and often opaque interactions with abundant nonnative fishes that occupy many or all niches available in the river. In spite of these potential complications, patterns suggested by these long-term Colorado pikeminnow data sets are

compelling. Managers should evaluate these findings and associated risks and act on them, even in the face of uncertainty, so that we have the best chance of conserving the native fish assemblage in the Green River subbasin, including the Colorado pikeminnow.

CONCLUSIONS

- Colorado pikeminnow reproduction occurred each year in the study period and in mid to late June in each of the Yampa River and lower Green River sites.
- Timing of first reproduction was positively related to peak flow level in spring and accumulated degree days in the Yampa River (negative relationship with degree days in the lower Green River), a metric of water temperatures prior to spawning.
- Abundance of larvae was similar at dawn, noon, dusk, and midnight in higher flow years, but was very low at all times except midnight in lower flow years.
- Abundance of larvae on an annual basis was positively related to flow magnitude, and few larvae were produced and transported downstream in low flow years.
- Abundance of larvae was highest up to 2000, but was lower after that, perhaps related to lower flow levels during drought and lower abundance of adults.
- Abundance of larvae limited abundance of age-0 Colorado pikeminnow in most low flow years, but larvae were typically abundant enough in higher flow years to produce an average or higher than average abundance of age-0 fish in autumn.
- High flows that prepare spawning substrate and base flows that incubate eggs and transport larvae are both considered important aspects of flows in spawning areas for reproductive success of Colorado pikeminnow.
- Production of Colorado pikeminnow larvae in the lower Yampa River was relatively stable throughout the study period. Thus, sufficient larvae are currently available to test predictions of the experimental base flows proposed below.
- Age-0 Colorado pikeminnow abundance declined in both the middle and lower Green River reaches over time, especially since 1994.
- Age-0 Colorado pikeminnow densities were higher in the lower Green River historically than the middle Green River, even though larvae abundance was lower.

- Fewer and smaller backwaters existed in the lower Green River than the middle Green River, which may play a role in density differences between reaches.
- Age-0 Colorado pikeminnow abundance was highest in the middle Green River in moderate flow years (1700-3000 ft³/sec), lower in some low flow years because larvae were fewer (< 1700 ft³/sec), and low in most high flow years (>3000 ft³/sec) because backwater habitat was reduced. Patterns were similar in the lower Green River except higher abundances of age-0 pikeminnow were in slightly higher flows.
- Growth of age-0 Colorado pikeminnow was highest in low flow years with warmer water temperatures and lower in high runoff years when cooler water temperatures prevailed. Pikeminnow growth was influenced by interactions among flow levels, water temperatures, and possibly nonnative fish densities in complex ways. However, higher abundance of age-0 fish was deemed more important than higher growth of age-0 fish.
- Growth rates and length of age-0 Colorado pikeminnow was relatively high at flows < 2500 cfs in the middle and lower Green River reaches; longer growing seasons increased growth and length.
- Abundance of age-0 Colorado pikeminnow was positively related to base flow level in the lower and middle Green River up to moderate flow levels (e.g., 3000 ft³/sec in the middle Green River), but declined at higher flows in each reach.
- Abundance of age-0 Colorado pikeminnow was positively related to transport abundance of larvae, a measure of annual spawning success based on captures of larvae made downstream of spawning areas.
- Both the middle and lower Green River nursery habitat reaches are needed to produce higher abundances of age-0 Colorado pikeminnow, similar to pre-1994 levels, to support additional recruitment of adult Colorado pikeminnow. Deference should be given to flows in the middle Green River because of the need to re-establish consistent year classes there and because adequate middle Green River flows support lower Green River flows.
- Middle Green River mean August-September base flows in the range of 48-85 m³/sec (1,700-3,000 ft³/sec) were correlated with higher densities of age-0 Colorado pikeminnow in autumn and with more backwater habitat. Flows between 2,500-3,000 ft³/sec less certain effects.

- Lower Green River base flows in the range of 48-108 m³/sec (1,700-3,800 ft³/sec) were correlated with higher densities of age-0 Colorado pikeminnow in autumn and with higher backwater habitat availability; the existing upper end of flow ranges in wetter flow year classifications may need to be reduced. Flows between 3,000-3,800 ft³/sec have less certain effects. Flow recommendations for the lower Green River naturally follow from flows in the upstream middle Green River.

RECOMMENDATIONS

- Continue drift sampling in the lower Yampa River and reinitiate sampling in the lower Green River to monitor the abundance of Colorado pikeminnow larvae transported downstream from spawning areas. Monitoring the abundance of drifting larvae is a proven method for documenting reproduction and measuring relative reproductive success of Colorado pikeminnow. Data are useful to link strength of survival of age-0 pikeminnow in autumn with flow levels and other environmental data.
- Continue drift net sampling so capture of Colorado pikeminnow larvae can be used to trigger appropriate base flow releases from Flaming Gorge Dam, which are essential to enhance survival of early life stages.
- Turbidity data are useful to understand variation in fish abundance patterns and captures and investigators may wish to add estimates of that parameter to field sampling investigations for nearly all life stages and fish species.
- Evaluate accuracy and precision of data collected by autumn *ISMP* sampling for estimating abundance of age-0 Colorado pikeminnow in backwaters. Acquisition of such data will ensure valid comparisons between abundance of larvae and recruitment of juveniles.
- Conduct taxonomic training or reinitiate preservation of *ISMP* samples, especially large quantities of nonnative fishes, after considering skill levels of crews to identify fishes in the field.
- Continue collection of monitoring data in Projects 22f, 115, 128, and 138, that are integral components of the experimental program recommended above.

- Timing of onset of base flow conditions should be linked with first presence of Colorado pikeminnow larvae in drift nets in the lower Yampa River to ensure adequate backwater conditions throughout the reproductive period and longer growing seasons for age-0 Colorado pikeminnow.
- Continue or expand nonnative fish control efforts throughout the Green River basin. Removal of threats such as large-bodied walleye and northern pike is a first priority. Protection of age-0 and juvenile recruitment areas, especially the lower Green River and the lower Colorado River, is also important. This is because small-bodied life stages are especially susceptible to predation by species such as walleye and smallmouth bass. Efforts to control these nonnative species in the lower and middle Green River should focus on removal rather than abundance estimation (releasing marked fish back to the river) to reduce their abundance and the chance of establishing reproduction in the river.
- Continue to evaluate importance of abiotic and biotic factors that influence intra- and inter-annual distribution, growth, and survival of early life stages of Colorado pikeminnow. Collection of such data will facilitate efforts to model population dynamics and long-term viability of Colorado pikeminnow.
- Continue to collect, long-term water temperature data year-round at several locations in the basin with continuously recording thermographs.
- Protect peak and base flows in the Yampa River and the Green River, as well as other tributaries such as the White River, to enhance reproduction of Colorado pikeminnow and provide for backwater habitat.
- Evaluate compatibility of competing demands for flow releases from Flaming Gorge Reservoir for various life stages of endangered and other native fishes in the Green River, and their effects on nonnative kinds.
- Initiate immediately, an experimental program of base flows in the middle and lower Green River that are higher than presently recommended for average and drier hydrologic conditions and begin those flows earlier in summer, with a goal to bolster populations of age-0, juvenile, and eventually adult, Colorado pikeminnow abundance in the Green River. Several successive years of base flows in a range consistent with regular production of larger year-classes of age-0 Colorado pikeminnow are needed to evaluate population response to flow manipulation.

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Table 1. Estimated dates of first, last, and peak reproduction and associated degree-day accumulation and days post-peak runoff for Colorado pikeminnow at the Yampa River and lower Green River spawning areas. Dates of first reproduction and first peak in reproduction were estimated by subtracting the average age of larvae at capture (6 d) and average incubation time of fertilized eggs at 18°C (6 d) from the dates that larvae were first captured in drift nets. The first peak of reproduction was qualitatively determined as the first substantial increase in abundance of captured larvae. Values are the mean of a five day period centered on the date of interest. Days > 18°C is the number of days to first reproduction when average water temperature met or exceeded that value. Days post-peak discharge is the number of days between the highest recorded daily average discharge recorded during spring runoff and first reproduction.

River	Year	Spawning period	First reproduction				First peak of reproduction		
			Temperature (C°)	Days >18°C	Days post-peak	Degree-days	Date	Temperature (C°)	Days >18°C
Yampa	1990	18 June - 16 July (29 d)	18.6	5	5	1098	24-Jun	22.1	11
	1991	26 June - 18 July (23 d)	17.8	5	33	1263	28-Jun	17.8	7
	1992	14 June - 20 July (38 d)	18.6	5	16	1482	17-Jun	17.6	7
	1993	30 June - 14 August (46 d)	17.4	0	39	1414	4-Jul	16.3	0
	1994	26 June - 21 July (26 d)	23.1	15	42	1646	26-Jun	23.1	15
	1995	1 July - 31 July (31 d)	16	1	24	1462	9-Jul	19.1	3
	1996	26 June - 1 August (37 d)	17.2	0	41	1539	30-Jun	18.4	2
	1997	—							
	1998	26 June - 31 July (36 d)	17.8	0	51	1076	7-Jul	22.1	11
	1999	29 June - 6 August (39 d)	18.7	4	33	1383	4-Jul	19.5	9
	2000	25 June - 27 July (33 d)	19.6	5	24	1565	28-Jun	20.3	8
	2001	16 June - 23 July (37 d)	17.3	5	28	1283	18-Jun	19	7
	2002	14 June - 16 July (32 d)	19.8	9	11	1229	21-Jun	21.1	16
	2003	21 June - 27 July (36 d)	17.5	4	17	1336	26-Jun	17.5	4
	2004	15 June - 19 July (34 d)	18.5	8	36	1397	23-Jun	19.1	16
	2005	29 June - 26 July (28 d)	17.4	1	35	1436	2-Jul	18.4	2
	2006	17 June - 24 July (37 d)	17.9	2	22	1255	19-Jun	19.1	3

	2007	14 June - 19 July (35 d)	19.8	6	28	1292	15-Jun	20.5	7
	2008	20 June - 4 August (45 d)	16.8	0	27	1010	10-Jul	22.2	12
	2009	26 June - 5 August (41 d)	19.7	2	29	1204	9-Jul	21	15
	2010	28 June - 2 August (35 d)	20.6	5	18	1125	29-Jun	20.6	6
	2011	12 July - 14 August (33 d)	17.7	0	33	1378	14-Jul	18.3	1
	2012	8 June - 30 July (52 d)	16.7	0	41	981	10-Jun	16.7	0
		mean	18.4	4	29	1312		19.5	7.4
		range	16-23.1	0-15	5-51	1010-1646		16.3-23.1	0-16
lower	1991	21 June - 23 July (33 d)	22	24	28	1608	21-Jun	22	28
Green	1992	9 June - 17 July (38 d)	20.6	38	26	1704	16-Jun	19.9	45
	1993	24 June - 6 August (44 d)	20.6	36	24	1701	24-Jun	20.6	36
	1994	9 June - 25 July (47 d)	19.8	9	12	1650	15-Jun	19.3	33
	1995	20 July - 5 August (17 d)	23	39	32	2395	21-Jul	23	40
	1996	24 June - 6 August (44 d)	20	13	32	1513	28-Jun	20.2	22
	1999	28 June - 25 July (28 d)	20.9	8	4	1598	30-Jun	21	10
		mean	21.0	23.9	22.6	1738.4		20.9	30.6
		range	19.8-23	8-39	4-32	1513-2395		19.9-23	10-45

Table 2. Type-III *F*-statistics for significant effects in the general linear model analysis of first (first) reproduction and first peak (peak) of reproduction by Colorado pikeminnow in the lower Yampa River, Colorado, and lower Green River, Utah. Degree days is the sum of mean daily water temperatures since 1 January until first or peak of reproduction in the year of interest, and D18 days is the number of days when mean daily water temperature was $\geq 18^{\circ}\text{C}$ before the peak of reproduction. Spring snowmelt runoff peak flow (Spring peak) is the highest mean daily flow annually of the Yampa River (USGS Deerlodge gauge # 09260050) or the lower Green River (Green River, Utah, gauge # 09315000).

Reach/Source	DF	Type III SS	Mean Square	<i>F</i> -Value	Pr > <i>F</i>
Yampa River					
First reproduction					
Degree days	1	127.28	127.28	6.05	0.0236
Spring peak flow (m ³ /sec)	1	730.30	730.30	34.73	<0.0001
First peak of reproduction					
Days > 18°C	1	254.36	254.36	13.62	0.0016
Spring peak flow (m ³ /sec)	1	1364.30	1364.30	73.03	<0.0001
Lower Green River					
First reproduction					
Degree days	1	57.70	57.70	3.22	0.1471
Spring peak flow (m ³ /sec)	1	262.05	262.05	14.63	0.0187
First peak of reproduction					
Days > 18°C	1	54.40	54.40	8.65	0.0423
Spring peak flow (m ³ /sec)	1	46.55	46.55	7.40	0.0529

Table 3. Mean number of Colorado pikeminnow larvae captured in dawn, noon, dusk, and midnight samples (N) in 24-hr periods (3 samples/period) in the Yampa River in summer 1991-2012 (no sampling in 1997). Samples are a composite of those collected during years classified as drought (1994, 2000-2002, 2007, 2012, mean of mean July-August flow = 5.1 m³/sec [180 ft³/sec], 0.8-8.9 m³/sec [28-313 ft³/sec]) and non-drought (all others, mean of mean July-August flow = 36.5 m³/sec [1,288 ft³/sec], 11.9-138.8 m³/sec [419-4,900 ft³/sec]) years. Abundance in different time periods was from density estimates (#/1,000 m³ water sampled) corrected for differences in the volume of water sampled and discharge during sampling periods so abundances are directly comparable within and among years. The coefficient of variation (CV; standard deviation/mean density * 100) reflects the relative variation in densities of larvae at different sample times across years; CL is confidence limit.

Time/Flow year	N	Mean	CV	Upper 95% CL	Lower 95% CL
Drought					
Dawn	40	97.8	269.8	182.1	13.4
Noon	40	77.6	407.6	178.7	-23.5
Dusk	39	220.4	406.0	510.4	-69.7
Midnight	39	1935.6	234.9	3409.5	461.6
Non-drought					
Dawn	102	610.4	257.4	919.0	301.8
Noon	97	512.1	201.7	720.3	304.0
Dusk	97	333.0	401.5	602.4	63.5
Midnight	92	561.5	181.0	771.9	351.0

Table 4. Effort and captures for middle Green River backwater sampling for Colorado pikeminnow, 1979-2012. #BW is the number of backwaters sampled that year, Seine Area is the backwater area swept with the seine, BW Area is the average backwater size per year (not available before 1986, “total” = mean size), YOY CP is the number of age-0 Colorado pikeminnow captured, Total CP is YOY CP plus the number of fish older than age-0 Colorado pikeminnow, and % BW w/CP is the percent of backwaters sampled where Colorado pikeminnow were found.

Year	Sample start	Sample end	# BW	Seine Area (m ²)	Seine Hauls	BW Area (m ²)	YOY CP	Total CP	% BW w/CP
1979	12-Sep	12-Oct	71	3798	106	na	925	925	63.4
1980	16-Sep	10-Oct	35	3630	71	na	559	560	60.0
1981	14-Sep	16-Oct	33	1788	39	na	283	284	36.4
1982	27-Sep	5-Oct	41	2620	87	na	474	474	53.7
1983	17-Oct	10-Nov	42	4232	86	na	21	21	14.3
1984	16-Oct	26-Oct	39	2795	82	na	25	25	28.2
1985	11-Oct	29-Oct	45	2386	89	na	63	63	42.2
1986	29-Sep	3-Oct	42	4298	84	1071	493	496	71.4
1987	29-Sep	2-Oct	41	3256	80	783	218	219	46.3
1988	28-Sep	4-Oct	42	3978	84	1070	919	920	73.8
1989	27-Sep	29-Sep	42	4221	84	894	62	62	40.5
1990	24-Sep	26-Sep	42	4845	84	1354	339	341	73.8
1991	19-Sep	26-Sep	40	5107	80	1195	527	527	80.0
1992	22-Sep	7-Oct	39	4697	80	986	182	183	69.2
1993	27-Sep	29-Sep	40	3950	80	1885	305	305	47.5
1994	27-Sep	7-Oct	42	4356	84	1083	12	15	7.1
1995	26-Sep	5-Oct	42	3784	84	656	75	75	31.0
1996	1-Oct	3-Oct	42	3898	84	1233	79	79	35.7
1997	6-Oct	8-Oct	39	3137	78	1399	23	23	17.9
1998	22-Sep	24-Sep	42	4987	84	1948	74	74	26.2
1999	21-Sep	23-Sep	41	3896	82	2114	12	12	19.5
2000	26-Sep	29-Sep	42	3830	84	1232	78	87	23.8
2001	17-Sep	21-Sep	42	4156	84	1316	10	10	16.7
2002	23-Sep	26-Sep	42	5202	84	1490	0	0	0.0
2003	8-Sep	11-Sep	41	4740	82	1216	2	2	4.9
2004	27-Sep	6-Oct	42	4686	84	1403	60	60	45.2
2005	29-Sep	18-Oct	55	10856	219	1701	60	60	23.6
2006	13-Sep	3-Oct	52	8831	143	2241	5	5	5.8
2007	24-Sep	5-Oct	54	7982	116	1968	5	10	11.1
2008	22-Sep	2-Oct	57	7739	138	1517	20	20	8.8
2009	22-Sep	1-Oct	58	10698	123	1743	641	642	44.8
2010	20-Sep	29-Sep	56	8348	138	1673	493	494	53.6
2011	27-Sep	6-Oct	55	11570	128	1432	0	3	5.5
2012	17-Sep	27-Sep	37	10247	143	1644	2	2	5.4
totals			1,515	178,542	3,278	1,417	7,046	7,078	34.9

Table 5. Effort and captures for lower Green River backwater sampling for Colorado pikeminnow, 1979-2012. #BW is the number of backwaters sampled that year, Seine Area is the backwater area swept with the seine, BW Area is the average backwater size per year (not available before 1986, “total” = mean size), YOY CP is the number of age-0 Colorado pikeminnow captured, Total CP is YOY CP plus the number of fish older than age-0 Colorado pikeminnow, and % BW w/CP is the percent of backwaters sampled where Colorado pikeminnow were found.

Year	Sample start	Sample end	# BW	Seine Area (m ²)	Seine Hauls	BW Area (m ²)	YOY CP	Total CP	% BW w/CP
1979	19-Sep	27-Sep	30	2152	48	na	547	548	93.3
1980	8-Sep	25-Sep	31	1520	55	na	1070	1070	80.6
1981	15-Sep	17-Sep	24	1571	34	na	133	135	70.8
1982	21-Sep	5-Oct	38	2450	71	na	166	172	68.4
1983	18-Oct	21-Oct	24	1736	47	na	29	33	37.5
1984	10-Oct	11-Oct	12	336	16	na	2	2	16.7
1985	1-Oct	17-Oct	36	1980	69	na	182	182	61.1
1986	29-Sep	3-Oct	28	1964	50	772	845	845	85.7
1987	21-Sep	23-Sep	35	2938	71	978	857	859	80.0
1988	24-Sep	28-Sep	42	3215	82	1004	2961	3009	97.6
1989	20-Sep	23-Sep	47	4248	94	1160	1625	1664	95.7
1990	17-Sep	16-Oct	46	6609	92	2117	439	443	80.4
1991	16-Sep	19-Sep	34	3007	68	1211	186	189	70.6
1992	20-Sep	24-Sep	50	4182	94	774	133	134	48.0
1993	21-Sep	30-Sep	47	4574	89	878	1618	1619	85.1
1994	20-Sep	23-Sep	47	3844	94	906	306	354	74.5
1995	19-Sep	22-Sep	43	2548	81	534	57	58	53.5
1996	24-Sep	27-Sep	50	2981	91	360	407	411	84.0
1997	15-Sep	18-Sep	47	2940	94	438	40	48	42.6
1998	22-Sep	25-Sep	48	3235	92	489	258	258	60.4
1999	13-Sep	16-Sep	44	4102	82	942	384	384	54.5
2000	18-Sep	21-Sep	38	5760	72	1606	704	708	81.6
2001	2-Sep	5-Sep	35	5962	62	1751	18	18	31.4
2002	16-Sep	23-Sep	31	4645	60	771	18	22	32.3
2003	22-Sep	25-Sep	48	4052	95	2302	107	124	41.7
2004	15-Sep	18-Sep	21	1974	44	798	79	80	52.4
2005	7-Sep	10-Sep	32	2938	63	1022	70	71	65.6
2006	11-Sep	14-Sep	41	4936	80	2243	326	331	70.7
2007	4-Sep	7-Sep	40	3138	80	970	681	688	70.0
2008	16-Sep	19-Sep	34	1950	66	783	60	61	52.9
2009	13-Sep	15-Sep	35	2500	67	692	427	427	91.4
2010	12-Sep	14-Sep	29	2868	53	652	131	134	62.1
2011	11-Sep	12-Sep	27	1796	46	752	17	17	11.1
2012	6-Sep	16-Sep	36	4716	62	1153	254	293	63.9
totals			1,250	109,366	2,364	1,039	15,137	15,391	63.8

Table 6. Numbers of fish captured by year in the first seine haul in each primary backwater sampled in the middle Green River, 1979-2012. Species are grouped, native fishes first ending with razorback sucker, followed by nonnative fishes, starting with the three most common species, fathead minnow, red shiner, and sand shiner, to allow for easier comparisons, followed by the remainder. Species lists are for the entire river so some species have no abundance data because none were captured, but this format allows for easier comparisons across middle and lower Green River reaches. "S?" were unidentified fishes, mostly cyprinids.

Species	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012			
Native species																																					
bluehead sucker									277	1	80	9	9	115	80	26	25	25	30	48	11	12				1	1			8	3	19		7			
flannelmouth sucker									67	120	16		2	2	54	26	15	8	9	19	12	6	69	3		8	6	5	7	3	19	2	1	2			
Colorado pikeminnow	710	167	283	269	18	14	44	107	27	252	13	85	144	47	83	1	43	14	4	46	6	3				25	7	1			39	32					
Gila	691	44	10	40		8	3	43	19	5	41	22	10	5	30	11	5	4	26	19	34	4	6	3	1	7			1		7						
mottled sculpin																																					
speckled dace	290	81	29	4	22	12	18	149	2	6	3	2	5	11	7	6	11	4	2	4	9	2				1	1							1			
razorback sucker																			3	1																	
Nonnative species																																					
fathead minnow	567	152	598	809	564	883	1472	2003	873	650	865	1386	518	1653	1538	2685	1304	486	1067	1569	407	1436	371	1303	89	337	204	1431	327	149	108	231	867	189			
red shiner	7433	3123	7185	2435	625	579	2148	6727	9757	4072	4025	5395	3301	3178	4835	41290	3229	2871	1010	2400	1832	10860	4510	11516	3847	5524	3654	19365	5754	1090	2101	3566	1682	2379			
sand shiner	3	17	7		1	3		154	462	159	284	87	38	440	50	1898	188	1265	1152	474	533	8072	283	1059	49	1207	552	2060	3940	816	417	959	301	583			
black bullhead					1		11	3	20			2			1					7	3	2	1							9	1		1	5			
black crappie																																			3		
bluegill																									1				3								
brown trout																																					
channel catfish	15	10	27	26				1	1	7	7	1	14	3	17								6			4	1		10	3		1		6			
common carp	248	5	4	30	20	3	20	20	3	2	43	4	5	15	13	2	6	5	11	8	23	12		1	48	1	1	98	16	38	17	38	13	1			
brook stickleback																1			4	11	3	3	10	5	1	1	18	7		10	4						
gambusia																																					
green sunfish		2	118	48	12	8	10	124	8	13	22		5	5	3	1	1	8	3	17	68	15		39		8		1		102	1	15	14				
gizzard shad																													5	3		2			22		
largemouth bass																																					
northern pike								1													1																
plains killifish																																					
rainbow trout																																					
redside shiner	300				1																																
smallmouth bass																		1		1										6	5	1		2	1		
S?																													2197								
unknown sucker	1708	406	91	199	136	7	62	93						108		1	2		1	1	16																
unidentified						1		1																													
unknown minnow													8																								
walleye																																					
white sucker													1							3	1					1		5		3	13	7	5	8			
yellow bullhead																																					
Total	11965	4007	8352	3861	1399	1529	3780	9443	11496	5289	5399	6991	4060	5583	6710	45948	4830	4690	3326	4630	2954	20431	5259	13931	4036	7129	4444	25176	10094	2227	2740	4854	2895	3183			

Table 7. Numbers of fish captured by year in the first seine haul in each primary backwater sampled in the lower Green River, 1979-2012. Species are grouped, native fishes first ending with razorback sucker, followed by nonnative fishes, starting with the three most common species, fathead minnow, red shiner, and sand shiner, to allow for easier comparisons, followed by the remainder. Species lists are for the entire river so some species have no abundance data because none were captured, but this format allows for easier comparisons across middle and lower Green River reaches. "S?" were unidentified fishes, mostly cyprinids.

Species	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012			
Native species																																					
bluehead sucker										1				1	7	9		7	13		3	2												2			
flannelmouth sucker										5	2	15			2		3					10			2		1			8		5	1	6			
Colorado pikeminnow	303	775	53	72	12	1	65	271	352	875	341	130	53	38	212	139	17	166	15	34	71	190	3	9	23	26	13	103	297	29	203	60	1	149			
Gila		3	7		8		6	9			1				18	1	2			1		2			1	4		6	1		1						
mottled sculpin																																					
speckled dace		36	3	7	31	19	14	20		1			1	4	22		16	9	1	24	6	4	3	1	1					1	2	8					
razorback sucker																																				1	
Nonnative species																																					
fathead minnow	101	252	194	245	235	135	90	87	34	1790	170	228	386	500	249	500	363	1097	79	120	340	234	1564	14721	201	215	142	1187	2183	1074	1044	125	310	3085			
red shiner	699	3078	2416	1286	498	171	415	663	1303	4363	5826	9599	9060	2737	3443	8007	3478	11858	855	1709	845	3591	11727	26710	4707	297	344	8623	8807	4458	2766	1003	1820	2043			
sand shiner		140	21	29	36	45	14	4	4	38	113	129	1135	180	1362	1196	969	3751	320	178	156	574	1168	2135	43	190	95		35	250	15	925	1056	8620			
black bullhead	7	1	4		7			7		1	1	1		1	1		7					3			5	3	35	2									
black crappie																				6	1									2				8			
bluegill																																					
brown trout																																					
channel catfish	69	241	51	80	3	1	7	4	1	110	73	37	8	70	11	6	4		17		2	12	7	122	11	7	10	6	23	13	3		6	5			
common carp	6	5	13	11	8	1	2	12		2	1	4	3	1	1	8	16		1	1	37	3		2	1		9	3		116			15	5			
brook stickleback																																					
gambusia										7						1		2	4	17	1							1									
green sunfish	2			1	26	2		9	5	1	3		2		8	6	2	3				1		1	12	1		4					5				
gizzard shad																														1	1	1	4			15	
largemouth bass																												1	2	1							
northern pike																																					
plains killifish																																					
rainbow trout																																					
redside shiner																																					
smallmouth bass																																					
S?																																					
unknown sucker	86	18	1	13	43	38	35	25																													
unidentified																							40							206							
unknown minnow								5						11	17	8	7	8		2		2197	19														
walleye																																					
white sucker																				1			4														
yellow bullhead																																		6			3
Total	1276	4553	2756	1752	899	413	648	1116	1705	7190	6544	10128	10649	3569	5327	9874	4895	16906	1297	2094	1473	6813	14531	43704	5008	739	650	9937	11349	6165	4035	2137	3217	13932			

Table 8. Parameter estimates for significant effects in the general linear model analysis of age-0 Colorado pikeminnow length in autumn in the middle and lower Green River as a function of red shiner density, mean July-August water temperature, and spring peak flow, the highest mean daily flow for that year in the middle (Jensen, Utah gauge) or the lower Green River (Green River, Utah, gauge).

Parameter	Estimate	Standard			R^2
		Error	t -Value	Pr > t	
Middle Green River					0.85
Intercept	-51.338	20.558	-2.500	0.022	
Red shiner density (#/10 m ²)	0.059	0.014	4.150	0.001	
Water temperature (°C)	4.925	0.926	5.320	< 0.0001	
Spring peak (m ³ /sec)	-0.024	0.006	-4.200	0.001	
Lower Green River					0.72
Intercept	-32.064	31.000	-1.030	0.315	
Red shiner density (#/10 m ²)	0.052	0.034	1.550	0.139	
Water temperature (°C)	3.347	1.264	2.650	0.016	
Spring peak (m ³ /sec)	-0.019	0.005	-3.600	0.002	

Table 9. Type-III *F*-statistics for significant effects in the general linear model analysis of age-0 Colorado pikeminnow length in autumn in the middle and lower Green River as a function of red shiner density, mean July-August water temperature, and spring peak flow, the highest mean daily flow for that year in the middle (Jensen, Utah gauge) or the lower Green River (Green River, Utah, gauge).

Source	DF	Type III SS	Mean Square	<i>F</i> -Value	Pr > <i>F</i>
Middle Green River					
Red shiner density (#/10 m ²)	1	307.36	307.36	17.24	0.0005
Water temperature (°C)	1	504.68	504.68	28.31	<0.0001
Spring peak (m ³ /sec)	1	314.02	314.02	17.61	0.0005
Lower Green River					
Red shiner density (#/10 m ²)	1	71.39	71.39	2.4	0.1387
Water temperature (°C)	1	208.40	208.40	7.01	0.0164
Spring peak (m ³ /sec)	1	385.19	385.19	12.95	0.0021

Table 10. Comparison of base flow levels in Muth et al. (2000) and those proposed in this report for the middle and lower Green River, Utah. The higher upper ends of flow ranges in Muth et al. (2000) for the lower Green River reflect uncertainty about tributary inputs, while proposed targets represent preferred ranges.

Hydrologic classification	Reach 2, Middle Green River flows		Reach 3, Lower Green River flows	
	2000 (Muth et al.)	Proposed	2000 (Muth et al.)	Proposed
Dry (10% of years, 0 to 10% exceedance)	26-31 m ³ /s (900-1,100 ft ³ /s)	48-51 m ³ /s (1,700-1,800 ft ³ /s)	37-74 m ³ /s (1,300-2,600 ft ³ /s)	48-57 m ³ /s (1,700-2,000 ft ³ /s)
Moderately dry (20% of years)	31-43 m ³ /s (1,100-1,500 ft ³ /s)	51-57 m ³ /s (1,800-2,000 ft ³ /s)	42-96 m ³ /s (1,500-3,400 ft ³ /s)	57-65 m ³ /s (2,000-2,300 ft ³ /s)
Average (40% of years)	43-68 m ³ /s (1,500-2,400 ft ³ /s)	57-74 m ³ /s (2,000-2,600 ft ³ /s)	51-119 m ³ /s (1,800-4,200 ft ³ /s)	65-79 m ³ /s (2,300-2,800 ft ³ /s)
Moderately wet (20% of years)	68-79 m ³ /s (2,400-2,800 ft ³ /s)	62-79 m ³ /s (2,200-2,800 ft ³ /s)	77-133 m ³ /s (2,700-4,700 ft ³ /s)	74-91 m ³ /s (2,600-3,200 ft ³ /s)
Wet (10% of years, 90 to 100% exceedance)	79-85 m ³ /s (2,800-3,000 ft ³ /s)	68-85 m ³ /s (2,400-3,000 ft ³ /s)	91-133 m ³ /s (3,200-4,700 ft ³ /s)	79-108 m ³ /s (2,800-3,800 ft ³ /s)

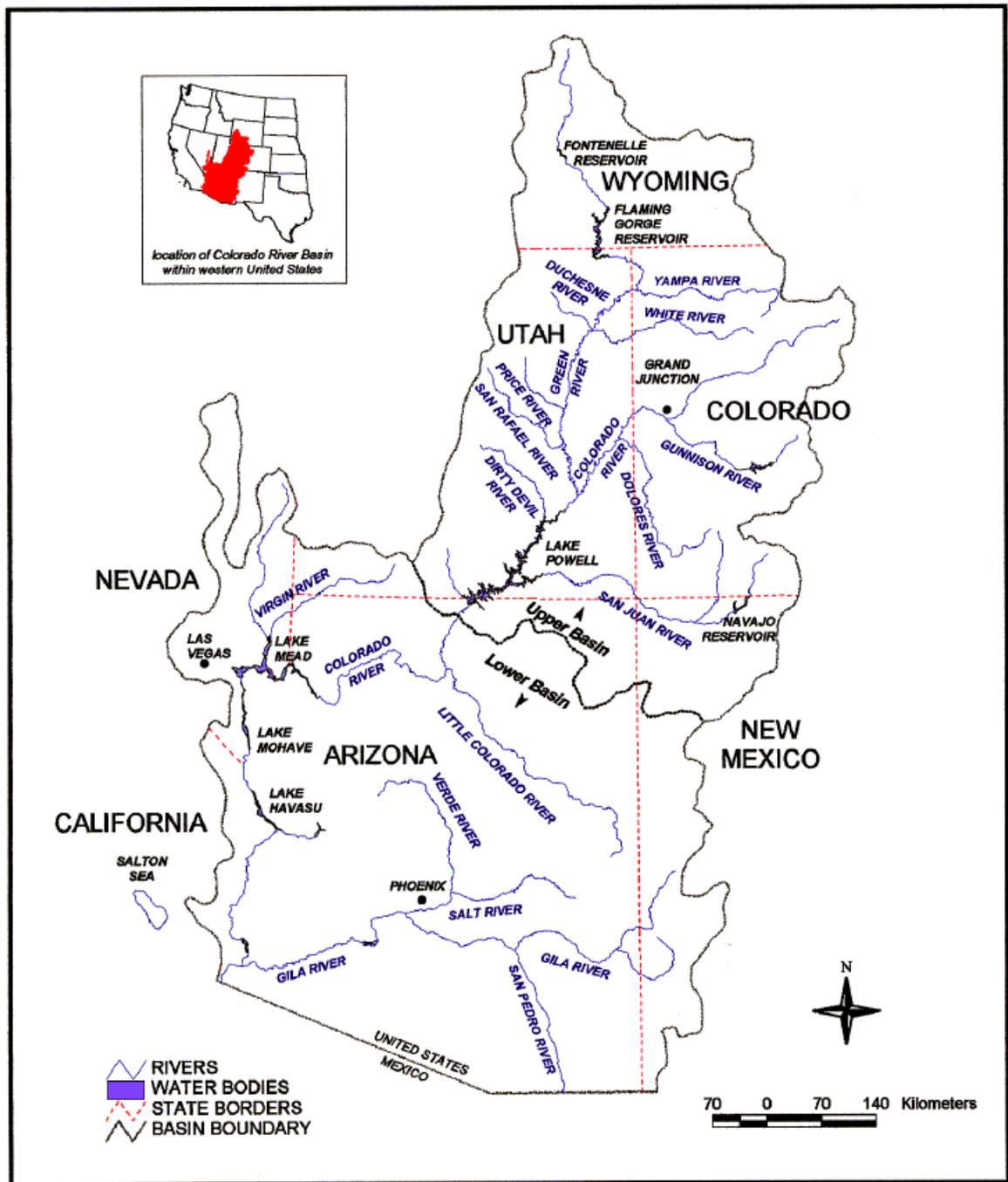
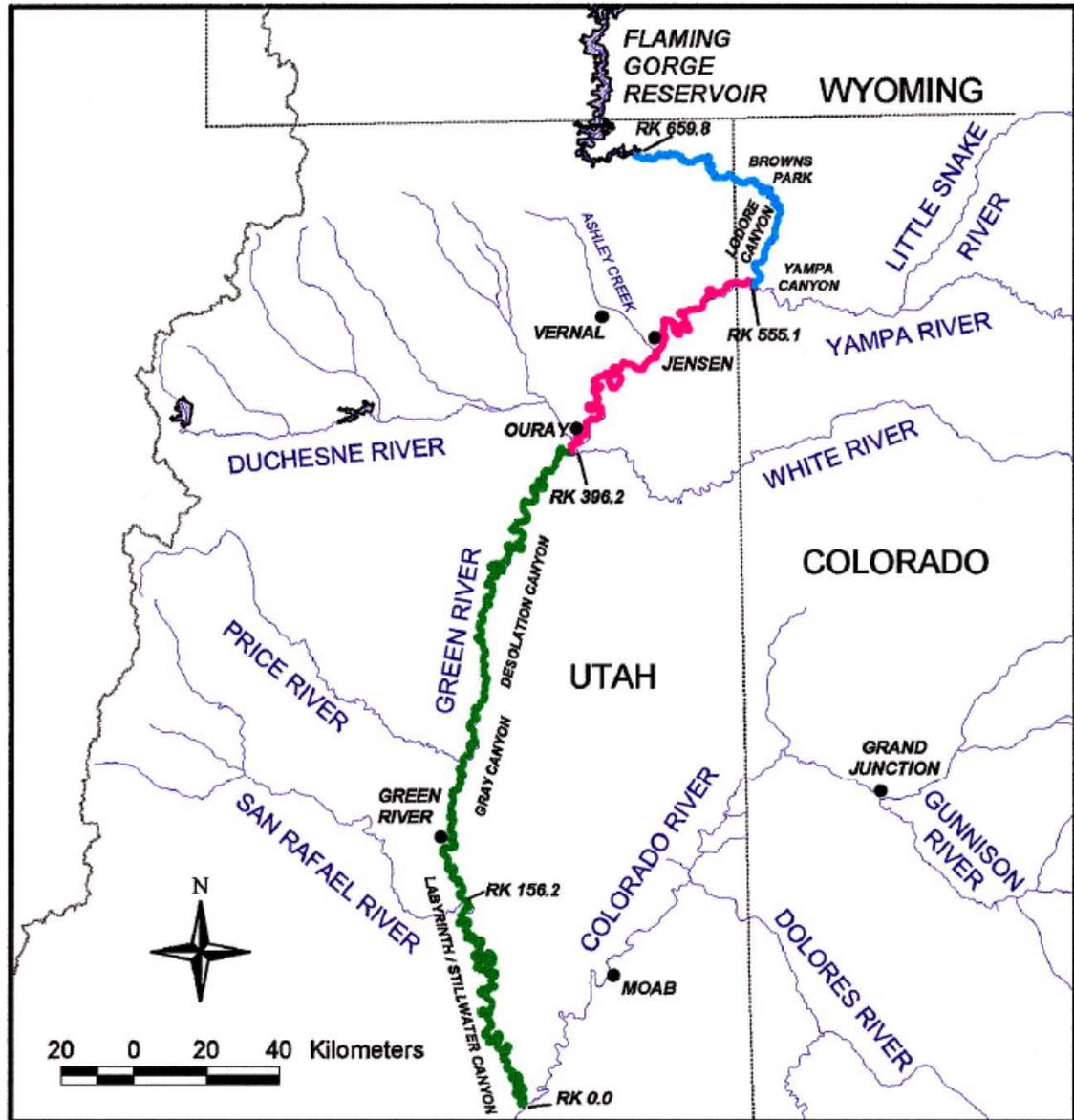


Figure 1. Map of Colorado River basin rivers and major water storage structures (from Muth et al. 2000). The upper and lower portions of the basin are demarcated by the heavy line just downstream of Lake Powell.



LEGEND

- | | |
|---|---|
|  REACH 1 |  STATE BORDERS |
|  REACH 2 |  WATER BODIES |
|  REACH 3 |  RIVER BASIN |
|  RIVERS | |

Figure 2. Map of Green River subbasin rivers and major water storage structures (from Muth et al. 2000). The three main reaches of the Green River (1, upper Green River; 2, middle Green River; and 3, lower Green River) as defined by the Recovery Program. River kilometer (RK) designations depict important landmarks or confluence points.

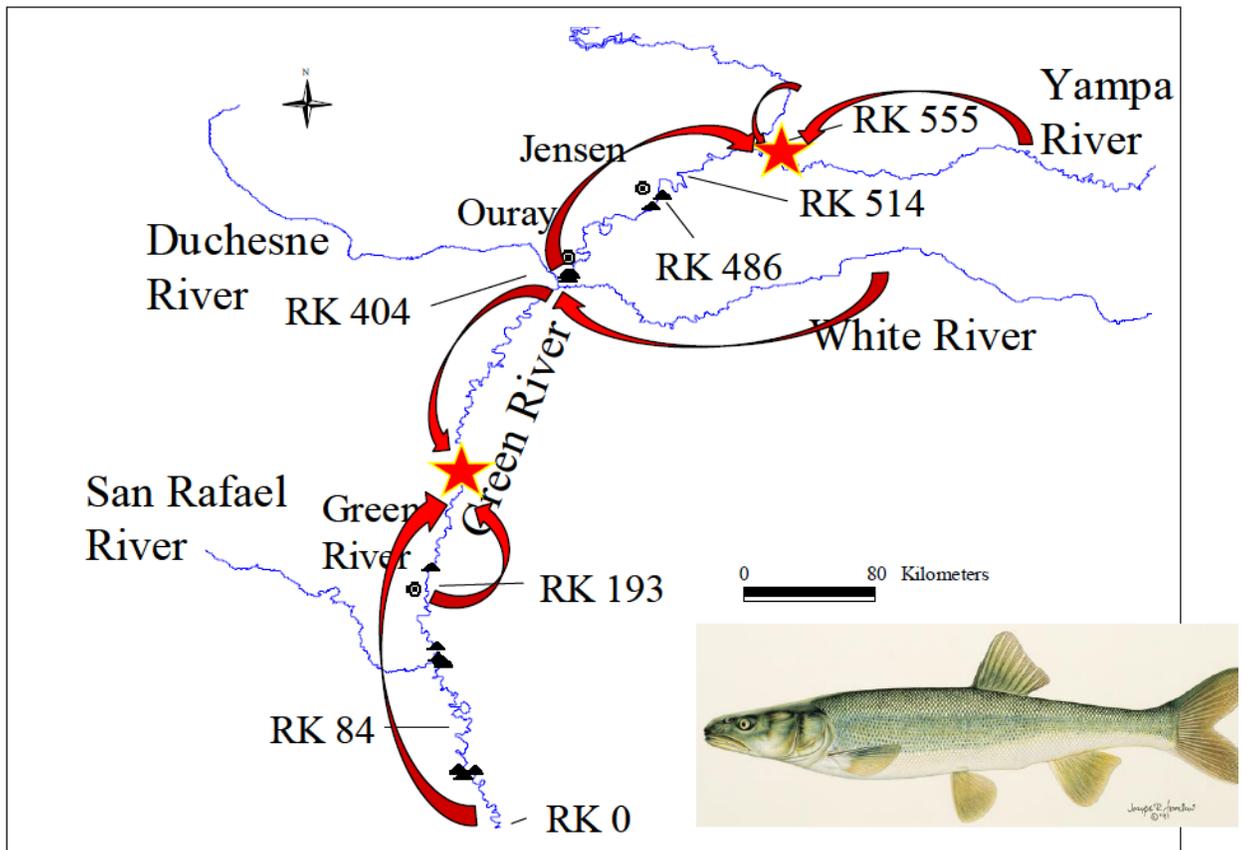


Figure 3. Movements by radio-telemetered adult Colorado pikeminnow (arrows) from various reaches of the Green River subbasin to two known spawning areas (stars), one in Gray Canyon, lower Green River, and one in the lower Yampa River. Pikeminnow return to home ranges after spawning.

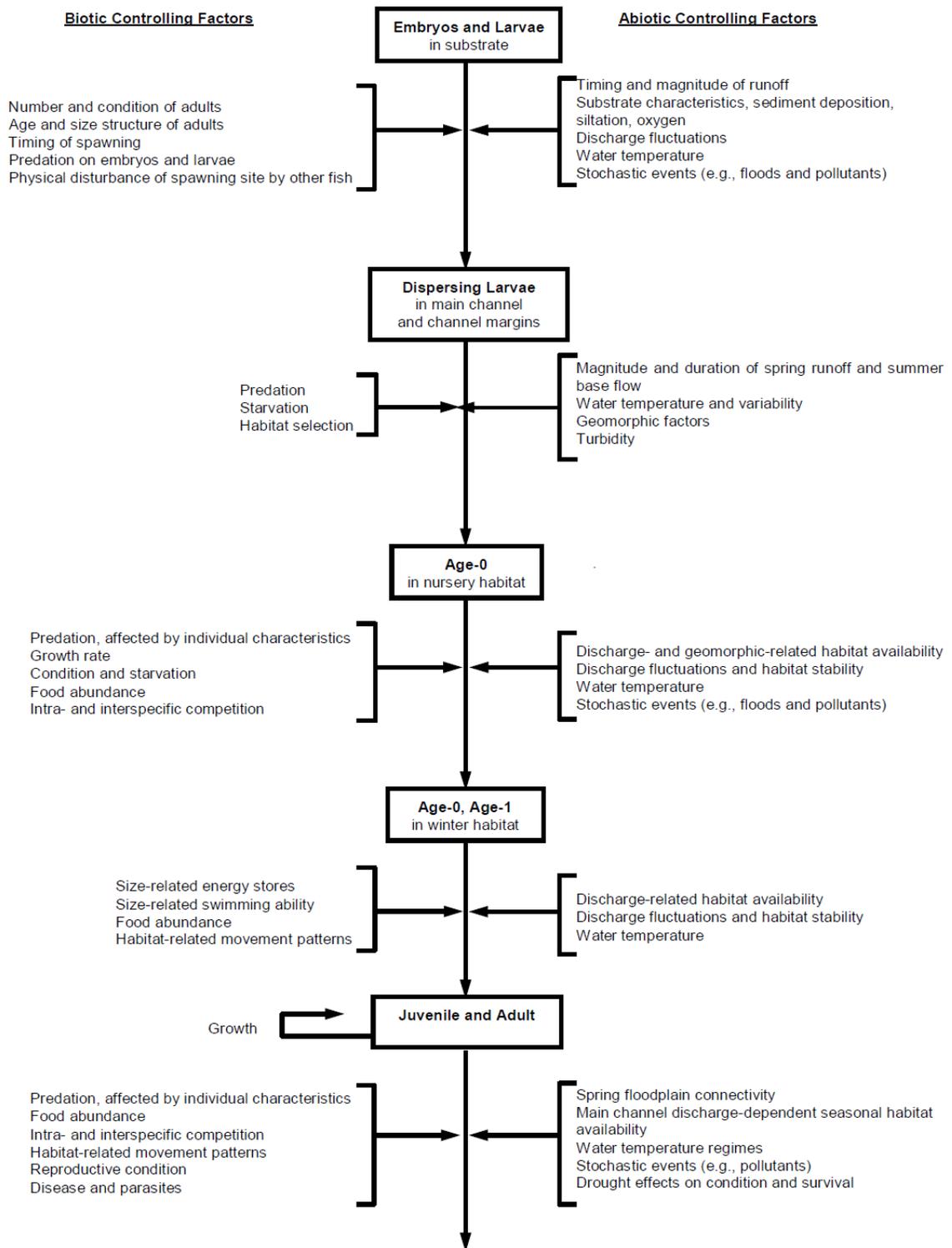


Figure 4. Conceptual life history model of Colorado pikeminnow recruitment to various developmental stages, and important biotic and abiotic controlling factors that affect them.

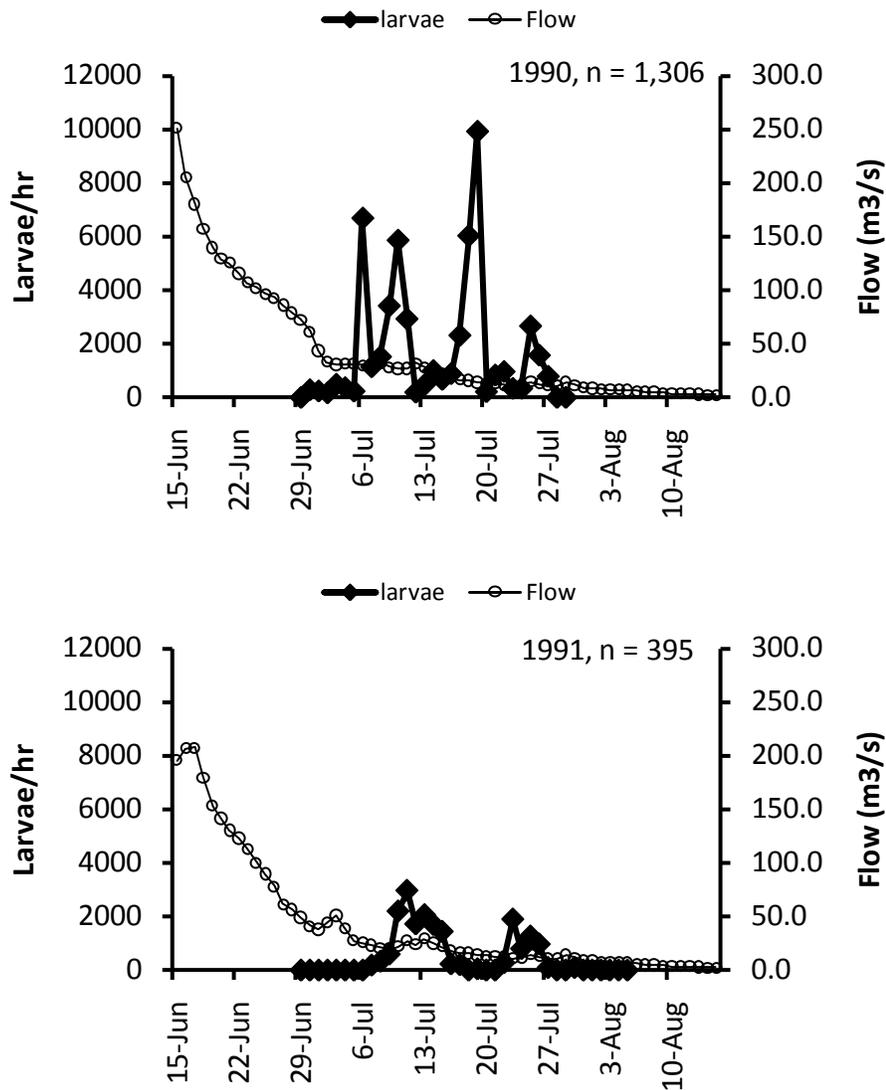


Figure 5. Abundance of Colorado pikeminnow larvae transported downstream past the lower Yampa River sampling station near the confluence with the Green River, Dinosaur National Monument in summers 1990-2012 (no sampling in 1997). Transport abundance was estimated by dividing the number of larvae captured ($n = \text{total in season}$) in three dawn nearshore drift net samples adjusted to an hourly rate by the estimated proportion of total discharge that was sampled.

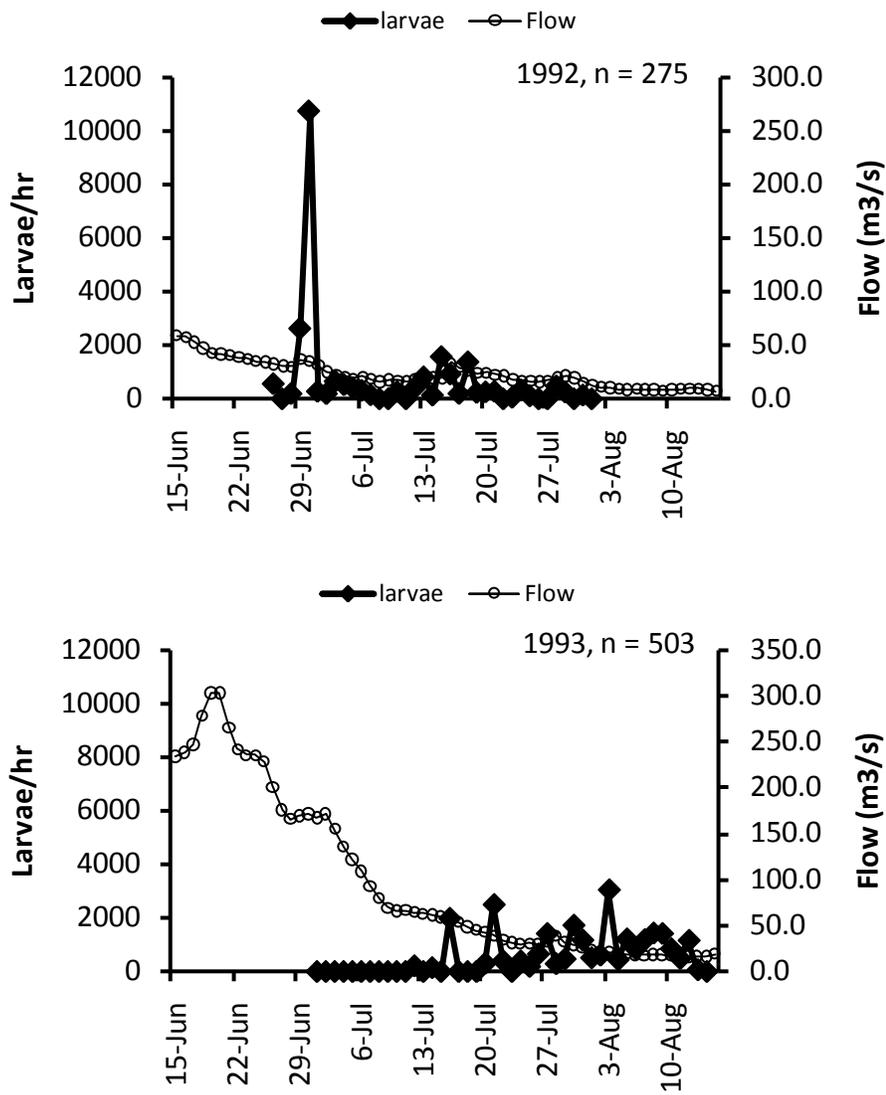


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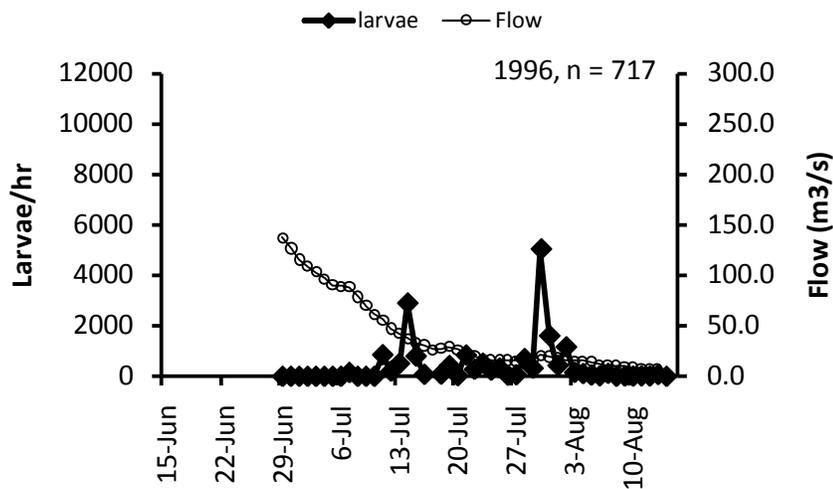
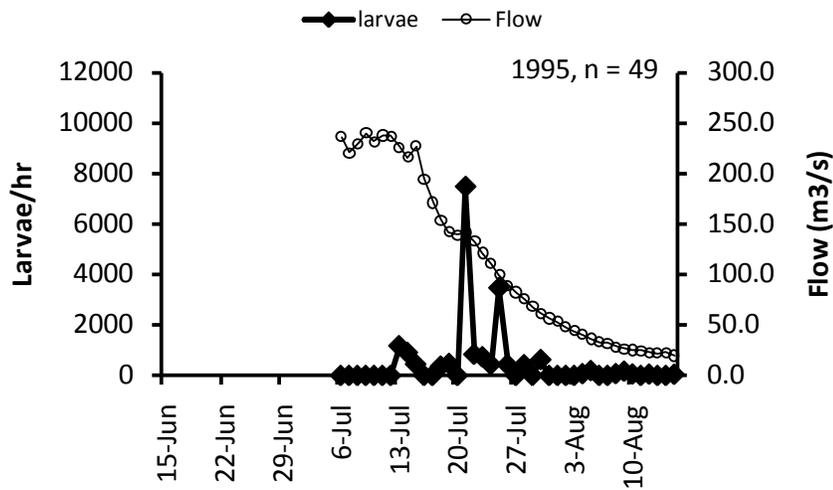
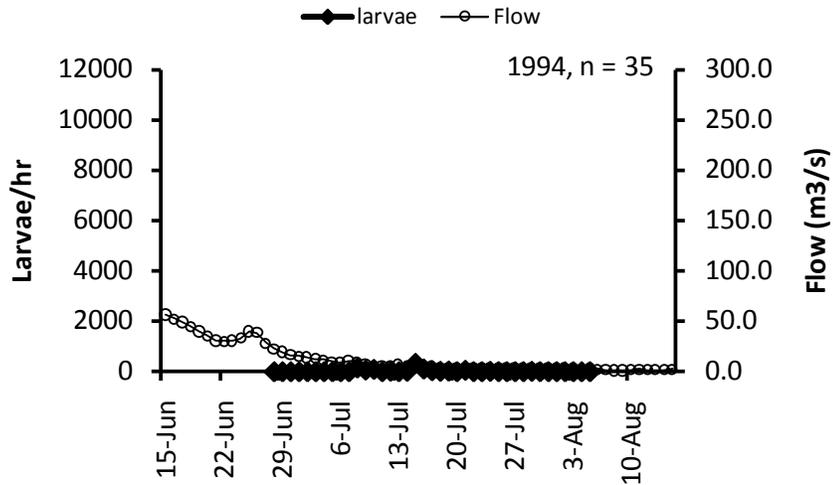


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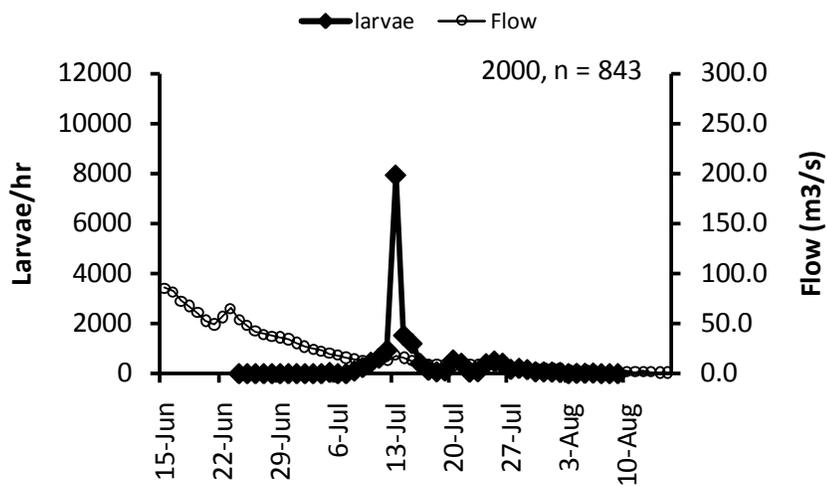
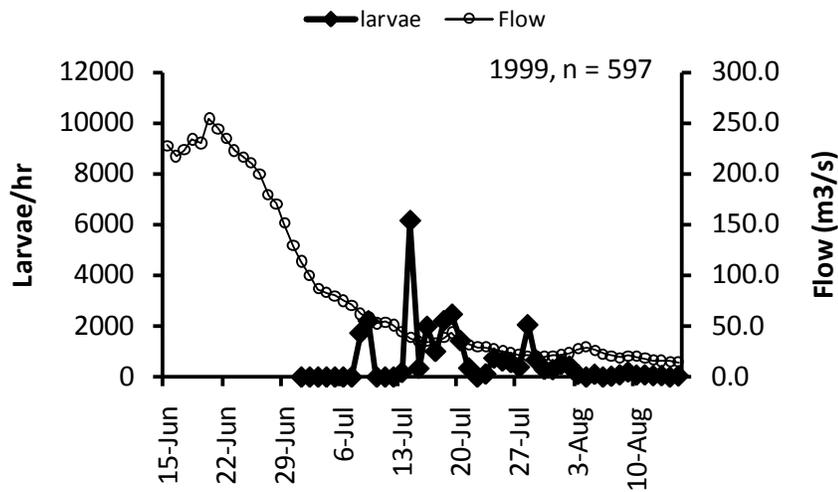
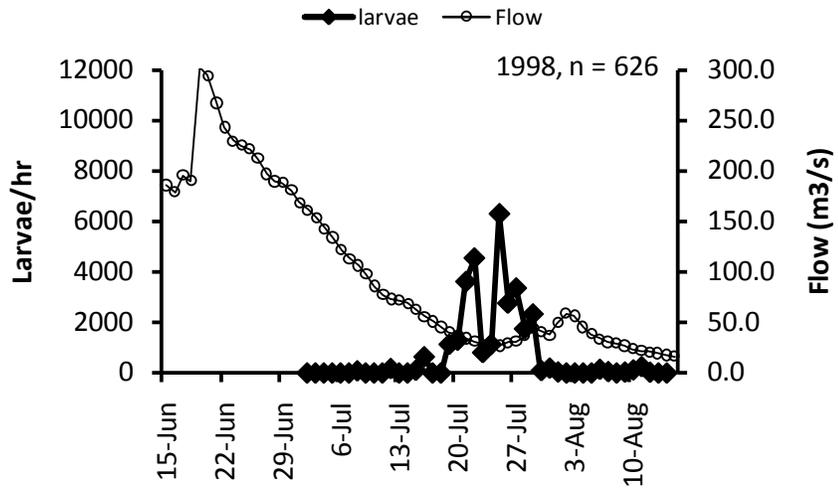


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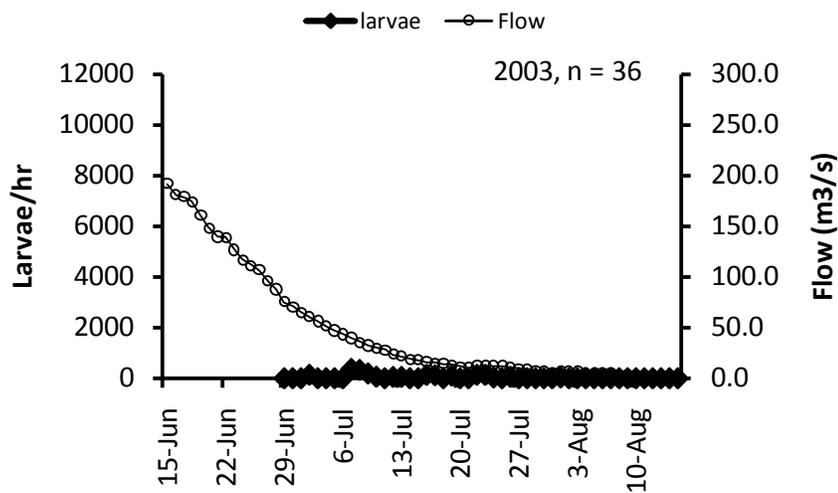
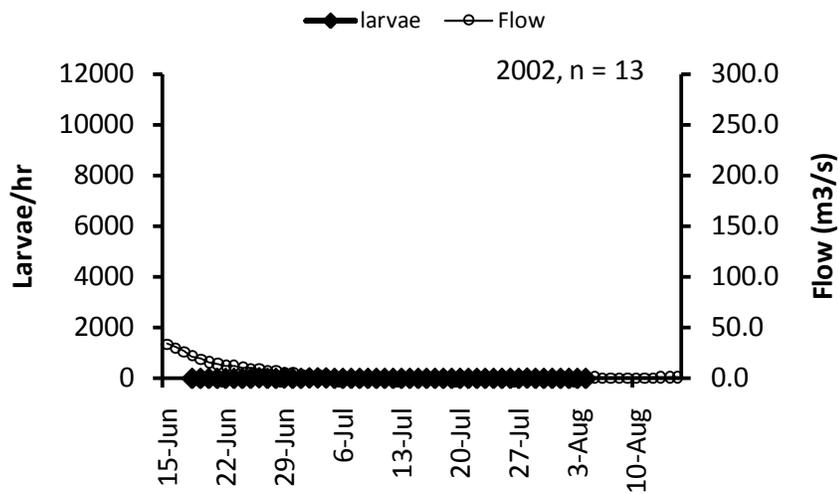
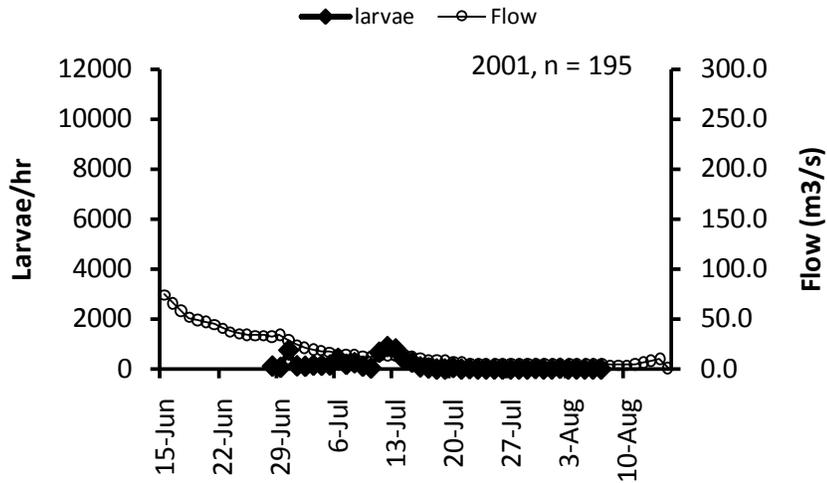


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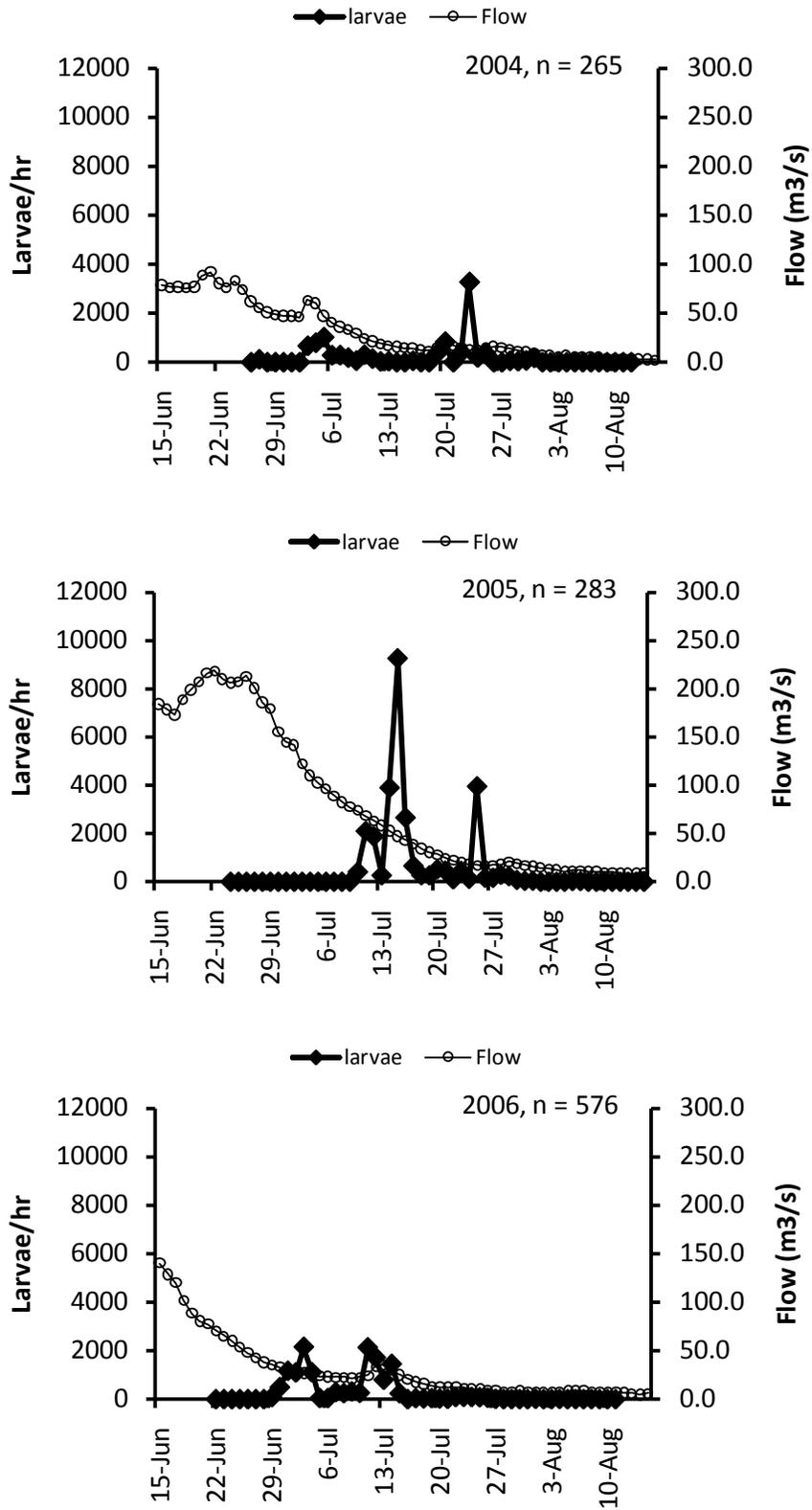


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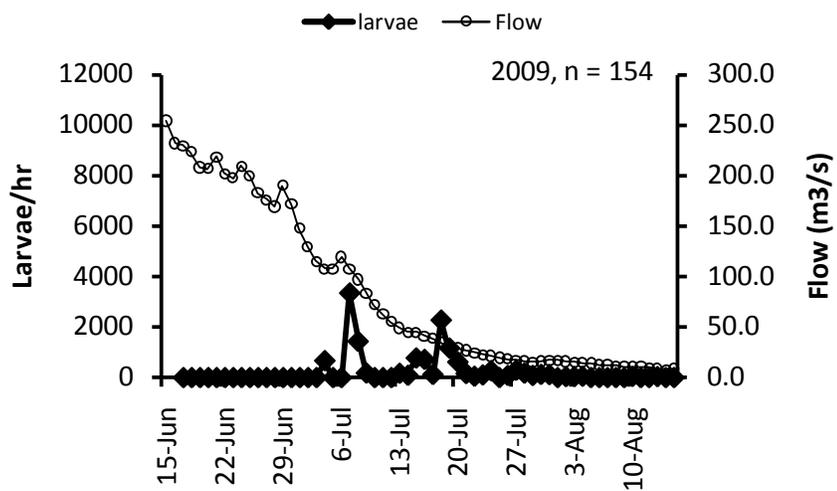
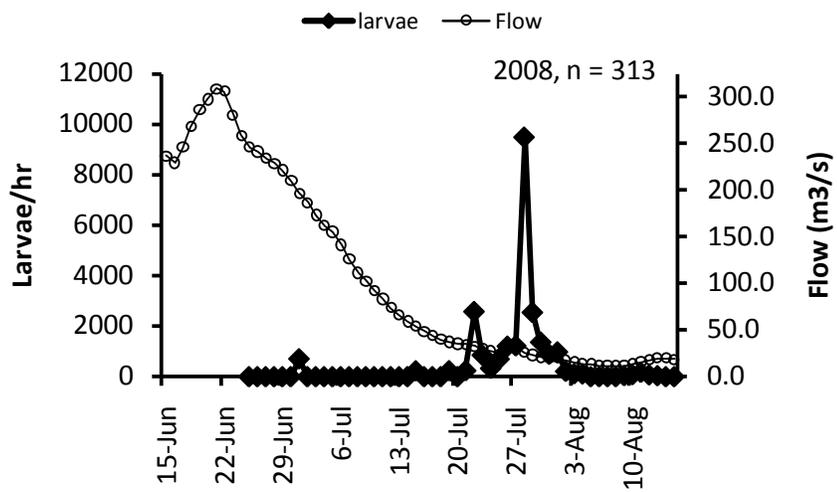
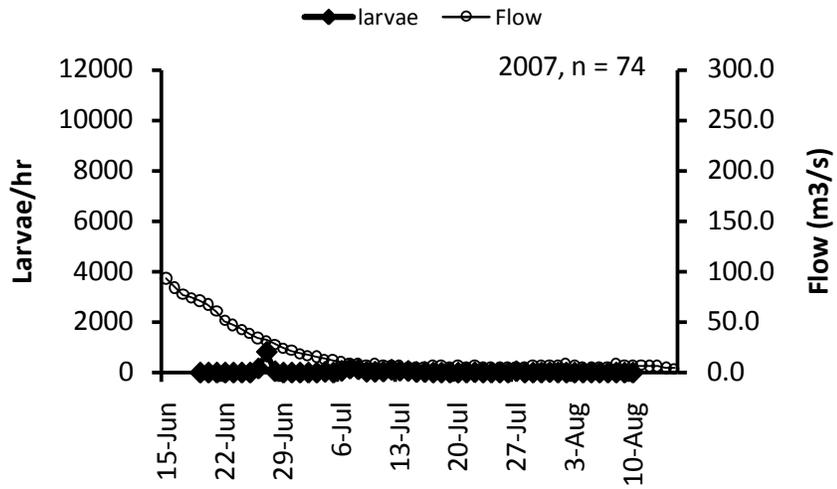


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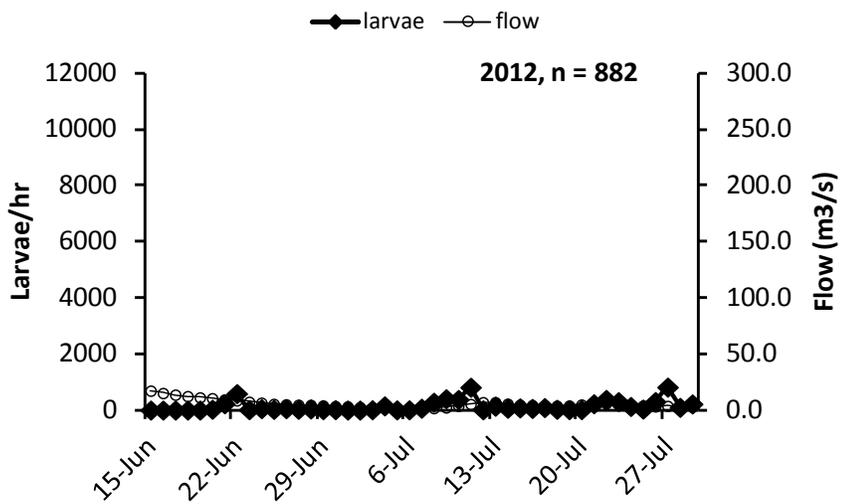
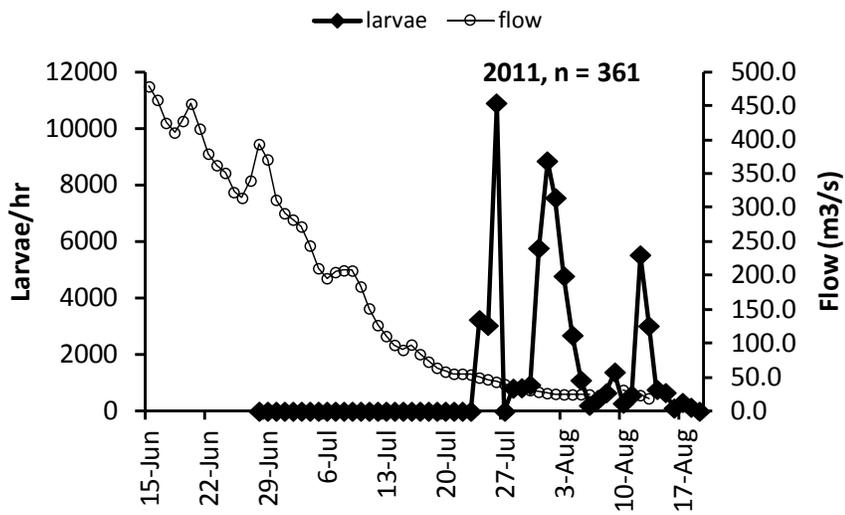
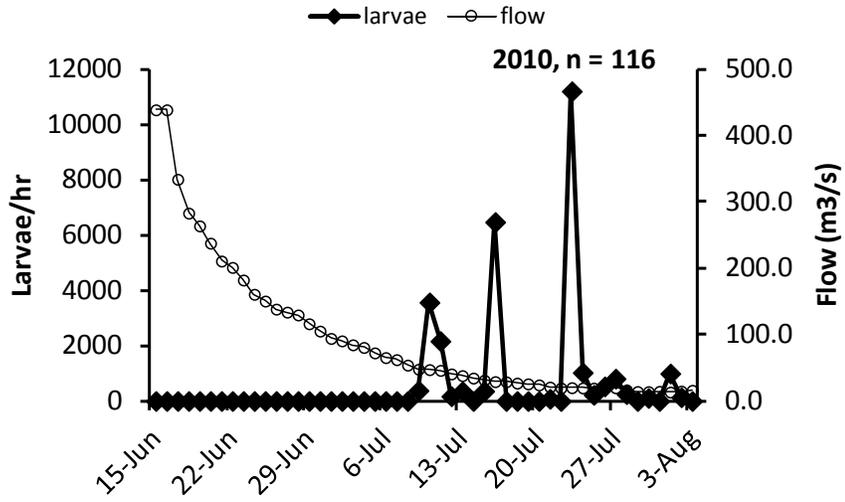


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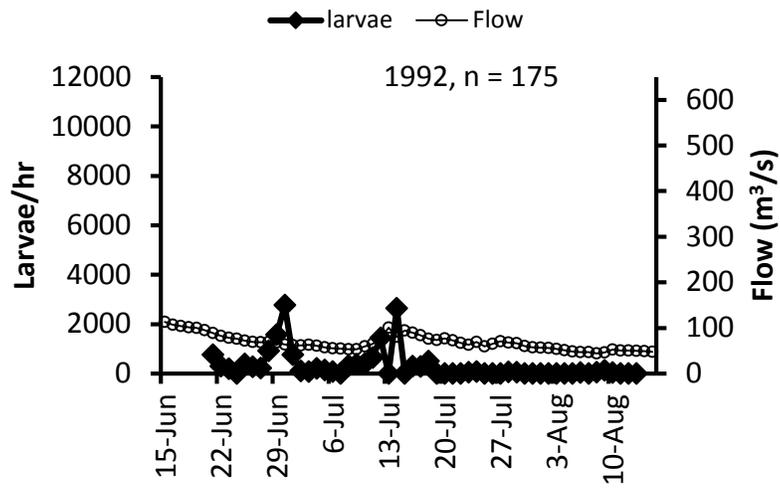
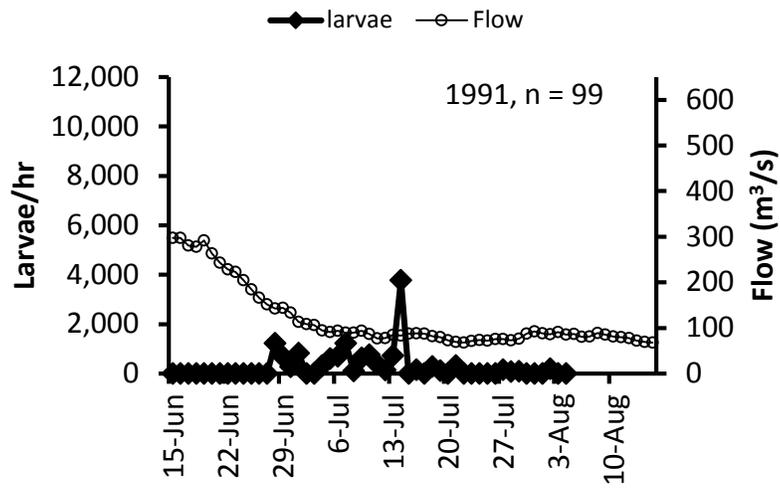


Figure 6. Abundance of Colorado pikeminnow larvae transported downstream past the lower Green River sampling station near Green River, Utah, in summers 1991-1996 and 1999. Transport abundance was estimated by dividing the number of larvae captured (n = total in season) in three dawn nearshore drift net samples adjusted to an hourly rate by the estimated proportion of total discharge that was sampled.

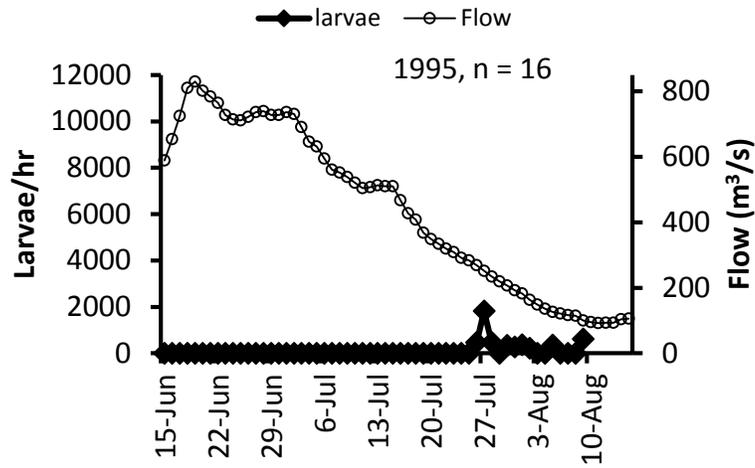
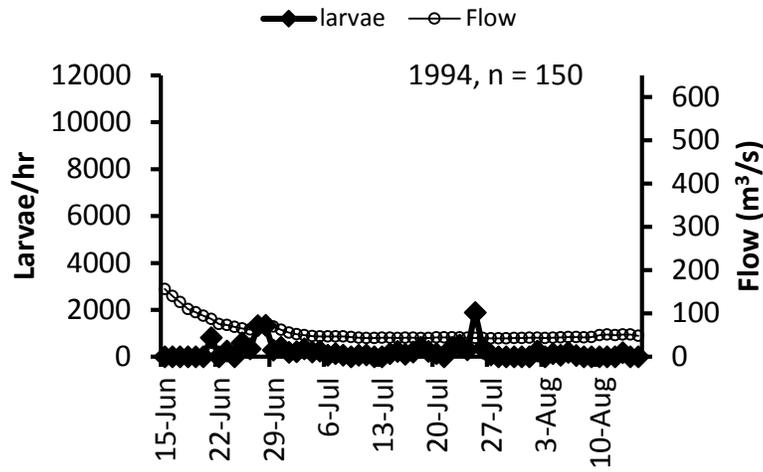
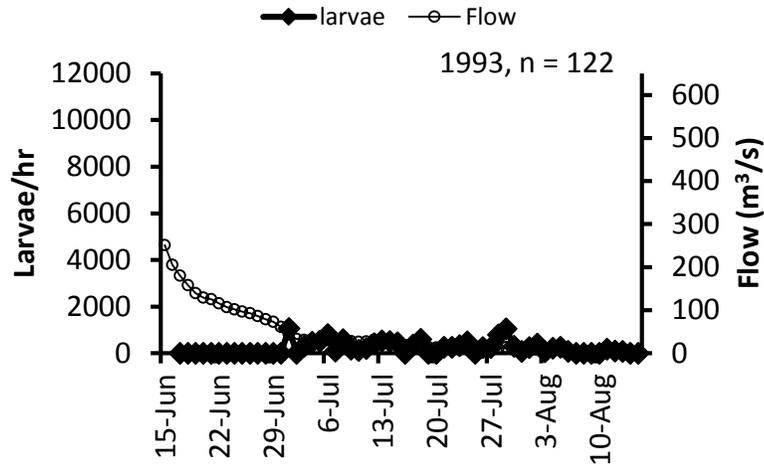


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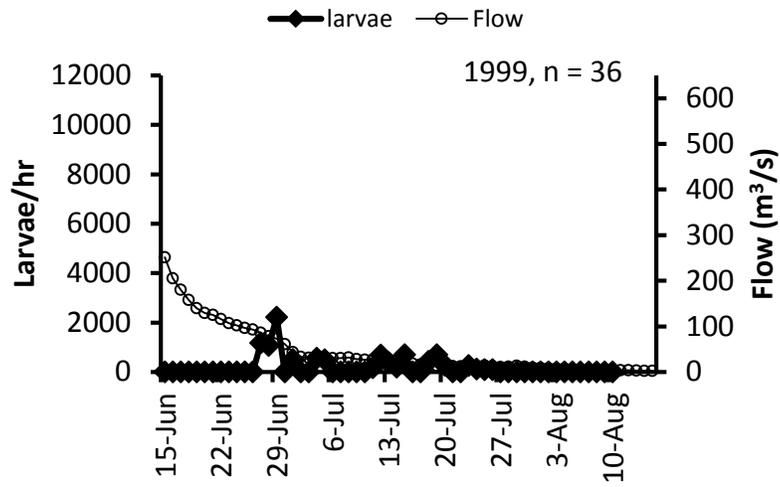
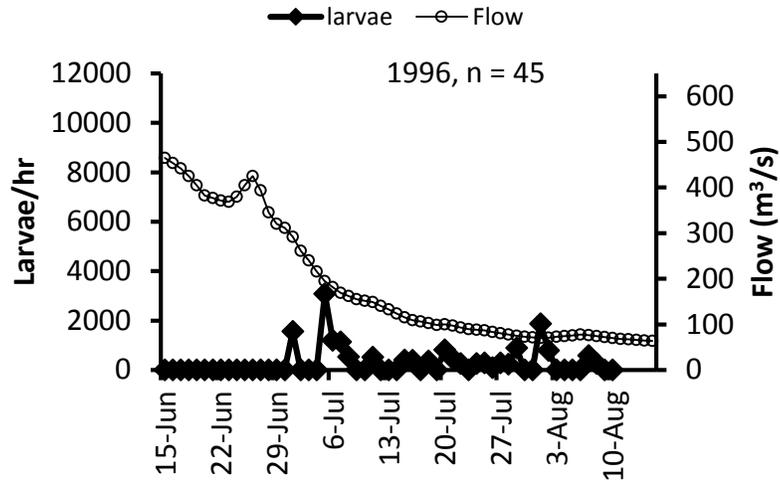


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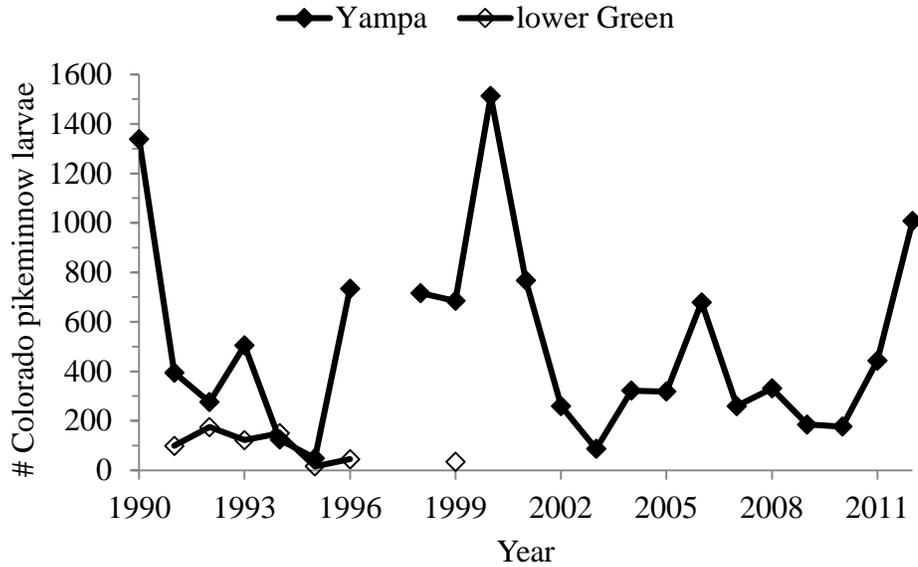


Figure 7. Number of Colorado pikeminnow larvae captured in drift nets by year, lower Yampa River, Colorado, and lower Green River, Utah.

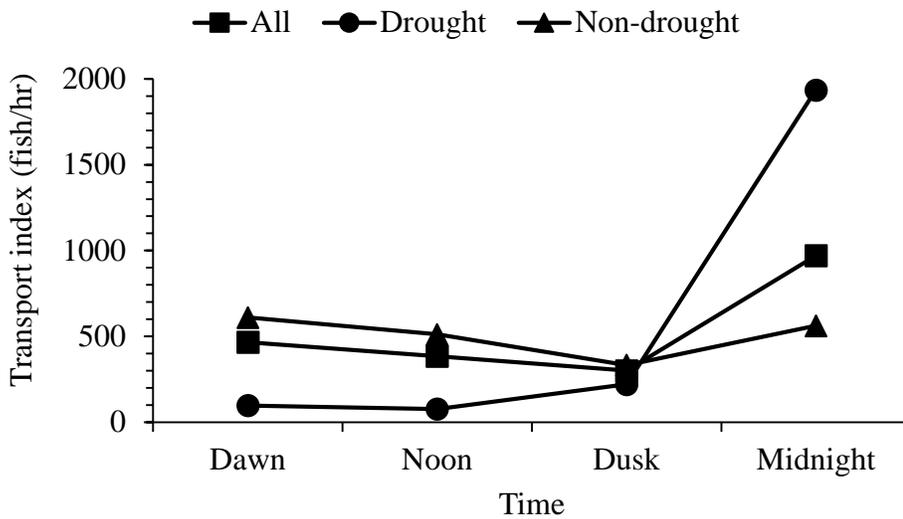


Figure 8. Diel drift patterns of Colorado pikeminnow, lower Yampa River, 1991-2012 (no sampling in 1997). Samples are a composite of those collected during years classified as drought (1994, 2000-2002, 2007, 2012, mean of mean July-August flow = $5.1 \text{ m}^3/\text{sec}$ [$180 \text{ ft}^3/\text{sec}$], $0.8\text{-}8.9 \text{ m}^3/\text{sec}$ [$28\text{-}313 \text{ ft}^3/\text{sec}$]) and non-drought (all others, mean of mean July-August flow = $36.5 \text{ m}^3/\text{sec}$ [$1,288 \text{ ft}^3/\text{sec}$], $11.9\text{-}138.8 \text{ m}^3/\text{sec}$ [$419\text{-}4,900 \text{ ft}^3/\text{sec}$]) years. All is all years. Transport abundance was estimated by dividing the number of larvae captured in three dawn nearshore drift net samples adjusted to an hourly rate by the estimated proportion of total discharge that was sampled.

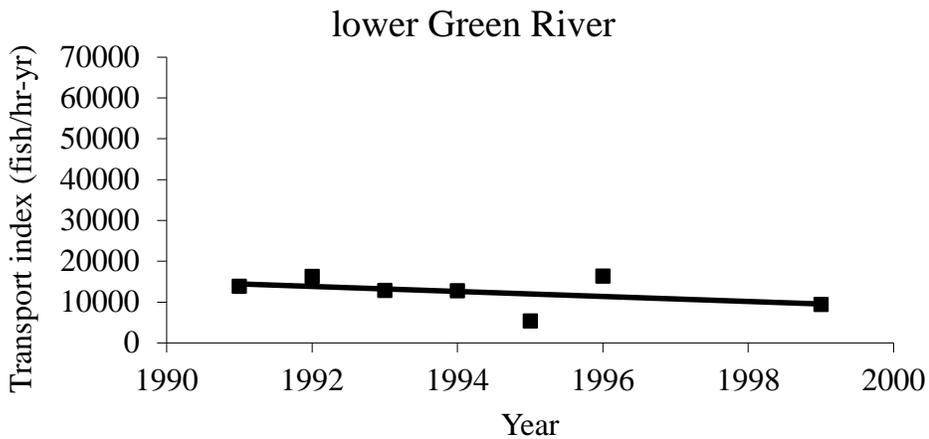
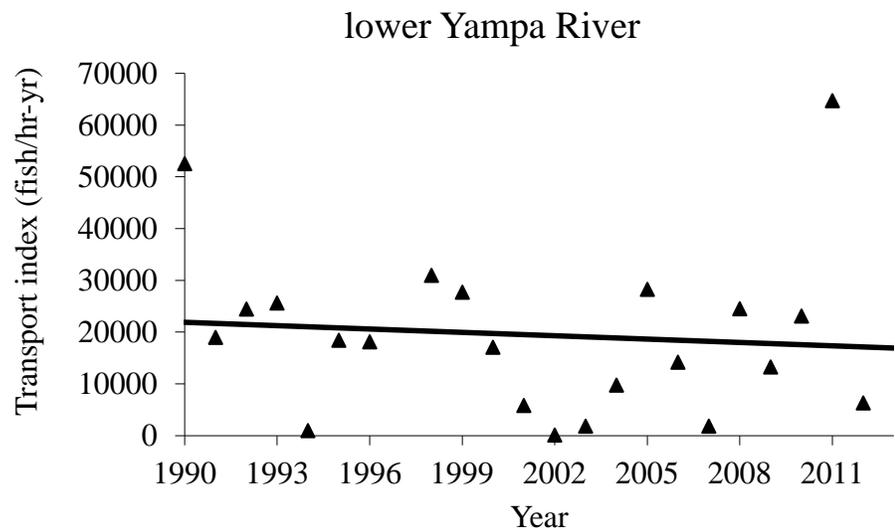


Figure 9. Transport index as a function of year, lower Yampa River (1990-2012, no sampling in 1997) and lower Green River (1991-1996, 1999). Transport abundance was estimated by dividing the number of larvae captured in three dawn nearshore drift net samples adjusted to an hourly rate by the estimated proportion of total discharge that was sampled.

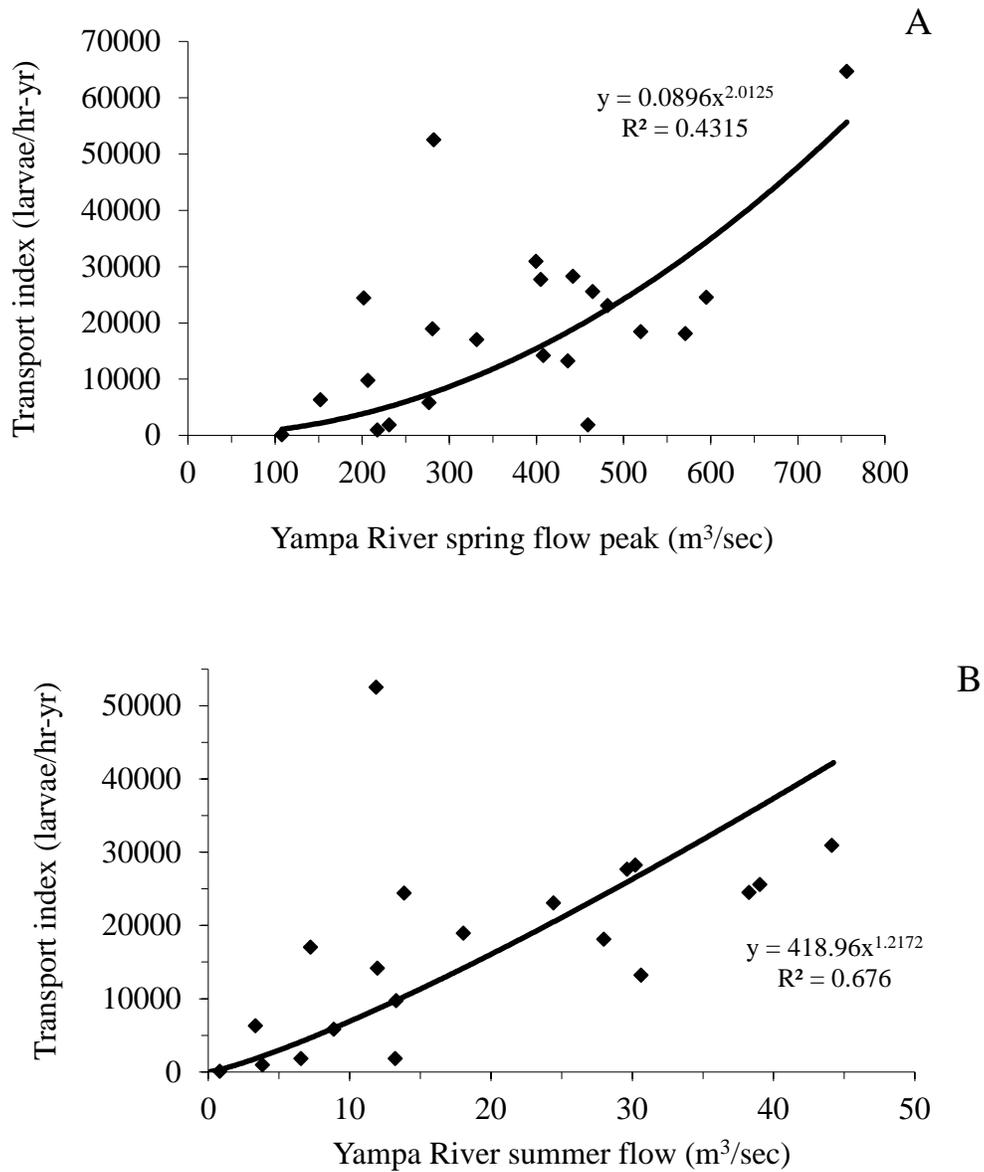


Figure 10. Colorado pikeminnow larvae transport index as a function of spring peak flow (panel A) and mean July-August summer base flow (panel B), lower Yampa River, Colorado, 1990-2012 (no sampling in 1997). Transport abundance was estimated by dividing the number of larvae captured in three dawn nearshore drift net samples adjusted to an hourly rate by the estimated proportion of total discharge that was sampled.

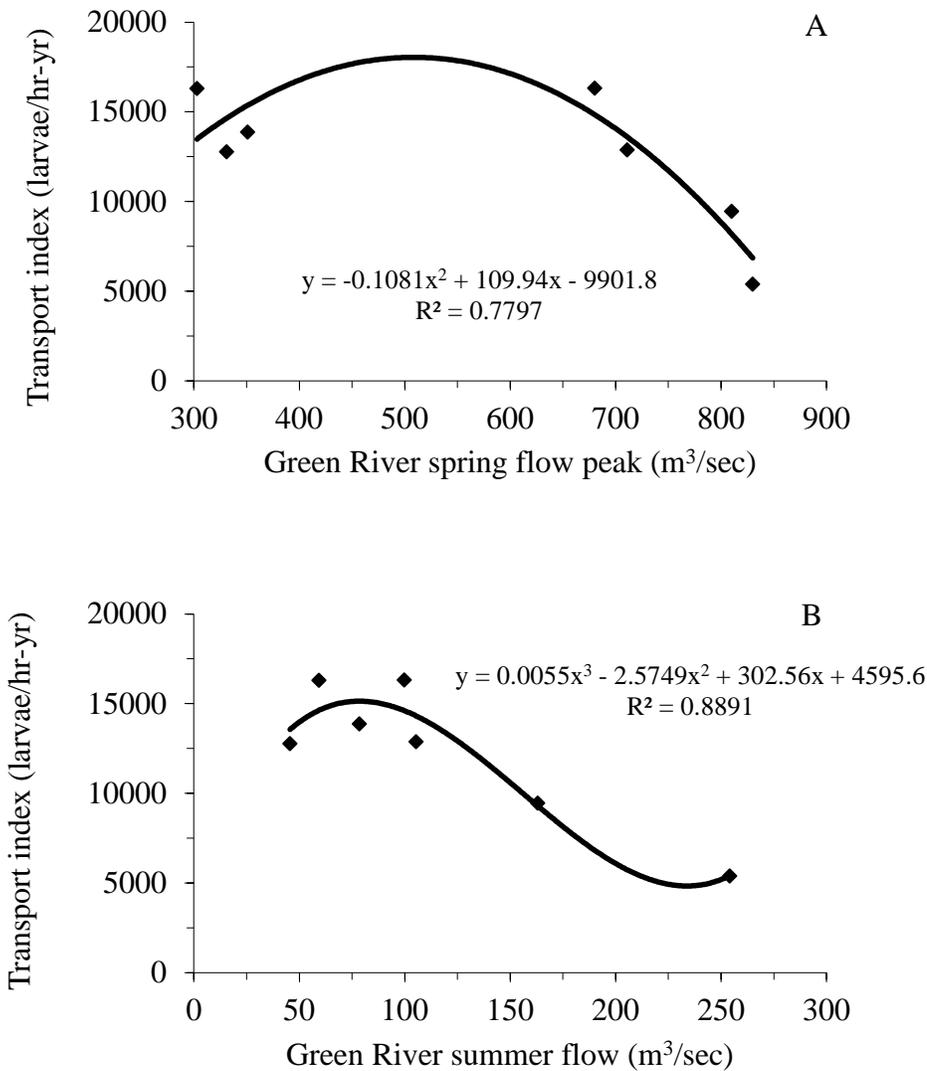


Figure 11. Colorado pikeminnow larvae transport index as a function of spring peak flow (panel A) and mean July-August summer base flow (panel B), lower Green River, Utah, 1991-1996, 1999. Transport abundance was estimated by dividing the number of larvae captured in three dawn nearshore drift net samples adjusted to an hourly rate by the estimated proportion of total discharge that was sampled.

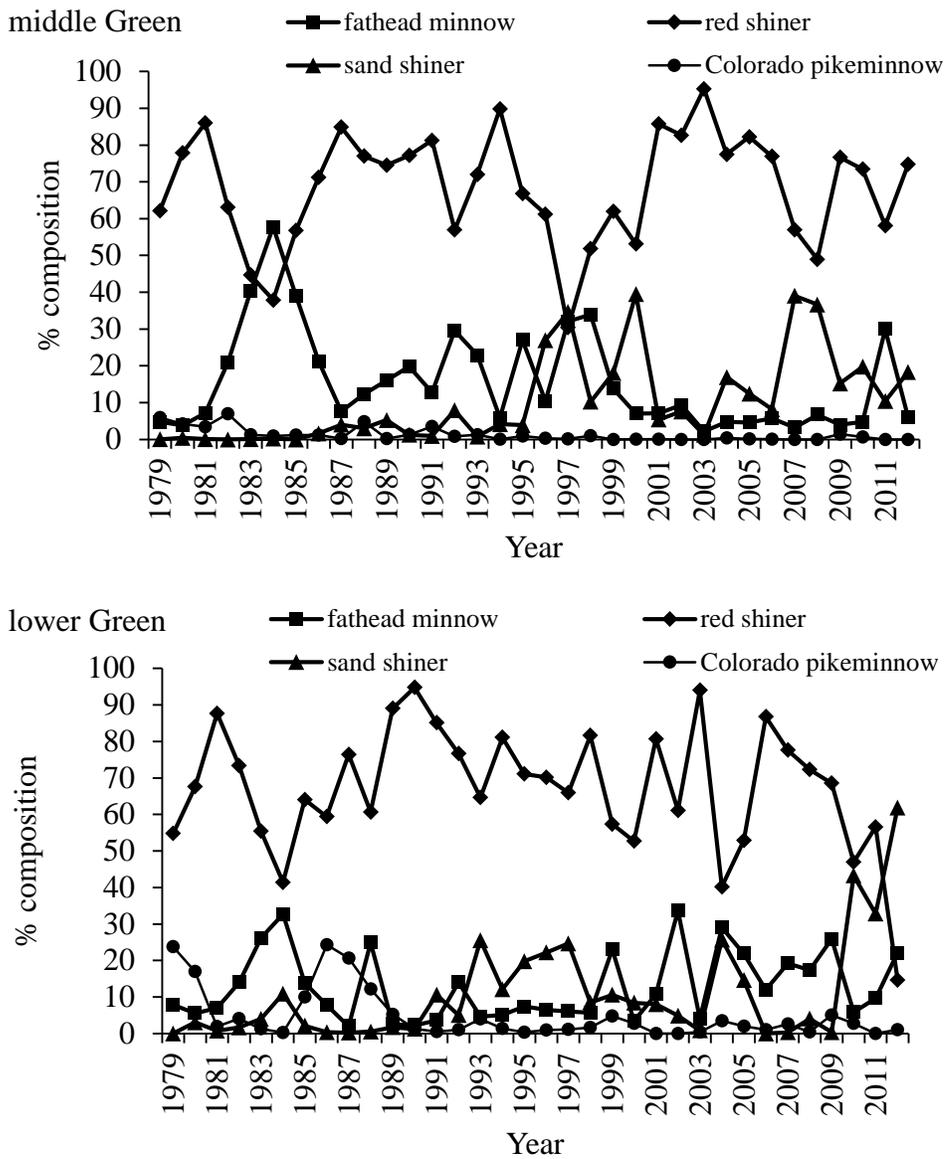


Figure 12. Abundance (% composition in samples) of native Colorado pikeminnow and nonnative red shiner, sand shiner, and fathead minnow in backwaters of the middle and lower Green River, 1979-2012.

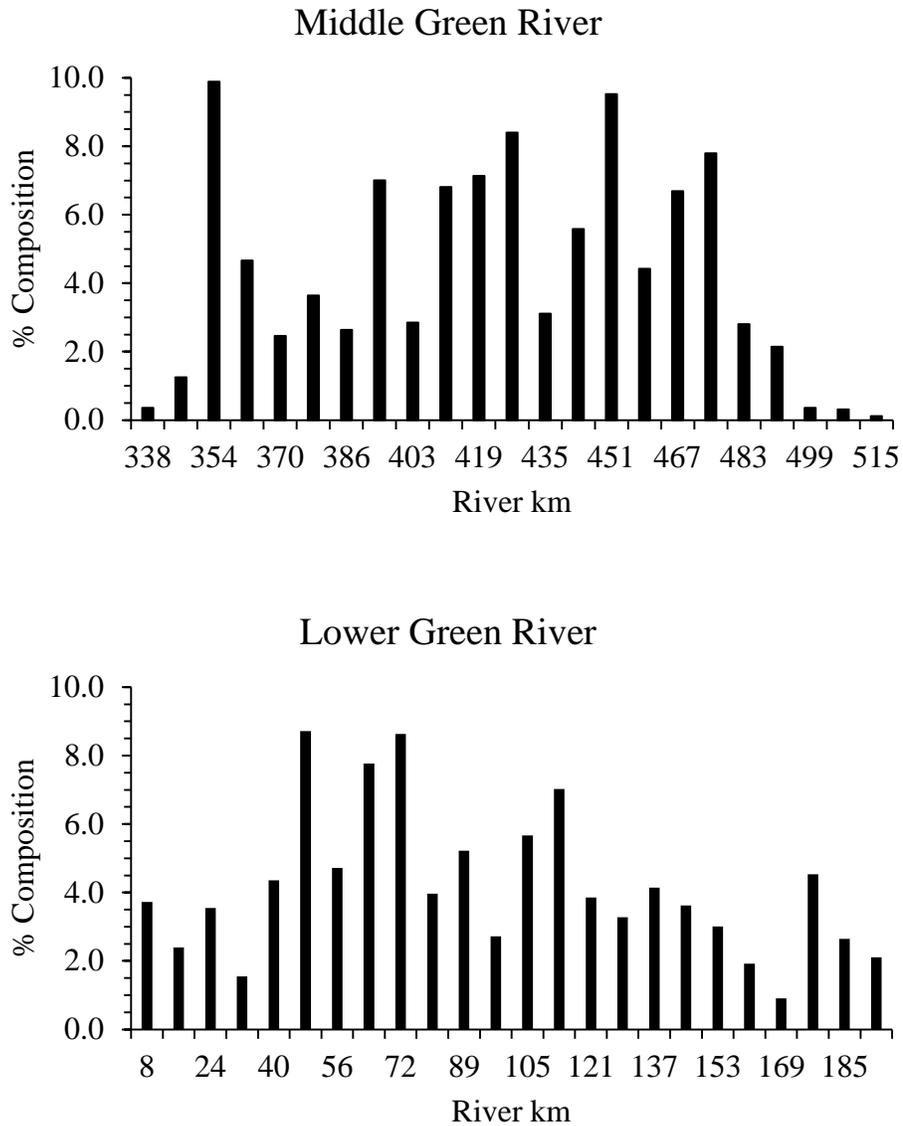


Figure 13. Distribution of age-0 Colorado pikeminnow by river km and abundance (as % composition) captured in backwaters of the middle and lower Green River 1979-2012. Totals of 6,068 and 14,231 age-0 Colorado pikeminnow were captured over the study period in the respective reaches.

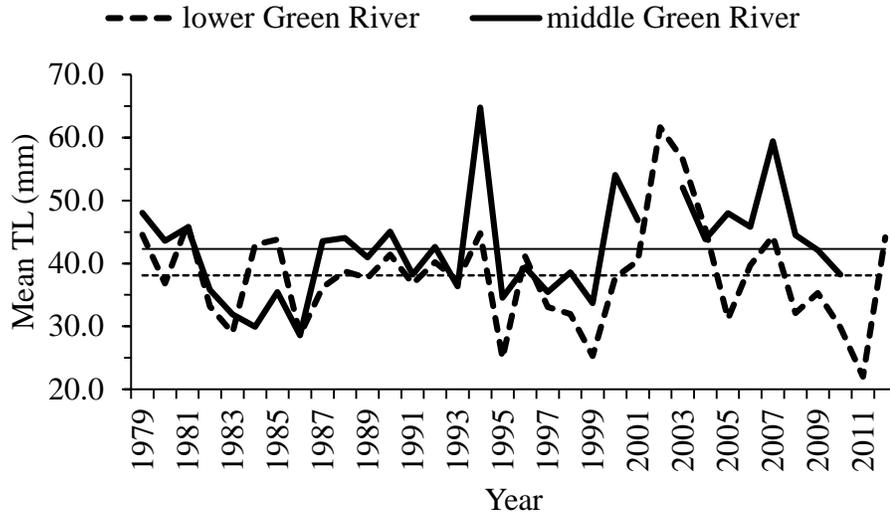


Figure 14. Mean total length (TL) of Colorado pikeminnow captured in backwaters of the middle and lower Green River 1979-2012. Horizontal lines represent mean TL for each reach over all years; no estimates available for the middle Green River in 2002 and 2011 because no pikeminnow were captured.

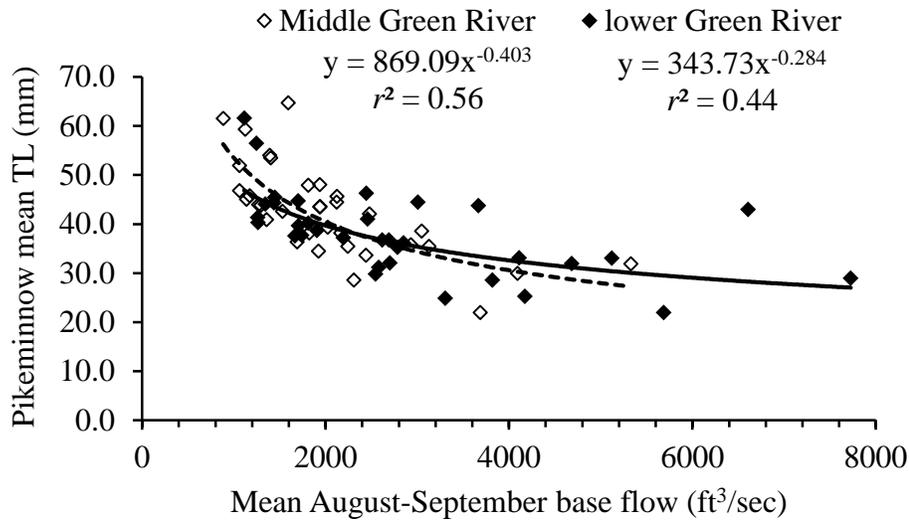


Figure 15. Age-0 Colorado pikeminnow TL (mm) as a function of mean August-September base flow in the middle (dashed line) and lower (solid line) Green River reaches, Utah, 1979-2012.

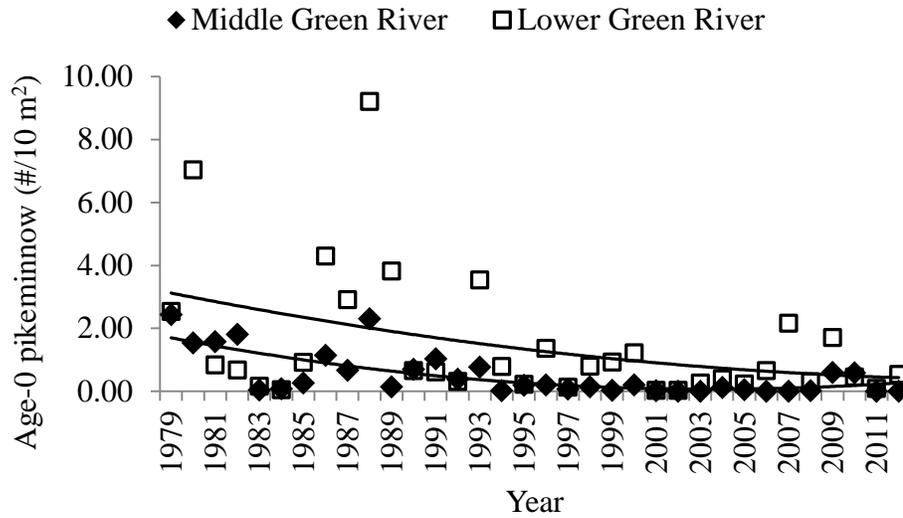


Figure 16. Mean annual density of age-0 Colorado pikeminnow captured in backwaters of the middle and lower Green River, 1979-2012. Density is number of pikeminnow captured in backwaters in the area swept by a seine.

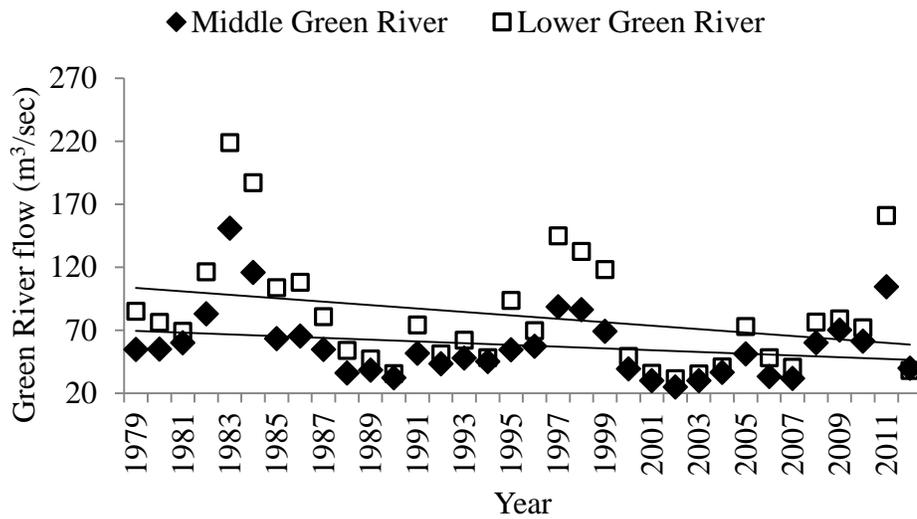


Figure 17. Mean August-September base flow of the middle (Gauge # 09261000) and lower Green River (Gauge # 09315000) reaches, Utah.

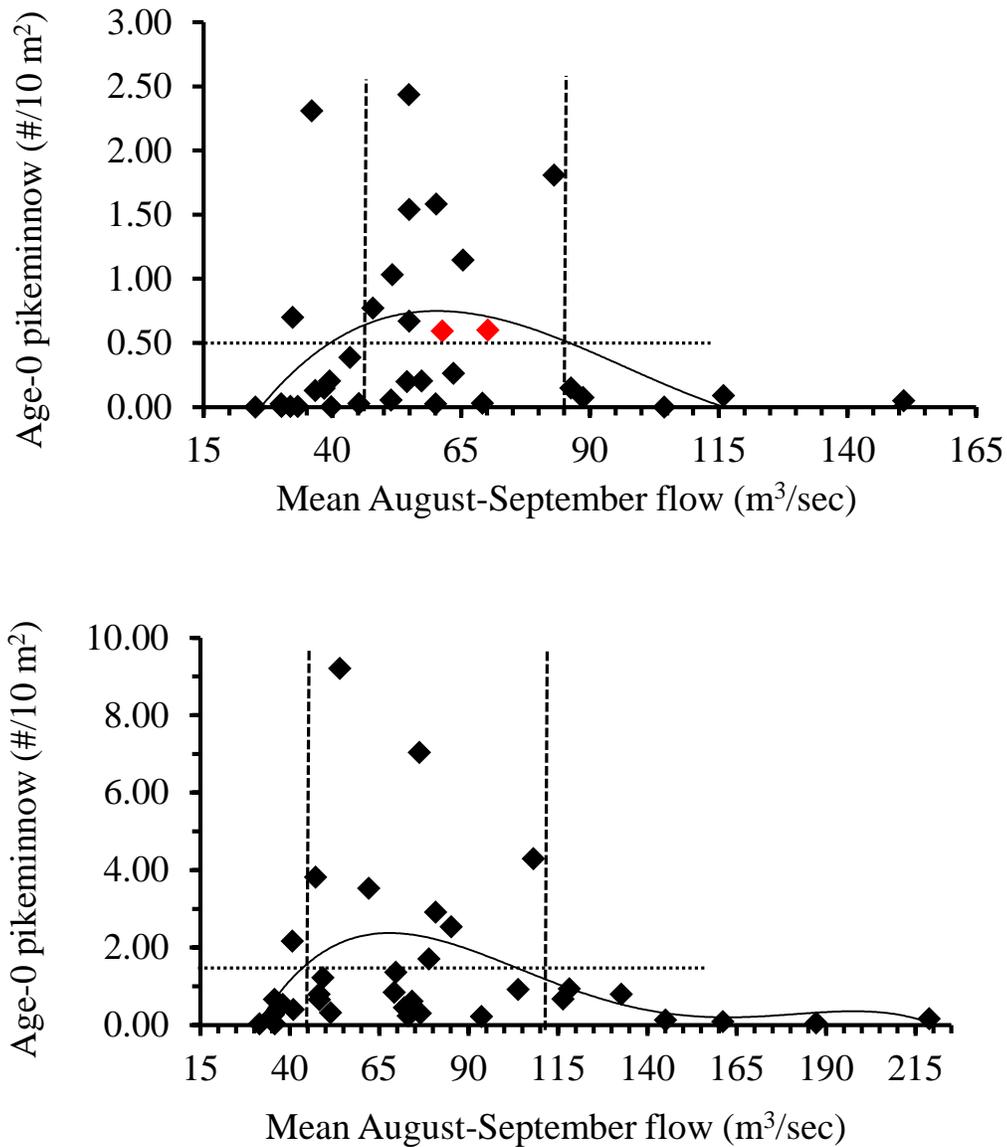


Figure 18. Mean annual density of age-0 Colorado pikeminnow captured in backwaters of the middle (upper panel) and lower (lower panel) Green River as a function of mean August-September flow, 1979-2012. Density is number of pikeminnow captured in area of backwaters swept by a seine. The middle Green River 2009 and 2010 data are red triangles. Dashed vertical lines encompass the flow ranges in each reach when the proportion of above average recruitment years is highest, and the horizontal dotted line is the mean density for the period of record. Polynomial regression relationships illustrate the dome-shaped nature of the recruitment relationship at intermediate flow levels. Green River flows were measured at the Jensen, Utah gauge (09261000) for the middle Green River reach and at the Green River, Utah gauge (09315000) for the lower Green River reach.

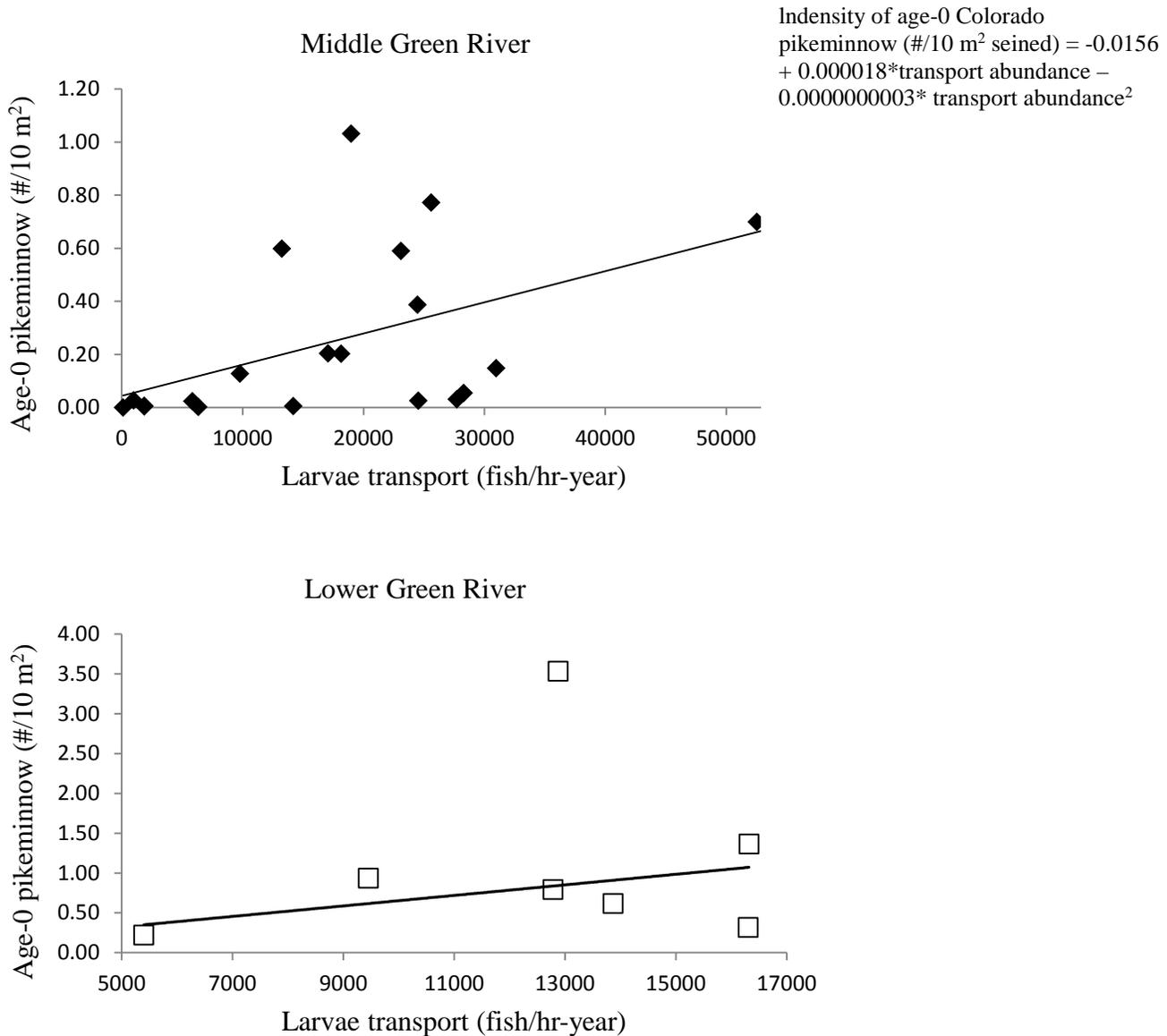


Figure 19. Mean density of age-0 Colorado pikeminnow captured in backwaters of the middle (upper panel) and lower (lower panel) Green River as a function of transport abundance of larvae. Density is number of pikeminnow captured per area of backwater swept by a seine. Larvae transport abundance was estimated by dividing the number of larvae captured (n = total in season) in three dawn nearshore drift net samples adjusted to an hourly rate by the estimated proportion of total discharge that was sampled. Years with high flows (> 85.0 m³/sec [3000 ft³/sec] in middle Green River and > 107.6 m³/sec [3800 ft³/sec] in lower Green River) were omitted because backwaters were few in those low recruitment years.

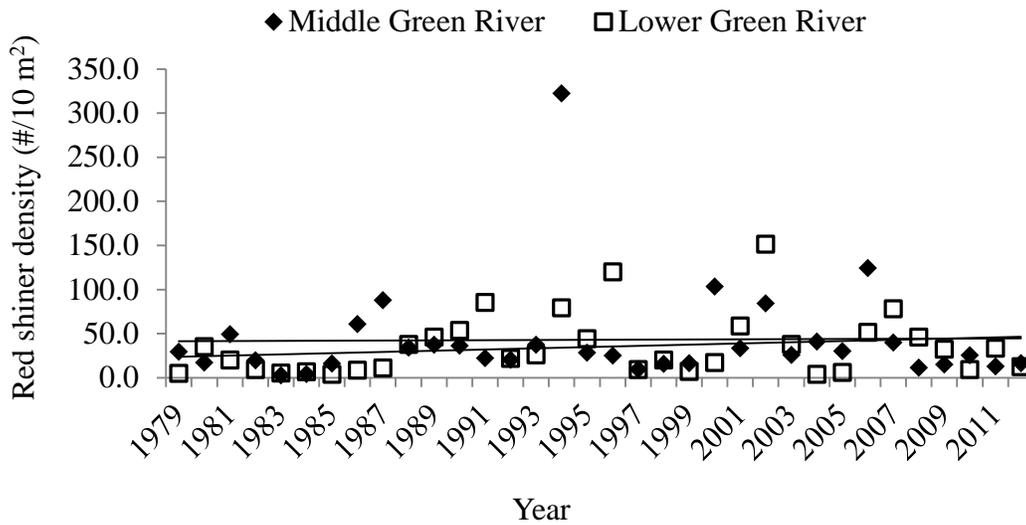


Figure 20. Red shiner density as a function of year in the middle and lower reaches of the Green River, 1979-2012.

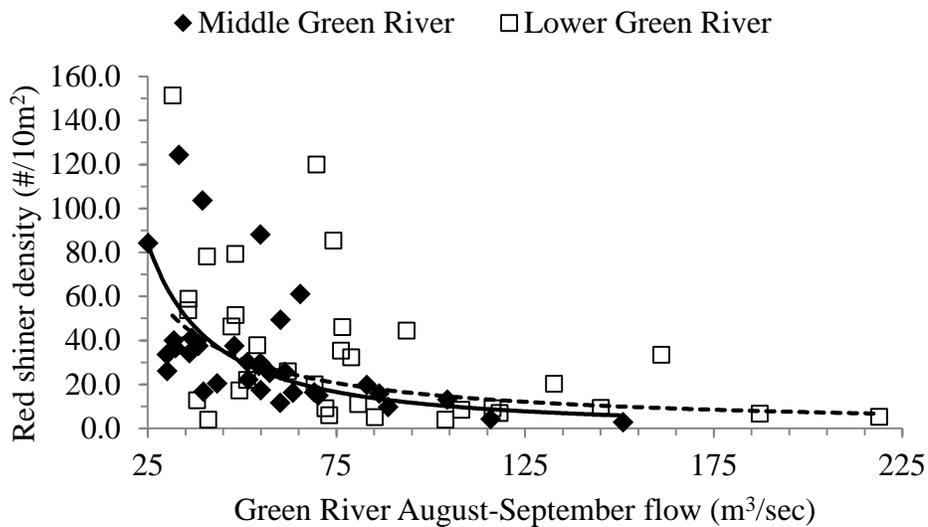


Figure 21. Red shiner density as a function of mean August-September flow in the middle and lower reaches of the Green River, 1979-2012. The 1994 middle Green River red shiner density estimate (323/10 m²) is not shown to better illustrate remaining data. Green River flows were measured at the Jensen, Utah gauge (09261000) for the middle Green River reach and at the Green River, Utah gauge (09315000) for the lower Green River reach.

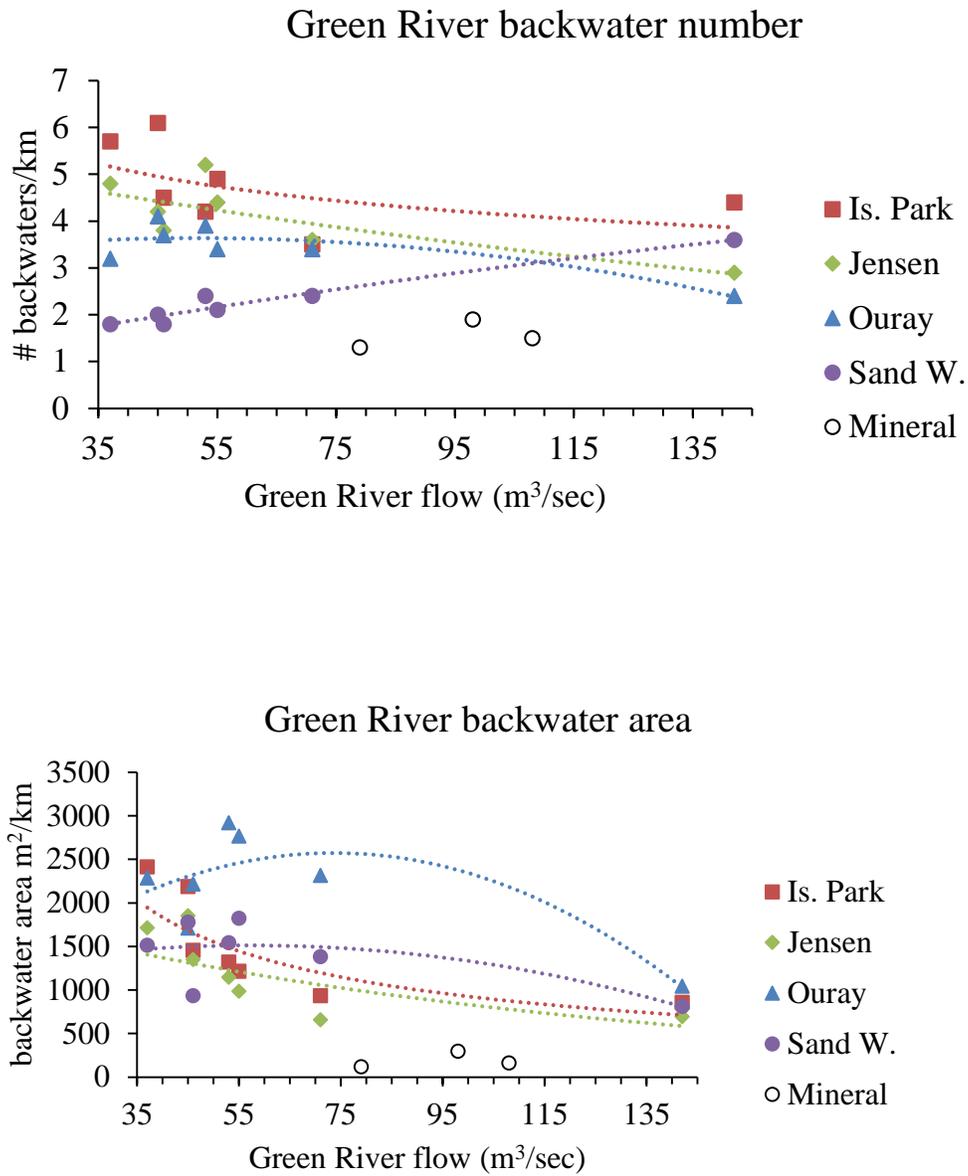


Figure 22. Green River backwater number (upper panel) and area (lower panel) per river km in Island Park, Jensen, Ouray, Sand Wash (all in middle Green River reach), and Mineral Bottom (lower Green River) reaches, 1987. Mineral Bottom data not fit with a line because only three occasions were measured. Green River flows were measured at the Jensen, Utah gauge (09261000) for all but the Mineral Bottom site, which were measured at the Green River, Utah gauge (09315000).

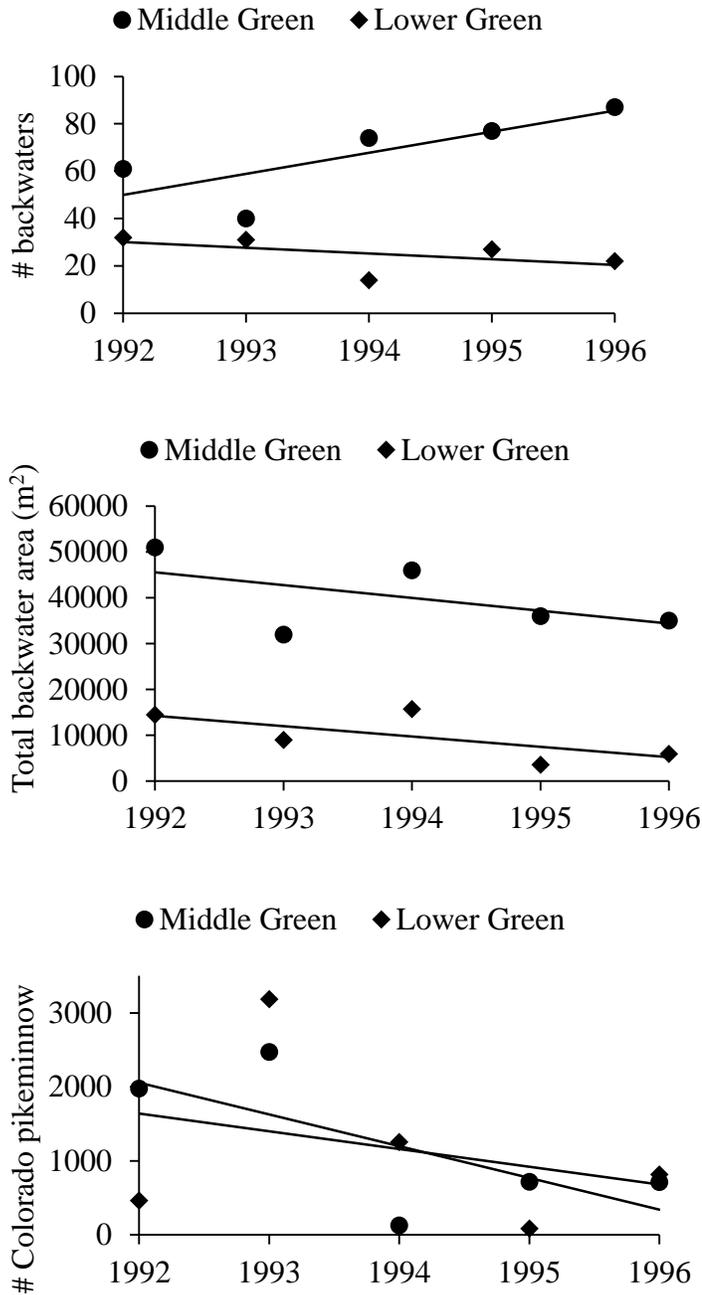


Figure 23. Number of backwaters (upper panel), total backwater area (middle panel), and estimated age-0 Colorado pikeminnow density (lower panel) in 16 river km reaches of the middle Green River (Ouray National Wildlife Refuge, RK 421.6-405.5), and the lower Green River (Mineral Bottom area, RK 91.7-75.7), Utah, 1992-1996. Similarity in Colorado pikeminnow abundance is due to higher density in the lower Green River in spite of lower number and area of backwaters.

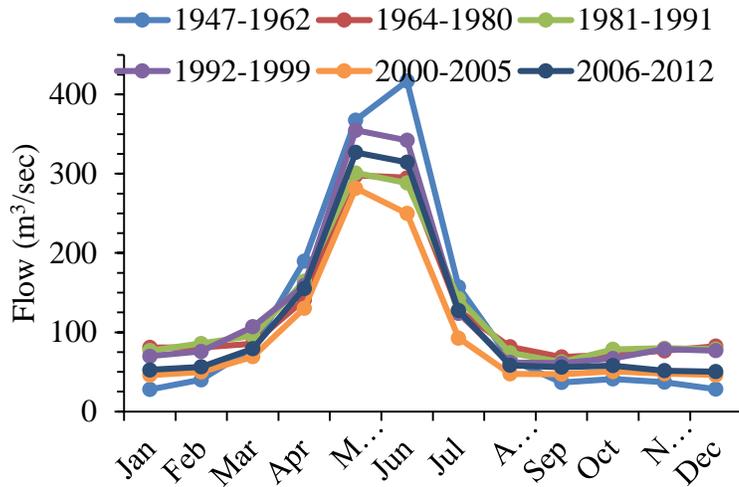


Figure 24. Mean monthly flow of the Green River (Jensen, Utah, gauge 09261000) in five time periods, the pre-dam period, 1947-1962, the post-dam period without a temperature control device installed, 1964-1980, the post-temperature control device period, 1981-1991, the first flow recommendations period, 1992-1999, and the later flow recommendations period, 2000-2012, which was approximately when the flow recommendations of Muth et al. (2000) were implemented. The 1964 data were not portrayed in the first year that Flaming Gorge Dam was being filled.

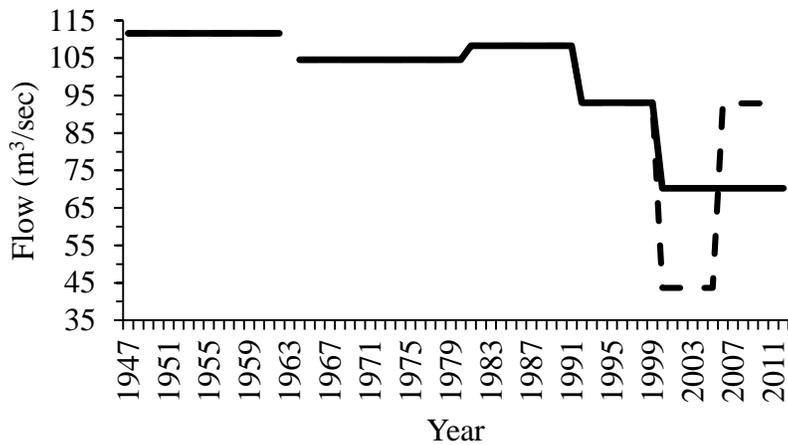


Figure 25. Mean July-August flow of the Green River (Jensen, Utah, gauge 09261000) in five time periods (solid line): the pre-dam period, 1947-1962, the post-dam period without a temperature control device installed, 1964-1980, the post-temperature control device period, 1981-1991, the first flow recommendations period, 1992-1999, and the later flow recommendations period, 2000-2012, which was approximately when portions of the flow recommendations of Muth et al. (2000) were implemented. The dashed line represents the 2000-2012 period broken into 2000-2005 pre-Record of Decision flows and 2006-2012 post Record of Decision period. The 1964 data were not portrayed in the first year that Flaming Gorge Dam was being filled.

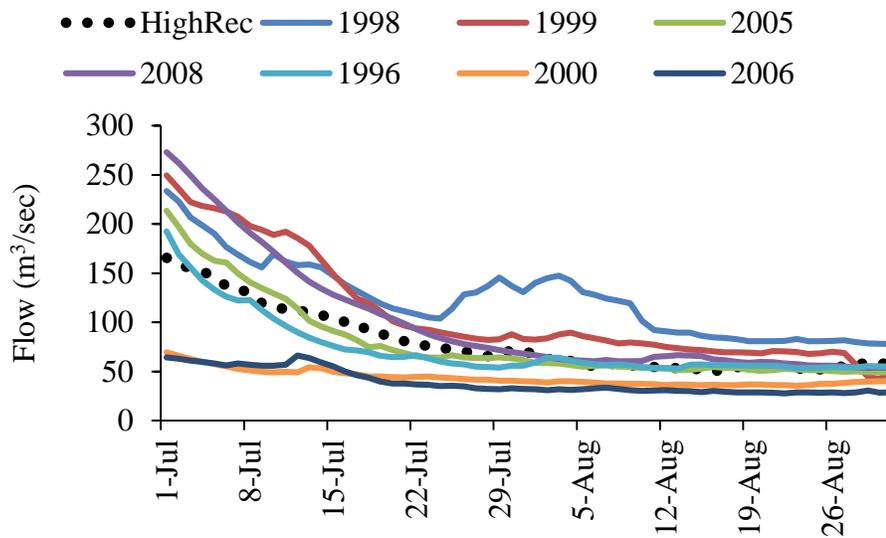
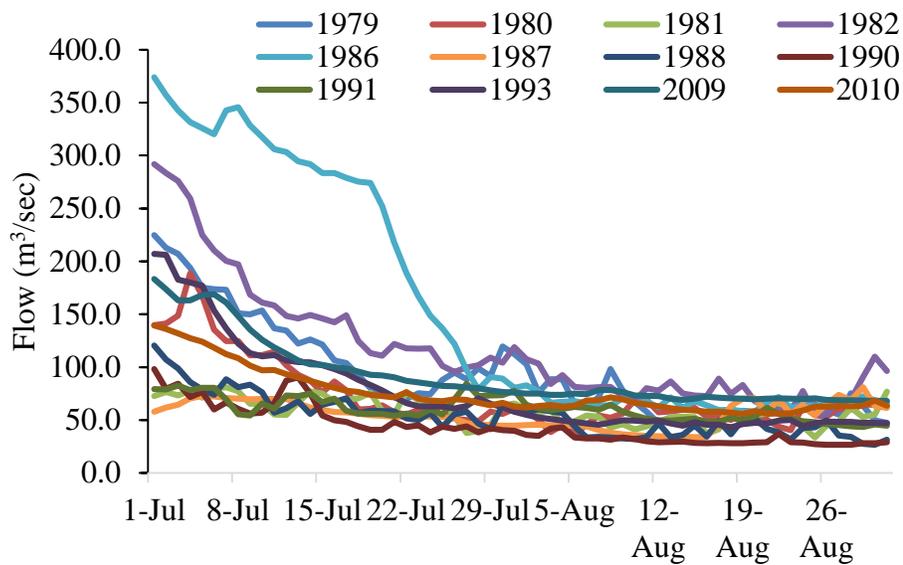


Figure 26. Upper panel shows variation of mean daily flow from 1 July-31 August of the Green River (Jensen, Utah, gauge 09261000) in 12 relatively high recruitment years for age-0 Colorado pikeminnow in the middle Green River in the period 1979-2012. Lower panel shows the mean daily flows for the 12 high recruitment years (HighRec, pictured in upper panel) and for seven other years that all had low recruitment.

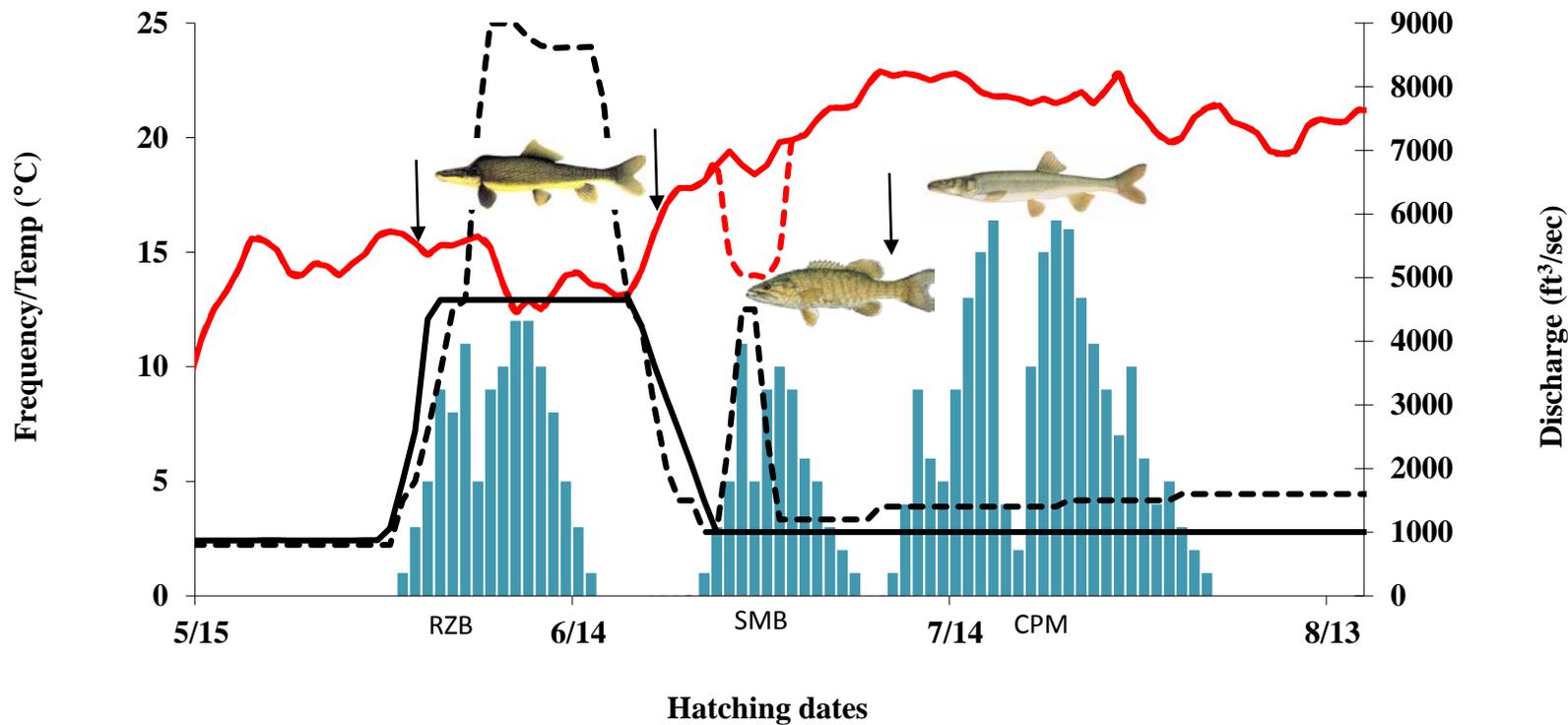


Figure 27. Conceptual diagram showing temporal sequencing of flow and water temperature regimes to benefit native razorback sucker and Colorado pikeminnow and disadvantage invasive smallmouth bass in the Green River, downstream of Flaming Gorge Dam. Hatching date initiation for each species (indicated 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.