

DISSERTATION  
COLD SUMMER STREAM TEMPERATURES REDUCE RECRUITMENT OF  
NATIVE CUTTHROAT TROUT POPULATIONS

Submitted by

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Fish, Wildlife, and Conservation Biology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

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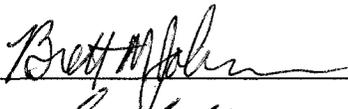
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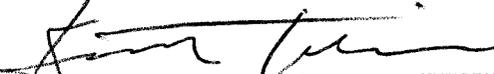
  
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ABSTRACT OF DISSERTATION  
COLD SUMMER STREAM TEMPERATURES REDUCE RECRUITMENT OF  
NATIVE CUTTHROAT TROUT POPULATIONS

Translocation is a key strategy for conserving subspecies of native cutthroat trout *Oncorhynchus clarkii*, which have declined markedly throughout their native ranges in North America. Previous research showed that translocation success in high-elevation southern Rocky Mountain streams was more likely in warmer streams, and suggested that cold temperatures could limit juvenile trout recruitment and explain translocation failures. However, the effects of cold temperature on recruitment had not been previously investigated. I studied these effects using an integrated laboratory and field approach. In the lab, age-0 Colorado River cutthroat trout *O. c. pleuriticus* were subjected to one of three natural temperature regimes during two years, which averaged 7°C, 8.5°C and 10.0°C during the warmest summer month. From hatching to swimup, mean survival was high during both years, ranging from 97% (warm regime) to 85% (cold). After swimup, warm regime fry had much greater survival and grew more than 60% larger, on average, than cold regime fry by the onset of winter in the 2003 experiment. The pattern of lower survival in colder temperature regimes held through mid-winter, with 76% survival (warm regime), 62% (intermediate), and 29% (cold). Likewise, during the 2004 experiment, survival to early winter ranged from 44% (warm regime) to 10% (cold). Most mortality in all treatments occurred during a recruitment bottleneck encompassing a 4- to 6-week period following swimup. A response surface

analysis of percent dry weight data indicated that the energy content of fry at swimup was lower in colder regimes, and declined during the recruitment bottleneck in all regimes. In the field, I monitored temperatures and conducted surveys to estimate densities of age-0 fry at peak emergence in six headwater streams that varied in thermal characteristics. Density and growth increased with Celsius degree days during the growing season. My results indicate a strong recruitment bottleneck after swimup, when temperature-related energy deficits probably cause significant mortality. Fisheries managers in the southern Rocky Mountains may increase translocation success of native cutthroat trout by selecting sites with  $\geq 800$ -900 degree days during the growing season, and fry grow to  $\geq 30$ -35 mm by the end of the growing season.

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## DEDICATION

This dissertation is dedicated to the two most inspiring people in my life – my father, and my wife. My father, Sidney Coleman, continues to inspire me by persevering more than twenty years after his faculties were diminished by four brain aneurysms. He continues to be a great man, and I attribute many of my skills and accomplishments to his influences on me when I was young. My wife, Cecelia Coleman (Cele), despite facing a cancer diagnosis and several months of chemotherapy during the second year of my graduate program, maintained her support of me with an optimum combination of pats on the back and kicks in the rear.

Facing the very sobering prospects of mortality or the sudden loss of one's faculties would be difficult under any circumstance. I have learned that facing the prospects of these things happening to your loved ones may be no less challenging. While my loved ones faced their challenges with grace and dignity, my empathy for them threatened to erode my resolve and dampen my ambitions. In the long run, their challenges have helped place mine (completing my graduate program) in perspective.

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## INTRODUCTION

Colorado River cutthroat trout (CRCT; *Oncorhynchus clarkii pleuriticus*) have declined throughout their native range in the headwaters of the Colorado River basin, due to overfishing, habitat degradation, and invasions by nonnative salmonids (Behnke 1992; Young et al. 1996). Estimates of their current distribution have varied, but the most recent estimates suggest that CRCT now occupy about 14% of their historic native range (Hirsch et al. 2005). Due to their decline, CRCT were considered a Federal Category 2 “candidate species” proposed for listing under the Endangered Species Act (ESA) before the categories were dropped in 1996 (CRCT Coordination Team 2006). Although no longer federally listed under the ESA, CRCT have been granted special status by the states of Colorado, Utah, and Wyoming, and the U.S. Forest Service and Bureau of Land Management. These state and federal agencies formed the CRCT Coordination Team to coordinate efforts to increase the distribution and abundance of CRCT, and thereby reduce or eliminate the threats that warrant its special status (CRCT Coordination Team 2006).

One strategy used by fisheries managers to prevent listing has been to establish new populations by translocating genetically pure CRCT to streams where no trout occurred originally (e.g., above natural barriers), or where nonnative trout (usually brook trout, *Salvelinus fontinalis*) that displaced CRCT were removed. An objective of the CRCT Conservation Agreement (CRCT Coordination Team 2006) is to increase the number of stream populations of CRCT in the three states, by restoring them to streams within their native range. Managers report that current restoration projects cost \$50,000

to \$100,000 or more, so these translocations will require substantial resources to complete (Bruce Rosenlund, U.S. Fish and Wildlife Service, personal communication). The primary goals of this research were to: 1) identify the lower thermal limits on translocation success of native cutthroat trout in high-elevation streams in Colorado, and 2) identify ways to use thermal criteria for selecting streams where translocations are most likely to succeed, and thereby reduce the costs, in time and money, that often hinder such conservation efforts.

With regard to habitat, Harig and Fausch (2002) reported that low summer stream temperature was correlated with low translocation success of native cutthroat trout in 27 streams in Colorado and New Mexico. These streams made up nearly the entire set of 28 streams where translocations of greenback (*O. c. stomias*) and Rio Grande cutthroat trout (*O. c. virginalis*), two subspecies closely related and with similar ecologies to the Colorado River cutthroat trout, had been attempted up to 1995. Harig and Fausch (2002) found that most streams where cutthroat trout had been translocated reached only 6-11°C (average daily temperature) during summer when cutthroat trout spawn and their fry mature, and remain near freezing during winter. An incubation temperature of 2°C reduced survival in embryos of rainbow trout *O. mykiss* and cutthroat trout (Hubert et al. 1994; Stonecypher et al. 1994; Hubert and Gern 1995), and decrease metabolic efficiency during egg development (Morrison and Smith 1980; Dwyer et al. 1981). However, survival rates were high (86-95%) for cutthroat trout embryos incubated at either 4 or 7°C (Stonecypher et al. 1994), temperatures that lie at or below the cold end of the range of summer temperatures for southern Rocky Mountain streams where translocations had been attempted (A. Harig and K. Fausch, unpublished data). Therefore, cold

temperatures during incubation are unlikely to explain low translocation success. Harig and Fausch (2002) hypothesized that cold summer temperatures had caused translocation failures by slowing growth and development and reducing recruitment of age-0 fry, a hypothesis not previously tested in either the laboratory or field.

Herein, I summarize the results of a three-year integrated laboratory and field study that investigated the effects of cold summer temperature on growth and recruitment of age-0 cutthroat trout between hatching and mid-winter. Chapter 2 summarizes the results of laboratory experiments conducted during 2003 and 2004 (Coleman and Fausch in press a). In both years, I subjected newly hatched Colorado River cutthroat trout fry to three temperature regimes that covered a range similar to those where translocations of greenback and Rio Grande cutthroat trout had resulted in absent, low-, or high-abundance populations. Through these experiments, I identified a strong, temperature-related recruitment bottleneck that occurs after swimup, during the critical period when fry are making the transition from using yolk as their primary energy source, to consuming exogenous prey (Harig and Fausch 2002; Coleman and Fausch in press a). Chapter 3 summarizes a field study, in which I monitored temperatures and conducted surveys to estimate fry abundance and size at peak emergence in six streams where I predicted cutthroat trout recruitment would be low or high based on summer temperature regimes (Harig and Fausch 2002; Coleman and Fausch in press b). I further used laboratory derived estimates of survival from swimup to the start of winter to estimate the proportion of these fry that would survive to the start of winter in their natal streams, and identified probability thresholds in growing season temperatures and size at the start of

winter that will be useful in prioritizing streams for translocations or other conservation actions in the future.

### **Project objectives**

The objectives of the laboratory experiments were to test the effects of low water temperature on cutthroat trout fry growth and survival in the laboratory under controlled conditions, relate them to the findings in the field, and to investigate the mechanisms underlying cold-temperature limitation of recruitment in Colorado River cutthroat trout. The objective of the field study was to relate recruitment (i.e., abundance) of fry of native cutthroat trout to stream temperatures. Together, the laboratory experiments and field study serve to test the overall hypothesis of Harig and Fausch (2002) that low translocation success of native cutthroat trout is caused in large part by low summer water temperatures, to evaluate the mechanisms of this recruitment bottleneck, and to refine thermal guidelines for successful translocations of native cutthroat trout in high elevation streams in the southern Rocky Mountains.

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**CHAPTER 2: Cold Summer Temperature Regimes Cause a Recruitment  
Bottleneck in Age-0 Colorado River Cutthroat Trout Reared in Laboratory Streams**

Accepted for Publication in *Transactions of the American Fisheries Society*.

## **Abstract**

Native salmonids are increasingly restricted to upstream habitats that may be too cold to sustain recruitment, and recruitment limitation due to cold temperatures is a main hypothesis to explain translocation failures of native cutthroat trout *Oncorhynchus clarkii* in high-elevation streams in the southern Rocky Mountains. I subjected Colorado River cutthroat trout fry to one of three temperature regimes (cold, intermediate, or warm) in laboratory streams during each of two years, which averaged 7°C, 8.5°C and 10°C during the warmest summer month. The regimes mimicked those of natural streams where translocated fish had died out, or produced populations of cutthroat trout of low or high abundance. Mean fry survival rate from hatching through swimup was high during both experiments, ranging from 97% in the warm regime to 85% in the cold. After swimup, fry in the warm regime grew more than 60% larger on average than those in the cold regime by the onset of winter in 2003, during a 22-week period. Survival rates through mid-winter were also higher in the warm regime (76%) than in the intermediate (62%) and cold (29%) regimes. A similar pattern of temperature-related growth and mortality was apparent in the 2004 experiment (12 weeks), in which survival rates to early winter ranged from 44% in the warm regime to 10% in the cold. Most mortality in all three treatments occurred during a recruitment bottleneck encompassing a 4- to 6-week period following swimup. Analyses of size and percent dry weight indicated that the energy content of fry after swimup was lower in colder regimes, and declined during the recruitment bottleneck in all three regimes. My findings indicate a strong recruitment bottleneck after swimup when temperature-related energy deficits apparently cause

significant mortality. Analysis of degree days accumulated during the growing season in the test regimes indicated that managers may increase viability of translocated populations by selecting sites that accumulate >900 degree days.

## **Introduction**

Native salmonids worldwide are commonly relegated to small portions of their original range due to invasions by nonnative fishes, habitat degradation, and overfishing (Kitano 2004; Fausch et al. 2006). For those affected strongly by invasions, managers often intentionally isolate populations above migration barriers to prevent hybridization, competition, or predation from nonnative salmonids downstream, and preserve genetically pure native stocks (Hilderbrand 2003; Novinger and Rahel 2003). However, such isolation may increase the risk of local extinction from harsh abiotic factors or stochastic demographic effects (Caughley 1994, McElhaney et al. 2000; Morita and Yamamoto 2002). In particular, habitats now occupied by native salmonids at high latitudes or high elevation may be too cold for recruitment needed to sustain these populations (Harig and Fausch 2002; Borgström and Museth 2005).

Isolation management is commonly used for native cutthroat trout *Oncorhynchus clarkii*, whose populations have decreased drastically since the modern settlement of the western U.S. (Young 1995; Harig et al. 2000). The cutthroat trout is a polytypic species, originally widely distributed in the West and arranged in 14 subspecies (Behnke 1992, 2002). Three closely related subspecies with similar ecologies inhabit the southern Rocky Mountain region, including the Colorado River *O. c. pleuriticus*, greenback *O. c. stomias*, and Rio Grande cutthroat trout *O. c. virginialis*. All three are the subject of conservation management plans aimed at increasing their distribution and abundance, to

prevent further endangerment and listing under the Endangered Species Act (USFWS 1998; CDOW 2003; CRCT Coordination Team 2006). The main strategies to achieve this goal are reconnaissance in remote watersheds to find undiscovered populations of genetically pure native cutthroat trout, and translocation of pure native trout into streams and lakes above barriers where nonnative salmonids have been removed or no trout occurred originally. Translocations are expensive and time-consuming, however, so fisheries biologists in Colorado have sought to understand better the factors determining translocation success in high-elevation streams.

Harig and Fausch (2002) reported that cold summer stream temperature was an important factor limiting translocation success in greenback and Rio Grande cutthroat trout, in conjunction with physical habitat. Translocation success, measured in three categories of adult fish abundance, was correlated with mean July stream temperatures, bankfull pool width, and the number of deep pools. Model predictions indicated that translocations would likely fail to establish populations in streams with mean July temperatures  $<7.1^{\circ}\text{C}$  (at the average width and number of pools). In otherwise similar streams with mean July temperatures averaging  $7.8^{\circ}\text{C}$  and  $10.0^{\circ}\text{C}$ , the model predicted low and high abundance populations, respectively. State and federal fisheries managers throughout the central and southern Rocky Mountains have recently begun applying the model of Harig and Fausch (2002) to evaluate potential translocation sites and the expected long-term success of current populations in streams (cf., Young and Guenther-Gloss 2004; Young et al. 2005). Although this model is widely used, its accuracy may be limited because it is based on correlative evidence from a modest number of streams ( $n=27$ ). This sample included nearly all the streams where these two subspecies of

cutthroat trout had been translocated (there had been few translocations of Colorado River cutthroat trout), but only six of these were cases where the fish had died out. Therefore, there is potential for error when predictions are made for other streams if other unmeasured factors that are correlated with July temperature or other habitat variables actually control translocation success.

Previous research and field data suggest that the mechanism for poor translocation success at cold temperatures may be mortality of age-0 fish during their first few months of life. High-elevation streams where cutthroat trout have been translocated are cold. Most reach only 6-11°C during summer when cutthroat trout spawn and their fry mature, and remain near freezing during winter (Harig and Fausch 2002). Incubation temperatures still colder than this (2°C) are known to reduce survival in embryos of rainbow trout *O. mykiss* and cutthroat trout (Hubert et al. 1994; Stonecypher et al. 1994; Hubert and Gern 1995), and decrease metabolic efficiency during egg development (Morrison and Smith 1980; Dwyer et al. 1981). However, survival rates were high (86-95%) for cutthroat trout embryos incubated at either 4 or 7°C (Stonecypher et al. 1994), temperatures that extend well below the cold end of the range for high-elevation translocation streams in the southern Rocky Mountains (A. Harig, Trout Unlimited, Boise, Idaho and K. Fausch, unpublished data). This suggests that incubation temperatures there do not severely limit embryo survival, and thus recruitment limitation due to cold temperature regimes may be more severe after swimup. Harig and Fausch (2002) speculated that cold temperature regimes may also reduce growth of age-0 fry, which may reduce their survival during their first summer or the ensuing winter (Borgström and Museth 2005). This is consistent with a demographic model of native

cutthroat populations, which revealed that survival of age-0 fish was an important factor determining population growth rates in isolated populations (Hilderbrand 2003).

However, to date no experiments have been conducted to measure how cold temperatures affect survival and growth after hatching, particularly using realistic temperature regimes that mimic those in natural streams.

Here I describe the results of laboratory experiments conducted as part of an integrated laboratory and field study of the effects of cold temperature regimes on translocation success of native cutthroat trout (Coleman and Fausch in press). My first objective was to test the hypothesis proposed by Harig and Fausch (2002) that cold summer temperatures reduce growth and survival of age-0 cutthroat trout, and may thereby contribute to the failure of translocations in cold streams by limiting recruitment. My second objective was to characterize the temporal pattern of mortality, growth, and energy content in fish subjected to different cold temperature regimes to identify any recruitment bottlenecks (i.e., discrete periods of high mortality), and determine whether mortality could be caused by effects of cold temperature on metabolism.

## **Methods**

I tested the effect of three natural temperature regimes on growth and survival of age-0 Colorado River cutthroat trout from hatching through mid-winter, during a 26-week laboratory experiment in summer and fall of 2003 that consisted of two phases. The first (Phase 1) encompassed the early larval stage from hatching to swimup, when fish are referred to as 'sac fry'. The second (Phase 2) encompassed the late-larval and early juvenile stages from swimup through mid-winter. I repeated this experiment during 2004, but modified the experimental design to accommodate destructive sampling of fish

throughout the experiment to more thoroughly assess the growth and energy content of fish raised in each thermal regime. This second experiment encompassed the first 17 weeks after hatching, which included the period after swimup during which I observed the highest mortality in the 2003 experiment.

Because translocation success was lower in high-elevation streams in Colorado with colder summer temperatures (Harig and Fausch 2002), I predicted that survival rates would be lower in colder temperature regimes during both years. Further, I predicted that a recruitment bottleneck would occur during Phase 1 or Phase 2, with greater mortality rates in colder temperature regimes. For the 2004 experiment, I also predicted that the energy content of fish would decrease as yolk was depleted during the period shortly after swimup, and then increase as fish adapted to exogenous food consumption. I expected that this rate of increase would be faster in the warmer regimes, where fish were exposed to a greater number of thermal units following the transition to exogenous foods.

### ***Subjects and acclimation***

For the 2003 experiment, I obtained eyed embryos of Nanita Lake Colorado River cutthroat trout on 15 July 2003 (Colorado Division of Wildlife Hatchery, Glenwood Springs). The Nanita Lake strain was originally translocated from Trappers Lake, Colorado at 2940 m elevation (Behnke 1992), and is cold adapted. The embryos had been maintained at a constant temperature of 8.8°C for 29 days after spawning. I transported moist embryos in a vented plastic container, resting on ice, to the Foothills Fisheries Facility at Colorado State University, then rehydrated and acclimated the embryos from 8.0°C to 7.0°C over a 30-minute period. I then sanitized the embryos in PVP solution (100 mg/L, Providone iodine in water). Embryos were incubated in three

half-full, aerated 40-L aquaria at a constant 7.0°C through hatching, and half the volume of each tank was replaced daily.

For the 2004 experiment, I obtained a second set of eyed embryos of Nanita Lake Colorado River cutthroat trout on 2 July 2004 from the same source. These embryos were maintained at a constant temperature of 8.0°C for 29 days at the hatchery, then shipped via overnight courier to Colorado State University. Upon receipt, the embryos were gradually acclimated and sanitized as before, and incubated using the same apparatus at 7.5°C until hatching.

### *Temperature regimes*

I synthesized temperature regimes (Figure 1) to mimic those of relatively cold high-elevation streams where cutthroat trout translocations had resulted in absent, low, or high abundance populations. I used thermograph data collected by Harig and Fausch (2002, and unpublished data) during 1996-1998 from 27 streams studied in the southern Rocky Mountains in Colorado and New Mexico. Temperatures were averaged across streams in each set for each day of the year, and across years, and the results smoothed using a 31-d moving average. To differentiate the regimes evenly based on average summer temperatures, I increased daily temperature in the warm regime to 106% of synthesized values, and decreased daily temperature in the cold regime to 90%. This resulted in three clearly differentiated temperature regimes with mean August temperatures evenly spaced at approximately 7.0°C, 8.5°C, and 10.0°C. During the 2003 experiment, thermographs placed in the head tanks supplying water to each temperature regime (Onset Tidbit dataloggers, Onset Computer, Bourne, Massachusetts) indicated that mean weekly regime temperatures exceeded those planned only slightly, averaging

0.3°C (SE=0.28), 0.2 °C (SE=0.048), and 0.4 °C (SE =0.094) higher than planned in the warm, intermediate, and cold regimes, respectively. During the 2004 experiment, the respective mean weekly head tank temperatures averaged 0.4°C (SE=0.074) , 1.1°C (SE=0.13), and 0.9°C (SE=0.13) higher than planned. These differences were due to the inability to maintain precise control of low temperatures as they dropped during the onset of winter through the end of the experiment. I also measured temperature daily before the first feeding using a thermocouple thermometer (Model #39658-K, Atkins Technical Inc., Gainesville, Florida), and found that temperature variation among tanks within each treatment was no greater than 0.2 °C during the 2004 experiment. During 2003, variation within treatments was  $\leq 0.3$  °C, except during one three day period when hard water deposits partially occluded the inlet pipes in three streams, causing variation to increase briefly in the cold and intermediate regimes, to  $\leq 0.9$  °C. Additional thermographs placed at the outlet of one (2003) or two (2004) stream tanks in each treatment showed that outlet temperatures ranged from 0.3 to 0.5 °C warmer than the head tanks throughout the study. Head tank temperatures were used for all analyses because they represent the temperature of water supplied at the inlet of every stream in the treatment, whereas outlet temperatures represent the maximum to which fish were exposed and may not be representative of all tanks in a treatment due to sampling error.

### ***Artificial stream apparatus***

The apparatus consisted of 24 independent artificial streams (8 for each temperature regime) to which well water was supplied at a rate of 4.0 L/min. Each tank was 117 cm long, 51 cm wide, and 25 cm high and had a pea gravel substrate. Screen dividers were used to exclude the fish from turbulence at the inlet and from the standpipe

at the outlet, so tank area accessible to fish was approximately 434 cm<sup>2</sup> (92.5 cm by 49.2 cm). Approximately 116 cm<sup>2</sup> near the inlet screen was occupied by the outlets of two air lift pumps, which drew water downward through the gravel, provided under-gravel filtration, and generated additional current at the inlet screen. Water depth in each tank ranged from 2.5 cm at the inlet screen to 7.5 cm at the outlet screen. Water velocity in the streams ranged from 1.0 to 7.0 cm/s, and averaged 2.2 cm/s when measured at 50% depth at 32 evenly spaced locations in each of two tanks from each regime. Velocities were not different among treatments ( $P=0.68$ ) or tanks ( $P=0.31$ ) according to ANOVA with a fixed factor of tank nested within treatment (PROC ANOVA, SAS v9.1).

Tanks within each treatment were grouped together and enclosed in insulation to maintain the cold temperatures needed for the study. Although each tank was an independent unit with its own water supply, grouping the tanks also allowed the water supply pipes within treatments to be of equal length to reduce temperature variation among tanks. The insulated enclosures were lighted with fluorescent fixtures with 5000 K tubes, controlled by a light timer, and photoperiod was adjusted weekly to mimic the natural photoperiod. Therefore, although treatments could not be randomly assigned to tanks, clustering tanks within each treatment allowed maintaining the cold temperatures needed, and minimized differences in temperature and light intensity among tanks.

Temperature regimes were generated using a water chilling system and adjustable thermostatic mixing valves. Water chilled by a refrigeration unit and held in a 190 L sump supplied the cold regime treatment, and was mixed with warmer well water to supply the intermediate and warm regime treatments. After use, most water was returned to the sump, but some was diverted to a drain and replaced by pre-chilled well water

through a float valve in the sump. Thus, water was shared among treatments and partially recirculated with a continuous fresh water exchange. Tanks were gently cleaned with a siphon weekly to remove excess food and other detritus.

### ***Feeding***

When the first fry reached swimup near the end of Phase 1, fish were fed Rangen Trout Starter Diet #0 (Rangen Feeds, Boise, Idaho) *ad libitum* once or twice daily. During Phase 2 of the 2003 experiment, fish were fed 75% of the optimum ration of Rangen Trout Starter Diet daily using automatic feeders that dropped food particles into the inlet flow continuously to simulate invertebrate drift. However, the feeder mechanisms were not reliable, and the small food particles often clung to the feeders and had to be brushed into the tanks later, so during 2004 fish were fed the same daily ration in two to three daily feedings until regime temperatures dropped below 4°C, after which feedings occurred once per day. The optimum ration was calculated each week based on treatment temperature, fish length, and the number of fish remaining using a commercial feeding chart. I fed 75% rather than 100% of the optimum ration, because cold high-elevation streams are relatively unproductive (Scarnecchia and Bergersen 1986) and the amount of food available to cutthroat trout fry is likely suboptimal. The swimup fry in my study averaged about 22.5 mm TL, much smaller than the 30 mm minimum on the feeding chart. I was concerned that the minute rations resulting from extrapolation to smaller fish might hinder the development of feeding behavior, so I fed swimup fry the same ration calculated for 30-mm fish.

### ***Phase 1***

To determine survival rates of hatchling cutthroat trout fry to swimup in each temperature regime, I placed 100 sacfry during 2003 ( $n=2400$ ) and 101 sacfry during 2004 ( $n=2424$ ) within 5 days of hatching in each of the 24 artificial streams. I acclimated sacfry for 1 h in plastic bags filled with 7.0°C water from the incubation tanks, due to a 0-3°C difference between incubation and starting temperatures of the experimental regimes (see below). No acute mortality was observed during this acclimation period. Sacfry were held in screen boxes (28 cm by 18 cm by 10 cm deep) with opaque covers to shield them from light, prevent burrowing into the gravel, and allow daily mortality counts. I started the experiment at the point in each synthesized temperature regime that matched the number of degree days to which the embryos and fry had already been exposed since spawning (egg take). I estimated the spawning date as the day in each regime that temperatures first exceeded 5°C, because this is the temperature at which native cutthroat trout have been observed to spawn in Colorado (USFWS 1998; B. Rosenlund, U.S. Fish and Wildlife Service, Lakewood, Colorado, personal communication).

I recorded mortalities daily, and estimated the proportion of fish that had reached swimup. During the first two days, mortalities were assumed to be caused by handling, and were replaced with extra hatchling fry that were maintained at the incubation temperature (7°C). Phase 1 for each treatment ended when I judged that >50% of sacfry had reached swimup (i.e., the median swimup time). I considered fish to have reached swimup when external signs of remaining yolk were no longer visible, and fish held positions in the water column rather than resting on the bottom. The proportion of fry

reaching swimup was estimated after observers remained motionless for 2 minutes, to allow fish to become acclimated to their presence. The experimental design and procedures were the same during both years for Phase 1, but improved temperature control during 2004 resulted in slight differences in incubation and treatment temperatures, so I analyzed results for each year separately.

## *Phase 2*

**2003 experiment.** At >50% swimup in each treatment, I selected 20 swimup fry randomly from the basket in each tank, and measured their total lengths (TL) and wet weights. I released these fry into the stream tank and euthanized remaining fry in all but one tank in each treatment. These ‘extra’ fry were used to replace mortalities during the first two days of Phase 2, which I assumed were due to acute effects of handling. Due to the different rates of development in the different temperature regimes, the start of Phase 2 was synchronized to life-history stage (50% swimup) for each treatment, rather than calendar date. As a result, Phase 2 began 14 d later in the cold treatment, and 7 d later in the intermediate treatment, than in the warm treatment (Figure 1). Tanks were inspected daily for mortalities, which were removed and their TL measured, when possible, beginning the fourth week of Phase 2 (dead fry were inadvertently not measured the first three weeks).

To measure survival, I carefully counted surviving fish each week. I considered any missing fish as mortalities in my weekly counts, because they could not escape from tanks. A few retreated beneath the gravel and were missed on some counts, but were added to previous counts if they reappeared. I measured the total length (TL) and wet weight (WW) of each surviving fish at the onset of winter, defined as the week in each

regime that temperatures first dropped below 4°C, and at the end of the study, after 14 weeks of simulated winter temperatures. Fish were measured only three times to minimize handling mortality (only two fish died from handling). I measured the total length of each fish to the nearest 0.5 mm, and wet weight to the nearest 0.0001 g (Scientech analytical balance, model SA-210, Bradford, Massachusetts). I captured each fish in a fine-mesh nylon aquarium net, carefully blotted excess water from the fish and net on a damp natural sponge for 5 seconds, and then transferred the fish into a beaker containing approximately 10 ml of water for which my balance had been tared. At the end of Phase 2, fish were euthanized before weighing by the same procedure.

A minor infestation of the parasite *Ichthyobodo* (formerly *Costia*) was discovered during weeks two through five after swimup (depending on treatment) during the 2003 experiments (identified by Mike Minniear and Pete Walker, Fish Pathologists, Colorado Division of Wildlife). The infestation was found when mortality increased sharply, particularly in the cold treatment. Within two days of detecting the increased mortalities, I began successful treatment by flushing the artificial streams twice, seven days apart, for 30 minutes with dilute formalin (1:4000), as recommended. There were no acute mortalities during the 48 h after treatments that could be attributed to the prophylaxis, and a subsequent examination showed that the treatment was successful.

**2004 experiment.** At >50% swimup in each treatment, I selected 37 swimup fry randomly from the basket in each tank, and measured their total lengths (TL) and wet weights as in 2003. I released these fry into the stream tank and euthanized remaining fry in all but one tank in each treatment to replace mortalities during the first two days as before. The number of fry per tank was increased in 2004 to accommodate sampling of

fish during Phase 2 for dry weight measurements. As in 2003, Phase 2 began 14 days later in the cold treatment, and 7 days later in the intermediate treatment, than in the warm treatment (Figure 1).

Tanks were inspected daily for mortalities, which were removed and frozen in water. To measure survival, I carefully counted surviving fish each week. Moribund fish, which were dark gray or black over at least the caudal half of their body and had lost equilibrium, were counted as mortalities and removed from tanks. I measured the total length and wet weight of each surviving fish at the end of the experiment, after 5 to 6 weeks of simulated winter temperatures, using the same methods as in 2003. Fish were not measured at the onset of winter during the 2004 experiment because higher mortality rates had occurred in the preceding weeks, and I was concerned that mortality due to handling might reduce fish numbers in the cold treatment and jeopardize planned analyses. At swimup and weekly during the 5 (cold regime) to 6 (intermediate and warm regimes) weeks before the onset of winter temperatures, I randomly sampled one fry from each artificial stream tank. These and a sample of the surviving fish at the end of the experiment were euthanized and frozen in water for later energy content estimates.

Fish sampled from tanks and frozen were later thawed to estimate energy content. I measured the total lengths and wet weights of whole thawed fish, removed the viscera under a dissecting microscope from esophagus to vent, and recorded eviscerated wet weight. Eviscerated carcasses were freeze-dried in a lyophilizer, and their dry weight measured. All weights were measured to the nearest 0.00001 g (AE 240 Analytical Balance, Mettler-Toledo, Inc., Columbus, Ohio). I used the eviscerated wet:eviscerated dry weight ratios (percent dry weight) as a surrogate for energy content for relative

comparisons among treatment groups. Percent dry weight has been shown to be closely related to energy density in many species of fish (Hartman & Brandt 1995).

### ***Data analysis***

**Phase 1: Hatching to Swimup.** For Phase 1 survival and daily mortality rates I used one-way analysis of variance (ANOVA) with posthoc least squares means (LSMEANS) comparisons to test for statistical differences in survival among treatments (PROC GLM, SAS v9.1). Such differences could be due to the life stage duration alone (assuming constant daily mortality rate), differences in daily mortality rate, or both (Houde 1987). Therefore, I analyzed arcsine-squareroot transformed survival and daily mortality rates (the proportion that died divided by the duration of Phase 1 in days) through >50% swim-up for each treatment.

**Phase 2: After Swimup.** For Phase 2 of the 2003 experiment, I compared the total lengths and wet weights of fish among treatments using a linear model with repeated measures, and used the Satterthwaite method to calculate denominator degrees of freedom (PROC MIXED, SAS v9.1). Because fish were not individually identified, the tank was the experimental unit for this analysis, and the size data were log transformed to correct for the variance increasing with size. Condition indices (i.e., relative weights) were not analyzed, because length-weight relationships are unstable for salmonid age-0 swim-up fry due to morphological changes as fish mature to the juvenile stage, and because such indices may not reflect proximate body composition (see Simpkins et al. 2003).

*Survival.* I compared survival rates among treatments for Phase 2 using the normal approximation of the binomial for both 2003 and 2004 data. I calculated Kaplan-

Meier 95% confidence intervals (Newman 1995) on survival from swimup to each week of Phase 2. The data for 2004 were back-corrected (censored) to account for fish sampled during each week for dry weight measurements. Therefore, my 2003 results were better suited for a detailed hazard analysis to identify and describe any temperature-related recruitment bottleneck apparent in the survival data, because no fish were sampled for other analyses. For the 2003 data, I fit a logistic-normal model to binomial weekly hazard risk (proportion surviving through each weekly interval) to characterize the hazard function and estimate variation due to random tank effects (PROC NLMIXED, SAS v9.1).

I modeled the hazard function (weekly survival) using accumulated degree days since egg take (DD), dummy variables for treatment (TRT), the DD $\times$ TRT interaction, and a random tank effect. In some models, I also included a quadratic term (DD<sup>2</sup>) and the DD<sup>2</sup> $\times$ TRT interaction, due to an obvious dip in weekly survival rates during the weeks preceding winter that appeared to differ among treatments. Accumulated degree days was chosen as a covariate to integrate both time and temperature in a single variable that is biologically pertinent as an approximation of “physiological time” (Schmidt-Nielsen 1984). I fit four logistic models representing mechanistic hypotheses to determine which covariates best explained variation in the hazard data. These included a full quadratic-logistic model with DD<sup>2</sup>, TRT, and DD $\times$ TRT and DD<sup>2</sup> $\times$ TRT interactions, a reduced quadratic-logistic model that excluded the TRT effects and interactions, and full and reduced linear-logistic models that were identical to their quadratic counterparts but excluded the quadratic terms (DD<sup>2</sup>). I used an information-theoretic approach to select the best fitting model based on Akaike’s Information Criteria corrected for small samples

size ( $AIC_c$ ), which allows objectively selecting the model most consistent with the data, while balancing the trade-off between precision and bias (Franklin et al. 2000; Burnham and Anderson 2002). The models were ranked in ascending order based on  $AIC_c$ , and the model with the lowest  $AIC_c$  was considered the best fitting. Likelihood ratio tests (LRT) were used to distinguish the top model from the other three candidate models.

The best fitting hazard model for the 2003 Phase 2 results lacked a hierarchical structure, which made parameter interpretation problematic, and standard posthoc tests for group comparisons were not possible. So, to compare hazard curves among groups, I excluded data from one treatment group at a time, and fit the full (with TRT and interactions) and reduced quadratic models (no TRT or interactions) to test differences between all three possible treatment pairs. For each group comparison, I used LRT to determine whether models accounting for variation among treatment pairs explained weekly survival significantly better than models that did not. A lower  $AIC_c$  for the full model and a significant LRT were taken as evidence of a statistical difference between treatment pairs.

*Size-related mortality.* I used a regression approach to determine whether mortality was size-related within each treatment during Phase 2 of the 2003 experiment. A model was fit to describe the relationship between time and fry total lengths at swimup, the start of winter, and the end of the experiment. A similar model was fit to the total lengths of fry that died during this period. A third model was fit to the relationship between time and total lengths of all fry (live and dead). The error sums of squares for the three models were used to calculate an approximate F-test to determine whether the curve predicting size of living fry differed from that for fry that died during the

experiment (P. Chapman, Department of Statistics, Colorado State University, personal communication).

*Growth and relative energy content.* Because I sampled fish from experimental tanks during Phase 2 of the experiment during 2004, I was able to conduct a more thorough analysis of growth and changes in relative energy content among treatments. Energy content was estimated as percent dry weight, to which an arcsine-squareroot transformation was applied to adjust for skew in the variance of proportion data with values below 30%. Total length, eviscerated dry weight, and percent dry weight were analyzed using analysis of covariance (ANCOVA) with interaction (Proc MIXED, SAS v9.1), including a term for variation due to random tank effects. I used likelihood ratio tests (LRT) to determine whether inclusion of the random effect in the models significantly improved model fits. The test allowed for different variances among treatment regimes for total length data, and resulted in approximate F-tests of group differences. Approximate tests were deemed acceptable in this case due to a relatively large sample size. All weight data were log-transformed due to increasing variance.

I also fit quadratic response surfaces (Proc RSREG, SAS v9.1), to describe the relationships of total length, eviscerated dry weight, and energy content to time and thermal regime during Phase 2 in 2004. The thermal regimes were represented by the number of degree days that accumulated during the growing season (spawning to the onset of winter when temperatures dropped below 4°C). Calculating degree-days converts the class variable for the thermal regimes (cold, intermediate, and warm), to a continuous variable that is more meaningful in an ecological context. Response surfaces

were not predicted from the 2003 experiment, because fry were not sampled throughout the study to provide appropriate data.

## **Results**

### ***Phase 1: Hatching to Swimup***

During the 2003 experiment, survival was lowest and daily mortality rates were highest in the cold temperature regime (Table 1). The proportion of sac fry surviving from hatching to swimup differed among treatments (one-way ANOVA:  $P=0.0009$ ), and was lower in the cold regime than in the intermediate (LSMEANS:  $P=0.004$ ) and warm ( $P=0.0003$ ) regimes. The time required for >50% of sac fry to swim up varied by 14 d among temperature regimes and was only about half as long in the warm versus cold treatment. Daily percentage mortality also differed among treatments (one-way ANOVA:  $P=0.015$ ) and was higher in the cold regime than in the intermediate (LSMEANS:  $P=0.02$ ) and warm ( $P=0.007$ ) regimes. Survival was slightly higher and daily mortality rate lower in the warm vs. intermediate treatments during Phase 1, but the differences were not statistically significant ( $P\geq 0.3$ ).

During the 2004 experiment, survival was again significantly different among regimes (ANOVA:  $P=0.02$ ). However, in contrast to my 2003 results, the intermediate regime had significantly lower survival than both the cold (LSMEANS:  $P=0.008$ ) and warm (LSMEANS:  $P=0.0008$ ) regimes, which were not significantly different. Daily mortality rates also differed significantly among regimes (ANOVA:  $P=0.03$ ), with the intermediate regime significantly lower than the cold (LSMEANS:  $P=0.001$ ) and warm (LSMEANS:  $P=0.008$ ) regimes, which were not significantly different. The time

required to >50% swimup again varied by 14 days, and in the warm regimes was only 65% of that in the cold regime.

### ***Phase 2: After Swimup***

**2003 Experiment.** Cold temperatures strongly reduced growth in age-0 Colorado River cutthroat trout fry during the interval from swimup to the onset of winter temperatures (4°C), and from this point through 14 weeks of simulated winter (Figure 2). Fry growth, measured in total length and wet weight, differed among the three temperature regimes (i.e., interactions between temperature regime and period were significant for both; ANOVA:  $P < 0.0001$ ), so I compared sizes separately for each period. Fry lengths and weights differed significantly among the three temperature regimes at the start of winter and the end of the experiment (LSMEANS:  $P < 0.0001$  for all comparisons). Growth was highest between swimup and the start of winter, when fish in the warm temperature regime achieved an average length over 60% greater than those in the cold regime.

A surprising finding was that surviving fish in all treatments were larger, on average, after 14 weeks of simulated winter than at the start of winter temperatures (LSMEANS:  $P < 0.0001$ ). This apparent growth was not due solely to size-selective mortality because mean total length of survivors at the end of the experiment plus those that died after the onset of winter (see below), were only 0.9-2.5 mm shorter than the mean lengths without these mortalities. The survivors were also significantly longer than mean lengths at the onset of winter ( $P < 0.05$  based on non-overlapping confidence intervals). Thus, it is apparent that fish in the warm and intermediate treatments grew in

size at temperatures below 4°C when sufficient food was available, similar to Bear Lake Bonneville cutthroat trout (*O. c. utah*; Behnke 1992).

Cold temperatures also reduced survival rates of age-0 Colorado River cutthroat trout fry from swimup to the onset of winter temperatures, and through mid-winter (Figure 3). Survival from swimup was lower in the cold treatment by the onset of winter, and was less than half that in the two warmer treatments after 14 weeks at winter temperatures, a significant difference based on non-overlapping Kaplan-Meier 95% confidence intervals. Moreover, the proportion of fry surviving in the cold treatment dropped rapidly from swimup through the first three weeks of winter, suggesting that this 7-week period posed a strong bottleneck for survival of cutthroat trout fry reared at these cold temperatures. In contrast, the proportion of fry surviving in the intermediate and warm temperature regimes dropped most rapidly during the 4 weeks before the onset of winter, and slowly thereafter during winter.

This period of high mortality was best reflected in the hazard data (i.e., survival from week to week) as a sharp dip in weekly survival during the 8 weeks following swimup in each treatment (Figure 4). My analysis indicated that the full quadratic model fit the data significantly better (LRT:  $P < 0.0001$ ) than each of the three remaining models ( $\Delta AIC > 2.0$ ), and held nearly all of the Akaike weight (Table 2). In addition, the two quadratic models also outranked the two linear-logistic models. The presence of  $DD^2$  in the top two models and significant LRT indicates that the dip in weekly survival during the first 8 weeks after swimup was significant, and the presence of TRT and  $DD^2 \times TRT$  interactions in the best fitting model indicate that the dip varied among temperature regimes, being greater at colder temperatures. The random tank effect was both small

and did not differ statistically from zero ( $t=0.59$ ;  $df=23$ ;  $P=0.56$ ) in the top model. My likelihood ratio tests for treatment differences showed that including treatment effects in the full quadratic-logistic model resulted in a significantly better fit than the reduced model including only main effects of DD and DD<sup>2</sup> in all three cases (Table 3). Thus, all treatment combinations were significantly different ( $P \leq 0.007$ ).

At the time of death, fish that died were almost all smaller than expected compared to their living counterparts (Figure 5). Approximate F-tests indicated that this difference in size between fish that died vs. the estimated size of living fish was significant in the cold ( $F=50.37$ ;  $df=2, 346$ ;  $P<0.0001$ ) and intermediate temperature regimes ( $F=10.83$ ;  $df=2, 364$ ;  $P<0.0001$ ), but not in the warm regime ( $F=0.99$ ;  $df=2, 404$ ;  $P=0.37$ ). The total lengths of nearly all fish that died in the intermediate and cold regimes fell below the growth trajectory of survivors, based on the predictions of the statistical models fitting the measurements at swimup, the start of winter, and the end of the 2003 experiment. In contrast, after some early mortality in the warm regime of both larger and smaller trout, only one fish died during the winter, but was not measured (so is not shown).

**2004 experiment.** The pattern of growth among treatments during Phase 2 of the 2004 experiment was similar to that in 2003. Swimup fry in all treatments started at about the same size, but those in the warmer treatment grew more by the end of the study (Figure 6), as indicated by a significant period by temperature regime interaction (ANOVA:  $P<0.0001$ ). Fish in all three temperature regimes grew significantly in both length and weight, and differed significantly in size by the end of the experiment (LSMEANS:  $P<0.0001$  for each comparison). Fish in the warm regime were 40%

longer than those in the cold regime by the end of the study. Overall, growth was lower in 2004 than in 2003, possibly due to differences in density early in phase 2 due to increased sample size to accommodate sampling of fish during the recruitment bottleneck period (compare Figure 6 to Figure 2). During Phase 2, the pattern of survival among treatments (Figure 7) was similar to that in the 2003 experiment, but final survival in the 2004 experiment was 20-45% lower than in 2003, even though there was no parasite infestation or disease outbreak in 2004.

Total length, eviscerated wet weight, eviscerated dry weight, and relative energy content (percent dry weight) were all related to both temperature regime (as a class variable), and the number of estimated Celsius degree days fish had been exposed to from fertilization to the time they were sampled (cumulative degree days) in 2004 (Figure 8). Variation due to random tank effects was not significant (LRT:  $P > 0.3$  in all cases), so the random tank effect was not included in the final ANCOVA models. One very low dry weight value was excluded from all analyses involving dry weights, because it was assumed to have been a measurement error, and was as an influential outlier (LRT:  $P = 0.0001$ ). In all of the analyses, there was a significant interaction between temperature regime and accumulated degree days (Table 4). Main effects for both variables were also significant, except in the analysis of eviscerated dry weights, where only cumulative degree days was significant. Thus, the relationship between the growth and energy content of fish to accumulated degree days varied among temperature regimes.

The quadratic response surfaces for total length and dry weight indicated that growth increased with the number of degree days accumulated during the growing season and through time within each regime in a nearly linear fashion (Figures 9a and 9b). By

contrast, the response surface for percent dry weight (index of energy content) indicated a curvilinear relationship between energy content and time (Figure 9c), reaching an apparent minimum in energy content of growing fish during the first 3-6 weeks following swimup, depending on treatment. This coincided with the period of peak mortality apparent in the survival data (Figure 7). There was also a trend of increasing energy content in fish exposed to higher temperatures throughout the experiment.

## **Discussion**

The results of this experiment support the prediction that cold summer temperature regimes like those of natural streams where past translocations of native cutthroat trout were not successful can strongly reduce growth, energy stores, and survival of age-0 cutthroat trout after swimup during their first summer and winter. My data show that survival from hatching to swimup was high during both years of the study in all temperature regimes, but the cold temperature regime delayed development so that by swimup only 4 to 5 weeks of growing season remained before the onset of winter. Temperatures were also dropping rapidly during this period. Moreover, survival from swimup through midwinter was much lower in the cold than intermediate or warm regimes, even though the mean summer temperatures were spaced evenly at 1.5°C intervals among regimes. Because survival rates in my cold treatment were low by the end of experiments during both years of the study (2003: <30%; 2004: <10%), I consider cold summer temperatures a plausible mechanism to explain the low recruitment reported for cold, high-elevation streams in recent field studies (Harig and Fausch 2002; Peterson et al. 2004; Coleman and Fausch in press).

Most mortality in all treatments was due to a strong recruitment bottleneck, a discrete period of decreased week-to-week survival rates preceding the onset of winter. Moreover, this bottleneck grew more severe with colder temperature regimes. The hazard analysis, based on the 2003 experiment, showed that in the cold temperature regime mortality was greatest during the 4 weeks before the onset of winter, and for 3 weeks afterwards. Swimup occurred closer to the start of winter in this regime, and the recruitment bottleneck occurred immediately after swimup. This pattern of high mortality for 5-6 weeks after swimup that was more severe in cold regimes also occurred in the 2004 experiment, when overall survival was lower than in 2003. The lower survival rates may have been due to differences in actual thermal regimes achieved, annual or batch variation in quality of embryos obtained from the hatchery, differences in density of fish (20 per tank at the beginning of 2003 experiment, but 37 per tank in 2004), or other small differences in experimental design between years. Despite differences in absolute mortality between years, the pattern of mortality relative to temperature regimes was consistent. After swimup, a critical period for salmonid larvae occurs when yolk is depleted and fish must find exogenous prey to survive (Houde 1987; Elliott 1989; Pottinger and Mosuwe 1994). Mechanisms invoked to explain mortality during this period include inability to gain territories (Elliott 1990), starvation (Houde 2002), or physiological mechanisms such as increased stress response and decreased immune response (Pottinger and Mosuwe 1994), all of which are known to be affected by temperature.

Taken together, my growth and survival data collected during two long-term laboratory experiments constitute several lines of evidence that indicate cold summer

temperature increases mortality by increasing the severity of energy deficits during a critical period in development. This result is consistent with previous research indicating that mortality in other stream-resident trout may be related to early winter energy deficits (Cunjak & Power 1987; Cunjack et al. 1987). During my 2003 experiment, necropsies of fry that died in the cold treatment during Phase 2 indicated that several had yolk remaining inside their body cavity, which had not closed (buttoned up), several weeks after swimup. These fish had died of apparent starvation, suggesting that temperatures were too cold to allow fish to metabolize their yolk and develop normally. My analysis of percent dry weight of fish sampled throughout the 2004 experiment showed a lower energy content in the colder temperature regime at swimup, even though this developmental stage occurred later in this regime than in the others, and then a further decline in energy content during the first few weeks afterwards. Further, mortality during the recruitment bottleneck and through the first half of winter in the 2003 experiment was size-dependent in the two colder temperature regimes, where mortality rates were highest, and suggested that fry must likely exceed some size threshold to survive through winter. Most fish that died were smaller than the average size of their living counterparts, and in the two colder regimes many of these died during winter. In contrast, in the warm regime nearly all those that survived to the onset of winter also survived to the end of the experiment. Other researchers also have found that smaller salmonids appear to use the little energy they have stored more rapidly than their larger counterparts (Berg and Bremset 1998; Post and Parkinson 2001). Thus, cold summer temperature regimes like those studied here are near the physiological threshold for

cutthroat trout recruitment, even though adult fish can persist in streams with similar temperatures (Coleman and Fausch in press).

Other evidence from field studies also suggests a size threshold for recruitment. During an intensive 4-year field study of four cutthroat trout populations (Peterson and Fausch 2002; Peterson et al. 2004), no age-0 and few age-1 trout were captured during annual late summer electrofishing of long segments in two cold, high-elevation streams with mean July temperatures of 6.6°C and 6.9°C. However, careful extensive fry sampling of the same streams in September during the final year revealed small numbers of age-0 cutthroat trout of 26 mm and 30 mm median length, respectively. In contrast, age-1 fry were relatively abundant in two warmer, mid-elevation streams with mean July temperatures of 12.7°C and 12.4°C, and the median lengths of age-0 trout captured during careful surveys in September were 45 mm and 69 mm, respectively. These observations and my own experimental results suggest that age-0 cutthroat trout fry must reach a threshold length of 30-35 mm to survive over winter (Figure 5). Thus, in cold temperature regimes, survival to the start of winter is low due to a severe recruitment bottleneck, and the few surviving fry are likely too small to survive over winter when other harsh physical processes, like spring snowmelt runoff, may contribute further to mortality.

My experiments cannot clearly distinguish between density-dependent and density-independent mechanisms governing mortality, but instead suggests that some combination of both types of effects integrated over time may lead to high mortality rates. The chronic mechanisms leading to metabolic deficits and poor survival could have resulted through density-dependent behavioral mechanisms, such as failure to gain

profitable feeding territories (Elliott 1990). My data suggest, however, that there were also direct effects of temperature, because fry in colder regimes in my 2004 experiment had lower estimated energy content, on average, than those in warmer regimes. This was just after the sacfry (alevin) stage, during which survival is typically governed by abiotic, density-independent processes (Houde 1987, 2002).

During the 2003 experiment, the parasite infestation (*Ichthyobodo*) affected all treatments due to extensive water sharing, and may have increased mortality after swimup. However, the infestation can only explain a small portion of the mortality observed, because it was discovered quickly and treated successfully. No acute mortalities occurred within 48 h after treatment, and the infestation did not recur. Further, during the 2004 experiment, when no parasite infestation was observed, a similar pattern of high mortality during the period after swimup was also found, as well as greater mortality rates overall. Regardless, fry may be more susceptible to parasite irruptions during the critical period (Pottinger and Mosuwe 1994), especially in cold temperatures due to increased stress response or immunosuppression (Einarsdóttir et al. 2000; Watts et al. 2001). Thus, increased susceptibility to parasites and diseases may be one of several proximate mechanisms accounting for increased mortality due to cold temperatures.

My results show that recruitment bottlenecks at cold temperatures can explain the reduced success of native cutthroat trout translocations in cold high-elevation streams in the southern Rocky Mountain region. A similar mechanism may also explain low recruitment rates for populations of brown trout in high-elevation lakes in northern Europe (Borgström and Museth 2005). My data indicate that cold temperature regimes

do not provide sufficient thermal units for adequate development and growth of fry, which are needed to ensure survival during the subsequent winter. These results are corroborated by a companion field study which showed that growth and recruitment declined markedly in streams with mean August temperatures below 8.5°C, where <900 degree days accumulated during the growing season, on average (Coleman and Fausch in press) and were most successful in streams with >900 degree days. Without adequate recruitment, fish populations remain small and are susceptible to local extinction due to environmental fluctuations (Rieman and McIntyre 1993; Caughley 1994; McElhane et al. 2000). As a result, translocated populations of cutthroat trout are likely to be more susceptible to extinction at high elevations within their ranges (Myers 1998), due to the cold temperature regimes. Recent data on other salmonid species suggests that the isolation of these populations to streams with small habitat areas relative to their historic range may further increase this risk (Morita and Yamamoto 2002; Hilderbrand 2003). Despite this, cold temperature is often overlooked as a factor limiting salmonid populations. The results of my integrated laboratory and field study indicate that locating streams with growing seasons warm enough to support consistent recruitment (>900 degree days) will be a key to increasing translocation success of native cutthroat trout in southern Rocky Mountain streams.

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## **Tables**

Table 1. Proportion of age-0 Colorado River cutthroat trout fry surviving from hatching to swimup and their percent daily mortality in the three temperature regimes in Phase 1 of the experiment during both 2003 and 2004. The 95% confidence intervals (CI) are shown in parentheses.

| Study year | Temperature regime | Days to >50% swimup | Survival to swimup (95% CI)     | Percent daily mortality (95% CI) |
|------------|--------------------|---------------------|---------------------------------|----------------------------------|
| 2003       | Cold               | 31                  | 0.85 (0.79 - 0.90) <sup>a</sup> | 0.45 (0.28 - 0.65) <sup>b</sup>  |
|            | Intermediate       | 24                  | 0.95 (0.91 - 0.98)              | 0.19 (0.09 - 0.33)               |
|            | Warm               | 17                  | 0.97 (0.94 - 0.99)              | 0.15 (0.06 - 0.28)               |
| 2004       | Cold               | 40                  | 0.95 (0.91 - 0.98)              | 0.14 (0.13 - 0.14)               |
|            | Intermediate       | 32                  | 0.91 (0.86 - 0.95) <sup>c</sup> | 0.29 (0.24 - 0.32) <sup>c</sup>  |
|            | Warm               | 26                  | 0.96 (0.92 - 0.99)              | 0.17 (0.14 - 0.20)               |

<sup>a</sup> Significantly different from other regimes ( $P \leq 0.004$ ).

<sup>b</sup> Significantly different from other regimes ( $P \leq 0.02$ ).

<sup>c</sup> Significantly different from other regimes ( $P \leq 0.008$ ).

Table 2. Logistic regression models of hazard data (weekly survival) as a function of accumulated degree days (DD) and treatment (TRT). Models were ranked in ascending order, based on Akaike's Information Criterion (AIC). The  $AIC_c$  is the AIC corrected for small sample size,  $K$  is the number of parameters estimated in the model, and  $\Delta AIC_c$  is the difference in  $AIC_c$  between the candidate model and the model with the lowest  $AIC_c$ . The Akaike weights ( $w_i$ ) sum to 1.0. Likelihood ratio tests (LRT) indicate that the top model fit the data significantly better than the three other candidate models. The predictions of the top model (in bold) are plotted in Figure 4.

| Model<br>(included variables)   | $AIC_c$      | $K$      | $\Delta AIC_c$ | $w_i$       | LRT<br>$P(\chi^2, df)$ |
|---|--------------|----------|----------------|-------------|------------------------|
| <b>Full quadratic<br/>(DD, DD<sup>2</sup>, TRT, DD×TRT,<br/>DD<sup>2</sup>×TRT)</b> | <b>659.8</b> | <b>9</b> | <b>0.0</b>     | <b>1.00</b> | --                     |
| Reduced quadratic<br>(DD, DD <sup>2</sup> )   | 720.9        | 3        | 61.1           | 0.00        | <0.0001<br>(73.5, 6)   |
| Full linear<br>(DD, TRT, DD×TRT)  | 738.4        | 6        | 78.6           | 0.00        | <0.0001<br>(84.9, 3)   |
| Reduced linear<br>(DD)  | 754.2        | 2        | 94.4           | 0.00        | <0.0001<br>(108.9, 7)  |

Table 3. Likelihood ratio tests (LRT) for treatment differences. The full quadratic model includes accumulated degree days (DD), DD<sup>2</sup>, temperature regime (TRT), and the interactions DD×TRT and DD<sup>2</sup>×TRT. The reduced models include only the DD and the DD<sup>2</sup> covariates. In each row, a lower AIC<sub>c</sub> indicates a better fit, and the LRT tests are for differences between the full and reduced model. Comparisons of AIC<sub>c</sub> among rows are not valid, because the statistics in each row are based on a different subset of the data.

| Group comparisons     | AIC <sub>c</sub> |                   | LRT                      |
|-----------------------|------------------|-------------------|--------------------------|
|                       | Full quadratic   | Reduced quadratic | <i>P</i> ( $\chi^2$ ,df) |
| Cold vs. Intermediate | 474.6            | 480.7             | =0.007 (12.2, 3)         |
| Cold vs. Warm         | 452.7            | 490.1             | <0.001 (43.5, 3)         |
| Intermediate vs. Warm | 455.6            | 465.2             | =0.001 (15.8, 3)         |

Table 4. The P-values for factors included in final models of analysis of covariance (ANCOVA) testing group effects of temperature regime treatments on several dependent variables describing growth (lengths and weights), and estimated relative energy content (percent dry weight). Differences in sample sizes for each test arose from missing total length data, and exclusion of one dry weight datum that was presumed to be a measurement error (see text). Predictions from the final models for total length, eviscerated dry weight, and percent dry weight are plotted in Figure 8.

| Dependent variable                            | Main effects                              |   | Temperature regime<br>× accumulated<br>degree-days<br>interaction |
|---|---|---|---|
|   | Temperature<br>regime (class<br>variable) | Accumulated<br>degree-days at<br>sampling |   |
| Total length<br>( <i>n</i> =182)              | <0.0001                                   | <0.0001                                   | <0.0001   |
| Eviscerated wet<br>weight<br>( <i>n</i> =187) | 0.023                                     | <0.0001                                   | 0.0002  |
| Eviscerated dry<br>weight<br>( <i>n</i> =186) | 0.21                                      | <0.0001                                   | 0.0027  |
| Percent dry weight<br>( <i>n</i> =186)        | 0.0045                                    | <0.0001                                   | <0.0001   |

## Figures

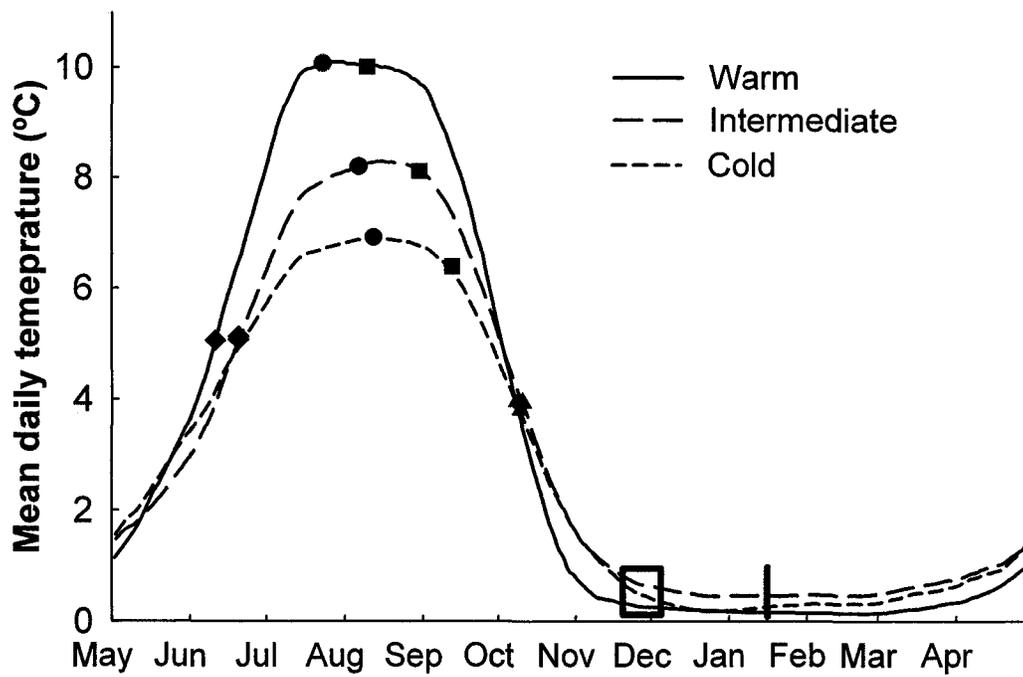


Figure 1.

Figure 1. The three synthesized temperature regimes used in the experiments, based on mean daily temperatures from streams studied by Harig and Fausch (2002). The regimes correspond to streams where translocations resulted in absent (cold,  $n=6$ ), low (intermediate,  $n=8$ ), or high (warm,  $n=13$ ) abundance cutthroat trout populations (see text). The diamonds show the point in the regime where I estimate fish spawned, and the solid circles show the start of Phase 1 of the experiment, soon after fry hatched. The squares show the start of Phase 2, when >50% of fry had reached swimup. The triangles mark the onset of winter for each regime, the vertical line marks the end of the 2003 experiment, and the open box marks the end of the 2004 experiment when the experiment was ended one week earlier relative to the start of winter in the cold than in the intermediate and warm treatments.

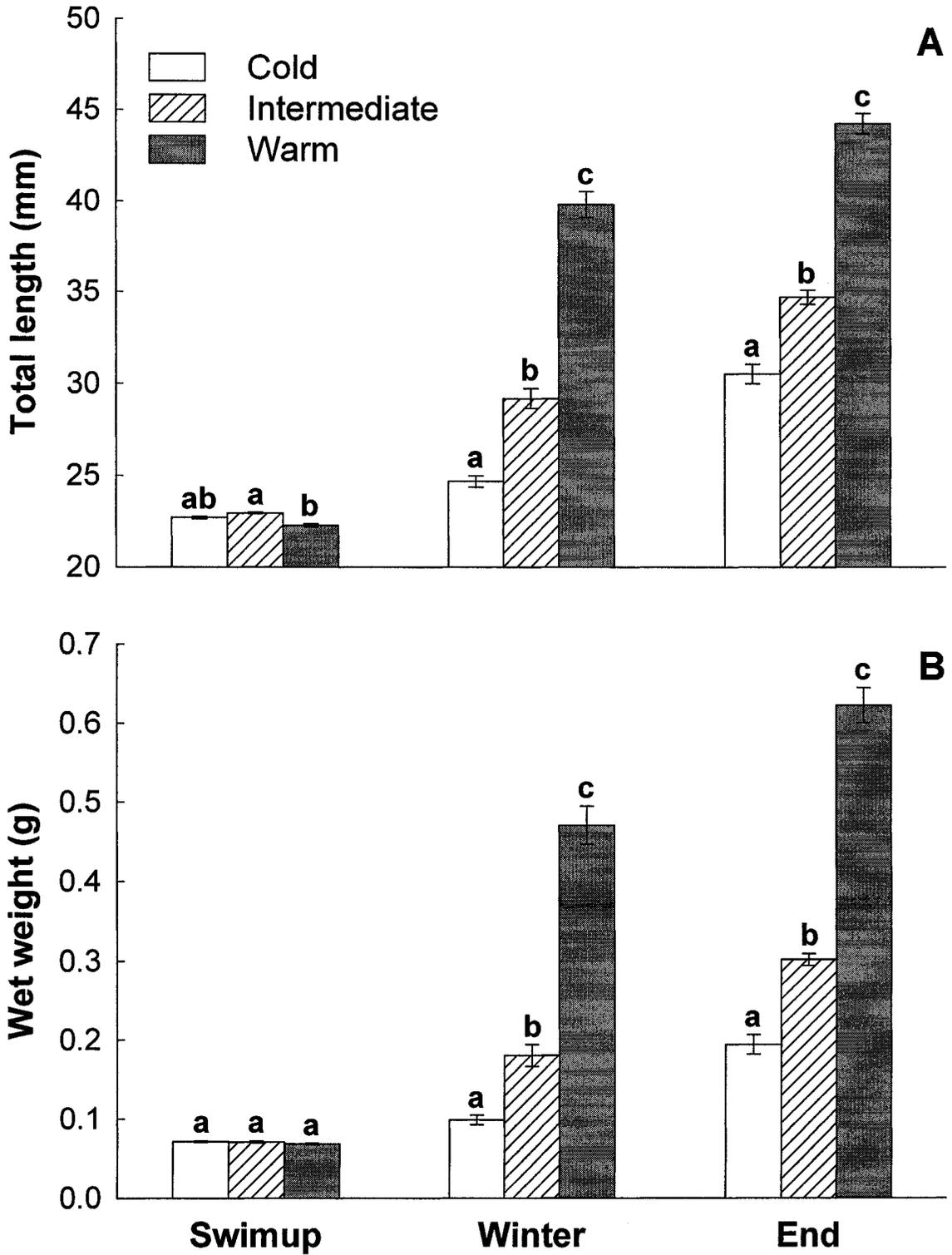


Figure 2.

Figure 2. A) Total lengths and B) wet weights of fry at swimup, the start of winter when temperatures dropped below 4°C, and at the end of Phase 2, in the 2003 experiment after 14 weeks of winter temperatures. Bars show  $\pm 1$  SE, based on raw data, with tank as the experimental unit ( $n=8$  for each treatment). Within each period, bars with different letters are significantly different ( $P<0.05$ ) by comparison of least squares means (see text). The difference in total length between the warm and intermediate treatment at swimup was statistically significant ( $P=0.04$ ), but small (0.65 mm) and biologically insignificant.

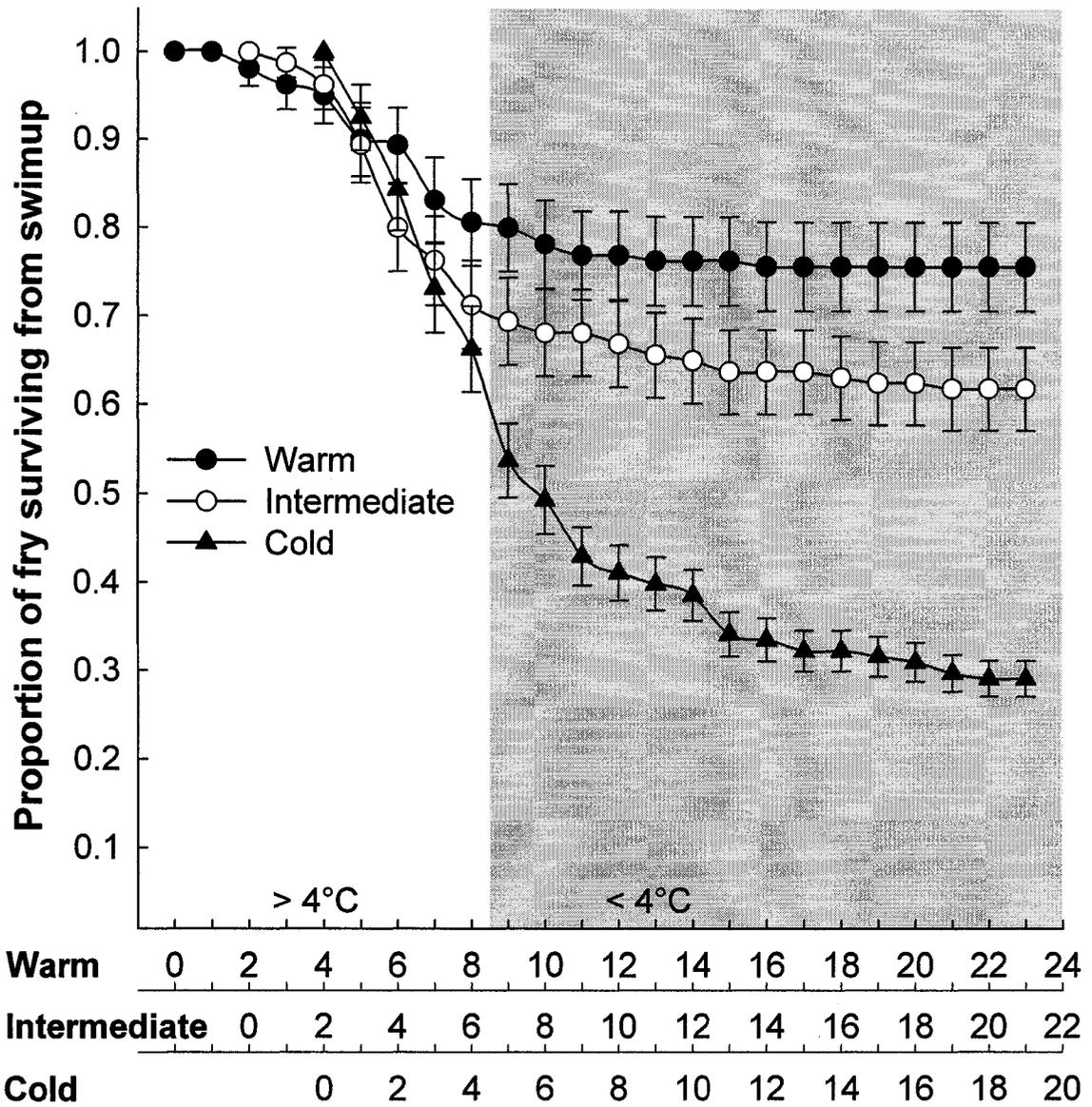


Figure 3.

Figure 3. Proportion of age-0 Colorado River cutthroat trout surviving from swim-up to each week during Phase 2 of the 2003 experiment. The survival curves for each regime have been shifted along the horizontal axis to synchronize them based on the timing for onset of winter temperatures. Bars show Kaplan-Meier 95% confidence intervals.

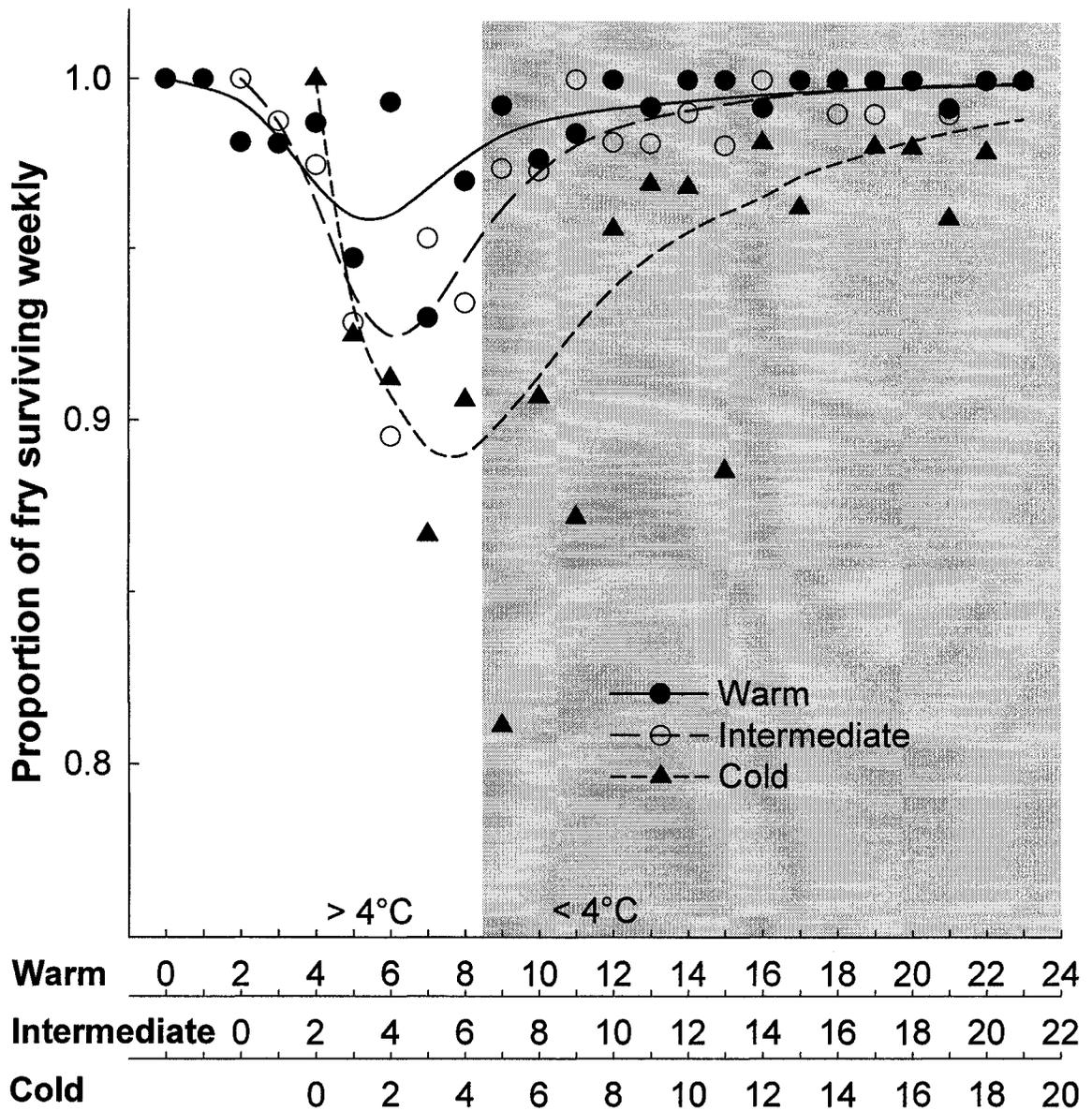


Figure 4.

Figure 4. Hazard plots showing survival of age-0 Colorado River cutthroat trout fry each week during Phase 2 of the 2003 experiment for the three temperature regimes. Logistic regression curves from the best fitting model are shown in Table 2. The curves have been shifted along the horizontal axis as in Figure 3.

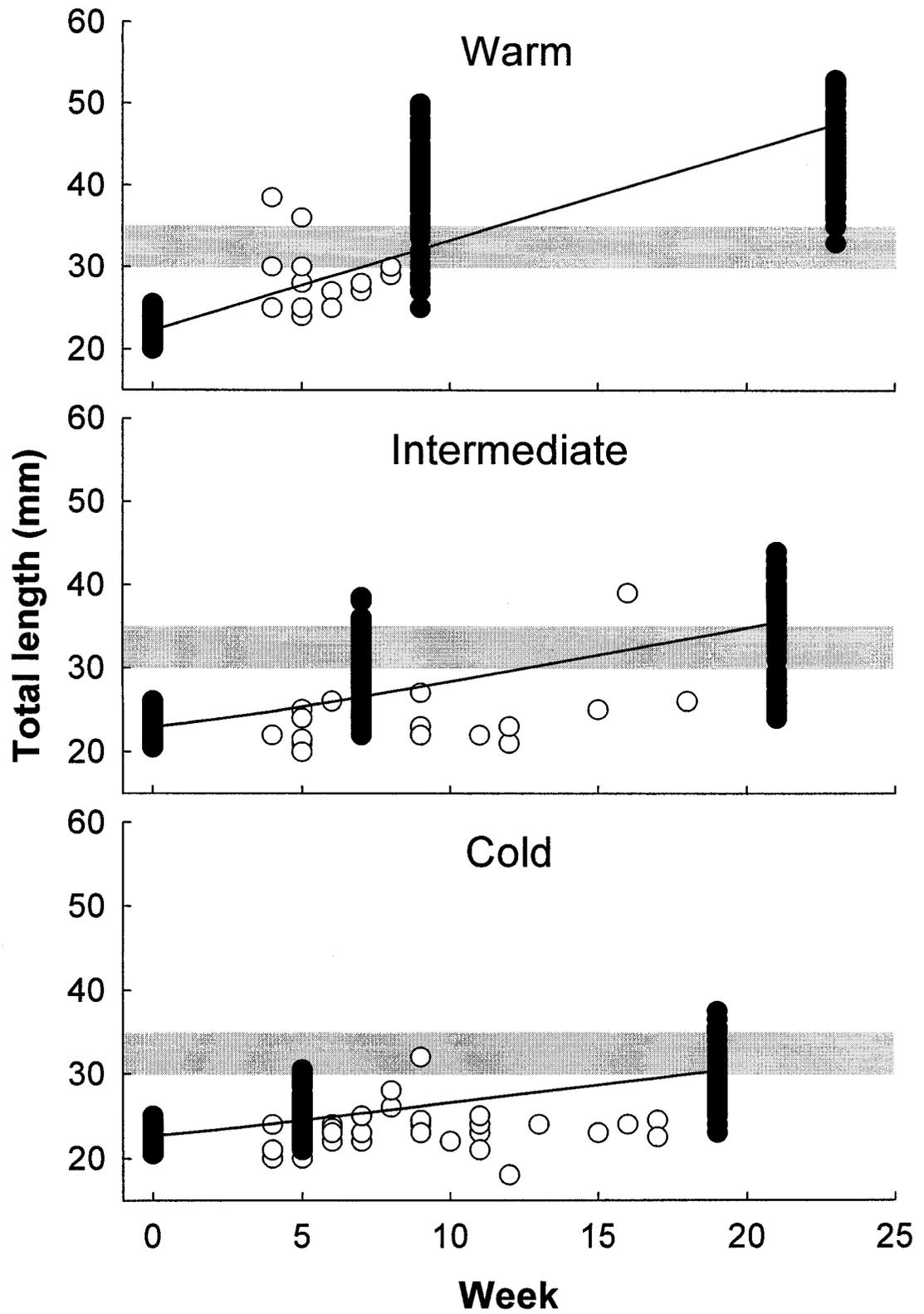


Figure 5.

Figure 5. Total lengths of living and dead fish for each temperature regime during Phase 2 of the 2003 experiment. Living fish (filled symbols) were measured three times (swimup, start of winter, and the end of the experiment). Dead fish (open symbols) were measured at their time of death. The relationship shown is the nonlinear best fit to measurements of live fish. The shaded area shows the approximate minimum size threshold for overwinter survival derived from previous field research (Peterson and Fausch 2002; Peterson et al. 2004).

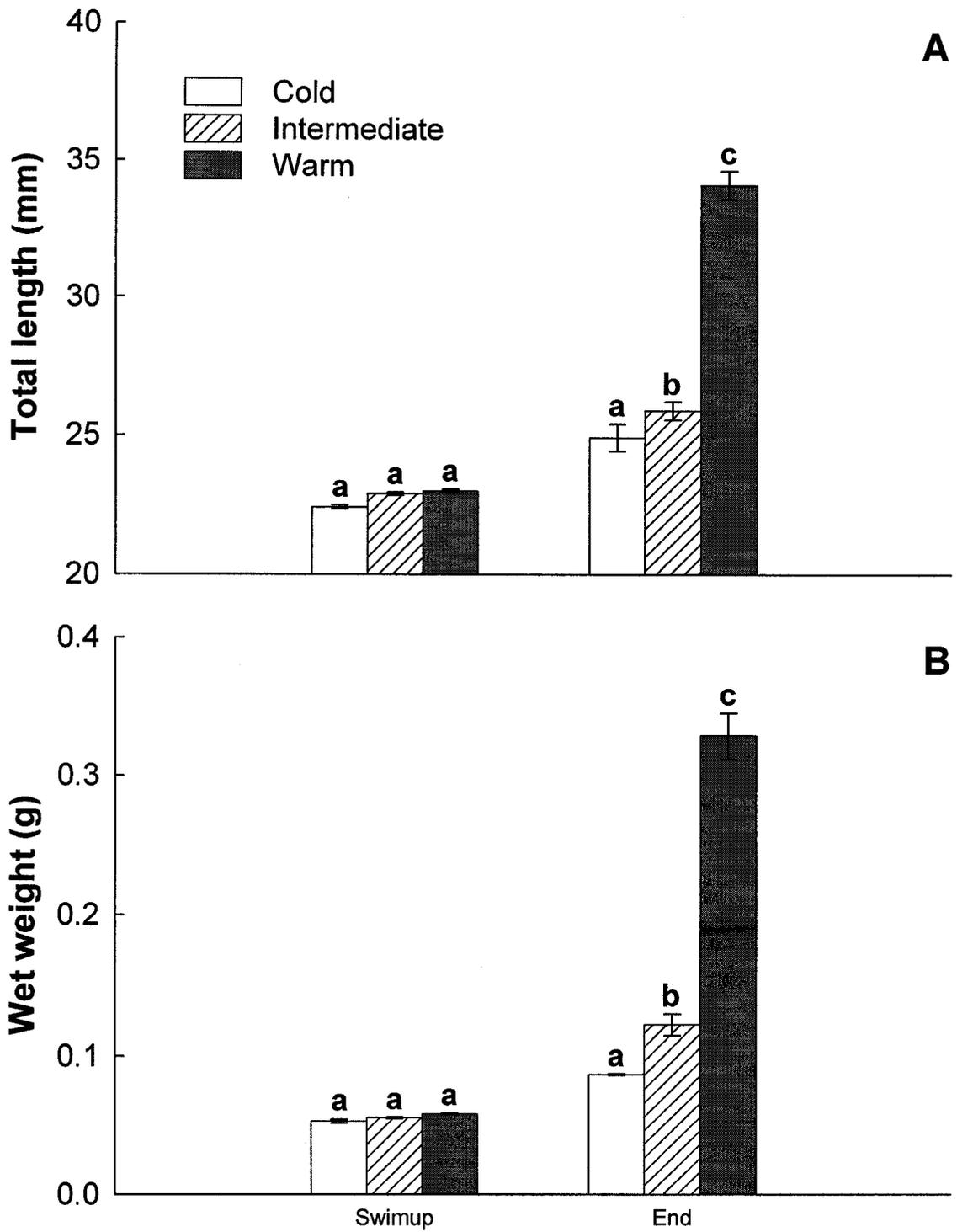


Figure 6.

Figure 6. A) Total lengths and B) wet weights of fry at swimup, and the end of the 2004 experiment, after 6 to 7 weeks of winter temperatures ( $<4^{\circ}\text{C}$ ). Bars show  $\pm 1$  SE, based on raw data, with tank as the experimental unit. Within each period, bars with different letters are significantly different ( $P<0.05$ ) by comparison of least squares means (see text).

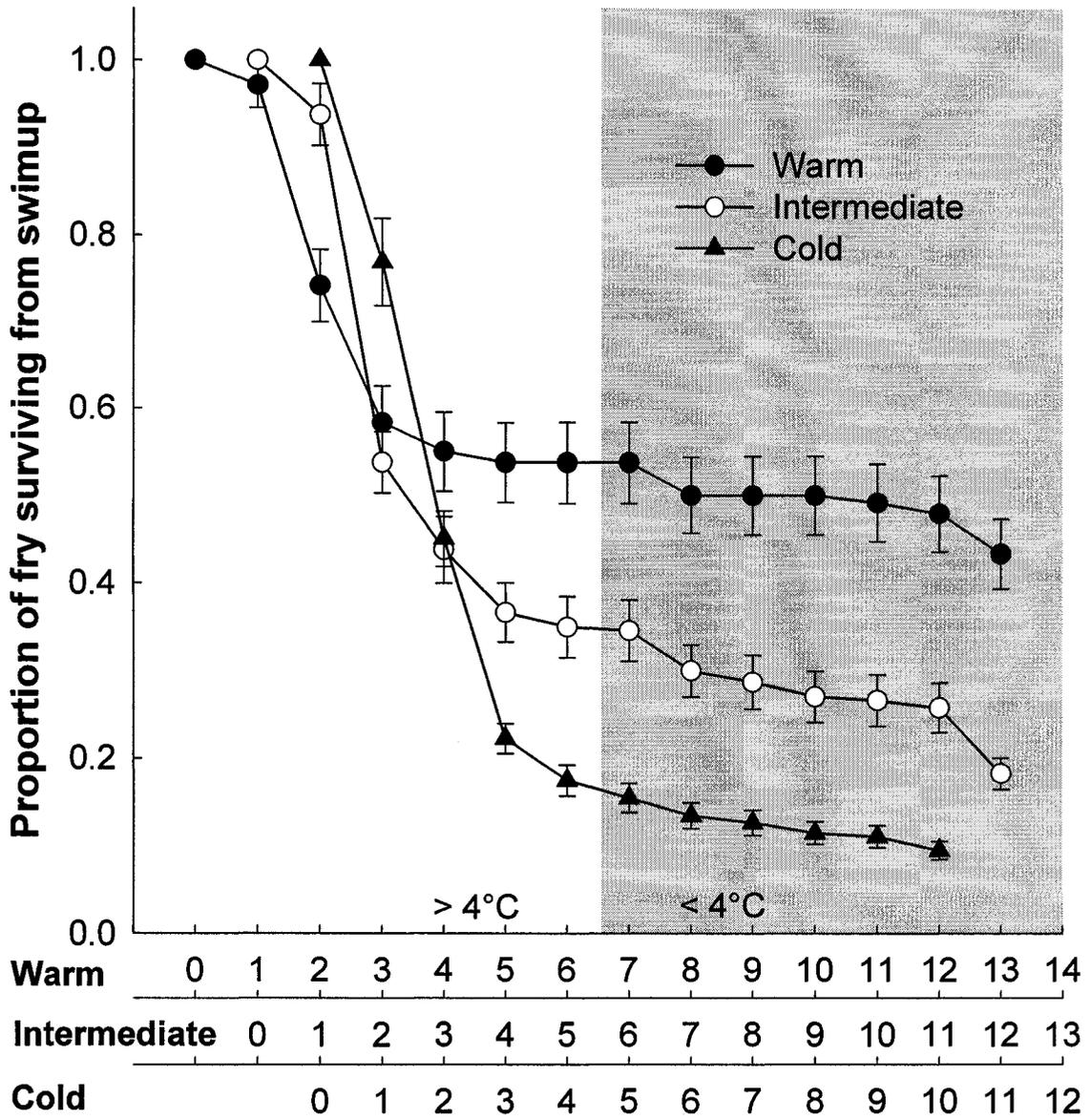


Figure 7.

Figure 7. Proportion of age-0 Colorado River cutthroat trout surviving from swim-up to each week during Phase 2 of the 2004 experiment. The survival curves for each regime have been shifted along the horizontal axis to synchronize them based on the timing for onset of winter temperatures. Bars show Kaplan-Meier 95% confidence intervals.

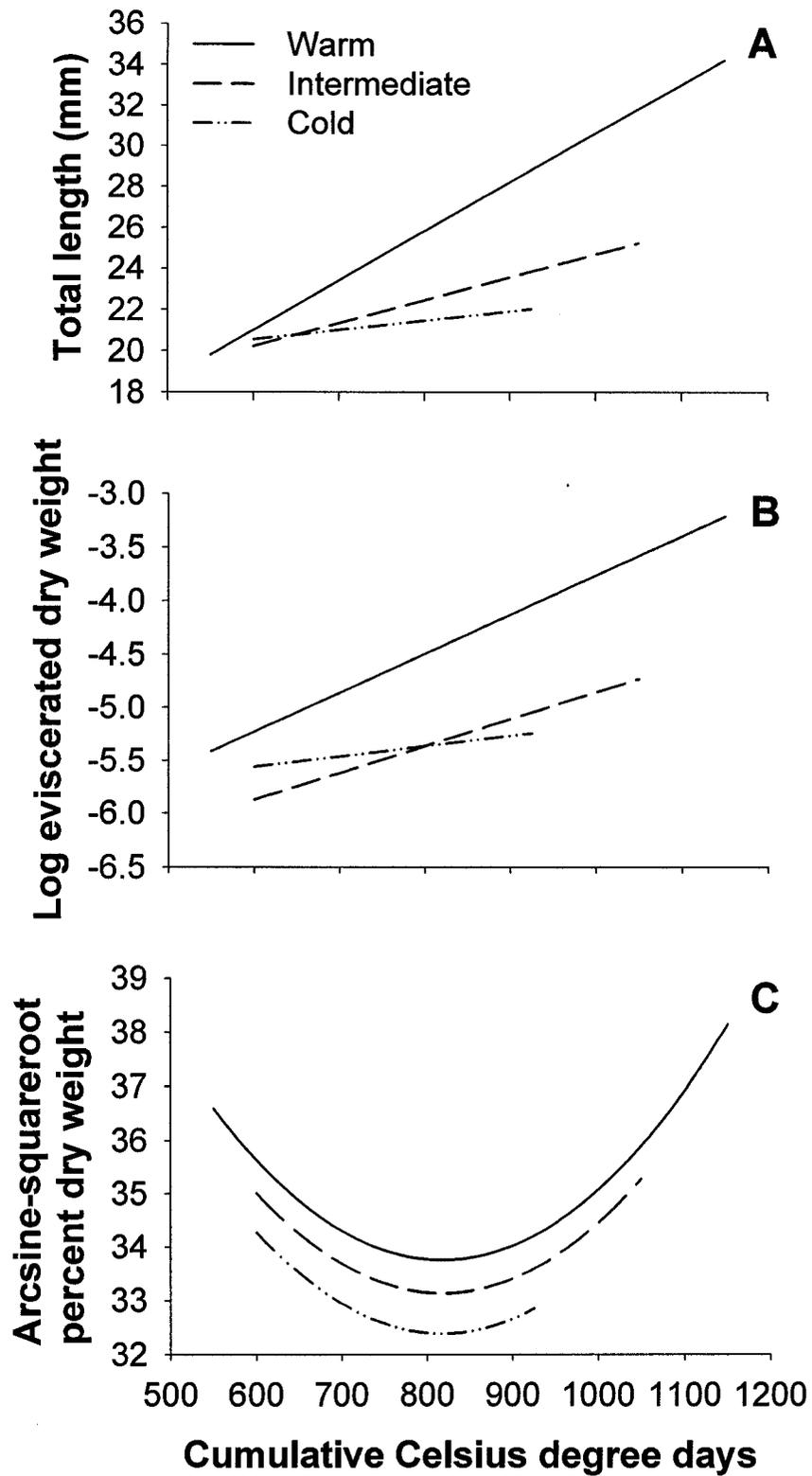


Figure 8.

Figure 8. Predicted A) total lengths, B) log eviscerated dry weights, and C) arcsine-squareroot percent dry weights of fry from the 2004 experiment, based on regression models fitting each of these variables. There was a significant interaction between accumulated degree days and treatment in all analyses (see Table 4).

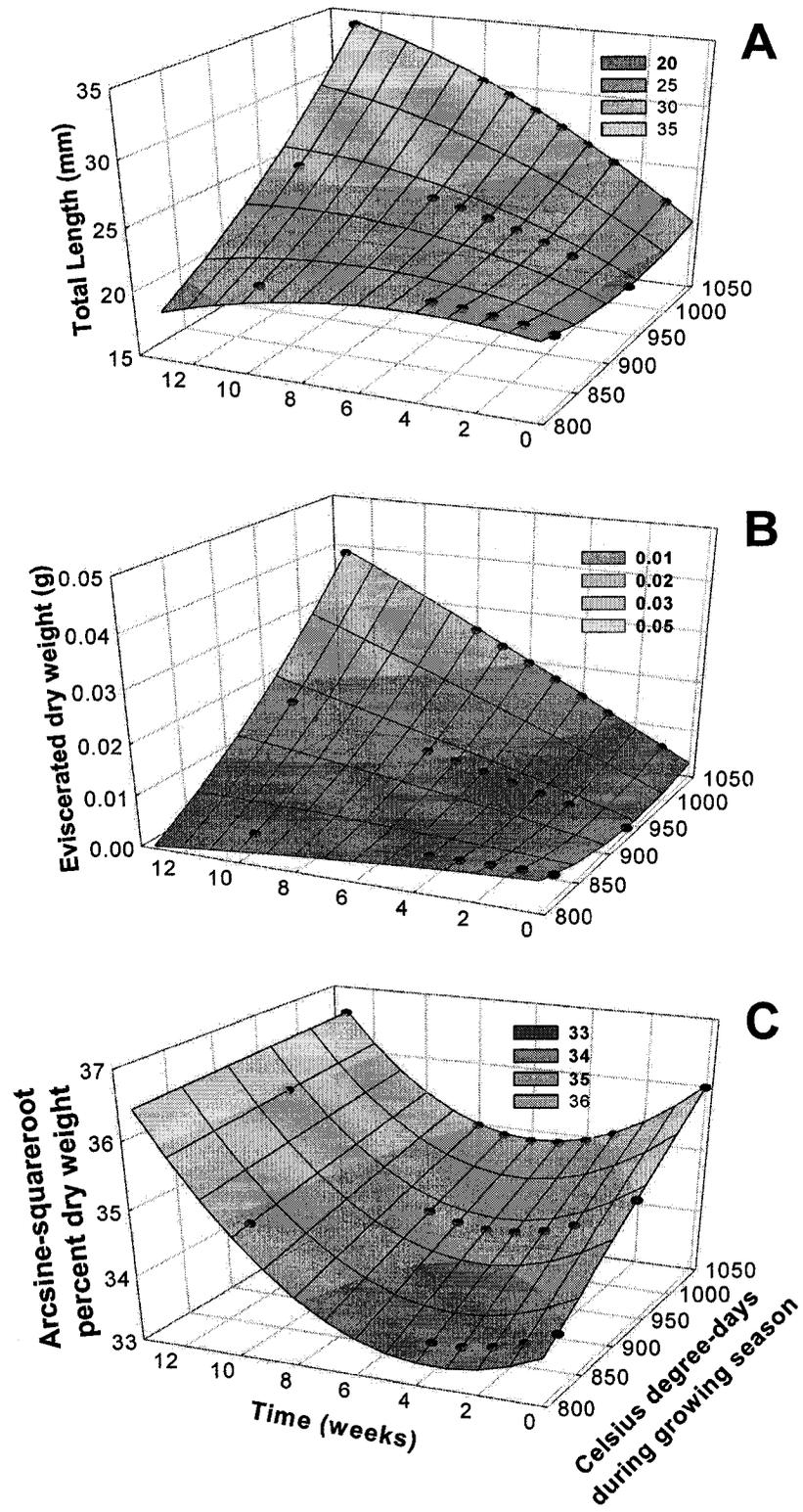


Figure 9.

Figure 9. Response surfaces for A) total length, B) eviscerated dry weight, and C) arcsine-squareroot percent dry weight of age-0 Colorado River cutthroat trout fry sampled from experimental tanks during Phase 2 of the 2004 experiment. The dots show when sample fish were collected in each of the three temperature regimes. Fish were subjected to 818, 932, and 1044 growing season degree-days during the 2004 experiment in the cold, intermediate, and warm regimes, respectively.

**CHAPTER 3: Cold Summer Temperature Limits Recruitment of Age-0 Cutthroat  
Trout in High-Elevation Colorado Streams**

Accepted for Publication in *Transactions of the American Fisheries Society*

## **Abstract**

Translocation is a key strategy for conserving native cutthroat trout *Oncorhynchus clarkii* subspecies that have declined markedly throughout their native range. Previous research showed that successful translocations of cutthroat trout in high-elevation southern Rocky Mountain streams were more likely in those with warmer summer water temperatures, and lead to the hypothesis that cold summer temperatures govern translocation success by limiting recruitment. I tested this by measuring density and size of age-0 cutthroat trout (greenback *O. c. stomias* and Colorado River cutthroat trout *O. c. pleuriticus*) in six headwater streams in north central Colorado that varied in thermal characteristics. Surveys were conducted at peak emergence during three years in two widely-spaced study reaches in each stream. Fry density increased with Celsius degree days accumulated during the growing season, but did not vary significantly among years. Laboratory data on growth and survivorship of age-0 cutthroat trout in three temperature regimes similar to those studied in the field was used to determine expected survivorship and size of fry at the start of winter, which occurred several weeks after peak emergence in the warmer reaches and coincided with emergence in colder reaches. The results support the hypothesis that recruitment of native cutthroat trout in Colorado is limited by cold water temperatures that reduce growth and recruitment. High-elevation streams like those studied that accumulate 900-1200 Celsius degree days during the growing season afford the best opportunity for cutthroat trout recruitment and translocation success. Streams that provide 800-900 degree days likely sustain recruitment in some years, and those with less than 800 degree days are generally unsuitable for translocations due to a

greater risk of recruitment failures and smaller sizes attained by fry by the onset of winter.

## **Introduction**

Recruitment in fishes is critical to population abundance and persistence, and is controlled by interacting abiotic and biotic factors (Hjort 1914; Houde 1987; Myers 2001). The relative importance of abiotic vs. biotic factors in determining recruitment may vary at different life history stages and in different environments. Abiotic factors are typically more important during larval and early juvenile stages in fishes, when fish rely on yolk energy stores and are not food limited, whereas biotic factors are more important once fish have depleted their yolks and begin to compete for exogenous prey (Houde 1987, 2002). However, in harsh environments, the role of abiotic factors such as temperature and salinity may outweigh biotic factors like competition and predation in causing bottlenecks throughout the period of juvenile recruitment (Shuter and Post 1990; Myers 1998). Such a case may exist for salmonids in regions of high latitude and high elevation, where temperatures are cold and growing seasons short (Biro et al. 2004). In these thermally marginal environments, mechanisms that underlie recruitment bottlenecks may include delayed spawning and prolonged egg incubation (Stonecypher et al. 1994), and delayed larval development and slow growth (Coleman and Fausch in press), which may eventually lead to energetic deficits that cause starvation during winter (Cunjak and Power 1987; Cunjak et al. 1987).

Recruitment bottlenecks like these may have important effects on population persistence of native cutthroat trout *Oncorhynchus clarkii* in high-elevation streams in the western U.S. The cutthroat trout has 14 recognized subspecies (two are functionally

extinct), but most of those remaining occupy only small proportions of their native ranges due to overfishing, invasions by nonnative species, and habitat loss (Young 1995; Young and Harig 2001; Behnke 2002; Hirsch et al. 2006). The three extant subspecies native to the southern Rocky Mountains are the Colorado River *O. c. pleuriticus*, greenback *O. c. stomias*, and Rio Grande *O. c. virginialis* cutthroat trout, which have diverged relatively recently from a common ancestor and are thus both phylogenetically and ecologically similar (Behnke 1992; 2002). Populations of these subspecies are frequently translocated into headwater streams and isolated above migration barriers to prevent introgressive hybridization and competition with nonnative fishes downstream (Harig et al. 2000; Novinger and Rahel 2003; Fausch et al. 2006). Such translocations are a key management strategy used to conserve native cutthroat trout stocks (USFWS 1998; CDOW 2003; CRCT Coordination Team 2006). However, recent research indicates that translocation success for two subspecies in Colorado may be hampered by low temperatures in about half of the high-elevation streams to which they were introduced (Harig and Fausch 2002; Coleman and Fausch in press).

Harig and Fausch (2002) reported that cold summer stream temperature in conjunction with lack of physical habitat were important factors limiting translocation success in greenback and Rio Grande cutthroat trout. Translocation success, measured in three categories of adult fish abundance, was correlated with mean July stream temperatures, bankfull pool width, and the number of deep pools. Model predictions indicated that translocations would likely fail to establish populations in streams with mean July temperatures  $<7.1^{\circ}\text{C}$  (at the average width and number of pools), and establish low and high abundance populations, respectively, with mean July temperatures

averaging 7.8°C and 10.0°C. Harig and Fausch (2002) hypothesized that low translocation success in cold streams had been caused by recruitment failures due to cold summer temperatures. These proximate effects on recruitment over successive generations may ultimately limit the final adult population size achieved through translocations to cold high-elevation streams.

The goal of this study was to test this hypothesis directly by measuring recruitment of translocated Colorado River and greenback cutthroat trout populations in headwater streams that span the range of temperature regimes of streams studied by Harig and Fausch (2002). I predicted that growth and recruitment of age-0 trout would be greater in streams with warmer regimes. This study was conducted simultaneously with a laboratory study (Coleman and Fausch in press) that measured growth and survival in controlled temperature regimes developed from the three groups of streams defined by Harig and Fausch (2002), with absent, low abundance, or high abundance populations. The results show that growth and abundance of age-0 cutthroat trout were greater in warmer streams, and use laboratory data to predict their growth and prospects for survival to onset of winter, after a severe recruitment bottleneck that coincides with declining temperature at the end of the growing season. These results can be used to validate guidelines developed from the companion laboratory study for selecting streams with thermal regimes sufficient to promote successful future translocations of these native cutthroat trout.

### **Study sites**

Six first- or second-order headwater streams in the southern Rocky Mountains in north central Colorado were selected for study (Table 1). All were located in the

Arapaho-Roosevelt National Forest or Rocky Mountain National Park, and contained allopatric populations of either greenback or Colorado River cutthroat trout that had been sustained by natural reproduction for at least 20 years above barriers to nonnative trout invasion. As such, they were representative of small headwater streams where native cutthroat trout persist in northern Colorado. The streams spanned the range of temperatures for which the model of Harig and Fausch (2002) predicted that recruitment would occur either intermittently, and produce a low abundance of adult trout, or consistently, and produce high adult trout abundance. In each stream, two study reaches were selected near the upstream and downstream end of cutthroat trout distribution that were approximately 500 m long and appeared physically similar. Fry densities can be low and their distribution patchy, so long study reaches were chosen to improve the accuracy of the fry density estimates. The reaches were spaced as far apart as possible to measure the effects of thermal differences within streams, but excluded low gradient reaches containing beaver ponds. The reaches ranged from 2633-3068 m in elevation at their downstream ends, 2.5-9.0% in gradient, and 3.0-4.4 m in bankfull width. Measured reach lengths ranged from 486-534 m, except in Columbine Creek, a short headwater stream segment where beaver ponds further limited study reaches to 349 and 311 m. Substrates in study reaches were dominated by gravel to cobble sized bed material, and riparian vegetation was dominated by a combination of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*), interspersed with willows (*Salix* spp.).

## Methods

Stream temperatures were monitored year-round in each study reach and body length and abundance of age-0 cutthroat trout were measured each fall during three years (2002 to 2004). During summer 2004, surveys of adult trout and spawning habitat were conducted. I predicted age-0 cutthroat trout lengths and recruitment at the onset of winter using field and laboratory data to account for additional growth and mortality after fry surveys. The start of the growing season was defined as the beginning of the first week that average stream temperatures exceeded and remained above 5°C for the season, and the end as the last day of the first week that average stream temperature dropped below 4°C. These criteria were based on previous work indicating that adult native cutthroat trout in Colorado spawn when stream temperatures reach 5 - 8°C (USFWS 1998), and that growth typically occurs in trout at water temperatures approximately 4°C and above (Piper et al. 1982).

*Stream temperature monitoring.* Water temperature in the 12 study reaches was monitored using two to four thermographs per stream (HOBO Water Temp Pro temperature data loggers, Onset Computer Corporation, Pocasset, ME), deployed during June and July 2002. A small tributary entered near the midpoint of each study reach in Cabin Creek, so additional thermographs were placed downstream to measure their thermal influence. The tributary in the downstream reach was found during the 2002 fry survey, so the additional thermograph was deployed in 2003. These 14 thermographs measured temperature at 1-h intervals through the final fry recruitment surveys in September 2004.

*Predicting temperature for periods not measured.* Temperature monitoring began after several weeks of the growing season had elapsed during 2002 and ended several weeks before the end of the growing season in most streams during 2004, so local air temperature and precipitation were used to predict mean weekly stream temperatures for these unmeasured periods. The goal was to identify a model that best predicted stream temperatures in each study reach, rather than to determine the relative importance of individual predictor variables. Segmented linear models were used to predict stream temperature for each of my thermograph stations (Proc NLIN, SAS v9.1) and a model selection procedure was used to choose the best model for each site. The segmented regressions fit different conjoined linear relationships for summer and winter data, identifying the best fitting lines for each period based on the predictor variables and the transition point between the two lines (i.e., at the change of seasons). The slope of the line predicting winter temperatures was zero in every case, because winter temperatures stabilize when surface ice forms, but the segmented fit ensured that the lack of an air-water temperature relationship during winter did not detract from the summer fit.

The primary predictor was local air temperature (see Cassie et al. 2001; Sloat et al. 2005), with or without a 1-wk lag due to the potential for delayed effects on water temperature. Water temperatures recorded in the same place at different times are not independent, but instead are related to prior water temperatures. Rather than using an autoregressive time-series approach to predict temperatures for the unmeasured periods, the lack of independence between measurements was accounted for using one of three covariates. For these covariates, air temperature served as a surrogate for stream temperature, because the two are positively correlated (Gu and Li 2002; Isaak and Hubert

2004; Sloat et al. 2005). The covariates were the difference between air temperature used and that of the previous week, or the average of the previous two or three weeks. Using this approach, time-series extrapolations were avoided, and instead predictions were based primarily on air temperatures for prediction periods, which were within the range of air temperature for the period during which actual stream temperature data were collected.

To improve model precision, three precipitation covariates were included to account for additional variation in stream temperature not accounted for by air temperature. These were spring snowpack (proportion of average) measured on May 31 each year, summer precipitation (cm) measured from June 1 to August 31 each year, and the Palmer Drought Severity Index, which incorporates temperature and rainfall (Palmer 1965). Spring snowpack and summer precipitation were calculated using data from the National Weather Service Cooperative (NWSC) station nearest each stream that had complete data for 2002-2004 (mean distance = 10.2 km, range 7.1 – 15.3). The Palmer Drought Severity Index was reported by the Colorado Climate Center (Colorado State University, Fort Collins).

An information-theoretic approach was used to select the “best approximating” segmented linear model using Akaike’s Information Criteria (AIC). This allows objectively selecting the model most consistent with the data, while balancing the trade-off between precision and bias (Franklin et al. 2000; Burnham and Anderson 2002). The model with the lowest  $AIC_c$  (AIC corrected for small sample bias) was considered to be the best approximating model among a set of 12 models predicting stream temperature as a function of local air temperature and the precipitation covariates for each of the 14

thermograph locations. These best approximating models were then used to predict weekly mean water temperatures for the periods during the growing season at each study site not measured in 2002 and 2004. Finally, the accumulated degree days during the unmeasured period for each stream was calculated by multiplying the mean weekly temperatures by seven to extrapolate the sum of the mean daily temperatures. For the measured period, daily mean temperatures were simply summed to calculate degree-days. The sum for the two periods, termed 'growing season degree days' (GSDD), is a continuous variable that integrates the thermal regime for the entire growing season in each stream.

*Surveys of adult trout and spawning habitat.* Visual surveys were conducted during July 2004 to determine whether adult cutthroat trout abundance and available spawning habitat was sufficient to sustain recruitment in study reaches. Surveys were conducted early in the growing season to count fish in or near the areas where they spawn, in case adults emigrated after spawning (see Young 1996; Northcote 1997; Schmetterling 2001). During summer, adult cutthroat trout most often inhabit pools (Young 1996), so the visual survey methods used by Harig and Fausch (2002) were adapted to estimate adult trout abundance. Two observers wearing polarized sunglasses moved slowly upstream, counting all adult fish ( $\geq 125$  mm) observed in each channel unit (i.e., riffle, run, pool). One observer probed beneath undercut banks and around boulders and large woody debris with a wood staff to detect additional fish hiding beneath cover. The other observer held a partly concealed position on the bank and made a second count from this higher vantage point. The two counts were reconciled and recorded. A recent study suggested this method is conservative, detecting 16% of adult abundance estimated

by removal electrofishing (Young and Guenther-Gloss 2004). During the same survey the number of patches of spawning habitat were recorded, defined as small areas ( $\geq 0.5$ - $2.0 \text{ m}^2$ ) of clean gravel substrate ( $< 25\%$  embedded with fine substrate) approximately 0.5-3.0 cm diameter, the range of sizes used for spawning by other small salmonids (Kondolf and Wolman 1993). Most study reaches also had one or more large accumulations of spawning gravel  $> 2.0 \text{ m}^2$  trapped upstream of boulders or woody debris jams, so the length and width of these patches were measured to estimate area. Data on adult cutthroat trout abundance collected by other researchers in my study streams between 1997 and 2002 was also compiled (M. Young and P. Guenther-Gloss, US Department of Agriculture Forest Service [USDAFS], unpublished data; B. Rosenlund and C. Kennedy, USFWS, unpublished data; USFWS 1998; Harig and Fausch 2002).

*Fry surveys.* Cutthroat trout begin to spawn in Colorado mountain streams when mean daily water temperatures reach  $5^\circ\text{C}$  in June or July (USFWS 1998; B. Rosenlund, USFWS, unpublished data), and fry begin to emerge from redds after 570-600 Celsius degree days have accumulated (Coleman and Fausch in press), from mid-August through early October. Spawning may occur over two to three weeks once the growing season begins, so 100-200 degree days may have accumulated before some fish spawn. As a result, peak fry emergence was predicted to occur approximately 600-800 degree days after spawning. Annual fry surveys were conducted to estimate abundance of recently-emerged cutthroat trout fry in each study reach during late August to early October when this period was predicted to occur. In the warmer reaches, several weeks of growing season remained at the time of my fry surveys, whereas in the colder reaches, fry surveys were conducted at the end of the growing season (see Table 2). In general, streams were

surveyed in order from warmest to coldest, based on prior summer temperature data provided by the Arapaho and Roosevelt National Forests (K. Sexton, USDAFS, unpublished data), Rocky Mountain National Park (B. Rosenlund and C. Kennedy, USFWS, unpublished data), and previous research (Harig and Fausch 2002).

Temperature data collected during this study (Table 2) generally confirmed this order.

Each year, surveys began after pilot sampling at Roaring Creek, the warmest stream, confirmed that fry had recently emerged and their total lengths were between 20-25 mm. Age-0 cutthroat trout fry less than 30 mm long are weak swimmers and are confined to backwaters, isolated pools, or small shallow sheltered depressions, with very low water velocity (Moore and Gregory 1988), which I termed “pockets.” A systematic sample of  $n = 1771$  pockets in all streams measured during 2002 averaged  $0.64 \text{ m}^2$  (SE =  $0.02 \text{ m}^2$ ) in area and  $0.12 \text{ m}$  (SE =  $0.0014 \text{ m}$ ) deep. Nearly all of the pockets were located along channel margins. Pilot surveys showed that newly emerged fry are not easily disturbed by observers approaching carefully, and when startled they seek cover within pockets rather than fleeing into adjacent flowing waters that would wash them away. Because small age-0 fry are confined to pockets, where they are relatively easy to find and count compared to larger fry, a visual survey method to estimate fry abundance at peak emergence was possible. Fry counts were interpreted as an index of fry recruitment resulting from recruitment limitation over several generations, and not simply due to year-to-year differences.

The fry surveys consisted of pocket-by-pocket visual counts by two observers wearing polarized sunglasses. One observer moved slowly upstream along each bank, counting all age-0 cutthroat trout fry in each pocket encountered. Observers first

identified pockets from downstream and conducted a primary visual scan during a careful upstream approach, followed by a close visual count of fry. After the primary count, observers gently disturbed all available cover in the pocket with a blunt probe to reveal any hidden fry. Pocket cover included undercut banks, crevices under and between substrate particles, and any other gaps that small age-0 cutthroat trout fry might enter. Accurate fry counts resulted, because the number of fry per pocket was low (in 2002, 97% contained  $\leq 1$  fry,  $n = 4381$ ) and observers took care not to suspend silt. In 2002, some fry in two of the warmest study reaches had grown larger than 30 mm and moved from pockets to the margins of the main channel, so observers also surveyed this habitat and counted all larger fry. Each year, observers also captured a sample of up to 10 fry from throughout each reach using fine-meshed dip nets and measured their total lengths to the nearest 0.5 mm. After processing, fry were immediately returned to their pocket. Fry were not counted in West Creek or the lower study reach in Roaring Creek during 2003 due to logistical constraints, and other minor differences in reach lengths sampled are shown in Table 1.

*Validation of visual fry counts.* Previous research using a careful searching technique for age-0 Colorado River cutthroat trout fry (Bozek and Rahel 1991) indicated that observers saw 78% of the fry (20-52 mm total length [TL]) estimated to be present by three-pass depletion electrofishing, and that their visual counts were significantly correlated with the electrofishing estimates ( $r = 0.92$ ,  $P < 0.05$ ). By comparison, most fry observed during field surveys had emerged recently and were smaller (20-35 mm TL), and so were confined to pockets due to their weak swimming ability (Moore and Gregory 1988). To determine whether visual counts of fry in pockets were accurate, two trials

were conducted during July and August 2003, just below the upper reach of Roaring Creek and just above the lower reach of Cabin Creek, to compare my visual counts to the number of fish captured by electrofishing.

For this validation study, an observer worked upstream, carefully counting fry in pockets as described previously (including disturbing pockets with a blunt probe) and placing flags about 50 cm from pockets to mark them for follow-up electrofishing. The observer was careful to select pockets far enough apart that electrofishing in one would not disturb fry in the next, and did not communicate the results to the electrofishing crew. Fry were observed not to leave pockets either during or after the visual counts, and before electrofishing was conducted. The two-person electrofishing crew, equipped with a backpack electrofishing unit (Coffelt Inc., Model BP-4) operated at 350-400 V at 30 Hz, sampled each pocket within 5 min after the visual counts were conducted. Each pocket was surrounded with dip nets on the offshore side to enclose any fry present (usually 0-2 in each pocket), and workers captured fry during two separate thorough electrofishing passes made to sample all habitat in each pocket. Shocking duration was typically 15-30 s on each pass, and 60-90 s elapsed between passes. When observers captured fry on the second pass, they conducted additional passes until no more fry were captured. The total was summed to estimate the number of fry in each pocket.

I evaluated several approaches for calibrating visual counts using the electrofishing estimates. Regression procedures describing the relationship between two variables that are both subject to measurement error (i.e., Model II regression) were considered, primarily Major Axis Regression (Sokal and Rohlf 1995) because it is most useful when both variables are measured in the same units. However, this method

assumes the two variables are continuous and that errors are randomly distributed. In contrast, count data are multinomial and display a Poisson distribution, for which there is no established procedure for Model II regression. In addition, the results indicated that electrofishing sometimes underestimated fry abundance, and so could not be used as a calibration standard (see Results). Therefore, both methods produced similarly biased estimates of true abundance, with true fry abundance being proportionally higher, so correlation analysis was used to compare them (Proc CORR, SAS v9.1).

*Statistical Analyses and Model Selection.* The goal of the first stage analyses was to determine the relationships of the fry recruitment at peak emergence to GSDD, and whether this relationship differed by year. An information-theoretic approach was used to select the best approximating model (or subset of models) from among a set of three regression models that predicted fry counts as a function of GSDD, year (a class variable), and the GSDD $\times$ year interaction. Growing season degree days was selected as the primary predictor and included in all models, because it quantitatively describes stream temperature regimes (more degree days accumulate in a growing season in warmer regimes), and integrates most stream temperature variation that occurs over time during the summer growing season, when eggs and fry are developing. It thus accounts for the most pervasive factor that influences fish physiology and ecology, namely temperature (Brett 1964; Coutant 1976; Magnuson et al. 1979). Therefore, GSDD is a continuous variable that is useful for fitting predictive models of recruitment and growth that managers can apply with greater accuracy to a broad variety of streams.

I developed models predicting fry density using Poisson regression (Proc GENMOD, SAS v9.1). The dispersion parameter was scaled to the deviance of the

global model, which included all covariates and interactions, to account for overdispersion (Burnham and Anderson 2002), and a log-link function was used to account for non-normality and heterogeneous variance, which are typical in count data. The same model selection procedure based on AIC values was used as for predicting stream temperatures (Franklin et al. 2000; Burnham and Anderson 2002). The model with the lowest AIC<sub>c</sub> was considered to be the best approximating model and variables were considered important for predicting fry counts if they occurred in the top model.

Although fry were counted at peak emergence (at swimup) in each stream, streams were surveyed over a 4-6-week period each year, and those with warmer temperatures had several weeks of growing season remaining before the onset of winter. Peak emergence in colder streams occurs later, and thus closer to the onset of winter, so fry surveys in the coldest streams coincided with the end of the growing season. A concurrent laboratory experiment in 2003 (Coleman and Fausch in press) that mimicked temperature regimes in high-elevation streams in Colorado indicated that a severe recruitment bottleneck occurs for fry of Colorado River cutthroat trout after swimup and before the onset of winter. Survival rates through this bottleneck were highest in the warmest temperatures tested and lowest in the coldest (7, 8.5, and 10°C mean daily summer temperature). Thus, my fry counts, which were made during the estimated period of peak emergence, were indicative of recruitment to swimup among streams and reaches in general, but do not reflect recruitment to the onset of winter during a period when my laboratory data indicated the greatest mortality may occur. Therefore a logistic regression model was fit describing the relationship between survival from swimup (peak emergence) to the start of winter from the laboratory data (Coleman and Fausch in press)

and used this to predict survivorship of fry in each of the field study reaches from peak emergence to the onset of winter.

I used fry total length measurements from both the 2003 laboratory experiment (Coleman and Fausch in press) and fry collected in the field during this study to predict the total length of fry at the onset of winter. Subsequent growth was likely at warmer study sites where temperatures remained sufficient for growth for several weeks after fry surveys. Fry surveys were conducted to coincide with peak fry emergence, but survey timing varied somewhat relative to this period annually, and between reaches within streams. Degree days accumulated from estimated spawning (water temps > 5°C) to fry surveys (DD) ranged from 511-866 in 11 of 12 study reaches over three years, and was 1045 in one reach during 2002. Linear and exponential regression models were fit to describe growth from swimup to the start of winter as a function of accumulated degree-days at measurement (Proc NLIN, SAS v9.1). These DD describe only the relationship between size and degree days to which fish have been exposed from spawning to the time they were measured, and differs from GSDD, which is degree days in the stream temperature regimes from spawning to the onset of winter. However, when GSDD for each study reach is substituted for DD in the best-fitting model (with lowest AIC<sub>c</sub>), the model provides an estimate of expected mean total lengths of fry at the onset of winter.

## **Results**

*Adult trout abundance and spawning habitat.* Data on adult cutthroat trout from all available sources indicated that sufficient numbers were present in my study reaches for successful spawning and recruitment, given favorable conditions (Table 2). The visual surveys during summer 2004 detected 10-54 adult fish in each study reach,

although comparison to abundance estimates from removal electrofishing by other investigators suggested that these underestimated abundance by 2-10 times (cf., Young and Guenther-Gloss 2004). Adult surveys could not be conducted at West Creek due to high flows, but visual surveys by Harig and Fausch (2002) in 1998 in the same reaches using the same method indicated similar numbers of adults as in my visual surveys of other reaches. Large deep pools in the upper reach likely obscured their visual counts, further underestimating abundance. Overall, the presence of adult fish indicated that adults use habitat in the study reaches during summer, and thus probably spawn there.

My surveys also indicated that habitat in the study reaches was sufficient for adult trout to spawn (Table 2). The density of habitat patches deemed potentially suitable for spawning (i.e.,  $>0.5 \text{ m}^2$ ) averaged from 2.9 to 14.0 per 100 m, after accounting for reach length. Likewise, the total area of patches  $>2.0 \text{ m}^2$  ranged from 0.0 to  $10.4 \text{ m}^2$  per 100 m in the study reaches. Overall, the lower reach of Columbine Creek (one of the warmest reaches surveyed) had the least spawning habitat and the upper reach of East Fork Sheep Creek (one of the coldest) had the most. High flows prevented a habitat survey in West Creek during 2004, so the availability of spawning habitat was judged from data collected in 1998 by Harig and Fausch (2002). Their field surveys indicated at least one patch of spawning habitat at the downstream end of each pool, and my field notes described large patches of suitable spawning gravel in the downstream study reach.

***Stream temperature monitoring.*** Mean August temperature in my study reaches ranged from 6.8 to 9.9°C during the three years of study (Table 2). Complete temperature data were measured for August of each year, whereas temperatures were predicted for parts of July 2002 before monitoring began. Nevertheless, temperature was

similar for the two months each year. When mean July temperatures for both reaches of each study stream were averaged, the temperatures for the three colder streams were 7.1, 7.4, and 7.6°C, and for the three warmer streams were 8.1, 8.9, and 9.1°C. Thus, the study streams spanned the range of mean July temperatures predicted to support low (average 7.8°C) to high abundance (average 10.0°C) of cutthroat trout (Harig and Fausch 2002).

***Prediction of stream temperature.*** The model best describing stream temperature as a function of air temperature and precipitation covariates for each thermograph location was used to predict temperatures for the first few weeks of the growing season in 2002, before thermographs were deployed, and the last few weeks of the growing season in 2004, after thermographs were retrieved. The best fitting models accounted for most of the variation in measured stream temperature from midsummer 2002 through the fry surveys during fall 2004 ( $R^2 = 0.90-0.97$ ). Predicted temperatures were combined with actual data collected during thermograph deployment to estimate the full summer temperature regimes for 2002 and 2004. The total number of weeks for which temperatures were predicted ranged from 4-14 (median = 10) over three years for all but one study reach in Cabin Creek, where temperature was predicted for 26 weeks for one thermograph placed during 2003.

***Validation of visual fry surveys.*** A comparison of the careful visual survey technique to removal electrofishing showed that the two methods were nearly equivalent when counting recently emerged age-0 fry (20-35 mm TL). Overall, similar numbers of fry were counted using both the visual method and removal electrofishing (19 vs. 18 in Cabin Creek, 12 vs. 14 in Roaring Creek). Counts in each pocket were significantly

correlated ( $r = 0.75$ ,  $P < 0.0001$ ,  $n = 73$  pockets in Cabin Creek;  $r = 0.52$ ,  $P = < 0.0001$ ,  $n = 50$  pockets in Roaring Creek), but neither method detected all fry found by the other. Therefore, the visual survey technique was used throughout this study to avoid the risk of harmful effects of electrofishing on trout recruitment (Snyder 2003), and because it was faster and more efficient for making extensive fry surveys over long stream reaches that included large numbers of pockets. Moreover, calibration study results indicated that two-pass electrofishing was not a suitable standard for calibrating my visual survey method. In particular, electrofishing sometimes failed to detect fry that were seen, probably because some pockets were partly inaccessible by the electrofishing probe due to complex microhabitat.

***Recruitment of age-0 fry.*** Cutthroat trout fry were more abundant in the three warmer streams than the three colder streams over the three years of this study (Figure 1). A total of 10,218 pockets were surveyed in the six study streams, and the number of fry counted at peak emergence averaged 10.1 per 100 m in the three warmer streams, which accumulated more than 750 GSDD on average, versus 2.1 per 100 m in the three colder streams that averaged fewer than 700 GSDD. Moreover, fry counts varied among years. The highest fry counts in most study streams occurred during 2002, the driest year on record (257 mm precipitation) and one of the warmest (7.9°C mean annual temperature, ranked 12th) during the 110-year record in Colorado (National Climate Data Center, <http://www.ncdc.noaa.gov>). Fry counts were generally lower in 2003 and 2004, when precipitation was higher (361 and 434 mm, respectively), and mean annual temperatures remained high (8.6°C and 7.9°C, respectively).

Estimated abundance of age-0 cutthroat trout fry at peak emergence was higher in warmer stream reaches, when the two study reaches in each stream were considered separately. Fry density increased with GSDD alone (Figure 2), based on the best fitting model. This model, which held most of the Akaike weight ( $w_i = 0.81$ ), included only GSDD as a predictor (Table 3), and was clearly superior to two models that included year effects ( $\Delta AIC_c = 2.93$ ; 80.31). Fry density increased more rapidly with increasing stream temperatures in regimes with greater than about 800 GSDD.

Predictions of survivorship from peak emergence to the start of winter based on laboratory data (Figure 3) indicated that the few fish that do emerge in colder streams face a greater risk of mortality during the subsequent recruitment bottleneck (Coleman and Fausch in press; Table 4). Predicted survivorship ranged from 0.28 in the coldest reach, with a three-year mean of 581 GSDD, to 0.74 in the warmest reach, with a mean of 996 GSDD. The four reaches in which mean densities at peak emergence were highest and predicted survivorship through the post-swimup recruitment bottleneck was probable ( $>0.50$ ) averaged  $>800$  GSDD, indicating that swimup fry in stream segments with  $< 800$  GSDD are unlikely to survive to the onset of winter.

***Size of age-0 fry.*** Like recruitment, lengths of cutthroat trout fry were greater in warmer stream reaches. The best-fitting model described total length of fish measured in the field and laboratory as an exponential function of accumulated degree days from spawning to measurement (DD), location (LOC: field or lab), and the DD $\times$ LOC interaction (Figure 4). This model could not be clearly distinguished from the second-ranked model, which was the same but excluded the interaction ( $\Delta AIC_c = 0.45$ ). To ensure the most accurate predictions, the top-ranked model was selected. Substituting

GSDD for DD in the model provided estimates of fry total lengths at the onset of winter in my study reaches, which ranged from 23.1 mm in the coldest reach to 37.3 mm in the warmest study reach (Table 4).

## **Discussion**

The results of this study support the prediction that size and recruitment of age-0 cutthroat trout are greater in warmer streams, and lend support to the hypothesis of Harig and Fausch (2002) that translocation success in high-elevation Colorado streams is governed by negative effects of cold summer temperature on recruitment. Overall, these data corroborate the results of my laboratory experiment (Coleman and Fausch in press), and indicate that streams that accumulate <800 Celsius degree days during the growing season are unsuitable for translocations of the three subspecies of cutthroat trout native to Colorado due to their higher probability of recruitment failure. In contrast, streams reaching about 800-900 degree days may support adequate recruitment in some years, and those with about 900-1200 degree days are most suitable for translocations.

When combined with other field data and results of the companion laboratory experiment (Coleman and Fausch in press), these results suggest that cold summer water temperatures limit recruitment and translocation success via size-dependent effects on survival. Young and Guenther-Gloss (2004) found that abundance of age-1 cutthroat trout was positively correlated with summer water temperature in 12 Colorado streams during 1998-1999, which included two of the streams I studied. Peterson and Fausch (2002) reported that recruitment of age-0 cutthroat trout to the onset of winter, and to age-1 the following year, nearly always failed in cold segments of two high-elevation Colorado streams (mean July temperature 6.6 and 6.9°C) in which fry averaged only 26

and 30 mm TL by early September. In contrast, recruitment occurred consistently in segments of two other streams that were warmer (12.7 and 12.4°C), where fry reached 45 and 69 mm TL by mid-September. Likewise, Coleman and Fausch (in press) found in a second experiment that survival of age-0 Colorado River cutthroat trout in laboratory streams was >0.50 to the onset of winter in a warm treatment (1044 GSDD) where fry averaged 34 mm TL soon after the onset of winter, compared to two colder treatments (932 and 818 GSDD) where survival was only 18-35% to the onset of winter and survivors averaged only 26 and 25 mm TL. These data suggest that cutthroat trout fry need to reach a minimum of 30-35 mm TL by the onset of winter to allow recruitment to age-1 in temperature regimes like those of the streams I studied in the southern Rocky Mountains. If the 30-35 mm TL minimum size threshold I propose can be validated and generalized among streams, the abundance of age-0 fish reaching this threshold by the end of the growing season might be a useful index of recruitment for fisheries managers.

Overall, my results indicate that some high-elevation stream segments in the southern Rocky Mountains can be marginal habitats for native cutthroat trout due to cold temperatures that reduce fry survival and recruitment. Brett (1964) called temperature the “ecological master factor,” and its pervasive influences in fish ecology have long been widely recognized (Coutant 1976; Magnuson et al. 1979). Theoretically, abiotic factors such as temperature have their most marked effects on survival of larval fish (Houde 1987), because at this stage fish are not yet forced to compete for food. However, low temperature may also reduce fish production (e.g., Scarnecchia and Bergersen 1986) by reducing abundance and quality of invertebrate prey (see Hogg and Williams 1996) required by newly-feeding fry. In either case, in high-elevation streams

that approach the boundaries of the thermal niche for cutthroat trout, the effects of low temperature may be relatively strong and explain recruitment rates better than density-dependent mechanisms (Myers 1998).

Low or intermittent recruitment over many generations due to cold summer temperatures and short growing seasons would result in low abundance in translocated populations and reduce their long term viability. The results of the laboratory (Coleman and Fausch in press) and field research thus provide a mechanism to explain the results of Harig and Fausch (2002), which indicated that translocation success is improbable in streams with average July temperatures  $<7.8^{\circ}\text{C}$ . This was about the same threshold I found between streams with modest recruitment versus those with little recruitment to the onset of winter (i.e., 700 GSDD; Table 2, Figure 1). Harig and Fausch (2002) found the highest abundances of cutthroat trout in streams that averaged  $10.0^{\circ}\text{C}$  in July, a temperature achieved only in my warmest study reaches that had  $>900$  GSDD. Failures to recruit regularly and in sufficient numbers due to the proximate effects of cold summer stream temperatures over successive generations may lead to low population sizes in isolated headwater streams, and ultimately to translocation failures. Thus, my results provide further support for the use of empirically-derived thermal criteria to assess habitat suitability in high-elevation headwaters streams.

Based on my counts, fry abundance in the study reaches was lower than may be predicted based on adult abundance. These fry estimates are probably conservative, especially in the warmer streams, due to measurement error associated with single annual counts of swimup fry in complex habitats using available methods. However, in the colder streams two possible ecological explanations appear more likely. First, due to the

high energetic cost of producing eggs, migration, and spawning, female cutthroat trout may not spawn every year. The relatively low productivity and short growing season of cold headwater streams would exacerbate this problem, potentially decreasing fecundity, the frequency of spawning, or survival of adults after spawning. Second, mortality of eggs may be higher when incubated at colder temperatures. Laboratory studies suggest little to no effect on survival to hatching and swimup in Snake River cutthroat trout incubated at temperatures as low as 4°C (Hubert et al. 1994; Stonecypher et al. 1994; Hubert and Gern 1995), a range that extends well below average daily temperatures when eggs are incubating in my study streams. Thus, there is little evidence to suggest that fry abundance in streams like those I studied is drastically reduced by low survival rates due to cold incubation temperatures.

Although I would predict from my laboratory results that populations should die out in the coldest reaches studied, other mechanisms that operate at different scales probably allow them to persist. First, the coldest reaches were contiguous with warmer downstream habitats that likely provided recruitment that sustained the population throughout the whole stream segment. Therefore, these cold study reaches may be sink habitats supported by immigrants from larger source populations downstream. For example, the study reaches at East Fork Sheep Creek averaged only 581 GSDD upstream and 641 GSDD downstream, but there is a large source population in a meadow farther downstream. Second, cutthroat trout in cold high-elevation streams are long-lived and spawn over several years, which may provide opportunity for some recruitment during warmer years. For example, 2002 was the driest year on record in Colorado, and some fisheries biologists reported recruitment in cold streams where it had not previously been

observed. Third, some fry may find thermal microzones where temperatures are warmer and increase growth, enhancing their overwinter survival. Such microzones often occur in lateral backwater habitats like those where fry are found after they emerge.

Finally, geomorphic context may create discontinuity in temperatures along stream segments, providing additional opportunities for growth and recruitment. For example, both study reaches at Cabin Creek contained tributaries that cooled their lower sections. The upstream reach averaged 835 GSDD above the tributary, but only 621 GSDD downstream. The downstream reach averaged 909 GSDD above the tributary, but only 692 GSDD downstream. Therefore, spatial variation in stream temperature due to geomorphology can create patches of thermally suitable habitat alternating with unsuitable habitat along stream segments, and this thermal heterogeneity cannot be detected with a single thermograph. Longer stream segments provide more habitat, but also likely a greater diversity of thermally suitable habitats, which may help explain why stream length is positively related to cutthroat trout abundance in a wide range of Rocky Mountain streams (Hilderbrand 2003; Young et al. 2005). Given the importance of these factors that operate over larger spatial and temporal scales, I conclude that temperature measurements made at a single location or over a single season (e.g., mean July temperature) may provide only relatively coarse filter criteria for selecting translocation sites. A hierarchical approach to identifying thermally suitable streams for translocation may be useful, wherein short-term, small-scale temperature monitoring is used to identify thermally marginal streams where more detailed spatial and temporal temperature monitoring is warranted. More precise predictions of translocation success could be based on basin-wide temperature surveys and season-long monitoring at multiple

locations for several years. In the southern Rocky Mountain region such marginal streams make up a large proportion of the remaining streams where translocation are feasible. Given the time and expense required for each translocation, more detailed temperature surveys would be a prudent and economical approach for selecting the best of these streams for cutthroat trout translocations.

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## **Tables**

Table 1. Physical characteristics of habitat in survey reaches in the six study streams, listed from warmest to coldest (see Table 2). Geographic coordinates (UTM) were measured in the field at the lower ends of study reaches using a handheld global positioning system (GPS). Gradients were calculated from measurements of reach lengths made during 2004, and elevations estimated with a digital elevation model in a geographic information system (ArcMap v9, ESRI) for GPS coordinates taken in the field at the ends of each study reach. Stream bankfull widths were calculated by averaging measurements made at 100-m intervals in the study reaches during 2004.

| Stream             | CT subspecies <sup>a</sup> | Study reach | Georeference (UTM)  | Elevation at downstream end (m) | Gradient (% slope) | Reach Length (m) | Mean bankfull width (m; SE) |
|--------------------|----------------------------|-------------|---------------------|---------------------------------|--------------------|------------------|-----------------------------|
| Roaring Cr         | GBCT                       | upper       | 13 T 434831 4511287 | 2896                            | 9.0                | 486              | 3.1; 0.19                   |
|                    |                            | lower       | 13 T 435497 4509691 | 2735                            | 6.8                | 518 <sup>b</sup> | 4.2; 0.43                   |
| Columbine Cr       | CRCT                       | upper       | 13 T 433036 4448921 | 2788                            | 2.5                | 349 <sup>c</sup> | 3.5; 0.48                   |
|                    |                            | lower       | 13 T 432360 4448973 | 2761                            | 5.4                | 411 <sup>d</sup> | 3.8; 0.46                   |
| Cabin Cr           | CRCT                       | upper       | 13 S 439319 4426715 | 3068                            | 7.5                | 534 <sup>e</sup> | 3.9; 0.11                   |
|                    |                            | lower       | 13 S 438096 4426065 | 2951                            | 5.0                | 504              | 4.4; 0.48                   |
| Little Vasquez Cr  | CRCT                       | upper       | 13 S 431787 4414318 | 3021                            | 4.8                | 527 <sup>f</sup> | 3.1; 0.37                   |
|                    |                            | lower       | 13 S 432153 4415317 | 2935                            | 3.8                | 532              | 3.0; 0.31                   |
| West Cr            | GBCT                       | upper       | 13 T 454102 4479102 | 2668                            | 8.3                | 532 <sup>b</sup> | 4.3; 0.26 <sup>g</sup>      |
|                    |                            | lower       | 13 T 454791 4478631 | 2633                            | 4.8                | 505 <sup>b</sup> | 3.8; 0.45 <sup>g</sup>      |
| East Fork Sheep Cr | GBCT                       | upper       | 13 T 438697 4498420 | 3007                            | 6.3                | 527              | 3.5; 0.41                   |
|                    |                            | lower       | 13 T 437936 4499460 | 2949                            | 5.8                | 518              | 3.1; 0.12 <sup>g</sup>      |

- <sup>a</sup> Cutthroat trout (CT) subspecies studied were greenback (GBCT) and Colorado River cutthroat trout (CRCT).
- <sup>b</sup> Fry were not surveyed in this reach during 2003.
- <sup>c</sup> Only the lower 192 m was surveyed for fry during 2003.
- <sup>d</sup> Only the lower 311 m was surveyed for fry during 2003 and 2004, due to new beaver ponds in the upper 100 m.
- <sup>e</sup> Only the lower 484 m was surveyed for fry during 2003.
- <sup>f</sup> During 2003, the lower 100 m was not surveyed, but an additional 162 m was surveyed above the reach.
- <sup>g</sup> From data on bankfull widths of pools collected by Harig and Fausch (2002), where their survey overlapped my study reach.

Table 2. Measurements of adult trout abundance, and habitat and thermal characteristics of survey reaches in the six study streams, listed from warmest to coldest in terms of growing season degree days (GSDD). Previous surveys of adult trout were conducted by the USFWS and NPS in Rocky Mountain National Park, the USDAFS in the Arapaho-Roosevelt National Forest, and by Harig and Fausch (2002) in several streams. Unless otherwise reported, surveys of adult trout, pools, and spawning habitat were conducted during summer 2004.

| Stream             | Study reach | Counts of adult trout | Previous surveys of adult trout   | Pools $\geq$ 20 cm residual depth | Spawning habitat                      |   | Temperature ( $^{\circ}$ C) |                  |                  |
|--------------------|-------------|-----------------------|-----------------------------------|-----------------------------------|---------------------------------------|---|-----------------------------|------------------|------------------|
|                    |             |                       |                                   |                                   | No. patches $\geq$ 0.5 m <sup>2</sup> | Area (m <sup>2</sup> ) of patches $\geq$ 2.0 m <sup>2</sup> | Mean July                   | Mean August      | GSDD             |
| Roaring Cr         | upper       | 54                    | 530 <sup>a</sup>                  | 12                                | 43                                    | 4.8   | 8.4                         | 8.2              | 825              |
|                    | lower       | 39                    | 390 <sup>a</sup>                  | 17                                | 30                                    | 11.5  | 9.7 <sup>b</sup>            | 9.6 <sup>b</sup> | 996 <sup>b</sup> |
| Columbine Cr       | upper       | 15                    | 36 <sup>c</sup>                   | 1 <sup>d</sup>                    | 11                                    | 4.8   | 8.3                         | 8.5              | 771              |
|                    | lower       | 11                    | 24 <sup>c</sup>                   | 17                                | 9                                     | 0.0   | 9.5                         | 9.9              | 957              |
| Cabin Cr           | upper       | 25                    | 110 <sup>a</sup>                  | 25                                | 75                                    | 18.9  | 7.9                         | 7.9              | 728              |
|                    | lower       | 18                    | 100 <sup>a</sup>                  | 20                                | 15                                    | 2.2   | 8.2 <sup>e</sup>            | 7.9 <sup>e</sup> | 801 <sup>e</sup> |
| Little Vasquez Cr  | upper       | 11                    | - <sup>f</sup>                    | 19                                | 25                                    | 23.0  | 7.4                         | 7.2              | 627              |
|                    | lower       | 10                    | - <sup>f</sup>                    | 13                                | 16                                    | 41.3  | 7.4                         | 7.3              | 678              |
| West Cr            | upper       | - <sup>g</sup>        | 6 <sup>h</sup>                    | 10 <sup>h</sup>                   | 10 <sup>g,i</sup>                     | - <sup>g</sup>  | 7.3                         | 6.9              | 611              |
|                    | lower       | - <sup>g</sup>        | 19 <sup>h</sup>                   | 9 <sup>h</sup>                    | 9 <sup>g,i</sup>                      | - <sup>g</sup>  | 7.8                         | 6.8              | 675              |
| East Fork Sheep Cr | upper       | 28                    | 90 <sup>a</sup> , 11 <sup>h</sup> | 20                                | 55                                    | 54.6  | 7.1                         | 6.8              | 581              |
|                    | lower       | 13                    | 80 <sup>a</sup> , 14 <sup>h</sup> | 32 <sup>h</sup>                   | 40                                    | -   | 7.1                         | 7.6              | 641              |

- <sup>a</sup> Extrapolated from USDAFS electrofishing removal estimates during 1999-2000 from where my study reaches overlapped (M. Young, P. Guenther-Gloss, unpublished data)
- <sup>b</sup> Interpolated by averaging data from the upstream and downstream thermographs approximately equidistant from the study reach.
- <sup>c</sup> Extrapolated from USFWS/NPS electrofishing removal abundance estimates in 2002 from where my study reaches overlapped (B. Rosenlund and C. Kennedy, unpublished data).
- <sup>d</sup> A single beaver pond (~ 5 m wide, ~20 m long) present only during 2004 inundated several former pools which may have met my criteria.
- <sup>e</sup> Based partly on backward temperature predictions for the thermograph recording temperature in the upper 300 m of the reach above a tributary (see details in Methods).
- <sup>f</sup> Reports contracted by the USDAFS indicate a consistent presence of adult fish in pools located within my study reaches during 1998-2001.
- <sup>g</sup> Not surveyed due to high flows.
- <sup>h</sup> From data collected by Harig and Fausch (2002) in 1998, where my survey reaches overlapped.
- <sup>i</sup> All pools surveyed by Harig and Fausch (2002) had at least 25% clean gravel in the downstream quarter, which indicates presence of at least one spawning patch per pool within my study reaches based on the criteria used.

Table 3. Poisson regression models of fry density as a function of thermal and year effects. Models were ranked in ascending order, based on Akaike's Information Criterion (AIC). The  $AIC_c$  is the AIC corrected for small sample size,  $K$  is the number of parameters estimated in the model (including the intercept), and  $\Delta AIC_c$  is the difference in  $AIC_c$  between the candidate model and the model with the lowest  $AIC_c$ . The Akaike weights ( $w_i$ ) sum to 1.0. Year was entered as a class variable. The predicted fry densities from the best fitting model shown in bold italics are plotted in Figure 4.

| Model and parameters      | AIC <sub>c</sub> | K        | ΔAIC <sub>c</sub> | w <sub>i</sub> |
|---------------------------|------------------|----------|-------------------|----------------|
| <b>GSDD</b>               | <b>-154.76</b>   | <b>2</b> | <b>0</b>          | <b>0.813</b>   |
| GSDD, Year                | -151.82          | 4        | 2.93              | 0.188          |
| GSDD, Year, (GSDD * Year) | -74.45           | 6        | 80.31             | 0.000          |

Table 4. Age-0 cutthroat trout fry density by study reach, predicted survivorship, and predicted growth between the time of surveys and the start of winter in each study reach averaged over three years (2002-2004) and ranked in descending order from warmest to coldest based on growing season degree days (GSDD). Reaches where predicted survivorship > 0.50 are shown in bold, and those where it is predicted fry are likely to survive over winter (TL greater than 30 mm at the start of winter – see Discussion) are shown in bold italics. Predicted survivorship is based on a logistic regression of survival as a function of GSDD (Figure 3), fit using data from the 2003 laboratory experiment (Coleman and Fausch in press). Predicted growth is based on an exponential regression of fry total length as a function of accumulated degree days (Figure 4), fit using data from the 2003 laboratory experiment (Coleman and Fausch in press), and field data from this study.

| Stream              | Reach        | Density<br>(fry/100 m) | GSDD       | Predicted<br>survivorship | Predicted<br>total length (mm) |
|---------------------|--------------|------------------------|------------|---------------------------|--------------------------------|
| <i>Roaring Cr</i>   | <i>lower</i> | <i>11.2</i>            | <i>996</i> | <i>0.74</i>               | <i>37.3</i>                    |
| <i>Columbine Cr</i> | <i>lower</i> | <i>16.7</i>            | <i>957</i> | <i>0.71</i>               | <i>34.6</i>                    |
| <b>Roaring Cr</b>   | <b>upper</b> | <b>20.2</b>            | <b>825</b> | <b>0.56</b>               | <b>28.2</b>                    |
| <b>Cabin Cr</b>     | <b>lower</b> | <b>11.2</b>            | <b>801</b> | <b>0.53</b>               | <b>27.5</b>                    |
| Columbine Cr        | upper        | 3.5                    | 771        | 0.50                      | 26.6                           |
| Cabin Cr            | upper        | 4.4                    | 728        | 0.44                      | 25.5                           |
| Little Vasquez Cr   | lower        | 0.4                    | 678        | 0.39                      | 24.5                           |
| West Cr             | lower        | 10.6                   | 675        | 0.38                      | 24.5                           |
| East Fork Sheep Cr  | lower        | 2.6                    | 641        | 0.35                      | 23.9                           |
| Little Vasquez Cr   | upper        | 0.3                    | 627        | 0.33                      | 23.7                           |
| West Cr             | upper        | 0.0                    | 611        | 0.31                      | 23.5                           |
| East Fork Sheep Cr  | upper        | 0.5                    | 581        | 0.28                      | 23.1                           |

## **Figures**

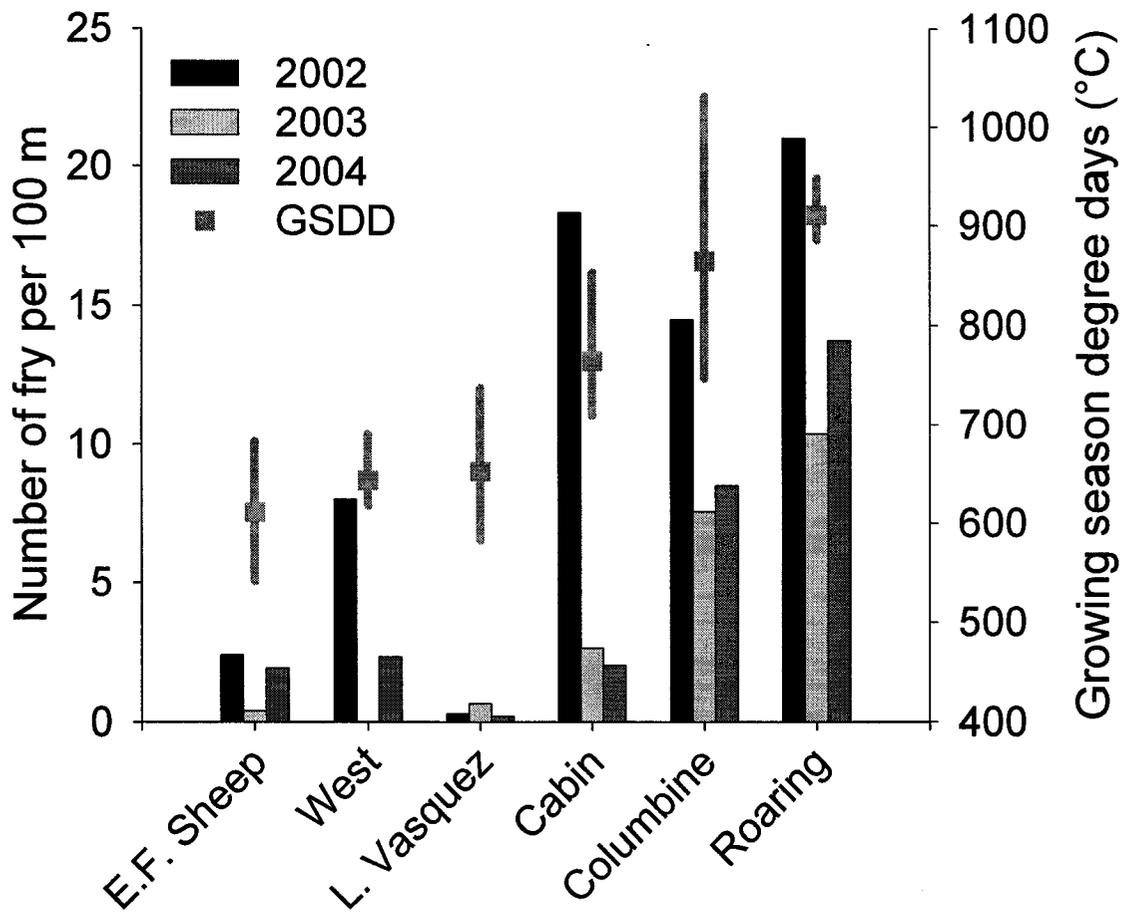


Figure 1.

Figure 1. Counts of cutthroat trout fry and average growing season degree days (GSDD) for study streams. Fry counts and GSDD were averaged across study reaches for each stream, and GSDD were averaged over the three years (bars show the range). Fry were not counted in West Creek or the lower study reach in Roaring Creek during 2003 (see text).

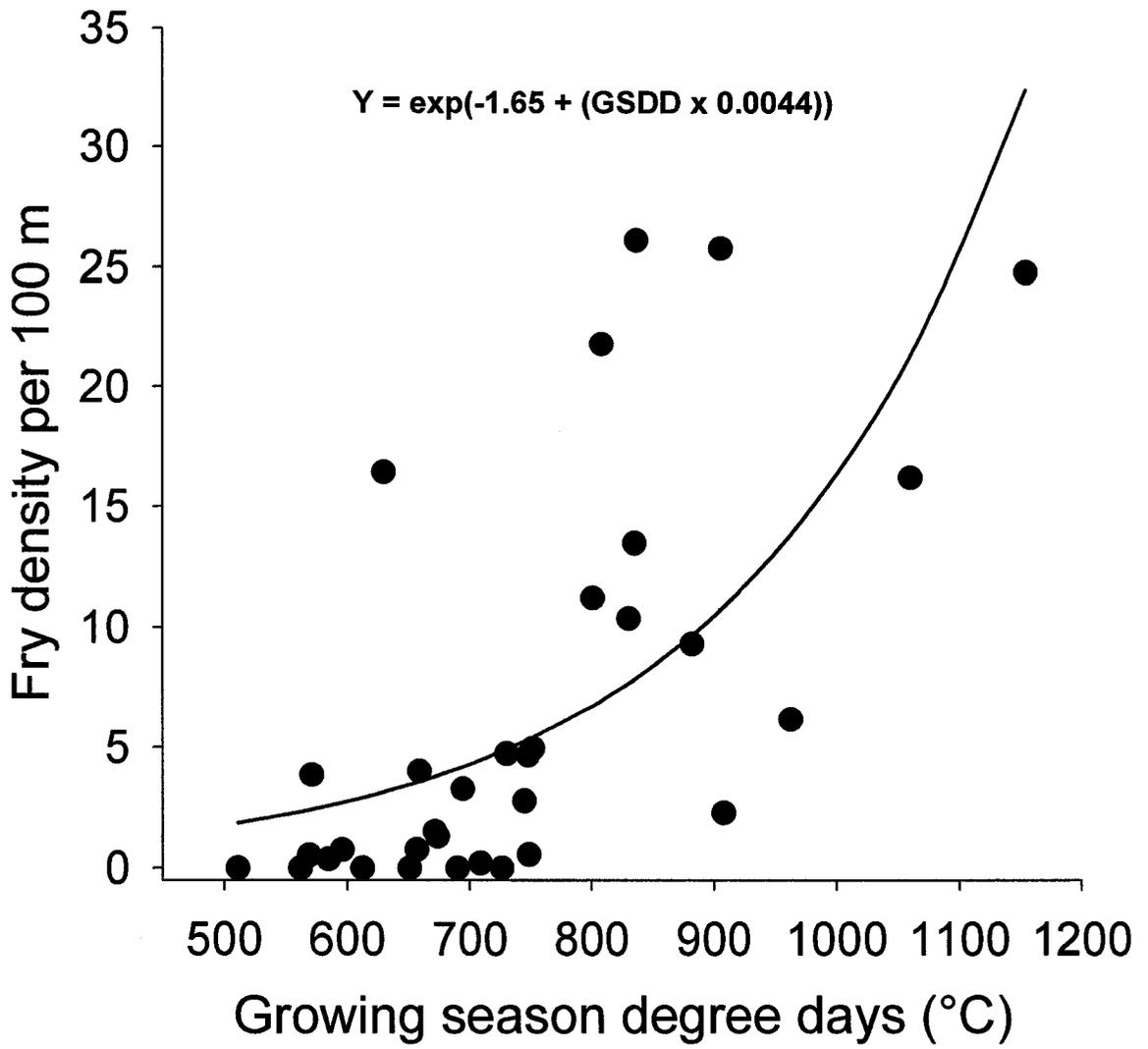


Figure 2.

Figure 2. Fry density as a function of growing season degree days for each study reach. The line plotted is from the best fitting Poisson regression model (see Table 3), which is shown. The model predictions fit the data based on a Scaled Pearson Goodness of Fit test ( $\chi^2=35.68$ ,  $P=0.26$ ,  $df=31$ ).

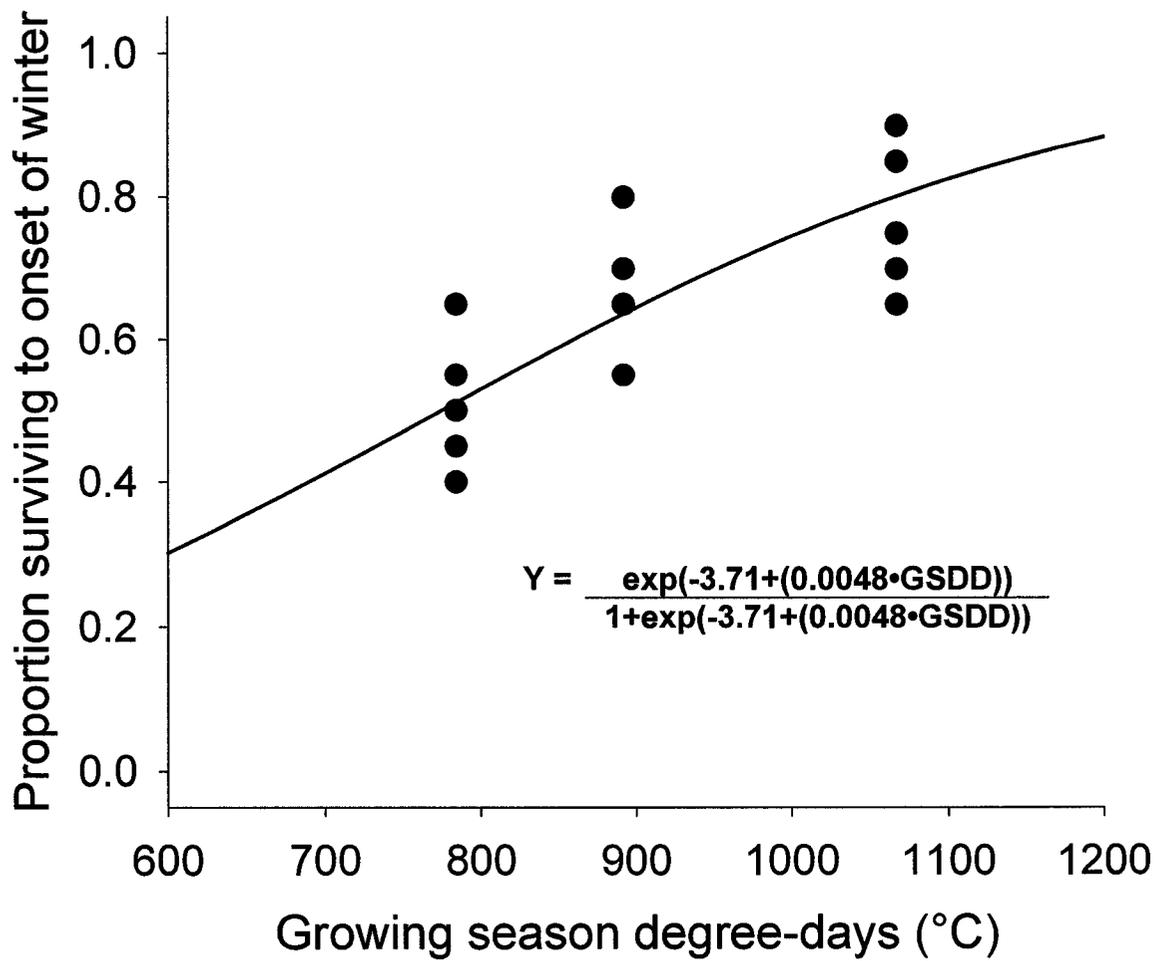


Figure 3.

Figure 3. Proportion of newly emerged Colorado River cutthroat trout surviving to the onset of winter as a function of growing season degree days for the laboratory experiment conducted during 2003 (after Coleman and Fausch in press). The data are proportion of fry surviving to the onset of winter for eight tanks at each of three temperatures (7.0, 8.5, and 10.0 °C; survival was identical in some tanks). The fitted relationship is a logistic regression model.

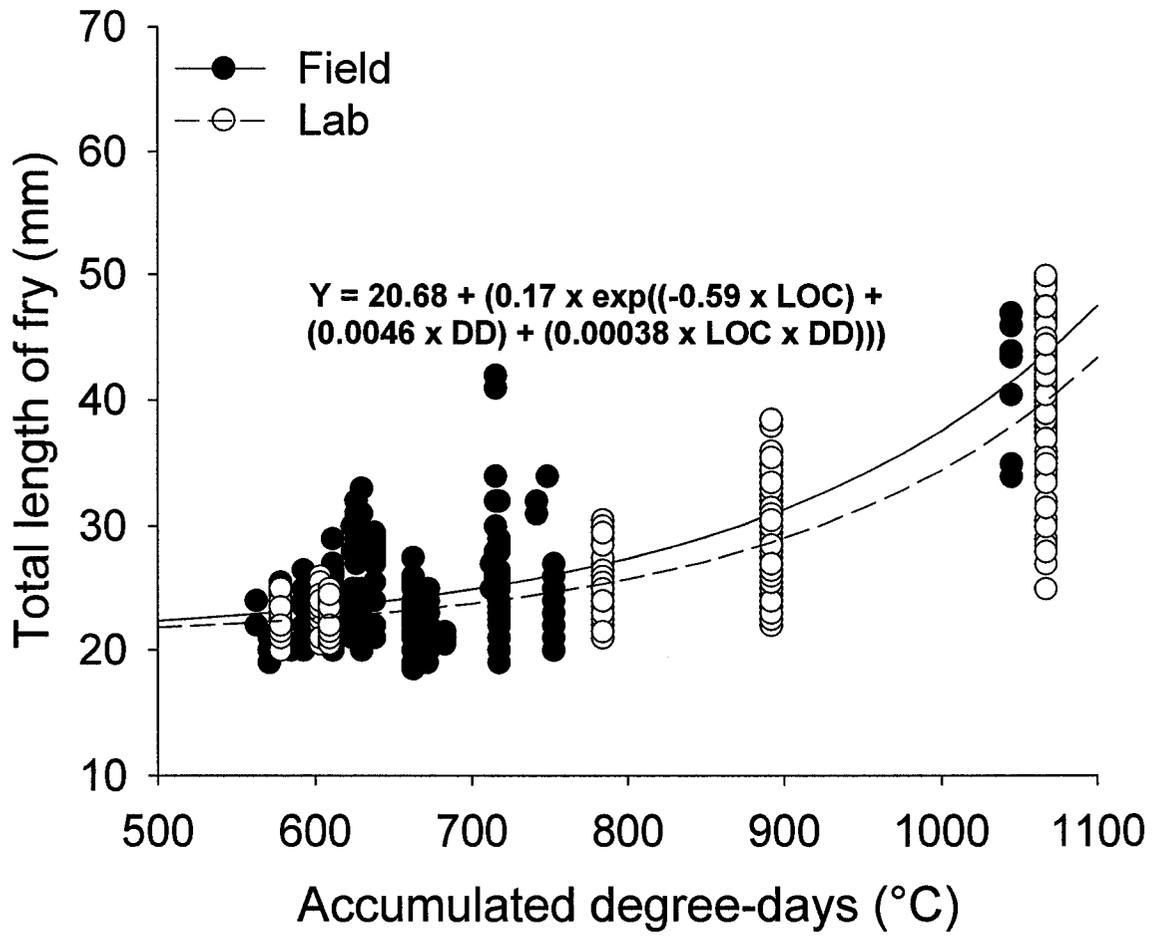


Figure 4.

Figure 4. Total lengths of Colorado River cutthroat trout fry measured in the 2003 laboratory experiment (open circles), and in each reach throughout the field study (filled circles) as a function of estimated degree days accumulated from spawning (field) or egg-take (lab) to the time of measurement (DD). The class variable used in the model to distinguish laboratory and field data is abbreviated as LOC. The fitted relationships shown are the predicted lengths of fry in the lab and field, based on an exponential model shown that included both laboratory and field data (see text).

## CONCLUSIONS

Recruitment bottlenecks at cold temperatures are a plausible explanation for the reduced success of native cutthroat trout translocations in cold high-elevation streams in the southern Rocky Mountain region. A similar mechanism may also explain low recruitment rates for populations of brown trout in high-elevation lakes in northern Europe (Borgström and Museth 2005). Cold temperature regimes do not appear to provide sufficient thermal units to ensure survival during the subsequent winter due to negative effects on development and growth of fry. Growth and survival decline markedly in streams with mean August temperatures below 8.5°C, where <800 degree days accumulated during the growing season, on average (Coleman and Fausch in press a) and regular recruitment is most likely in streams with >900 degree days (Coleman and Fausch in press a, in press b). This pattern was apparent in the laboratory study despite greater food abundance in two colder temperature regimes studied (Appendix: Figure 1), which may be indicative of differences in energy allocation of fish among regimes (Appendix: Figure 2, 3). Without adequate recruitment, fish populations in cold streams remain small and thus are susceptible to local extinction due to environmental fluctuations (Rieman and McIntyre 1993; Caughley 1994; McElhaney et al. 2000).

Recent data on cutthroat trout and other salmonid species suggest that the isolation of these populations to streams with small habitat areas relative to their historic range may further increase extinction risk (Morita and Yamamoto 2002; Hilderbrand 2003). Despite this, cold temperature is often overlooked as a factor limiting salmonid populations because salmonids are thought of as 'cold water' fish. The results of my

integrated laboratory and field study indicate that locating streams with growing seasons warm enough to support consistent recruitment (>900 degree days) will be a key to increasing translocation success of native cutthroat trout in southern Rocky Mountain streams with little or no lentic habitat.

Recruitment success changes markedly over just a few degrees in maximum summer temperatures in high-elevation streams (Coleman and Fausch in press a; in press b), so factors that influence temperature can play strong roles in streams that are thermally marginal. Lakes can create thermal refuges in shallow littoral habitats or in outlets that can act as a source of recruitment to sustain populations even where too few degree-days accumulate upstream to support regular recruitment. Temperature variation along stream channels due to hydrology (tributaries, springs, or seeps), geomorphology, and variation in shading can also create warmer “hotspots” for recruitment. For example, tributaries in both study reaches of Cabin Creek were cold, produced thermal conditions in the lower half of the study reaches that were not favorable for recruitment, and created a patchwork of thermally suitable and unsuitable habitat along the stream segment (Coleman and Fausch in press b). At Columbine Creek, a large alluvial meadow where the stream had been impounded by beavers created a thermal gradient through the meadow where upstream temperatures were unfavorable for recruitment, but downstream temperatures were highly favorable (Coleman and Fausch in press b). Therefore, thermal criteria for determining translocation success based on monitoring during a single season or at a single location can only be regarded as a coarse filter for selecting sites suitable for cutthroat trout translocations. More detailed spatially explicit surveys combined with

monitoring at multiple locations where factors that influence stream temperatures are identified is especially important in thermally marginal streams.

### **Selecting Translocation Sites – A Hierarchical Approach**

Due to the relative scarcity of streams where translocations are currently feasible, fisheries managers should refine the set of criteria used to determine the suitability of streams for translocations of native cutthroat trout. Considerable uncertainty is associated with model predictions based on temperature alone, which may have served as the basis for mean July temperature criteria that have been used widely by fisheries managers in the southern Rocky Mountain region. Harig and Fausch (2002) reported that translocated populations of Rio Grande and greenback cutthroat trout did not succeed in a sample of streams where mean July temperatures averaged 7.1°C, whereas low abundance populations were sustained in streams averaging 7.8°C, and high abundance populations were sustained in streams averaging 10.0°C. However, there was considerable variation in mean July temperatures within these three groups, and considerable overlap among them. This was particularly true for the two cold groups in which translocations had failed (range: 4.2-10.2°C) or produced low-abundance populations (6.0-9.2°C). This variation was explained partly by physical habitat variables (i.e., mean bankfull width of pools, and number of deep pools), but failure of mean July temperatures to adequately integrate the total thermal energy that age-0 fish in streams are exposed to during their first growing season may help explain still more of this variation. Based on the present study and previous research (Harig and Fausch 2002, Young et al. 2005), fisheries managers should continue to apply both physical habitat and thermal criteria, but should further refine their approach.

I recommend that fisheries managers use a hierarchical, or multi-tiered, approach to predict habitat suitability in small high-elevation stream segments in the southern Rocky Mountains that are likely to be thermally or physically marginal for native cutthroat trout. Previous research has shown that temperature and other physical habitat characteristics at various scales are positively correlated with translocation success (Harig and Fausch 2002) and population size (Young et al. 2005). I recommend that managers use the models presented by Harig and Fausch (2002) and Young et al. (2005) in the early stages of translocation site selection. Where streams are clearly warm enough, long enough, and have sufficient pool habitat, managers are justified in proceeding with translocation efforts. Translocations should not be further considered in stream segments that are too short, too narrow, and fail to meet mean July temperature criteria. However, in streams that are thermally marginal, but where stream length and physical habitat are otherwise acceptable, multiple years of season-long and spatially explicit stream temperature surveys should be conducted to better gage the probability of translocation success.

This hierarchical approach may be particularly valuable to fisheries managers, due to the high cost of conducting each translocation. Translocations in streams are increasingly becoming feasible only at high elevation on public lands where many available stream segments are either physically or thermally marginal, or both. As a result, fisheries managers using established landscape and stream scale criteria in the southern Rocky Mountains are forced to consider difficult decisions to attempt cutthroat trout translocations in streams where success is uncertain. Additional criteria that can

fine-tune predictions of habitat suitability and translocation success can help insure that resources are used more efficiently in support of native cutthroat trout conservation.

### **Implications of Climate Change**

It is accepted among climate scientists that the earth's climate is changing (Houghton et al. 2001). The change in global climate (i.e., "Global Warming") was first marked by observations that average temperatures at the earth's surface had been rising at an increasingly rapid rate since the Industrial Revolution. Although rapid on a geologic time-scale, the problem may be underestimated because within the span of a human lifespan, the change in global temperatures seems quite small, amounting to a 0.4-0.8°C increase during the 20<sup>th</sup> century (Committee on the Science of Climate Change 2002). However, my research suggests that even seemingly small changes in temperature, when integrated over time, can result in large differences in growth, development, and recruitment in cutthroat trout.

High-elevation cutthroat trout populations are largely at the mercy of their thermal environments. Although there can be important sources of thermal variation within these environments, overall they are generally cold. Further, barriers to upstream migration at the downstream ends of segments harboring native cutthroat trout populations may limit the opportunities to utilize warmer downstream habitats, because individuals that migrate downstream over barriers are lost. Cooney et al. (2005), in using a modeling approach to predict the probabilities of translocation success of native cutthroat trout in high elevation streams in the southern Rocky Mountains, predicted that warming would increase the probability of translocation success in the streams studied by Harig and Fausch (2002). However, this study did not account for predicted changes in

the temporal pattern of precipitation and snowmelt. Rising temperatures and large-scale decreases in ice and snow cover around the world are unlikely to leave precipitation patterns and hydrology unchanged.

Evidence is mounting that suggests snowpacks are melting and streamflows peaking earlier than they did 50 years ago (Mote et al. 2005, Stewart et al. 2005), which may have catastrophic effects on some cutthroat trout populations that appear to be thriving under current conditions. Some models predict greater precipitation at high-elevation sites in western North America, but suggest that the snowline will rise due to warmer temperatures (Kittel et al. 2002). If this is true, more precipitation may fall as rain, and snowmelt runoff will be earlier and the snow-free season longer. The reduced overall snowpack is predicted to reduce late summer flows (Wagner 2003). This is supported by observations of events during 2002, the driest year on record in Colorado, during an ongoing drought in the southern Rocky Mountains. Snowpack was nearly absent by spring of 2002 and snowmelt runoff negligible. Many headwater streams dried up, requiring some native cutthroat trout populations to be moved into hatcheries and later restocked when flows returned (R. Kolecki, T. Nesler, D. Krieger, Colorado Division of Wildlife, and B. Rosenlund, U.S. Fish and Wildlife Service personal communications). This drought has been linked to global warming by at least some scientists (Hoerling and Kumar 2003)

As global surface temperature has increased, the range of many species around the world at high latitudes has shifted or expanded to higher latitudes and elevations (Franco et al. 2006). Native cutthroat trout populations, however, are already near the upper terminus of aquatic habitats in their respective drainages. Indeed, once-suitable

habitat at lower elevations may become unsuitably warm, causing the distribution of invasive nonnative salmonids and other fishes to shift farther upstream. The closer proximity of nonnative salmonids to native cutthroat trout populations will likely increase the risk of nonnative salmonid invasions due to natural events or illegal translocation of fish above barriers (Fausch et al. 2006).

Rising stream temperatures and thermal regimes may also increase the risk of catastrophic disease outbreaks in isolated cutthroat trout populations. Kerans et al. (2005) determined that the whirling disease parasite *Myxobolus cerebralis* requires 1,320 and 1,456 degree days to develop at 8 and 15°C, respectively. Stream thermal regimes may therefore largely determine the timing of triactinomyxon (TAM) spore release during the year by their worm *Tubifex tubifex* hosts. The TAMs released are capable of infecting salmonids, and if they are released in the environment at high concentrations as salmonid swim-up fry are emerging from redds, a whirling disease epidemic may result that could decimate entire year classes of native cutthroat trout. Further, there are several strains of *T. tubifex* that appear to vary in susceptibility to infection by the myxospores of the whirling disease parasite, which are shed by infected fish (Nehring 2006). These strains also appear to vary in their optimum or preferred temperatures, as Kerans et al. (2005) found that the population size and biomass of two Gallatin River and Madison River *T. tubifex* strains in Montana were greatest at 8.0°C and 15.0°C, respectively. Therefore, greater probability of whirling disease may come about as headwater streams warm, due to improved synchrony in the life cycle of the parasite, *T. tubifex*, and fish, or due to an increase in density of *T. tubifex* strains that are more susceptible to infection. Both of these processes may be strongly influenced by even small changes in daily

temperature during the growing season. Furthermore, if nonnative salmonids that carry whirling disease shift upstream, inadvertent introduction of the parasite above upstream migration barriers may occur if infected fish or myxospores are translocated above barriers. Myxospores are highly durable and may be translocated on clothing, fishing, or research equipment, or by disposal of heads/entrails of fish in uninfected waters (Nehring 2006)

There is still uncertainty in how rising temperatures may affect fish, aquatic communities, and fish habitat. As a result, claims that worldwide increases in global temperatures will result in improved conditions for native cutthroat trout populations in the southern Rocky Mountains (e.g., see Cooney et al. 2005) are likely too simplistic. Some populations may increase in density, but available evidence and recent predictions suggest that changes in temporal and spatial patterns of precipitation may cause extinctions of other populations. The effects of climate change on streams and native cutthroat trout populations in the southern Rocky Mountains are difficult to predict, but the potential risks are great for native cutthroat trout subspecies that now occupy only a small portion of their native range in the region. Therefore, more detailed studies to investigate the risks posed by the interacting effects of temperature, hydrology, and disease in individual streams should be conducted, so these risks can be assessed and remedial actions can be planned to protect native trout populations in the future.

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## **APPENDIX**

### **Supplement: Feeding, Growth, and Energy Density**

Despite higher food abundance in the colder temperature regimes (Figure 1), fish in the colder regimes suffered greater mortality during the recruitment bottleneck period after swimup (Coleman and Fausch in press). Feeding records and wet weights of fish sampled from experimental tanks at swimup, during the recruitment bottleneck period, and after 6-7 weeks at winter temperatures ( $<4^{\circ}\text{C}$ ) during the 2004 experiment were used to estimate percent of body weight fed. Fish under 30 mm in length were fed at the rate prescribed for 30 mm fish, due to concerns that fish would have difficulty finding smaller quantities before they sank to the substrate as waste (Coleman and Fausch in press). The average size of randomly sampled fish in the cold and intermediate treatments remained below 30 mm throughout the study during 2004, which resulted in their food abundance relative to body size remaining higher throughout the study than in the warm treatment group. Average size in the warm treatment samples exceeded 30 mm by week 7 of Phase 2 (Coleman and Fausch in press).

Growth rates of fish appeared to vary little over the experiment, based on wet weight data from fish sampled during Phase 2 of the 2004 experiment (Figure 2). Daily percent change in weights were calculated for each sampling interval by dividing percent changes in weight over the sampling interval by the number of days in the interval. Growth decreased in the warm treatment throughout the experiment, as temperature dropped, but there is little evidence of trends in growth rates of fish in the cold and intermediate regimes, in which daily percent growth averaged around 0% and 2%, respectively, throughout Phase 2 of the 2004 experiment. Trends in growth in these two

cold treatments may be masked by size-dependent mortality of smaller fish in these treatments (Coleman and Fausch in press).

Plots of percent daily growth and energy density (expressed as percent dry weight), showed some evidence that fish in the three temperature regimes may have allocated energy differently (Figure 3). The energy density and daily percent growth plots diverged throughout Phase 2 of the 2004 experiment in the warm treatment, but not in the intermediate and cold treatments. This may indicate that in the warm treatment fish stored relatively more energy as lipid, and invested relatively less in growth of somatic tissues compared to fish from the intermediate and cold temperature regimes. This result is consistent with those from rainbow trout in British Columbia Lakes (Post and Parkinson 2001), which indicated that age-0 fish that reared in warmer lakes had greater body lipid content than those from colder lakes, which had a very low percentage of lipid in their bodies. The supplemental plots lend additional support to the hypothesis that the recruitment bottleneck and decreased survival of native cutthroat trout in cold high-elevation streams in the southern Rocky Mountains are due to energy deficits exacerbated by cold temperatures.

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## **Figures**

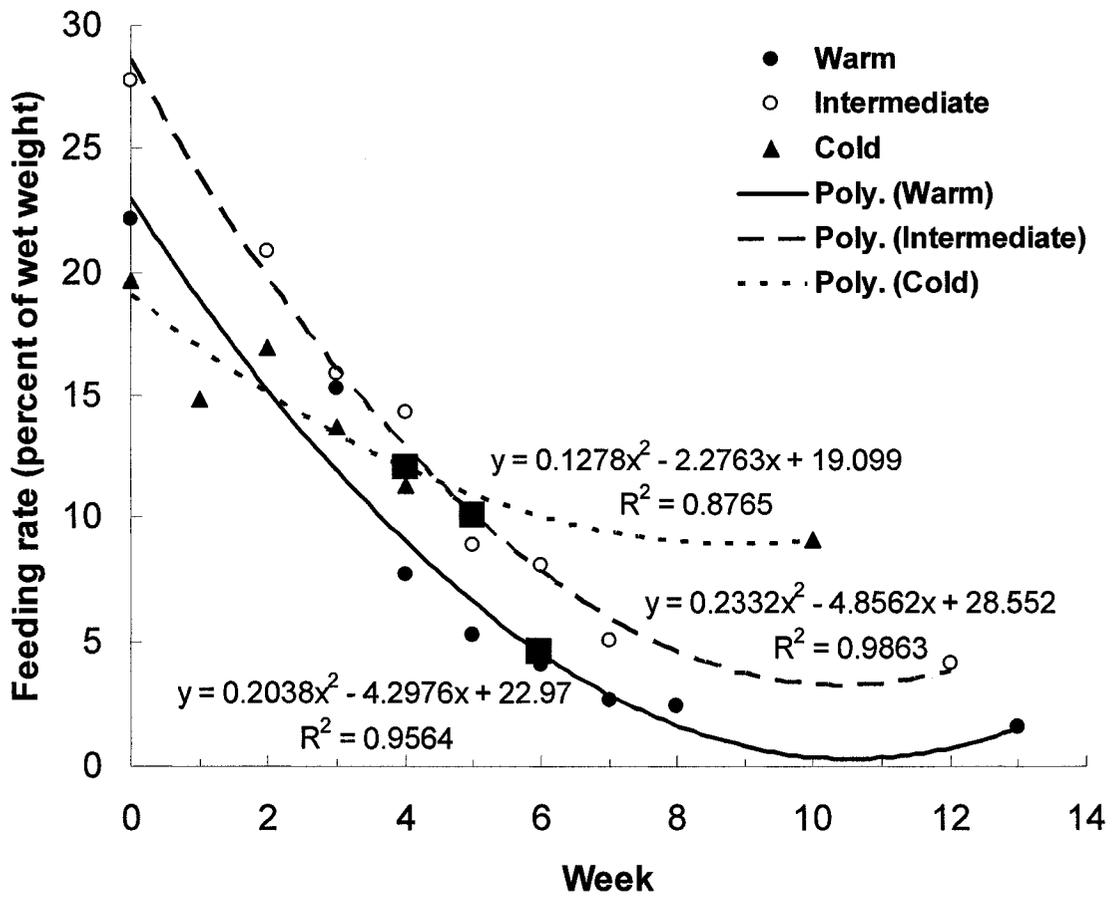


Figure 1.

Figure 1. The food abundance, in estimated percent of body weight of age-0 Colorado River cutthroat trout, during Phase 2 of the 2004 laboratory experiment, from swim-up through the end of the experiment (data from Coleman and Fausch in press). The lines are second-degree polynomial fits, and gray boxes indicate the start of winter ( $\leq 4^{\circ}\text{C}$ ) in each of the three temperature regimes studied. Warm regime temperatures started at  $10.0^{\circ}\text{C}$  at the beginning of Phase 2, whereas the intermediate regime started at  $8.5^{\circ}\text{C}$ , and the cold regime started at  $7.0^{\circ}\text{C}$ . In all three regimes, temperatures were decreased at a rate similar the natural thermal regimes to winter temperatures, with a minimum of about  $1.0^{\circ}\text{C}$  (Chapter 2; Coleman and Fausch in press).

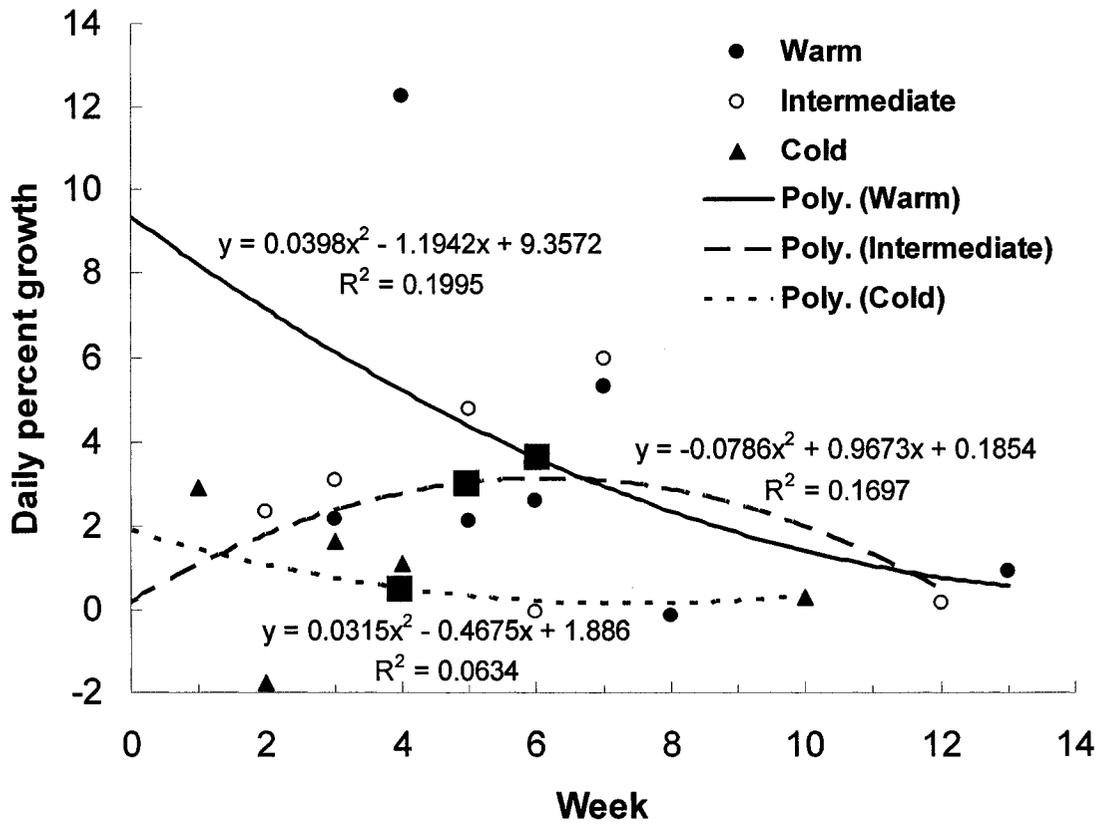


Figure 2.

Figure 2. Daily percent growth rates of age-0 Colorado River cutthroat trout during Phase 2 of the 2004 laboratory experiment (data from Coleman and Fausch in press). The lines are second-degree polynomial fits, and gray boxes indicate the start of winter ( $\leq 4^{\circ}\text{C}$ ) in each of the three temperature regimes studied. Warm regime temperatures started at  $10.0^{\circ}\text{C}$  at the beginning of Phase 2, whereas the Intermediate regimes started at  $8.5^{\circ}\text{C}$ , and the cold regime started at  $7.0^{\circ}\text{C}$ . All three were decreased at a rate similar the natural thermal regimes to winter temperatures, with a minimum of about  $1.0^{\circ}\text{C}$  (Chapter 2; Coleman and Fausch in press).

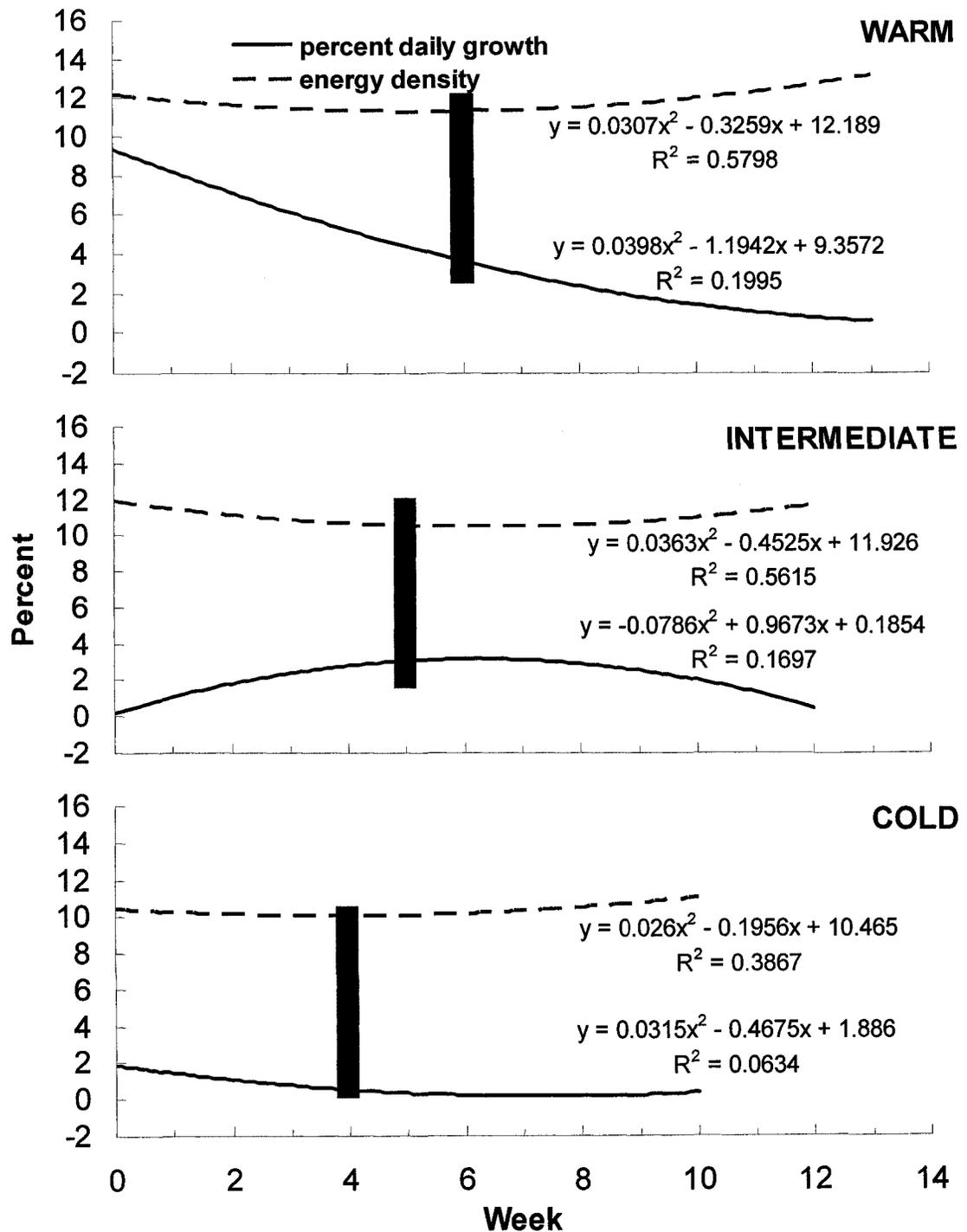


Figure 3.

Figure 3. Polynomial fits of daily percent growth and energy density (percent dry weight) for fish sampled during Phase 2 of the 2004 laboratory experiment (data from Coleman and Fausch in press). Percent dry weight numbers were not arcsine-squareroot transformed, as in Coleman and Fausch (in press), so that daily percent growth and energy density are expressed in the same units relative to eviscerated wet weight and can be plotted on the same axis. The lines are second-degree polynomial fits, and gray boxes indicate the start of winter in each regime, when temperature fell below 4°C.