Evaluation of the Effects of Stage Fluctuations on Overwinter Survival and Movement of Young Colorado Pikeminnow in the Green River, Utah, 1999–2002

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SYNOPSIS

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2004

REPORT A

Overwinter Survival and Movement of Young-of-Year Colorado Pikeminnow in the Green River, Utah, 1999–2002

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REPORT B

Movement Rates of Age-0 Colorado Pikeminnow Under Simulated Winter Conditions

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REPORT C

Development of a Bioenergetics Model for Evaluating Factors that Influence Overwinter Survival of Age-0 Colorado Pikeminnow in the Green River, Utah

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2004

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SYNOPSIS

INTRODUCTION

The Colorado pikeminnow *(Ptychocheilus lucius)* is the largest native minnow in North America and an endemic species in the Colorado River Basin. Historically, it was once widely distributed in the upper and lower Colorado River basins, but now the population range has been reduced by 80 percent because of interactions with introduced fishes, construction of dams, and other habitat modifications (Carlson and Muth 1989; U.S. Fish and Wildlife Service 1992; Tyus 1991). Although the Colorado pikeminnow no longer exists in lower basin, its populations still continue to thrive in the upper basin. The greatest numbers are found in the Green River subbasin (Tyus and McAda 1984; U.S. Fish and Wildlife Service 1990; Tyus 1991).

Colorado pikeminnow migrate during June and July to two spawning sites, Yampa Canyon or Gray/Desolation Canyon, where they spawn over cobble substrates. Newly hatched larvae drift downstream to one of two nursery areas in alluvial reaches of the Green River (McAda et al. 1998; Tyus and Haines 1991), one downstream of the Yampa Canyon spawning site in the middle Green River (RM 200–319), and the other downstream of the Gray/Desolation Canyon site in the lower Green River (RM 0–120). The numbers of age-0 Colorado pikeminnow in the nursery areas varies greatly from year to year (Bestgen et al. 1998; McAda et al. 1998), but standardized monitoring between 1986 and 1997 showed average catch was three times as great in the lower Green nursery (McAda et al. 1998). Age-0 Colorado pikeminnow occupy low-velocity backwater habitats and may have only two or three months to grow and accumulate fat reserves before entering their first winter (Thompson et al. 1991).

Overwinter survival during the first year of life is a primary factor determining year-class strength of most temperate zone fishes (Garvey et al. 1998), including Colorado pikeminnow (Haines et al. 1998). Winter is a period of reduced growth, depletion of energy reserves, and heightened mortality risk. Small changes in the rate of growth or mortality of eggs, larvae, and juvenile have been shown to substantially impact population recruitment (Houde 1987; Bestgen et al. 1997). Winter mortality is often size-selective, but the magnitude of size selectivity varies from year to year. To survive, young-of-year fishes must reach a threshold size by late fall of their first growing season, because overwinter mortality generally removes smaller individuals with low energy reserves (Oliver et al. 1979, Toneys and Coble 1979; Shuter et al. 1980; Post and Evans 1989; Schindler 1999). For larval and juvenile fishes, reaching this threshold size confers a host of advantages during a time when mortality is typically high, including lower probability of starvation due to higher prey capture rates, and decreased vulnerability to predators due to improved swimming ability (Garvey et al. 1998).

Although young-of-year fish may reach the threshold size, other environmental factors, such as ice formation, ice jams, cold water temperatures, and winter flow fluctuations, may impose additional threats to overwinter survival. Winter flows in the middle Green River are influenced by releases from Flaming Gorge Dam. It has been hypothesized that winter operations of Flaming Gorge Dam reduces survival of age-0 Colorado pikeminnow because fluctuating discharge and associated changes in water surface elevation modify the characteristics of nursery habitats which causes an increase in fish activity (Carlson and Muth 1989; U. S. Fish and Wildlife Service 1992; Haines et al. 1998; Valdez and Cowdell 1999). Yet, a study by Hayse et al. (2000) found that adverse winter conditions in backwater habitats including ice formation, ice jams, and flow-through conditions were likely more a function of local upstream conditions than winter flow fluctuations initiated at Flaming Gorge Dam. However, higher stage elevations produced by ice jams may inundate nursery backwater habitats and transform them into unsuitable flow-through areas. In addition, as flows decline, fish must search for suitable habitats to avoid being stranded. Winter flows may dismantle ice cover which acts as an insulator, allow the creation of frazil ice, and may result in ice jams that increase river stage and inundate backwaters (Valdez and Cowdell 1999). Each of these stressors may impact overwinter survival of young Colorado pikeminnow by causing fish to redistribute to more suitable habitats at a time that is very costly energetically.

However, the effects of winter flow fluctuations on overwinter survival, movement, and backwater habitats in the Green River downstream from Flaming Gorge Dam have not been demonstrated in the field.

The goals of this project were to: 1) evaluate the effects of winter operations of Flaming Gorge Dam on the survival, distribution, and nursery habitats of age-0 Colorado pikeminnow; 2) determine specific habitat changes and accompanying fish movements resulting from flow fluctuations; and 3) develop a bioenergetics model to assist in interpreting field data and predicting the effects of conditions other than those observed during the study. To address these goals, three interrelated studies were conducted. The effects of stage fluctuations induced by hydropower operations, should they exist, are presumed much greater at the nursery area in the middle Green River (91 miles below the dam) than in the lower Green River (290 miles below the dam).

The first study (Report A: Kitcheyan and Haines 2004) was designed to use capture-recapture procedures to estimate overwinter survival and monitor movement patterns of age-0 Colorado pikeminnow. Secondly, a mixture of deep and shallow backwaters were selected on the Ouray National Wildlife Refuge to evaluate the effects of fluctuating flows on these nursery habitats and fish found in them.

The second study (Report B: Plampin and Beyers 2004) described the range of spontaneous movement rates (activity) of age-0 Colorado pikeminnow in simulated winter conditions. Movement of individual Colorado pikeminnow was determined by measuring movement of individual fish at four water temperatures (1, 5, 10, and 15 ºC) and at three levels of disturbance (0, 1, and 2 disturbances/min).

The third study (Report C: Beyers and Plampin 2004) dealt with the construction of a bioenergetics model that described the energetics of age-0 Colorado pikeminnow in winter conditions. Energetic characteristics of age-0 Colorado pikeminnow were measured in the laboratory and integrated into a fish bioenergetics model. Accuracy of the model was evaluated by comparing predicted growth of

Colorado pikeminnow to observed growth in an independent investigation. Then the model was used to evaluate the potential for overwinter survival of age-0 Colorado pikeminnow to be influenced by changes in fish activity.

STUDY OBJECTIVES

Each component of the Flaming Gorge Winter study had specific objectives to address concerning the effects of winter operations of Flaming Gorge Dam on the survival, distribution, and nursery habitats of age-0 Colorado pikeminnow. In Table 1, study objectives for each project are presented and the reader is directed to the relevant draft report. The Colorado River Fish Project-Vernal, Utah, was responsible for conducting field investigations (i.e., population estimates, winter fish sampling, and monitoring stage fluctuations) in the alluvial reach occupied by age-0 Colorado pikeminnow. Colorado State University was responsible for characterizing movement rates under simulated winter conditions; and developing and evaluating a bioenergetics model for age-0 Colorado pikeminnow.

Table 1. Study objectives for Flaming Gorge Dam winter flow fluctuations on overwinter survival of young-of-year Colorado pikeminnow.

Objectives: Overwinter Survival and Movement of Young-of-Year Colorado Pikeminnow Component	**Addressed in:**[1]
Determine if overwinter survival of age-0 Colorado pikeminnow was affected by winter operations of Flaming Gorge Dam.	A
Determine if backwater habitats are physically affected by fluctuating releases from Flaming Gorge Dam during winter.	A
Determine if winter movements are related to fluctuating releases from Flaming Gorge Dam.	A
Evaluate the assumptions of overwinter survival estimates and specifically determine how Colorado pikeminnow movements affect these estimates	A
Evaluate alternative methods for collecting age-0 Colorado pikeminnow in backwater, embayments, eddy, and main-channel shoreline habitats during the winter.	A
Objectives: Movement Rates under Simulated Winter Conditions Component	
Describe the realistic range of spontaneous movement rates (activity) of age-0 Colorado pikeminnow in simulated winter conditions.	B
Objectives: Bioenergetics Model Component	
Construct a bioenergetics model that describes energetics of age-0 Colorado pikeminnow in winter conditions.	C
Evaluate the potential for overwinter survival of age-0 Colorado pikeminnow to be influenced by changes in fish activity.	C

[1] Reports are referenced as follows: A - Kitcheyan and Haines 2004; B - Plampin and Beyers 2004; and C - Beyers and Plampin 2004.

METHODS

Overwinter Survival and Movement of Young-of-Year Colorado Pikeminnow

Abundance Estimates and Overwinter Survival

Each year abundance estimates were conducted in autumn and again in spring using capture-recapture methods (Haines and Modde 1996; Haines et al. 1998). Abundance estimates for autumn and spring were computed using the computer program CAPTURE (White et al 1982). Our original study plan called for three sampling passes between Bonanza Bridge and Ouray Bridge, a 40-mile reach.

However, various problems required plan modification. In the fall of 1999, catch data from the Interagency Standardized Monitoring Program (ISMP) and preliminary sampling effort by our office showed low numbers of young-of-year Colorado pikeminnow in the middle Green River, suggesting catch rates would be too low to calculate a meaningful population estimate. As a result, sampling was confined to the Ouray Backwater Complex for fall 1999 and spring 2000, giving us the best opportunity to obtain recaptures. Population estimates were made for two backwaters in this reach. The entire 40-mile study reach was sampled in fall and spring, 2000, 2001, and 2002, although three passes were completed only once, and two passes on all other occasions. A sampling pass consisted of seining all backwaters > 30 m^2 in area within this reach. Backwaters were defined as shallow ephemeral embayments adjacent to the main river channel with no measurable water velocity. All Colorado pikeminnow <100 mm total length (TL) were marked with syringe-injected elastomer (Northwest Marine Technology, Shaw Island, Washington) and released into their backwater of origin. Fish recaptured in an intermediate pass were marked again before release.

Overwinter survival probability was calculated by dividing each spring estimate by the estimate from the previous autumn. Overwinter size selective growth and mortality were evaluated using quantile-quantile (q-q) plots of young-of-year Colorado pikeminnow length-frequency distributions from fall and spring (Post and Evans 1989; Converse et al. 1997; Post et al. 1998; McAda and Ryel 1999).

Movement

Young-of-year Colorado pikeminnow marked on each sampling pass were used to study movement patterns. The 40-mile reach was divided into eight 5-mile sections. Different colors (e.g., red, orange, yellow, green) and mark locations (i.e., base of the anal fin, left or right side of dorsal fin, posterior or anterior of the dorsal fin) were used to distinguish fish among sampling passes and 5-mile sections. Fish sampling began at Bonanza Bridge at river mile (RM) 289.4 and extended downstream to

Ouray Bridge (RM 249). When a fish was recaptured, the marks allowed identification of the 5-mile section or backwater where that individual fish was originally captured, capture history (e.g. if the fish was recaptured repeatedly between passes or seasons), and the number of days between captures.

Winter Flow Fluctuations

Three distinct flow regimes for winters 1999–2000, 2000–2001, and 2001–2002 were proposed to Bureau of Reclamation to evaluate the effects of fluctuating flows on the physical morphology of nursery habitats (e.g., changes in area, water depth, velocity, ice cover) and fish inhabiting them. Flow regimes for the first year were not manipulated but instead considered a stable flow regime. The second winter called for a series of 5-d periods of daily fluctuations followed by a 9-d period of stable flows to produce river stage changes at Jensen Gage (#9261000) of 0.10, 0.20, and 0.30. The final year of study proposed a 90-d period of flow fluctuations at a level shown to invoke fish movement.

Winter Habitat Description and Winter Sampling

In conjunction with the proposed flow scenarios, a mixture of deep and shallow backwaters were selected on the Ouray National Wildlife Refuge, a 12-mile section (RM 262-250) we call the Ouray Backwater Complex. Each winter, two or three backwaters were chosen in close proximity to evaluate effects of stage fluctuations. Three or four Optic StowAway® temperature loggers were placed into the backwaters. A Trimble GeoExplorer II® Global Positioning System (GPS) unit was used to outline each backwater and locate depth measurements, temperature loggers, and trap locations. Various fishing gears were utilized to capture small-bodied fish prior to, during, and after ice cover. Gear types included fyke nets, clover traps, minnow traps, and seines. An Aqua-Vu® underwater camera was used to monitor fish presence and behavior under ice for 6 to 8 h between1400 h and 0900 h (refer to Report A for a more in-depth discussion on methods).

Movement Rates under Simulated Winter Conditions Component

Young-of-year Colorado pikeminnow ranging from 45 to 55 mm TL were acclimated to laboratory conditions. Movement rates were quantified by video interpretation of movement of individual Colorado pikeminnow in an observation arena at four water temperatures (1, 5, 10, and 15°C) and at three levels of disturbance (0, 1, and 2 disturbance/min). Regression analysis was used to fit observed data to models that describe rates of movement as functions of water temperature and disturbance. The best approximating models were identified using Akaike's information criterion (Burnham and Anderson 1998).

Bioenergetics Model Component

<u>Construction and Evaluation of Bioenergetics Model</u>

The bioenergetics model was constructed specifically for Colorado pikeminnow life stages and temperature conditions that occur during winter in the Green River near Jensen, Utah. Energetic characteristics of age-0 Colorado pikeminnow that were measured included: food consumption as a function of fish size and water temperature; and metabolic rate as a function of fish size, water temperature, and activity. Performance of the bioenergetics model was evaluated in two steps. First, the model was used to estimate food consumption and respiration of Colorado pikeminnow in laboratory studies described in this paper and the predicted outcomes were compared to observed responses. The second evaluation step involved comparing modeled growth of Colorado pikeminnow to observed data from an independent experiment (Thompson 1989).

To evaluate the effect of increased activity on overwinter survival, six simulations were conducted using a variety of realistic fish sizes, temperature regimes, activity rates, and feeding conditions. Each simulation started with fish sizes of 35, 45, or 60 mm TL feeding at 10% of maximum ration for 118 d. At the end of each day, total length and fish condition (K) were updated. If fish growth was positive, total length was increased using a weight-length regression equation. If fish growth was negative, total length was held constant at the value for the previous day.

RESULTS AND DISCUSSION

Overwinter Survival and Movement of Young-of-Year Colorado Pikeminnow

Population and Overwinter Survival Estimates

Over a three year period of this study, a total of 732 young Colorado pikeminnow (30-100 mm TL) were captured, 404 were marked and released (fish captured on the last pass during spring sampling were not marked), and 38 fish were recaptured. In the first year of the study (fall 1999, spring 2000), we concentrated our sampling in the Ouray Backwater Complex and made population estimates for two backwaters (BA) for the fall and spring. In BA#1 the estimate was 218 fish in the fall and 153 fish in the spring; in BA#2 the estimate was 87 fish in the fall and 115 fish in the spring. All these estimates were imprecise, with the coefficient of variation (CV) ranging from 0.22 to 0.83, the result of small numbers of captures and recaptures. The probability of capture for individual fish was highly variable, ranging from 0.01 to 0.32.

The second kind of abundance estimate was for the 40-mile reach. For the autumn of 2000, we estimated 735 age-0 fish in the reach, and for the spring 2001, we estimated 260 age-1 fish. For autumn of 2001, the estimate was 670 age-0; for spring 2002, the estimate was 1,320 age-1 fish. These estimates were also highly variable, with CV ranging between 0.25 and 0.59. The probabilities of capture ranged from 0.03 to 0.16. In general, the probabilities of capture were smaller for the 40-mile reach than for the individual backwaters, because far fewer seine hauls per backwater were made.

Overwinter survival estimates for the 40-mile reach could not be calculated because population estimates were too imprecise. Two of four spring estimates were greater than the corresponding fall estimates. We looked at fall and spring length-frequency distributions for evidence of size-selective mortality. Among the three winter periods, the 1999–2000 winter was the mildest(i.e., shortest duration), and no overwinter size-selective mortality was observed. The 2000–2001 winter was intermediate in severity, and overwinter mortality occurred, but it was not strong. The 2001–2002 winter had the greatest severity and the greatest size-selective mortality. Others have also reported size-selective overwinter mortality for young Colorado pikeminnow (Converse et al. 1997, McAda and Ryel 1999, Thompson et al. 1991). Higher survival of large fish was presumably the result of more fat reserves (Thompson et al. 1991, Beyers and Plampin 2004), and size at the end of the growing season was probably the result of early arrival date in the nursery habitat (i.e., early hatching date resulting in longer growing season) and warm summer water temperatures (Bestgen et al. 1997), but habitat availability and food abundance may also have been important (Tyus and Haines 1991).

Winter Movements

Young Colorado pikeminnow moved only short distances both within autumn and spring sampling and between autumn and spring sampling. Within autumn and spring sampling, 95% of the recaptured young Colorado pikeminnow were within the same 5-mile section where they were originally marked. Of the recaptured fish for which we could determine the backwater of origin, 68% were recaptured in the backwater of origin, 94% were recaptured within 0.6 mile of the backwater of origin, and all were captured within 3 miles of the backwater of origin. These fish were at large between 5 and 42 d.

Overwinter movement (between autumn and spring sampling) was about 3 miles or less. Of 14 fish that were marked in the autumn and recaptured the following spring, 13 were recaptured in the same backwater and one fish was recaptured upstream 3 miles. We point out, however, that most of the fish we captured were caught in the downstream portion of the 40-mile study reach, and therefore we only sampled approximately 3 to 6 miles downstream from most marked fish, possibly underestimating the amount of downstream movement. Nevertheless, the evidence thus far suggests that most young Colorado pikeminnow moved less than 6 miles during the winter period.

We hypothesize that age-0 Colorado pikeminnow exhibit an adaptive behavior wherein in the summer and early fall they occupy backwater nursery habitats that provide refuge from the current, preferred thermal conditions, and a productive environment where prey are likely to be encountered (Tyus and Haines 1991). At this time, fish are widely distributed in the nursery area in deep and shallow backwaters. But as temperatures cool in the fall, the shallower backwaters become cooler than the main channel, even during the warmest part of the day. Fish tend to move downstream and congregate in the deepest and largest backwaters where temperatures at the mouth of the backwaters do not fall below the main channel temperature. It is in these large, deep backwaters that fish apparently overwinter (Haines and Tyus 1990; Tyus and Haines 1991; Day et al. 1999). Occasionally during the winter, the river stage increases, usually the result of an ice jam, and turns a backwater into a flow-through area. Some fish respond by moving out of the area in search of nearby low-velocity habitats, but others respond by finding low-velocity micro-habitats within the area of the original backwater, perhaps behind uneven bottom contours. After ice-out and spring runoff begins, more backwaters become flow-through areas, resulting in fish movement downstream.

Effects of Fluctuation Discharge from Flaming Gorge Dam

We were unable to test whether fluctuating flows from Flaming Gorge Dam influenced overwinter survival, primarily because there were too few age-0 Colorado pikeminnow in our study reach to make overwinter survival estimates, and secondarily because we could not obtain the winter flow fluctuations because of the national energy emergency during the winters of 2000–2001 and 2001–20002 . Hence, we worked with the fluctuations provided during the normal Flaming Gorge hydropower generation. Winter flows over three years ranged from 991 to 3,000 cubic feet per second (cfs), but the normal 24-hour releases usually ranged between 600 and 800 cfs, producing stage changes in the nursery area of <0.1 m at the upper end and <0.01 m and the lower end. These fluctuations did not alter physical morphology of backwaters studied in the Ouray Backwater Complex. These stage changes had only minimal affect on backwater habitats and were limited to the upper end of the nursery area.

In contrast to flow fluctuations, the formation of ice jams, as observed in the 1999–2000 winter, had far greater affect on backwater nursery habitats. Ice jams increased stage by 0.75-1.50 m, and transformed many backwater habitats into flow-through areas. In association with backwater transformation to flow-through environments, fish may be flushed into the surrounding system and incur increased risk of injury, predation, and metabolic cost associated with the search for another suitable nursery area (Haines et al. 1998; Muth et al. 2000). The role of fluctuating winter flows from Flaming Gorge in the creation of ice jams is unclear to us. Valdez and Cowdell (1999) speculated that fluctuating winter flows dismantle ice cover which facilitates the formation of frazil ice, and potentially results in ice jams that increase river stage several meters thus inundating many backwaters. However, Hayse et al. (2000) found that fluctuating winter flows did not dismantle ice cover or promote formation of frazil ice and ice jams. Whatever the cause, it is likely that ice jams form at several locations on the middle Green River nursery area in most years (Valdez and Cowdell 1999; Hayes et al. 2000).

Winter Sampling for Age-0 Colorado pikeminnow

Prior to ice formation, the most effective method for catching age-0 Colorado pikeminnow was seining. Seining was most effective when backwaters were warm and became less efficient as temperatures cooled. Colorado pikeminnow that occupied backwaters on the first pass during autumn sampling often vacated them prior to subsequent passes, especially when slush ice was found in the backwaters. During ice cover, all gear types were ineffective for capturing age-0 Colorado pikeminnow. Over the three year study period, only one young-of-year Colorado pikeminnow was captured under ice with a seine. Seining under the ice was very laborious, and effort was limited to one to three seine hauls per day.

The most efficient technique for under-ice sampling was the use of an underwater camera and video cassette recorder. The equipment could be set up at various locations in the backwater to observe diurnal, nocturnal, and crepuscular fish activity. Fish could be observed swimming in the water column or staging along the substrate. The total number of fish could be counted over a 6- to 8-h time frame. The information recorded, such as fish activity and temperature, was a representation of actual events occurring in the field. Ideally, most species and age-classes (i.e., juvenile or adult) could be identified in the video. Suckers and small cyprinids were easily identified. One or two suspected young-of-year Colorado pikeminnow were observed.

Movement Rates under Simulated Winter Condition Component

Results of the investigation showed that the temperature-dependent response of fish movement in the absence of disturbance was best approximated by an exponential model with the form $y=0.0895e^{0.1523t}$ where y is body lengths/s (bl/s) and t is temperature (°C). The influence of temperature on fish movement was not consistent when environmental disturbance was present. Disturbance increased fish movement at temperatures ≤10°C and decreased movement at 15 °C. Disturbance treatments were not intended to be ecologically relevant, but they may have elicited a natural response to a perceived threat. Casual observations revealed that fish frequently responded to the stimulus with rapid swimming followed by cessation of movement near the substrate. This pattern of swimming was not completely spontaneous, because a stimulus was required to elicit it, but the purpose of the disturbance treatments was to cause fish to move at relatively high rates so that maximum spontaneous movement rates could be approximated. This objective was achieved for temperatures ≤10°C. Maximum movement rates ranged from 0.82 bl/s at 1°C to 1.1 bl/s at 5°C. Other observations support the conclusion that these estimates approximate spontaneous rates. Beyers and Plampin (Report C) measured metabolic rates of Colorado pikeminnow in a swimming respirometer and reported that at 1.5°C, 42- to 46-mm TL fish could swim continuously for a minimum of 6 h at a velocity of 1 bl/s, but not at 2 bl/s.

Bioenergetics Model Component

Bioenergetics modeling predictions suggest that overwinter survival of age-0 Colorado pikeminnow may be negatively affected if fish activity increases in response to human-induced changes in the environment. Simulations showed that fish mass and condition consistently decline when water temperatures are below 5°C. Mass and condition of fish decline faster when activity is increased because energetic reserves must be used to offset the cost of higher metabolic rate.

Activity rates of age-0 Colorado pikeminnow in the Green River during winter are unknown because direct observations of fish are difficult to obtain. Consequently, the approach used in this investigation was to evaluate outcomes of realistic ranges of potential conditions including water temperature regimes, activity rates, and food consumption rates. Of the factors investigated, fish activity rates had the greatest influence on overwinter survival of age-0 Colorado pikeminnow. When activity rates were at a relatively low spontaneous level, or at a moderate level of 0.5 bl/s, fish survived to the end of the 118 d winter period. When activity was a relatively high level of 1 bl/s, age-0 fish did not survive to the end of the winter period regardless of their size.

SYNTHESIS

This study was unable to show that fluctuating winter flows due to releases from Flaming Gorge Dam to meet hydropower needs added additional stressors to overwintering young Colorado pikeminnow. Several investigators have hypothesized that winter operations of Flaming Gorge Dam influence age-0 fish survival (Carlson and Muth 1989; U. S. Fish and Wildlife Service 1992; Valdez and Cowdell 1996; Haines et al. 1999). A 24-hr hydropower release from Flaming Gorge Dam during this study fluctuated about 600 to 800 cfs, producing stage changes at the Jensen gage <0.1 m (93 miles downstream of Flaming Gorge) and about <0.01 m at the Ouray bridge. These stage changes had only minimal affect on backwater habitats and were limited to the upper end of the nursery area. These flow fluctuations did not alter the physical morphology of backwaters studied in the Ouray Backwater Complex. The formation of ice jams, however, had a far greater affect on the backwater nursery habitats, increasing stage by 0.75-1.50 m, resulting in the transformation of many backwater habitats into flow-through areas. The role of fluctuating winter flows from Flaming Gorge Dam in the creation of ice jams is unclear. Valdez and Cowdell (1999) speculated that fluctuating winter flows may dismantle ice cover which acts an insulator, allow the creation of frazil, and may result in ice jams that increase river stage several meters and inundate many backwaters. Hayse et al. (2000), however, found that fluctuating winter flows from Flaming Gorge Dam did not dismantle ice cover thereby promoting formation of frazil ice and ice jams. Whatever the cause, it is likely that ice jams form at several locations on the middle Green River nursery area in most years (Valdez and Masslich 1989; Valdez and Cowdell 1999; Hayse et al. 2000).

As a result, stage changes due to ice jams and frazil ice formation may force young fish to redistribute and seek alternate low-velocity channel-margin habitats (Muth et al. 2000). Young Colorado pikeminnow prefer low-velocity backwater habitats (Tyus and Haines 1991); when these habitats are inundated, the fish abandon them and move to other low-velocity habitats, sometimes to other backwaters several miles away and sometimes to low-velocity micro-habitats within close proximity of the inundated backwater from which they re-inhabit once the stage recedes. Other riverine fish have been documented to behave similarly in response to ice formation, which reduces physical space and changes depth and velocity. Atlantic salmon *(Salmo salar)* young-of-the-year redistributed to find suitable depth and velocity habitats (Whalen et al. 1999). Whalen et al. (1999) found that young Atlantic salmon exhibited a combination of strategies, first movement and then fidelity, suggesting an integration of strategies for winter survival.

Winter survival of small fish is related to their ability to accumulate energy reserves (Oliver et al. 1979; Shuter and Post 1990). Small fish are at a disadvantage because basal metabolism increases as size decreases, but there is no corresponding increase in energy storage capacity. Mortality of young Colorado pikeminnow during winter has been attributed to exhaustion of lipid reserves (Thompson et al. 1991). Body weight and condition decline faster when fish activity increases, because energetic reserves must be used to offset the higher metabolic rate. Bioenergetics model predictions suggest that overwinter survival of age-0 Colorado pikeminnow may be negatively affected if fish activity increases in response to human-induced changes in the environment. When activity rates were at low and moderate levels ($\leq$0.5 bl/s), age-0 fish survived to the end of the winter period. But when activity was at a high level (1.0 bl/s), fish did not survive to the end of the winter period regardless of their size.

The objective of this investigation was to evaluate the effects of winter operations (i.e. flow fluctuations) of Flaming Gorge Dam on the distribution, nursery habitat, and overwinter survival of age-0 Colorado pikeminnow. The magnitude of daily flow fluctuations in this study produced a stage change of <0.1 m at the Jensen gage and <0.01 m at the Ouray bridge. These flow fluctuations did not directly alter physical morphology of backwaters in the Ouray complex. Ice jams increased stage elevation by 0.75 to 1.50 m which transformed many backwater habitats into flow-through areas. Under these conditions, overwinter movement (between autumn and spring sampling) of young-of-year Colorado pikeminnow was about 3 miles or less. Mark-recapture population estimates were hampered by relatively low abundance of young Colorado pikeminnow during this investigation. Because few fish were captured, estimates were imprecise and reliable overwinter survival estimates could not be made. The fish bioenergetics analysis showed that in some circumstances, increased activity can reduce overwinter survival of young Colorado pikeminnow. Consequently, the bioenergetics analysis could not exclude the hypothesis that stage fluctuations caused by Flaming Gorge Dam operations influence overwinter survival of age-0 Colorado pikeminnow.

The effect of Flaming Gorge Dam on fish activity remains unknown because we were not able to observe changes in fish activity in response to flow fluctuations. For age-0 Colorado pikeminnow, winter conditions produce a negative energy balance where the costs of survival are greater than the energetic gains realized by food consumption. If it can be shown that the operation of Flaming Gorge Dam increases activity of age-0 Colorado pikeminnow in the Green River, then further evaluations should be conducted to determine the likelihood that natural mortality rates are affected.

CONCLUSIONS

Overwinter Survival and Movement of Young-of-Year Colorado Pikeminnow

- Population estimates for the 40-mile reach were imprecise; CV ranged from 0.25 to 0.59. The imprecision is the direct result of not catching, marking, and recapturing enough fish. Colorado pikeminnow young-of-year population densities, as measured by ISMP, were one-tenth the densities during the three years of this study compared to the 13 years prior to the study.
- Overwinter survival estimates could not be made because population estimates were too imprecise. Size-selective overwinter mortality does occur among young-of-year Colorado pikeminnow, but does not necessarily occur every winter.
- Young Colorado pikeminnow moved only short distances both within autumn and spring sampling and between autumn and spring sampling. Within autumn and spring sampling, 95% of

the recaptured young Colorado pikeminnow were within the same 5-mile section where they were originally marked.

- Overwinter movement (between autumn and spring sampling) was about 3 miles or less.
- Young Colorado pikeminnow apparently make local movements on a diel basis in response to environmental conditions.
- We were unable to draw conclusions about whether typical winter flow operations at Flaming Gorge Dam affected overwinter survival of young-of-year Colorado pikeminnow. Survival could not be estimated because population estimates of the fall and the following spring were too imprecise and the level of winter flow fluctuations may have been too low to affect survival.
- Ice jams were observed in the Ouray Backwater Complex that resulted in stage changes up to 0.75-1.50 m and transformed backwaters into flow-through environments.
- Prior to ice formation, seining was the most efficient method for catching age-0 Colorado pikeminnow. All gear types including baiting traps and using neon lights were ineffective in capturing young Colorado pikeminnow under ice. The most effective technique for under ice sampling was an underwater camera and video cassette recorder. Diurnal, nocturnal, and crepuscular fish activity were observed, and total number were counted over a 6 to 8 h time frame.

Movement Rates under Simulated Winter Conditions

- The temperature-dependent response of fish movement in the absence of disturbance (spontaneous) was best approximated by an exponential model with the form $y = 0.0895e^{0.1532t}$ where y is body lengths/s (bl/s) and t is temperature (°C).
- Activity declines exponentially with temperature, but young Colorado pikeminnow remain active during winter, even when water temperatures approached 0°C.

Bioenergetics Model Component

- Bioenergetics modeling predictions indicated that overwinter survival of age-0 Colorado pikeminnow may be negatively affected if fish activity increases in response to physical or natural changes in the environment. When activity rates were spontaneous or 0.5 bl/s, 35-, 45-, and 60-mm TL fish survived to the end of the winter period. When activity was 1.0 bl/s fish did not survive to the end of the winter period regardless of size.
- Simulations showed that fish mass and condition consistently decline when water temperatures are below 5°C.
- Mass and condition of fish decline faster when activity is increased because energetic reserves must be used to offset the cost of higher metabolic rate.
- Data describing fish growth and food consumption rates during winter are potentially useful for additional confirmation of the accuracy of bioenergetics model predictions. Required data are repeated measurements of mass (to nearest 0.01g) and total length (to nearest 1 mm) of individual fish before and after the winter period.

RECOMMENDATIONS

- Effects of stage fluctuations on overwinter survival could not be evaluated in this study, but the bioenergetics modeling predictions indicates that overwinter survival of age-0 Colorado pikeminnow may be negatively affected if fish activity increases in response to natural or physical changes in the environment. For age-0 Colorado pikeminnow, winter conditions produce a negative energy balance, where the costs of survival are greater than the energetic gains realized by food consumption. If it can be shown that the operation of Flaming Gorge Dam increases activity of age-0 Colorado pikeminnow in the Green River, then further evaluation should be conducted to determine the likelihood that natural mortality rates are affected.

- Because inadequate numbers of young-of-year Colorado pikeminnow were captured during this three year study, we recommend investigators review fall Interagency Standardized Monitoring Program catch data to determine if winter sampling would be feasible before initiating future winter studies .
- Ice jams in the Ouray Backwater complex were observed which increased stage levels and inundated nursery habitats. Past research indicates ice jams occur periodically, but frequency is unknown. We recommend selecting backwaters in the vicinity of documented ice jam locations, and monitoring magnitude and duration of stage fluctuations as result of winter flows or ice jams. Ice jams may be a contributing factor affecting overwinter survival.
- All sampling gears used under the ice were ineffective, except the underwater camera. We recommend the use of an underwater camera under ice cover be further evaluated as a sampling tool.

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REPORT A

Overwinter Survival and Movement of Young-of-Year Colorado Pikeminnow in the Green River, Utah, 1999–2002

FINAL REPORT

March 2004

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EXECUTIVE SUMMARY

Winter flows in the middle Green River nursery area consist primarily of releases from Flaming Gorge Dam. Several investigators have hypothesized that winter operations of Flaming Gorge Dam influence age-0 fish survival. As power demands increase, higher flows inundate nursery backwater habitats and transform them into unsuitable flow-through areas. It has been speculated that fluctuating winter flows may dismantle ice cover which acts an insulator, allow the creation of frazil ice, and may result in ice jams that increase river stage and inundate backwaters. As a result, each of these additional stressors may impact overwinter survival of young Colorado pikeminnow by causing the fish to redistribute to more suitable habitats at a time that is very costly bioenergetically. However, the effects of flow fluctuations on overwinter fish survival and nursery habitats have not been demonstrated in the field.

Previous studies in the Green River nursery area have shown that population estimates can be made in 20-mile reaches of river, but that accuracy of overwinter survival estimates is suspect, because of unknown immigration and emigration of fish to and from the study area. This study attempted to use capture-recapture procedures to estimate overwinter survival and movement of age-0 Colorado pikeminnow and relate the observed responses to stage fluctuations in the Green River induced by hydropower operations at Flaming Gorge Dam. The following objectives were developed for the study.

1) Determine if overwinter survival of age-0 Colorado pikeminnow is affected by winter operations of Flaming Gorge Dam.
2) Determine if backwater habitats are physically affected by fluctuating releases from Flaming Gorge Dam during winter.

3) Determine if fish movements in winter are related to fluctuating releases from Flaming Gorge Dam.
4) Evaluate the assumptions of overwinter survival estimates and specifically determine how Colorado pikeminnow movements affect these estimates.
5) Evaluate alternative methods for collecting age-0 Colorado pikeminnow in backwater, embayment, eddy, and main-channel shoreline habitats during the winter.

Over the three year period of this study, a total of 732 young Colorado pikeminnow were captured, 404 were marked and released (fish captured on the last pass during spring sampling were not marked), and 38 fish were recaptured. Population estimates were made that averaged 26 fish per river mile, with coefficients of variation (CV) that ranged between 0.25 and 0.59. The imprecision of our estimates was the direct result of not catching enough marked fish. Unfortunately, during the three years of this study, age-0 Colorado pikeminnow were only one-tenth as abundant as the average for the previous 13 years. As a result of the imprecision of the population estimates, we were unable to make overwinter survival estimates.

Age-0 fish marked in autumn and recaptured the following spring generally moved less than 10 miles downstream after being at large for 170 to 200 d. This result is consistent with other studies and gives us confidence that rate of movement between autumn and spring will not bias estimates of overwinter survival for a 40-mile reach, but it could be a problem for reaches less than 40 miles.

A number of techniques were attempted to sample for young Colorado pikeminnow under the ice that included seining, minnow traps, clover traps, fyke nets, and an underwater camera. The most effective approach was the use of an underwater camera and video cassette recorder. It allowed us to observe diurnal, nocturnal, and crepuscular patterns, swimming speeds, and activity levels of fish. Twenty-six hours of video showed 1,973 fish, of which one or two were suspect Colorado pikeminnow. With more experience, investigators can learn to identify the fish with more certainty.

This study was unable to show whether or not typical winter flow operations at Flaming Gorge Dam to meet hydropower needs influenced overwinter survival of young Colorado pikeminnow. Several investigators have hypothesized that winter operations of Flaming Gorge Dam reduce age-0 fish survival because fluctuating discharge and associated changes in water surface elevation modify the characteristics of nursery habitats which causes an increase in fish activity (Carlson and Muth 1989; U. S. Fish and Wildlife Service 1992; Valdez et al. 1999; Haines et al. 1999). A 24-hour hydropower release from Flaming Gorge Dam during this study usually fluctuated about 600 to 800 cfs, producing stage changes at the Jensen gage of <0.1 m (93 miles downstream of Flaming Gorge) and about <0.01 m at the Ouray bridge. These stage changes had only minimal affect on backwater habitats and were limited to the upper end of the nursery area. These flow fluctuations did not alter physical morphology of backwaters studied in the Ouray Backwater Complex. However, the formation of ice jams, as observed in the 1999–2000 winter, had far greater affect on backwater nursery areas, increasing stage by 0.75-1.50 m, and resulting in the transformation of many backwater habitats into flow-through areas. The role of fluctuating winter flows from Flaming Gorge Dam in the creation of ice jams is unclear to us. Some investigators have speculated that fluctuating winter flows may dismantle ice cover which acts an insulator, allow the creation of frazil ice, and may result in ice jams. However, a more recent study found that fluctuating winter flows from Flaming Gorge Dam during the winter of 1996–1997 did not dismantle ice cover or promote formation of frazil ice and ice jams. Whatever the cause, it is likely that ice jams form at several locations on the middle Green River nursery area in most years.

As a result of stage changes, ice jams, and frazil ice formation, young fish redistribute to more suitable habitats. Young Colorado pikeminnow prefer low-velocity backwater habitats, and when these habitats are inundated, the fish abandon them and move to other low-velocity habitats, sometimes to other backwaters several miles away and sometimes to low-velocity micro-habitats within close proximity of the inundated backwater from which they re-inhabit once the stage recedes.

When stage changes inundate nursery habitats and transform them into flow-through environments, resident fish are flushed into the surrounding system and incur increased risk of injury, predation, and metabolic costs associated with the search for another suitable nursery area. Body weight and condition decline faster when fish activity is increased because energetic reserves must be used to offset the cost of higher metabolic rate. The result may be higher overwinter mortality.

INTRODUCTION

The Colorado pikeminnow (*Ptychocheilus lucius*) is the largest native minnow in North America and an endemic species in the Colorado River basin. Historically, it was once widely distributed in the upper and lower Colorado River basins, but now the population range has been reduced by 80 percent. Construction of mainstem impoundments, which altered historic flows and temperature regimes, and the introduction of nonnative predators are believed to have reduced the Colorado pikeminnow population (Tyus 1991a; Tyus and Haines 1991; Irving and Modde 2000). By the 1970's, the Colorado pikeminnow was extirpated in the lower basin (Minckley 1973), but natural populations of Colorado pikeminnow continue to persist in the northern portion of its historical range. The greatest numbers are found in the Green River subbasin (Tyus and McAda 1984; USFWS 1990; Tyus 1991a).

In the Green River, Colorado pikeminnow migrate in June and July to two spawning sites, Yampa Canyon and Gray/Desolation Canyon, where they spawn over cobble substrate (Tyus 1990). Newly hatched larvae drift downstream to one of two nursery areas in alluvial reaches of the Green River (McAda et al. 1998; Tyus and Haines 1991), one downstream of the Yampa Canyon spawning site in the middle Green River (RM 200–319), and the other downstream of the Gray/Desolation Canyon site in the lower Green River (RM 0–120). The numbers of age-0 Colorado pikeminnow in the nursery areas varies greatly from year to year. In the middle Green River between 1986 and 1997 catches ranged from near zero to 1.9 fish per $10m^2$ seined (average = 0.4), and in the lower Green River for the same time period catches ranged from near zero to 5.6 fish per $10m^2$ seined (average = 1.4; McAda et al. 1998). Age-0 Colorado pikeminnow occupy low-velocity backwater habitats and may have only two or three months to grow and accumulate fat reserves before entering their first winter (Thompson et al. 1991).

Overwinter survival during first year of life is a primary factor determining year-class strength of most temperate zone fishes (Garvey et al. 1998), including Colorado pikeminnow (Haines et al. 1998). Winter is a period of reduced growth, depletion of energy, and heightened mortality risk. Small changes in the rate of growth or mortality of larvae and juvenile have been shown to substantially impact population recruitment (Houde 1987; Bestgen et al. 1997).

The effects of stage fluctuations induced by hydropower operations of Flaming Gorge Dam, should they exist, are presumed much greater at the nursery area in the middle Green River (91 miles below the dam) than in the lower Green River (290 miles below the dam). Winter flows in the middle Green River consists primarily of releases from Flaming Gorge Dam, and it has been hypothesized by several investigators that winter operations influences age-0 fish survival (Carlson and Muth 1989; U. S. Fish and Wildlife Service 1992; Valdez et al. 1999; Haines et al. 1998). As hydropower demands increase, higher flows may inundate nursery backwater habitats and transform them into unsuitable flow-through areas. It has been speculated that fluctuating winter flows may dismantle ice cover which acts as an insulator, allow the creation of frazil, and may result in ice jams that increase river stage and inundate backwaters (Valdez and Cowdell 1999). As a result, each of these factors may contribute additional stress to the overwinter survival of young Colorado pikeminnow by causing the fish to redistribute to more suitable habitats at a time that is very costly bioenergetically. However, the effects of flow fluctuations on overwinter fish survival and nursery habitats, should they exist, have not been demonstrated in the field.

Previous studies in the Green River nursery areas (Haines and Modde 1996; Haines et al. 1998) have shown that population estimates can be made in 20-mile reaches of river, but that accuracy of overwinter survival estimates is influenced by environmental conditions and fish movement into or out of sample reaches during winter. Obtaining accurate estimates of overwinter survival of age-0 Colorado pikeminnow is critical to understanding the life history of the species, modeling population dynamics, and determining the factors affecting survival to protect the species and its habitat. Capture-recapture population estimation is the best means for estimating abundance of age-0 Colorado pikeminnow because, unlike catch per unit of effort, it can account for the influence of environmental factors that may affect capture probabilities. In addition, capture-recapture can be used to estimate rates of immigration and emigration.

This study attempted to use capture-recapture procedures to estimate overwinter survival and movement of age-0 Colorado pikeminnow and relate the observed responses to stage fluctuations in the Green River induced by hydropower operations at Flaming Gorge Dam. The following objectives were developed for this study.

1) Determine if overwinter survival of age-0 Colorado pikeminnow is affected by winter operations of Flaming Gorge Dam.
2) Determine if backwater habitats are physically affected by fluctuating releases from Flaming Gorge Dam during winter.
3) Determine if fish movements in winter are related to fluctuating releases from Flaming Gorge Dam.
4) Evaluate the assumptions of overwinter survival estimates and specifically determine how Colorado pikeminnow movements affect these estimates.

5) Evaluate alternative methods for collecting age-0 Colorado pikeminnow in backwater, embayment, eddy, and main channel shoreline habitats during the winter.

STUDY AREA

The Green River, largest tributary of the Colorado River, originates in the Wind River Range of Wyoming and flows southward through the states of Utah and Colorado before entering the Colorado River 60 miles downstream of Moab, Utah. Flows of the Green River have been regulated since October 1962 by the operation of Flaming Gorge Dam. The dam has altered seasonal flow patterns and water temperatures, increased daily fluctuations in flows and river stages, and reduced sediment loads (Hayse et al. 2000). Our study area was located in the middle Green River, 119 miles downstream from Flaming Gorge Dam, in a low gradient alluvial reach that serves as an important Colorado pikeminnow nursery area (Tyus and Haines 1991, McAda et al. 1994, Haines et al. 1998). The study reach extended from Bonanza Bridge at river mile (RM) 289 to Ouray Bridge at RM 249 (Figure 1). The alluvial section was characterized as low gradient, consisting predominately of sand and silt substrates (Haines and Tyus 1990, Tyus and Haines 1991, McAda et al. 1994, Haines et al. 1998). During the winter ice-cover period, field work was confined to Ouray National Wildlife Refuge (NWR) between RM 250 and 260. This 10-mile section was selected because it was a known concentration of young-of-year Colorado pikeminnow (Tyus and Haines 1991, McAda et al. 1994) and accessible by road during the winter. We call this 10-mile reach the Ouray Backwater Complex (Figure 2).

METHODS

Capture and Marking of Young-of-Year Colorado Pikeminnow

Abundance estimates of young-of-year Colorado pikeminnow in autumn and the following spring were determined using capture-recapture population estimation methods (Otis et al. 1978, Seber 1982, Haines and Modde 1996, Haines et al. 1998). Our original study plan called for three sampling passes between Bonanza Bridge and Ouray Bridge, the 40-mile reach. However, various problems required plan modification. In the fall of 1999, catch data from the Interagency Standardized Monitoring Program (ISMP) and preliminary sampling by our office showed low numbers of young-of-year Colorado pikeminnow in the middle Green River, suggesting we would not catch enough fish to make a population estimate. As a result, sampling was confined to the Ouray Backwater Complex for fall 1999 and spring 2000, giving us the best opportunity to obtain recaptures. Population estimates were made for two backwaters in this reach The entire 40-mile study reach was sampled in fall and spring, 2000, 2001, and 2002, although three passes were completed only once, and two passes on all other occasions.

A sampling pass consisted of seining all backwaters >30 m^2 in area within this reach. Backwaters were defined as shallow ephemeral embayments adjacent to the main river channel with no measurable water velocity. Occasionally we also seined the shallow, low velocity, shoreline areas in the main channel adjacent to backwater habitats. Three different seine sizes were used: small seine, 4.5-m long x 1.9-m deep with 4.0-mm bar mesh; medium seine 9.0-m long x 1.9-m deep with 4.0-mm bar mesh; and large bag seine, 18-m long x 1.9-m deep with 4.0-mm bar mesh. For most backwaters, between 70 and 100% of the total surface area was seined. A few backwaters were large and deep, and only about 50% of the total area could be seined.

Catch per unit effort (CPUE) was calculated by considering the backwater as the primary sampling unit and defining CPUE as the number of Colorado pikeminnow captured per seine haul. Catch per unit effort for a single pass of all backwaters was estimated by averaging CPUE of each backwater for that pass.

All Colorado pikeminnow <100 mm total length (TL) were marked and released. The fish were placed into 20-L buckets filled with river water during seining. All pikeminnow were anesthetized with 100 mg/L aqueous solution of MS-222 and marked with syringe-injected elastomer (Northwest Marine Technology, Shaw Island, Washington). An attempt was made to record total length for all pikeminnow captured during each sampling pass. All fish were allowed to recover in a 20-L bucket of river water for 20 to 30 min before they were released into the backwater of origin.

Length-frequency histograms were constructed for each sampling season to examine size distributions between seasons (autumn versus spring). A Kolmogorov-Smirnov two-sample test was used to determine if there were significant differences between fall and spring length-frequency distributions. Mean total lengths in the fall versus mean total lengths in the spring were analyzed with a t-tests to determine if there were significant differences between samples.

Parameter Estimates

Abundance estimates for young-of-year Colorado pikeminnow in autumn and spring for each year were computed using the population estimators in the computer program CAPTURE (White et al. 1982). These estimators assume: 1) the population is closed; 2) all individuals in the population have an equal probability of capture; 3) animals do not lose their marks during each pass, nor is there differential mortality of marked and unmarked fish; and 4) marked animals are distinguished from unmarked animals (Otis et al. 1978). The second assumption, equal probability of capture, was the most difficult to satisfy because capture probability can vary among sample passes and individuals. Fortunately, program CAPTURE has abundance estimation models that detect and explicitly model recapture data for heterogeneity, behavioral, and time varying probabilities of capture (White et al. 1982). In this study, our recapture data was very sparse and we could not use the model selection procedure available in CAPTURE (i.e., not enough data to give reliable tests of the differing assumptions). Thus, we decided to use the Darroch (M_t) estimator because we know from previous studies that probability of capture changes with water temperature and thus from pass to pass (Haines et al. 1998). The Darroch estimator allows probability of capture to vary among sampling passes. The model gives maximum-likelihood estimates of population size, probability of capture for each pass, and profile likelihood confidence intervals.

Overwinter Size-Selective Mortality

Size-selective overwinter mortality was evaluated by comparing length-frequency distributions and quantile-quantile (q-q) plots of the same cohort collected in the fall (age-0) and following spring (age-1), using methods similar to Post and Evans 1989, Converse et al. 1997, Post et al. 1998, and McAda and Ryel 1999. To differentiate the youngest cohort from older fish, we followed Converse et al. (1997) and assumed the largest age-1 Colorado pikeminnow in March would be 80 mm. Therefore, pikeminnow > 80 mm TL were considered juveniles and excluded from the analysis.

The quantile plots were constructed by ranking the TLs from smallest to largest and assigning each to one of nine cumulative percentiles: 1, 5, 10, 25, 50, 75, 90, 95, and 99%. The fall quantile distribution was plotted on the x-axis and spring quantile distribution was plotted on the y-axis. The relationship was analyzed using linear regression to compute a regression coefficient (slope) and y-intercept. A t-test was used to determine if the slope differed from one and y-intercept differed from zero at $P<0.05$. Interpretation of the q-q plots and t-tests followed Post and Evans (1989), who described the results of various scenarios of overwinter growth and size-selective mortality.

For the length-frequency distributions, mean TL in the fall versus mean TL in the spring were analyzed with t-tests to determine if they were significantly different, and a Kolmogorov-Smirnov two-sample test was used to determine if the shape of the distributions were equal.

A winter severity index was calculated for each winter using the technique described by Hayse et al. (2000). Air temperature data was acquired from Ouray NWR to calculate daily average air temperature for each day; then average air temperature was subtracted from 0°C to determine number of freezing degree days for each day. Winter severity was computed by totaling the number of freezing degree days (accumulated freezing degree days, AFDD) for each winter period (November through March) (Hayse et al. 2000). The winter severity index was determined by the maximum AFDD that occurred during the winter; the greater the number, the more severe the winter.

Movement

Young-of-year Colorado pikeminnow marked on each sampling pass were used to study movement patterns. The 40-mile reach was divided into eight 5-mile sections. Different colors (i.e., red, orange, yellow, green) and mark locations (i.e., base of the anal fin, left or right side of the dorsal fin, posterior or anterior of the dorsal fin) were used to distinguish fish among sampling passes and 5-mile sections. The unique marks used to identify specific backwaters in the Ouray Backwater Complex in 1999 and 2000 are given in Table 1, and the marks used to identify 5-mile sections within the 40-mile reach are given in Table 2. When a fish was recaptured, the marks allowed identification of the section or backwater where that fish was originally captured and the number of days at large.

Histograms were developed to provide an overview of the longitudinal seasonal distributions of young-of-year Colorado pikeminnow captured within the 40-mile reach. In addition, the histograms also provided visual representations of year-to-year variation in numbers. Significant differences between the distribution of fish captured in fall and spring were analyzed with Kolmogorov-Smirnov two-sample tests.

Winter Sampling Under Ice

Each winter, two or three backwaters in the Ouray Backwater Complex were selected for under-ice sampling of young Colorado pikeminnow for the purpose of determining if the fish were using these habitats and if we could catch them. Selection criteria were based on accessibility and the presence of young Colorado pikeminnow during fall sampling. A number of sampling techniques were tried, including fyke nets, clover traps, minnow traps, and seines.

Four or five holes were made in the ice using an ice auger and chain saw. Minnow traps and fyke nets were placed near the mouth and mid-section of the backwater and left overnight. To increase capture efficiency, some traps were baited with Silver Cup Salmon Starter feed; some had a 12-V submersible green neon light placed inside (powered by 12-v battery attached to 61 cm cord); and some contained a combination of fish feed and neon light.

After fishing clover traps, minnow traps, and fyke nets overnight, two to three seine hauls were made underneath the ice. Seine hauls were made by first cutting with a chain saw two rectangular holes large enough to accommodate a seine; then drilling with an ice-auger a series of six to nine holes every 4.6 m on the left and right sides of the backwater; next threading nylon ropes under the ice between the holes using a 6-m polyvinyl chloride pole capped on each end (so it would float); finally, the seine was pulled the length of the backwater (32 to 41 m) and pulled out the rectangular hole at the tail end of the backwater (Figure 3); all fish captured were placed into a live well.

An Aqua-Vu® underwater camera was used to monitor fish presence and behavior under ice. The camera was connected to a video cassette recorder (VCR). The camera and underwater light was connected to a battery (12-V, 7.0 Ah); the battery (through a battery charger) and VCR were powered with a Honda® generator (model E6 1400X). The camera was placed in an ice hole and held approximately 0.3 m above the bottom. All equipment was placed under a dome tent. Fish activity was monitored for 6 to 8 h between 1400 h and 0900 h. One person re-visited the site around midnight and early morning to replace the video tape and refuel the generator.

Winter Habitat Descriptions

Within the Ouray Backwater Complex, two or three backwaters were chosen each year to describe winter habitat conditions. Each backwater had three to four Optic StowAway® temperature loggers placed into it before ice formation, and another logger was placed in the main channel. The temperature loggers were retrieved before spring runoff. A Trimble GeoExplorer II® Global Positioning System (GPS) unit was used to map the physical features of each backwater (e.g., area features). In addition, point features were located on each backwater. These point features represented temperature loggers, trap locations (i.e., fyke net, minnow trap, or clover trap), and locations of water velocity, water depth, and ice thickness measurements. Water velocity was measured with a Marsh-McBirney flow meter. All features collected with the GPS unit were downloaded onto a notebook computer using PathFinder Office® software to create uncorrected shape files. Although, selective availability of GPS satellites was not a factor in accuracy, we chose to differentially correct these files. Through PathFinder Office® and the internet, we used the Price, Utah, GPS base station to correct these data files. These corrected shape files were imported into ARC/View® to generate map images. The corrected shape files were overlaid onto digital orthophoto quarter quadrangles (DOQQ) to illustrate the backwater locations along the Green River and Ouray Backwater Complex.

Winter Flow Fluctuations

Three distinct flow regimes for winters 1999–2000, 2000–2001, and 2001–2002 were proposed to the Bureau of Reclamation to evaluate the effects of fluctuating flows on the physical morphology of nursery habitats (e.g., changes in area, water depth, velocity, ice cover) and fish inhabiting them. Flow regimes for the first year were not manipulated but instead considered a stable flow regime. The second winter called for a series of 5-d periods of daily fluctuations followed by a 9-d period of stable flows to produce river stage changes at Jensen Gage (#9261000) of 0.10, 0.20, and 0.30 m. The final year of the study proposed a 90-d period of flow fluctuations at a level shown to invoke fish movement. However, as explained in **Results**, these flows had to be modified considerably.

RESULTS

Field Catch Summary

Over the three year period of this study, a total of 732 young Colorado pikeminnow (30–100 mm) were captured, 404 were marked and released (fish captured on the last pass during spring sampling were not marked), and 38 fish were recaptured. In the autumn of 1999, we sampled the Ouray Backwater Complex. Three backwaters out of six contained age-0 Colorado pikeminnow. In one backwater (BA#1), 89 fish were captured, and in another (BA#2), 36 fish were captured. The following spring, just after ice-out, we again sampled the Ouray Backwater Complex. At that time, the complex contained seven backwaters, four with fish. In BA#1 we captured 28 fish, and in BA#2, we captured 30 fish (Tables 3 and 4).

In autumn of 2000, every backwater in the 40-mile reach was seined (first pass: 50 backwaters, 19 with young Colorado pikeminnow, 197 seine hauls; second pass: 49 backwaters, 16 with fish, 179 seine hauls). The two passes captured 114 age-0 Colorado pikeminnow. A third pass could not be made because early cold weather froze the backwaters for the winter (11 Nov), making them impossible to seine. In spring 2001 after ice out on 3 March, the 40-mile reach was again sampled (first pass: 32 backwaters, 13 with fish, 152 seine hauls; second pass 49 backwaters, 10 with fish, 210 seine hauls). Two passes captured 55 age-1 Colorado pikeminnow (Table 5).

In autumn of 2001, the backwaters in the 40-mile reach were again seined (first pass: 60 backwaters, 22 with young Colorado pikeminnow, 279 seine hauls; second pass: 50 backwaters, 14 with fish, 178 seine hauls; third pass: 39 backwaters, 10 with fish, 176 seine hauls). Three passes through the reach captured 102 age-0 Colorado pikeminnow. In spring 2002, the 40-mile reach was sampled (first pass: 41 backwaters, 21 with fish, 163 seine hauls; second pass: 49 backwaters, 41 with fish, 131 seine hauls); the two passes captured 278 fish (Table 6). Also captured in spring 2002 were 92 age-1 razorback sucker; 89 of these fish had a right pelvic fin clip, identifying them as hatchery fish stocked in October 2001; 3 had no fin clip and appeared to be wild fish (i.e., they were less robust and their keels were more prominent than the stocked fish). The length-frequency histogram for the razorback sucker catch is given in Appendix 1.

Catch Per Unit Effort and Abundance Estimates

Catch of young Colorado pikeminnow per seine haul in backwaters is summarized in Table 7. The highest CPUE was 2.36 fish per seine haul on the second pass for spring of 2002, and the lowest was 0.06 fish per seine haul for the same cohort the previous fall. The highest CPUE was associated with the highest main channel temperature, and in general we found that catch success was highly related to water temperature: warmer temperatures in the backwater caused more fish to congregate in the tail of the backwater and produced more successful seining. The CPUE for backwaters was highly variable, with CV ranging from 1.48 to 2.93.

This was the result of most backwaters not having any Colorado pikeminnow, some backwaters having a few, and a few backwaters having many (~200 fish) .

Abundance estimates are summarized in Table 8. These estimates were produced from the capture-recapture data in Tables 3–6 using the Darroch population estimator. Two kinds of population estimates were made, one for individual backwaters and one for the 40-mile reach. In the first year of the study (fall 1999, spring 2000), we concentrated our sampling in the Ouray Backwater Complex and made population estimates for two backwaters for the fall and spring. In BA#1, the estimate was 218 fish in the fall and 153 fish in the spring; in BA#2, the estimate was 87 fish in the fall and 115 fish in the spring. All these estimates were imprecise, with CV ranging from 0.22 to 0.83, the result of small numbers of captures and recaptures. The probability of capture for individual fish was highly variable, ranging from 0.01 to 0.32.

The second kind of abundance estimate was for the 40-mile reach. For the autumn of 2000, we estimated 735 age-0 fish in the reach, and for spring 2001, 260 age-1 fish. For autumn of 2001, the estimate was 670 age-0; for spring 2002, the estimate was 1,320. These estimates were also highly variable, with CV ranging between 0.25 and 0.59. The probabilities of capture ranged from 0.03 to 0.16. In general, the probabilities of capture were smaller for the 40-mile reach than for the individual backwaters, because far fewer seine hauls per backwater were made.

Overwinter Survival and Size-Selective Mortality

Overwinter survival estimates for the 40-mile reach could not be calculated because population estimates were too imprecise.   Two of four spring estimates were greater than the corresponding fall estimates. During 2000–2001 and 2001–2002, a total of 218 fish were marked in fall. Of these, none were recaptured the following spring.

Fall and spring length-frequency distributions were examined for evidence of size-selective mortality. In the first year, winter of 1999–2000, age-0 pikeminnow entered the winter with a mean length of 38.7 mm TL and ranged between 30 and 54 mm TL (Figure 4). At the end of winter, the mean length was similar (38 mm TL) to the previous fall (t-test, t=0.72, P=0.47). No fish >54 mm was captured in the fall or spring. The length-frequency distributions were also similar (Kolmogorov-Smirnov test, P>0.05, D_{max}=0.17, D=0.27; Figure 4), as were the cumulative length-frequency distributions (Figure 5) and the q-q plot (slope=1; Figure 6), suggesting no size-selective mortality or growth over the 1999–2000 winter period.

The winter duration for 1999–2000 was the shortest of the three years. Mean daily air temperatures declined and remained near or below freezing temperatures (0°C) from 30 November 1999 through 7 February 2000. The maximum number of freezing days was 153.6 and maximum AFDD was on 7 February 2001.

In the second year of the study (winter 2000–2001), age-0 fish captured in the fall of 2000 were much larger (mean=52.2 mm TL) than those captured the fall 1999 (mean=38.7 mm TL). Fish lengths for fall of 2000 ranged from 30 to 84 mm TL. The following spring, mean length increased to 57.5 mm TL, indicating significant difference between seasons (t-test; t=-3.65, P<0.05). The length-frequency distributions were also significantly different (Kolmogorov-Smirnov test, P<0.05, D_{max}=0.25, D=0.02; Figure 7). There was a distinct upward shift in length-frequency with some mortality evident at the tail end of the curve. The relative abundance of small fish (<54 mm) diminished overwinter. The cumulative length-frequency distributions (Figure 8), and the q-q plots (slope < 1) also indicated size-selective mortality on smaller individuals (<50 mm TL) over the winter 2000–2001 (Figure 9).

The 2000–2001 winter was intermediate in severity among the three years. Mean daily air temperatures declined and remained near or below freezing temperatures (0°C) from 10 November 1999 to 18 February 2000. The maximum number of freezing degree days was 429.2, and maximum AFDD occurred on 18 February 2001.

In the final year of sampling (winter 2001–2002), size-selective mortality was more evident, because there were more large fish going into the winter. Age-0 Colorado pikeminnow entered the 2001–2002 winter at a larger size (mean=55.3 mm TL). There was a much wider size distribution of fish, ranging from 30 to 89 mm TL (Figure 10). The length-frequency displayed a bi-modal distribution with two intermediate peaks toward the tail. The following spring, mean length of Colorado pikeminnow (mean=74.4 mm TL) was significantly greater than in the fall 2001 (t-test; t=-13.86. P<0.05). Size distributions in spring ranged from 40 to 104 mm TL. Length-frequency distributions between fall and spring were also significantly different (Kolmogorov-Smirnov test, P<0.05, D_{max}=0.58, D<0.05; Figure 10). The length-frequency histogram in the spring displayed a shift in size-class distributions to larger fish. The cumulative length-frequency (Figure 11) and the q-q plot (b < 1) indicated size-selective overwinter mortality for smaller individuals (Figure 12). Fish in size-classes <39 mm were absent from spring sampling and possibly suffered a high level of mortality. The relative abundance of fish in size classes 40-59 mm also decreased from fall to spring. The most likely cause of this shift was size-selective mortality; fish growth, however, cannot be completely ruled out, but we expect it would be small between November and April.

Winter severity was greatest for 2001–2002. Mean daily air temperatures dropped and remained near or below freezing from 24 November 2001 through 5 March 2002 and again from 14 March through 19 March 2002. The maximum number of freezing degree days was 731.9, and maximum AFDD occurred on 5 March 2002.

Age-0 Colorado Pikeminnow Movement

Individual Fish Movement.- Young Colorado pikeminnow recapture data for the Ouray Backwater Complex for fall of 1999 and spring 2000 are given in Table 9. Of 18 fish marked and recaptured within fall or spring sampling, 17 were recaptured within the backwater of origin, one fish moved upstream 3 miles. These fish were at large for 5–42 d. Fourteen fish that were marked in fall 1999 were recaptured in spring 2000; 12 were recaptured in the same backwater from which they were originally captured, one moved downstream 3 miles, and one moved upstream 3 miles. These fish had been at large for 127–149 d.

Colorado pikeminnow recaptures for the 40-mile study reach are given in Table 10. All of these recaptures occurred within either fall or spring sampling period. Of 13 recaptured fish that we could identify the backwater from which they were originally marked, 12 were recaptured within 0.6 mile of backwater of origin, and one moved downstream 2.6 miles. For two other fish we could not identify their exact backwater of origin, but at most one fish moved downstream 4.1 mile and the other upstream 1.1 mile. These fish were at large for 5 and 10 d, respectively.

Longitudinal Fish Distribution.- In the 40-mile study reach we looked at change in longitudinal fish distribution between fall and spring. In 2000–2001, no change was detected (Kolmogorov-Smirnov test, $P>0.05$; $D_{max}=0.25$, $D=0.91$; Figure 13). But in 2001–2002, the distribution shifted slightly downstream between fall and spring (Kolmogorov-Smirnov test, $P<0.05$; $D_{max}=0.96$, $D=0.000006$; Figure 13); in the fall 2001, the three uppermost 5-mile sections contained 65% of the catch, while in the spring 2002, the same three sections contained only 37% of the catch.

Winter Fish Sampling

Over the three year study period, minnow traps, fyke nets, clover traps and seines were used to collect fish under the ice in backwater habitats. Gear efficiency varied from winter to winter. Non-native fishes, such as sand shiners *(Notropis stramineus)* , red shiners *(Cyprinella lutrensis)*, and fathead minnows *(Pimephales promelas),* were the most abundant fishes captured. Very few native fishes, such as flannelmouth sucker *(Catostomus latipinnis)* and Colorado pikeminnow, were captured. One young-of-year Colorado pikeminnow was captured under the ice with a seine at Greasewood Corral backwater during 1999–2000 winter. Seining under the ice was ineffective and difficult for a couple of reasons. First, the seine floated against the bottom layer of ice and could not reach the bottom in the deepest portions of the backwater. Second, the seine got caught up in wood debris piles and was difficult to haul. Other gear types, including combinations with bait and light, were also ineffective in capturing young-of-year Colorado pikeminnow, but they were marginally effective at catching red shiners, fathead minnows, and sand shiners. Bait and light apparently were not helpful. Minnow traps were the least effective, catching only one green sunfish *(Lepomis cyanellus)*.

During 2001–2002 winter, an Aqua-Vu® underwater camera was setup at two backwaters to monitor fish activity. The camera was setup on five occasions between 27 February and 1 March at various time intervals at Johnson Bottom backwater. Twenty-nine hours of video footage was recorded, and 144 fish were counted. Some fish may have been counted more than once if they disappeared from the screen and then reappeared. The fish included a white sucker and numerous small cyprinids (i.e., red shiners, sand shiners, and fathead minnows). Fish were swimming above and along the substrate. On several occasions, fish were observed staging in a depression in the substrate. More fish were counted at night.

The camera was also set up on five occasions between 21 and 23 February 2002 at Greasewood Corral backwater. Water temperatures were slightly warmer in this backwater than in the Johnson Bottom backwater. Twenty-six hours of video footage was recorded, and 1,973 fish were counted. The average count rate was 1.3 fish per min. Small and large cyprinids (i.e., red shiners, sand shiners, fathead minnows) of various sizes (i.e., juveniles and adults) were more abundant than in the Johnson Bottom backwater. An occasional flannelmouth sucker and one suspect young-of-year Colorado pikeminnow were observed. All fish were swimming in the water column and not associated with the substrate. Fewer fish were counted during the day (1600 h to 2000 h) than the night (after 2000 h). On one occasion, video footage was recorded from 0520 h to 0719 h; 59 cyprinids were counted between 0520 h and 0604 h, and for the next hour, only 9 cyprinids were counted.

Winter Habitat Descriptions

Three backwaters were selected in the Ouray Backwater Complex during 1999–2000 for winter habitat description. The first was located at RM 252.8 near Greasewood Corral. It was 0.19 ha, and water depth averaged 0.9 m, ranging from 0.4 (mouth) to 2.1 m (tail). Three temperature loggers were placed in the backwater: at the mouth, mid-section, and tail. The second backwater, 0.40 has, was located above Old Charlie Wash outlet at RM 250.6. Two temperature loggers were placed in it, at the mouth and mid-section. The third backwater was located near Ouray National Fish Hatchery at RM 261.3. No temperature loggers were installed in this backwater.

On 10 January 2000, we noted that an ice jam had formed at the Ouray bridge and backed up water several miles upstream. River stage elevations increased from 0.75 to 1.50 m and turned all backwater habitats into flow-through areas. Also, a side channel near the hatchery backwater was flooded to depths of 0.45 to 0.61 m; originally, this channel was dry. By 18 January, the ice jam had broken and stage elevation had fallen back to the previous level. No water was flowing through the side channel near the hatchery backwater. All three flow-through areas returned to backwater habitats. The ice cover on the backwaters now consisted of two layers of ice (11 and 18 cm thick) separated by a free flowing water layer (17 cm). The ice jam episode resulted in loss of all temperature loggers and two staff gauges.

During 2000–2001 winter, three more backwaters were selected in the Ouray Backwater Complex for habitat description. All temperature loggers were placed in the backwaters on 22 December 2000. The first backwater was located near the Ouray National Fish Hatchery at RM 261.3. The backwater was 0.49 ha, and no temperature logger was placed in it. The second backwater was near Leota Bottom at RM 258.1. This backwater was 0.24 ha. Temperature loggers were placed at the mouth and tail of the backwater and in the main channel (Figure 14). Water temperatures at the mouth and tail of the backwater were much warmer compared to the main channel. Mean daily water temperatures reached freezing at the tail 24 December and the mouth 29 December 2000, and they remained near or below freezing until 7 March at the mouth and 3 January 2001 at the tail. Main channel temperatures rose above freezing after 27 February 2001. The third backwater was above Old Charlie Wash outlet at RM 250.6. It was 0.18 ha. Two temperature loggers were placed in this backwater: one at the mouth and one at the mid-section. However, after ice development, the temperature logger at the mouth was inundated by river-ice and lost. Water temperatures at the mid-section were much warmer compared to the main channel (Figure 15). Mid-section mean daily water temperatures did not reach freezing until 6 January 2001 and lasted until 6 March 2001. Main channel temperatures did not rise above freezing until after 27 February 2001. Unfortunately, the field notebook containing all descriptive data such as water depth, velocity, and ice thickness was lost.

During 2001–2002 winter, four backwaters were selected for habitat description. But physical dimensions and capture effort were documented for only two of the four sites. The first backwater was below Johnson Bottom at RM 260.4. This backwater was 0.10 ha. Four temperature loggers were installed in the backwater on 22 November 2001. The temperature logger between the tail and mid-section (3/4 of the distance from mouth to the tail) was lost when we accidently cut the cord with an ice auger. Mean daily water temperatures reached freezing on two different dates (Figure 16). The main channel and mouth of the backwater reached freezing on 28 December 2001 and remained that way until 11 March 2002. The tail and mid-section temperature loggers indicated freezing temperatures were reached on 29 November 2001. The mid-section rose above freezing after 10 March 2002, while the mean daily temperatures in the tail did not rise above freezing until after 18 March 2002. Average total depth (i.e., ice thickness plus standing free water) was 1.4 m and ranged from 0.68 to 1.95 m. Average water velocity in the eddy at the mouth of the backwater was 0.07 ft/s. Average ice thickness was 56 cm and ranged from 44 to 70 cm. Ice was thicker from the mid-section to the tail of the backwater. Average depth of standing free water was 0.84 m and ranged from 0.08 to 1.47 m. Standing free water was more available from the mid-section to the mouth of the backwater. The second backwater was at RM 252.8 near Greasewood Corral. It covered 0.34 ha. Four temperature loggers were installed on 21 November 2001. The temperature logger placed between tail and mid-section (i.e., 3/4) was destroyed by the ice auger. Mean daily water temperatures in the backwater reached freezing on three different dates (Figure 17). The tail reached freezing temperatures on 29 November 2001 and lasted until 21 March 2002. The temperature logger at the 3/4 section reached 0 ºC on 4 December. The main channel, mouth, and 1/4 section reached freezing temperatures on 28 November 2002. Both main channel and mouth temperatures rose above freezing on 10 March 2002, while the 1/4 section rose above freezing on 19 March 2002. Average depth (includes ice thickness and standing free water) was 86.25 cm and ranged from 56 to 172 cm. The only detectable water velocity was near the mouth at the backwater-main-channel eddy, where velocity ranged between 0.26 ft/s and 2.9 ft/s. Ice thickness averaged 51.8 cm and ranged from 37 cm to 64 cm. Average depth of standing free water was 34.4 cm and ranged from 4 cm to 122 cm. The last two backwaters (BA#1 and BA#2) were located at RM 251.7 and RM 251.6. Temperature loggers were placed at tail, 3/4, 1/4, and main channel for each of these backwaters (Figures 18 and 19). Finally, to illustrate the mean daily air temperature and mean daily main channel river temperature relation at the Ouray NWR, we offer Figure 20.

Winter Flow Fluctuations and Temperatures

The original study design called for three distinct flow regimes for the winters 1999–2000, 2000–2001, and 2001–2002. The first year was to be a stable flow regime. The second year was to be a series of 5-d periods of fluctuating flows to produce river stage changes at the Jensen Gauge of 0.1, 0.2, and 0.3 m followed by 9-d periods of stable flows. The third year was to be a 90-d period of flow fluctuations at a level shown to invoke fish movement. The planned Flaming Gorge Dam releases were not acquired, in part because of the national energy emergency during the winters of 2000–2001 and 2001–2002, and in part because there were not enough young-of-year Colorado pikeminnow to determine a response. Hence, we worked with the fluctuations provided during the normal Flaming Gorge Dam hydropower generation.

Among the three winter periods, flows varied considerably from year to year (Figure 21). The first winter (1 October 1999–28 February 2000), average daily flow at the Jensen gage was 2,563 cfs and ranged from 2,180 to 3,080 cfs. Within day flow fluctuations produced stage changes at the Jensen gage averaging 0.100 m (SD=0.037). The greatest flow and stage change occurred between 12 January 2000 and 3 February 2000. Mean discharge increased from 2,440 cfs to 3,080 cfs (between 12 and 26 January 2000) and declined to 2,450 cfs by 3 February 2000. From 12 January to 26 January 2000, stage rose 0.2 m. From 26 January to 3 February 2000, the stage gradually declined 0.24 m (Figure 22). Over the length of the winter period, the maximum stage change (i.e., difference between highest stage and lowest stage) was 0.40 m.

Mean daily river temperatures recorded from Ouray NWR during the first winter ranged from -0.06 °C to 14.2 °C. The temperatures reached freezing (0 °C) on 11 December 1999 and remained below freezing until 13 January 2000, a total of 32 days.

Winter flows for 2000–2001 were reduced by about 46% compared to 1999–2000 winter. Average daily discharge was 1,436 cfs, ranging between 1,250 and 1,570 cfs. Within day stage fluctuations averaged 0.050 m (SD=0.048). Occasional flow and stage increases occurred during the winter; mean daily flow increased by 160 cfs between 08 December and 16 December 2000, producing a stage rise of 0.14 m, then gradually descended 0.17 m (Figure 22). From 17 December 2000 until 2 February 2001, daily average flows fluctuated between 1,330 cfs and 1,470 cfs. Over the winter period, the maximum stage change was 0.78 m.

Mean daily river temperatures during winter of 2000–2001 ranged from -0.54 °C to 15.76 °C; temperatures were below freezing for 107 days, from 13 November 2000 to 27 February 2001.

During the 2001–2002 winter, flows receded by about 14% compared to the 2000–2001 winter. Average daily discharge was 1,222 cfs, and ranged between 991 and 1,400 cfs. Within day stage changes averaged 0.049 m (SD=0.074). Two notable stage increases were recorded at the Jensen gage. Between 24 December 2001 and 10 January 2002, stage level rose 0.65 m, then decreased 0.64 m. Another stage fluctuation occurred between 26 January and 21 February 2002. Stage levels increased from 0.73 m (26 January 2002) to 0.98 m (28 January 2002), an increase of 0.25 m. Stage levels remained at or above 0.91 m until 17 February 2002 before dropping to 0.69 m, a decline of 0.22 m. In both instances, mean daily discharge did not increase with stage fluctuations; the stage changes were apparently the result of ice jams downstream (Figure 22). Over the winter period, the maximum stage change was 0.88 m.

Mean daily main-channel water temperatures over the winter of 2001–2002 ranged between -0.14 and 18.63 °C. Temperatures did not reach freezing until 28 November 2001 and remained below freezing until 10 March 2002, a total of 102 d.

DISCUSSION

Population and Overwinter Survival Estimates

The Darroch population estimator has several assumptions: 1) the population is closed, 2) marks are retained for the duration of the study, 3) marks are correctly identified and recorded, 4) capture and marking do not affect probability of recapture, and 5) capture probabilities vary on each sampling pass (Otis et al. 1978). We believe that these assumptions were, for the most part, met for the autumn and spring population estimates.

Population closure is supported for the 40-mile study reach because two or three passes were completed within 18 d, a period too short for substantial recruitment (by growth or immigration), mortality, or emigration. The data from this study and from a similar study (Haines et al. 1998) showed that fish moved only small distances during this time.

Another issue related to closure is whether young-of-year Colorado pikeminnow are found only in backwater habitats. Tyus and Haines (1991) found that for September and October seining in the Green River nursery area, based on catch per 100 m^2 seined, 84% of the catch was from backwaters, and the remaining catch mostly from shallow shoreline and side channel habitats. If there is a subpopulation of fish that live outside of backwater habitats and do not mix with the fish in backwaters, then these fish would not have been sampled and the estimator would be biased too low. It is known, however, that age-0 Colorado pikeminnow move in and out of backwaters in response to diel temperature fluctuations (Haines et al. 1998, Tyus 1991). If there is a mixing of fish moving in and out of backwater habitats, as we believe, then the assumptions of the estimator hold.

Laboratory studies by Haines and Modde (1996) provide evidence that the second and third assumptions are met. They found that when the elastomer was used to mark age-0 Colorado pikeminnow, 98% of the fish retained their marks for at least 21 d. The elastomer did not appear to be degraded by environmental conditions overwinter; marks retained their color and were easily recognized.

The fourth assumption, that capture and marking did not affect probability of capture, is the assumption of most concern. Haines and Modde (1996) monitored survival of marked fish held in the laboratory and found no post-marking mortality after 21 d. In addition, they made extensive field observations on marked fish held overnight in enclosures, and survival averaged 95%. Haines et al. 1998 also held marked fish overnight in enclosures and, after discounting enclosure-induced mortality, observed 95% survival. Although we did not hold fish in enclosures overnight in this study, we used the same marking and recovery techniques as in the previously cited studies and believe our results are comparable. We did not attempt to correct our estimates for tag mortality.

The fifth assumption, capture probabilities vary on each sampling pass, characterizes the Darroch estimator. Our experiences have shown that varying environmental conditions, especially temperature, affect capture probabilities (Haines et al. 1998). Backwater temperatures can range from 13ºC down to 5ºC on subsequent passes, profoundly affecting fish behavior and capture probabilities from pass to pass.

Although we are confident that the five assumptions are mostly valid for population estimates for the 40-mile reach, we are far less confident of their validity for individual backwater estimates, like for BA#1 and BA#2 in autumn 1999 and spring 2000. The chance that a significant number of fish move into and out of the backwater during the 2- or 3-week sampling duration is too great to have much confidence that the first assumption holds, although the estimates are probably in the proper order of magnitude.

The greatest disappointment regarding our population estimates for the 40-mile study reach is the imprecision, where CV's ranged from 0.25 to 0.59. The imprecision is the direct result of not catching, marking, and recapturing enough fish. For example, in this study our autumn 2000 and 2001 catches averaged 46 fish per pass in a 40-mile reach, whereas in the Haines et al. (1998) study, autumn catches averaged 220 fish per pass in a 10-mile reach in 1992 and 536 per pass in a 20-mile reach in 1993; for these two estimates, CV < 0.15. Indeed, the reason our study reach was 40 miles long was to assure that we could catch and mark enough fish for relatively precise population estimates. The reason for poor catches in 2000 and 2001 apparently was low population densities. This study estimated 26 fish per mile compared to 277 fish per mile for 1992 and 1993. Finally, ISMP fall young of the year seining showed that 1999–2001 averaged 0.03 fish per 10 m^2 seined (range 0.02-0.05) (personal communication, C. McAda , USFWS, and R. Brunson, UDWR), whereas 1986–1998 catch rate averaged 0.34 fish per 10 m^2 seined (range 0.03-1.17; McAda et al. 1997). The average catch rate was over 10 times as great for the 13 years prior to our study compared to the 3 years during our study.

We could not estimate overwinter survival because the population estimates of fall and the following spring were too imprecise. One of the objectives in this study was to evaluate the assumption of geographical closure between autumn and spring, i.e., that there is minimal immigration and emigration of young Colorado pikeminnow to and from the 40-mile river reach. We found age-0 fish that were marked in autumn and recaptured the following spring generally moved less than 10 miles downstream after being at large for 170 to 200 d. This is in accordance with what Haines et al. (1998) found in the 20-mile reach upstream. Our opinion is that this rate of movement between autumn and spring may bias the overwinter survival estimate only slightly for a 40-mile reach but it could be a problem for reaches < 40 miles long.

Comparison of age-0 Colorado pikeminnow length-frequencies collected in the fall with those collected from the same cohort the following spring showed evidence of size-selective mortality, and the degree of this mortality was correlated with winter severity, although our study was only for three years. Among the three winter periods, the 1999–2000 winter was the mildest, and no overwinter size-selective mortality was observed. The 2000–2001 winter was intermediate in severity, and overwinter mortality occurred, but it was not strong. The 2001–2002 winter had the greatest severity and the greatest size-selective mortality. Others have also reported size-selective overwinter mortality for young Colorado pikeminnow (Converse et al. 1997, McAda and Ryel 1999, Thompson et al. 1991). Higher survival of large fish was presumably the result of more fat reserves (Thompson et al. 1991, Beyers and Plampin 2004), and size at the end of the growing season may have been the result of arrival date in the nursery habitat (i.e., early spawning date resulting in longer growing season) and summer water temperatures (Bestgen et al. 1997), but habitat availability and food abundance may also have been important (Tyus and Haines 1991).

Winter Movement

Young Colorado pikeminnow moved only short distances both within autumn and spring sampling and between autumn and spring sampling. Within autumn and spring sampling, 95% of the recaptured young Colorado pikeminnow were within the same 5-mile section where they were originally marked. One fish moved downstream 2.6 miles into the adjacent section. Of the recaptured fish that we could determine the backwater of origin, 68% were captured in the backwater of origin, 94% were captured within 0.6 miles of the backwater of origin, and all were captured within 3 miles of the backwater of origin. These fish were at large between 5 and 42 d. Haines et al. (1998) found a similar pattern, where 99% of the recaptured fish were in the 5-mile section. This data gives us confidence that our assumption of geographic closure is valid.

Overwinter movement (between autumn and spring sampling) was about 3 miles or less. Of 14 fish that were marked in the autumn and recaptured the following spring, 13 were recaptured in the same backwater and one fish was recaptured upstream 3 miles. Haines et al. (1998) found that 73% of their age-0 Colorado pikeminnow that were marked in autumn and recaptured the following spring were in the same 5-mile section where they were originally captured; 27% of the recaptures moved downstream only short distances; and one fish moved 4.6 miles upstream. We point out, however, that most of the fish we captured were caught in the downstream portion of the 40-mile study reach, and therefore we only sampled approximately 3 to 6 miles downstream from most marked fish, possibly underestimating the amount of downstream movement. Nevertheless, the evidence thus far suggests that most young Colorado pikeminnow move less than 6 miles during the winter period.

Although young Colorado pikeminnow do not make long-distance movements during the 5–30 d sampling periods, they apparently do make local movements on a diel basis in response to environmental conditions. The relatively low probability of capture for each sampling pass suggests that only a small fraction (<5%) of the population of young Colorado pikeminnow within the study reach were captured on each sampling occasion. We suspect that the small fraction of fish captured is the result of movement in and out of backwaters in response to diel temperature fluctuation. Our observations suggest that the fish were more likely to be caught in backwaters in the afternoon when water temperatures were warm, compared to the morning when water temperatures were cooler. Tyus (1991b) studied movements of young Colorado pikeminnow in the Green River during autumn and spring and found similar patterns. He reported that abundance in backwaters varied on a diel basis that was directly related to backwater temperature and inversely related to temperature of the main channel. He also observed that young Colorado pikeminnow were capable of local movements between a variety of habitats including backwaters, eddies, and other shoreline habitats, and the fish were able to cross the main channel without being transported downstream. Despite a high degree of local movement, some fish remained near the area where they were originally marked for a least one month (Tyus 1991b).

We hypothesize that age-0 Colorado pikeminnow exhibit an adaptive behavior wherein in the summer and early fall they occupy backwater nursery habitats that provide refuge from the current, preferred thermal conditions, and a productive environment where prey are likely to be encountered (Tyus and Haines 1991). At this time the fish are widely distributed in the nursery area in deep and shallow backwaters. But as temperatures cool in the fall, the shallower backwaters become cooler than the main channel, even during the warmest part of the day, and the fish tend to move downstream and congregate in the deepest and largest backwaters where temperatures at the mouth of the backwaters do not fall below the main channel temperature. It is in these large, deep backwaters that the fish apparently overwinter (Haines and Tyus 1990, Tyus and Haines 1991, Day et al. 1999). Occasionally during the winter, the river stage increases, usually the result of an ice jam, and turns a backwater into a flow-through area. Some fish respond by moving out of the area in search of nearby low-velocity habitats, but others respond by finding low-velocity micro-habitats within the area of the original backwater, perhaps behind uneven bottom contours. After ice-out and spring runoff begins, more backwaters become flow-through areas, resulting in fish movement downstream.

Effects of Fluctuating Discharge from Flaming Gorge Dam on Overwinter Survival

We were unable to test whether fluctuating flows from Flaming Gorge Dam influenced overwinter survival, primarily because there were too few age-0 Colorado pikeminnow in our study reach to make overwinter survival estimates, and secondarily because we could not obtain the winter flow fluctuations we needed to demonstrate the relation. However, we offer the following discussion based on our findings and other more circumstantial evidence of this relation.

Overwinter survival during first year of life is a primary factor determining year-class strength of most temperate zone fishes (Garvey et al. 1998), including Colorado pikeminnow Thompson et al. 1991, Haines et al. 1998). Winter is a period of reduced growth, depletion of energy, and heightened mortality risk. Small changes in the rate of growth or mortality of larvae and juveniles have been shown to substantially impact population recruitment (Houde 1987). Winter mortality is often size-selective because mortality generally removes small individuals with low energy reserves (Oliver et al. 1979; Tony and Coble 1979; Shuter et al. 1980; Post and Evans 1989; Schindler 1999; Thompson 1989). For larval and juvenile fish, achieving a threshold size gives many advantages during a time when mortality is typically high, including reduction of predation risks through improved swimming ability, higher prey capture rates, and lower probability of starvation (Garvey et al. 1998).

This study was unable to show whether or not typical winter flow operations at Flaming Gorge Dam to meet hydropower needs influenced overwinter survival of young Colorado pikeminnow. Several investigators have hypothesized that winter operations of Flaming Gorge Dam reduce age-0 fish survival because fluctuating discharge and associated changes in water surface elevation modify the characteristics of nursery habitats which causes an increase in fish activity (Carlson and Muth 1989; U. S. Fish and Wildlife Service 1992; Valdez et al. 1999; Haines et al. 1999). A 24-hour hydropower release from Flaming Gorge Dam during this study usually fluctuated about 600 to 800 cfs, producing stage changes at the Jensen gage of <0.1 m (93 miles downstream of Flaming Gorge) and about <0.01 m at the Ouray bridge. These stage changes had only minimal affect on backwater habitats and were limited to the upper end of the nursery area. These flow fluctuations did not alter physical morphology of backwaters studied in the Ouray Backwater Complex. However, the formation of ice jams, as observed in the 1999–2000 winter, had far greater affect on backwater nursery areas, increasing stage by 0.75-1.50 m, and resulting in the transformation of many backwater habitats into flow-through areas.

The role of fluctuating winter flows from Flaming Gorge Dam in the creation of ice jams is unclear to us. Valdez and Cowdell (1999) speculated that fluctuating winter flows may dismantle ice cover which acts an insulator, allow the creation of frazil ice, and may result in ice jams. Hayse et al. (2000), however, found that fluctuating winter flows from Flaming Gorge Dam during the winter of 1996–1997 did not dismantle ice cover or promote formation of frazil ice and ice jams. Whatever the cause, it is likely that ice jams form at several locations on the middle Green River nursery area in most years (Valdez and Cowdell 1999; Hayse et al. 2000).

As a result of stage changes, ice jams, and frazil ice formation, young fish redistribute to more suitable habitats. Young Colorado pikeminnow prefer low-velocity backwater habitats (Tyus and Haines 1991), and when these habitats are inundated, the fish abandon them and move to other low-velocity habitats, sometimes to other backwaters several miles away and sometimes to low-velocity micro-habitats within close proximity of the inundated backwater from which they re-inhabit the backwater once the stage recedes. Other riverine fishes have been documented to behave similarly. In response to ice formations that reduces physical space and changes depth and velocity, Atlantic salmon *(Salmo salar)* young-of-year redistributed to find suitable depth and velocity habitat (Whalen et al. 1999). Whalen et al. (1999) found that young Atlantic salmon exhibited a combination of strategies, first movement and then fidelity, suggesting an integration of strategies for winter survival.

When nursery habitats are inundated and transformed into flow-through environments, resident fish are flushed into the surrounding system and incur increased risk of injury, predation, and metabolic costs associated with the search for another suitable nursery area. Winter survival of small fish is related to their ability to accumulate energy reserves (Oliver et al. 1979; Shuter and Post 1990). Small fish are at a disadvantage because basal metabolism increases as size decreases, but there is no corresponding increase in energy storage capacity. Mortality of young Colorado pikeminnow during winter has been attributed to exhaustion of lipid reserves (Thompson et al. 1991). Body weight and condition decline faster when fish activity is increased because energetic reserves must be used to offset the cost of higher metabolic rate. The result may be higher overwinter mortality.

Winter sampling for age-0 Colorado pikeminnow

Prior to ice formation, the most effective method for catching age-0 Colorado pikeminnow was seining. Seining was most effective when backwaters were warm and became less efficient as temperatures cooled. Colorado pikeminnow that occupied backwaters on the first pass during autumn sampling often vacated them prior to subsequent passes, especially when slush ice was found in the backwaters. Haines et al. (1998) found fewer fish were likely to be caught during relatively cool environmental conditions. During cool conditions (<10ºC), large seines showed promise for sampling large, deep (1.8 m) backwaters, especially at the mouth. But the large seines were often difficult to handle, and sampling became restricted to one or two sites per day. Fyke nets, minnow traps, clover traps, and seines caught many non-target fish, but not Colorado pikeminnow.

During ice cover, all gear types were ineffective for capturing age-0 Colorado pikeminnow. Baiting the traps and using a neon lights did not increase the catch of young Colorado pikeminnow. Over the three year study period, only one young-of-year Colorado pikeminnow was captured under ice with a seine. But seining under the ice was very laborious, and effort was limited to one to three seine hauls per day. Most time and effort was spent cutting and removing ice within a backwater. Preparation for a seine haul took about 1.5 days.

The most efficient technique for under-ice sampling was the use of an underwater camera and video cassette recorder. The equipment could be set up at various locations in the backwater. The underwater camera allowed us to observe diurnal, nocturnal, and crepuscular fish activity. Fish could be observed swimming in the water column or staging along the substrate. The total number of fish could be counted over a 6- to 8-h time frame. The information recorded, such as fish activity and temperature, is a representation of actual events occurring in the field. Swimming speeds and activity levels could be determined and possibly integrated into bioenergetic models. Ideally, most species and age-classes (i.e., juvenile or adult) could be identified in the video. Suckers and small cyprinids were easily identified. One or two suspected young-of-year Colorado pikeminnow were observed. To overcome the uncertainty of pikeminnow identification by videography, one might collect some age-0 pikeminnow of various sizes and video-record them. From this information, physical characteristics can be documented. Another concern using an underwater camera was that the same fish may be counted more than once. Repeated counts can inflate the total number of fish actually present. To deal with this concern, one approach would be to place traps near the vicinity of underwater camera over a 24-h period. Afterward, the number of fish captured in the trap could be correlated with the number of fish observed to derive a correction factor. The correction factor applied to the number observed may provide a better representation of the number of fish actually present. And finally, one would have to take into account that fish may be attracted to the light and this could affect fish behavior in an unnatural way.

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Table 1. Unique marking locations for young-of-the-year Colorado pikeminnow to identify specific backwaters in the Ouray Backwater Complex, 1999 to 2000.

River Mile	Marking Locations	Color	Date
255.0	Anal	Green	02/23/00
252.5	Left dorsal, anterior	Orange	11/03/99
	Left dorsal, anterior	Red	11/08/99
	Left dorsal, anterior	Green	02/23/00
	Left dorsal, posterior	Green	03/14/00
	Right dorsal, posterior	Green	03/29/00
249.8	Right dorsal, anterior	Orange	11/04/99
	Right dorsal, anterior	Red	11/09/99
	Right dorsal, anterior	Green	02/29/00
	Anal	Green	03/29/00
	Left dorsal, anterior	Yellow	04/05/00
249.4	Anal	Green	02/29/00
248.3	Left dorsal, anterior	Green	03/01/00

Table 2. Marking locations for young-of-year Colorado pikeminnow in the 40-mile study reach.

River Mile	Marking Locations
289–284	Left dorsal, anterior + anal
284–279	Left dorsal, posterior + anal
279–274	Right dorsal, anterior + anal
274–269	Left dorsal, anterior
260–264	Left dorsal, posterior
264–259	Right dorsal, anterior
259–254	Right dorsal, posterior
254–247	Anal

Table 3. Capture-recapture data [a] for autumn 1999 and spring 2000 for BA#1, Green River, Ouray National Wildlife Refuge, RM 252.5.

Dates	j	M(j)	m(j)	u(j)	N	MC(C°)	BA(C°)
				Autumn 1999			
11/03	1	0	0	59	1	7.1	7.0
11/05	2	59	4	7	1	6.9	---
11/08[b]	3	66	9	23	1	7.0	---
				Spring 2000			
2/23[c]	1	0	0	1	1	4.9	5.9
3/14	2	1	0	21	1	8.1	7.4
3/29	3	22	1	6	1	10.4	10.4

[a] j = sample occasion, M(j) = number of marked fish prior to sample, m(j) = number of marked fish caught, u(j) = number of unmarked fish caught, N = number of backwaters or low velocity sites sampled, MC = average main channel temperature, BA = average backwater temperature.
[b] 2 mortalities on the 3rd pass, 1 while seining and 1 after marking.
[c] 1 mortality on the 1st pass.

Table 4. Capture-recapture data [a] for autumn 1999 and spring 2000 for BA#2, Green River, Ouray National Wildlife Refuge, RM 250.6.

Dates	j	M(j)	m(j)	u(j)	N	MC(C°)	BA(C°)
			Autumn 1999				
11/04	1	0	0	26	1	6.9	5.3
11/09	2	26	4	10	1	7.4	7.9
			Spring 2000				
2/23	1	0	0	2	1	5.5	10.0
3/14[b]	2	2	0	14	1	7.7	13.2
3/29	3	16	2	14	1	10.4	13.2

[a] j = sample occasion, M(j) = number of marked fish prior to sample, m(j) = number of marked fish caught, u(j) = number of unmarked fish caught, N = number of backwaters or low velocity sites sampled, MC = average main channel temperature, BA = average backwater temperature.
[b] 2 mortalities on the 2^{nd} pass, 1 while seining and 1 after marking.

Table 5. Capture-recapture data [a] for autumn 2000 and spring 2001, Green River, 40-mile reach.

Dates	j	M(j)	m(j)	u(j)	N	MC(C°)	BA(C°)
			Autumn 2000				
10/17-10/23	1	0	0	73	50	10.1	12.6
10/25-11/03	2	73	2	41	49	9.1	11.3
			Spring 2001				
3/07-3/16	1	0	0	42	32	6.9	---
3/16-3/21	2	42	2	13	49	6.6	—

[a] j = sample occasion, M(j) = number of marked fish prior to sample, m(j) = number of marked fish caught, u(j) = number of unmarked fish caught, N = number of backwaters or low velocity sites sampled, MC = average main channel temperature, BA = average backwater temperature.

Table 6. Capture-recapture data [a] for autumn 2001 and spring 2002, Green River, 40-mile reach.

Dates	j	M(j)	m(j)	u(j)	N	MC(C°)	BA(C°)
			Autumn 2001				
10/24-10/30	1	0	0	55	60	8.4	---
10/31-11/02	2	55	2	30	50	10.0	---
11/05-11/09	3	85	0	17	39	8.8	---
			Spring 2002				
3/25-4/03	1	0	0	74	41	7.1	13.5
4/04/4/11	2	74	12	204	49	11.6	15.2

[a] j = sample occasion, M(j) = number of marked fish prior to sample, m(j) = number of marked fish caught, u(j) = number of unmarked fish caught, N = number of backwaters or low velocity sites sampled, MC = average main channel temperature, BA = average backwater temperature.

Table 7. Catch per unit effort (CPUE)[a] of young Colorado pikeminnow for backwaters in the 40-mile study reach, 1999–2002.

Season/year	Pass	CPUE	CV	Number of seine hauls	Number fish
Autumn 99		1.12	1.48	73	142
Spring 00		0.32	1.65	75	127
Autumn 00	1	0.24	1.96	197	73
	2	0.14	2.12	179	41
Spring 01	1	0.19	1.81	152	31
	2	0.12	2.93	210	24
Autumn 01	1	0.18	1.74	279	55
	2	0.12	2.03	178	50
	3	0.06	2.21	176	39
Spring 02	1	0.38	2.23	163	74
	2	2.36	1.32	131	216

[a] CPUE was calculated by determining catch per seine haul for each backwater and then averaging the backwaters.

Table 8. Population estimates (Ñ), standard error (SE), coefficient of variation (CV), profile likelihood interval (PFI), number of passes (n), probability of capture for each sampling pass p(j), and density for 1999–2002.

Occasion	Ñ	SE	CV	PFI	n	p(1)	p(2)	p(3)	Density
					Ouray Complex				
BA#1 Autumn 99	218	48.3	0.22	150–367	3	0.32	0.06	0.15	1,090 per ha
BA#1 Spring 00	153	126.9	0.83	52–676	3	0.01	0.13	0.05	765 per ha
BA#2 Autumn 99	87	31.0	0.36	50–234	2	0.30	0.16	----	217 per ha
BA#2 Spring 00	115	66.9	0.58	48–623	3	0.02	0.19	0.14	287 per ha
					40-mile Reach				
Autumn 00	735	265.5	0.36	452–12773	2	0.10	0.06	----	11.4 per mile
Spring 01	260	154.9	0.59	104–1424	2	0.16	0.05	----	4.0 per mile
Autumn 01	670	218.7	0.33	444–13400	3	0.08	0.05	0.03	10.4 per mile
Spring 02	1320	335.5	0.25	848–2339	2	0.06	0.16	----	20.5 per mile

Table 9. Capture-recapture information, net movement, and days at large for young-of-year Colorado pikeminnow (CPM) collected in the Ouray Backwater Complex, 1999–2000.

Recapture Date	# of CPM	RM Recap	RM Origin	RM Change[a]	Days Since First Marked
11/08/99	9	252.5	252.5	0	5
11/09/99	4	249.5	249.5	0	5
03/14/99	3	252.5	252.5	0	132
	2	252.5	252.5	0	127
03/29/00	1	252.5	252.5	0	15
	1	252.5	252.5	0	147
	2	249.5	249.5	0	141
	2	249.5	249.5	0	146
	1	249.5	252.5	- 3	142
04/05/00	1	249.5	249.5	0	36
	1	249.5	249.5	0	7
	1	252.5	249.5	+ 3	42
	1	252.5	249.5	+ 3	149
	2	249.5	249.5	0	148
	1	249.5	249.5	0	7

[a] Plus sign indicates upstream movement and negative sign indicates downstream movement.

Table 10. Capture-recapture information, net movement, and days at large for young-of-year Colorado pikeminnow (CPM) collected in the 40-mile reach, 2000–2001 and 2001–2002.

Recapture Date	# of CPM	CPM Remain w/in 5-mi Section	RM Recap	RM Origin	RM Change[a]	Days Since First Marked
10/26/00	1	Yes	270.3	270.3	0.0	5
11/02/00	1	Yes	258.1	258.1	0.0	8
03/12/01	1	Yes	288.1	288.4	+ 0.3	5
03/21/01	1	Yes	255.5	255.5	0.0	5
10/31/01	1	Yes	287.0	287.0	0.0	6
11/02/01	1	Yes	253.9	253.7	+ 0.2	9
04/04/02	1[b]	Yes	285.7 285.7	289.8 285.5	- 4.1 + 0.2	10 9
04/05/02	1	Yes	278.0	277.7	+ 0.3	9
	1	Yes	278.0	278.5	- 0.5	9
	1[c]	Yes	279.8	279.0	+ 0.8	9
		No	279.8	278.7	+ 1.1	9
04/09/02	1	Yes	265.4	265.0	+ 0.4	7
	1	Yes	255.8	255.5	+ 0.3	6
04/11/02	1	No	253.2	255.8	- 2.6	8
	1	Yes	252.4	252.5	- 0.1	7
	1	Yes	250.8	250.6	+ 0.2	7

[a] Plus sign indicates upstream movement while the negative sign indicates downstream movement.
[b] Two possible movement scenarios for this fish with regards to backwater of origin: it was recaptured at river mile 285.7 on river left; it could have originated from a backwater at river mile 289.8 on river right or a backwater on river left at river mile 285.5.
[C] Two possible movement scenarios for this fish with regards to backwater origin: it was recaptured at river mile 279.8 on river right; it could have originated from a backwater at river mile 279.0 on river right or from a backwater downstream on river right at river mile 278.7.

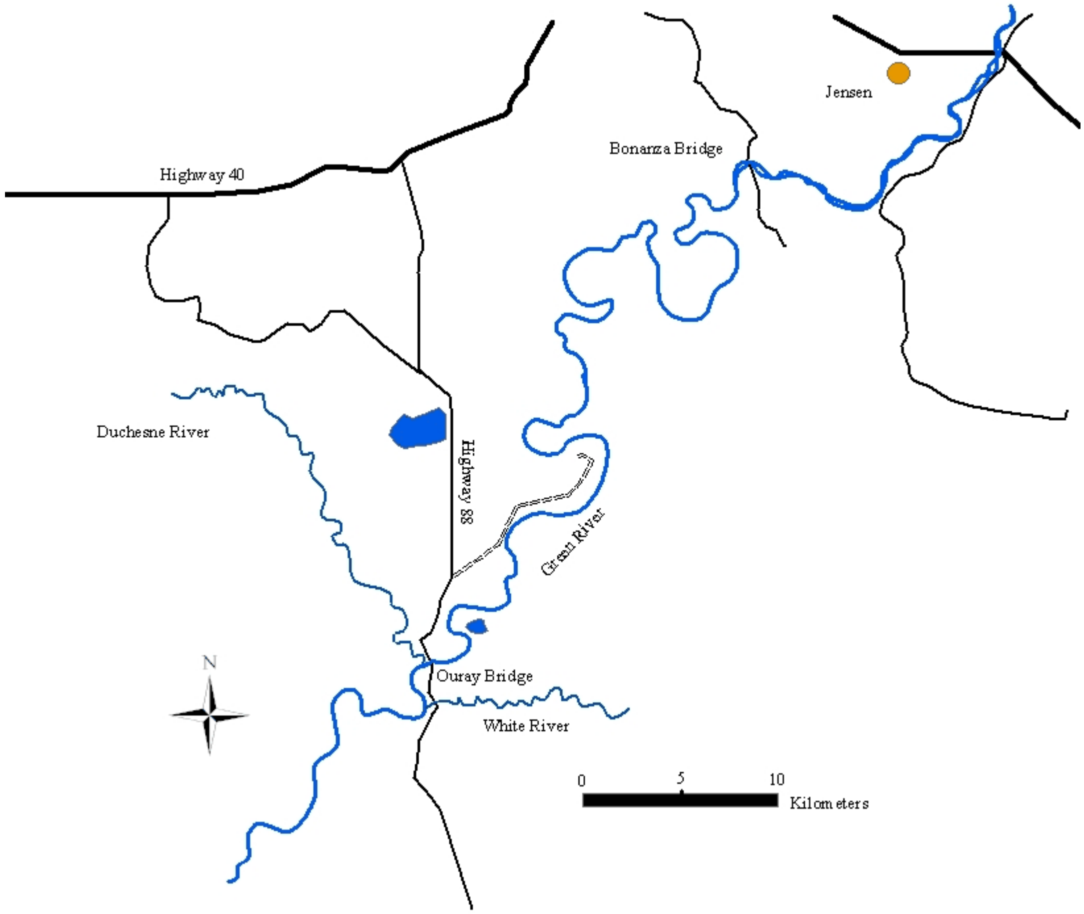


Figure 1. 40-mi study reach between Bonanza Bridge (RM 289.5) to Ouray Bridge (RM 248.2).

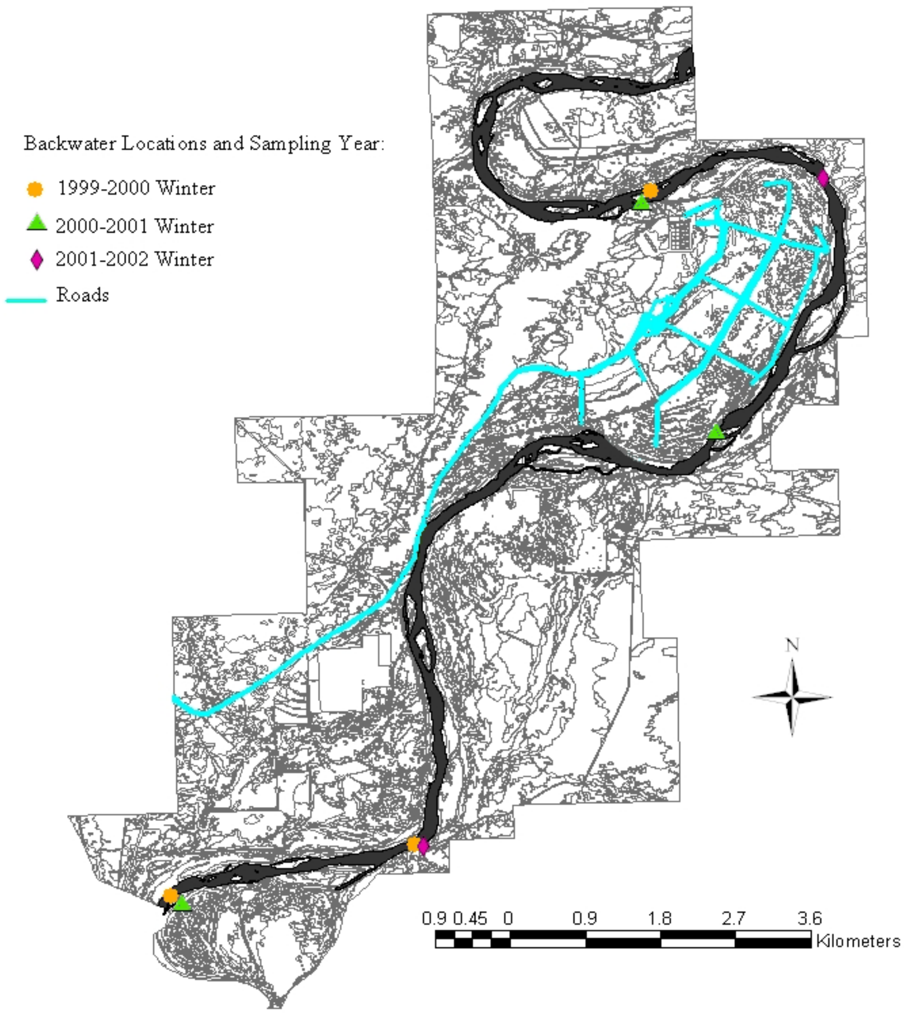
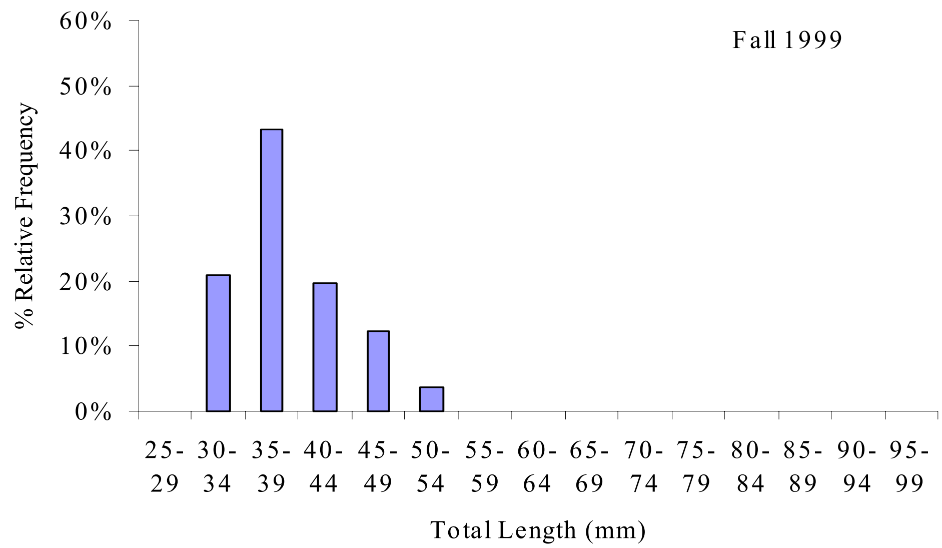


Figure 2. Ouray Backwater Complex, Ouray National Wildlife Refuge.

Figure 3. Seining under the ice at Greasewood Coral Backwater, RM 252.8, during 1999--2000 winter.



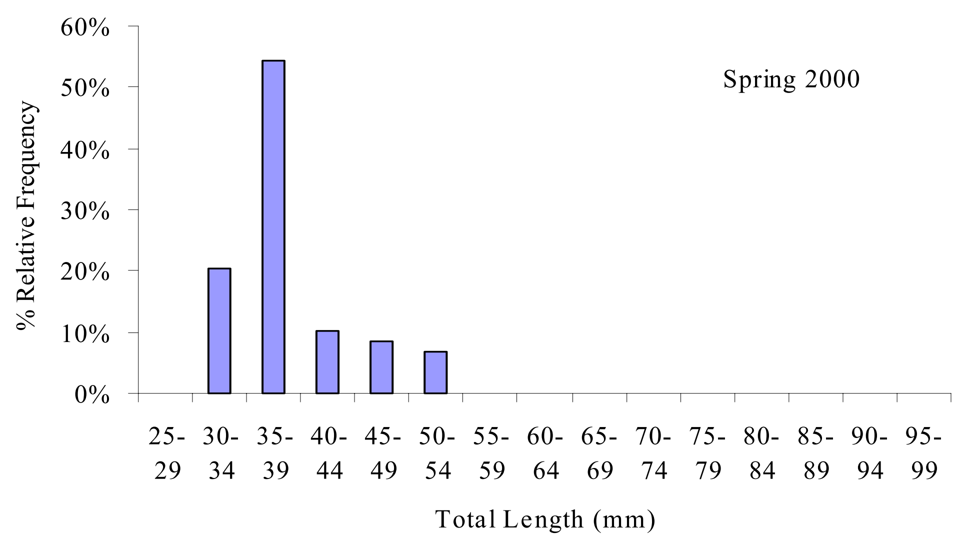


Figure 4. Length-frequency histograms for age-0 and age-1 Colorado pikeminnow in the 40-mile reach, autumn 1999 (81 fish) and spring 2000 (59 fish).

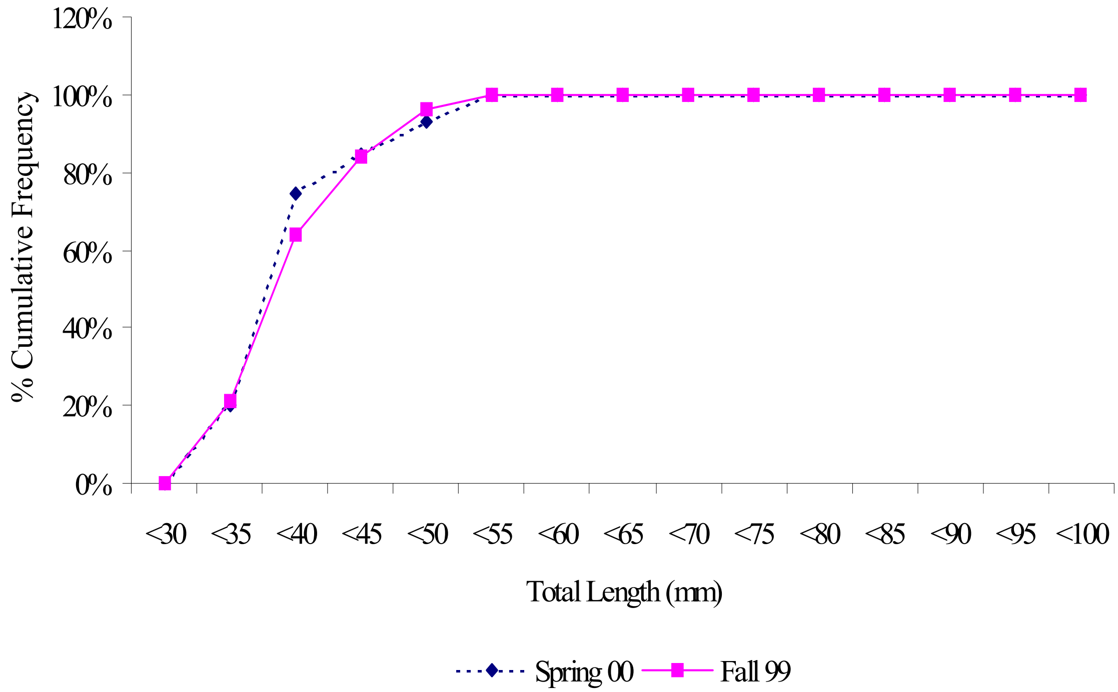


Figure 5. Cumulative length-frequency distributions of young-of-year Colorado pikeminnow, fall 1999 (81 fish) and spring 2000 (59 fish).

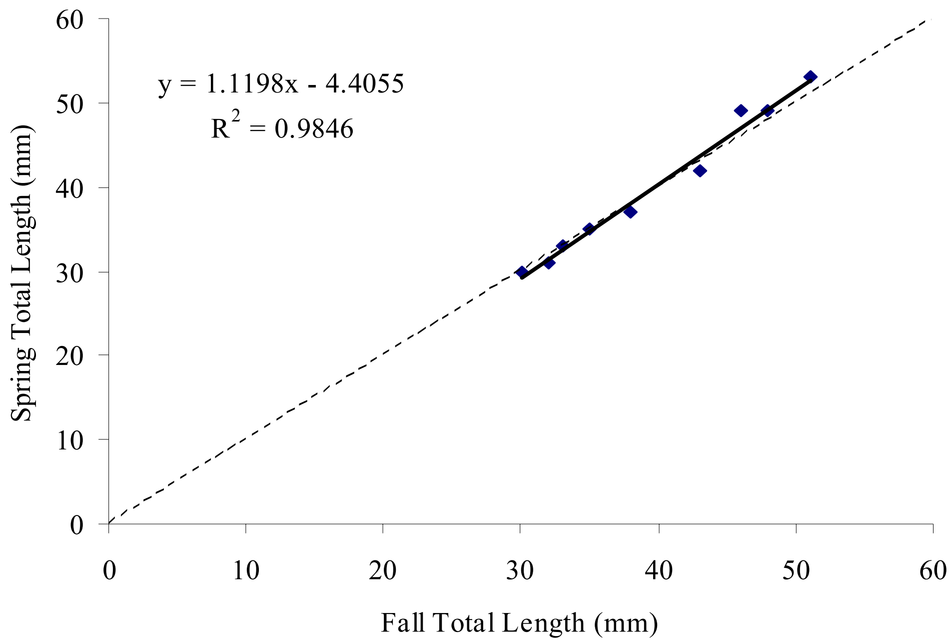


Figure 6. Quantile-quantile plot for fall 1999 and spring 2000 age-0 Colorado pikeminnow. The broken line represents a 1:1 relationship and indicates no change in length distribution. The solid line represents the least squares regression and indicates presence and magnitude of overwinter size dependent growth or mortality. Points represent 1, 5, 10, 75, 90, 95, and 100% of the cumulative length-frequency distributions for fall (81 fish) and spring (59 fish).

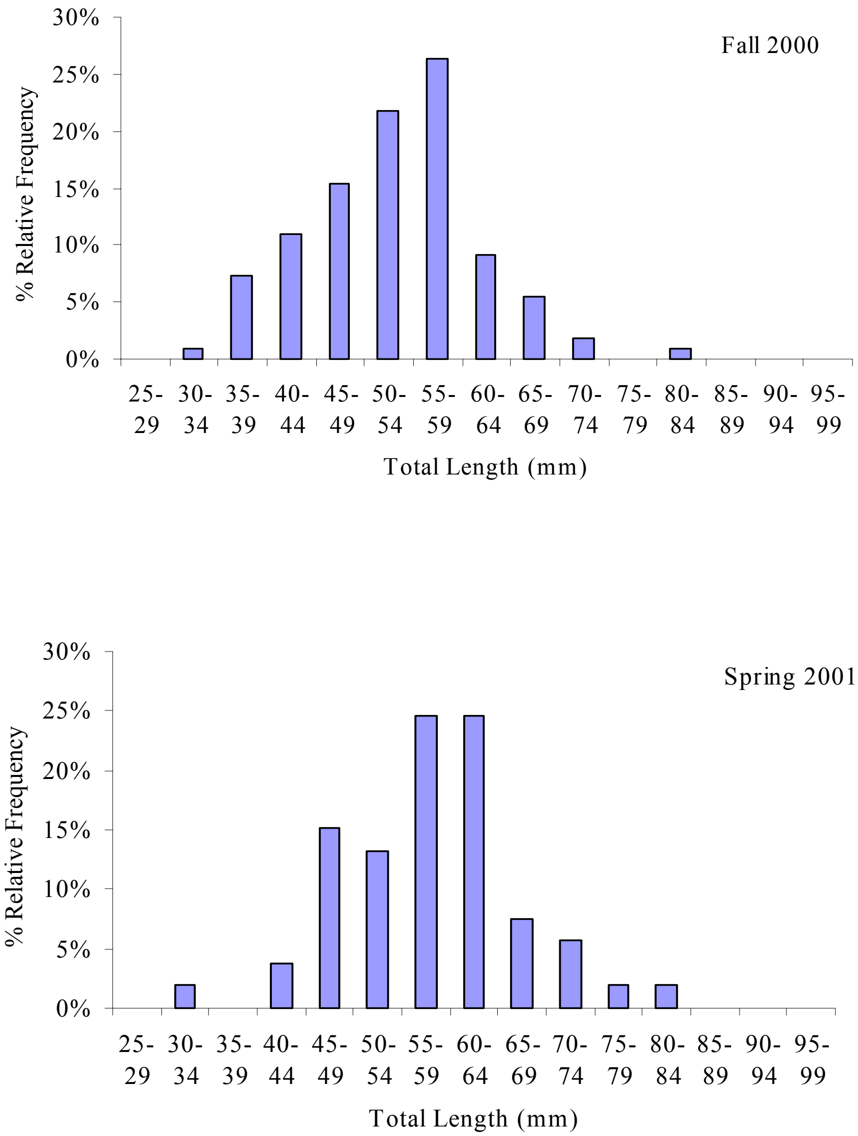


Figure 7. Length-frequency histograms for age-0 and age-1 Colorado pikeminnow in the 40-mile reach, autumn 2000 (110 fish) and spring 2001 (53 fish).

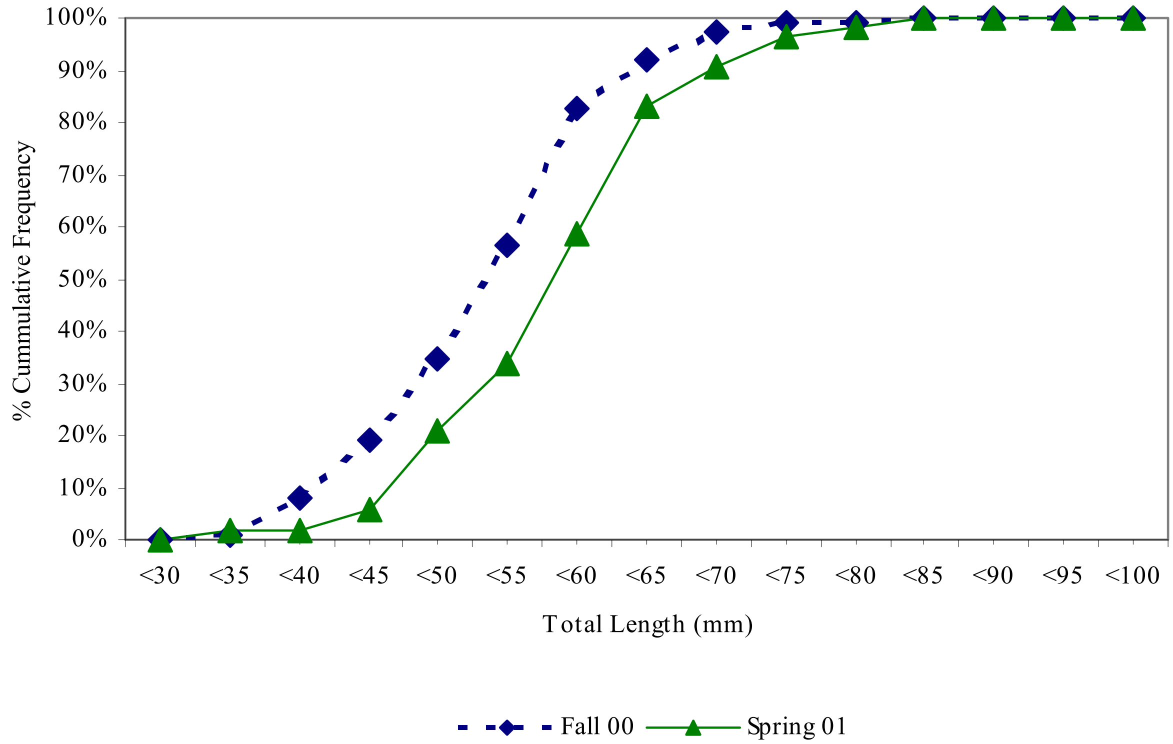


Figure 8. Cumulative length-frequency distributions of young-of-year Colorado pikeminnow, 2000 (110 fish) to 2001 (53 fish).

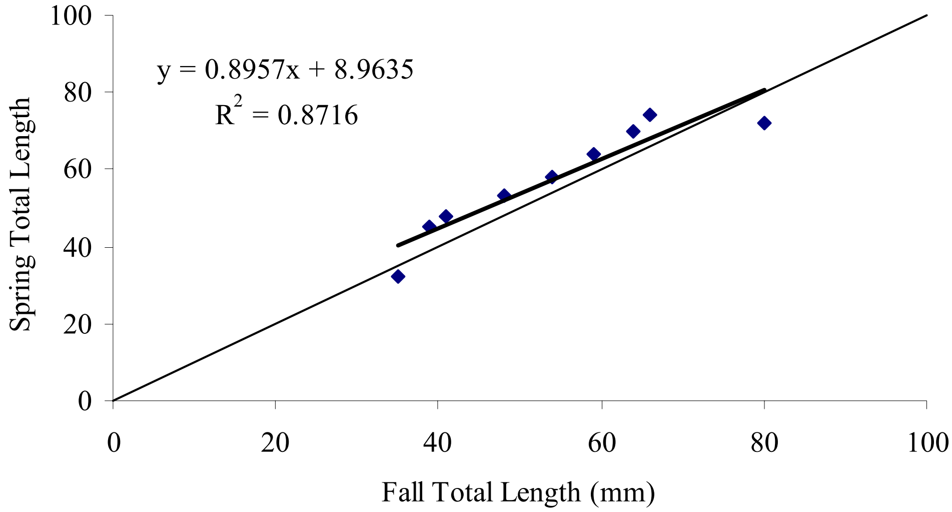
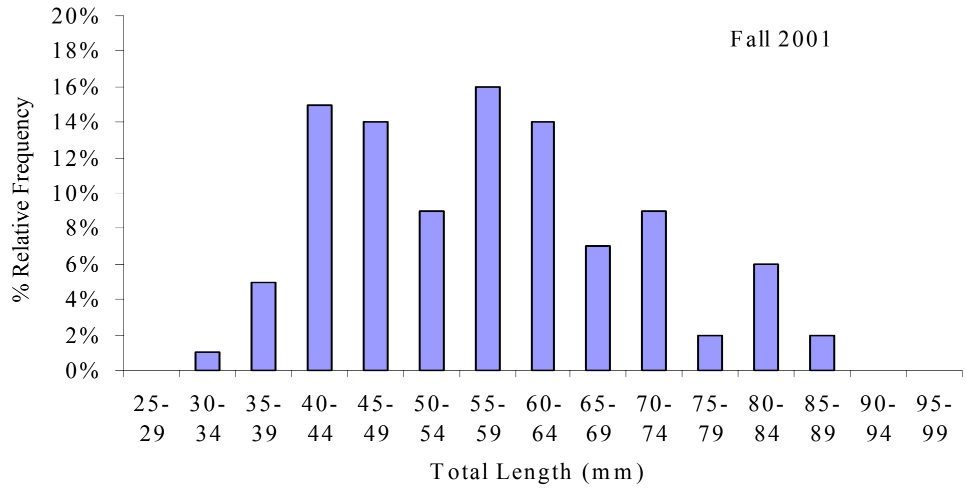


Figure 9. Quantile-quantile plot for fall 2000 and spring 2001 age-0 Colorado pikeminnow. The broken line represents a 1:1 relationship and indicates no change in length distribution. The solid line represents the least squares regression and indicates presence and magnitude of overwinter size dependent growth or mortality. Points represent 1, 5, 10, 75, 90, 95, and 100% of the cumulative length-frequency distributions for fall (109 fish) and spring (53 fish).



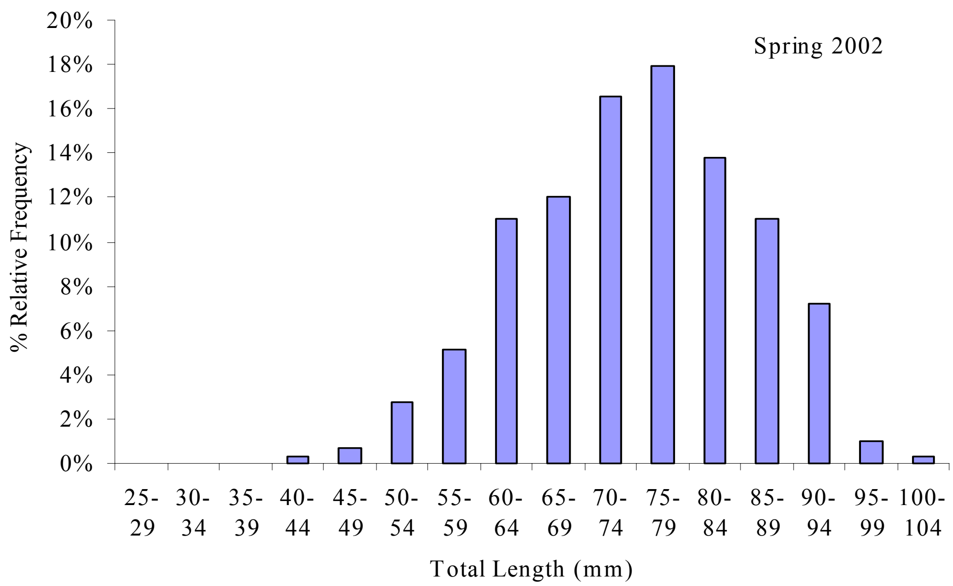
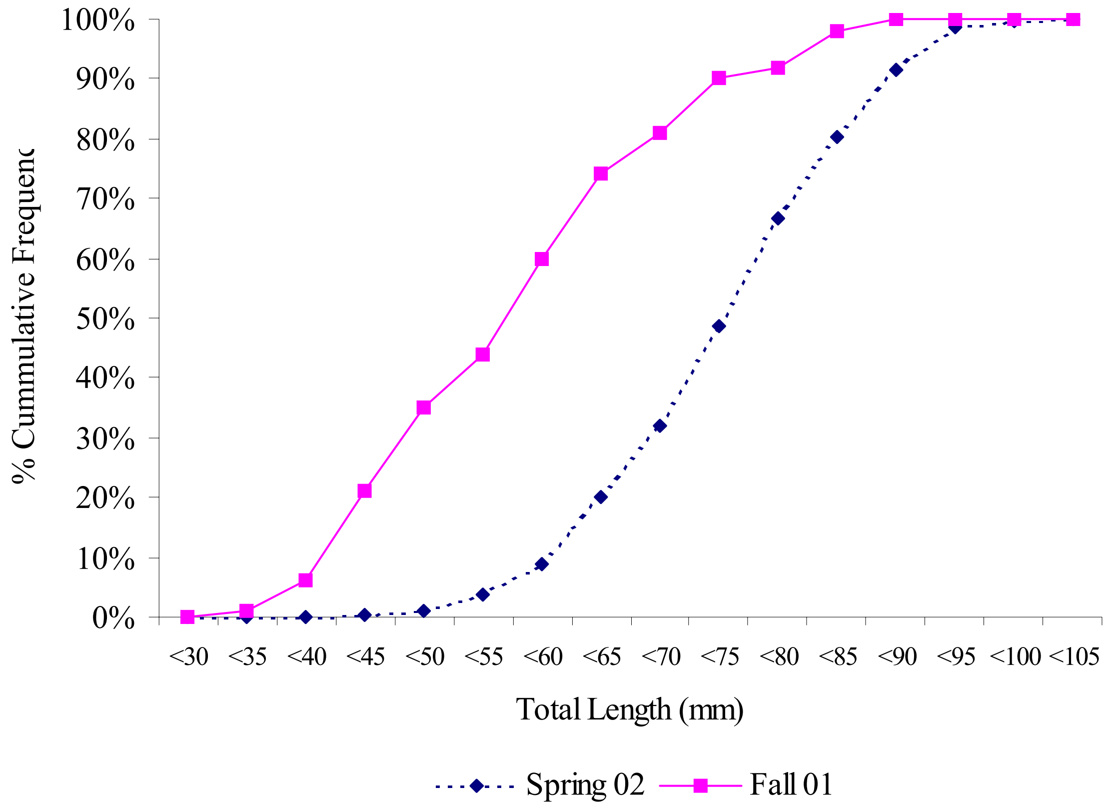


Figure 10. Length frequency histograms for age-0 and age-1 Colorado pikeminnow in the 40-mile reach, autumn 2001 (100 fish) and spring 2002 (290 fish).



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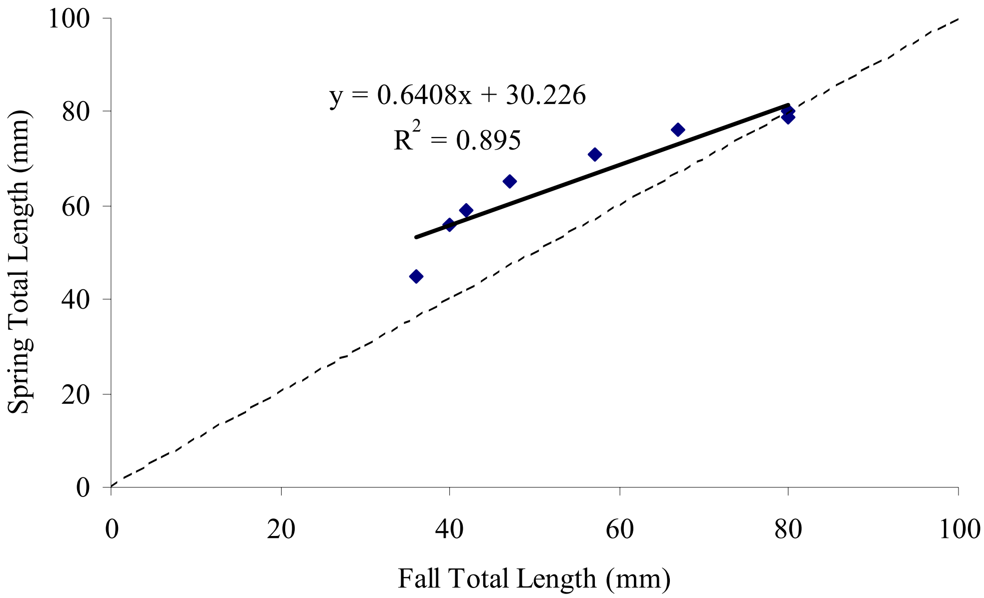


Figure12. Quantile-quantile plot for fall 2001 and spring 2002 age-0 Colorado pikeminnow. The broken line represents a 1:1 relationship and indicates no change in length distribution. The solid line represents the least squares regression and indicates presence and magnitude of overwinter size dependent growth or mortality. Points represent 1, 5, 10, 75, 90, 95, and 100% of the cumulative length-frequency distributions fall (96 fish) and spring (201 fish).

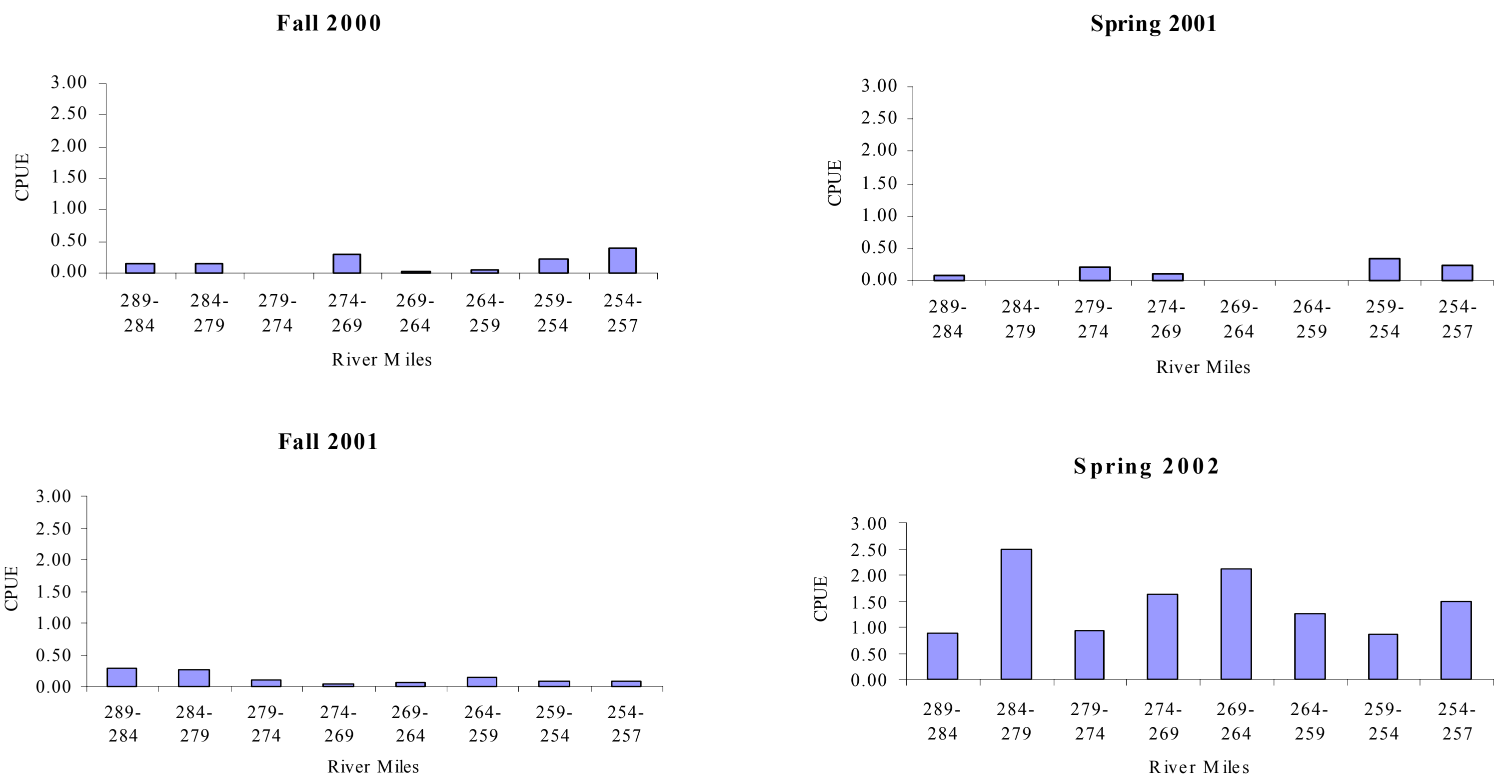


Figure 13. Fall and spring distributions of young-of-year Colorado pikeminnow collected in the 40-mile study reach, 2000–2001 (110 fish in fall, 53 fish in spring) and 2001–2002 (100 fish in fall, 290 fish in spring).

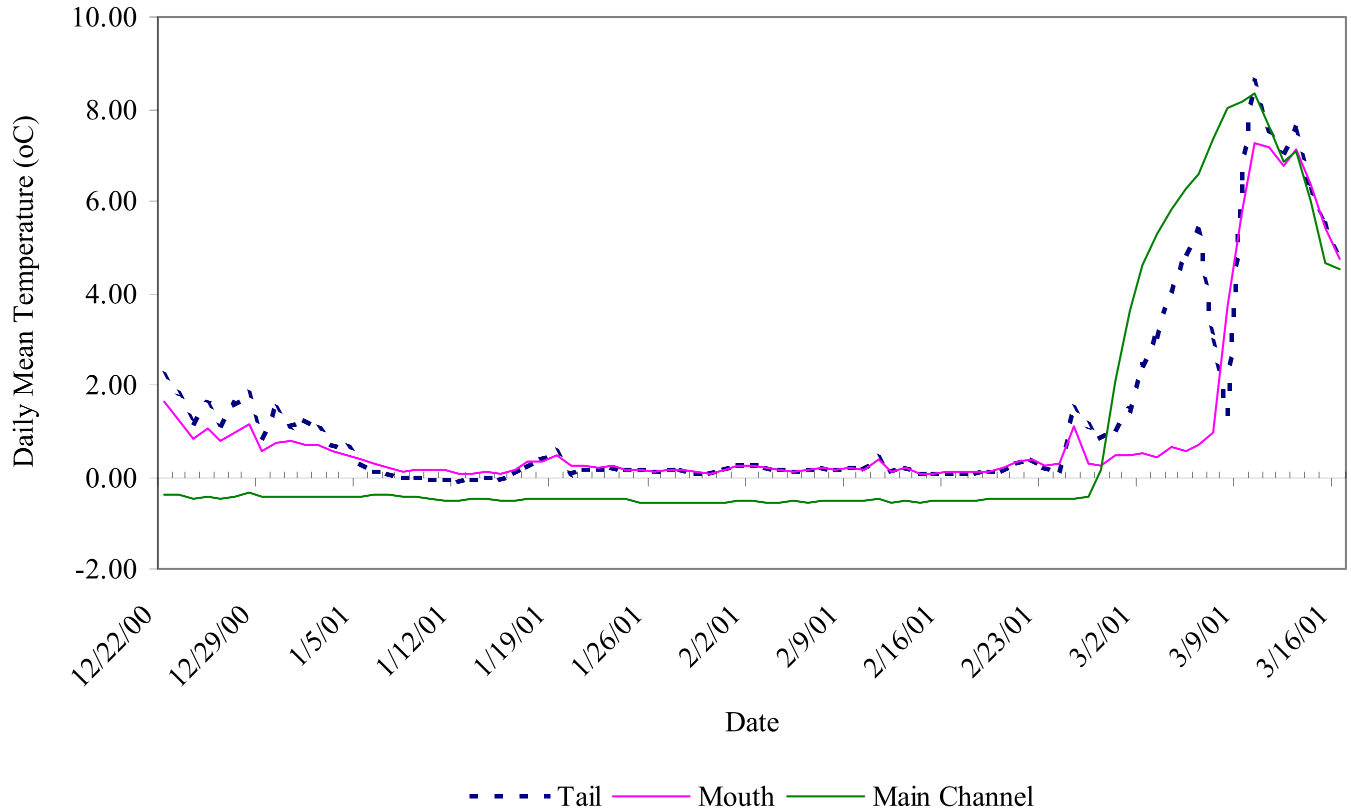
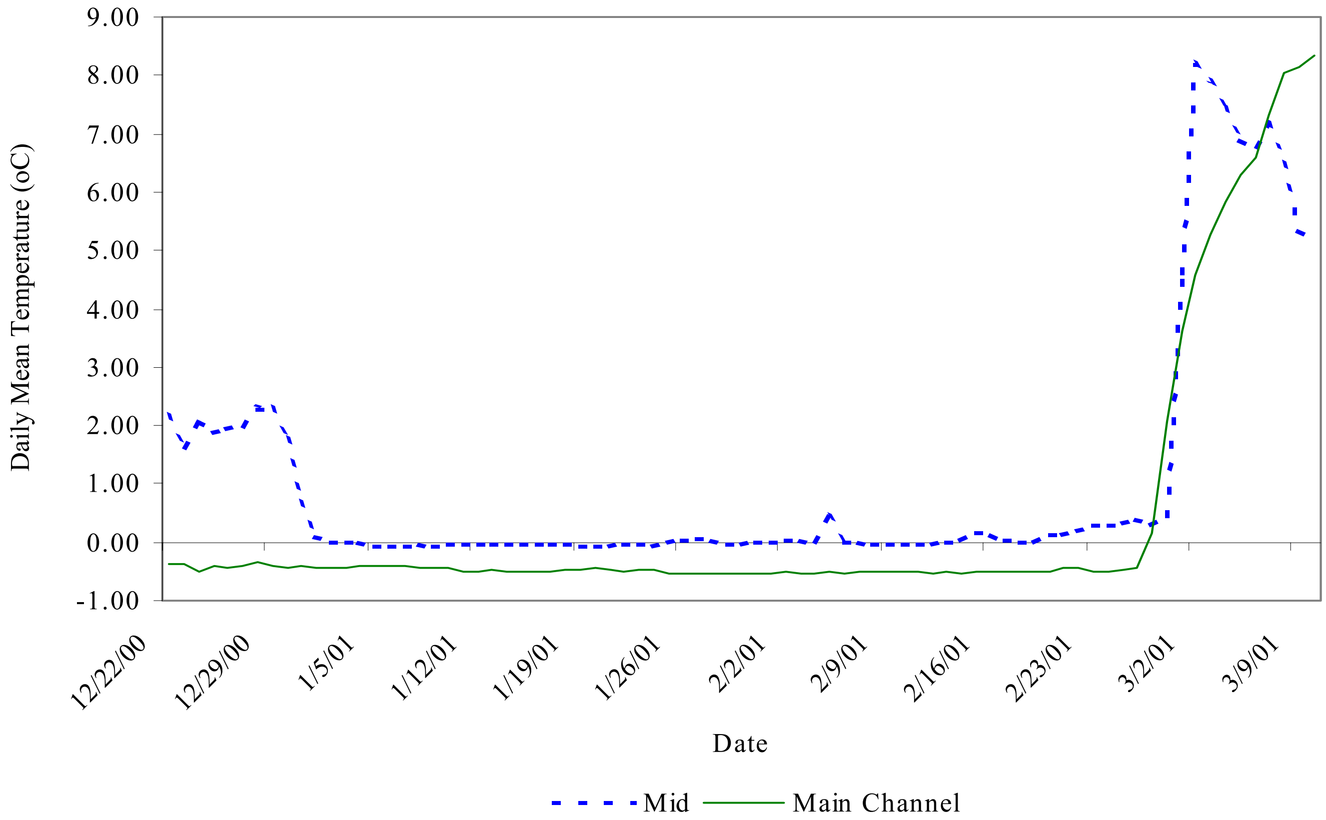


Figure 14. Daily mean water temperature profile of Leota Backwater at river mile 258.1.



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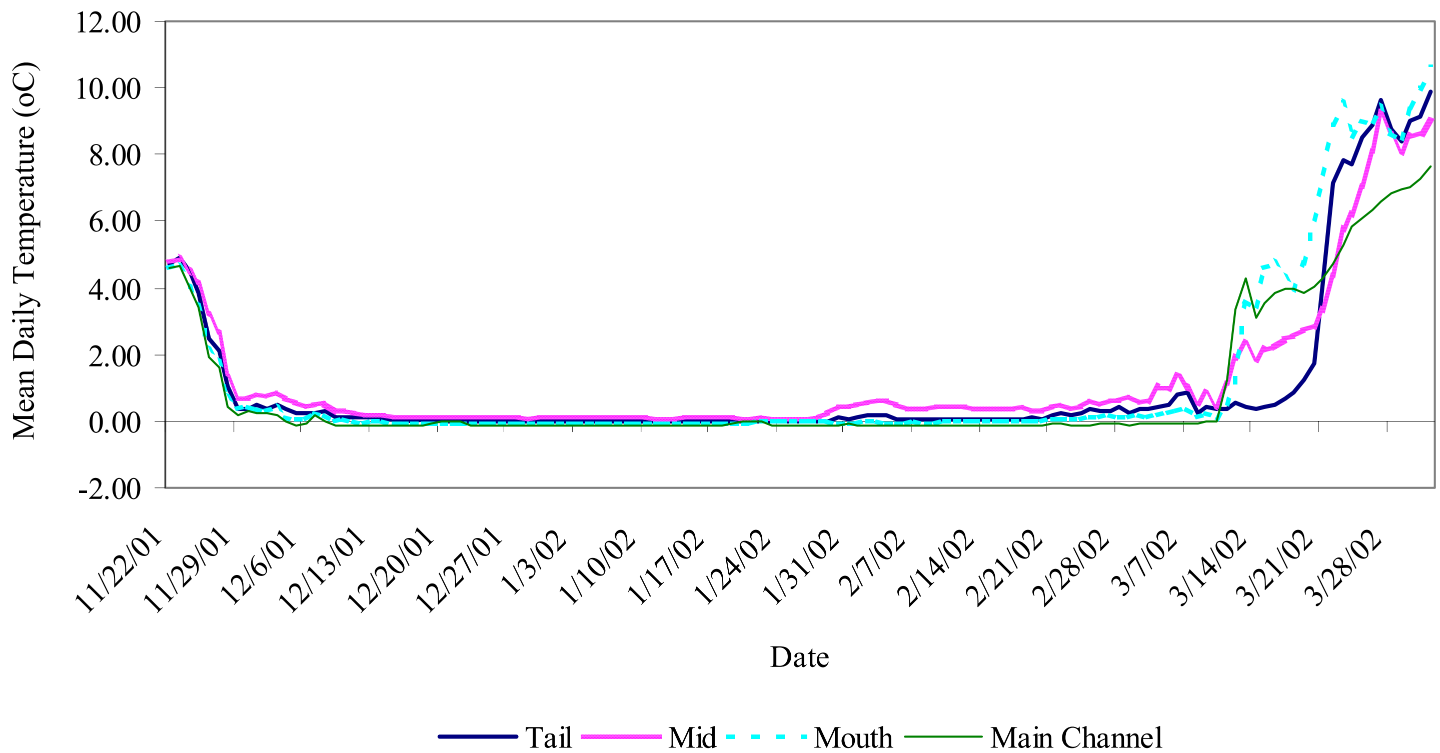

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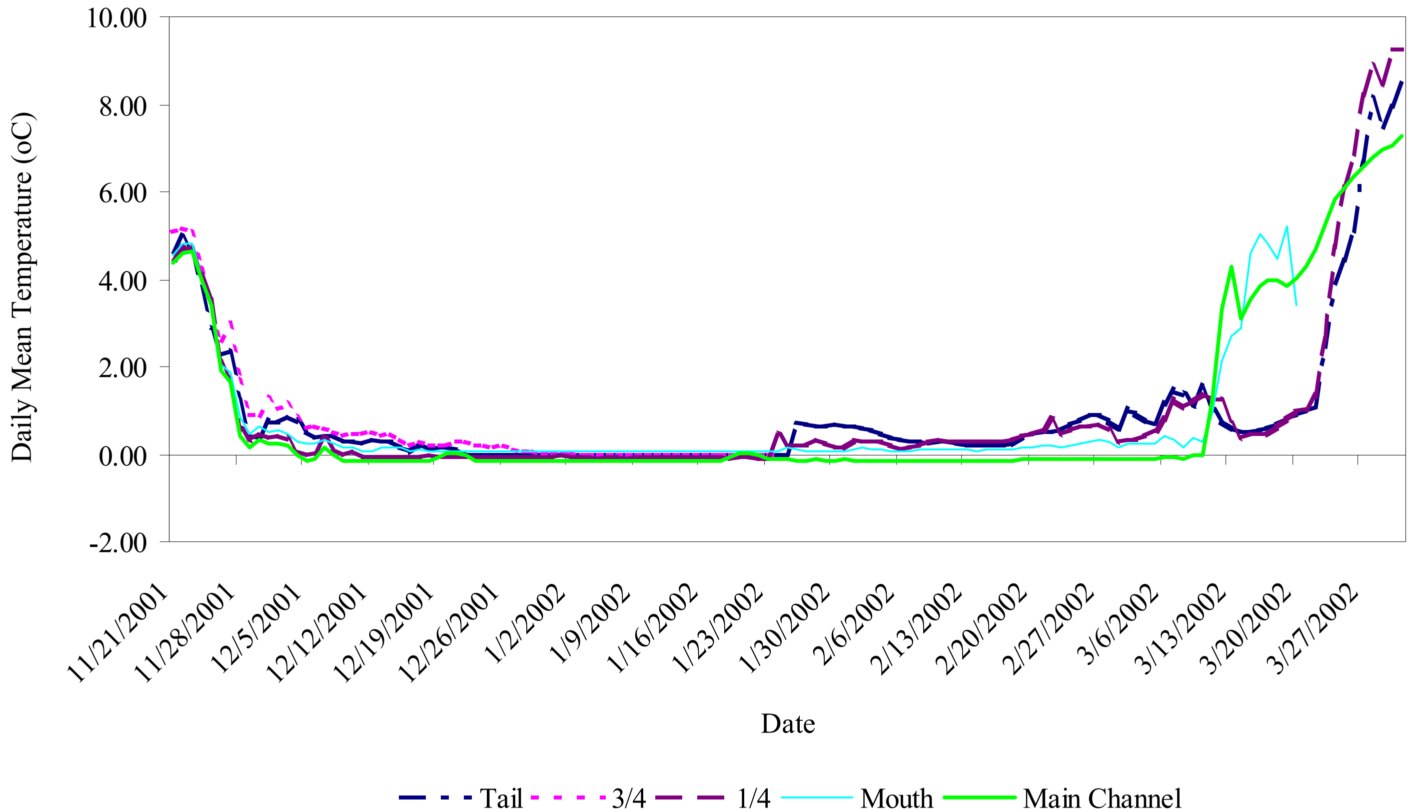

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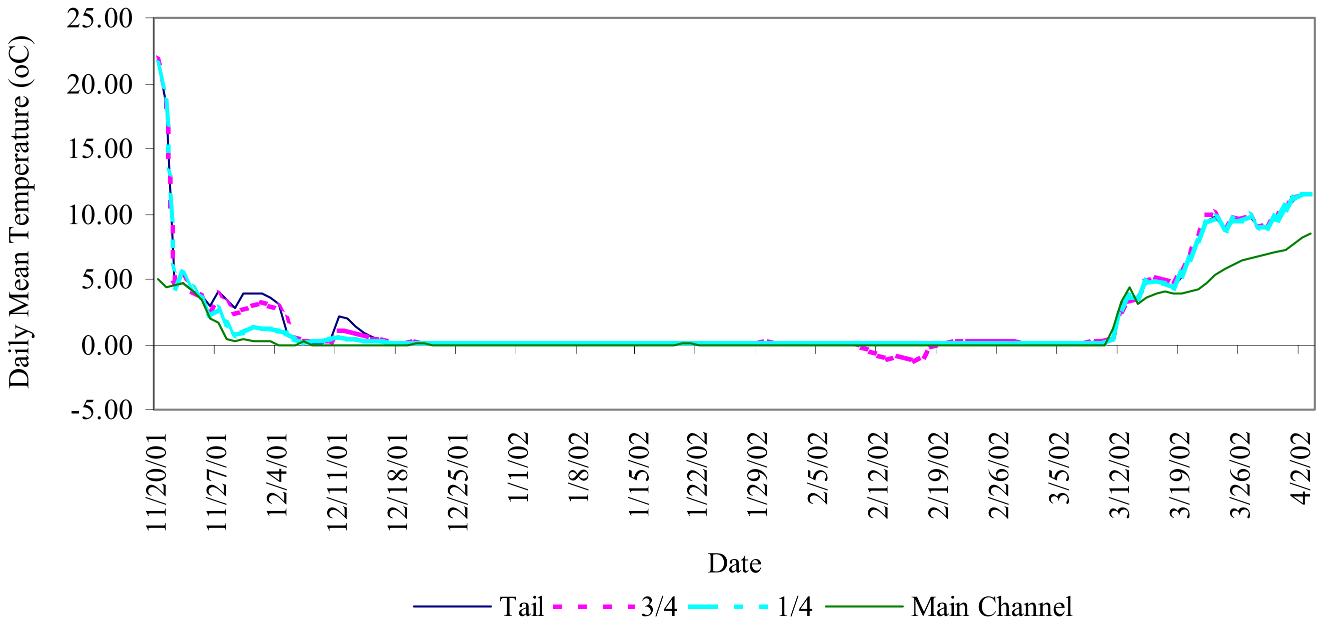
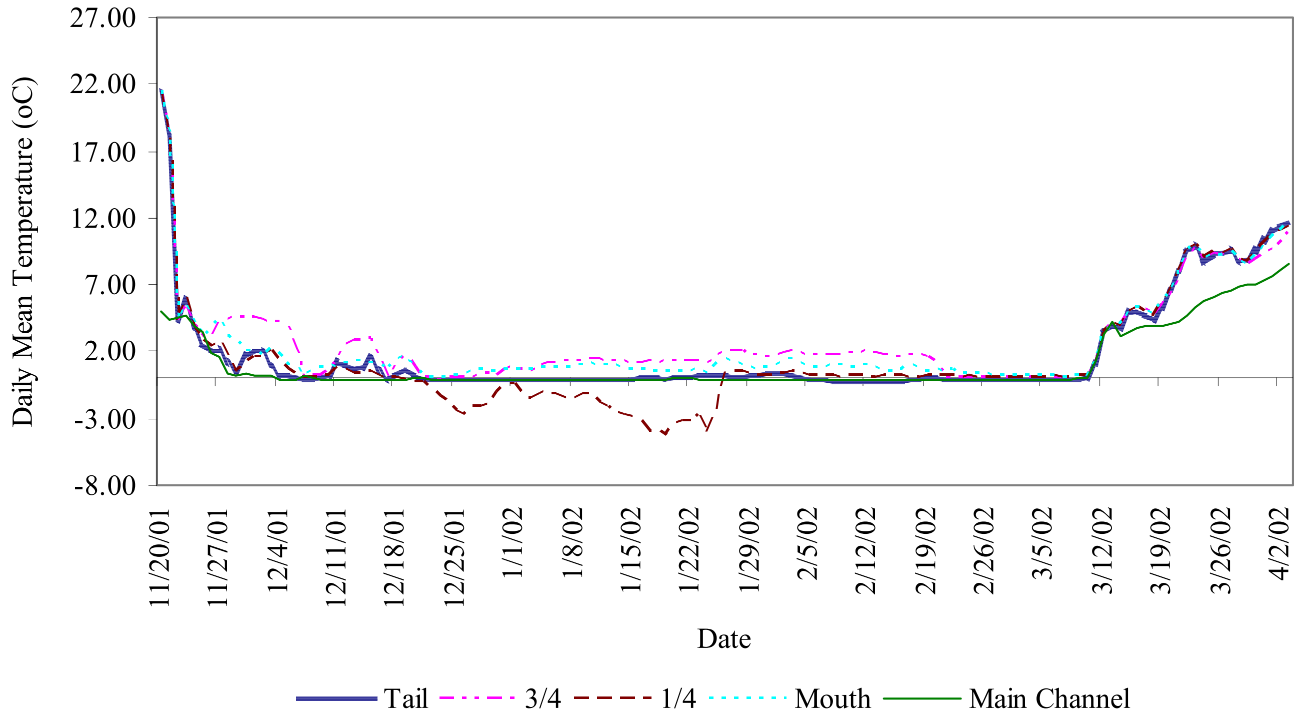


Figure 18. Daily mean water temperature of backwater #1 at river mile 251.7.



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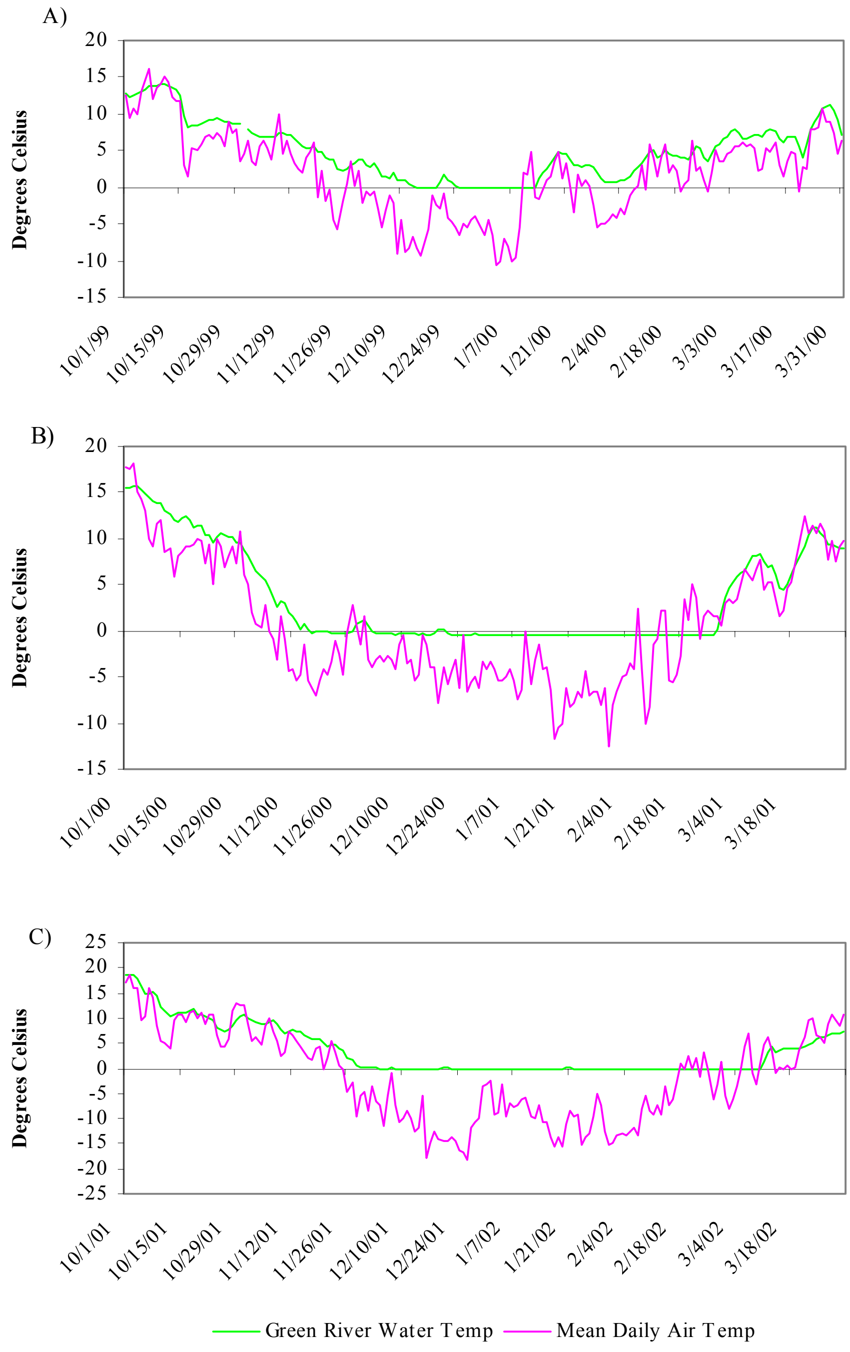

Figure 20. Mean daily air and river temperature of the Green River at Ouray National Wildlife Refuge for three consecutive winters: a) 1999–2000, b) 2000–2001, and c) 2001–2002.

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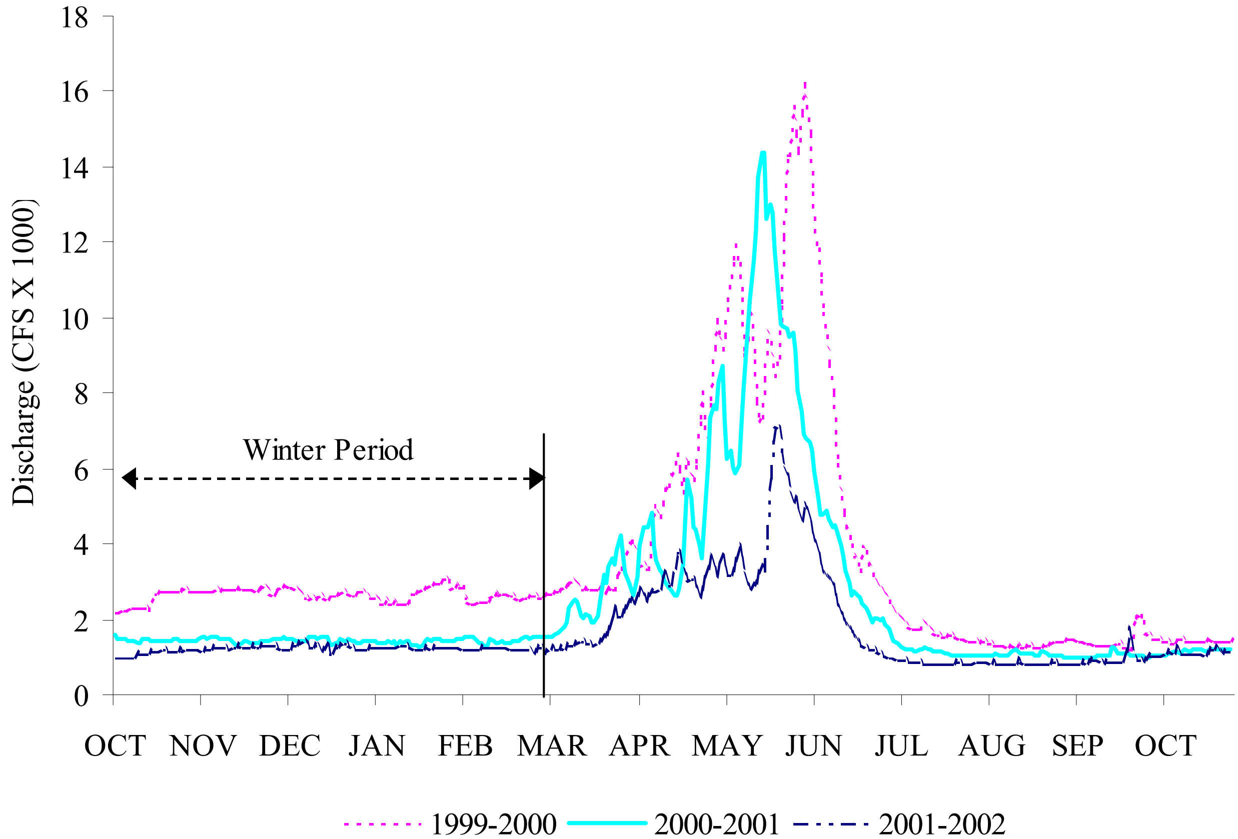

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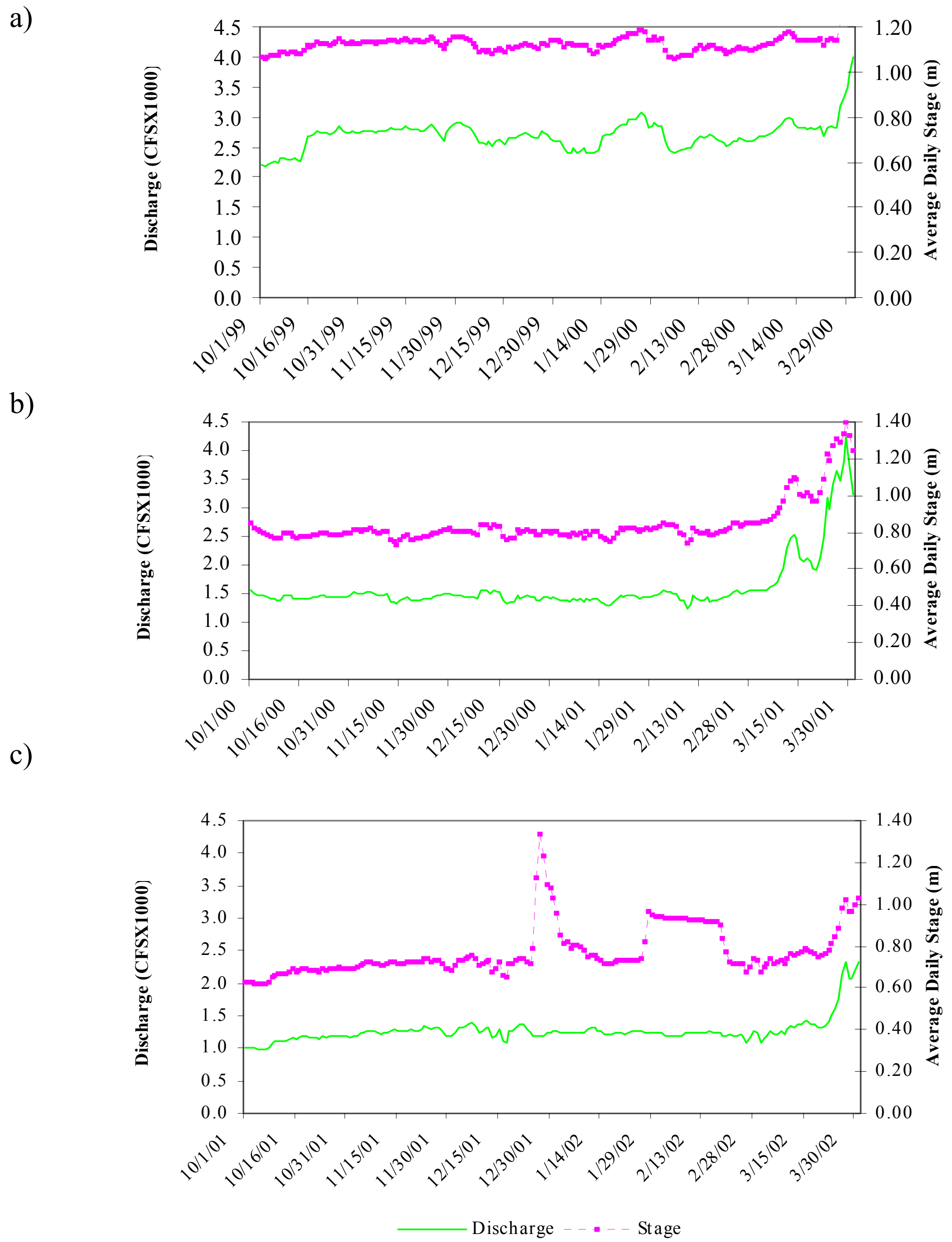

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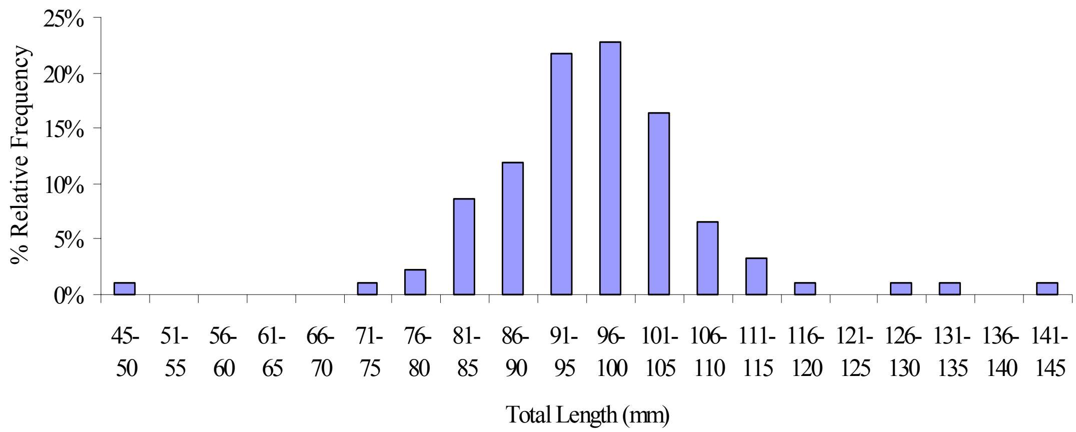
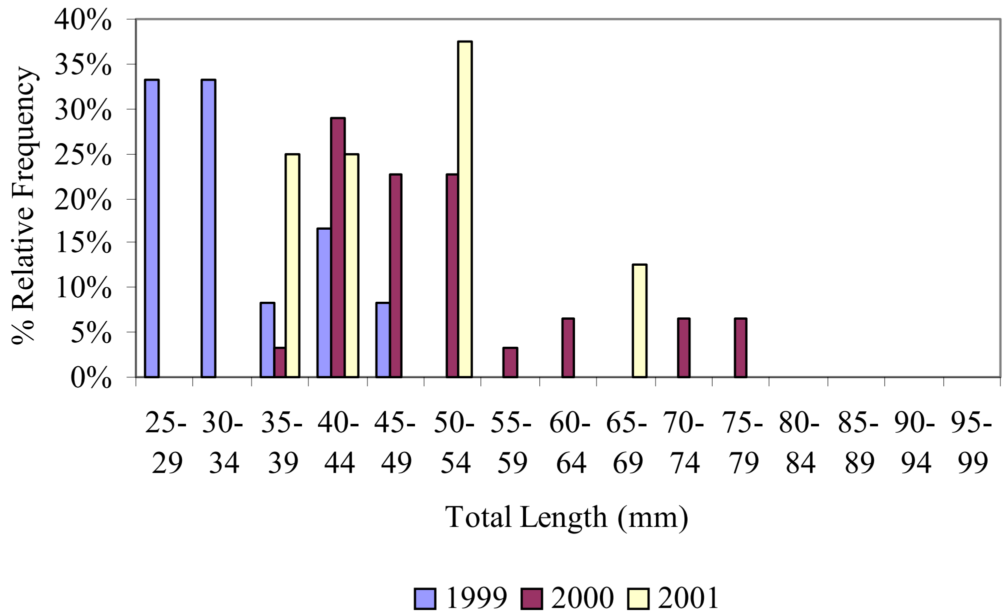


Appendix 1. Length-frequency histogram for 92 juvenile razorback suckers collected in the Green River in the 40-mile reach, spring 2002.



Appendix 2. Length-frequency histogram for age-0 Colorado pikeminnow collected in the Green River from Split Mountain Campground downstream 120 miles to Sand Wash (Reach 4) during the Interagency Standardized Monitoring Program from 1999–2001.

REPORT B

Movement Rates of Age-0 Colorado Pikeminnow Under Simulated Winter Conditions

FINAL REPORT

March 2004

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EXECUTIVE SUMMARY

This investigation estimated rates of spontaneous movement (activity) of age-0 Colorado pikeminnow in simulated winter conditions for fish bioenergetics modeling (REPORT C). Movement rates were quantified using video interpretation of movement of individual Colorado pikeminnow in an observation arena at four water temperatures (1, 5, 10, and 15 ºC) and at three levels of disturbance (0, 1, and 2 disturbances/min). Regression analysis was used to fit observed data to models that describe rates of movement as functions of water temperature and disturbance. The best approximating models were identified using Akaike's information criterion. The temperature-dependent response of fish movement in the absence of disturbance was best approximated by an exponential model with the form $y = 0.0895e^{0.1532t}$ where y is body lengths/s (bl/s) and t is temperature (ºC). Average observed movement rates of Colorado pikeminnow in the absence of disturbance ranged from 0.11 to 0.89 bl/s at 1 and 15ºC, respectively. Two models, intercept ($y = 0.60$) and linear-disturbance ($y = 0.44 + 0.10x$ where $x = 1$ or 2 disturbances/min) gave approximately equal descriptions of the combined effect of disturbance and water temperature. Neither model includes a temperature effect which suggests that the disturbance treatment overwhelmed the temperature-dependent response described above. Disturbance stimuli were intended to encourage fish to move at relatively high rates so that maximum spontaneous movement rates in winter conditions could be estimated. This outcome was achieved for fish in 1, 5, and 10°C treatments which had maximum movement rates of 0.82, 1.1, and 1.1 bl/s, respectively. The fitted models can be used to estimate rates of spontaneous movement of young Colorado pikeminnow at water temperatures ranging from 1 to 15°C.

INTRODUCTION

The Colorado pikeminnow *(Ptychocheilus lucius)* is a large cyprinid endemic to the Colorado River Basin. Historically, the Colorado pikeminnow was widespread in warm-water streams and rivers, but the species was listed as federally endangered in 1967 in response to declining populations (U.S. Department of Interior 1967). The decline of Colorado pikeminnow is commonly attributed to interactions with introduced fishes, construction of dams, and other adverse habitat modification (Carlson and Muth 1989; U.S. Fish and Wildlife Service 1992; Tyus 1991).

An important element of Colorado pikeminnow life history is reliance of early life stages on nursery habitats. Nursery habitats for Colorado pikeminnow have been identified as backwaters and other low-velocity areas that occur along shorelines of rivers (Tyus 1991). Young fish occupy these habitats throughout their first year of life.

The Green River in Utah is the largest tributary to the Colorado River and is one of the strongholds for Colorado pikeminnow populations. Winter discharge in the Green River downstream from Flaming Gorge Dam is influenced by releases from the dam. It has been hypothesized that winter operations of Flaming Gorge Dam reduce survival of age-0 fish (Carlson and Muth 1989; U.S. Fish and Wildlife Service 1992; Valdez and Cowdell 1996; Haines et al. 1998), but negative effects on overwinter survival have not been demonstrated. One possible mechanism for reduced survival is that winter operations increase activity of young Colorado pikeminnow. Higher metabolic rate associated with increased movement may be detrimental during winter when thermal conditions are below optimum for Colorado pikeminnow. A first step toward evaluating the potential energetic cost of increased activity is quantifying the potential range of spontaneous movement rates. However, no data describing spontaneous movement rates are available for Colorado pikeminnow. Some data describing swimming performance of Colorado pikeminnow in stamina tunnels are available (Berry and Pimentel 1985; Childs and Clarkson 1996), but these investigations do not reveal movement rates in low-velocity conditions like nursery habitats. These investigations also emphasized swimming ability under relatively warm spring and summer thermal conditions (10 to 26°C). Consequently, little is known about swimming ability of young warm-water fish like Colorado pikeminnow in winter conditions, even though temperature has been shown to be an important environmental variable affecting fish physiology and behavior (Schaefer 1986; Hurst and Conover 2001).

The purpose of this investigation was to describe the realistic range of spontaneous movement rates (activity) of age-0 Colorado pikeminnow in simulated winter conditions for fish bioenergetics modeling (REPORT C). This objective was achieved by measuring movement of individual Colorado pikeminnow in an observation arena at four water temperatures (1, 5, 10, and 15 °C) and at three levels of disturbance (0, 1, and 2 disturbances/min). Regression analysis was used to fit observed data to statistical models that describe rates of movement as functions of water temperature and disturbance. The resulting models can be used to estimate rates of spontaneous movement of young Colorado pikeminnow at water temperatures ranging from 1 to 15°C.

METHODS

Experimental animals.

Colorado pikeminnow were obtained from Dexter National Fish Hatchery and Technology Center (Dexter, NM). Fish were fed a mixture of live $\leq$ 24-h-old brine shrimp nauplii (Aquarium Products, Glen Burnie, MD) and a commercially prepared flake diet (TetraMin®; TetraWerke, Melle, Germany) twice daily. Fish ranged from 45 to 55 mm TL (mean= 54.7 mm).

Experimental design and observation system

Experimental treatments were assigned to individual fish using a balanced, randomized factorial design with four temperature treatments (1, 5, 10, 15^{o}C) and three disturbance treatments (0, 1, and 2 disturbances/min). Temperature treatments were studied in a random order (5, 15, 10, 1^{o}C) and five fish (*n*=5) were assigned randomly to each experimental treatment combination. Fish were acclimated to each temperature for at least 14 d. After temperature acclimation, an individual fish (experimental unit) was transferred to the observation arena. The observation arena was a plastic-coated 1.2-m diameter round steel tank. Water depth was 5 cm and the bottom of the arena was covered with sand. The arena was positioned in a temperature-controlled water bath and enclosed within a blind. An observation port in the blind allowed access for a video camera lens from above. Two fluorescent lamps provided illumination 12 h in each 24-h period. Fish were allowed to acclimate to the arena for 24 h before observations were made. At conclusion of the acclimation period, the 0-disturbance observations were made by video taping fish movements for 3 min. Then fish movements were video taped for an additional

3 min initiated by a 1 or 2 disturbance/min treatment (treatment selected *a priori* by coin flip). The disturbance was applied by touching the surface of the water directly above a fish with a meter stick for 1 s. After conclusion of the disturbance observation, 2 h were allowed to elapse before the remaining disturbance treatment was applied. Thus, each of 20 fish was exposed to all three disturbance treatments and observed for 3 min/treatment such that total observation time was 180 min.

Video interpretation

Fish movement was interpreted by viewing video recordings on a monitor and tracing each fish's position onto a transparency. Distance traveled was estimated using image analysis software (Optimus, Seattle, Washington). Distance traveled was converted to swimming speed by dividing total distance by elapsed time, or by fish total length and elapsed time to give estimates with units of cm/s or body lengths/s (bl/s).

Statistical analysis

Statistical analysis was based on a model-selection philosophy advocated by Burnham and Anderson (1998). The general method of analysis was to identify likely candidate models from fish bioenergetics literature and then fit the dependent variable (i.e., movement rate) as a function of independent variables (e.g., water temperature) for each model using nonlinear regression (NLIN procedure; SAS 1990). Best approximating models were identified using Akaike's information criterion with small-sample bias adjustment (AIC_c). In some cases, candidate models had AIC_c values that differed by less than 2 AIC_c units. Models that differ by less than 2 AIC_c approximate the data equally well (Burnham and Anderson 1998). Data from the 0-disturbance treatment were analyzed separately from the other data, because it was anticipated that fish behavior might be qualitatively different in the presence versus absence of disturbance stimuli. Three candidate models for describing the response of activity as a function of water temperature were fit: intercept, linear, and exponential. The intercept model ($y = a$) represents the null hypothesis that movement rate (y; bl/s) is not influenced by water temperature. The linear model ($y = a + bt$) represents the alternative hypothesis that movement increases directly with water temperature (t). The exponential model ($y = ae^{bt}$) is widely used to estimate changes in metabolism of fish as a function of water temperature (Peters 1983; Hanson et al. 1997).

For the remaining data, disturbance was treated as a continuous variable, so that the influence of the magnitude of disturbance (1 or 2 disturbances/min) could be described. Candidate models included intercept, linear function of disturbance, linear function of disturbance and temperature, and linear function of disturbance and exponential function of temperature. Nonlinear regression was used to fit each model to movement rate as a function of respective experimental treatments.

RESULTS

The model that best explained movement in the absence of disturbance was the exponential model (Table 1; Figure 1). The model had the form $y = 0.0895e^{0.1532t}$ (y = bl/s; t = °C) and explained 53% of variation in movement rates. Mean movement rates of undisturbed Colorado pikeminnow ranged from 0.11 to 0.89 bl/s at 1 and 15°C, respectively (Table 2). A linear model ($y = - 0.0244 + 0.0550t$) explained almost as much variation (51% of variation) as the exponential. However, inspection of data and residual plots showed that observed values and mean estimates of movement rates were better described by the exponential model. In general, as water temperatures increased, so did the magnitude of individual variation in movement. At 1°C, movement rates ranged from 0.0012 to 0.20 bl/s (coefficient of variation = 72%) compared to 0.11 to 2.2 bl/s (coefficient of variation = 110%) at 15°C.

Two models, intercept and linear-disturbance, gave approximately equal descriptions of the combined effect of disturbance and water temperature (Table 1; Figure 1). The intercept model had the form $y = 0.60$. The linear-disturbance model had the form $y = 0.44 + 0.10x$, where x = 1 or 2 disturbances/min. Neither model includes a temperature effect which suggests that the disturbance treatment overwhelmed the temperature-dependent response described above. The AIC_c values for the approximating models differed by 0.53 units. The intercept model had the lowest (best) AIC_c value (Table 1), but the linear-disturbance model explained the largest fraction (86.2 versus 85.6%) of total sums of squares. This result suggests that there may be a disturbance effect, but it is relatively subtle and the data are inadequate to reliably describe it. Inspection of data and residual plots could not identify which model best described observed values and mean estimates. Disturbance stimuli were intended to encourage fish to move at relatively high rates so that maximum spontaneous movement rates could be estimated. This outcome was achieved for fish in 1, 5, and 10°C treatments, but not at 15°C (Table 2). Maximum movement rates were 0.82, 1.1, and 1.1 bl/s for fish exposed to 2 disturbances/min at 1, 5, and 10°C, respectively.

DISCUSSION

We measured spontaneous movement rates of age-0 Colorado pikeminnow at water temperatures ranging from 1 to 15°C. Our objective was to obtain data that describe the potential range of spontaneous movement rates that can be demonstrated by wild fish in winter conditions. The data collected in this investigation are valuable because winter operations of Flaming Gorge Dam may influence Colorado pikeminnow movement rates. The energetic cost of increased movement is unknown, but can be estimated using fish bioenergetics if movement rates of fish in the field can be approximated (REPORT C). Most investigations of fish swimming ability have used experimental conditions where fish were forced to swim at known velocities. Relatively little is known about spontaneous movement rates, and even less is known about activity of age-0 fish under winter conditions. Results of this investigation show that activity declines exponentially with temperature, but young Colorado pikeminnow remain active during winter, even when water temperatures approach 0°C. This interpretation is consistent with results of Thompson et al. (1991) who studied feeding, growth, and condition of three sizes ($\bar{x}$ = 30, 36, and 44 mm TL) of age-0 Colorado pikeminnow in aquaria for 210 d using winter conditions (3 to 5°C) and concluded that the fish "feed readily and remain active at 4°C."

The influence of temperature on fish movement was not consistent when environmental disturbance was present. Disturbance increased fish movement at temperatures ≤10°C and decreased movement at 15°C. Disturbance treatments were not intended to be ecologically relevant, but they may have elicited a natural response to a perceived threat. Casual observations revealed that fish frequently responded to the stimulus with rapid swimming followed by cessation of movement near the substrate. This pattern of swimming was not completely spontaneous, because a stimulus was required to elicit it, but the purpose of the disturbance treatments was to cause fish to move at relatively high rates so that maximum spontaneous movement rates could be approximated. This objective was achieved for temperatures ≤10°C. Maximum movement rates ranged from 0.82 bl/s at 1°C to 1.1 bl/s at 5°C. Other observations support the conclusion that these estimates approximate maximum spontaneous rates. Beyers and Plampin (REPORT C) measured swimming metabolic rates of Colorado pikeminnow in a Brett-type respirometer and reported that at 1.5°C, 42- to 46-mm fish could swim continuously for a minimum of 6 h at a velocity of 1 bl/s, but not at 2 bl/s.

Individual variability in spontaneous movement rates increased with water temperature when disturbance was not present (Figure 1). At 15°C, movement rates of fish in the absence of disturbance ranged from 0.11 to 2.2 bl/s. This magnitude of variability was probably due to real behavioral differences that may reflect individual differences in habitat preferences, hunger, and energy reserves. Similar results have been reported by other investigators, but are usually attributed to variation in fish size (Berry and Pimentel 1985; Hurst and Conover 2001). It is unlikely that the individual variability in fish movement rates that we observed was due to fish size because we studied a narrow size range (45 to 55 mm TL). In addition, when a disturbance was present, variability in movement increased at 1 and 5°C and decreased at 15°C compared to undisturbed fish at the same temperatures. This disturbance effect tended to equalize variability of individual movement rates across temperature treatments. This outcome would not have been observed if individual differences in movement were caused by fish size.

Spontaneous movement rates of undisturbed Colorado pikeminnow ranged from 0.0012 to 2.2 bl/s, and decreased with declining water temperature. Other researchers using different methods have described similar relationships for age-0 and subadult Colorado pikeminnow (Berry and Pimentel 1985; Childs and Clarkson 1996), age-0 smallmouth bass *(Micropterus dolomieu)* fry (Larimore and Duever 1968), age-0 bonytail *(Gila elegans)*, humpback chub *(G. cypha)* (Berry and Pimentel 1985), white crappie *(Pomoxis annularis)* (Smiley and Parsons 1997), lake whitefish *(Coregonus clupeaformis)* (Bernatchez and Dodson 1985), brook trout *(Salvelinus fontinalis)* (Tang et al. 2000), and age-0 striped bass *(Morone saxatilis)* (Hurst and Conover 2001). There are three primary explanations for this general response. First, biochemical reactions within any organism slow with decreased temperature. At cooler temperatures, food is metabolized more slowly, energy conversion is less efficient, muscle reaction, and nervous system response times are longer. Second, prolonged exposure to winter conditions and low temperatures may reduce energy reserves in fish (Thompson et al. 1991). By modifying behavior and reducing activity, overwintering fish may be able to minimize the energetic costs of survival until food and thermal conditions improve in the spring. Thus, fish may conserve energy at colder temperatures by reducing activity unless a stimulus forces them to move. A third explanation for reduced movement in cold conditions is that fish may be less motivated to move because habitats may be isolated by winter conditions or food may be scarce (Childs and Clarkson 1996).

Information about spontaneous rates of movement of young Colorado pikeminnow is important because it can contribute to an understanding of factors that influence growth and survival of wild fish during their first year of life. Accurate estimates of fish swimming ability can contribute to an understanding of potential effects of the operation of hydroelectric facilities.

Estimates of fish activity can also be used to refine fish bioenergetics models as well as increase our knowledge of basic ecology of rare and interesting fishes like the Colorado pikeminnow.

CONCLUSION

Relatively little is known about swimming ability of young warm-water fish like Colorado pikeminnow in winter conditions. The data presented in this investigation describe the realistic range of spontaneous movement rates (activity) of age-0 Colorado pikeminnow in simulated winter conditions. In the absence of disturbance, fish movement rates can be approximated by a temperature-dependent model with the form $y = 0.0895e^{0.1532t}$ where y is bl/s and t is temperature (^{o}C). When a disturbance is present, Colorado pikeminnow can increase their activity up to a level of about 1 bl/s. These data are useful for estimating rates of movement of young Colorado pikeminnow at water temperatures ranging from 1 to 15^{o}C.

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Table 1. - AIC_c values for candidate models describing spontaneous movement rates of Colorado pikeminnow. Better approximating models have lower AIC_c values.

Model	Residual sums of squares	Total sums of squares	AIC_c	Δ AIC_c
Movement in absence of disturbance				
Intercept	6.260	9.488	-18.52	4.14
Linear	4.586	9.488	-21.95	0.71
Exponential	4.426	9.488	-22.66	0
Movement in presence of disturbance				
Intercept	2.406	16.739	-108.11	0
Linear disturbance	2.299	16.739	-107.58	0.53
Linear disturbance and linear temperature	2.287	16.739	-105.32	2.79
Linear disturbance and exponential temperature	2.288	16.739	-105.30	2.81

Δ AIC_c = the difference between each AIC_c value and the minimum value.

Table 2. - Mean and standard deviation (in parentheses) of movement rates (bl/s) of Colorado pikeminnow at experimental water temperatures and disturbance-level combinations (n = 5).

Disturbances/min	Water Temperature			
	1°C	5°C	10°C	15°C
0	0.11(0.078)	0.20(0.12)	0.40(0.34)	0.89(0.98)
1	0.45(0.13)	0.54(0.18)	0.58(0.33)	0.61(0.29)
2	0.64(0.17)	0.66(0.26)	0.73(0.33)	0.56(0.30)

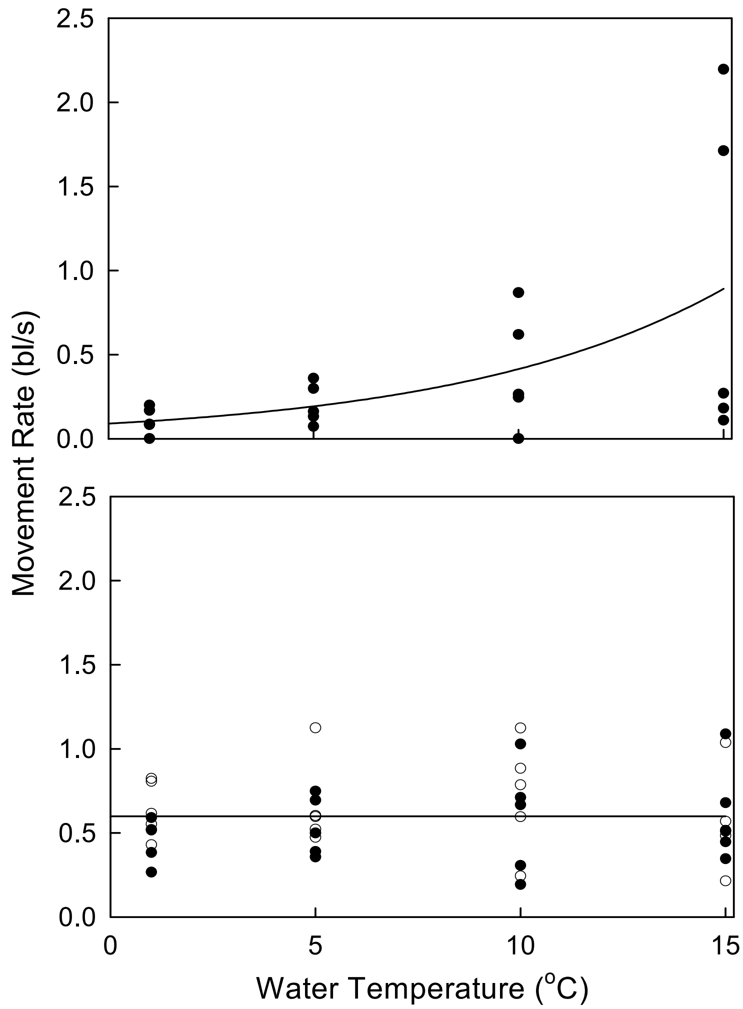

Figure 1. – Spontaneous movement rates of age-0 Colorado pikeminnow in the absence (top; $y = 0.0895e^{0.1532t}$) and presence (bottom; $y = 0.60$) of a disturbance stimulus. Plots show the observed responses (markers) and fitted models (lines) for movement as a function of water temperature. Filled markers represent 1 disturbance/min; unfilled markers, 2 disturbances/min.

REPORT C

Development of a Bioenergetics Model for Evaluating Factors that Influence Overwinter Survival of Age-0 Colorado Pikeminnow in the Green River, Utah

FINAL REPORT

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EXECUTIVE SUMMARY

This investigation used a bioenergetics-based approach to evaluate if overwinter survival of age-0 Colorado pikeminnow can potentially be influenced by human-induced changes in fish activity. A bioenergetics model was constructed specifically for Colorado pikeminnow life stages and temperature conditions that occur during winter in the Green River near Jensen, Utah. Accuracy of the model was confirmed by comparing predictions to observed fish growth in an independent investigation. To evaluate the effect of increased activity, fish growth was simulated for a 118-d period using combinations of a winter temperature regime and three activity levels: temperature-dependent spontaneous activity having a mean of about 0.1 body lengths/s (bl/s); or constant activity of 0.5 or 1.0 bl/s. When activity rates were spontaneous or 0.5 bl/s, 35-, 45-, and 60-mm TL fish survived to the end of the winter period. When activity was 1.0 bl/s fish did not survive to the end of the winter period regardless of size. Consequently, the bioenergetics analysis could not exclude the hypothesis that human-induced changes in activity can affect overwinter survival of age-0 Colorado pikeminnow in the Green River near Jensen, Utah. The bioenergetics model is useful for evaluating potential effects of factors like fish size in fall, winter temperature regime, and human-induced changes in fish activity on overwinter survival of age-0 Colorado pikeminnow.

INTRODUCTION

The Colorado pikeminnow *(Ptychocheilus lucius)* is a large cyprinid endemic to the Colorado River Basin. Historically, the Colorado pikeminnow was widespread in warm-water streams and rivers, but the species was listed as federally endangered in 1967 in response to declining populations (U.S. Department of Interior 1967). The decline of Colorado pikeminnow is commonly attributed to interactions with introduced fishes, construction of dams, and habitat modification (Carlson and Muth 1989; U.S. Fish and Wildlife Service 1992; Tyus 1991).

An important element of Colorado pikeminnow life history is the reliance of early life stages on nursery habitats. Nursery habitats for Colorado pikeminnow have been identified as backwaters and other low-velocity areas that occur along shorelines of rivers (Tyus 1991). Young fish occupy these habitats throughout their first year of life.

The Green River in Utah is a large tributary to the Colorado River and is one of the strongholds for Colorado pikeminnow populations. Winter discharge in the Green River is influenced by releases from Flaming Gorge Dam. It has been hypothesized that winter operations of Flaming Gorge Dam reduce survival of age-0 Colorado pikeminnow (Carlson and Muth 1989; U.S. Fish and Wildlife Service 1992; Valdez and Cowdell 1996; Haines et al. 1998); but, negative effects on overwinter survival have not been demonstrated. One possible mechanism for reduced survival of fish is that winter operations increase activity of young Colorado pikeminnow.

The potential effect on young Colorado pikeminnow of increased energetic cost of activity caused by winter operations of Flaming Gorge Dam is unknown, but can be estimated using a fish bioenergetics model. Bioenergetics models have been used for over 20 years to evaluate affects on fish of a wide range of natural and anthropogenic stressors (Beyers and Rice 2002). Model-evaluation studies have demonstrated that when inputs are well-known there is good agreement between predicted and observed responses (Rice and Cochran 1984; Whitledge et al. 1998; Beyers et al. 1999; Madenjian et al. 2000). In addition, sensitivity analysis has been used to evaluate model behavior and predictions (Kitchell et al. 1977; Stewart et al. 1983; Bartell et al. 1986; Beyers et al. 1999).

The purpose of this investigation was to construct a bioenergetic model that describes energetics of age-0 Colorado pikeminnow in winter conditions, and use the model to evaluate the potential influence of activity on overwinter survival of fish in the Green River near Jensen, Utah. These objectives were achieved by measuring a variety of energetic characteristics of age-0 Colorado pikeminnow including: food consumption as a function of fish size and water temperature; metabolic rate as a function of fish size and water temperature; and metabolic rate as a function of activity. Equations describing each response were integrated into a fish bioenergetics model that is based on a widely used format (Hanson et al. 1997). Accuracy of the model was evaluated by comparing predicted growth of Colorado pikeminnow to observed growth in an independent investigation (Thompson 1989). The fish bioenergetics model was then used to evaluate the influence of water temperature, fish size, changes in fish activity, and food consumption rates on overwinter survival of age-0 Colorado pikeminnow.

MATERIALS AND METHODS

Laboratory data

Experimental animals

Larval Colorado pikeminnow were obtained from Dexter National Fish Hatchery and Technology Center (Dexter, New Mexico). Juvenile Colorado pikeminnow were obtained from the Grand Valley Propagation Facility (Grand Junction, Colorado). Fish were reared in mass cultures in laboratory facilities at Colorado State University (Fort Collins, Colorado). Culture-facility water temperature was 18°C. For the investigations described below, fish were acclimated to study temperatures for at least 14 d by randomly selecting fish and transferring them to separate mass cultures where target temperatures were held ±2°C. Not all fish used in the investigation were age 0. Older, larger fish were included in several experiments so that size-dependent relationships could be accurately estimated. Fish used in the investigation ranged from 28 to 164 mm total length (TL) and 0.100 to 29.20 g blotted wet mass.

The freshwater oligochaete *(Lumbriculus variegatus)* was used as a surrogate for natural prey in food-consumption studies described below. *L. variegatus* were obtained from in-house cultures and Aquatic BioSystems (Fort Collins, Colorado).

Weight-length relationship

Total lengths (to the nearest 1mm) and blotted wet mass (to the nearest 0.001 g) of 86 live Colorado pikeminnow were measured during the investigation. The data were collected to estimate a weight-length relationship using standardized methods (Anderson and Gutreuter 1983).

Food consumption as a function of fish size

The relationship between maximum food consumption and fish size, also known as weight dependence of consumption $C f(W)$), was estimated by offering fish, ranging in mass from 0.120 to 2.254 g, known rations of *L. variegatus*. Experimental treatments were assigned to 20 aquaria using a balanced, randomized design with each of four fish-size treatments (approximately 0.2, 0.4, 0.8, and 2 g) assigned to five aquaria ($n = 5$). One Colorado pikeminnow (experimental unit) was randomly assigned to each aquarium. Aquaria were 40 × 20 × 25 cm high, and water depth was 20 cm. Aquaria were arranged within a water bath and a water temperature of 15±1°C was maintained. Water temperature was recorded continuously using a chart recorder. Colorado pikeminnow were transferred from mass cultures to aquaria for acclimation 48 h before feeding experiments were conducted. Food was withheld during the acclimation period. Water in aquaria was replaced at a flow rate of about 75 mL/min. The water source was the same as that used for mass cultures. Cool-white fluorescent lamps were the only source of illumination (530 lx), and a 8-h light, 16-h dark photoperiod was maintained.

At conclusion of the acclimation period, an initial ration (blotted wet mass) of live *L. variegatus* equal to about 20% of fish mass was introduced into each aquarium. After 24 h, aquaria were inspected and an additional ration was given if ≥75% of the first ration was consumed. Feeding was stopped at 48 h when remaining *L. variegatus* were removed by siphoning, and their mass was determined. Colorado pikeminnow were left in aquaria for an additional 48 h to allow for gut clearance, then each fish's mass and TL were determined. A preliminary study showed that mass of *L. variegatus* changed with time during the 48-h feeding period. Consequently, five additional rations were placed in separate aquaria without fish so that the background change in mass could be estimated. After correcting for background mass loss of *L. variegatus*, observed food consumption of each fish was expressed as a mass-specific rate (g prey $\cdot$ g fish^{-1} $\cdot$ d^{-1}).

Food consumption as a function of water temperature

Temperature dependence of food consumption *(C f*(*T*)) was estimated by exposing Colorado pikeminnow to water temperatures ranging from 1.5 to 15°C and offering them known rations of *L. variegatus*. Fish in each treatment had approximately the same mass ($\bar{x}$ = 0.889g; range = 0.808 to 0.979 g). Experimental treatments were assigned to 20 aquaria using a balanced, randomized design with each of four temperature treatments (1, 5, 10, and 15 ± 1°C) assigned to five replicate aquaria (n = 5). Characteristics of aquaria, temperature-control system, acclimation procedures, and food consumption methodology were identical to those described above.

Respiration as a function of fish size

Weight dependence of respiration *(R f*(*W*)) was estimated by measuring metabolic rates of resting fish ranging from 0.100 to 12.42 g. Five fish from each of six size treatments (approximately 0.2, 0.4, 0.8, 2, 5, and 11 g) were assigned to static respirometers (Cech 1990) using a balanced, randomized design (n = 5). Not all fish sizes were available simultaneously, so a completely randomized study design could not be used. However, fish of different sizes were obtained from two sources so the order of measurement of metabolic rates of each group was interspersed (0.2, 0.4, 5, 11, 0.8, and 2 g). Respirometers were 14-cm long × 4-cm diameter plastic cylinders having a volume of approximately 180 mL for 0.2- to 0.8-g fish, and 21-cm long × 9-cm diameter glass jars having a volume of approximately 1,500 mL for 2- to 11-g fish. Respirometers were arranged within a water bath, and a water temperature of 15±1°C was maintained. A blind surrounded the water bath so that sampling could be conducted without disturbing the fish. Light intensity in the blind was less than 1 lx. Food was withheld from fish for 48 h before respirometry measurements. Colorado pikeminnow were transferred for acclimation from mass cultures to respirometers about 12 h before measurements were made. During acclimation, water in respirometers was replaced about twice per hour. The water source was the same as that used for mass cultures.

At the end of the acclimation period, respiration rate of each fish was measured using the following standard respirometry protocol. The flow of water to each respirometer was interrupted and initial oxygen concentration was measured using an external water pump that recirculated water from closed respirometers to an oxygen meter (Model 57, Yellow Springs Instrument Company, Yellow Springs, Ohio). A final measurement was taken after 1 to 3 h depending on the rate of oxygen decline. Initial dissolved oxygen concentrations ranged from 6.6 to 8.4 mg/L. Final measurements were made before dissolved oxygen concentrations declined to less than 5.0 mg/L. Then mass and TL of each fish were determined. After correcting for biological oxygen demand of respirometers, observed oxygen consumption of each fish was expressed as its mass-specific rate (mg $O_2 \cdot$ g fish$^{-1} \cdot$ d^{-1}).

Respiration as a function of water temperature

Temperature dependence of respiration *(R f(T))* was estimated by exposing Colorado pikeminnow to water temperatures ranging from 1.1 to 15.6°C and measuring metabolic rates as described above. Fish in each treatment had approximately the same mass ($\bar{x}$ = 0.893 g; range = 0.794 to 1.033 g). Individual fish were assigned to static respirometers using a balanced, randomized design (n = 5) with four temperature treatments (1, 5, 10, and 15 ± 1°C). Characteristics of respirometers, temperature-control system, acclimation procedures, and respirometry methodology were identical to those described above. Initial dissolved oxygen concentrations ranged from 6.60 to 10.92 mg/L.

Respiration as a function of activity

Activity dependence of respiration *(R f(A))* was estimated by measuring swimming metabolic rates of Colorado pikeminnow using a swimming respirometer (Cech 1990). Fish in each treatment had approximately the same mass ($\bar{x}$ = .487 g; range = 0.407 to .610 g). Individual fish were assigned to the respirometer using a balanced, randomized design (n = 5) with three swimming-speed treatments of 0.5, 1, or 2 body lengths/second (bl/s). It was assumed that respiration estimates for fish in weight- and temperature-dependent studies (described above) represented metabolic rates at 0 bl/s since fish were quiescent in static respirometer chambers. The swimming respirometer consisted of a closed loop of transparent plastic pipe with a variable speed centrifugal pump. Diameter of the respirometer at the point occupied by fish was 4 cm. This size was selected to minimize solid blocking effects within the respirometer, since fish cross-sectional area was less than 10% of the cross-sectional area of the apparatus (Cech 1990). The respirometer had a volume of approximately 900 mL. The respirometer was placed within a water bath and a water temperature of 1.5±0.5°C was maintained. Total lengths of Colorado pikeminnow were measured when fish were transferred from mass cultures to holding aquaria 48-h before respirometry trials. Other acclimation procedures were identical to respirometry studies described above.

At the end of the acclimation period, water velocity in the respirometer was gradually increased over a period of 30 s from 0 to 1 or 0 to 2 bl/s depending on each fish's TL and respective treatment. Respiration rate of each fish was measured using the standard respirometry protocol with final measurements taken after about 5 h. Initial dissolved oxygen concentrations ranged from 12.90 to 12.72 mg/L. After correcting for biological oxygen demand of the respirometer, observed oxygen consumption of each fish was expressed as its mass-specific rate (mg $O_2 \cdot$ g fish$^{-1} \cdot$ d^{-1}).

Field data

Temperature data were recorded from a nursery habitat (Johnson Backwater) on the Green River, Utah, where Colorado pikeminnow occur (see REPORT A for description of locality). Temperature measurements were made at the mouth, midpoint, and tail of the backwater, as well as in the main channel of the river. Two temperature regimes ("preferred" and "midpoint") were extracted from the data. The preferred regime was assembled from the warmest average daily temperatures of all of the recording locations. Thus, the regime mimics the thermal conditions that fish might encounter if they preferentially selected the warmest microhabitats. The midpoint regime was assembled directly from the average daily temperatures recorded at the midpoint of the backwater. This regime represents conditions that fish might encounter if they occupy the relatively persistent, low-velocity portion of the backwater. Both temperature regimes started on 22 November 2001 and ended on 19 March 2002 (118 d). Water temperature was ≤ 5°C for the entire period, and ice covered the habitat from 29 November 2001 to 19 March 2002.

Statistical analysis

General approach

Statistical analysis was based on a model-selection philosophy advocated by Burnham and Anderson (1998). The general method of analysis was to identify likely candidate models from fish bioenergetics literature (Adams and Breck 1990; Hanson et al. 1997) and then fit dependent variables as functions of independent variables for each model using nonlinear regression (NLIN procedure; SAS 1990). Commonly used models included linear ($y = a + bx$), exponential ($y = e^{ax}$), and power ($y = ax^b$) functions where y is the dependent variable, x is the independent variable, and a and b are constants. An intercept model ($y = a$) was also fit to each data set because it represents the null hypothesis of no relationship between dependent and independent variables. Best approximating models were identified using Akaike's information criterion with small-sample bias adjustment (AIC_c). In some cases, candidate models had AIC_c values that differed by less than 2 AIC_c units. Models that differ by less than 2 AIC_c approximate the data equally well (Burnham and Anderson 1998). When this occurred, one of the models was selected based on traditional principles of fish bioenergetics. Fit of best approximating models was evaluated by interpretation of data and residual plots.

Weight-length relationship

The generally accepted model for describing the relationship between fish weight and length is the power function, where y = fish mass (g) and x = TL (mm). This model is so universally accepted (Anderson and Gutreuter 1983) that the intercept model was the only other model evaluated.

Food consumption characteristics

Size dependence of consumption is typically described using a power function, where y = specific food consumption (g prey $\cdot$ g fish^{-1} $\cdot$ d^{-1}) and x = fish mass (g). Intercept and linear models were also evaluated (Hanson et al. 1997).

A variety of models have been used to describe the temperature-dependent relationship of food consumption (Hanson et al. 1997). Several of the models account for reduced food consumption when water temperatures are above the physiological optimum of a fish. The emphasis of this investigation was on the influence of winter conditions. Winter water temperatures are below the physiological optimum for Colorado pikeminnow. Consequently, food-consumption data were collected over a temperature range that was below the optimum and a relatively simple exponential model, where y = specific food consumption (g prey $\cdot$ g fish^{-1} $\cdot$ d^{-1}) and x = water temperature (°C), is commonly used to describe the relationship. Intercept and linear models were also evaluated.

Respiration characteristics

Size dependence of respiration is typically described using a power function, where y = specific respiration ($mg\ O_2 \cdot g\ fish^{-1} \cdot d^{-1}$) and x = fish mass (g). Intercept and linear models were also evaluated.

Below-optimum water temperatures affect respiration in the same fashion as food consumption. Therefore, the exponential model, where y = specific respiration ($mg\ O_2 \cdot g\ fish^{-1} \cdot d^{-1}$) and x = water temperature (°C), was used to describe the relationship. Intercept and linear models were also evaluated.

Activity dependence of respiration was described by fitting a linear model where y = specific respiration ($mg\ O_2 \cdot g\ fish^{-1} \cdot d^{-1}$) and x = swimming speed (bl/s). The intercept model was the only other model fit to the data. Model selection for activity dependence of respiration was limited by availability of reliable data. Respiration estimates at 0.5 bl/s were unreliable because fish did not swim continuously at that speed. Estimates at 2 bl/s were unreliable because only one of five fish swam for the duration of the measurement period. Consequently, data for only two swimming-speed treatments (0 and 1 bl/s) were available for analysis.

Bioenergetics modeling

Equations and parameters

Bioenergetics models for fish derive from the same general equation (Warren 1971; Brett and Groves 1979; Kitchell 1983). The equation represents an energy budget that balances energy intake from prey consumption against expenditures for metabolism, waste production, and storage of surplus energy in the form of growth. The general equation for growth is:

growth = consumption - respiration - egestion - excretion

For purposes of simulation modeling, each component of the general equation has been reformulated to describe growth as an integration of rate-specific physiological processes. We used the format described by Hanson et al. (1997). Parameters for each equation (Table 1) were estimated during this investigation or obtained from the literature.

Daily food consumption (C) has the general form $C = C\,f(W) \cdot p \cdot C\,f(T)$ where $C\,f(W) = CA \cdot W^{CB}$, p = the realized proportion of maximum consumption, and $C\,f(T) = e^{CQ \cdot T}$. The parameter CA was 0.00991, estimated using the intercept value of 0.0107 from the regression equation for temperature-dependent feeding adjusted for a 1-g fish. Other parameters were obtained directly from respective regression equations (Table 1).

Activity-dependent respiration (R) was modeled as $R = R\,f(W) \cdot R\,f(T) + R\,f(A)$ where $R\,f(W) = RA \cdot W^{RB}$, $R\,f(T) = e^{RQ \cdot T}$, and $R\,f(A) = AB \cdot \mathrm{ACT}$. The parameter RA was 0.258, estimated using the intercept value of 0.262 from the regression equation for temperature-dependent respiration adjusted for a 1-g fish. Other parameters were obtained directly from respective regression equations (Table 1). Temperature-dependent spontaneous activity (ACT) of age-0 Colorado pikeminnow was estimated using the model described by Plampin and Beyers (REPORT B): $\mathrm{ACT} = 0.0895e^{0.153 \cdot T}$ where ACT = bl/s. Respiration rate (mg $O_2 \cdot$ g fish$^{-1} \cdot$ d^{-1}) was transformed to its energetic equivalent using the conversion 13.556 J/mg O_2 (Elliot and Davidson 1975).

Experimental data describing rates of specific dynamic action, egestion, and excretion were not collected during this investigation and specific values are not available. Simple proportional models presented in Hanson et al. (1997) were used. The equation for egestion has the form $F = FA \cdot C$; excretion has the form $U = UA \cdot C - F$); and specific dynamic action has the form $S = \mathrm{SDA} \cdot C - F$). Parameter estimates for FA, UA, and SDA are general values suggested by Hanson et al. (1997). Model analysis has demonstrated that bioenergetics-based predictions are not sensitive to parameter values for egestion, excretion, or specific dynamic action (Bartell et al. 1986; Beyers et al. (1999). Therefore, general estimates can be substituted for unknown species-specific values without creating unacceptable bias in model predictions.

Energy densities of Colorado pikeminnow and prey

Thompson et al. (1991) measured lipid content (14.9%) in wild age-0 Colorado pikeminnow from the Colorado River and presented an equation that can be used to calculate body-water percentage (BW%) based on lipid content: BW% = (220.89 - lipid%)/2.54. Based on this equation, dry-mass percentage (DM%) was calculated, and wet-mass energy density (ED) expressed as J/g was estimated using an equation for Cyprinidae given by Hartman and Brandt (1995): ED = -981 +251.1 · DM%. Calculations yielded a dry-mass percentage of 18.9 and a predicted wet-mass energy density of 3,765 J/g.

Diet of wild Colorado pikeminnow (31 to 73 mm TL) comprises about 53% dipteran larvae, 27% fish, and 20% miscellaneous aquatic invertebrate larvae and adults, and debris (Muth and Snyder 1995). We assumed that the wet-mass energy density of dipteran larvae (1,047 J/g; Hanson et al. 1997) approximated the energy density of the miscellaneous fraction of the diet. A wet-mass energy density of 1,781 J/g was calculated for the typical diet of Colorado pikeminnow in winter assuming a diet of 73% dipteran larvae or energetically equivalent food items, and 27% fish larvae having the same energy density as Colorado pikeminnow. Energy densities of Colorado pikeminnow and prey were assumed to be constant throughout winter.

Estimate of p for food consumption

Most fish bioenergetics applications solve for p using an iterative technique that fits model outcomes to observed growth data so that food consumption can be predicted. A similar approach was used in this investigation. The value of p was estimated using results of a laboratory feeding study (Thompson 1989), where age-0 Colorado pikeminnow were fed an *ad libitum* ration of brine shrimp nauplii for 210 d under winter conditions (3.5°C). Brine shrimp nauplii were assumed to have a wet-mass energy density of 2,370 J/g (D.W. Beyers, unpublished data). Laboratory fish grew from a mean TL of 30.1 mm to a mean TL of 31.3 mm, but mean mass (0.14 g) remained the same after 210 d. Mean fish condition declined from 0.52 to 0.46 which is an 11.5% reduction. Because growth of fish was not completely characterized by fish TL or mass, the relative change in condition was used to estimate p. The bioenergetics model was used to simulate growth of a 0.14-g fish for 210 d at 3.5°C. Condition (K) was calculated as $K = (\mathrm{W} \times 10^5)/(\mathrm{TL})^3$. Fish length was calculated using the weight-length regression equation. The value of p was manipulated to obtain an 11.5% reduction in fish condition at the end of the simulation. The final p value was 0.10, and in the simulations that follow, we assumed that this value was appropriate for wild fish.

Model evaluation

Performance of the bioenergetics model was evaluated in two steps. First, the model was used to estimate food consumption and respiration of Colorado pikeminnow in laboratory studies described in this paper and the predicted outcomes were compared to observed responses. Use of this observed data set represents a circular demonstration of model performance, because the data were used to construct the model. However, this evaluation step was important for confirming that the model was functioning properly. No adjustment to parameter values or model structure resulted from the analysis.

The second evaluation step involved comparing modeled growth of Colorado pikeminnow to observed data from an independent experiment. Thompson (1989) studied growth of two sizes ($\bar{x}$ = 0.14 and 0.62 g) of age-0 Colorado pikeminnow in the laboratory using winter conditions (3.5°C). One component of the investigation involved observing the decline in mass and condition of unfed fish for up to 210 d. Food consumption of fish in the investigation was known (i.e., 0); therefore, growth of fish was predicted using the bioenergetics model. The simulation started with 0.14- or 0.62-g fish that were not fed (p = 0) for the duration of the growth period. Growth was simulated for 70 or 210 d, which were the respective intervals for small and large fish in the laboratory experiment. The thermal regime was a constant 3.5°C. Laboratory data were available to estimate means and 95% confidence intervals for small fish at 0 and 70 d, and for large fish at 0, 70, 140, and 210 d. These observed data were plotted as a function of time so that they could be compared to bioenergetics model predictions.

Simulations

Six simulations were conducted to describe the relative influence of water-temperature regime, fish size, fish activity, and % maximum consumption on Colorado pikeminnow growth. Each simulation started with a 35-, 45-, or 60-mm TL (0.228, 0.495, and 1.201 g, respectively) Colorado pikeminnow feeding at 10% (p = 0.10; unless noted otherwise) of maximum ration for 118 d. At the end of each day, total length and fish condition (K) were updated. If fish growth was positive, total length was increased using the weight-length regression equation. If fish growth was negative, total length was held constant at the value for the previous day. Fish condition was calculated using the condition index described above. Thompson et al. (1991) used the same condition index and reported that the mean value for dying fish was 0.36. Therefore, if $K \leq 0.36$ the simulation was stopped.

In the first simulation, the model was used to predict growth of fish using the preferred backwater temperature regime. This combination of environmental conditions, fish bioenergetics, and fish behavior is probably the closest representation of all the simulations to undisturbed natural fish growth in winter conditions. The simulation illustrates differences in growth that result from initial size and also represents a baseline for evaluating effects of other factors on Colorado pikeminnow growth.

The second simulation was identical to the first, but used the midpoint backwater temperature regime. Thus, the simulation quantifies the affect on growth of a slightly cooler water temperature regime.

The third simulation was based on the first, but was modified to demonstrate the potential influence of a disturbance-induced change in fish activity. Plampin and Beyers (REPORT B) showed that spontaneous activity of age-0 Colorado pikeminnow can increase from a mean of 0.104 bl/s at 1°C for undisturbed fish, to a mean of 0.60 bl/s at 1 to 5°C in the presence of physical disturbance. To evaluate the influence of increased activity on fish growth, swimming speed was constrained to 0.5 bl/s for the duration of the simulation. The simulation shows how growth and condition of fish would be affected if human disturbance causes approximately a five-fold increase in fish activity.

The fourth simulation had the same conditions used in the previous example, except activity was increased to an even higher magnitude. Plampin and Beyers (REPORT B) showed that activity of fish exposed to physical disturbance can increase up to 1.1 bl/s at 5°C. This magnitude of increased activity was evaluated by constraining swimming speed to 1 bl/s for the duration of the simulation.

The fifth simulation evaluates the effect of an episodic increase in activity. Conditions were identical to simulation 4, but it was assumed that activity increased to 1 bl/s on only 6 d out of each week. This pattern mimics the regime that might be produced if human disturbance is high on Monday through Saturday, and relatively low on Sunday.

The last simulation illustrates the importance and potential sensitivity of the model to the value of p. Conditions were identical to simulation 4 except % maximum consumption (p) was increased to 0.2. Results of this simulation are important because p is not known for wild age-0 Colorado pikeminnow in the Green River. In this investigation, the value of p for wild fish was estimated using Thompson's (1989) data (p = 0.1). Sensitivity of the model to the parameter value for % maximum consumption can be evaluated by comparing predictions when p = 0.2 to results when p = 0.1 (simulation 4).

RESULTS

Laboratory data

Weight-length relationship

A power function provided a good description of weight-length data (Figure 1) and explained more than 99% of variation based on sums of squares (Table 2). The equation had the form $y = 4.01\times10^{-6} x^{3.08}$.

Food consumption characteristics

The model that best described the size-dependent relationship of food consumption was a power function (Table 2) . The model explained about 90% of variation based on sums of squares. The equation had the form: $y = 0.0527x^{-0.673}$ (Figure 2).

Two models, linear and exponential, gave approximately equal descriptions of the temperature-dependent relationship of food consumption (Table 2). The AIC_c values for the models differed by about 0.3 units. When water temperatures are below the physiological optimum of a fish, the data are typically modeled using an exponential model. Consequently, the exponential model was selected for consistency with current fish bioenergetics-modeling practices. The model explained about 90% of variation based on sums of squares. The equation had the form: $y = 0.0107e^{0.108x}$ (Figure 2).

Respiration characteristics

Two models, linear and power, were about equal in their approximation of the data for weight dependence of respiration (Table 2). The AIC_c values for the models differed by about

1.6 units. A power model is typically used to describe weight dependence of respiration. The data have the general shape of a power curve (Figure 3), but unexplained variation from estimated respiration rates for 0.4-g fish reduced model fit. This interpretation was confirmed by re-running the analysis with the 0.4-g data omitted. With the modified data set, the power model gave the best approximation by an AIC_c margin of 9.73. No methodological reason could be identified for the unexplained variation in respiration rates. Because it is possible that the data reflect real developmental changes in metabolic rates of Colorado pikeminnow, the original power function was selected as the best approximating model. The model explained about 90% of variation based on sums of squares. The equation had the form: $y = 3.108x^{-0.142}$.

The model that best described temperature dependence of respiration was an exponential function (Table 2) . The model explained about 96% of variation based on sums of squares. The equation had the form: $y = 0.262e^{0.161x}$ (Figure 3).

A linear model provided a good description of activity dependence of respiration (Figure 4) and explained about 92% of variation based on sums of squares (Table 2). The equation had the form: $y = 0.620 + 1.12x$. Respiration rates were measured by swimming fish for 4 to 6 hours. All fish swam for the duration of the measurement periods at 1 bl/s.

Bioenergetics modeling

Model evaluation

Estimates of Colorado pikeminnow growth in the 210-d laboratory experiment were in close agreement with observed responses (Figure 5). The difference between mean predicted and observed responses for large fish was 5.6, 7.4, and 3.8% after 70, 140, and 210 d of growth.

The difference for small fish was 3.9% after 70 d of growth. None of the small fish in Thompson's (1989) investigation survived to 140 d, so additional growth data were not available for comparison. However, the model did predict that small fish would not survive to 140 d.

Simulations

Under simulated winter conditions using the preferred temperature regime (simulation 1), all three sizes of Colorado pikeminnow lost mass and had decreasing condition with time (Figure 6; Table 3). All size groups survived. The lowest condition factor observed (0.478) was for 45-mm fish. Condition trajectories for 35- and 45-mm fish crossed at about day 92. This effect is due to interactions of model parameters and nonlinear relationships within the model such that the relative influence of simulated conditions is not constant for all fish sizes.

The slightly cooler midpoint temperature regime (simulation 2) had a relatively small affect on growth of Colorado pikeminnow compared to the preferred regime (Table 3). Mean temperatures for the midpoint and preferred regimes were 0.66 and 0.80°C, respectively, and the ranges were identical (0.1 to 4.9°C). At the end of the simulation, fish in the midpoint regime were larger than those in the preferred regime, and the growth effect ranged from 0.001 g for 35-mm fish to 0.005 g for 60-mm fish. Fish condition followed a similar pattern. Slower mass loss in the cooler temperature regime was probably caused by a temperature-induced reduction in metabolic rate.

Increasing activity of fish to a constant 0.5 bl/s (simulation 3) produced about a 17% decrease in fish mass and condition at the end of the simulation (Table 3). All fish survived the simulated winter period with ending condition factors ranging from 0.400 to 0.396.

Increasing activity of fish to a constant 1.0 bl/s (simulation 4) resulted in mortality of all sizes of fish after 89 to 92 d (Figure 7; Table 3). Fish mass at the time of death was about 25% less than at the start of the simulation.

When activity of fish was 1 bl/s for 6 d of each week, and spontaneous for the last day of each week (simulation 5), mortality was delayed for about 11 d compared to simulation 4 (Figure 8; Table 3). This outcome reveals the benefit of lower energetic cost of spontaneous activity compared to increased activity. A total of 14 d of spontaneous activity occurred during the time period that fish were alive (100 to 103 d).

Sensitivity of model predictions to the value of *p* varied with fish size (simulation 6; Table 3). Model conditions for simulations 4 and 6 were identical except for different *p* values. Thus, the direct effect of changing *p* can be observed by comparing outcomes of the two simulations. Doubling the value of *p* from 0.1 to 0.2 increased survival times by 24, 13, and 6 d for 35-, 45-, and 60-mm fish respectfully. Although survival times were longer when *p* was larger, the ultimate outcomes of simulations 4 and 6 were similar because mortality occurred before the winter period ended in every case.

DISCUSSION

Biological significance of increased activity

Bioenergetics modeling predictions suggest that overwinter survival of age-0 Colorado pikeminnow may be negatively affected if fish activity increases in response to human-induced changes in the environment. Simulations showed that fish mass and condition consistently decline when water temperatures are below 5°C. Mass and condition of fish decline faster when activity is increased because energetic reserves must be used to offset the cost of higher metabolic rate.

Activity rates of age-0 Colorado pikeminnow in the Green River during winter are unknown because direct observations of fish are difficult to obtain. Consequently, the approach used in this investigation was to evaluate outcomes of realistic ranges of potential conditions including water temperature regimes, activity rates, and food consumption rates. Of the factors investigated, fish activity rates had the greatest influence on overwinter survival of age-0 Colorado pikeminnow. When activity rates were at a relatively low spontaneous level (simulation 1), or at a moderate level of 0.5 bl/s (simulation 3), fish survived to the end of the 118 d winter period. When activity was at a relatively high level of 1 bl/s (simulation 4), age-0 fish did not survive to the end of the winter period regardless of their size. The strong influence of activity on winter bioenergetics of Colorado pikeminnow was confirmed by running an additional simulation with a two-fold increase in food consumption (simulation 6). Doubling the food consumption rate extended the survival time of Colorado pikeminnow, but the energetic increase was insufficient to offset the cost of a 1 bl/s activity rate.

Data needs suggested by model evaluation

Sensitivity of model predictions to the value of *p* suggests that it is more important to obtain additional information about food consumption rates of small fish than for large fish. When *p* was increased from 0.1 to 0.2 (simulation 6), survival times increased by 24 d for 35-mm fish, but only 6 d for 60-mm Colorado pikeminnow. The effect on model predictions was 4× greater for 35-mm fish compared to 60-mm fish, which suggests that inaccuracy in the estimate of *p* for small fish will produce a similarly biased model prediction. This does not imply that the current model is inaccurate. It does suggest that additional data describing the magnitude of *p* for small fish are potentially valuable, because it is important to confirm that current estimates are accurate. Data that are required for estimating *p* for wild Colorado pikeminnow are repeated measurements of mass (to nearest 0.01g) and total length (to nearest 1 mm) of individual fish before and after the winter period. Once the change in individual fish mass during winter is known, *p* can be estimated with the fish bioenergetics model using the same procedure described in the methods section of this paper.

CONCLUSIONS

Numerous natural and anthropogenic factors influence environmental conditions of winter habitats occupied by age-0 Colorado pikeminnow. Isolating the effects of these factors on overwintering fish is impossible under field conditions because the environment cannot be controlled. It has been hypothesized that winter operations of Flaming Gorge Dam reduce survival of age-0 Colorado pikeminnow because changes in the physical environment may cause an increase in fish activity. The bioenergetics model presented in this investigation, represents a mechanistic-based attempt at evaluating if it is possible for disturbance-induced changes in fish activity to negatively influence survival of age-0 Colorado pikeminnow in winter conditions. Six simulations were conducted using a variety of realistic fish sizes, temperature regimes, activity rates, and feeding conditions. The simulations showed that when movement rates (activity) were $\leq$ 0.5 bl/s, fish always survived to the end of the simulated winter period. In contrast, when movement rates were 1 bl/s for at least 6 d of each week, none of the fish survived the winter period. Consequently, the bioenergetics analysis could not exclude the hypothesis that human-induced changes in fish activity can affect overwinter survival of age-0 Colorado pikeminnow in the Green River near Jensen, Utah. For age-0 Colorado pikeminnow, winter conditions produce a negative energy balance, where the costs of survival are greater than the energetic gains realized by food consumption. If it can be shown that the operation of Flaming Gorge Dam increases activity of age-0 Colorado pikeminnow in the Green River, then further evaluations should be conducted to determine the likelihood that natural mortality rates are affected.

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Table 1. - Parameter values and standard error of estimates (in parentheses) for age-0 Colorado pikeminnow bioenergetics model.

Parameter[a]	Parameter description	Value	Source[b]
	Consumption		
CA	Intercept of weight-dependence function	0.00991(0.00304)	1
CB	Slope of weight-dependence function	-0.673 (0.110)	1
CQ	Slope of temperature-dependence function	0.108(0.021)	1
	Respiration		
RA	Intercept of weight-dependence function	0.258(0.071)	1
RB	Slope of weight-dependence function	-0.142(0.044)	1
RQ	Slope of temperature-dependence function	0.161(0.019)	1
AB	Slope of activity-dependence function	1.12(0.23)	1
SDA	Specific dynamic action	0.175	2
	Egestion and excretion		
FA	Proportion of consumption egested	0.15	2
UA	Proportion of consumption excreted	0.1	2

[a]Parameter notation after Hanson et al. (1997).

[b]Sources: 1 = this investigation; 2 = Hanson et al. (1997).

Table 2. - AIC_c values for candidate models describing bioenergetics of Colorado pikeminnow. Better approximating models have lower AIC_c values.

Model	Residual sums of squares	Total sums of squares	AIC_c	$\Delta\ AIC_c$
Weight-length relationship				
Intercept	3662	5143	326.7	433.8
Power	23.0	5143	-107.1	0
Food consumption as a function of size				
Intercept	0.0797	0.2355	-112.3	23.90
Linear	0.0401	0.2355	-124.0	12.22
Power	0.0224	0.2355	-136.2	0
Food consumption as a function of water temperature				
Intercept	0.0079	0.0249	-151.9	19.71
Linear	0.0025	0.0249	-171.6	0
Exponential	0.0026	0.0249	-171.3	0.3077
Respiration as a function of size				
Intercept	41.88	317.0	14.45	6.867
Linear	32.40	317.0	9.231	1.646
Power	30.67	317.0	7.585	0
Respiration as a function of water temperature				
Intercept	26.46	66.99	10.30	41.10
Linear	6.682	66.99	-14.42	16.37
Exponential	2.947	66.99	-30.79	0
Respiration as a function of activity				
Intercept	3.989	15.25	-1.323	6.101
Linear	1.188	15.25	-7.424	0

$\Delta\ AIC_c$ = the difference between each AIC_c value and the minimum value.

Table 3. - Conditions and outcomes of simulations using a bioenergetics model for age-0 Colorado pikeminnow in winter conditions. Final mass and condition of 35-, 45-, and 60-mm TL fish are given for each simulation.

Simulation	Temperature regime	Activity (bl/s)	% maximum consumption	Initial length (mm)	Simulation length (d)[a]	Final mass (g)	Final condition (*K*)
1	Preferred	Spontaneous	0.1	35	118	0.206	0.481
				45	118	0.435	0.478
				60	118	1.044	0.484
2	Midpoint	Spontaneous	0.1	35	118	0.207	0.483
				45	118	0.437	0.480
				60	118	1.049	0.486
3	Preferred	0.5	0.1	35	118	0.171	0.400
				45	118	0.361	0.396
				60	118	0.864	0.400
4	Preferred	1	0.1	35	90	0.153	<0.36
				45	89	0.327	<0.36
				60	92	0.775	<0.36
5	Preferred	Spontaneous, 1	0.1	35	101	0.153	<0.36
				45	100	0.327	<0.36
				60	103	0.773	<0.36
6	Preferred	1	0.2	35	114	0.153	<0.36
				45	102	0.326	<0.36
				60	98	0.776	<0.36

[a]Simulation length was 118 d unless fish condition declined below the minimum value for survival (0.36).

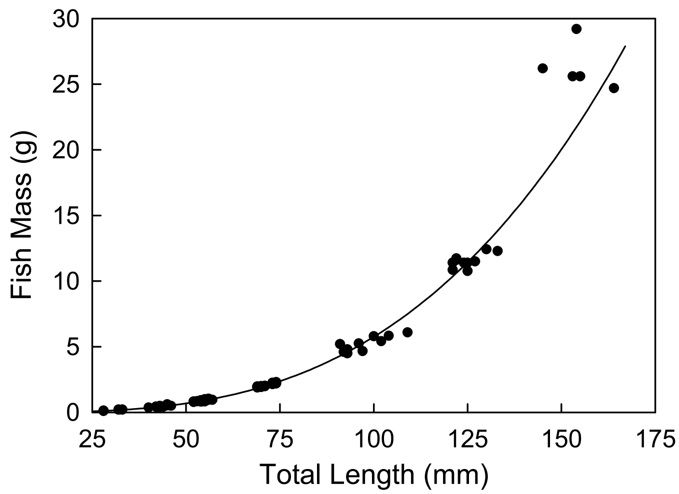

Figure 1. Weight-length relationship for laboratory-reared Colorado pikeminnow. The predicted relationship has the form $y = 4.01{\times}10^{-6}\,x^{3.08}$.

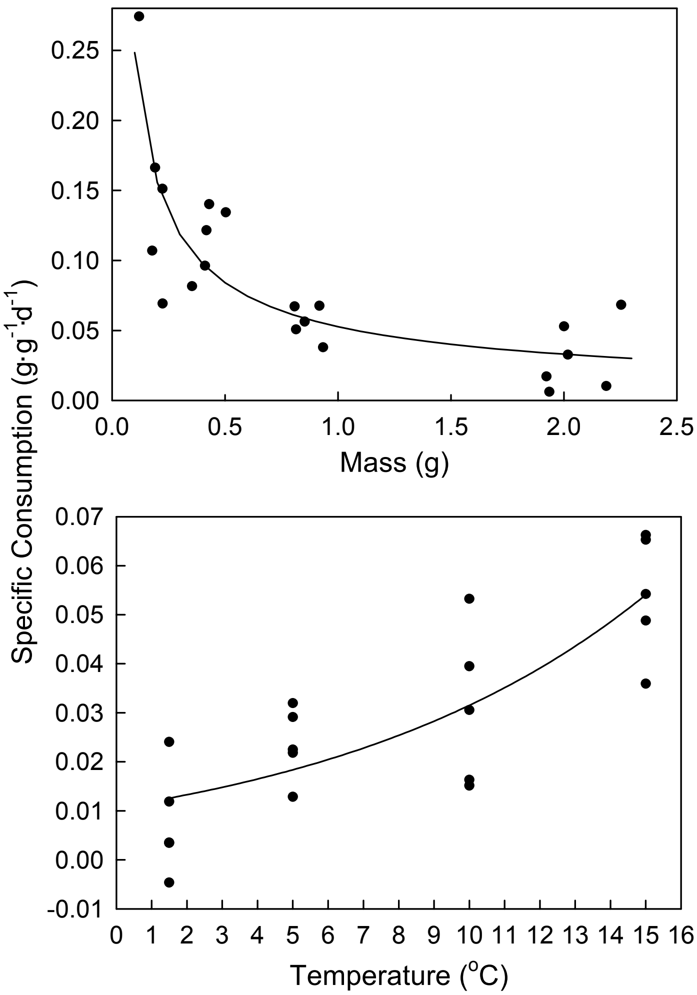

Figure 2. Observed and predicted responses of maximum specific consumption as functions of fish size (top) and water temperature (bottom). The predicted relationship for size-dependence of consumption is: $y = 0.0527x^{-0.673}$; the predicted relationship for temperature-dependence of consumption is $y = 0.0107e^{0.108x}$.

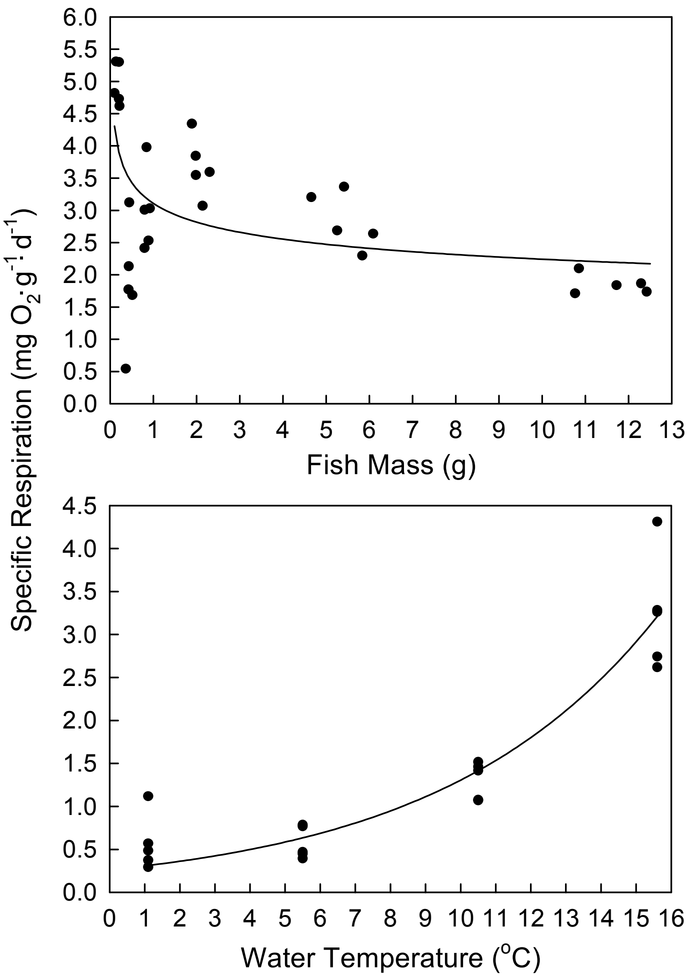

Figure 3. Observed and predicted responses of specific respiration as functions of fish size (top) and water temperature (bottom). The predicted relationship for size-dependence of respiration is $y = 3.108x^{-0.142}$; the predicted relationship for temperature-dependence of respiration is $y = 0.262e^{0.161x}$.

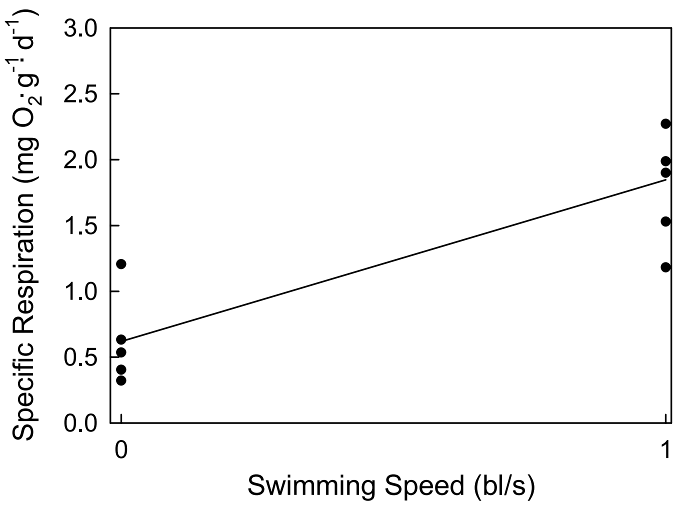

Figure 4. Observed and predicted responses of specific respiration as a function of activity. The predicted relationship for activity-dependence of respiration is: $y = 0.620 + 1.12x$.

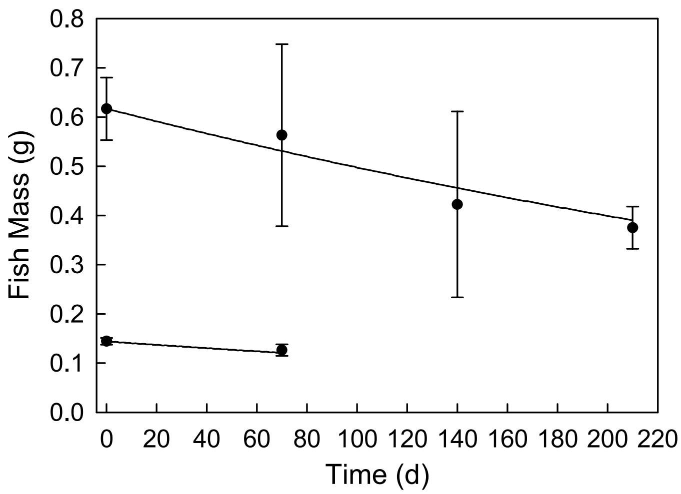

Figure 5. Comparison of bioenergetics model predictions (line) and observed growth (mean and 95% confidence intervals) for two sizes of Colorado pikeminnow in 70- and 210-d growth experiments. Observed data from Thompson (1989).

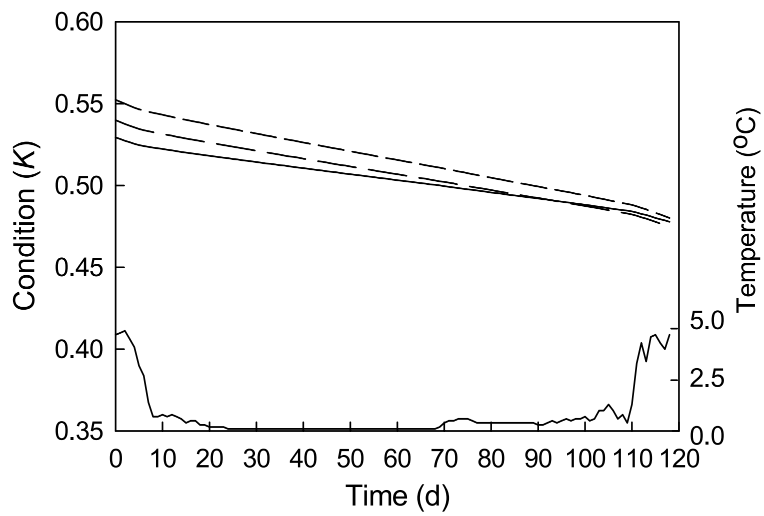

Figure 6. Simulated growth (simulation 1) of age-0 Colorado pikeminnow with a spontaneous activity rate and a natural temperature regime collected in a backwater from 22 November 2001 to 19 March 2002 (118 d). Condition (*K*) of 35- (solid line), 45- (long-dash line), and 60-mm TL (short-dash line) fish are shown.

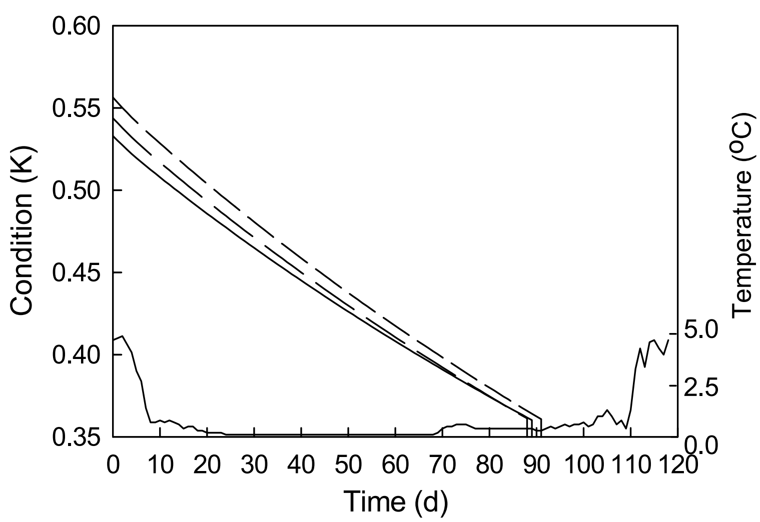

Figure 7. Simulated growth (simulation 4) of age-0 Colorado pikeminnow with an activity rate of 1 bl/s and a natural temperature regime collected in a backwater from 22 November 2001 to 19 March 2002 (118 d). Condition (*K*) of 35- (solid line), 45- (long-dash line), and 60-mm TL (short-dash line) fish are shown.

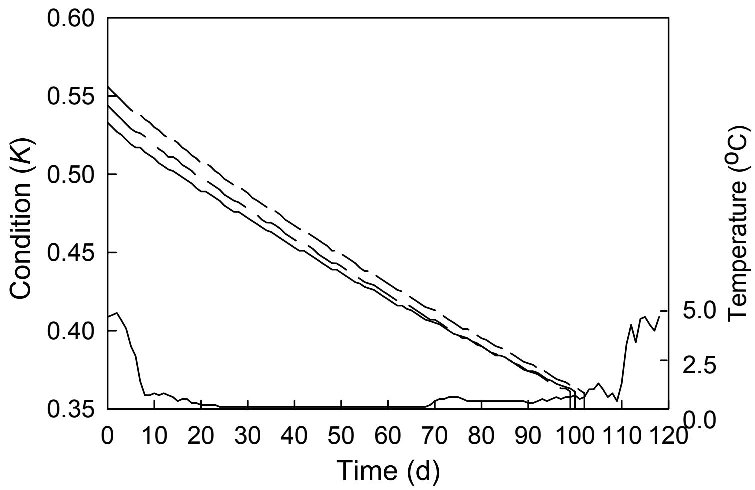

Figure 8. Simulated growth (simulation 6) of age-0 Colorado pikeminnow with an activity rate of 1 bl/s for 6 consecutive days then spontaneous for 1 day each week, and a natural temperature regime collected in a backwater from 22 November 2001 to 19 March 2002 (118 d). Condition (*K*) of 35- (solid line), 45- (long-dash line), and 60-mm TL (short-dash line) fish are shown.