Implications of a Depressed Thermal Regime on Native Fish Species of the North Fork of the Cache la Poudre River

C. Nathan Cathcart and Kurt D. Fausch

Department of Fish, Wildlife, and Conservation Biology

Colorado State University

May 2010

Executive Summary

Population growth along the Front Range in Colorado has created an increase in the demand for municipal water, which has led to a proposal to expand both Halligan and Milton Seaman Reservoirs on the North Fork Cache la Poudre River. Dams alter aquatic ecosystems in three primary ways, affecting: connectivity of critical habitat, the natural flow regime, and the thermal regime. Depressed thermal regimes are often caused by releasing water from the bottom of the reservoir (i.e., hypolimnial releases). Although this effect is not as visible as homogenized flow patterns and connectivity loss, understanding the thermal regime is critical to persistence of native fishes because temperature affects essentially all physiological, biochemical, and life history processes of all fishes.

The river segment between Halligan and Milton Seaman reservoirs is important habitat for fishes along the Front Range of northern Colorado. This area between the plains and mountains (elevation 1400 – 1650 m; 4593 – 5413 ft), known as the transition zone, supports a representative assemblage of fishes that require cool water and coarse, silt-free substrate to sustain populations. Many of these fish are at the fringe of their natural distribution and thus are likely to be ecologically, genetically, and morphologically distinct from the same fish species near the center of their range (e.g., in the Great Lakes region). Urbanization and water storage are two main factors that have caused loss of transition zone habitat, and subsequent declines in native fishes. For example, the segment of the North Fork between the two reservoirs originally supported an assemblage of nine native species (suckers, minnows, and darters), of which two have not been captured since 1959.

The focus of this report is on the potential for reservoir expansion to produce water downstream that is too cold for the persistence of native fishes in the North Fork Cache la Poudre River. Thermal biology of many fishes has been studied extensively, but there are few useful data for assessing the effects of depressed thermal regimes on native transition-zone fishes. Most thermal tolerance studies are conducted in the lab and have focused on game and food fish species, not small-bodied fishes. Moreover, these studies focus on the acute thermal limits of fish, not chronic effects of temperature on populations. We conducted a literature review on cold thermal tolerances of the fishes native to the North Fork, to assess the risk of altering the thermal regime of the river segment. We relied on data from laboratory and field studies with emphasis on survival, growth, spawning, and hatching of early life stages. Although data were lacking for species in several of these categories, we were able to infer basic temperature requirements for the fish assemblage.

The main conclusions from the literature review on cold thermal tolerances of these native fishes are:

1. The native fishes in the North Fork between the reservoirs can **survive** to temperatures as low as 0°C, based on the available data (four of nine species).

2. Few data were available for the lower limits of **growth** of the native species (only three of nine species), and these limits varied substantially, from 1°C to >10°C

3. Eggs, larvae, and juvenile stages of fishes are the most sensitive to temperature, and these life stages are critical for populations to persist. Most native fish in the North Fork require 10°C to initiate **spawning** (data were available for eight of nine species), and this represents an important thermal limit for these native fishes.

4. Stream temperatures need to reach about 15°C for all species to **hatch** successfully. **Moreover, we infer from the limited data on the existing thermal regimes in the North Fork, and those for the main stem Poudre River in Fort Collins (where the same assemblage of fishes is native), that average daily temperatures will need to reach at least 20°C for a month or more to allow sufficient growth of fish larvae to achieve high overwinter survival (i.e., recruitment) for many of these native species.**

5. Overall, data on thermal minima required for survival, growth, and successful recruitment of early life stages of these species are sparse, and often come from other regions. For example, no data were available for bigmouth shiner for any category. More detailed data would be needed to make more accurate predictions specific to this region.

6. Case studies of the effects of depressed or altered thermal regimes on fishes in other rivers were reviewed, and showed:

a. Spawning and migration cues can be disrupted by altered thermal regimes, leading to population declines, such as has occurred for native minnows and suckers in the Colorado River system, and for native burbot (a type of cod) in the Kootenai River in the northern Rockies.

b. Growth and survival can be inhibited in streams with depressed thermal regimes, also leading to population declines, such as for the Colorado River fishes, and native cutthroat trout in high-altitude mountain streams in Colorado.

c. Fish may cope with altered thermal regimes by either compensation or adaptation. A population of darters in an eastern U.S. river compensated for cold temperatures by reducing growth and egg production, and delayed spawning. In contrast, a population of minnows in Texas apparently underwent rapid evolution, as evidenced by altered thermal preferenda in a laboratory test.

The implications of this study extend beyond the Front Range of Colorado. As demand for water increases in the western United States, it is to be expected that reservoirs will be expanded, and may lower temperature regimes that could potentially have adverse effects on native stream fish assemblages. **If a conservation goal for the North Fork Cache la Poudre River is to maintain suitable habitat for the assemblage of native fish species, then their thermal requirements will need to be a primary consideration.** New research likely will be needed to establish these requirements for many species.

Introduction

Population growth in Fort Collins and Greeley, Colorado has created an increase in the demand for municipal water. Increased demand has led to a proposal to expand both Halligan and Milton Seaman reservoirs on the North Fork of the Cache la Poudre River by 2029 (Figure 1; www.halligan-seaman.org). Water storage in Halligan Reservoir would increase nearly four fold, from 6400 acre-feet (ac ft) to 23,000 ac ft, and that in Milton Seaman Reservoir would increase more than 10 fold, from 5000 ac ft to 53,000 ac ft, for a collective 76,000 acre feet more water stored annually after completion. Depending on water storage capacities, the expanded reservoir areas could cause up to a 6 km loss in river habitat. The goal of expanding water storage in the basin is to provide water to the increasing populations in Greeley and Fort Collins, and to provide increased water system reliability in the event of a 1-in-50-year drought. Also, there is a relatively small component of the Halligan Reservoir expansion that is intended to provide additional water to the North Poudre Irrigation Company. Between 2010 and 2040, Greeley is estimated to double to 200,000 people and Fort Collins' population is predicted to grow by 15% up to 165,000 people (www.halligan-seaman.org).

Dams alter aquatic ecosystems in several ways, including creating barriers to fish movement (loss of connectivity), altering the timing and quantity of stream flow (i.e., the natural flow regime), and changing the thermal regime. First, dams sever connections within the river system, which prevents movement of fishes among habitats critical to different life stages (Schlosser 1995; Fausch et al. 2002; Helfman 2007). Second, the natural flow regime is modified because dams often homogenize flow and downstream habitats, often by decreasing peak flows and increasing base flows. This can cause loss of important ecological cues to fishes, such as increased discharge needed to initiate spawning (Poff et al. 1997). Third, thermal regimes are often stabilized, and depressed. This can affect fishes by inhibiting growth, spawning, and movement cues (Fausch 2007; Paragamian 2009).

When dams are constructed, alterations to these three critical factors interact and can lead to declines in native fish populations, including economically and ecologically valuable fishes such as Pacific salmonids, the Colorado River native fishes, and the Kootenai River burbot (*Lota lota*; Poff et al. 1997; Helfman 2007; Paragamian 2009). Depressed thermal regimes are often caused by releasing water from the bottom of the reservoir (i.e. hypolimnial releases). Although this effect is not as visible as homogenized flow patterns and connectivity loss, understanding the thermal regime is critical to persistence of native fishes because temperature affects essentially all physiological, biochemical, and life history processes of all fishes (Beitinger et al. 2000). All three of these effects currently manifest on the North Fork Cache la Poudre River, where the dams and at least one other diversion structure present a complete barrier to upstream movement, average winter flows are in the bottom 10^{th} percentile of natural flows, and stream temperatures are depressed as much as 6 degrees C during bottom releases from Halligan Reservoir (Figures 2 and 3). It is conceivable that these factors have already contributed to the extirpation of several species and reduced populations of others in the North Fork, although there is no clear way to evaluate this possibility.

The river segment between Halligan and Milton Seaman reservoirs is important habitat for fishes along the Front Range of northern Colorado. This area between the plains and mountains (elevation 1400 – 1650 m; 4593 – 5413 ft), known as the transition zone, supports a representative assemblage of fishes that require cool water and coarse silt-free substrate to sustain populations (Fausch and Bestgen 1997). The project proponents in the Shared Vision Planning water management process (promoted by the US Corps of Engineers) have identified the native fish populations of the North Fork as a primary environmental target in project planning. Several of these species, such as the common shiner (*Luxilus cornutus*) and the Iowa darter (*Etheostoma exile*), are glacial relicts. These fish once occurred throughout the Great Plains during cooler and wetter periods after the most recent glaciations, but were extirpated from watersheds on the Great Plains of eastern Colorado as the climate became warmer and drier. Both common shiner and Iowa darter have special conservation status in Colorado, being state threatened and a species of special concern, respectively (Woodling 2006; Hubert and Gordon 2007). Loss of transition zone habitat and subsequent declines in the fish communities have been caused by urbanization and water diversion and storage driven by population growth (Li 1968; Fausch and Bestgen 1997). Continued anthropogenic impacts such as climate change pose thermal challenges and ultimately could lead to the transition zone shrinking farther or shifting to higher elevations (McCullough et al. 2009). Therefore, the river segment between Halligan and Milton Seaman reservoirs is critical habitat for the conservation of these native fishes.

Thermal biology of many fishes has been studied extensively, but many of the criteria are not relevant or are difficult to use for assessing the effects of depressed thermal regimes on native transition zone fishes, for three reasons. First, the majority of studies on thermal relationships in fishes have been conducted in the laboratory using simple endpoints as predictive tools, such as mortality. Two approaches to quantifying temperature tolerance in fishes are universally recognized: the incipient lethal temperature (ILT) technique and the critical thermal method (CTM; Beitinger et al. 2000). The ILT technique, also known as the plunge method, involves placing fish acclimated at a given temperature into several different water temperatures approaching their upper and lower limits, and exposing them for prescribed time intervals (12, 24, 48, or 96 h). The temperature at which 50% mortality occurs over this time period is then estimated. In the CTM, acclimated fish are subjected to a constant linear rate of change until a predefined sublethal effect occurs (loss of equilibrium, muscle spasms; Beitinger et al. 2000). However, both of these methods measure only upper and lower tolerance limits of a species and are not necessarily good indicators of the chronic effects of temperature. Second, the literature related to thermal maxima outnumbers thermal minima data 10 to 1, so data on thermal minima are available for relatively few species (Beitinger, pers. comm.). Third, most of the fish studied have been large-bodied food or sport fishes, not small-bodied fishes such as those found in the North Fork Cache la Poudre River (Wismer and Christie 1987; Beitinger et al. 2000).

We conducted a literature review on thermal tolerances of fishes native to the North Fork Cache la Poudre River to assess the risk of altering the thermal regime of the river segment. Although data are sparse for many of the species native to the North Fork, this problem was addressed by combining different sources of data collected using different methods over various life stages of the target species. We relied on data from laboratory and field studies with emphasis on growth, spawning, and early life stages. We also reviewed studies documenting the effects of tailwater operations on other fish species due to depressed (or altered) thermal regimes to offer insight based on results from other regions.

Methods

Study Area

The North Fork Cache la Poudre River flows through the Rocky Mountain foothills in Larimer County, Colorado, and into the main stem of the Cache la Poudre River near Fort Collins. Halligan Reservoir, completed in 1910, holds water for the North Poudre Irrigation Company and lies upstream of Milton-Seaman Reservoir, finished in 1943, which holds water for the city of Greeley. The river segment of interest lies between these reservoirs and is presently approximately 20 km long (Figure 1). The segment directly downstream of Halligan Reservoir descends through land owned by The Nature Conservancy including the narrow Phantom Canyon. The valley then opens and the river traverses rolling private grasslands, lands owned by Larimer County (Eagle's Nest Open Space), and other private, U.S. Forest Service, and state lands before entering Seaman Reservoir. River habitat in Phantom Canyon includes deep pools formed against the rock faces, whereas in the downstream reaches pools are formed by a combination of boulders and natural fluvial processes in the gravel and cobble bed. During summer baseflow, Halligan Reservoir dam releases water from the bottom of the reservoir (i.e., hypolimnial release) resulting in coldwater habitat downstream.

Target Species

Historical sampling records of the fish fauna in the North Fork Cache la Poudre River show that the river supports an assemblage native and non-native fishes. Non-native rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), yellow perch (*Perca flavescens*), and brook stickleback (*Culaea inconstans*), species reported from the study area, are not addressed specifically in this report. Yellow perch and brook stickleback were recently found near Milton-Seaman Reservoir and are associated with this still-water habitat more than the river (K. Fausch, Colorado State University, and K. Kehmeier, Colorado Division of Wildlife, unpublished data). Halligan Reservoir is currently operated to discharge hypolimnial water, and creates coldwater habitat downstream that supports thriving populations of nonnative brown trout and rainbow trout. The thermal regimes required by these trout species are well understood and are currently being met. Therefore, the focus of this report will be on thermal regimes required to support native fishes found currently or in the past, which include nine native fishes (Table 1).

The assemblage of native fishes included two suckers (Family Catostomidae), five minnows (Family Cyprinidae; the minnow, dace, chub, and shiners), and two darters (Family Percidae; see Table 1 for scientific names of all species, and Appendix I for their life history). Most require relatively cool to warm water to successfully reproduce and grow, and along the Front Range of Colorado several of these species are found primarily or only in transition zone streams or ponds. Fishes within the North Fork display a wide range of biology and life history within this narrow habitat type. Some of these fish are long-lived and large-bodied, whereas some are small-bodied, short-lived fish. The fish assemblage is comprised of all spring or early summer spawners. However, some will spawn only once each year (e.g., suckers), whereas others will spawn multiple times in a season (e.g., fathead minnow), whenever conditions are adequate. Spawning substrate requirements vary, with six of nine species preferring gravel, two favoring sand, and one spawning in vegetation. Although two species have special conservation status in Colorado, none are federally endangered or threatened, and all have widespread distributions throughout other parts of the Mississippi River basin farther east (e.g, see Becker 1983). However, because the target species are glacial relicts in Colorado, they are likely to be ecologically, genetically, and morphologically distinct from their Great Lakes counterparts (Scheurer et al. 2003). In fact, many have disjunct distributions, with the next closest populations found hundreds of miles to the east. Two of the minnows, bigmouth shiner and common shiner, have not been collected in this river segment since the first collections in 1959, and may now be extirpated from the segment. Nevertheless, other fishes were rediscovered in the transition zone along the Front Range after a long hiatus (Bestgen et al. 1991) or have been collected for the first time only recently (Platania et al. 1986).

Literature review of thermal minima

Three sources of data were relevant to this study on the fishes historically present in the North Fork Cache la Poudre River. First, thermal tolerance data determined in the laboratory using the ILT technique were compiled for native fishes in the North Fork. Second, data reported from the laboratory and field on thermal requirements for growth, spawning, and egg and fry development were assembled for these species. Last, field data on effects of depressed or altered thermal regimes on other fish species downstream of hypolimnial release reservoirs are presented as examples of impacts that could be incurred by the native fishes. These case studies involved species in some of the same genera (*Etheostoma*) and families (Cyprinidae) found in the North Fork, as well as other species.

Many of the data found on thermal minima for fishes were from Canada and the Great Lakes region. However, if data were plentiful and the source was known, we selected those from the most appropriate locations to present (i.e., Colorado data were selected over Great Lakes region data) to account for regional variability that may occur within a species. Data are presented to illustrate both the limits of thermal tolerances and the necessary temperatures for the various fishes throughout their life histories (i.e. egg, larvae, juvenile, adult). Ranges for lower incipient lethal temperatures vary depending on the acclimation temperature tested, so the acclimation temperatures are also presented.

Temperature data

Miller Ecological collected thermal data on the North Fork Cache la Poudre River using temperature loggers in 2003 (unpublished data provided by W. Miller). These data will be used to model the current and future thermal regimes based on different management strategies as part of the Halligan-Seaman expansion project. We used the average daily temperatures from three sites along the North Fork to assess the thermal regime to which the native fish community was exposed. The three sites sampled were above Halligan Reservoir, below Halligan Reservoir, and below Phantom Canyon (Figure 1).

Results

Overall, data were sparse for the thermal biology of most of the native fishes of the North Fork Cache la Poudre River. We were able to find relatively complete data (i.e., on temperature tolerances, and thermal requirements for growth and spawning) for only two of the nine species, white sucker and fathead minnow. For three species (creek chub, longnose dace, and common shiner) data were available for two of the three attributes, and for another three (Iowa darter, johnny darter, and longnose sucker) data for only one attribute were found. One species, bigmouth shiner, had no temperature data available and only general spawning times were found. The most prevalent data were on spawning temperatures (available for eight of nine species), whereas data on growth were available for only three of nine species, and data on tolerances to low temperatures were available for only four of nine species.

Lower incipient lethal thermal tolerances

Data on lower incipient lethal temperatures (LILT) were found for only four species: white sucker, creek chub, common shiner, and fathead minnow (Table 2). Acclimation temperatures are shown in the table to help explain variation in LILT within species. The ranges of LILT were assumed to extend between those tested, because often the data did not include intermediate acclimation temperatures (i.e. acclimation temperatures tested included 20ºC and 25ºC but none between). The four fish tested can survive to temperatures as low as 0-2°C. Data on lower thermal tolerances may be sparse due to the assumption that most temperate fishes can survive at temperatures at or approaching 0°C (Beitinger et al. 2000).

Growth

Data on minimum temperature requirements for growth were limited to three species: white sucker, longnose dace, and fathead minnow (Table 3). Fish were held for long periods at different temperatures, or their growth was measured in the field, so acclimation temperatures are not an issue. White sucker stop growing at temperatures lower than about 12ºC, based on data from Colorado (Wismer and Christie 1969). Fathead minnow can continue to grow at temperatures as low as 7ºC, and longnose dace can sustain some growth to 1ºC. Below these temperatures for each species, fish are expected to stop growing. In contrast, optimum temperatures for growth are usually close to the upper incipient lethal temperature for most fishes. For example, optimum growth for white sucker occurs at 24-27ºC, close to the upper incipient lethal temperature of 29ºC. Minimum temperatures for growth were the least available thermal data type reported by temperatures by Wismer and Christie (1987) possibly due to the difficulty (and cost) of determining temperature requirements for growth during relatively long experiments at cold temperatures, which are difficult to maintain.

Spawning and development

Thermal requirements for spawning and hatching of eggs were found for all species except bigmouth shiner (Table 4). The data available show that most native fish require water temperatures to warm to 10°C or higher to initiate spawning, and require continued warming for successful development, hatching, and growth. Moreover, as temperatures decrease, incubation and hatching times increase (Figure 5). The development of spawning characteristics, including breeding colors and nuptial tubercles in males (projections on the head and fins used in courtship) and ovulation in females, appear to be temperature dependent (Becker 1983). Just as the onset of spawning can be induced by temperature, a significant drop in temperature will delay spawning activity by days in common shiner and fathead minnow (Carlander 1969; Becker 1983). Native fishes spawn during different periods based on water temperature, with darters and suckers tending to be early spring spawners, and minnows tending to spawn during summer (Figure 6).

Current thermal regime

The current thermal regimes show that temperatures reach levels required for all species in the native fish community to spawn in the three reaches for which data were available (above and below Halligan Reservoir, and below Phantom Canyon; Figures 2-4, Table 4). Average daily temperatures in the sampled reaches approached or exceeded 20°C during summer (Figures 2-4). While there are no temperature data available for spring and early summer to assess conditions for early-spawning fish, these fish begin spawning at lower temperatures so we assume that their requirements are being met as well. Temperatures do not reach optima for growth of some species, such as white sucker and fathead minnow, and it is unknown whether thermal units are sufficient to allow larvae of some minnows to grow sufficiently to survive well during the subsequent winter. Additional studies on the thermal requirements for first-year growth and survival of these species would be needed to predict "recruitment" success (see Coleman and Fausch 2007a, 2007b for an example with trout).

Case studies on effects of altered thermal regimes

Reports of the effects of altered thermal regimes in rivers below reservoirs on several species of native fish from throughout North America provide evidence of the importance of these potential effects on fish populations and their persistence. These studies also indicate the role of thermal disruption on multiple life history stages for native fishes. Here, we provide examples of 1) disrupted spawning cues for a burbot population, 2) limited growth and population bottlenecks in trout caused by low temperature regimes, 3) the contribution of depressed thermal regimes to the decline of native minnows and suckers in the mainstem Colorado River, 4) adaptive responses of a minnow to an altered thermal regime, and 5) comparisons of growth and fecundity of a darter species in awarm water segment versus a colder tailwater.

1) Effects of Libby Dam on Kootenai River burbot.- The Kootenai River in Idaho, USA and Kootenay Lake in British Columbia, Canada, both historically supported popular recreational and valuable commercial fisheries for burbot, a freshwater cod (Dunnigan and Sinclair 2008; Paragamian et al. 2008). Libby Dam was completed in 1972 and the fishery had collapsed within the decade. By 1992 the burbot fishery was closed, and now even careful sampling reveals only a few burbot each year. The population is estimated at only 25 fish (V. Paragamian, personal communication). Altered temperature has been shown to be a detriment to migration and life history patterns in many fishes, including burbot (Paragamian et al. 2008). Before Libby Dam, temperatures during the winter pre-spawning period (December-February) averaged 0-2°C whereas temperatures after dam closure during the same months have averaged 2.5-8°C. Coupled with increased discharge from the dam, these consistently warmer temperatures are thought to have disrupted spawning cues as well as actual spawning by the burbot population in the Kootenai River and Kootenay Lake (Paragamian 2009). Although in this example, *warmer* temperatures created downstream from a dam are the issue, it is an excellent illustration of how homogenizing temperature regimes can put populations at risk of extinction.

2) Low temperatures create recruitment bottlenecks for trout. – Success of translocations of native cutthroat trout (*O. clarkii*) to start new populations in small high-elevation Colorado mountain streams is highly dependent on thermal conditions. Harig and Fausch (2002) reported that temperatures in July (the warmest month) averaged 10.0ºC in streams where translocations started successfully reproducing populations, but averaged 7.1ºC in those where transplanted fish died out and translocations failed. Further laboratory experiments by Coleman and Fausch (2007b) showed that the mechanism explaining these differences was low cutthroat trout fry survival at cold temperatures (about 75% vs. 30% from fry swim-up to 20 weeks after hatching, in the warm vs. cold regimes described above). Low temperatures delayed egg incubation and reduced growth of fry, which in turn reduced their survival during early winter due to lack of metabolic reserves. Based on additional field surveys of fry survival, Coleman and Fausch (2007a) reported that 900-1000 Growing Season Degree Days (GSDD) are required for successful recruitment of native cutthroat trout. The GSDD are defined as the cumulative average daily temperatures from when temperature exceeds 5ºC in early summer, which initiates spawning, until it drops permanently below 4ºC in the fall, when growth nearly ceases.

Rainbow trout apparently have similar thermal requirements for successful fry recruitment. Prior to 1985, age-0 rainbow trout were absent from the reach below Ruedi Dam on the Fryingpan River, Colorado due to the cold thermal regime caused by the hypolimnial release of water (670 GSDD by 1 October; Fausch 2007). In contrast, after modifications of the outlet structure to release warmer water (900 GSDD by 1 October), fry survival and recruitment increased and age-0 trout became prevalent. These studies show that even coldwater fishes like two species of trout can be inhibited if temperature regimes are too cold.

3) Effects of depressed thermal regimes on Colorado River fishes. – Entire fish communities in the Colorado River and its major tributaries have been largely extirpated by dam construction and the subsequent releases of cold water from the hypolimnion of reservoirs (Clarkson and Childs 2000). For example, after the 1962 closure of Flaming Gorge Dam on the Green River, Utah, spring-summer water temperatures were lowered to 6ºC from the former range of 7-21ºC. Several native species such as speckled dace (*R. osculus*), roundtail chub (*Gila robusta*), and federally endangered native species like Colorado pikeminnow (*Ptychochelius lucius*) and humpback chub (*G. cypha*) disappeared from the 104-km segment downstream of the dam to the confluence with the Yampa River. Reproduction did not occur throughout this entire segment until modifications to the outflow were made. Even then, the 13ºC maximum has allowed only limited spawning, and only in the lower reaches. Glen Canyon Dam on the Colorado River in Arizona had similar effects after it was completed in 1963. Tailwater operations led to a constant 10ºC thermal regime downstream. Colorado pikeminnow, roundtail chub, and bonytail chub (*G. elegans*), among others, were all extirpated. These losses of native fishes can be attributed to the cold water temperatures that lowered fecundity, inhibited spawning, and caused recruitment bottlenecks due to low overwinter survival of young-of-year fish (Clarkson and Childs 2000).

4) Adaptive response of a minnow to a depressed thermal regime. - Calhoun et al. (1982) studied the effect of hypolimnial releases from Morris Sheppard Dam on the Brazos River, Texas on the genetic make-up of red shiner (*Cyprinella lutrensis*). They found that the fish in the regulated tailwater had a much lower thermal preferendum (23.3ºC) when tested in the laboratory, compared with red shiner from a nearby unregulated river (30ºC). Environmental selective pressures due to the lowered thermal regime and the adaptive responses (i.e., rapid evolution; Stockwell et al. 2003) by red shiner are thought to have caused this variation between populations.

5) Compensatory responses by tessellated darters in modified thermal regimes. - Rocky Gorge Dam began operations on the Patuxent River, Maryland in 1954. Tessellated darters (*Etheostoma olmstedi*) have been shown to persist in the river downstream from the dam, despite cold hypolimnial releases. Due to a relatively short life span (commonly to only age 2), the darter was chosen to assess the effects of thermal modifications on fish populations in the river. The data showed that the population abundance and age-class proportions in the affected tailwater were similar to those in a downstream segment of the same river that was warmed by wastewater effluent (age-1 and age-2 fish made up 99.6% of the sample; Tsai 1972). However, fecundity, growth, and abundance of mature fish were lower. Likewise, spawning time was delayed by at least two weeks in the tailwater section compared to the warmer segment. Although the darter was apparently able to compensate for the colder thermal regime, the energetic cost of this compensation may ultimately prove too high, and lead to localized extirpation and a downstream shift of the population to more favorable habitat. The results of this study might be applicable to species in the North Fork in the genus *Etheostoma*, such as native Iowa and johnny darters, especially if temperatures are colder after reservoir expansion.

Conclusions and implications for native fishes in the North Fork

Our review shows that most native suckers, minnows, and darters in the North Fork Cache la Poudre River require water temperatures to warm above 10ºC to spawn successfully, and we surmise that an extended period of warmer temperatures will be needed for the fish larvae and juveniles to grow sufficiently to survive the winter (i.e., for successful recruitment to age 1). Based on data for the current thermal regime for the North Fork, and the main stem Cache la Poudre River, we surmise that growth and recruitment targets could be achieved with mean daily stream temperatures of at least 20°C for at least a month or more. Limited data on the summer thermal regime of the North Fork from one year (2003) indicates that average temperatures reached about 20ºC for about a month, although this may be below the optimum for some native species. Likewise, the thermal regime of the main stem Poudre River in Fort Collins, where all of these fishes were also native, also averages about 20°C for about a month during summer (Dr. Kevin Bestgen, Larval Fish Laboratory, Colorado State University, unpublished data). As a result, if a conservation target is to maintain suitable habitat in the segment for these native fish species, then their thermal requirements should be a primary consideration. New research could establish these requirements for many species.

Overall, data were sparse on the minimum thermal requirements needed to sustain native fishes of the North Fork. Wismer and Christie (1987) and Beitinger et al. (2000) also noted the scarcity of thermal data on non-game and small-bodied fishes, such as suckers, minnows, and darters. Nevertheless, these families include species that are among the most thermally sensitive of fishes (Wismer and Christie 1987).

The data reviewed suggest that cold temperatures directly influence life history patterns seen in these fishes. Data on lower incipient lethal temperatures, and that fact that all these fishes can survive in water with surface ice, support the assumption that fish can survive to temperatures approaching 0ºC. However, these data show only whether an individual of a species can survive a laboratory test, not the chronic effects on a population. Data pertaining to growth were few (three species) and should be investigated further to explore the effects on the fish assemblage, since growth can determine the success of whole year classes. The most striking data found were on spawning and development, where a threshold of 10°C must be met to suit the needs of all but one species in the present community (longnose sucker need colder temperatures for spawning). This trend of increasing sensitivity of biological requirements in fishes follows Shelford's Law of Tolerance (Shelford 1911, in Kendeigh 1961) where survival can occur over the widest range in temperature, growth is positive over a narrower range, and spawning and development of larvae are the most sensitive to environmental extremes and thus occur over the narrowest range of temperatures.

Case studies documenting the responses of fishes to depressed and homogenized thermal regimes below reservoirs provide real-world examples of how altered temperatures can strongly reduce or extirpate fish populations in some locations, and how fish compensate for, or adapt to, altered thermal regimes in other locations. Examples of effects on burbot and two trout species (one trout species is native in Colorado) as well as those on minnows, suckers, and darters (families that are native to the North Fork) all demonstrate that reduced thermal regimes can strongly delay or alter spawning, egg incubation and hatching, and fry growth and survival, leading to recruitment bottlenecks and, in some cases, extirpation of entire populations. Indeed, even small changes in temperature accumulate to result in large changes in fish life history, due to the cumulative nature of changes in development and growth (e.g., Coleman and Fausch 2007a, 2007b). In addition, temperature provides cues for fish to move to spawning habitat, and cues spawning behavior itself, further demonstrating how temperature is a master variable controlling all aspects of the life history of ectotherms (i.e., cold-blooded animals). Nevertheless, if thermal changes are not too extreme, compensation could occur, as in the tessellated darters that persisted, despite lower fecundity, slower growth, and delayed spawning. Likewise, rapid evolution and adaptation are also possible (Stockwell et al. 2003), such as in the red shiner population that evolved a lower thermal preferendum within relatively few generations in response to a depressed thermal regime. While thermal requirements for the native fish community are apparently met at present in the summer in the North Fork of the Cache la Poudre River between the reservoirs, there is sufficient evidence for deleterious effects on fish species to warrant cautious management strategies in the future regarding thermal regimes.

Data on thermal maxima are much more common for fishes than those on thermal minima. This large discrepancy could be explained by several factors. First, it is relatively difficult to test lower thermal tolerances of fishes because they often approach

0ºC, and these temperatures are difficult to create and maintain in the laboratory (see Coleman and Fausch 2007b). Second, there is a stubborn perception that high temperatures are more limiting than lower temperatures, even though more fish kills are caused by low temperatures than extremely high temperatures (Beitinger 2000). Third, most regulatory guidelines for fish thermal limits are based solely on thermal maxima (McCullough et al. 2009). For example, the database recently developed by the Colorado Division of Wildlife, and used for regulation, contained sparse or no data on thermal minima for most species in the North Fork, including Iowa darter, longnose sucker, common shiner, bigmouth shiner, creek chub, and longnose dace (Todd et al. 2008).

This study focused on the potential effects of the least visible result of hypolimnial release dams, but the other obvious changes caused by dams cannot be ignored. Flow regime, connectivity, sediment transport, and the fish assemblage have all been altered drastically from their historical states. For example, impoundments serve as suitable source habitats for introduced fishes, all of which may compete or prey on native fishes at various life history stages. Furthermore, the reaches downstream of the dams provide habitat where nonnative brown and rainbow trout thrive and most likely prey on native fish, which have little to no evolutionary history with these highly piscivorous fishes. Finally, many of these fish are at the western edge of their natural distribution and likely have unique genetic adaptations to the harsh environment, some of which may be lost due to recent anthropogenic modifications of the environment. Synergistic effects of these various factors could also induce further loss in these fish populations.

The implications of this study expand beyond the Front Range of Colorado. As human populations and demand for water increase in the western United States, it is to be expected that the number and size of reservoirs will increase, and often cause adverse effects on native stream fish assemblages. Several of the transition zone fish species are glacial relicts at the fringe of their natural distribution and are likely distinct from other populations found in the Great Lakes and Mississippi River basins (Scheurer et al. 2003). Comprehending the mechanisms that shape native stream fish communities will be crucial in attempts to develop management strategies at the proper scales (Fausch et al. 2002). By recognizing the needs of these distinct transition zone stream fishes for key factors such as thermal regimes, conservation measures can be refined to enhance their persistence.

Acknowledgments

We thank K. Bestgen for insight into the native fishes, K. Kehmeier for compiling sampling data, J. Sanderson for collaboration with the project's Shared Vision planning group, and W. Miller and T. Beitinger for guidance during the literature review. We thank K. Bestgen and J. Sanderson for insightful comments on a draft manuscript. The research and preparation of this paper was funded by a grant from The Nature Conservancy to K. Fausch and other faculty at Colorado State University.

References cited

Becker, G.C. 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison, Wisconsin.

Beitinger, T.L., W.A. Bennett, and R.W. McCauley. 2000. Temperature tolerances of North American freshwater fishes exposed to dynamic changes in temperature. Environmental Biology of Fishes 58: 237-275.

Bestgen, K.R., K.D. Fausch, and S.C. Riley. 1991. Rediscovery of a relict southern population of lake chub, *Couesius plumbeus*, in Colorado. The Southwestern Naturalist 36:125-127.

Calhoun, S.W., E.G. Zimmerman, and T.L. Beitinger. 1982. Stream regulation alters acute temperature preferenda of red shiners, *Notropis lutrensis*. Canadian Journal of Fisheries and Aquatic Sciences 39:360-363.

Carlander, K.D. 1969. Handbook of freshwater fishery biology. Volume 1. The Iowa State University Press, Ames, Iowa.

Clarkson, R.W. and M.R. Childs. 2000. Temperature effects of hypolimnial-release dams on early life stages of Colorado River basin big-river fishes. Copeia 2:402-412.

Coleman, M.A. and K.D. Fausch. 2007a. Cold summer temperature limits recruitment in age-0 cutthroat trout in high elevation Colorado streams. Transactions of the American Fisheries Society 136: 1231-1244.

Coleman, M.A. and K.D. Fausch. 2007b. Cold summer temperature regimes cause a recruitment bottleneck in age-0 Colorado River cutthroat trout reared in laboratory streams. Transactions of the American Fisheries Society 136: 639-654.

Dunnigan, J.L., and C.L. Sinclair. 2008. Home range and movement patterns of burbot in Koocanusa Reservoir, Montana, USA. Pages 43-54 *in* V.L. Paragamian and D.H. Bennett, editors. Burbot: ecology, management, and culture. American Fisheries Society, Symposium 59, Bethesda, Maryland.

Etnier, D.A., and W.C. Starnes. 2001. Fishes of Tennessee. University of Tennessee Press. Knoxville, Tennessee.

Fausch, K.D. 2007. Introduction, establishment and effects of non-native salmonids: considering the risk of rainbow trout invasion in the United Kingdom. Journal of Fish Biology 71:1-32.

Fausch, K.D. and K.R. Bestgen. 1997. Ecology of fishes indigenous to the central and southwestern Great Plains. Pages 131-166 *in* F.L. Knopf and F.B. Samson, editors. Ecology and conservation of Great Plains vertebrates. Springer-Verlag, New York.

Fausch, K.D., C.E. Torgersen, C.V. Baxter, and H.W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52: 483-498.

www.halligan-seaman.org. Halligan-Seaman water management project. September 2009.

Harig, A.L., and K.D. Fausch. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. Ecological Applications 12:535-551.

Helfman, G.S. 2007. Fish conservation. Island Press. Washington, D.C.

Hubert, W.A., and K.M. Gordon. 2007. Great Plains fishes declining or threatened with extirpation in Montana, Wyoming, or Colorado. Pages 3-13 *in* M.J. Brouder and J.A. Scheurer, editors. Status, distribution, and conservation of freshwater fishes of western North America: a symposium proceedings. American Fisheries Society, Symposium 53, Bethesda, Maryland.

Kendeigh, S.C. 1961. Animal ecology. Prentice-Hall. Englewood Cliffs, NJ.

Li, H. 1968. Fishes of the South Platte River basin. Masters Thesis. Colorado State University. Fort Collins.

McCullough, D.A., J.M. Bartholow, H.I. Jager, R.L. Beschta, E.F. Cheslak, M.L. Deas, J.L. Ebersole, J.S. Foott, S.L. Johnson, K.R. Marine, M.G. Mesa, J.H. Peterson, Y. Souchon, K.F. Tiffan, W.A. Wurtsbaugh. 2009. Research in thermal biology: burning questions for coldwater stream fishes. Reviews in Fisheries Science 17: 90-115.

Paragamian, V.L., and V.D. Wakkinen. 2008. Seasonal movement of burbot in relation to temperature and discharge in the Kootenai River, Idaho, USA and British Columbia, Canada. Pages 55-77 *in* V.L. Paragamian and D.H. Bennett, editors. Burbot: ecology, management, and culture. American Fisheries Society, Symposium 59, Bethesda, Maryland.

Paragamian, V.L., B.J. Pyper, M.J. Daigneault, R.C.P. Beamesderfer, S.C. Ireland. 2008. Population dynamics and extinction risk of burbot in the Kootenai River, Idaho, USA and British Columbia, Canada. Pages 213-234 *in* V.L. Paragamian and D.H. Bennett, editors. Burbot: ecology, management, and culture. American Fisheries Society, Symposium 59, Bethesda, Maryland.

Paragamian, V.L., and M.J. Hansen. 2009. Rehabilitation needs for burbot in the Kootenai River, Idaho, USA and British Columbia, Canada. North American Journal of Fisheries Management 29:768-777.

Platania, S.P., T.R. Cummings, and K.J. Kehmeier. 1986. First verified record of the stonecat, *Noturus flavus* (Ictaluridae), in the South Platte River system, Colorado, with notes on an albinistic specimen. The Southwestern Naturalist 31: 553-555.

Poff, N.L., J.D. Allan, M.B. Bain, J.R. Karr, K.L. Prestegaard, B.D. Richter, R.E. Sparks, and J.C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience 47: 769-784.

Roberts, J.H. and G.D. Grossman. 2001. Reproductive characteristics of female longnose dace in the Coweeta Creek drainage, North Carolina, USA. Ecology of Freshwater Fish 10:184-190

Schlosser, I.J. 1995. Critical landscape attributes that influence fish population dynamics in headwater streams. Hydrobiologia 303:71-81.

Simon, T.P., and D.J. Faber. 1987. Descriptions of eggs, larvae, and early juveniles of the Iowa darter, *Etheostoma exile* (Girard), from Lac Heney, Quebec. Canadian Journal of Zoology 65:1264-1269

Schuerer, J.A., K.R. Bestgen, and K.D. Fausch. 2003. Resolving taxonomy and historic distribution for conservation of rare Great Plains fishes: Hybognathus (Telostei: Cyprinidae) in eastern Colorado basins. Copeia 2003:1-12.

Smith, R.K., and K.D. Fausch. 1997. Thermal tolerance and vegetation of Arkansas darter and johnny darter from Colorado plains streams. Transactions of the American Fisheries Society 126:676-686.

Stewart, K.W. and D.A. Watkinson. 2004. The freshwater fishes of Manitoba. University of Manitoba Press.

Stockwell, C.A., A.P. Hendry, and M.T. Kinnison. 2003. Contemporary evolution meets conservation biology. Trends in Ecology and Evolution. 18: 94-101.

Todd, A.S., M.A. Coleman, A.M. Konowal, M.K. May, S. Johnson, N.K.M. Vieira, and J.F. Saunders. 2008. Development of new water temperature criteria to protect Colorado's fisheries. Fisheries 33:433-443.

Tsai, C. 1972. Life history of the Eastern johnny darter, *Etheostoma olmstedi* Storer, in cold tailwater and sewage-polluted water. Transactions of the American Fisheries Society 1:80-88.

Walford, C.D., and K.R. Bestgen. 2008. The nonnative Iowa darter (*Etheostoma exile*) established in the Yampa River, Colorado and Green River, Utah. The Southwestern Naturalist 53: 529-533.

Wismer, D.A. and A.E. Christie. 1987. Temperature relationships of Great Lakes fishes: a data compilation. Great Lakes fishery commission special publication 87-3. 165 p.

Woodling, J. 1985. Colorado’s little fish: a guide to the minnows and other lesser known fishes in the state of Colorado. Colorado Division of Wildlife, Denver.

Table 1. Native fishes of the North Fork of the Cache la Poudre River, Colorado collected in the segment between Halligan and Seaman Reservoirs, between 1959 and 2009.

Family	Species	Scientific name	Conservation Status	Last Seen
Catostomidae	longnose sucker	*Catostomus catostomus*	-	2006[2]
Catostomidae	white sucker	*Catostomus commersoni*	-	2009[3]
Cyprinidae	fathead minnow	*Pimephales promelas*	-	2009[3]
Cyprinidae	longnose dace	*Rhinichthys cataractae*	-	2009[3]
Cyprinidae	bigmouth shiner	*Notropis dorsalis*	-	1959[1]
Cyprinidae	common shiner	*Luxilus cornutus*	state threatened	1959[1]
Cyprinidae	creek chub	*Semotilus atromaculatus*	-	2009[3]
Percidae	johnny darter	*Etheostoma nigrum*	-	2009[3]
Percidae	Iowa darter	*Etheostoma exile*	species of concern	2006[2]

[1]Collected by Frank Cross, University of Kansas Ichthyological Survey
[2]Collected by Ken Kehmeier, Colorado Division of Wildlife monitoring
[3]Collected by Ken Kehmeier and Kurt Fausch, CSU Fish Conservation Class FW400

Table 2. Lower incipient lethal temperatures for the native fishes of the North Fork of the Cache la Poudre River, Colorado (compiled by Carlander 1969). Numbers within boxes show the acclimation temperatures (°C) tested. Yellow shading shows the assumed range of lower incipient lethal temperatures over the range of acclimation temperatures tested. Blue shading shows the fishes for which no data exist.

	Temperature (C°)												
SPECIES	0	1	2	3	4	5	6	7	8	9	10	11	12
White sucker			20	20			25						
Longnose sucker													
Longnose dace													
Creek chub	15	20	22		25								
Bigmouth shiner													
Iowa darter													
Johnny darter													
Common shiner	15	20	20	20	20	20	20	25					
Fathead minnow			20								30		

Lower Incipient Lethal Temperature with Acclimation Temperature

Lacks Data

Table 3. The relationships of growth and temperature for native fishes of the North Fork of the Cache la Poudre River, Colorado. All values were estimates from laboratory studies compiled by Wismer and Christie (1987). Optimum (O) is the temperature at which maximum growth rate occurs. The lower limit (LL) is the point below which no growth is possible. The upper limit (UL) is also shown if it was explicitly stated, rather than assumed. Blue shows the fishes for which data do not exist.

	Temperature (C°)																														
SPECIES	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
White sucker													LL												O	O	O	O		UL	
Longnose sucker																															
Longnose dace		LL																													
Creek chub																															
Bigmouth shiner																															
Iowa darter																															
Johnny darter																															
Common shiner																															
Fathead minnow								LL																		O	O				

LL=Lower Limit

UL=Upper Limit

O=Optimum

Within Tolerable Range

Lacks Data

Table 4. Spawning and hatching as a function of temperature for native fishes of the North Fork of the Cache la Poudre River, Colorado. Yellow shows the temperature range where spawning is known to occur. The symbol H shows known hatching temperatures which may overlap with spawning temperatures. The symbol O stands for the optimum temperature at which spawning events occur most frequently. No data were found for bigmouth shiner.

	Temperature (C°)																														
SPECIES	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
White sucker[1]											O	O			H	H	H														
Longnose sucker[1]						O						H	H	H	H																
Longnose dace[1]															H	H	H														
Creek chub[2]														O	O	O	O	O													
Bigmouth shiner																															
Iowa darter[2]*														H	H	H	H														
Johnny darter[1]														H	H	H	H	H	H	H	H	H	H	H	H						
Common shiner[1]																			O	O	O										
Fathead minnow[1]																									H	H	H				

H=Hatching

O=Optimum Spawning

Within Tolerable Range of Spawning

Lacks Data

[1]Wismer and Christie 1987
[2]Becker 1983
*Simon and Faber 1987

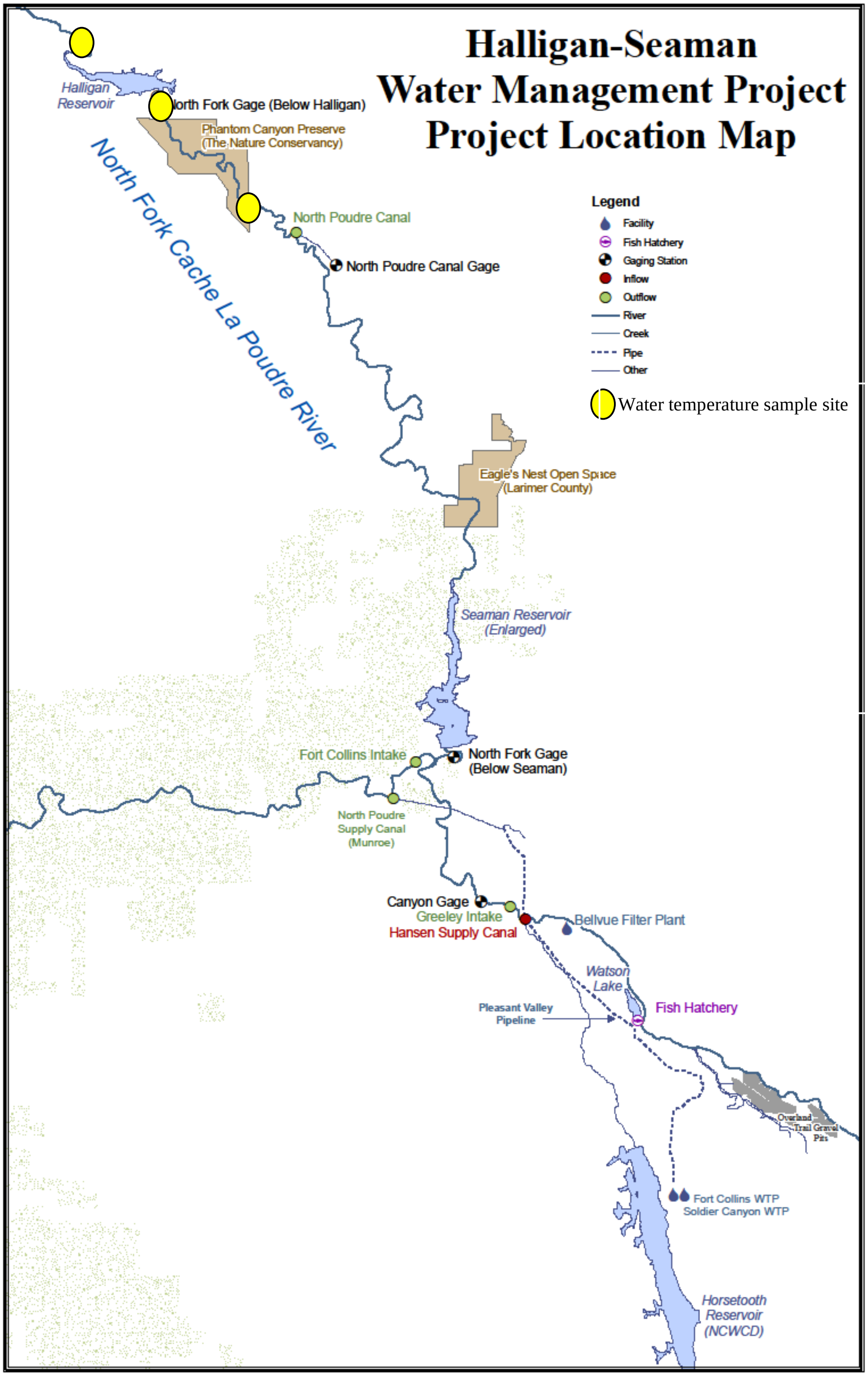

Figure 1. The North Fork Cache la Poudre River and Halligan-Seaman Water Management Project location map with water temperature sampling sites from 2003.

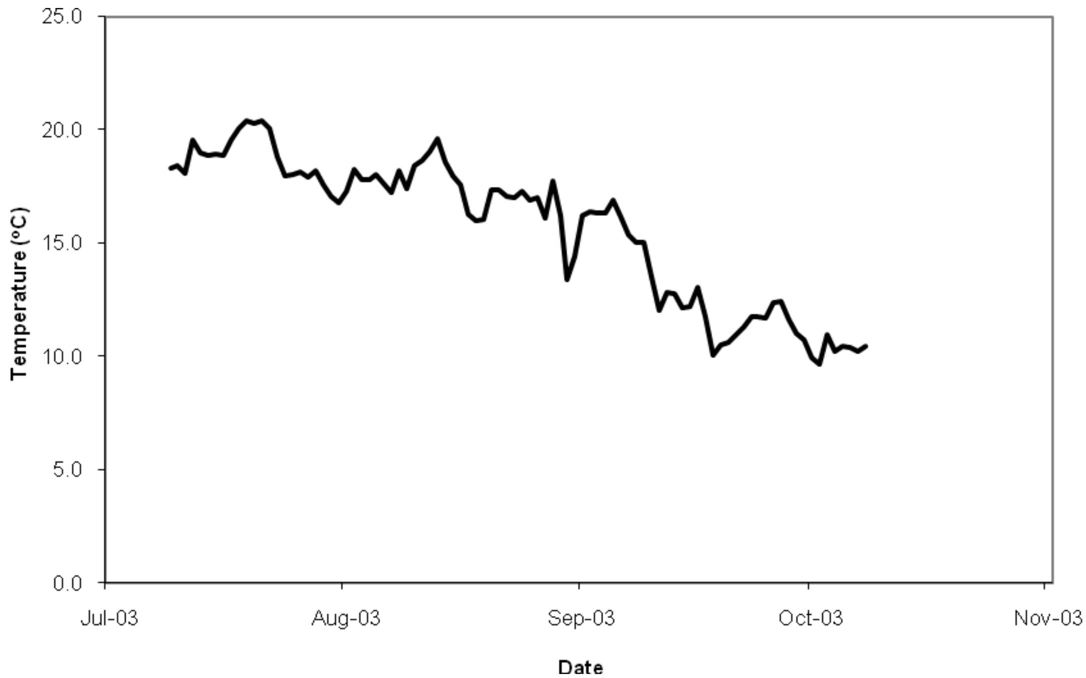

Figure 2. Average daily water temperatures in the North Fork of the Cache la Poudre River above Halligan Reservoir in 2003.

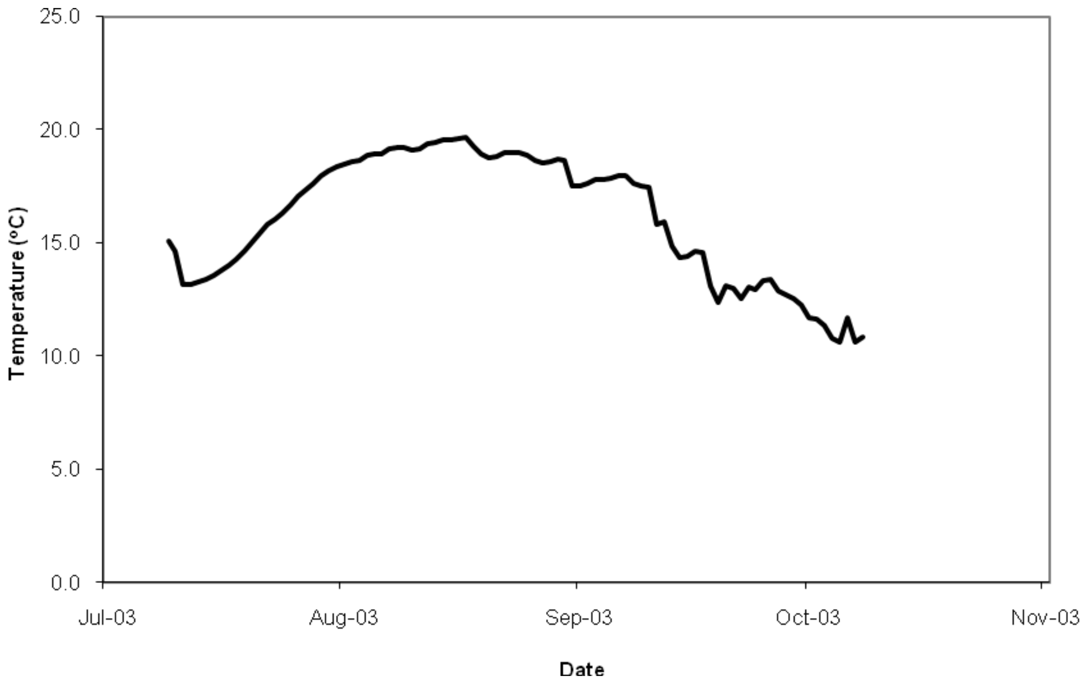

Figure 3. Average daily water temperatures in the North Fork of the Cache la Poudre River below Halligan Reservoir in 2003.

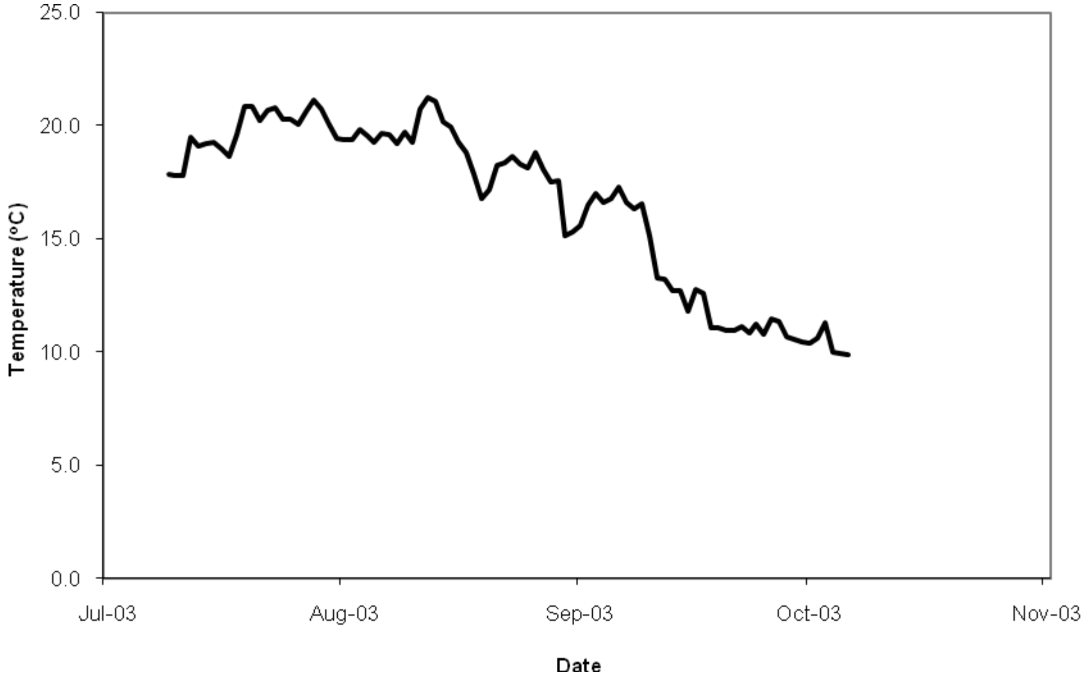

Figure 4. Average daily water temperatures in the North Fork of the Cache la Poudre River below Phantom Canyon in 2003.

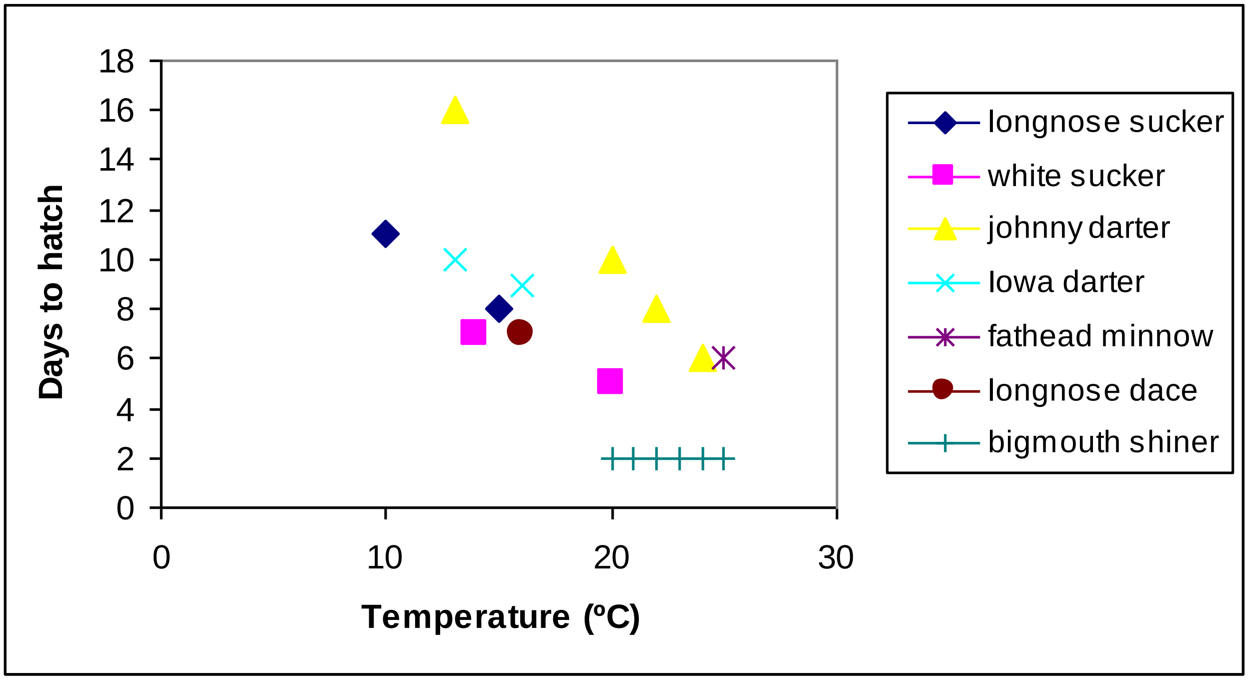

Figure 5. The number of days required for eggs to hatch as a function of water temperature in native fishes found in the North Fork of the Cache la Poudre River, Colorado (data from Carlander 1969, Becker 1983).

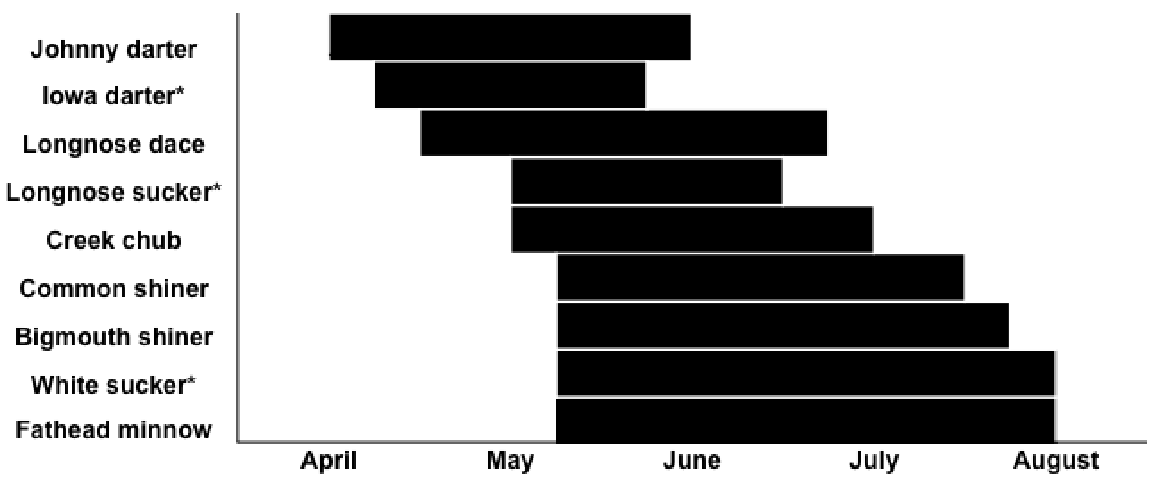

Figure 6. A phenology of spawning periods for the native fishes of the North Fork of the Cache la Poudre River, Colorado (Becker 1983). An asterisk (*) denotes species for which data were available on spawning period from Colorado (Carlander 1969; Faber and Simon 1987).

Appendix I

Life History of Native Fishes in the North Fork Cache la Poudre River

Sucker Family (Catostomidae)

Catostomus catostomus – longnose sucker

Longnose suckers spawn over gravel from mid-April to June in Colorado and when coexisting with white sucker, spawn earlier. This earlier spawning at colder temperatures could explain why longnose sucker are found at higher elevations than white sucker (Li 1968; Carlander 1969). Males mature sexually at age 2 and females at age 3 in Colorado (Carlander 1969). It is probable that longnose suckers would use the reservoirs within the drainage when possible and use the stream mainly for spawning and rearing (Stewart and Watkinson 2004). Longnose sucker are widespread in North America, ranging from Alaska south to Colorado, and east to Maryland and Labrador (Becker 1983). Colorado is the southernmost state within the native range of the longnose sucker.

Catostomus commersoni – white sucker

Spawning occurs over gravel and coarse sand from late-May into August in Colorado (Carlander 1969). White sucker reach sexual maturity at age 2 in males and age 4 in females and have been reported to live to age 17 in Colorado (Carlander 1969; Etnier and Starnes 2001). Natural hybrids of white and longnose suckers are known to occur although different spawning times could act as a preventative mechanism (Stewart and Watkinson 2004). White suckers have one of the most widespread ranges of suckers occurring from Labrador southward to New Mexico and north to the Northwest

Territories and British Columbia. White sucker can also be important energy sources for the ecosystem. They are widespread in Colorado and are tolerant of a wide range of environmental conditions (Becker 1983).

Minnow Family (Cyprinidae)

Luxilus cornutus – common shiner (**a threatened species in Colorado**)

Spawning occurs from late May to mid-July over gravel substrates in Wisconsin and is often associated with nest building species such as creek chub (Becker 1983). This species prefers coarse substrates for nest building and clear waters. The average life span is four years with some individuals reaching age 6 and in one case, age 9. Sexual maturity is reached at age 2 or age 3.

Common shiner are abundant throughout the Great Lakes and Mississippi River basin but also includes a range spanning from Newfoundland to Ontario and south to Kansas. This fish is a glacial relict and Colorado is the westward extent of their distribution. Listed as Threatened species in the state of Colorado, the beginning of a continuing decline of common shiners was documented by Li (1968). Their distribution within the state presumably shifted upstream to cleaner portions of the South Platte basin with more consistent flow, although it has not been collected in the North Fork of the Cache la Poudre since 1959.

Notropis dorsalis – bigmouth shiner

The limited reproductive biology data suggests spawning occurs from late May to early August in the Midwest (Becker 1983). There have been no studies conducted on the spawning habits of this species. Bigmouth shiner prefer gravel and sandy substrates in clear water. Rainfall and possibly flood events are also thought to cue spawning in this species. The average bigmouth shiner lives to age 2 with some reaching age 4 (Carlander 1969; Becker 1983). Sexual maturity is thought to be reached at age 2; it was suggested that bigmouth shiners matured at age-1 in Missouri (Becker 1983).

Bigmouth shiner show disjunct distributions throughout the Great Lakes basin and are found from Minnesota to Missouri within the Mississippi River basin. The Front Range in Colorado and Wyoming is the westward limit of distribution of the bigmouth shiner (Becker 1983). In midwestern U.S. and Canadian streams, bigmouth shiner often can attain high abundance and therefore could act as a significant source of energy and nutrient flow within the fish community (Stewart and Watkinson 2004).

Pimephales promelas – fathead minnow

Fathead minnow spawn on sand from May through August and can spawn multiple times (Carlander 1969). However, in Colorado plains streams they likely spawn any month that water temperatures are suitable (K. Fausch and K. Bestgen, unpublished observations). Maturity appears variable at age 1 to age 2 but has been recorded as early as age 0 as far north as Minnesota (Carlander 1969; Becker 1983). Fish often live to age 2 with few individuals surviving to age 3. The fathead minnow is one of the most abundant and widespread cyprinids in North America. Their range spans from the Maine to California and from Alberta southward to Mexico, because of its wide range of tolerances to various water quality parameters and habitats (Becker 1983).

Rhinichthys cataractae – longnose dace

Longnose dace spawn between May and July throughout their range and can spawn multiple times in a season over coarse sand and gravel substrates (Roberts and Grossman 2001). Fish live to age 4 and mature at age 2 (Becker 1983). This species favors riffles and rocky substrate and is tolerant of a wide range of turbidity and temperature (Stewart and Watkinson 2004). The longnose dace is the most widely distributed cyprinid in North America occurring from the Northwest Territories and the Pacific Northwest in the U.S. east to Labrador, and south to Mexico (Roberts and Grossman 2001).

Semotilus atromaculatus – creek chub

Creek chub spawn from May to July in gravel nests created by males (Becker 1983). Creek chub can reach age 8 although few live past age 4. Maturity is reached at age 1 in females and age 3 in males, which could possibly account for faster growth of males. Creek chub are an efficient predator on invertebrates and small fish, making them an intermediate and top predator in small stream food webs (Stewart and Watkinson 2004). This species prefers cool, and clear to slightly turbid water with coarse gravel and sand substrates. Creek chub are found from Quebec to Florida and westward to Wyoming (Becker 1983).

Darter Family (Percidae)

Etheostoma exile – Iowa darter (**a species of special concern in Colorado**)

This species occurs in cool, clear, slower-moving streams and rivers with aquatic vegetation. It can reach age 4 although most populations are composed mainly of age 1 and age 2 fish (Becker 1983; Woodling 2006; Walford and Bestgen 2008). Adult fish spawn at temperatures from 12º-15ºC from late April to early June in Colorado (Simon and Faber 1987). Adhesive eggs are attached to vegetation and exposed tree roots.

The Iowa darter is thought to be a glacial relict at the western edge of its range, native only to the South Platte River basin in Colorado (Scott and Crossman 1973; Walford and Bestgen 2008). The natural distribution extends from the Great Lakes basin to Alberta and south to Colorado. A Colorado state species of special concern, Li (1968) documented a decline of this fish in the South Platte basin in the 1960's, presumably from habitat degradation.

Etheostoma nigrum – johnny darter

Spawning generally occurs from April through June over sand (Becker 1983). Johnny darters may reach sexual maturity at age 1 with life-spans rarely reaching age 3. Unlike Iowa darters, johnny darters prefer habitat with sandy substrate and no vegetation cover. Johnny darters are habitat generalists which could explain their widespread distribution throughout North America from northern Ontario south to Alabama, west to Colorado and east to North Carolina. Their generalist nature could also explain high abundances in the South Platte River basin of northeast Colorado (Becker 1983; Smith and Fausch 1997).