

NATIVE FISH RESPONSE TO REMOVAL OF NON-NATIVE PREDATOR FISH IN THE YAMPA RIVER, COLORADO

By

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EXECUTIVE SUMMARY

Sampling was undertaken in a reach of the Yampa River (RK 161-199.6), near Maybell, Colorado, from 2003-2006 to determine native fish response in control and treatment reaches to removal of non-native predator fishes in treatment reach. Removal in the treatment reach focused on larger, age-1 or older smallmouth bass and northern pike in all years and was conducted under a separate study. In 2005 and 2006, increased effort was allocated to remove small-bodied age-0 smallmouth bass from the treatment reach. Sampling to understand native fish response to removal was conducted in both a 19.3 RK control reach and a 19.3 RK treatment reach and focused mostly on age-0, small-bodied native fishes, because response of that life stage would likely be easiest to detect. Yampa River habitat has changed since drought began in 2000, with lower stream flows and higher water temperatures. These factors were likely associated with a fish community shift since 1999 to increased abundance of smallmouth bass, and decreased diversity and abundance of native fishes in 2003-2006, in spite of predator fish removals. Sampling of 249 individual habitat areas, distributed among an array of habitat types in control and treatment reaches, showed that native mottled sculpin are no longer found in the study area despite presence of adequate riffle habitat. All other native fishes are now rare in mainstem Yampa River habitat and smallmouth bass is the dominant species captured in most years in both control and treatment reaches. No difference in presence or abundance of native fishes was detected in control and treatment reaches. Native fishes were captured in isolated pool habitat, in both control and treatment reaches, in significantly higher frequencies and abundances. In isolated pools, abundance of native fishes was negatively associated with presence and abundance of smallmouth bass. We also examined utility of smallmouth bass otolith analysis to better understand timing of spawning and growth rates of this species. Preliminary studies showed promise and additional information gathered under different flow

and water temperature conditions should provide a basis for understanding critical spawning periods and means to reduce bass survival. Otolith evidence also suggested fast growth of age-0 smallmouth bass to a predatory size in the Yampa River, which has negative consequences for native fish survival. Evidence we gathered collectively suggested that habitat changes during drought, and associated higher abundances of smallmouth bass, have resulted in reduced diversity, distribution, and abundance of native fishes in the study area. There are several hypotheses that may explain why native fishes have not responded to predator removal in the study area. The first is that an insufficient number of predator fish may have been removed. A second and associated hypothesis is that habitat change, in the form of altered flows and water temperatures, has differentially favored smallmouth bass and reduced native fishes during the recent drought period. However, a direct effect of habitat change on much reduced abundance of small-bodied native fishes seems unlikely. A third potential explanation for lack of a small-bodied native fish response to predator removal may be an insufficient number of adult native fish available to produce larvae. A final hypothesis for lack of small-bodied native fish response to bass removal in the treatment reach was compensatory increases in small bass survival because of large bass removal. However, this hypothesis is not supported by capture rates of age-0 smallmouth bass in control and treatment areas because capture rates in control areas are as high or higher than those in the treatment reaches in each year. We recommend continued sampling as currently conducted to monitor response of native fishes. More extensive and intensive predator removal and changes in environmental conditions may yield insights into native fish response. We also recommend investigating whether abundance levels of adult native fishes are sufficient to produce enough larvae to elicit a response to predator removal and discuss means to accomplish that. Additional investigations of early life history of smallmouth bass may assist with efforts to reduce their survival and recruitment.

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KEY WORDS

Fish removal, non-native predators, smallmouth bass, roundtail chub, flannelmouth sucker, bluehead sucker, speckled dace, mottled sculpin, drought, restoration, endangered fishes, water temperature, stream flow

INTRODUCTION

Introduction and establishment of non-native fish in western rivers of the USA is a major threat to conservation of native fish assemblages (Minckley and Deacon 1968, Stanford and Ward 1986, Moyle et al. 1986, Carlson and Muth 1989, Minckley and Deacon 1991, Olden et al. 2006). In the upper Colorado River Basin, non-native fish invasions began over 100 years ago, with introduction of channel catfish *Ictalurus punctatus*, common carp *Cyprinus carpio*, and salmonids for sport fishery purposes. In the 1960's, small-bodied species such as red shiner were relatively rare in the Green River sub-basin of the Upper Colorado River Basin (Vanicek et al. 1970), but by the 1970's were expanding rapidly (Holden and Stalnaker 1975a and 1975b). By the 1980's, red shiner was a dominant species in low-velocity habitat used by early life stages of native fishes, and potential negative effects of that species and other small-bodied fishes have been documented (Haines and Tyus 1990; Dunsmoor 1993; Ruppert et al. 1993; Muth and Snyder 1995; Bestgen et al. 1997; 2006a). More recently, piscivores such as smallmouth bass *Micropterus dolomieu* and northern pike *Esox lucius* have established and are common in the lower Yampa River and the upper and middle Green River basins (Anderson 2002, 2005; Bestgen et al. 2006b; Finney 2006).

The predatory threat of these large-bodied taxa is substantial and programs for their control via mechanical removal have been implemented in different rivers of the upper Colorado River Basin. However, effects of removal on restoration of native fishes is unknown. Estimating the response of the native fish community to predator removal is needed to understand if removal programs are having the desired effect. Therefore, the goal of this project is to document fish community changes in response to predaceous fish removals in a reach of the Yampa River, Colorado.

Specific objectives necessary to achieve the goal for Yampa River fish removal evaluation studies are as follows:

1. Select treatment and reference areas for study.

2. Assess abundance of predators in treatment and reference reaches to determine removal effects.
3. Implement removal of smallmouth bass and northern pike in treatment reaches in spring (mostly conducted in a different study).
4. Estimate response of native fishes in autumn after spring-summer predator removal.

STUDY AREA

The Yampa River drains mountainous and high desert portions of south-central Wyoming and northwestern Colorado and is the largest tributary of the Green River. The mainstem Yampa River begins in Colorado and flows west from near Steamboat Springs, CO, downstream to the Green River confluence in Dinosaur National Monument. The main study area was in the vicinity of Little Yampa Canyon, just downstream of Craig, Colorado. The length of the study area expanded over the study period from 19.4 RK in 2003 to 38.6 RK in 2006 (RK's 161-199.6). The original 19.4 RK study area reach had a 9.7 RK upstream treatment and a 9.7 RK downstream control reach. Non-native fish predators were removed from the treatment reach in spring and summer (J. A. Hawkins, RIP annual reports). The length of each of the treatment and control reaches was doubled in 2004 and reach positions were swapped, with the treatment reach extended downstream and the control reach extended upstream by 9.7 RK each. Thus, each reach was then 19.4 RK (12 river miles) long. This was done because movement of tagged smallmouth bass among the smaller treatment and control reaches was substantial.

Each of the treatment and control reaches was geomorphically similar because portions of each were within Little Yampa Canyon, and portions were in less constrained valley reaches. In the late summer and autumn low-flow sampling season, habitat consists mostly of low-velocity pools separated by shallow, higher-velocity riffles. Substrate is typically a mix of boulder, cobble, gravel, and sand in low velocity areas, and cobble and gravel in riffles. Backwaters and isolated pools are created mostly by cutoff high-flow side channels and are shallow to deep, with cobble, gravel, and fine-grained substrate.

METHODS

Fish removal studies background.— Although not specifically part of this study (see Hawkins 2005, 2006), the structure and effort allocated to predator fish removal in the study area is detailed below to assist the reader with understanding important aspects of the experimental design for this study. In 2003-2005, smallmouth bass sampling was stratified by treatment and control reaches. The first sampling pass was typically a marking pass for northern pike and smallmouth bass and recapture data from subsequent passes were used to conduct abundance estimates for those species by reach. Smallmouth bass captured after the first pass in the treatment reach were removed from the river but in the control reach, bass were released alive. Northern pike were removed from all areas after marking passes were completed (e.g., no control reach). Removal sampling was mainly directed at larger-bodied age-1+ smallmouth bass and pike. In 2006, the entire 38.6 RK study area was a removal (treatment) area for bass as well as northern pike. This was done because smallmouth bass movement was extensive within the shorter control and treatment reaches, such that removal efforts were confounded.

The control-treatment aspect of this study was maintained by additional removal of small-bodied smallmouth bass (mostly age-0, some age 1 bass) and other predators from the treatment reach in late July through early September, beginning in 2005 and 2006 (Hawkins 2005, 2006). This additional removal was the result of insufficient reductions of larger-bodied smallmouth bass that would subsequently spawn and produce large numbers of small-bodied smallmouth bass. Because we thought a response to non-native predator removal would be first and most easily observed in small-bodied native fishes, and that small-bodied bass were mostly likely the strongest predatory influence on small-bodied native and other fishes, increased removal of small-bodied bass seemed a logical addition to achieving study objectives. This logic also led us to focus exclusively on sampling small-bodied fish to document response to non-native fish removals.

Small-bodied smallmouth bass removal in 2005 and 2006 in the 19 RK treatment reach was mainly with a crew of four or five and a 10 m-long electric seine (Hawkins 2005, 2006).

Most habitat in the treatment reach suitable to support small-bodied smallmouth bass was sampled on three sampling passes conducted from late-July/early August to early September, each pass taking about 9 days to complete. That period was targeted for removal because young smallmouth bass that had hatched in late June through July were of a size sufficient for efficient capture using the electric seine. Main areas sampled were shallow, had low-velocity, and were typically shorelines of pools and runs with cobble or large substrate. A sampling pass was also completed during this time frame in the control area so that small-bodied smallmouth bass abundance could be compared to that in the treatment area.

Native fish evaluation sampling.-- Sampling for this study typically began by early to mid-September and extended into late-October until the river froze. In each year, three to four sampling trips of 7 to 9 nine days each were conducted, and similar per trip sampling effort was usually expended in the control and treatment reaches. Sampling in both reaches during each pass would reduce confounding of comparisons of fish abundance through time if river-wide changes in water temperature, flows, turbidity or other factors were responsible for changes which may otherwise be attributable to a reach (removal) effect.

We attempted to sample a mix of channel areas across the reaches, including backwaters, eddies, pools, riffles, runs, pools isolated from the main channel, and low velocity shorelines of pools and runs. The number of channel area types sampled was about proportional to their availability, except that most isolated pools were sampled because they were an unusual and biologically interesting habitat type. We attempted to sample a similar number of habitat areas in each of the control and treatment reaches, although differences in the mix of habitat types in each reach did not always allow for that. Some sites were accessible by vehicle but most were sampled from canoes during this low-flow autumn period. Low flows also limited access by rafts or other craft capable of transporting heavier boat-based electrofishers that may be more efficient at sampling the longer and deeper pools in some reaches. Anderson (2005) was able to sample a couple pools in the Duffy Tunnel area with a raft electrofisher. When we tried this gear type, we could not navigate longer river reaches, and found that water depth and limited mobility

made large-bodied fish captures difficult. Since we decided to focus mostly on small-bodied life stages anyway, this was not a serious impediment.

We experimented with a variety of gears in 2003 and 2004, including seines, backpack electrofishing (Coffelt and Smith-Root units), shore-based, generator-powered electrofishing gear (Smith-Root unit), and an electric seine. Comparisons of electrofishing gears and seines conducted in 2003 suggested that electrofishing captured more species ($N = 17$ + hybrid suckers) and individuals than seines ($N = 6$, Table 1). Seines were effective only in low-velocity habitat types with sand or silt substrate, a relatively rare substrate type in this river reach, and captured mostly sand shiners, a species that is typically found over sand substrate. Seines were less effective in areas with heavy cover (some pools) or coarse substrate where smallmouth bass tended to occur. In 2004, we made additional comparisons of backpack electrofishers, shore-based electrofishers, and electric seines. Each gear type captured about the same number of species, but backpack shockers were limited by the small effective sampling area and limited battery life. The large generator and heavy cable required by the shore-based electrofisher limited mobility of this gear type, even when floated in a barge, which was problematic in this mostly shallow and difficult-to-navigate river. The electric seine was a good compromise because it efficiently captured the species in the habitat type, was canoe-portable with the small and lightweight generator, had a large effective sampling area, was reliable and relatively efficient in open areas as well as those with cover. In 2005 and 2006, we sampled exclusively with the electric seine. A down side to the electric seine (or any electrofishing gear) was that fish capture success was reduced when the water was turbid. With a few exceptions (e.g., autumn 2004), water was generally clear.

At each habitat location, a discrete area was chosen (e.g., a shoreline reach, a single eddy, one pool) for sampling so fish abundance could be related to habitat type. Sampling usually proceeded in an upstream direction and the area was thoroughly covered by the sampling gear. All fish available for capture were netted during a timed sampling effort and the dimensions and characteristics of each habitat area were estimated. Fish were identified to species and if samples were large, a subsample of each was measured and weighed. If fish were relatively few,

all were measured and weighed. Special care was taken to identify potential catostomid hybrids. We identified these based on morphological characteristics of the mouth and body that were intermediate between putative parental types and on intermediate squamation patterns and scale counts in the lateral series (Hubbs and Miller 1953). Smallmouth bass captured in the treatment reach during native fish response evaluation sampling were also removed. Some of those smallmouth bass were also preserved in ethanol to provide specimens for studies of timing and duration of spawning via otolith analysis. Small numbers of voucher specimens of unusual (darters) or difficult to identify taxa (small suckers) were preserved and are housed at the Larval Fish Laboratory, Colorado State University.

Stream flow and water temperature data collection and presentation.—Most streamflow data were from the State Highway 40 bridge site near Maybell, CO, (U. S. Geological Survey gauge 09251000), which is near the downstream end of the study area.. Temperature data were collected at that site and at Government bridge (G. Smith, U. S. Fish and Wildlife Service, Denver, Colorado); USGS data were used to supplement Recovery Program information. We characterized flows in a historical period (1979-1999), which starts just after the time intensive sampling began in this area. We used water temperature data collected since 1991 to describe thermal conditions in pre-drought (1991-1999, 1996 missing) and drought (2000-2005, full 2006 data not yet available) periods. Flow and water temperature data from periods prior to 2000 are contrasted with that from drought years 2000 to 2006 to provide a perspective on differences in physical habitat among the periods and that available during fish sampling from 2003 to 2006.

Age-0 smallmouth bass age and growth.—In order to gain more information about smallmouth bass ecology in the study area, we undertook some preliminary studies of otolith microincrement structure. We initiated these studies with fish collected in 2005, with an eye towards demonstrating the utility of the technique and possible expansion to other river reaches and years if the technique is successful. Fish were randomly selected from a series of ethanol-preserved samples collected throughout the late summer and early autumn. Fish were measured and otoliths extracted, attached to microscope slides with glue, and polished on one side until increments were visible. Increments were counted via techniques in the published literature

(Graham and Orth 1987; Bestgen and Bundy 1998; Bundy and Bestgen 2001). Increment counts were verified with a second reader. In general, otolith increments were obvious and easy to read. Smallmouth bass hatching dates were estimated by subtracting age in days from the date of capture, assuming that the first daily increment was deposited at hatching. Per the literature, a 1:1 relationship between age in days and otolith microincrement count was assumed. Fish growth rate was estimated by subtracting length at hatching (mean literature value of 5.5 mm TL, Carlander 1977) from length at capture, and dividing by age in days.

Native fish evaluation data analysis.—Data analysis for this report was mostly via presentation of species richness and percent composition of fishes by control and treatment reach and habitat type. We rely on this approach because that is the main data presentation technique for historical data, with which we make comparisons to our own data. We also conducted logistic regression analyses to estimate presence of native fishes as a function of year of sampling, control or treatment reach, habitat type (isolated pool or main channel), and smallmouth bass presence and abundance. We also conducted logistic regression analyses to estimate proportion of native fishes as a function of year of sampling, control or treatment reach, habitat type (isolated pool or main channel), and smallmouth bass presence and abundance. Overdispersion in these models was corrected by multiplying the standard errors of the parameter estimates by the square root of the deviance. This approach gives more realistic and larger estimates of the variance and generally results in fewer significant statistical tests for estimates, so it is a conservative approach. Model selection was by AIC. Analyses were conducted with Statistical Analysis Systems software, Proc Genmod and Proc GLM (SAS, Cary NC).

RESULTS AND DISCUSSION

Yampa River stream flow and water temperatures.—We present extensive information on historical and present-day streamflow and temperature patterns of the Yampa River because we believe they are a significant influence on recent changes in fish distribution and abundance

patterns. The relatively unregulated Yampa River exhibits great seasonal flow variability, with a 20-yr mean flow peak (1979-1999) of about 223 m³/sec, and an associated base flow (August-February) of about 10 m³/sec (Fig.1). Mean daily flows during the summer (15 June to 15 September) were 43.7 m³/sec from 1979-1999. During the recent drought period of 2000-2006, annual peak flow exceeded the 20-year average peak in all years except 2002 and 2004, but base flows were much lower and began earlier (Figs 1-3). Flows during summer (15 June to 15 September) averaged only 17.5 m³/sec from 2000-2006 and generally reached seasonal lows by around the first of July rather than the first of August. An exception to this was 2005, when the onset and level of base flows closely mimicked the pre-drought 1979-1999 average.

Lower flows, and likely warmer air temperatures, in the 2000-2006 drought period, resulted in higher water temperatures in the Yampa River study area. For the period 1991-1999 (no data for 1996 were available), water temperatures warmed earlier (mid May, Fig. 4) than in the drought period 2000-2005 (a full summer of 2006 water temperatures was not yet available), and were substantially higher in summer, particularly June and July. For example, mean daily water temperature from 15 June to 15 September (a main period for fish growth) from 1979-1999 was 19.0°C compared to 20.5°C in 2000-2005. In every year in the 2000-2005 period, mid-June to late July water temperatures were substantially warmer and warmed earlier than in the 20-year 1979-1999 pre-drought period (Figs. 4-6). For example, average water temperature of the Yampa River was sustained at 16°C in the 1979-1999 by 25 June, whereas in the 2000-2005 drought period, water temperature was sustained or above 16°C by 14 June, 8 June, 29 May, 26 June, 14 June, and 22 June, in the years 2000 to 2005, respectively. Lower temperatures later in the year in 2003 and 2005 were associated with relatively high flows later in the year.

Yampa River habitat sampled.—A total of 257 individual habitat units was sampled during this study, 249 of which supported fish (Table 2). Number of habitat areas sampled was relatively low in 2004 because of effort expended in gear sampling efficiency evaluations and because of high flows through most of October. A few additional samples were collected with

2004 funds in spring 2005, but those results were incorporated into 2005 results. Effort in other years varied between 64 and 95 total samples.

Shorelines were the most common habitat type sampled, followed by backwaters, embayments, riffles, eddies, and isolated pools. Except for shoreline areas, deep runs and large pools were only rarely sampled because discrete habitat areas and samples were difficult to obtain. The total number of samples and total samples per habitat type varied among years, but was generally similar over the study period.

Yampa River fishes, species composition.—Composition of fishes in the Yampa River study area, 2003-2006, has changed since 1981-1982, based on comparisons of our samples to nearshore, low-velocity habitat seine and dip net samples of Wick et al. (1985) collected in 1981-1982 (Table 3), and Anderson (2002) in our study area. Of six native fishes historically found, we captured only four, bluehead and flannelmouth sucker, roundtail chub, and speckled dace. We did not capture mottled sculpin, a species taken regularly by Anderson (2002) as recently as 1999, even though we sampled several riffles that appeared to be suitable for sculpins. We also did not capture mountain whitefish, although mainstem electrofishing with boats captured that species in 2005 and 2006 (Hawkins 2005; 2006).

Many more non-native fishes occur in the study area in the recent period compared to 1981-1982. Only seven non-native fishes occurred in samples collected in 1981-1982, compared to 16 in the 2003-2006 period. Only red shiner, a rare species in 1981-1982, was not collected in 2003-2006.

Many of the species that have invaded the Yampa River and established since the 1981-1982 period are potentially piscivorous including black bullhead, black crappie, bluegill, northern pike, and smallmouth bass. Northern pike were likely in the study area in low numbers as adults in 1981-1982 (Nesler 1995), but are now found as YOY in low velocity habitats as well. Species such as pumpkinseed, largemouth bass, and brown trout are rare in the study area.

Species continue to invade the Yampa River study area. Iowa darter appears to be the most recent, being first detected in samples in 2003 in low numbers, but increasing since. Iowa darter was apparently not present in 2001 or before (Anderson 2002). Since it is distinctive,

relatively abundant and thus, not likely to be missed in sampling efforts, it likely represents a new introduction or invasion from upstream.

Yampa River fishes, relative abundance.—Relative abundance (% composition of a species in a sample) of species in the fish community in the study area also appears to have changed between the 1981-1982 period and our study, 2003-2006. Native species comprised about 27% of samples collected in 1981-1982 (23-32%, Wick et al. 1985) compared to 3.8% (1.3-9.2%) in 2003-2006 (Table 4). Roundtail chub were the most abundant native species present in each period.

Relative abundance of native fishes during this study was highest in 2004, when relative abundance of smallmouth bass (19.3%) was the lowest observed in the 2003-2006 period. This may also be related to the relatively high proportion of isolated pools sampled in 2004, relative to other years, where bass are less abundant.

Data from Anderson (2002, his Table 5) suggested that declines in small-bodied native fish abundance occurred relatively recently, based on seines samples collected in our study area. As recently as 1999, flannelmouth sucker (1%, n = 23 individuals), roundtail chub (34%, n = 733), and speckled dace (24%, n = 538) comprised 59% of the fish community (n = 2,272 fish collected) in low-velocity nearshore habitat seine samples. In 2001 in the same study area (no samples collected in 2000), no flannelmouth sucker or speckled dace were captured (n = 803 fish collected), and only 11 roundtail chub were captured, for a total native fish relative abundance of 1.4%. White sucker relative abundance also decreased from 21.9% in 1999 to 1.2% in 2001.

The main shift in non-native species abundances from 1999 to 2001 appeared to be related to smallmouth bass, which increased from 2.5% (n = 57) in 1999 to 67% (n = 540) in 2001 (Anderson 2002). Water temperatures in 1999 were relatively cool, but were warmer in 2000 and 2001. Anderson (2002) suggested that increased water temperatures may be related to the large increase in age-0 smallmouth bass abundance in 2001, and continued warm water temperatures in the drought period 2003-2006 may be contributing to continued high smallmouth bass abundance in the study area. The increase in relative and absolute abundance of

smallmouth bass from 1999 to 2001, and the decline in native fish in the same period, may also be related.

Other elements of the non-native fish community also changed between the two periods. In 1981-1982, redbreast shiners comprised about 50% of fish captured in all samples, and fathead minnows an additional 10-20%. Sand shiners were relatively rare, at 5% or less of the fish community. In 2003-2006, redbreast shiners were rare (0.3%) and sand shiners were the second-most abundant species (28.6%); fathead minnow remained relatively common (7%). Shifts in species composition of shiners may be related to shifts in water temperatures, which were warmer in the study area in the 2003-2006 period than historically occurred. Redbreast shiners are generally a more cool-water tolerant species occurring upstream in higher abundance and sand shiners are more common in downstream reaches with warmer water. Warmer water in recent years may be responsible for declines in redbreast shiner and increased abundance of sand shiner. Anderson (2002) also noted reduced abundance of redbreast shiner and increased abundance of sand shiner in samples collected in 1999 and 2001 in the same area. This upstream-downstream abundance pattern shift is repeated in the Green River where redbreast shiners were more abundant in cooler upstream reaches of Browns Park and upper Lodore Canyon and sand shiner is more abundant in the warmer reaches of lower Lodore Canyon and Whirlpool Canyon (Bestgen and Crist 2000; Bestgen et al. 2006b).

Yampa River fishes, control-treatment reach comparisons.—In the first two years of smallmouth bass removals, 2003 and 2004, a relatively small proportion of bass were removed, and all fish removed were age-1 or older (Hawkins 2005, 2006). For example, in 2003 smallmouth bass were removed on only one of six electrofishing passes, with a total of 294 bass removed, or about 11% of the estimated population (estimated abundance of about 2500 fish \geq 150 mm TL). In 2004, abundance of smallmouth bass \geq 150 mm TL in the treatment reach of the study area was estimated at 1,325 (CV = 30%); 1600 smallmouth bass of all sizes were handled in the treatment reach in 2004 and 919 of those were $>$ 150 mm TL and were removed. Thus, the 2004 removal rate was about 69% for that size group.

Greater numbers of smallmouth bass were removed in 2005 and 2006, due to greater effort. Years 2005 and 2006 were also the first years of removal of age-0 smallmouth bass from the treatment reach (Hawkins 2005, 2006). In 2005, an abundance estimate of 1,223 smallmouth bass ≥ 150 mm total length (CV = 18%, 2-pass capture-recapture estimate) and a removal of 1,404 bass suggested a removal of $> 100\%$ of the population with boat electrofishing over eight removal passes. Another 848 bass were removed that were < 150 mm TL. Many additional fish may have immigrated into the study reach due to escapement of smallmouth bass from Elkhead Reservoir or movement from other adjacent reaches, which is a likely explanation for the number of fish removed being greater than the estimated abundance. Evidence of escapement of fish from Elkhead Reservoir is based on recapture of tagged fish that were moved from the Yampa River to the reservoir in prior years or the same year, and were recaptured in the study area. The hypothesis of fish immigration into the study area was also based on an abundance estimate over 5-passes of 2,846 (CV = 11%), which occurred during the time when bass likely immigrated into the area. A large influx of bass into the study area would result in an inflated estimate, based on a lowered proportion of marked fish that were recaptured in later passes after fish had moved in. It is also possible that abundance estimates were biased low.

In 2005, an additional 9,528 small-bodied smallmouth bass (most age-0) were removed by electric seining efforts from late-July to early September. We do not know what proportion of smallmouth bass were removed because there was not an accompanying abundance estimate. Age-0 smallmouth bass abundance in control and treatment reaches started at low levels in mid-July based on electric seine sampling results (Fig. 7A). Mid- to late-July was about the time smallmouth bass finished reproduction in that relatively high and cool flow year (KRB, unpublished otolith aging information). Bass abundance in samples (CPUE) increased rapidly by late August to early September in control and treatment reaches. Smallmouth bass abundance in the treatment reach never achieved the level that they did in the control reach, perhaps because of continuous removals. Smallmouth bass abundance in the control reach remained high and constant through late September, but declined sharply in the treatment reach, a difference that is likely due to removal efforts. Between late September and mid-October, smallmouth bass

abundance in the control reach also declined rapidly, perhaps due to mortality, movement out of relatively shallow and colder, low-velocity areas that we sampled, or due to increased turbidity. However, control reach bass abundance was still more than two times that of the treatment reach. Treatment reach smallmouth bass abundance in mid-October was similar to that in late September.

In 2006, smallmouth bass abundance was estimated at 1,347 fish \geq 150 mm TL; 642 of those fish were removed from the treatment reach of the study area with boat electrofishing over six removal passes, a removal of about 48% of the population (Hawkins 2006). An additional 7,909 small-bodied smallmouth bass (most age-0) were removed by electric seining efforts from late-July to early September. Again, we do not know what proportion of smallmouth bass were removed because there was not accompanying abundance estimate. Age-0 smallmouth bass abundance in samples in the treatment reach started at a low level in late-July based on electric seine sampling results (Fig. 7B). Bass abundance increased rapidly by mid-August, and was about two times as high in the control reach as in the treatment reach. By late September, smallmouth bass abundance in control and treatment reaches declined, but smallmouth bass abundance in the control reach was still more than twice that of the treatment reach in October.

Over the 2003-2006 period, smallmouth bass removals via boat electrofishing were sometimes large, but the treatment effect for these larger bass was not sustained because bass abundance was high in the beginning of each spring removal period ($>$ about 1,300 fish \geq 150 mm TL, Hawkins, 2005, 2006, 2007). In 2005 and 2006, removal of age-0 smallmouth bass in the treatment reach was also substantial, and levels in the control reach were often twice as high as that in the treatment reach. Declines in abundance did not occur until relatively late in September, and there was also a large seasonal component in each reach, as age-0 bass abundance apparently declined in both control and treatment reaches. Consistent declines in each reach suggest mortality of age-0 bass, reduced capture probability, or both.

Number of fish captured in control and treatment reaches varied among years but was consistent between the reaches within years (Table 5), reflecting a similar number of habitat areas sampled in each reach (Table 2). The percentage of native fish in samples was consistently

low compared to historical samples and showed no consistent pattern between control and treatment reaches. Only in 2003 was the percentage of native fish substantially larger in the treatment reach than in the control reach (5.1 % vs 1.2 %), but that was in a year when nearly no fish removal occurred in the treatment reach and when most native fishes in the treatment reach occurred in isolated pools, a special habitat type. Native fish abundance in 2004 was highest in the entire study period 2003-2006, and was consistent in control and treatment reaches at 9% and 9.7%, respectively. This was also the year when smallmouth bass relative abundance was relatively low in the study area, 21.5% in the control reach and 17.1 % in the treatment reach.

Native fish abundance was lower in 2005-2006 than in 2003-2004 throughout the study area. In 2005, native fish comprised 2.2% of the fish community in the control reach, and 0.3% in the treatment reach. This pattern of reduced native fish abundance in 2005 and 2006 compared to 2002 and 2003, and reduced abundance in treatment reaches compared to controls, is opposite the pattern one might expect if removal of predaceous smallmouth bass was having a positive effect. Ironically, this occurred in the first year, 2005, that substantial removal of age-0 (with electric seine) and larger smallmouth bass both occurred. Smallmouth bass abundance was much higher in the control reach (55.3%) than in the treatment reach (29.2%), perhaps due to removal efforts for those age-0 fish. Non-natives sand shiner and white sucker were more abundant in treatment reaches than in the control reach in 2005, perhaps indicating a release from predation due to the effect of removal smallmouth bass. Reductions in relative abundance of age-0 native fish in the reach in 2005-2006 was consistent with reductions of larger-bodied native fish and increased abundance of smallmouth bass in boat electrofishing samples in the same period (J. Hawkins, 2007 draft report).

In 2006, a pattern similar to that for 2005 was observed as native fish comprised 2.3% of the fish community in the control reach, and 0.3% in the treatment reach. However, smallmouth bass abundance was higher in the treatment reach (46.2 %) after substantial removals had occurred than in the control reach (37.4%). Years 2005 and 2006 had the highest composite abundance of smallmouth bass in the study area, regardless of treatment or control reach, which was surprising given substantial efforts to remove age-0 and larger smallmouth bass in these

years compared to 2003 and 2004. Sand shiner was more abundant in the treatment reach than the control reach in 2006, and white sucker abundance was about equal. High abundance of black bullhead that occurred mainly in the control reach was unusual and most were captured in a few samples.

Continued low native fish abundance, and inconsistent response of native fishes and selected non-native taxa to smallmouth bass removal, suggested that removals conducted at the present levels are not having the expected effect. Mechanisms may include predation rates that are too high to allow recruitment, changes in habitat quality, or levels of reproduction by adult fishes that are too low to permit sufficient recruitment to occur. It appears that smallmouth bass abundance levels in the main channel of the Yampa River remain too high, even in the relatively low abundance year of 2004 (about 19 % relative abundance), to allow recruitment of native fishes at levels that were observed as recently as 1999.

Yampa River fishes, isolated pool and main stem river comparisons.—Support for the thesis that smallmouth bass may be negatively impacting abundance of native fishes in low-velocity habitats comes from comparison of the few places where native fishes do exist in the study area in relatively high numbers, isolated pools, to places where native fishes do not survive, the main channel in both the control and treatment reaches. A total of 19 isolated pools were sampled in the study area in the four years of study, 10 in the control reach and 9 in the treatment reach (Table 2).

In general, the proportion of samples from isolated pool samples were low, with the exception of 2004, when isolated pools were relatively common and fewer main channel samples were obtained. Native fishes were more common in isolated pools than in the main channel (Table 6). For example, 13 of 19 (68 %) isolated pools that held fish supported native fishes, while only 50 of 230 main channel samples (22 %) supported native fishes. From 2003-2006, native fish relative abundance in isolated pools was 14%, compared to < 1% in the main channel. Conversely, mean relative abundance of smallmouth bass in isolated pools was < 5 %, but in the main channel approached 50 %.

Abundance of smallmouth bass in isolated pools was inversely proportional to abundance of native fishes. For example, mean native fish relative abundance in isolated pools averaged 16.7% (2.3 - 43.5 %, n = 10) of all fishes captured when smallmouth bass abundance was < 1% (mean = 0.2%), and was highest when bass were not found (Fig. 8). Native fish relative abundance averaged only 4.5 % (0 - 8.3 %, n = 4) when smallmouth bass abundance was > 10% (mean = 22%, 11 - 31%). Fathead minnow and white sucker abundance was also higher in isolated pools than the main channel, again perhaps indicating release from predation by smallmouth bass. These data suggested that native fishes and other small-bodied taxa could cohabit areas with smallmouth bass, but survived in higher numbers only when smallmouth bass abundance was quite low. Native fish abundance in isolated pools was still quite low compared to abundance in main channel Yampa River habitat as recently as 1999.

Yampa River fishes, statistical comparisons.—The patterns of native fish presence or absence in the Yampa River based on descriptive data from the main channel and isolated pools were supported by logistic regression analysis. The probability of native fish presence in a sample was significantly higher if it was from an isolated pool than if it was from the main channel habitat (Table 7, *Chi-square* value = 9.30; $p = 0.002$); the large chi-square value indicates this was, by far, the largest effect. Probability of finding native fish in the sample was also negatively associated (*Chi-square* value = 4.50; $p = 0.034$) with the percentage of smallmouth bass in the sample. Solving the equation in the table, assuming for simplicity that the percentage of smallmouth bass was zero, predicted that the probability (as a %) of finding native fish in the sample was 69% if it was from an isolated pool habitat. That probability was reduced to 29% if the sample was from a main channel habitat. Probability of native fish presence in a sample was not affected by whether the sample was from a control or treatment reach (*Chi square* value = 0.19; $p = 0.66$). One would expect a positive and significant association of native fish presence with the treatment reach if predator removal was having a significant and positive effect on survival of native fishes. The year effect was significant but was dropped here, and for native fish abundance analyses (just below), because it only demonstrated that the proportion of habitat areas that supported native fish varied by year (2003,

6 of 56; 2004, 9 of 20; 2005, 24/95; 2006, 25/78). The proportion was high in 2004 because we chose to sample relatively more isolated pools, places where native fishes tended to reside, and obtained relatively few samples in other habitat types.

Patterns of native fish abundance in the Yampa River were also supported by logistic regression analysis and showed essentially the same patterns as those for native fish presence. The proportion of native fish in a sample was significantly higher if it was from an isolated pool habitat but lower if it was from main channel habitat (Table 8, *Chi-square* = 197.2, $p < 0.0001$); the large chi-square value indicates again that this was, by far, the largest effect. Proportion of native fish in the sample was higher if smallmouth bass were absent in the sample (*Chi-square* = 18.4, $p < 0.0001$) but decreased as number of smallmouth bass in the sample increased (*Chi-square* = 3.9, $p < 0.049$). Solving the equation in the table, assuming that the sample was from an isolated pool with no smallmouth bass, predicted that the proportion of native fish in the sample (as a %) should be 15%. Note that the 15% value matches up well with previous descriptive data reported for isolated pools (e.g., 16.7% native fish in isolated pools where bass abundance was very low). Solving the equation in the table, assuming that the sample was from the main channel and bass were present ($n = 1$), predicted that the proportion of native fish in the sample (as a %) should be $< 0.1\%$. The proportion of native fish in a sample was not affected by whether the sample was from a control or treatment reach (*Chi square* value = 0.31; $p = 0.58$). Again, one would expect the proportion of native fish in samples collected in the treatment reach to be higher than in the control reach if treatment reach predator removal was having a significant and positive effect on survival of native fishes.

Most smallmouth bass and native fishes captured in isolated pools were age-0 fish, based on their size at capture. Higher relative abundance of native fishes in isolated pools could be a function of timing of reproduction relative to high flows. Areas that eventually become isolated pools may be available to fish in the main channel mostly during higher flow events relatively early in the summer, but are cut off only after native fishes invade these areas and are subsequently isolated. Perhaps the majority of smallmouth bass do not spawn in time to access areas that eventually become isolated pools, and thus, are relatively rare. It may also be that

isolated pools are not desirable habitat for smallmouth bass. Regardless, fish composition data from isolated pools supports the notion that native fish can survive in the areas with limited bass abundance, but in areas where smallmouth bass are abundant such as in main channels, native fishes do not persist.

Yampa River age-0 smallmouth bass age and growth.—Smallmouth bass sagittal otolith daily increments were obvious and generally easy to read, a trait that was enhanced by the large size of the otolith relative to cypriniform fishes. Limited smallmouth bass hatching in the Yampa River in 2005 began in mid-June and extended into late July, but the bulk of fish hatched from early to mid-July in about a 2-3 week period (Fig. 9). Regular spawning (about 5-8 d incubation time prior to hatching, depending on water temperature) began when water temperatures were consistently above about 16°C.

Smallmouth bass growth was water temperature dependent and typically very fast, even when water temperatures were cooler (Fig. 10). For example, fish collected in mid-August grew on average about 1.2 mm/d at those warm water temperatures. Even fish collected in late September, which experienced a warm summer and a cooler September period, grew at a rate of about 0.7 mm/day. These are very high growth rates, compared to native cypriniform fishes. For example, mean growth rates of Colorado pikeminnow larvae in laboratory studies and in backwaters of the Green River grew from 0.3-0.5 mm/day, under high growth conditions (Bestgen 1996, Bestgen et al. 2006a). Growth rates of razorback suckers are even lower (Bundy and Bestgen 2001).

Yampa River smallmouth bass hatching and growth rate information is specific to only 2005. This is especially true since we only examined a relatively small sample and because the thermal and flow regime of the Yampa River in 2005 was quite different than in other years in the recent period (see earlier figures). However, results of preliminary studies presented here showed that otolith information may be useful to identify the timing and duration of smallmouth bass spawning seasons in Upper Colorado River Basin streams. Collection of such data under a variety of flow and temperature regimes, including using data from historical bass samples, may be useful to be able to predict timing and intensity of spawning. This information will be useful

if efforts are undertaken to disrupt spawning and reduce survival of early life stages of smallmouth bass.

Fast growth of smallmouth bass observed in the Yampa River in 2005 suggests that smallmouth bass may be even more problematic than previously thought. This is because our unpublished simulations showed that age-0 smallmouth bass should grow fast enough in most years to grow to a size large enough to capture and consume most age-0 native fishes in the same summer. This should be true even if native fish hatched substantially earlier than smallmouth bass. Higher flows in non-drought periods and accompanying cooler water temperatures may partially ameliorate this situation by slowing growth of age-0 bass. It also seems clear that smallmouth bass abundance needs to be reduced in order to increase survival rate of native fishes. It is not clear if a return to more normal hydrologic conditions will restore native fishes now that smallmouth bass are so well established.

Yampa River fishes, hypotheses regarding native fish response.—There are several hypotheses that may explain why native fishes have not responded to predator removal (J. A. Hawkins, annual reports) in the study area. The first and most obvious explanation is that an insufficient number of predator fish may have been removed. Evidence from Anderson (2002) and our own isolated pool data suggest that in the recent past and now, that native fishes are able to survive in the Yampa River in certain situations. Those situations have a common factor, low or no smallmouth bass present. Even though present removal efforts are intensive and reasonably successful, many smallmouth bass still remain in the study area. It may be that removal efforts need to be increased both within the study area, and outside of it, to prevent immigration. It may also be that age-0 smallmouth bass reductions in the treatment reach happen too late in the year to benefit native fishes. However, first sampling to remove age-0 smallmouth bass occurs just after smallmouth bass swim-up. Further reductions in age-0 smallmouth bass abundance may also be realized if hydrologic conditions return to a non-drought state. Higher and cooler flows will likely reduce the suitability of the Yampa River for smallmouth bass and may act as a riverwide mechanism to reduce bass abundance.

A second and associated hypothesis is that habitat change, in the form of altered flows and water temperatures, has differentially favored smallmouth bass and reduced native fishes during the recent drought period. There is no doubt that warmer water temperatures and associated lower flows have benefitted smallmouth bass in the Yampa River (Anderson 2002; 2005). Warmer water and lower and earlier flow peaks has resulted in earlier bass spawning, longer growing seasons, and increased growth rates. Increased size of age-0 bass in summer has likely increased overwinter survival, which likely increases recruitment to the adult population.

Reduced habitat size apparently reduced biomass of large juvenile and adult native fishes and other taxa during this drought period in the Yampa River while smallmouth bass abundance increased (Anderson 2002, 2005). However, a direct effect of habitat change on much reduced abundance of small-bodied native fishes seems unlikely. Native fishes have tolerated flow and thermal regimes like the ones present in the Yampa River during these drought years throughout their history. If anything, warmer thermal regimes and increased low-velocity habitat would likely increase growth and abundance of small-bodied native fishes in the absence of smallmouth bass. A logical explanation for reductions in small-bodied native fishes are that changes in habitat allowed bass numbers to increase, and likely increased predation on small-bodied native fishes. This hypothesis is supported because native fishes were common just before age-0 smallmouth bass abundance increased in low velocity habitats between 1999 and 2001. Further evidence that suggests smallmouth bass as suppressing native fishes comes from isolated pools sampled in this study. Thus, habitat change affected age-0 native fishes indirectly by increasing predatory smallmouth bass abundance. Another direct mechanism for reductions of small-bodied native fishes may be competition with smallmouth bass. This hypothesis seems less likely given the high growth rates observed for bass, which suggest that resource limitation usually associated with competition, is not a factor.

Another potential explanation for lack of a native fish response to predator removal may be an insufficient number of adults available to produce larvae. This question is difficult to answer, because even though adults of each of the large-bodied species (flannelmouth and bluehead suckers and roundtail chub) occur in the study (J. Hawkins draft report, 2007), what a

“sufficient” number constitutes is unknown, and is likely to remain so. We do know that native fish are reproducing in the study area because we capture age-0 individuals in main channel and isolated pool habitat each year. A possible means to test the veracity of this hypothesis is to supplement early life stages of native fishes in various habitat types in both the control and treatment reaches. Such fish could be marked via tetracycline immersion to differentiate them from wild-produced fish, and changes in their relative abundance in samples compared to previous years, and between control and treatment reaches, could be tracked. Such information may provide data to determine if an adequate number of large-bodied adult fish are present to produce larvae in a number sufficient to benefit from predator fish reductions in the treatment area. Small-bodied native species such as mottled sculpin and speckled dace may need to be added as adults to test the sufficient reproduction hypothesis for those species.

A final hypothesis for lack of small-bodied native fish response to bass removal in the treatment reach, and one that is related to the first hypothesis discussed, is related to our own actions of removing bass. Removal activities reduce the size structure and abundance of adult smallmouth bass in the treatment reach, an action that has been realized (Hawkins 2006) and one that may have the compensatory effect of reducing predation pressure on age-0 smallmouth bass. This would increase survival and abundance of age-0 smallmouth bass in the treatment reach, and by extension, increase predation pressure on small-bodied native fishes as well. This scenario is supported, in part, by relatively low relative abundance of age-0 smallmouth bass in the study area in 2003 and 2004 (Table 4), which was prior to increased removal efforts in 2005 and 2006. Higher relative abundance of age-0 bass in 2005 and 2006 when removals of adult bass were higher, supports this idea. However, this hypothesis is not supported by capture rates of age-0 smallmouth bass in control and treatment areas (Figs 7A and 7B) because capture rates in control areas are as high or higher than those in the treatment reaches in each year. This is opposite what one would expect if larger and more abundant smallmouth bass in the control reach were suppressing survival of age-0 bass.

CONCLUSIONS

- ◆ Species diversity in the study area has declined compared to historic times as mottled sculpin has disappeared and several other species are rare.
- ◆ Abundance of remaining native small-bodied fishes has been reduced in all habitat types but particularly in the main stem Yampa River, compared to samples collected as recently as 1999.
- ◆ Smallmouth bass abundance in the study area has increased markedly since 1999.
- ◆ Those fish community changes were associated with lower flows and warmer water temperatures associated with drought conditions that began in 2000.
- ◆ Positive response of small-bodied native fish in the main channel of the Yampa River to removal of small and large-bodied predators such as smallmouth bass and northern pike has not been detected based on sampling in control (no predator removal) and treatment (predator removal) reaches.
- ◆ Isolated pools in both the control and treatment reach support the highest abundance of native fish in the study area, but typically only when pools have few or no smallmouth bass.
- ◆ Smallmouth bass may be limiting survival and recruitment of small-bodied native fishes in the Yampa River study area. Other factors such as environmental changes and reduced abundance of adults and larvae may also be limiting the response of native fishes to predator removal.
- ◆ Otolith aging may be a useful technique to understand timing and duration of the smallmouth bass reproductive season, and to understand other aspects of smallmouth bass early life history.

RECOMMENDATIONS

- ◆ Continue sampling as currently conducted to monitor response of native fishes. More extensive and intensive predator removal and changes in environmental conditions may yield insights into native fish response.

- ◆ Investigate abundance levels of adult native fishes to understand if sufficient numbers remain to produce enough larvae to elicit a response to predator removal.
- ◆ Determine if supplementing early life stages of native fishes in study area is a viable means to better understand native fish response to predator removal. One approach would be to supplement marked fish in a few habitat types in a small area (e.g., a few RK) within the treatment reach where smallmouth bass have been subject to an even more focused removal effort.
- ◆ Investigate early life history of smallmouth bass to understand timing and duration of reproduction, information which may assist with efforts to reduce their survival and recruitment.

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Table 1. Comparison of electrofishing (EL) and seine (SE) sampling to estimate species richness and relative abundance (% composition in samples) in control (C) and treatment (T) reaches of the Yampa River near Maybell, Colorado, 2003.

SPECIES	T-EL	C-EL	T-SE	C-SE
native suckers	0.92	1.54	0	0
roundtail chub	0.92	0.62	0	0
black bullhead	0.33	13.95	0	0
black crappie	0.38	1.23	0	0.10
bluegill	0.05	0.41	0	0
brook stickleback	6.07	0.92	0	0.10
common carp	3.20	0.82	8.33	0.10
creek chub	6.89	9.03	0	0
fathead minnow	18.71	11.38	8.33	0.39
Iowa darter	0.05	0	0	0
northern pike	0	0.41	0	0
plains killifish	0.22	0	0	0
reeside shiner	0.05	0	0	0
speckled dace	3.36	0.21	0	0
smallmouth bass	38.18	43.28	8.33	0.39
sand shiner	7.38	9.54	75	98.93
white sucker	13.07	6.46	0	0
hybrid suckers	0.22	0.21	0	0
total fish	1844	975	100	1028

Table 2. Number of samples and habitat types sampled in control (C) and treatment (T) reaches, Yampa River, RK 161-199.6, near Maybell, Colorado, 2003-2006

Sample types	2003		2004		2005		2006		Total	
	C	T	C	T	C	T	C	T	C	T
# of samples	33	31	12	8	46	49	35	43	126	131
Samples with fish	31	25	12	8	46	49	35	43	124	125
Backwater	9	6	2	1	9	9	6	8	26	24
Eddy	1			1	5	4	7	5	13	10
Embayment	4	5		1	9	13	5	7	18	26
Isolated Pool	2	4	3	2	1		4	3	10	9
Riffle	6	6	3	3	2	2	1	1	12	12
Shoreline	7	8	2		18	20	10	16	37	44
Runs	2	2	2		1	1	2	2	7	5
Pool	2				1			1	3	1

Table 3. Composition of fishes of the Yampa River, near Maybell Colorado, 1981 and 2003-2006, collected in low velocity habitats. The 1981 data are from Wick et al. (1985) and represent samples collected in 1981 and 1982.

Species	1981	2003	2004	2005	2006
flannelmouth sucker	X	X	X	X	X
bluehead sucker	X	X		X	X
mottled sculpin ¹	X				
mountain whitefish ²	X			X	X
roundtail chub	X	X	X	X	X
speckled dace	X	X	X	X	X
black bullhead		X	X	X	X
black crappie		X		X	X
bluegill		X		X	X
brown trout				X	
brook stickleback		X	X	X	X
common carp	X	X	X	X	X
creek chub	X	X	X	X	X
fathead minnow	X	X	X	X	X
Iowa darter		X	X	X	X
northern pike		X	X	X	X
plains killifish		X	X	X	
pumpkinseed					X
redside shiner	X	X		X	X
red shiner	X				
smallmouth bass		X	X	X	X
sand shiner	X	X	X	X	X
white sucker	X	X	X	X	X
unknown suckers ³		X	X		
sucker hybrids		X	X	X	X

¹ Sculpin presence based on presence in other sampling in the study area including that of Anderson (2000; 2002; 2005).

² Whitefish presence based other sampling including boat electrofishing in the study area (Hawkins 2006).

³ Unknown suckers and sucker hybrids unidentifiable based on size, condition, or hybridization.

Table 4. Relative abundance (% composition) of fishes collected in low-velocity habitat of the Yampa River, near Maybell, Colorado, from 2003-2006

Species	2003	2004	2005	2006	2003-2006
Bluehead sucker	0.6	0.2	0.1	0.5	0.4
Flannelmouth sucker	0.2	1.6	0.3	0.7	0.7
Roundtail chub	0.6	4.5	0.6	0.1	1.4
Speckled dace	1.7	3.0	0.3	0.4	1.3
Black bullhead	3.7	3.5	1.0	11.3	4.9
Black crappie	0.5	0.0	1.5	< 0.1	0.7
Bluegill	0.1	0.0	0.1	0.1	0.1
Brown trout	0.0	0.0	< 0.1	0.0	0.0
Brook stickleback	3.1	0.8	0.6	1.5	1.5
Common carp	1.8	0.5	0.1	0.3	0.7
Creek chub	5.5	7.3	2.1	0.8	3.9
Fathead minnow	11.9	0.9	7.5	7.7	7.0
Green sunfish	0.0	0.0	0.9	0.1	0.2
Iowa darter	0.0	1.0	1.1	1.3	0.8
Largemouth bass	0.0	0.0	< 0.01	0.0	0.0
Northern pike	0.1	< 0.1	0.1	0.1	0.1
Plains killifish	0.1	0.3	0.6	0.0	0.3
Pumpkinseed	0.0	0.0	0.0	< 0.1	0.0
Redside shiner	< 0.1	0.0	0.9	0.3	0.4
Smallmouth bass	29.1	19.3	42.8	41.0	33.1
Sand shiner	32.3	44.7	23.1	14.3	28.6
Unknown sucker	0.6	< 0.1	0.0	0.0	0.2
White sucker	7.8	12.3	16.0	19.1	13.8
White x bluehead sucker hybrid	0.0	0.0	0.0	0.0	0.0
White x flannelmouth sucker hybrid	0.1	0.1	0.2	0.3	0.2
Bluehead x flannelmouth sucker hybrid	0.0	0.0	0.0	0.0	0.0
% native fish	3.1	9.2	1.3	1.8	3.8
% non-native fish	96.9	90.7	98.7	98.2	96.5
Total fish sampled	3882	2425	13537	12553	32397

Table 5. Relative abundance (% composition) of fishes collected in low-velocity habitat areas in control and treatment reaches of the Yampa River, near Maybell, Colorado, 2003-2006.

Species	2003		2004		2005		2006	
	C	T	C	T	C	T	C	T
Bluehead sucker	0.7	0.6	0	0.3	0.2	0	0.5	0.6
Flannelmouth sucker	0.1	0.3	1.3	1.9	0.4	0.1	1.1	0.2
Roundtail chub	0.3	0.9	1.8	7.3	1.1	0.2	0.1	0.2
Speckled dace	0.1	3.3	5.6	0.2	0.6	0.1	0.7	<0.1
Black bullhead	6.8	0.3	0	7.3	2.0	0	19.2	0.2
Black crappie	0.7	0.4	0	0	2.3	0.7	<0.1	<0.1
Bluegill	0.2	0.1	0	0	0.1	<0.1	0.1	0.1
Brown trout	0	0	0	0	0	0	0	0
Brook stickleback	0.5	6.0	1.5	0.1	0.7	0.4	1.8	1.0
Common carp	0.5	3.2	0.9	0.1	0.1	0.2	<0.1	0.7
Creek chub	4.4	6.8	2.9	12.1	2.2	2.0	0.8	0.8
Fathead minnow	5.7	18.4	0.5	1.4	6.5	8.6	10.8	3.2
Green sunfish	0	0	0	0	1.6	0.1	0.1	0.1
Iowa darter	0	0.1	0.9	1.0	1.4	0.7	1.6	1.0
Largemouth bass	0	0	0	0	0	0	0.1	0.1
Northern pike	0.2	0	0.1	0	0.1	0.1	<0.1	0
Plains killifish	0	0.2	0.1	0.6	0	1.3	0	0
Pumpkinseed	0	0	0	0	0	0	<0.1	0
Redside shiner	0	0.1	0	0	1.7	0	<0.1	0.6
Smallmouth bass	21.3	37.5	21.5	17.1	55.3	29.2	37.4	46.2
Sand shiner	55.4	7.7	54.4	34.2	10.3	37.1	5.5	26.9
Unknown sucker	0	1.2	0	0.1	0	0	0	0
White sucker	3.2	12.8	8.7	16.3	13.2	19.1	19.9	18.0
White bluehead hybrid	0	0.1	0	0	0.1	0	0	0
White flannelmouth hybrid	0.1	0.2	0	0.2	0.2	0.2	0.5	0.1
Bluehead flannelmouth hybrid	0.1	0	0	0	0	0	0	0
Total fish captured	2003	1879	1258	1167	7053	6484	7354	5199

Table 6. Relative abundance (% composition) of fishes collected in low-velocity habitat of the main channel and in isolated pools of the Yampa River, near Maybell, Colorado, 2003-2006.

Species	2003		2004		2005		2006	
	MC	IP	MC	IP	MC	IP	MC	IP
Bluehead sucker	0	1.7	0	0.2	<0.1	3.7	0	2.7
Flannelmouth sucker	0	0.5	1.3	1.7	0.2	5.4	0.1	3.2
Roundtail chub	0	1.5	0	6.6	0.1	23.1	0.1	0.3
Speckled dace	0.3	3.9	0.1	4.4	0.1	11.2	0.1	1.7
Black bullhead	1.1	7.7	0.3	5.0	1.1	0	14.1	0
Black crappie	0.7	0.3	0	0	1.5	0	<0.1	<0.1
Bluegill	0.2	0.1	0	0	0.1	0	0.1	0
Brown trout	0	0	0	0	<0.1	0	0	0
Brook stickleback	0.6	7.2	0.4	1.0	0.5	5.4	0.7	4.4
Common carp	0.2	4.3	0.8	0.4	0.1	0.3	0.4	0.1
Creek chub	4.2	7.7	18.8	1.9	2.1	0.3	0.8	1.1
Fathead minnow	3.3	25.4	0.3	1.2	7.4	11.6	3.4	24.7
Green sunfish	0	0	0	0	0.9	0	0.1	0.1
Iowa darter	<0.1	0	2.7	0.1	1.1	0.7	1.4	1.0
Largemouth bass	0	0	0	0	<0.1	0	0	0
Northern pike	0	0.3	0.1	0	0.1	0	0.1	0.1
Plains killifish	0.1	0.1	1	0	0.7	0	0	0
Pumpinseed	0	0	0	0	0	0	<0.1	0
Redside shiner	0	0.1	0	0	0.9	0	0	1.3
Smallmouth bass	38.9	13.7	59.9	0.2	43.7	0	51.1	0.3
Sand shiner	49.9	4.6	5.7	63.1	23.6	2.0	16.0	7.5
Unknown sucker	0	1.5	0	0.1	0	0	0	0
White sucker	0.5	19.4	8.8	14.0	15.6	34.0	11.5	49.8
White bluehead hybrid	0	0.1	0	0	0	1.4	0	0
White flannelmouth hybrid	0	0.3	0	0.1	0.2	0.7	<0.1	1.6
Bluehead flannelmouth hybrid	0	0.1	0	0	0	0	0	0
Grand Total	2376	1503	777	1648	13243	294	10059	2494
% native fish	0.3	8	1	13	0.4	44	0.3	8

Table 7. Parameter estimates for a logistic regression analysis of native fish presence (as logit) in the Yampa River as a function of whether the sample was from an isolated pool ((IP (Y)) or not ((IP (N)), and the percent smallmouth bass in the sample. The effect of whether the sample was from a control or treatment reach was not significant (*Chi-square* = 0.01, *p* = 0.94). The logit values returned by the equation can be transformed to probabilities, here the probability of finding native fish present in the sample, by the equation $e^y/(1+e^y)$, where *y* is the logit value.

Parameter	DF	Estimate	Standard Error	Wald 95% Confidence Limits		Chi-Square	Pr > ChiSq
Intercept	1	0.8172	0.5080	-0.1784	1.8127	2.59	0.1077
IP (N)	1	-1.6935	0.5553	-2.7819	-0.6051	9.30	0.0023
IP (Y)	0	0.0000					
SMBPerc	1	-0.8980	0.4231	-1.7273	-0.0687	4.50	0.0338

Table 8. Parameter estimates for a logistic regression model analysis of native fish abundance (as the logit of the proportion in sample) in the Yampa River as a function of whether the sample was from an isolated pool ((IP (Y)) or not ((IP (N))), and the presence and number of smallmouth bass in the sample. The effect of whether the sample was from a control or treatment reach was not significant (*Chi-square* = 0.19, *p* = 0.66). The logit values returned by the equation can be transformed to proportions, here the proportion of native fish in the sample, by the equation $e^y/(1+e^y)$, where *y* is the logit value.

Parameter	DF	Estimate	Standard Error	Wald 95% Confidence Limits		Chi-Square	Pr > ChiSq
Intercept	1	-2.4067	0.1193	-2.6405	-2.1729	406.93	< 0.0001
IP (N)	1	-3.0832	0.2195	-3.5135	-2.6528	197.21	< 0.0001
IP (Y)	0	0.0000					
SMBP (N)	1	0.6364	0.1485	0.3453	0.9275	18.36	< 0.0001
SMBP (Y)	0	0.0000					
SMB #	1	-0.0037	0.0019	-0.0074	-0.0000	3.85	0.0496

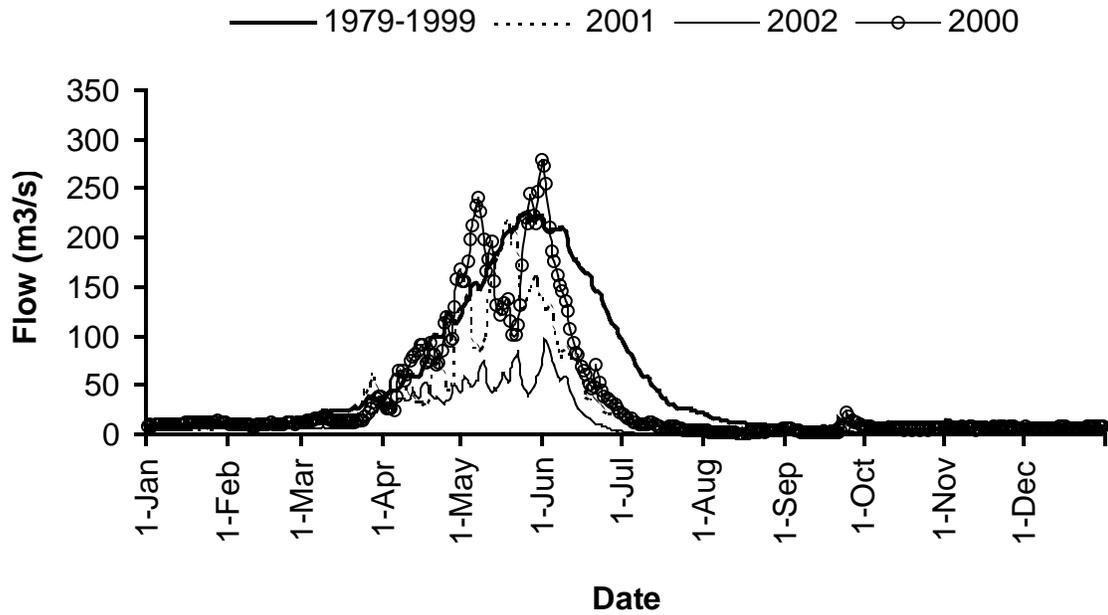


Figure 1. Mean daily flows for the Yampa River near Maybell, CO, in the pre-drought (1979-1999) and recent drought years, 2000-2002 (USGS gauge # 09251000).

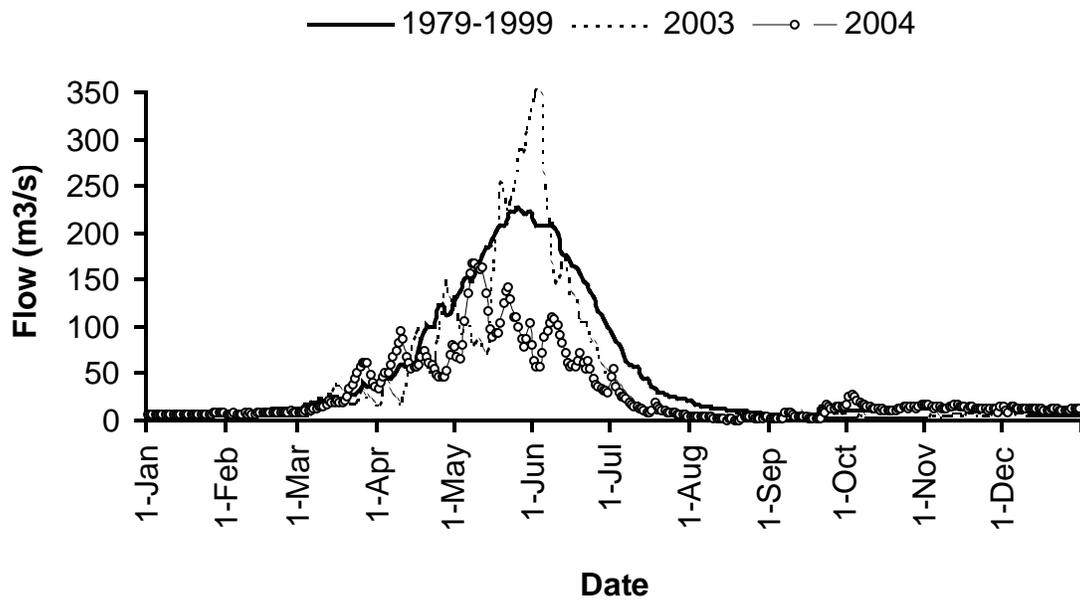


Figure 2. Mean daily flows for the Yampa River near Maybell, CO, in the pre-drought (1979-1999) and recent drought years, 2003 and 2004 (USGS gauge # 09251000).

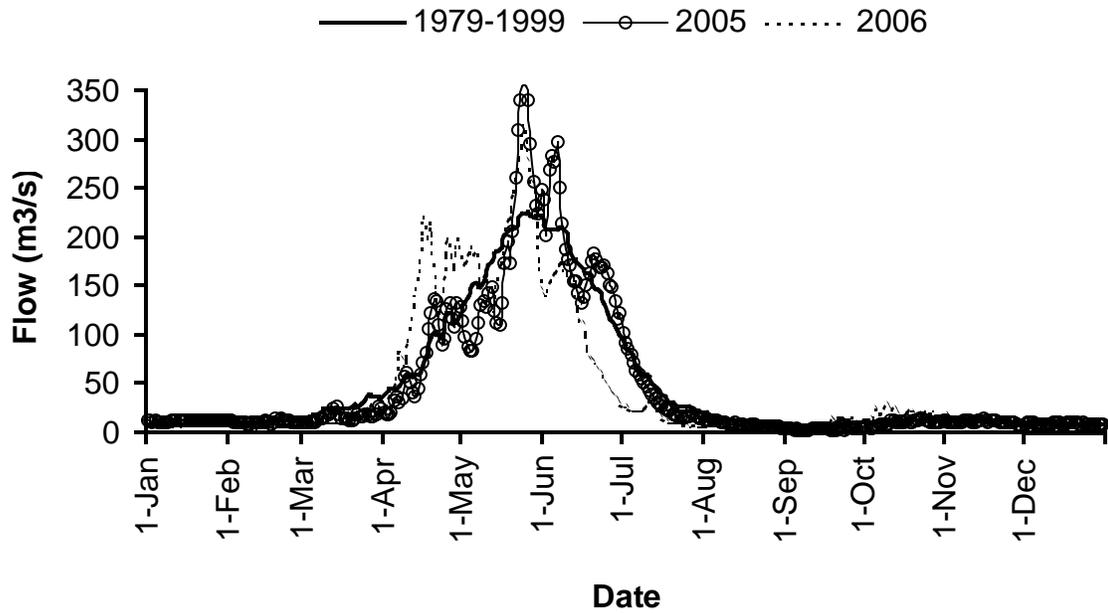


Figure 3. Mean daily flows for the Yampa River near Maybell, CO, in the pre-drought (1979-1999) and recent drought years, 2005 and 2006 (USGS gauge # 09251000).

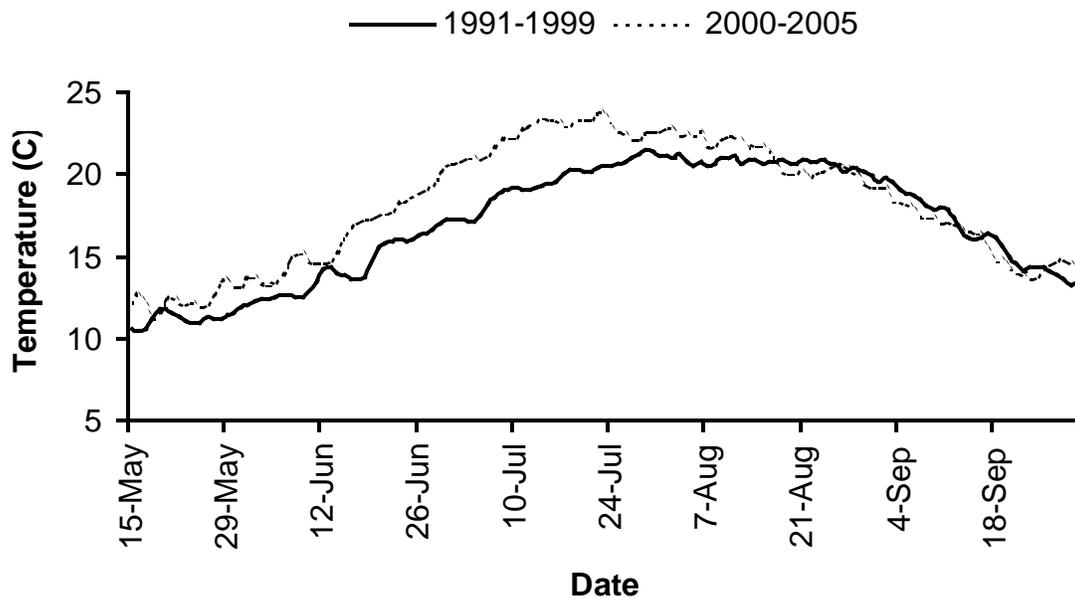


Figure 4. Mean daily water temperatures for the Yampa River near Maybell, CO, in the pre-drought (1979-1999) and drought (2000-2005) periods (USGS gauge # 09251000, in part).

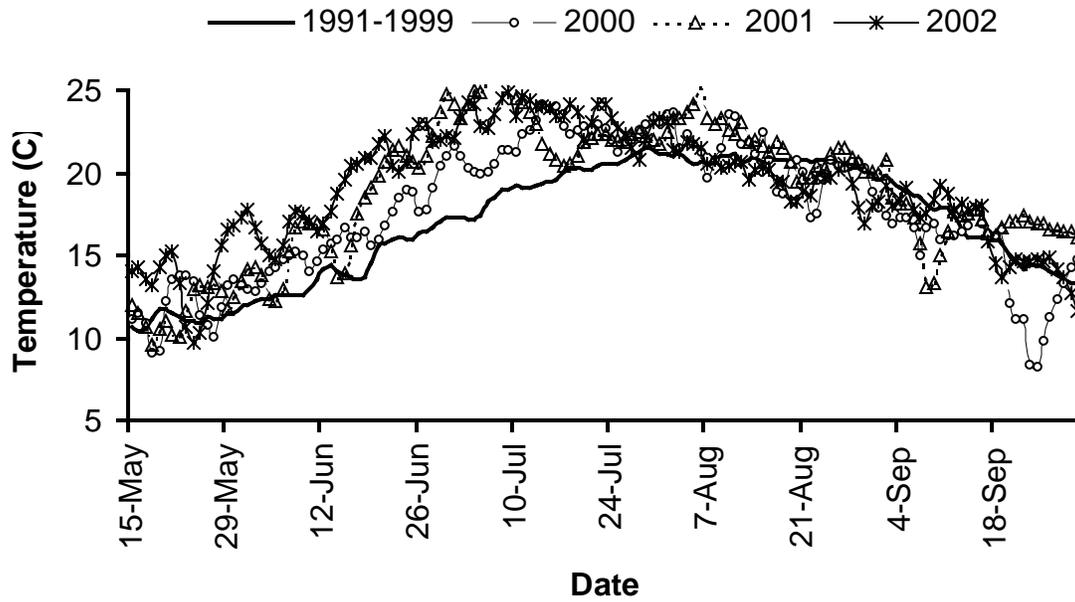


Figure 5. Mean daily water temperatures for the Yampa River near Maybell, CO, in the pre-drought (1979-1999) and drought years 2000, 2001, and 2002 (USGS gauge # 09251000, in part).

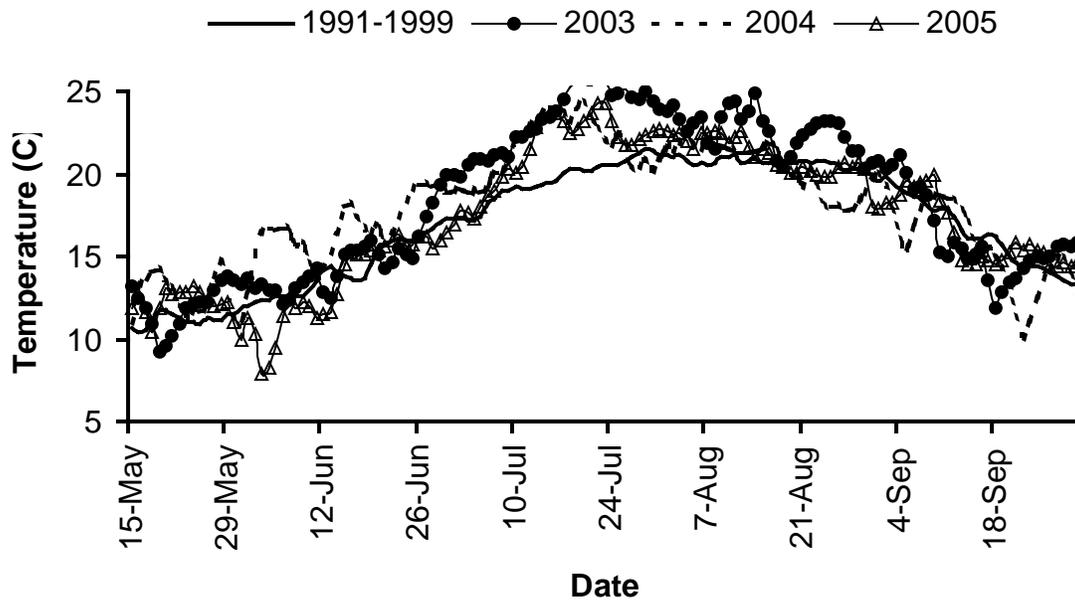


Figure 6. Mean daily water temperatures for the Yampa River near Maybell, CO, in the pre-drought (1979-1999) and drought years 2003, 2004, and 2005 (USGS gauge # 09251000, in part)

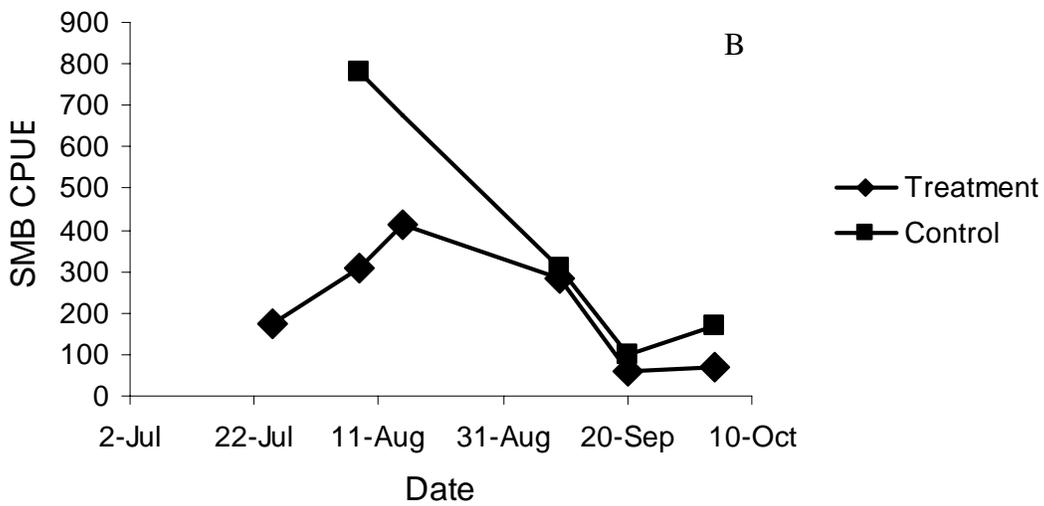
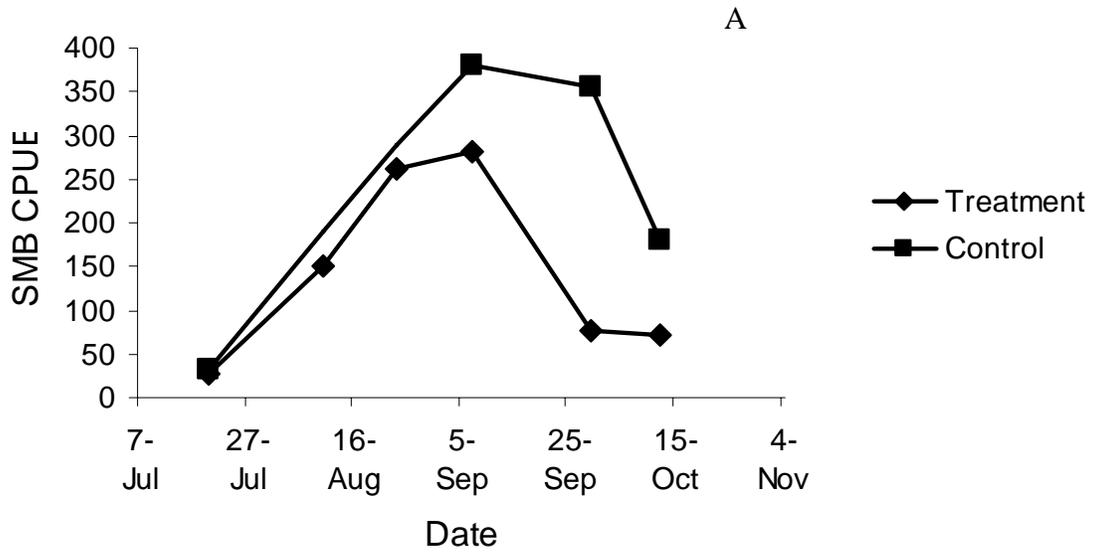


Figure 7. Catch per unit effort of smallmouth bass captured in the Yampa River, near Maybell, Colorado, in 2005 (A) and 2006 (B) in control and treatment reaches.

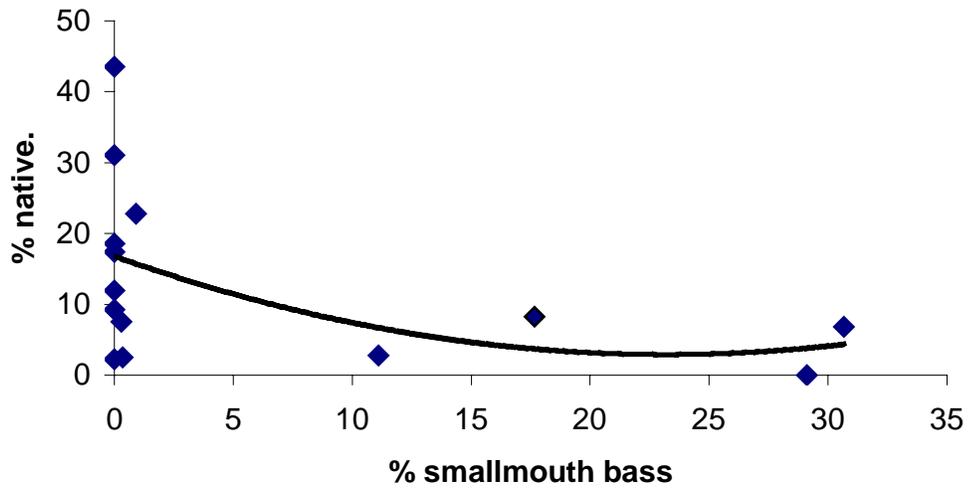


Figure 8. Percent native fish in isolated pools as a function of the percent of smallmouth bass in the Yampa River, near Maybell, Colorado, 2003-2006.

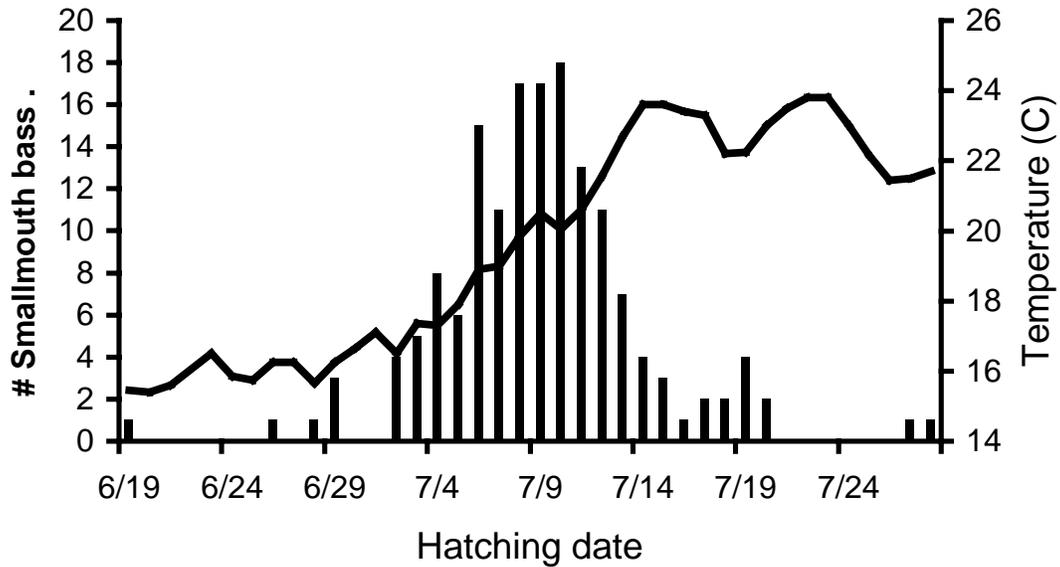


Figure 9. Distribution of hatching dates of otolith-aged smallmouth bass captured in the Yampa River, summer 2005. Water temperature ($^{\circ}\text{C}$) of the Yampa River is depicted by the line.

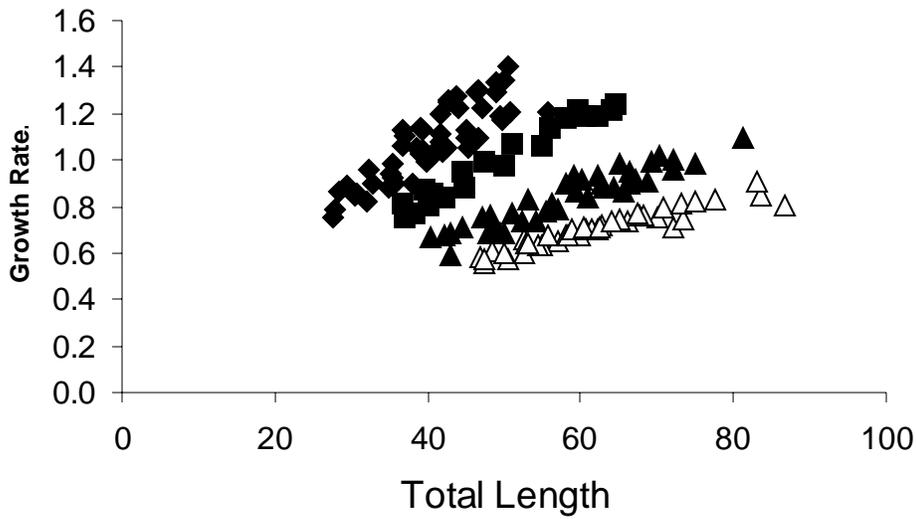


Figure 10. Growth rate of age-0 smallmouth bass (mm/day), estimated from otolith age and size at capture, as a function of total length, for fish collected in the Yampa River, RM 100-124, summer 2005. Diamonds are for samples collected on 10-12 August, at a mean pre-collection water temperature of 22.5 C, squares on 24 August at 22.1 C, filled triangles on 7-13 September, at 21.4 C, and open triangles on 30 September - 3 October, at 19.9 C.