Overwinter survival of westslope cutthroat trout in Cache Creek, Montana
by Matthew Joseph Handy

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biological Sciences
Montana State University

Abstract:
Little is know about the winter ecology of westslope cutthroat trout Oncorhynchus clarki lewisi and other headwater, resident salmonids. A great deal of uncertainty exists in areas such as critical habitat requirements, size- or age-specific survival, energy budget, and their interrelationships. Specific objectives of my study were to examine: (1) size- specific overwinter mortality of cutthroat trout in Cache Creek; (2) the relationship between mortality and fish body size, lipid content, and condition factor; (3) the relationship between habitat quality and overwinter survival; and (4) winter conditions within the system and their potential influence on westslope cutthroat trout movement. Using pre- and post-winter population samples, no size-specific survival was evident, suggesting possible adaptive advantages of westslope cutthroat which allows them to persist in systems experiencing severe and prolonged winter conditions. Fenced habitat enclosures failed to withstand severe winter conditions and the relationship between habitat quality and survival remains unknown. Body lipid content of samples pooled by size class exhibited a general decline from autumn to spring. The majority of the lipid decline occurred in early winter, supporting the notion of the "critical" nature of this period. Relatively high end-of-winter lipid levels and relatively low percentage lipid declines of the smallest sized fish may provide indirect support for the proposed "metabolic deficit" hypothesis. Mean condition factors, especially when generated from small samples, were poorly correlated with lipid content of pooled samples. Moisture content was inversely related to lipid content, and moisture uptake by fish overwinter may be limiting the usefulness of condition factors in assessing changes in energetic reserves during this period. Groundwater inputs throughout Cache Creek influenced winter habitat conditions, and should be included in any future assessment of the relationship between habitat and survival within the system. Timing and directionality of fish movement support the significance of temperature cues in regulating fish behavior, and further suggests the importance and suitability of Cache Creek as an overwintering area for westslope cutthroat trout within the Taylor Fork drainage.

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MONTANA STATE UNIVERSITY
Bozeman, Montana

August 1997

APPROVAL

of a thesis submitted by

Matthew J. Handy

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ACKNOWLEDGMENTS

I would like to extend my sincere appreciation to those who assisted me in this effort. Dr. Thomas McMahon directed the study and offered guidance throughout. Drs. Al Zale and Cal Kaya reviewed the manuscript and provided helpful advice. Bob Coby and the USFWS Bozeman Fish Technology Center provided laboratory facilities and technical assistance. Russ Thurow of the Forest Service Intermountain Research Station provided funding and advice. The staff of the Biology department, especially Dee Topp and Harry Fenelson, were helpful, in their own ways, in making the entire process go as smoothly as possible. Most especially, I thank my technicians, volunteers, and a certain group of fellow graduate students (you know who you are) for providing both physical, technical, and moral support from beginning to end.

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ABSTRACT

Little is know about the winter ecology of westslope cutthroat trout *Oncorhynchus clarki lewisi* and other headwater, resident salmonids. A great deal of uncertainty exists in areas such as critical habitat requirements, size- or age-specific survival, energy budget, and their interrelationships. Specific objectives of my study were to examine: (1) size-specific overwinter mortality of cutthroat trout in Cache Creek; (2) the relationship between mortality and fish body size, lipid content, and condition factor; (3) the relationship between habitat quality and overwinter survival; and (4) winter conditions within the system and their potential influence on westslope cutthroat trout movement. Using pre- and post-winter population samples, no size-specific survival was evident, suggesting possible adaptive advantages of westslope cutthroat which allows them to persist in systems experiencing severe and prolonged winter conditions. Fenced habitat enclosures failed to withstand severe winter conditions and the relationship between habitat quality and survival remains unknown. Body lipid content of samples pooled by size class exhibited a general decline from autumn to spring. The majority of the lipid decline occurred in early winter, supporting the notion of the "critical" nature of this period. Relatively high end-of-winter lipid levels and relatively low percentage lipid declines of the smallest sized fish may provide indirect support for the proposed "metabolic deficit" hypothesis. Mean condition factors, especially when generated from small samples, were poorly correlated with lipid content of pooled samples. Moisture content was inversely related to lipid content, and moisture uptake by fish overwinter may be limiting the usefulness of condition factors in assessing changes in energetic reserves during this period. Groundwater inputs throughout Cache Creek influenced winter habitat conditions, and should be included in any future assessment of the relationship between habitat and survival within the system. Timing and directionality of fish movement support the significance of temperature cues in regulating fish behavior, and further suggests the importance and suitability of Cache Creek as an overwintering area for westslope cutthroat trout within the Taylor Fork drainage.

INTRODUCTION

The need for fisheries research during winter was emphasized by Hubbs and Trautman (1935) over 60 years ago, and has been increasingly recognized over the past few decades. Whereas a substantial increase in research focusing on the winter ecology of stream fishes has occurred, there still remains a great deal of uncertainty concerning many issues specific to this period (Cunjak 1996). These include survival, energy budget, critical habitat requirements, and their interrelationships. Winter ecology of interior salmonids remains one of the most critical research areas in the Rocky Mountain region (Marcus et al. 1990).

The percentage of annual mortality that is specific to the winter period is generally unknown for salmonid populations. Age- or length-specific survival rates are also largely unknown, although age-0 fish are thought to suffer higher mortality rates during the winter than larger, older fish (Cooper 1953; Reimers 1963; Hunt 1969; Smith and Griffith 1994). Average first-winter survival rate in 24 salmonid populations was 49.8% (SD = 18.0%) (Smith and Griffith 1994). Such information on age-specific mortality rates is an important variable in population viability models (Rieman and McIntyre 1993).

I examined overwinter survival of westslope cutthroat trout *Oncorhynchus clarki lewisi* in Cache Creek, a subbasin of the Taylor Fork drainage in southwestern Montana. This system experiences severe and prolonged winter conditions typical of many of the high elevation, headwater stream environments where most remaining populations of this subspecies now persist (Liknes and Graham 1988). Additionally, the Cache Creek drainage provides a unique opportunity to assess aspects of the winter ecology of cutthroat trout in a system with naturally high levels of fine sediments.

Overwinter mortality is strongly size-related for juvenile salmonids (Cooper 1953; Reimers 1963; Hunt 1969). Similar relationships between size and mortality exists for non-salmonid fishes (Oliver et al. 1979; Wicker and Johnson 1987; Miranda and Hubbard 1994; Thompson et al. 1991). The prevailing hypothesis for size-specific differences in mortality rates is that both lipid level and metabolic rate are related to size. Smaller fish have higher basal metabolism and lower lipid content per unit weight than larger fish. Therefore, metabolic requirements during the transition period of rapidly decreasing water temperatures from autumn to winter are thought to result in more rapid lipid depletion and higher overwinter mortality among smaller individuals (Shuter et al. 1980, Shuter and Post 1990).

It has been proposed that salmonids incur a "metabolic deficit" as the price for acclimating to these rapidly changing conditions in early winter, and that size-related factors such as lipid reserves may be important for overwinter survival (Cunjak et al. 1987; Cunjak and Power 1987b; Cunjak 1988b). Ninety-five percent of the total overwinter mortality of rainbow trout in the Henry's Fork, Idaho, occurred within the first seven weeks of low water temperature (100% of mortality occurred within 14 weeks) (Smith and Griffith 1994). Survival was size related, with survival of 130-160 mm fish exceeding 95% while fish < 100 mm suffered 100% mortality. Condition factor (K), as a surrogate for energy reserves, was also an effective predictor of individual overwinter survival, with 0% survival of fish with late-autumn K values below 0.77 to 0.82. The interaction of size, energy reserves, and winter survival clearly has implications for younger fish and, in turn, for population recruitment.

Habitat quality likely influences the size-related factors associated with winter mortality. Habitat features that require minimum energy expenditure, such as the low velocity areas associated with deep pools, complex woody debris, and interstitial cover, may be important for minimizing depletion of energy reserves during winter. When such features are lacking, mortality can result directly from overexpenditure of lipid reserves, or indirectly as a result of acute or chronic stress. Such stress can result in nutritional deficiencies which can have debilitating effects on a fish's defense system and its ability to resist infection (Pickering and Pottinger 1988).

A variety of habitat features are known to be important to both juvenile and adult salmonids during winter. Instream cover is valuable to both brown trout *Salmo trutta* and brook trout *Salvelinus fontinalis* (Cunjak and Power 1986; 1987a). Juvenile coho salmon *Oncorhynchus kisutch* select for both instream and overhead cover (Swales et al. 1986) and cover complexity is correlated with use (McMahon and Hartman 1989). Brook trout select for both reduced current velocity and deep pools in winter (Chisholm et al. 1987).

Preference and selection for substrate particle size and degree of embeddedness, particularly by juveniles, has been demonstrated (Rimmer et al. 1983; Cunjak 1988a; Griffith and Smith 1993). The addition of cobble substrate in a highly sedimented system resulted in an eight-fold increase in juvenile chinook salmon *Oncorhynchus tshawytscha* density over the previous winter (Hillman et al. 1987). Densities declined to levels similar to those found previously after these cobble piles became embedded.

Juvenile salmonids move into interstitial spaces of cobble or boulder substrate as water temperatures drop in early winter in what Griffith and Smith (1993) referred to as concealment behavior. Ambient water temperatures in these spaces can be 0.2-1.0° C higher than that of the overlying water (Smith and Griffith 1994). These areas also provide juveniles with a refuge from harsh icing conditions (Chapman 1966; Bjornn 1971; Rimmer et al. 1983).

Much of the winter research conducted to date has been undertaken in environments that were ice-free or in which ice formation was minimal (Cunjak et al. 1987; Cunjak and Power 1987b; Cunjak 1988b). A strong link between high winter mortality rates of trout and severe winter ice conditions has been suggested (Needham et al. 1945; Maciolek and Needham 1952; Nielson et al. 1957). Similarly, snow and ice conditions had a greater influence on the overwinter mortality of rainbow trout *Oncorhynchus mykiss* than did either food limitations or prolonged low water temperatures (Reimers 1957; Needham and Jones 1959).

Salmonids select for sites with groundwater input that can moderate fluctuation in winter water temperatures. Brook trout and brown trout in a southern Ontario river in winter formed aggregations close to sources of groundwater discharge (Cunjak and Power 1986). Cutthroat trout in the Ram River, Alberta, moved, both upstream and downstream, into overwintering areas that were influenced by springs or upwelling groundwater (Brown and Mackay 1995). Movement into groundwater-fed sites moderates the effects of frazil and anchor ice (Brown and Mackay 1995) and the winter metabolic deficit (Cunjak et al. 1987).

Little is known about how habitat quality directly influences overwinter survival. In the case of Cache Creek, the unusually high loads of fine sediment likely affect both habitat availability and quality during winter. This situation appears to be further exacerbated by timber harvesting and livestock grazing within the basin (Magee et al. 1996). Sediment deposition within Cache Creek severely limits the availability of cobble substrates as well as other critical winter habitat features, and the overall habitat quality in the system appears poor. However, high summer and autumn densities of cutthroat trout, the highest reported in the literature (Ireland 1993), suggests high winter survival rates.

The overall objective of my study was to examine how the interaction of habitat quality, and body size and condition influences overwinter survival. Specific objectives of my study were to examine: (1) size-specific overwinter mortality of cutthroat trout in Cache Creek; (2) the relationship between mortality and fish body size, lipid content, and condition factor; (3) the relationship between habitat quality and overwinter survival; and (4) winter conditions within the system and their potential influence on westslope cutthroat trout movement.

STUDY AREA

Cache Creek is a third-order tributary within the Taylor Fork drainage, a 160 km^2 basin located in the Gallatin National Forest (Figure 1). The drainage is near the northwestern boundary of Yellowstone National Park, and ranges in elevation from 3080 meters in the headwaters to 2032 meters at its confluence with the Gallatin River. From its highest point, Cache Creek flows through an alpine meadow before descending through coniferous forest (gradient > 2.5%) to its confluence with the mainstem Taylor Fork.

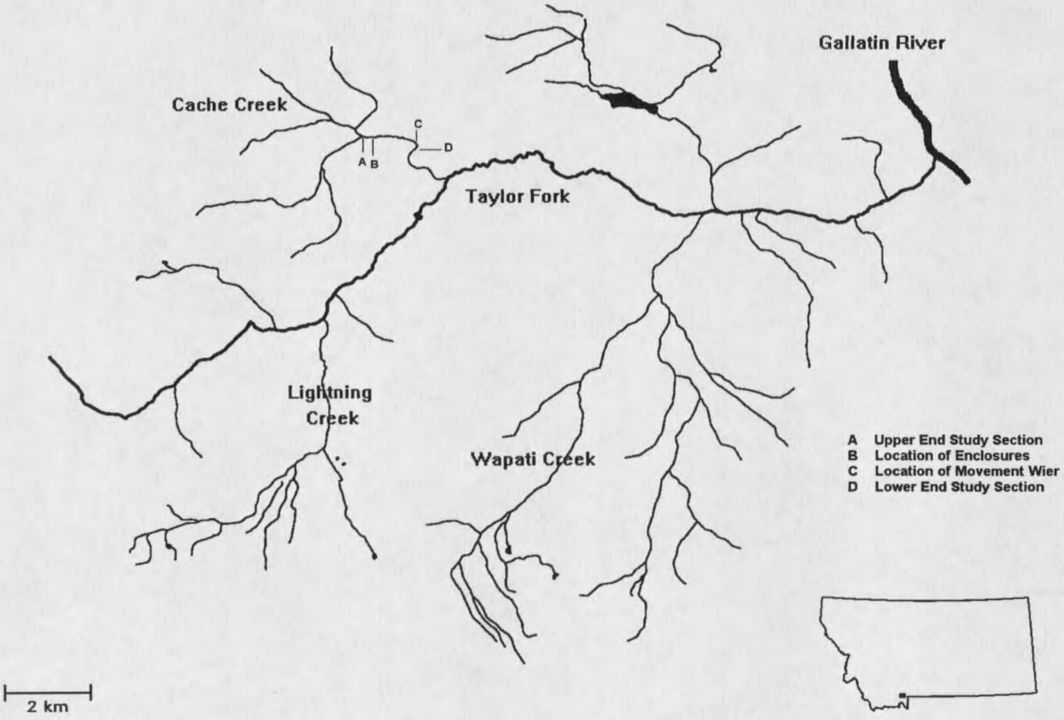


Figure 1. Map of Cache Creek and the Taylor Fork drainage.

The entire Taylor Fork drainage is composed of highly erosive, soft sedimentary rock that elicits high suspended sediment loads during spring runoff and high rainfall. The majority of stream banks within the drainage are unstable (Snyder et al. 1978), and livestock grazing practices are apparently compounding the naturally high fine sediment load (Magee et al. 1996).

Westslope cutthroat trout appear to be concentrated largely in Cache and Wapiti creeks within the Taylor Fork drainage (Ireland 1993; Magee 1993). Whereas electrophoretic analysis has shown that westslope cutthroat trout in both creeks are introgressed with rainbow trout, those within the Cache Creek system are known to have maintained higher (>85%) genetic purity (Magee et al. 1996).

The importance of the alpine meadow reach of Cache Creek as an overwintering area has been demonstrated (Ireland 1993). This information, along with the greater accessibility of the drainage, made the Cache Creek population the most appropriate choice within the larger drainage for this study. The study section encompassed the entire length of the Cache Creek mainstem within the alpine meadow environment, above the higher gradient, forested reach (Figure 1).

METHODS

Winter Survival

I estimated winter survival by conducting population sampling throughout the entire study section on the Cache Creek mainstem (about 2 km) at the beginning and end of winter of 1994-1995. Westslope cutthroat trout move to their permanent winter habitat when water temperatures drop below 4-5° C (Liknes and Graham 1988; Ireland 1993). Initial sampling was conducted just prior to this temperature drop.

Fish were captured by electrofishing with a Coffelt-10 backpack shocker unit (Output range: 3-6 Amps), over the 2 km study section between 24 September - 1 October 1994. Fish were anesthetized with MS-222, measured, and weighed. Individuals >70 mm fork length were tagged with 12-mm Passive Integrated Transponder (PIT) tags using a 12-gauge needle and syringe. Tags were inserted into the body cavity at a point just posterior to the pectoral fins (Prentice et al. 1990a). All individuals <70 mm fork length received an adipose clip. A recapture sample was obtained on 9 October 1994 by electrofishing. I estimated pre-winter population abundance using program MRPE, which incorporates mark-recapture data to generate the maximum likelihood estimate (MLE) using Bayesian statistics (Gazey and Staley 1986; Gustafson 1990).

Post-winter population sampling was conducted by electrofishing the same 2 km reach of Cache Creek on 16 May 1995. Tagged individuals were identified using a PIT-tag reader, weighed, and measured. Spring values were then compared to the initial values. Individuals without tags were also weighed and measured, and were used along with tagged individuals to determine the length-frequency distribution of the population. Pre- and post-winter length frequency distributions were compared to assess size-specific survival.

I omitted fish < 80 mm from length-frequency comparisons due to perceived differences in catchability between sampling periods. Post-winter sampling was conducted during a period of high stream discharge associated with the initial stages of runoff. Fish within the smallest size class were captured and observed with high frequency in flooded, shallow, low-velocity areas that were not available during sampling efforts of autumn 1994.

A Mann-Whitney test was used in comparing seasonal population sample mean lengths. Autumn versus spring length-frequency distributions were compared using chi-square and Kolmogorov-Smirnov two-sample tests. One-way analysis of variance (ANOVA) was used to compare among size class differences in average overwinter change in length, weight, and condition of recaptured fish. A significance level of $P \leq 0.05$ was used for all tests.

Habitat/Survival Relationship

I examined overwinter survival over a range of habitat conditions using a field experimental approach (Ratti and Garton 1994; Smith and Griffith 1994). I used larger enclosures than those used by Smith and Griffith (1994) to simulate a more natural winter environment. Habitat units were selected along the length of the study section to represent combinations of the three variables thought to influence winter habitat quality: depth (i.e., shallow (<0.75m) or deep pools (>0.75m)), substrate crevices (embedded or unembedded), and bank cover (presence or absence). The study design involved enclosing replicated habitat units with these features, and measuring survival, condition, and growth of tagged fish within each unit over winter. The winter period was defined as beginning just prior to the formation of seasonal ice cover and ending at breakup of surface ice.

Selected habitat units were enclosed with 1/2-inch metal or nylon mesh secured to fencing frames (supported with 1/2-inch conduit) and/or posts placed in the stream bed. The ends of each fence were secured to posts placed within the stream bank, reburied, and supported with sandbags. Fencing sections at point bars were extended to a point above the anticipated maximum stream water level. Sections thought to be at the greatest risk of ice-damming were further supported with metal cable attached to fence posts on shore. Surface area within enclosures ranged from 21.2 - 82.2 m^2.

Only the habitat variables of depth and cover were examined because unembedded substrate is very rare in Cache Creek. The total number of replicates of each combination were based on availability within the system and were established as follows:

WINTER 1994-1995

deep pool\undercut bank	(3 replicates)
deep pool\no undercut bank	(3 replicates)
shallow pool\undercut bank	(4 replicates)
shallow pool\no undercut bank	(3 replicates)

WINTER 1995-1996

deep pool\undercut bank	(3 replicates)
deep pool\no undercut bank	(2 replicates)
shallow pool\undercut bank	(4 replicates)
shallow pool\no undercut bank	(2 replicates)

Cover within all enclosures was limited to that provided by undercut banks.

Only 5 of the 13 designated habitat units were fully enclosed in the winter of 1994-1995. Measurements of length, average width, and maximum depth were made within all units. Ice-over occurred before measurements of relative cover could be made, and prior to the addition of tagged fish to the enclosures. After breaking through and removing surface ice within these enclosure, fish ranging in size from 88 - 234 mm (fork length) were obtained by electrofishing. Fish were weighed, measured, PIT-tagged, and placed within the five enclosures. Enclosures represented the following treatments: shallow/undercut bank (N = 3), deep/undercut bank (N =1), and deep/no undercut bank (N = 1).

Habitat measurements (i.e., length, average width, maximum depth, average depth, relative abundance of cover) were made on the 11 units in the winter of 1995-1996, immediately prior to surface ice formation. Each habitat unit was enclosed for the duration of the winter, after water temperatures had dropped to 4-5° C in late October 1995.

Fish ranging in size from 81 mm to 244 mm (fork length) were obtained by electrofishing both inside and outside of the enclosures. All fish were weighed, measured for fork length, PIT-tagged, and placed in enclosures at densities of 0.5-0.7 fish/m^2, based on estimates of Ireland (1993) for winter densities within pools. In all tagging efforts in 1995-96, tag needles were sterilized with 70% ethanol.

Body Condition

Whole body lipid and moisture composition of westslope cutthroat trout were determined over the course of the autumn-winter period to assess how size-related differences in energy reserves influenced survival. I also examined the relationship between lipid content and condition factor to assess the usefulness of condition factor as an index of relative lipid level. Samples were obtained by electrofishing, beginning in September, at two- to four-week intervals until early winter when complete ice-over occurred. A final sample was obtained in the spring in both years. All fish collected were weighed, measured for fork length, and frozen for subsequent body condition analysis.

Average lipid and moisture content were determined from pooled samples of 2-14 fish within each of five different size classes. Designated size classes (mm fork length) were 50-80, 81-125, 126-150, 151-175, and ≥176 in 1994-1995. Size classes (mm fork length) were 65-99, 100-124, 125-149, 150-179, and ≥180 in 1995-96. Slightly different size class ranges were used in 1995-96 in an attempt to limit the number of pooled samples containing three or fewer individuals. In samples from 1995-96, fish smaller than 65 mm could not be collected consistently and were excluded from the analysis.

Frozen samples were homogenized in a blender (homogenization of samples enhanced fragmentation). Two moisture subsamples (about 0.5 g) were taken from each pooled, homogenized sample. All subsamples were weighed and then dried, along with the remaining volume of the original, homogenized sample, at 100° C for a minimum of 24 hours.

Dried moisture subsamples were weighed immediately upon removal from drying oven. Initial, homogenized samples were crushed to powder form, and two lipid subsamples of approximately 0.5 g were taken and used for Soxlet extraction using ethyl ether. The resulting lipid residue was air dried and weighed. Calculation of both moisture and lipid content was based on average weights of the two respective subsamples (AOAC 1984).

A Fulton-type condition factor (**K**) was generated for all individuals obtained throughout the study. Size-class condition factors were generated from average **K** values for individuals within each respective group. This index is of the form:

$$\mathbf{K = 100,000(W/L^3)}$$

where **W** equals weight in grams, and **L** equals length in millimeters (Anderson and Gutreuter 1983). All comparisons of condition based on this index were restricted to individuals or pooled samples within identical size classes.

Kruskal-Wallis nonparametric analysis of variance tests were used to determine if average condition factor (K) and average lipid content changed significantly over the winter period. When significant differences were found, Tukey's multiple comparison tests were used to compare within each size class. A significance level of $P \leq 0.05$ was used for all tests.

Winter Stream Conditions

High variation exists in water temperature and stream ice thickness in high-elevation streams (Chisholm et al. 1987; Berg 1994; Smith and Griffith 1994). I measured both variables throughout the study section to assess such spatial variations which may influence survival. Thermographs (three in the winter of 1994-1995 and five in the winter of 1995-1999) were installed at about even intervals along the entire stream length. Both Onset HOBO-TEMP and Ryan TempMentor temperature loggers were used. Temperatures were recorded at about hourly intervals. Comparisons of temperatures at thermograph sites were made based on centigrade temperature units (CTU's), which are defined as the sum of average daily temperatures over 0° C over a specific time period (Rieman and Apperson 1989).

Detailed measurements of temperature and ice thickness were made in winter of 1995-1996. A series of five pool habitat units, spaced at about 150 m intervals starting from the lowest enclosure and extending downstream to the lowermost thermograph site (about 750 m), were marked and sampled periodically, beginning on 22 November, 1995, through mid-winter. On each sampling occasion, a visual estimate of relative pool ice cover was made at each station. Two sites at each station were then chosen at locations along the estimated thalweg. Ice thickness and water depth were then measured with a meter stick placed in 2.5 cm holes augured through the ice. These measurements can be seen only as potential depths, as it was not possible to identify air pockets between the bottom of the ice and the surface of the water. Snow depth and water temperature were also measured at each site. Measurements of ice, snow, and water depth were also made within all eleven habitat enclosures. Stream snow cover and site access limitations prevented sampling after 17 December 1995.

Movement

A two-way weir (1/2-inch metal mesh) was placed at the lower end of the study section on 1 October 1994 to identify any directional or temporal patterns in movement in or out of the Cache Creek. The trap was checked about every two to three weeks from 1 October to 18 December 1994. Sampling ceased when ice clogged the weir.

RESULTS

Winter Survival

Between 24 September and 1 October 1994, 463 fish representing all size categories were captured by electrofishing and PIT-tagged (Figure 2). Of the 389 fish recaptured on 9 October, 50 were marked, yielding an autumn population abundance estimate of 3,726 (95% confidence interval: 2,894-4,588). Using Ireland's (1993) average width measurements of 2.9 m for this section of Cache Creek, this equates to an approximate density estimate of 64.2 trout/100 m^2 throughout the length of the study section (about 2 km).

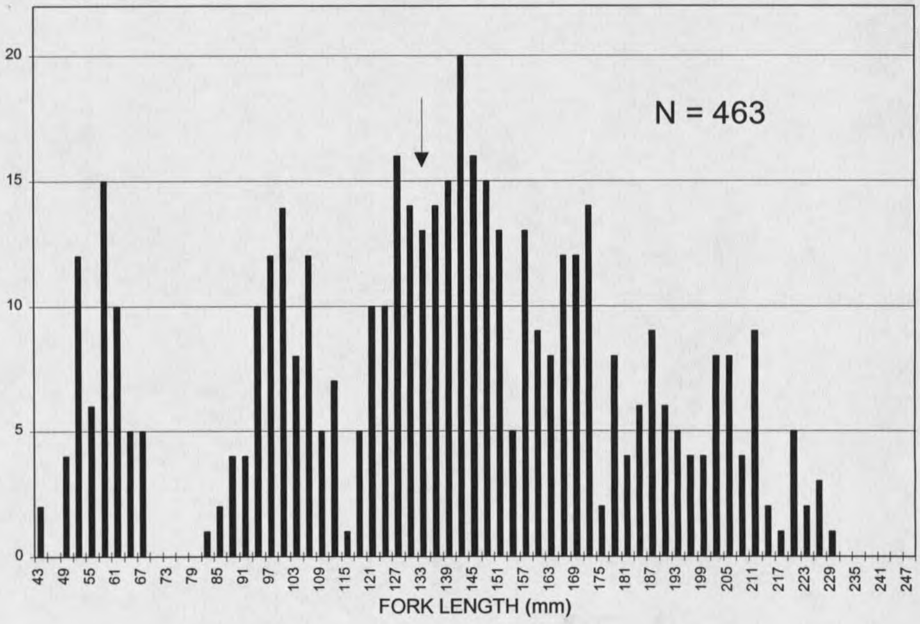


Figure 2. Length-frequency distribution of fish captured in Cache Creek mainstem (autumn 1994). Sample mean length (135.9 mm) indicated with arrow.

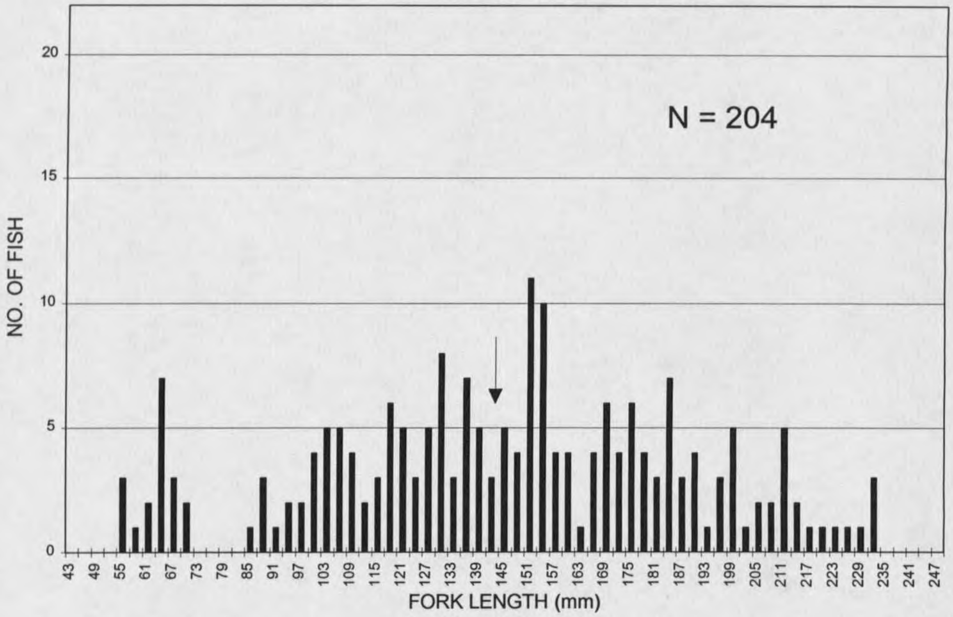


Figure 3. Length-frequency distribution for all fish captured in Cache Creek mainstem (spring 1995). Sample mean length (143.9 mm) indicated with arrow.

After ice-out (16 May 1995), 204 fish, representing all size categories, were collected (Figure 3). Of this total, 58 fish, ranging from 85 mm - 230 mm, had been previously tagged. For recaptured individuals, average change in length, weight, and percent condition factor were +4.3 mm, -0.2 g, and -8.2%, respectively. Change in average length of all tagged fish was significant ($t = 9.59$, $P < 0.0001$), and in all subsequent pre- versus post-winter size class comparisons, spring size groupings were increased by 4 mm over comparable autumn groupings. No significant differences were found among size classes in any category using one-way ANOVA (Table 1).

Table 1. Average overwinter change in length, weight, and condition factor (K) for fish recaptured in Spring 1995. Standard deviation in parentheses. No significant differences existed between any size class in any category.

	Size Class (mm fork length)				
	80-125 n = 11	126-150 n = 11	151-175 n = 15	176-200 n = 13	≥201 n = 8
Average Change in Length(mm)	+4.5 (3.6)	+4.1 (2.4)	+4.7 (3.2)	+3.9 (3.8)	+4.4 (4.7)
Average Change in Weight(g)	+0.4 (3.2)	-1.1 (2.3)	+0.3 (4.7)	+0.2 (5.4)	0.0 (5.9)
Average Change in K (%)	-8.5 (17.3)	-10.5 (7.4)	-7.4 (4.6)	-6.0 (6.2)	-5.9 (8.7)

Because only a single recapture run was conducted in the spring of 1995, population abundance at the end of winter could not be estimated. However, I found no evidence of size-dependent mortality. Excluding fish < 80 mm, mean sample lengths were 147.1 mm in autumn 1994 and 151.8 mm in spring 1995 (Mann-Whitney, P = 0.13). Length-frequency distributions also were not significantly different (Kolmogorov-Smirnov, P = 0.15). Additionally, comparisons of size-class frequencies for autumn versus spring population samples (Table 2) did not support the postulated decreases in fish < 100 mm (chi-square, P = 0.99).

Table 2. Proportion of sample within each size class (Spring 1995 sample accounts for 4 mm growth over winter).

Sample	Size Class (mm fork length)					
	<100	101-125	126-150	151-175	176-200	201+
Autumn 1994 (n = 406)	0.09	0.15	0.31	0.22	0.11	0.11
Spring 1995 (n = 186)	0.09	0.19	0.25	0.19	0.16	0.10

PIT-tagging appeared to have little effect on fish condition, as no differences were observed in K between tagged and untagged fish (Table 3). However, recapture rates of tagged fish were low, resulting in small sample sizes for many of the size classes.

In general, PIT-tag effectiveness was high. Only one of 58 fish (1.7%) known to be tagged failed to produce a PIT-tag reader response (it was uncertain whether this was due to tag failure or tag loss). However, several individuals recaptured in 1995 did exhibit infections that were potentially related to either the presence of the tag or the tagging procedure. Thus, more antiseptic techniques involving needle sterilization between each use was used in subsequent tagging efforts.

Table 3. Condition factors of fish with and without PIT-tags. No significant difference existed within any size class.

	Size Class (mm fork length)				
	90-125	126-150	151-175	176-200	200+
Fish with Tags	1.08z (n=11)	1.04z (n=11)	1.07z (n=15)	1.03z (n=13)	1.08z (n=8)
Fish without Tags	1.02z (n=35)	1.03z (n=34)	1.06z (n=30)	1.03z (n=18)	1.12z (n=11)

Habitat/Survival Relationship

Study enclosures were nearly completely lost during each of the two winters. In the first winter of the study, all five enclosures were breached by winter ice and failed. Two of the five units appeared to be intact upon inspection, but electrofishing indicated that movement of substantial numbers of untagged fish into the enclosures had occurred.

In spring 1996, visual inspection found that none of the 11 established enclosures remained intact. In many cases, fencing frames and conduit supports were severely buckled. Similar buckling occurred with many supporting fence posts, leaving many sections of mesh completely below the water surface. Pressure and stress on bent frames severed all metal cable supports, and substantial scouring eroded stream banks used as anchor points for several enclosures. It is unclear whether failure of enclosures was due to snow and ice or to runoff after ice-out. Site access was limited from mid-December 1995 to early May 1996.

Body Condition

Lipid composition and condition factor (K) were highly variable both within and among size classes (Tables 4 and 5). Mean lipid levels declined from late autumn through early spring in both years. Levels for all size classes combined declined 34% (6.4% to 4.2%) in 1994-95 and 52% (4.5% to 2.2%) in 1995-96.

Lipid depletion overwinter also varied within size classes. Relative declines ranged from 6% to 56% in 1994-95 and from 26% to 46% in 1995-96. In both years, the greatest percentage decline (56% and 46% in 1994-95 and 1995-96, respectively) occurred in the largest fish (≥176 mm). Conversely, lipid levels of the two smallest size categories (≤125 mm) exhibited relatively moderate or low percentage declines (24% and 25% in 1994-95 and 1995-96, respectively).

Lipid levels among size classes were also highly variable. However, lipid values at the end-of-winter were lower for the largest fish (≥176 mm) than those for the smallest fish (<100 mm) in both years. Values for largest verses smallest size classes were 2.8% versus 3.4% in 1994-95, and 2.1% versus 3.5% in 1995-96. Conversely, autumn lipid values for the largest fish were higher than those of smallest fish in 1994-95, but were lower than those of the smallest fish in the autumn of 1995-96. Also, in 1995-96, percent lipid composition of the largest size class was very low (< 2.0%) in all late-autumn and winter samples, and were lower than that of the smallest class throughout the entire period.

Most lipid depletion occurred in early winter. In 1994-95, 86% of the overall decline in lipids occurred during the six-week period between 17 September and 4 November. Levels of largest sized fish (≥ 176 mm) declined 22% during this period, while levels for the smallest fish (≤ 80 mm) increased 9%. The greatest percentage declines were exhibited by the intermediate sized fish (126 - 175 mm). In 1995-96, 46% of the overall decline occurred between 15 September and 26 November. Levels of largest sized fish (≥ 180 mm) declined 53% during this period, while levels for the smallest fish (≤ 100 mm) remained about the same. Mean lipid levels for the initial, late autumn sample were about 50% lower at the onset of winter in 1995-96 than in 1994-95.

Table 4. Change in average condition factor (K), lipid content, and moisture content over winter 1994-1995 (standard deviation in parentheses). Results of Kruskal-Wallis and Tukey's HSD test for unequal sample size comparisons of K are shown. Letters **a-b** indicate among date tests (values with letters in common are not significantly different). Values for lipid and moisture content represent mean value and standard deviation of two subsamples from a single pooled sample. No significant difference in lipid content existed either among dates or size classes.

Sample	Size Class (mm fork length)				
Date	50-80	81-125	126-150	151-175	≥176
9/17/94	n = 6	n = 6	n = 3	n = 3	n = 2
K	1.17(0.24)**a**	1.14(0.22)**a**	1.13(0.01)**a**	1.07(0.06)**a**	1.16(0.01)**a**
%lipid	4.5(0.1)	7.1(0.0)	7.5(0.0)	6.8(0.0)	6.3(0.1)
%moisture	80.3(0.2)	74.1(0.1)	73.6(0.5)	71.2(0.5)	74.0(0.2)
10/20/94	n = 5	n = 4	n = 2	n = 3	n = 2
K	1.12(0.24)**a**	1.09(0.10)**a**	1.03(0.04)**a**	1.07(0.05)**a**	1.10(0.02)**a,b**
%lipid	4.6(0.2)	7.8(0.2)	5.2(0.1)	4.4(0.1)	6.1(0.0)
%moisture	79.1(0.0)	73.7(0.6)	75.9(0.1)	75.1(0.2)	73.5(1.9)
11/4/94	n = 6	n = 2	n = 4	n = 2	n = 5
K	1.13(0.26)**a**	1.11(0.07)**a**	1.02(0.05)**a**	1.04(0.13)**a**	1.08(0.08)**a,b**
%lipid	4.9(0.1)	4.7(0.1)	4.4(0.1)	3.8(0.1)	4.9(0.1)
%moisture	78.1(0.4)	77.4(0.0)	75.8(0.1)	75.9(0.5)	74.1(1.3)
5/16/95	n = 6	n = 8	n = 9	n = 6	n = 6
K	0.94(0.13)**a**	1.00(0.09)**a**	1.07(0.09)**a**	1.05(0.13)**a**	0.99(0.04)**b**
%lipid	3.4(0.0)	6.7(0.1)	4.3(0.0)	3.9(0.1)	2.8(0.1)
%moisture	78.9(0.5)	74.6(0.3)	75.2(0.2)	76.6(0.0)	77.1(1.3)

Table 5. Change in average condition factor (K), lipid content, and moisture content over winter 1995-1996 (standard deviation in parentheses). Results of Kruskal-Wallis and Tukey's HSD test for unequal sample size comparisons of K are shown. Letters **a-d** indicate among date tests (values with letters in common are not significantly different). Values for lipid and moisture content represent mean value and standard deviation of two subsamples from a single pooled sample. No significant difference in lipid content existed either among dates or size classes.

Sample	Size Class (mm fork length)				
Date	65-99	100-124	125-149	150-179	≥180
9/15/95	n = 14	n = 3	n = 5	n = 3	n = 3
K	1.02(0.10)**a**	1.12(0.08)**a**	1.06(0.02)**a,b,d**	1.09(0.05)**a**	1.03(0.05)**a,b**
%lipid	4.7(0.1)	5.8(0.2)	5.0(0.0)	3.1(0.1)	3.9(0.1)
%moisture	77.0(0.0)	75.4(0.3)	74.6(0.7)	76.8(0.0)	75.7(1.3)
10/26/95	n = 2	n = 5	n = 7	n = 10	n = 3
K	1.08(0.01)**a,c**	1.15(0.14)**a**	1.19(0.11)**a,d**	1.10(0.11)**a**	0.98(0.08)**a,b**
%lipid	5.2(0.0)	6.0(0.1)	3.4(0.1)	3.1(0.0)	0.9(0.0)
%moisture	76.8(0.6)	75.6(0.0)	76.4(0.1)	77.1(0.3)	78.8(0.6)
11/12/95	n = 9	n = 5	n = 5	n = 4	n = 4
K	1.05(0.06)**a,c**	1.04(0.06)**a**	0.98(0.10)**b**	1.08(0.02)**a**	1.00(0.03)**a,b**
%lipid	4.9(0.0)	4.8(0.1)	3.8(0.0)	3.7(0.1)	1.8(0.1)
%moisture	76.5(0.0)	76.6(0.0)	75.8(0.3)	75.5(0.3)	79.2(0.1)
11/26/95	n = 12	n = 6	n = 6	n = 14	n = 7
K	0.97(0.11)**a**	1.02(0.14)**a**	1.02(0.04)**a,b,c**	1.05(0.05)**a**	0.91(0.10)**a**
%lipid	4.8(0.0)	5.6(0.1)	3.0(0.0)	2.7(0.0)	1.1(0.0)
%moisture	77.3(0.2)	75.1(0.1)	76.0(0.3)	77.0(0.3)	79.9(0.6)
5/16/96	n = 5	n = 9	n = 11	n = 13	n = 12
K	1.22(0.10)**b,c**	1.13(0.13)**a**	1.13(0.09)**c,d**	1.12(0.11)**a**	1.15(0.12)**b**
%lipid	3.5(0.0)	3.6(0.0)	2.7(0.0)	2.4(0.0)	2.1(0.0)
%moisture	77.6(0.5)	76.4(0.4)	77.8(0.5)	77.9(0.1)	77.8(0.1)

In contrast, mean moisture content generally increased over winter and was inversely related to lipid level (Figure 4). Mean moisture content for all size classes combined increased from 74.6% to 76.4% in 1994-95 and from 75.9% to 77.5% in 1995-96. In the 1994-95 samples, 94% of the overall mean increase occurred between 17 September and 4 November and, in 1995-96 samples, 75% of the increase occurred between 15 September and 26 November. Although relative changes within size classes were variable in both years, relative moisture content of the two smallest size classes (fish <125 mm) either declined (i.e., autumn versus spring) or had the least increase among all size classes.

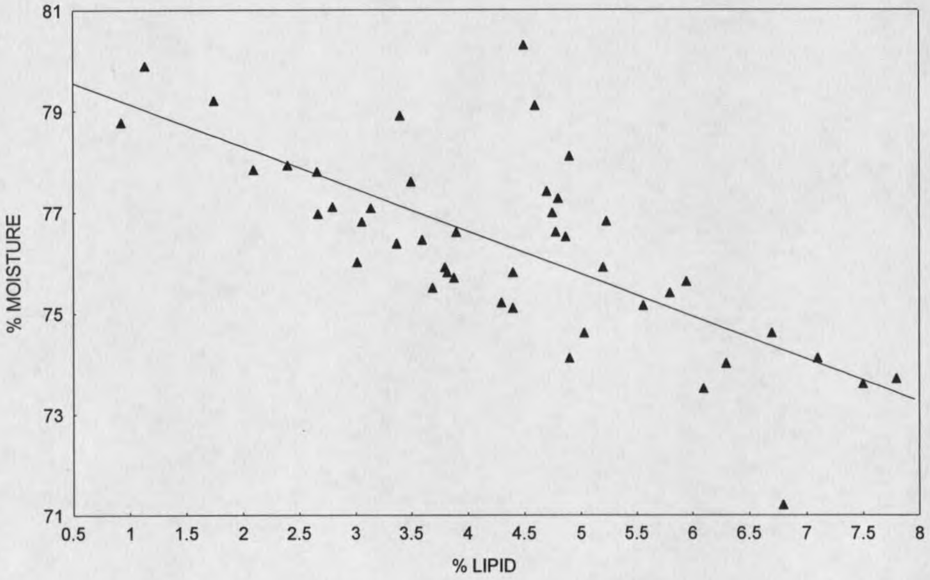


Figure 4. Relationship between body lipid content and moisture content (N = 45, $R^2 = 0.526$, $P < 0.0001$).

Condition factors of fish analyzed for lipid and moisture content in winter 1994-95 declined generally for all size classes combined; mean condition factor decreased from 1.13 to 1.01 from autumn to spring. In contrast, mean condition factor for the 1995-96 season declined from 1.06 to 0.99 from mid-September to late-November, then increased to 1.15 at the end of winter. Although this pattern was generally seen within all size classes, mean condition factors were significantly lower in autumn 1995-96 than in autumn 1994-95 (Mann-Whitney, P = 0.03). Mean condition factor with samples for both years combined was poorly correlated with both average lipid content (Figure 5) and average moisture content (Figure 6).

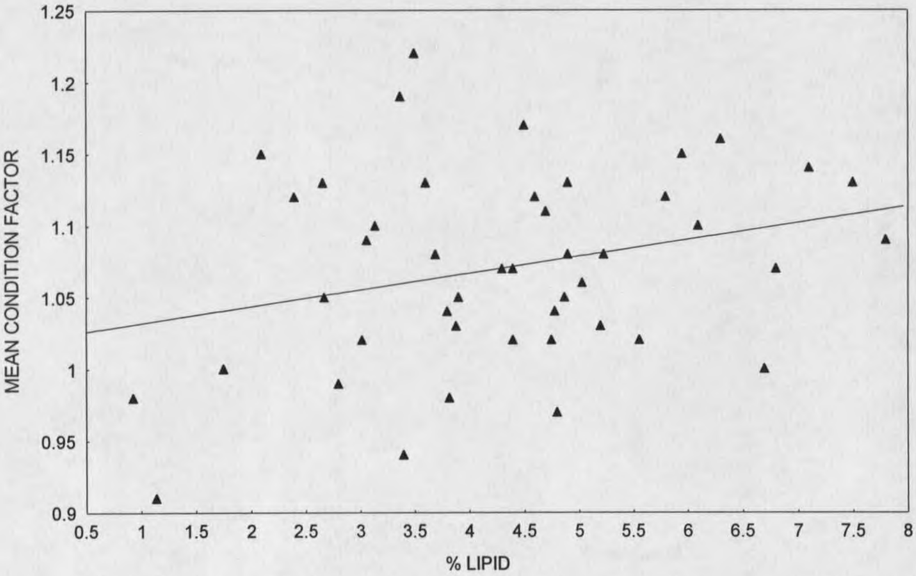


Figure 5. Relationship between mean condition factor (K) and body lipid content (N = 45, R^2 = 0.076, P < 0.0001).

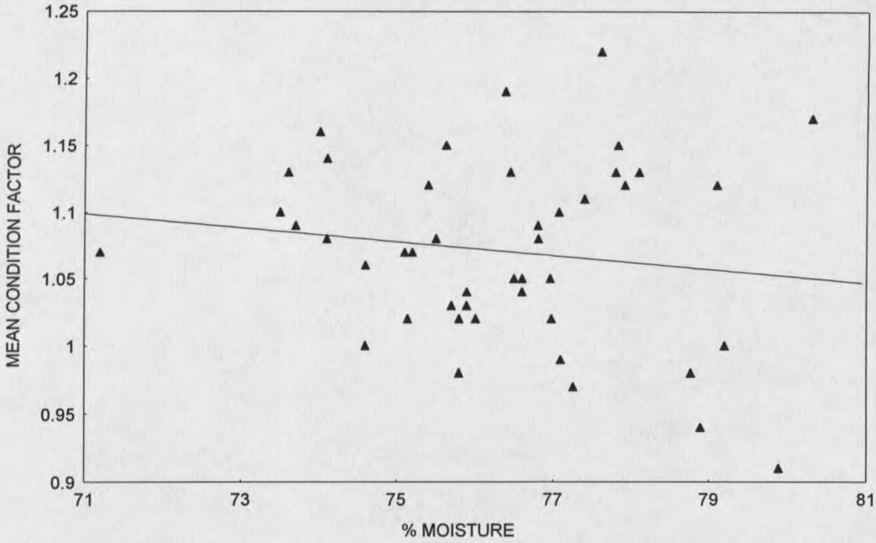


Figure 6. Relationship between mean condition factor (K) and body moisture content ($N = 45$, $R^2 = 0.021$, $P < 0.0011$).

Site access limitations in the springs of both years prevented sampling until after runoff had initiated; fish sampled at this time may have already begun feeding and increasing in weight. Therefore, spring condition factors may not be representative of the actual end-of-winter values. However, this increase was not found to occur with lipid levels, further suggesting a poor correlation between condition factor and lipid content.

Table 6. Autumn versus spring condition factor comparison (size class averages). Spring sample accounts for average 4 mm growth over winter. Values with letter in common are not significantly different.

Sample	Size Class (mm fork length)						
	45-75	76-100	101-125	126-150	151-175	176-200	201+
Autumn 1994	1.17x n=56	1.18x n=46	1.14x n=65	1.14x n=125	1.11x n=80	1.09z n=48	1.10z n=41
Spring 1995	0.95y n=18	1.00y n=20	1.04y n=35	1.04y n=52	1.05y n=34	1.05z n=26	1.09z n=18

The decline in condition factor seen in fish for the 1994-95 lipid samples was similar to that seen in the population samples obtained during the same period (Table 6). The anticipated overwinter drop in condition factor was strongly correlated with size, with the smallest size classes exhibiting the most pronounced drop (Figure 7).

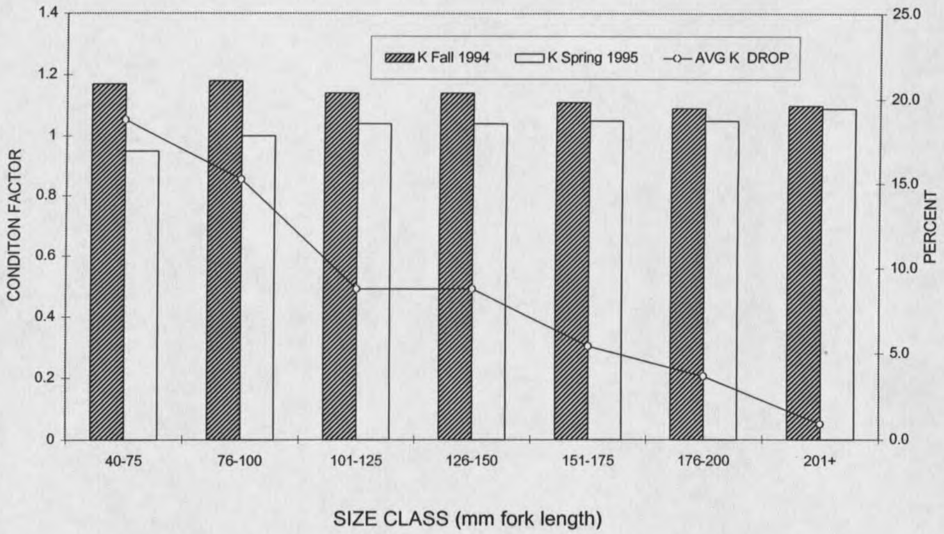


Figure 7. Change in population sample condition factor (K) in winter 1994-95 (by size class).

Winter Stream Conditions

In 1995-96, water temperatures within Cache Creek exhibited a series of sharp drops in early- to mid-October and fell below 4° C by the beginning of November (Figure 8). With the exception of the uppermost thermograph location (site 1), water temperatures fell below 2° C at the beginning of December, and did not rise above this point until after the first week of March at site 2 and until after the first week of April at sites 3 and 4. Water temperatures rose to above 4° C at all sites by mid-April.

Winter stream temperatures varied considerably within Cache Creek. Centigrade thermal units (CTU's) varied three to four times among sites (Table 7), and showed evidence of groundwater influence at the uppermost site. Despite daily average air temperatures of < 0° C for much of the winter, thermograph site 1 maintained average daily stream temperatures above 1° C from October through December 1995, and above 2° C from January through the remainder of winter. The section of stream below the groundwater input was free of surface ice through November, 1995. The extent of this ice-free area varied considerably throughout early winter and, at maximum, extended to between 100 and 150 meters downstream. Site access limitations in mid- to late-winter prevented visual inspection of the site, and the extent of groundwater warming during this period is unknown.

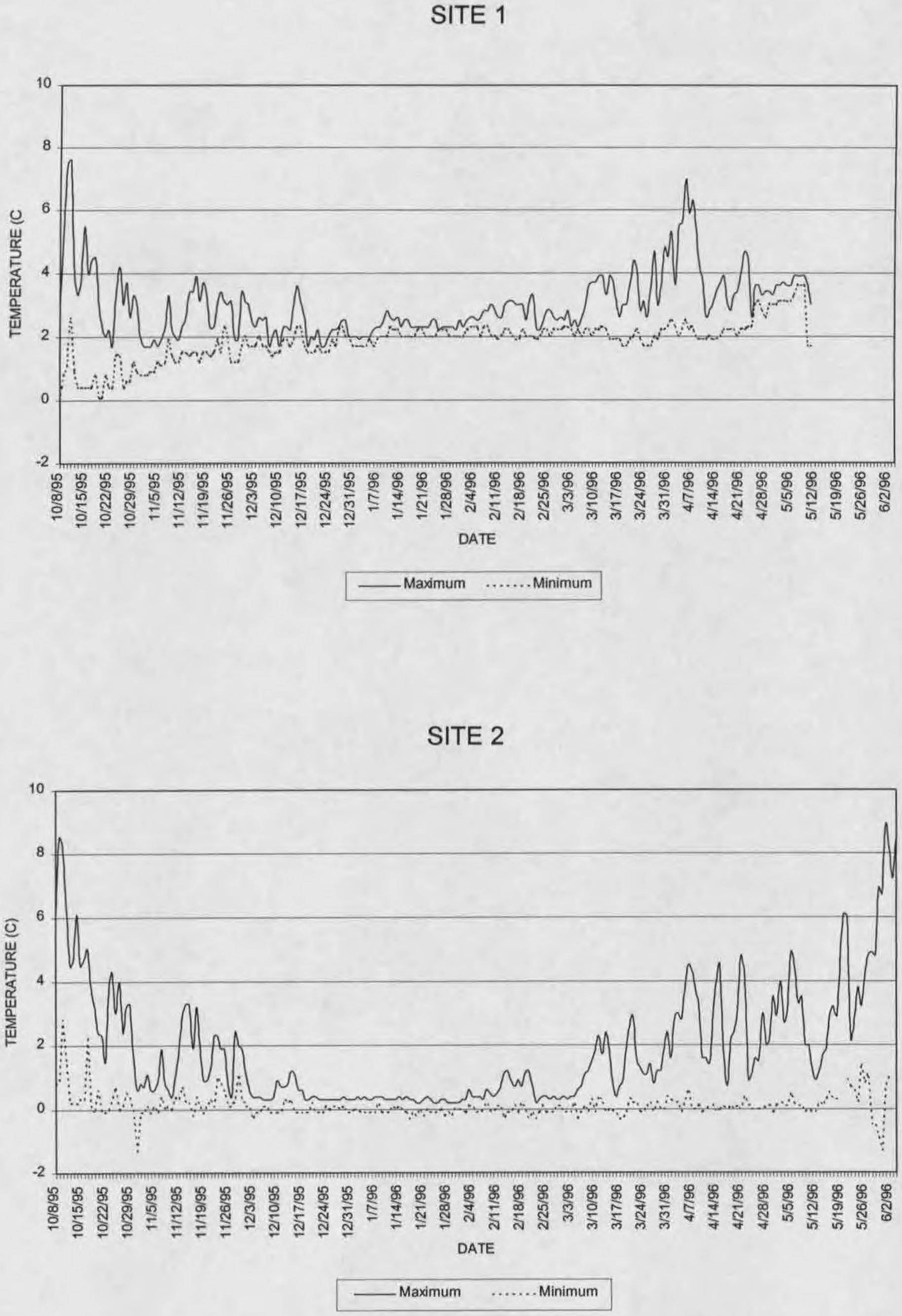
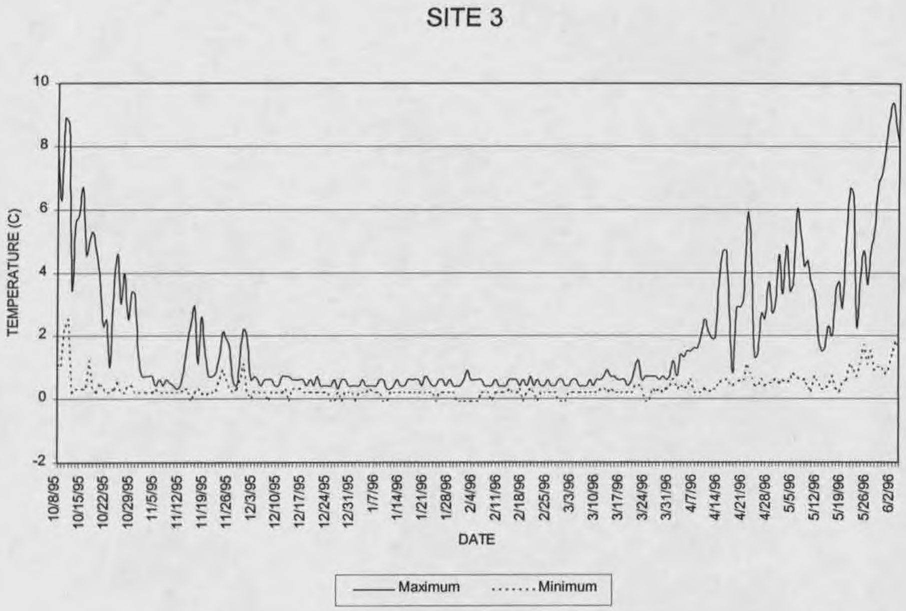


Figure 8. Daily temperature ranges over a longitudinal gradient within Cache Creek (thermograph at site 1 uppermost, thermograph at site 4 lowest).



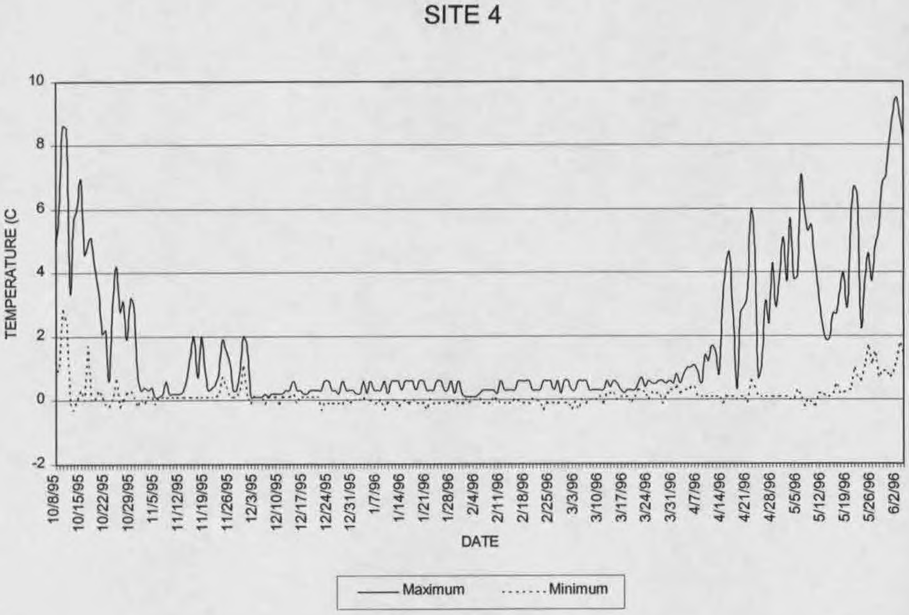


Figure 8 continued.

Stream temperatures at downstream sites (2-4) remained from 0-1° C from mid-December 1995 to early April 1996. At site 2, sharp drops in minimum daily temperatures to below 0.0° C were recorded in early November, 1995 and early June, 1996, and may have been the result of either supercooling of the water or instrument malfunction. An additional thermograph located downstream of Site 4 and immediately below another known groundwater input site malfunctioned and was excluded from the study.

Table 7. Centigrade temperature unit (CTU) comparison for thermograph sites 1-4 from 8 October 1995 to 11 May 1996 (Site 1 uppermost, site 4 lowest).

Thermograph Location	Centigrade Temperature Units (CTU's)
Site 1	502
Site 2	144
Site 3	165
Site 4	121

The thickness of stream surface ice generally increased between the two sampling periods in early winter, and exhibited considerable longitudinal variability (Figure 9). However, only ice and snow depth measurements from within the habitat unit enclosures, located within the upper stream reaches and including the area of the most pronounced level of groundwater input, were examined. Solar input was thought to be uniform over the range of locations allowing for assessment of the influence of water temperature alone. Although these sites were not uniformly spaced, they still serve to illustrate the likely impact of groundwater discharge. Site K was 1 - 2° C warmer than site H, and was ice-free on both sampling occasions, influenced by the presence of the groundwater input demonstrated by thermograph 1. Sites I and H showed considerable surface ice formation and, along with thermograph 2, serve to illustrate the decreasing influence of the upstream groundwater input. Ice depths at sites E and G were relatively low in comparison with areas adjacent to them and likely showed the influence of other groundwater discharge points.

Stream snow cover was present only on 17 December, and averaged from 9 cm to 11 cm in depth for all sites with over 4 cm of surface ice. Sites with ≤ 4 cm of ice cover (sites E, G, J, and K) possessed no measurable snow cover.

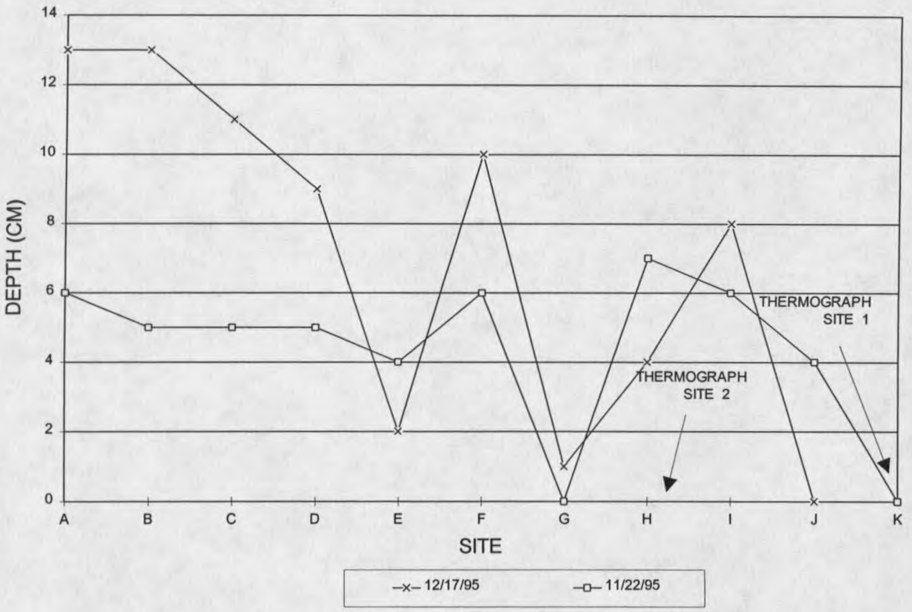


Figure 9. Change in ice depth along the length of Cache Creek (Site A lowest, site K uppermost). Locations of thermographs indicated with arrows (thermographs 3 and 4 were downstream from ice depth site A).

Movement

From 6 October to 20 November 1994, a total 82 fish were captured moving upstream (Figure 10). Of this total, 37 (45%) moved upstream over the 11-day period from 10 - 20 October. In contrast, only seven fish were found in the downstream trap, all on 6 October, 1994; no downstream movement was detected after this date. Upstream movement coincided with the sharp drop in water temperatures below 4° C in mid to late October.

Attempts to maintain and monitor the two-way weir after the beginning of December were hampered by ice and snow conditions. Formation of an ice dam eventually destroyed the trap.

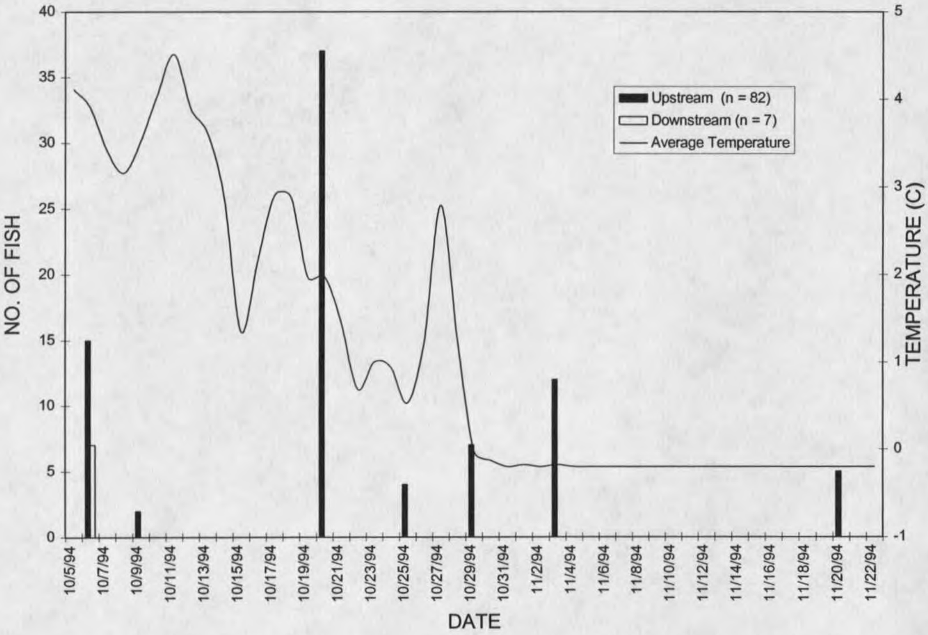


Figure 10. Upstream movement in relation to temperature changes in Cache Creek (Autumn 1994). Average daily temperatures were obtained from a thermograph placed at the weir site.

DISCUSSION

Winter Survival

Westslope cutthroat trout were relatively abundant in the Cache Creek (64/100 m^2), with densities in late autumn exceeding the 29-33 fish/100 m^2 reported by Ireland (1993). This suggests that cutthroat density within the system was relatively high going into the winter period. Also, actual autumn population abundance was likely even higher than estimated, as size-related capture probability was not consistent in all mark-recapture sampling efforts, and age-0 fish may have been substantially underrepresented in recapture sampling.

Increases in mean length over winter have been used as indications of size-specific mortality within populations and within year-classes (Oliver et al. 1979; Toneys and Coble 1979; Miranda and Hubbard 1994). However, I found no evidence for size-specific mortality of smaller size classes in Cache Creek. With age-0 fish excluded from analysis (due to apparent differences in seasonal capture probability) neither the upward shift in mean length nor the overall differences in distributions were significant. This is in sharp contrast to findings of many other researchers who have noted an increase in mean length, consistent with higher winter mortality of smaller fish, among a wide range of different species (Cooper 1953; Reimers 1963; Hunt 1969; Oliver et al. 1979; Wicker and Johnson 1987; Thompson et al. 1991; Miranda and Hubbard 1994; Smith and Griffith 1994).

Despite capture inefficiencies, many of the smallest individuals in Cache Creek did survive winter. This contradicts the findings of Smith and Griffith (1994) on rainbow trout, who found 0% overwinter survival among fish < 100 mm in October. This apparent ability of westslope cutthroat trout to survive winter at very small body sizes (< 60 mm) suggests adaptations to severe winter conditions in headwater streams, and may account for their ability to persist in high elevation systems in the presence of nonnative salmonids (Bozek and Hubert 1992).

The feasibility of using PIT-tags in salmonid species generally has been demonstrated (Prentice et al. 1990a, b). This study supports these findings, suggesting the suitability of these tags for use in westslope cutthroat trout. Tag retention was high among all size classes, and condition factor comparisons suggested no deleterious effects on fish health or body condition. The recovery of tagged fish did, however, highlight the need for standardized practices in needle and tag preparation. Because several individuals were found to have infections near tag insertion locations, our first season of tagging (1994-1995) probably lacked sufficient sterilization procedures.

Habitat/Survival Relationships

Winter habitat use patterns of salmonids have been used to suggest a link between habitat type and quality and overwinter survival (Rimmer et al. 1983; Cunjak and Power 1986; Swales et al. 1986; Hillman et al. 1987; Griffith and Smith 1993). The work of Smith and Griffith (1996) is one of the first attempts to experimentally examine this relationship. Yet, other attempts to directly measure survival under different habitat conditions will continue to be needed if we are to fully understand this link.

The failure of the habitat enclosures highlights the difficulty of winter research aimed at defining critical habitat requirements. Although it remains unclear as to whether ice or spring runoff had the greatest impact on the failure of fencing structures, my results suggest that a different approach may be needed in examining potential relationships between habitat quality and survival. In environments with similar conditions and frequency of supercooling, fencing practices that are substantially more aggressive and invasive may ultimately be required to hold adequate numbers of fish, or enclosure designs employing fencing sections may need to be abandoned entirely.

A possible alternative approach to fencing stream sections could include the use of smaller-scale holding structures, such as those employed by Smith and Griffith (1994) in their study of first-year winter survival of rainbow trout in the Henrys Fork of the Snake River. Their study design entailed placing fish in reinforced wire mesh cages, which had habitat manipulated internally. Such a design is useful in that the holding structure could also be sealed on top and submersed below the level of anticipated ice cover. This approach would be less able to directly link survival with natural habitat conditions. However, it would likely have a higher probability of withstanding severe winter conditions while still providing useful information on habitat-survival relationships.

However, large-scale habitat enclosures are valuable for their potential to measure actual *in situ* overwinter survival. Such a design may be highly effective in systems that experience infrequent supercooling events and, thus, are less likely to develop frazil ice and subsequent anchor ice formations. Additionally, systems with greater overall winter accessibility would allow for needed monitoring and maintenance of fencing sections. In such situations, anticipated ice-off could be also more accurately predicted, and fish removal could be more effectively timed. Because of the potential for enclosure failures in even seemingly ideal conditions, systems which allow for the development of numerous habitat unit replicates would be most desirable.

Body Condition

Lipid levels generally declined (though non-significant) over the winter (late autumn to early spring) within all size classes in both seasons. Over all size classes, lipid levels ranged from 2.8 to 7.8% in winter of 1994-95, and from 0.9 to 6.0% in winter of 1995-96. These values are consistent with ranges found for other salmonids. Ranges of 3 to 7% and 1.7 to 7.7% have been documented for Atlantic salmon (Gardiner and Geddes 1980) and brook trout (Cunjak 1988b), respectively. The severity of this decline within each size class varied considerably and the results of comparisons among size ranges were unexpected. In both seasons, the smallest size class had higher end-of-winter lipid levels than did the largest size class, and experienced a lower percentage drop (24% versus 56%

in 1994-95, and 27% versus 72% in 1995-96). This result is in contrast with previous studies showing greatest rates of lipid utilization among smaller size classes for the winter period (Shuter et al. 1980; Post and Evans 1989; Shuter and Post 1990).

It has been proposed that early winter is the most stressful period for salmonids (Gardiner and Geddes 1980; Cunjak et al. 1987; Cunjak and Power 1987; Cunjak 1988b). The rapidly changing environmental conditions during this period, especially sharp declines in water temperature within a relatively short time, are thought to cause rapid depletion of energetic reserves. For example, 95% of the total winter mortality of rainbow trout in the Henry's Fork occurred within the first 7 weeks (Smith and Griffith 1994). In my study, 40-100% of the overall lipid decline over winter occurred within the first 8 weeks of declining water temperatures. Similar early winter declines in energy content have been documented for other salmonids (Gardiner and Geddes 1980; Cunjak 1988b).

Declines in lipid level coincided with rapid declines in water temperatures. Between the second week of October and the first week of November 1995, maximum daily stream temperatures declined by about 8° C. These results generally support the hypothesis of early winter metabolic deficit. A notable contradiction to this is seen in the changes in early winter lipid composition within the smallest size class. These smallest fish would have been expected to exhibit the most pronounced early winter drop. However, in both years, early season lipid levels for this size class remained the same or increased.

One possible explanation for this lack of decline in lipids in small fish is that it may be an artifact of using pooled samples for analysis; there may have been substantial variation among individuals that was not evident in combination. However, another possible explanation for this, as well as for the results of the previous comparisons of the largest and smallest size classes, is a positive bias in sampling. That is, smaller individuals with lower lipid levels may have died, and only those with higher lipids remained (Gardiner and Geddes 1980). If true, this would further support the proposed metabolic deficit hypothesis, especially in relation to size-specific susceptibility.

Like lipids, mean condition factors (K) generally showed a nonsignificant decline over the winter. This is in contrast to the findings of many researchers who reported significant declines in condition factors for trout over the winter (Reimers 1963; Power and Coleman 1967; Hunt 1969; Cunjak and Power 1987b). Because of the inverse relation between lipids and moisture, it may be the case that increased moisture levels maintained body weight while lipids declined. Mean condition factor (K) would therefore be of little use in assessing changes in actual condition. Such a result was reported by Gardiner and Geddes (1980), where wet weight of overwintering juvenile Atlantic salmon stabilized or, in some cases, slightly increased due to net water uptake despite continual declines in energy content.

Moreover, K values for the pooled population samples obtained in autumn 1994 and spring 1995 did suggest that smaller size classes experienced the greatest drop in K. Other factors, however, may also have influenced changes in K over winter, and my affect the usefulness of the measure as an index of energy content. Mean fork length of recaptured, tagged fish increased by about the same amount among all size classes, but weights remained essentially the same. If these values are considered representative of the entire population, then the apparent differences in condition factor (K) decline between size class may simply be a function of the two in combination. Specifically, while the average overwinter increase in length was similar for all size classes, the impact of this increase, in terms of relative condition factor (K), becomes more pronounced with decreasing fish size. That is, the roughly 4 mm increase in length is a greater percentage of overall length of smaller fish, and thus results in a greater drop in K than for the larger size classes.

The question remains, therefore, as to whether K values are a good indication of any specific physiological condition of salmonids. Mean condition factor (K) of fish from the smaller pooled lipid samples exhibited a very poor correlation with both moisture and lipid content. This is similar to the findings of a weak relationship between K and seasonal energy levels for age-0 and age-1 muskellunge *Esox masquinongy* (Jonas et al. 1996). It may be that mean condition factor (K), especially when generated for relatively small pooled samples such as the ones used in this study, has only limited use as a measure of the condition of energy reserves in some fish species.

Winter Stream Conditions/Movement

Water temperatures within Cache Creek showed considerable variation, despite prolonged and severe winter air temperatures of < 0° C, as a result of multiple groundwater input sites. Salmonids typically select areas associated with groundwater discharges as overwintering habitat (Cunjak and Power 1986;

Brown and Mackay 1995). Brown and Mackay (1995) found trout overwintering in groundwater influenced areas as shallow as 8 cm, and suggested that "warm" water may be a more important criterion for choice of winter habitat than depth.

Groundwater inputs had an apparent influence on surface ice formation. Known groundwater input sites precluded complete ice-over, locally, until late into the winter. Whereas the findings of this study tend to support the importance of groundwater input in regulating winter environmental conditions, the actual extent to which they ultimately influenced overwinter survival of the resident cutthroat trout remains uncertain. However, several studies have shown a positive correlation between winter temperature and salmonid survival (Hunt 1969; Seelbach 1987). Similarly, whereas all rainbow trout in enclosures at a spring-fed site in the Henry's Fork survived, only 63% of fish at the coldest study site survived (Smith and Griffith 1994).

Movement of westslope cutthroat trout within the system seemed to correspond to the pronounced drop in stream temperatures to below 4° C in late October. Ireland (1993) also found a distinct shift in habitat use by cutthroat trout in Cache Creek at about this same time. This data suggests the importance of temperature cues in regulating shifts in winter behavior. However, it remains uncertain as to whether the movement response was triggered by a drop in temperatures to below a certain minimum level (i.e., 4° C) or by the magnitude and duration of the change (average daily temperatures dropped from 4.5° C to below 1° C within a 14-day period). Movement to overwintering habitat in response to temperature changes have also been documented for other salmonids (McFadden 1961; Bjornn and Mallet 1964; Chapman and Bjornn 1969; Hunt 1969).

Limited movement of salmonids from fall to winter in areas with habitat suitable for both periods has been reported (Miller 1954, 1957; Chisholm et al. 1987). In the case of westslope cutthroat trout in Cache Creek, Ireland (1993) has suggested the importance of this system as habitat in all seasons given the generally poor habitat quality of the mainstem Taylor Fork. Cutthroat trout in the Ram River, Alberta, moved to areas of deep pools with ice cover when they were excluded from fall habitats by anchor ice (Brown and Mackay 1995). The mainstem Taylor Fork is largely shallow and braided as a result of historic land use practices, and is likely to experience similar ice conditions. The lack of downstream movement, along with the limited and somewhat atypical upstream movement found in my study, suggests the importance of Cache Creek, which provides substantially greater pool depth along with the aforementioned groundwater discharges, as overwintering habitat within the Taylor Fork drainage. It has been further suggested that it is the combination of precisely these two winter habitat features, and not the presence of either feature alone, that is most valuable to trout as overwintering habitat (Brown et al. 1994).

CONCLUSION

My results show that Cache Creek, though highly sedimented and subject to extreme winter conditions, is suitable for the maintenance of a sizable population of westslope cutthroat trout. This is likely due to a combination of species and system characteristics. Despite the lack of unembedded substrate, it seems likely that adequate winter cover exists in the form of deep pools and undercut banks. Extensive groundwater inputs may also lessen the impacts of the harsh and prolonged winter period. Additionally, westslope cutthroat trout may have adaptations, likely physiological, which allow them to tolerate the restrictions and requirements imposed by this high elevation system better than other salmonids.

Although westslope cutthroat trout are abundant, the question of size-specific overwinter survival at the population level remains largely unanswered. Although the results I obtained hint at uniform mortality among size classes for this period, a more rigorous approach will be needed to assess size-specific differences with any degree of certainty. This will likely require long term data from multi-year, multiple mark-recapture sampling.

Similarly, critical habitat requirements of trout within the system still need to be defined for the winter period. While the results I obtained further suggest the importance of Cache Creek as an overwintering area, the causal relationship between habitat features such as depth and cover and survival still needs to be addressed. Additionally, my assessment of winter conditions and the influence of groundwater inputs makes it clear that such groundwater discharges should be included, both alone and in combination with other habitat characteristics, in any assessment of habitat-survival relationships. Fisheries managers will need to rely on such winter-specific information if habitat protection, restoration, or enhancement activities are to be effective in the long run. First, however, alternate enclosure designs or approaches will need to be developed that are better suited to the harsh winter conditions experienced within this system.

The results I obtained from analyses of overwinter change in body lipid content lend support the proposed metabolic deficit hypothesis. Specifically, the data demonstrate that, on the whole, lipid levels were depleted most rapidly in the early winter. Such results are consistent with the suggestion that this period is most critical for overwinter survival of fish in general.

Conversely, no clear, direct evidence was found of size-specific differences in this early season depletion rate. However, the possibility of sampling bias due to mortality of all but the most fit of the smallest individuals from the populations may itself lend indirect support to this hypothesis. Clearly, this is far from certain, and can likely be answered only through analysis of lipid content of individuals maintained and monitored in a controlled environment, where all mortality can be identified and quantified.

The results I obtained from comparisons of lipid and moisture content suggest that Fulton-type condition factors, either from individuals or pooled samples, may have limited use in assessing actual fish condition. Its reliance on absolute weight as a measure of energy reserves, along with its other potential biases, may limit its value only to use as a rough measure of the minimum weight-at-length needed for survival. As such, mangers may need to reevaluate their use of this index in assessing temporal changes within trout populations, especially over the winter period when moisture uptake may be compensating for declines in energy content.

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