

SUMMER RESOURCE LIMITATION AND OVER-WINTER MOVEMENT AND
SURVIVAL OF STREAM-RESIDENT COASTAL CUTTHROAT TROUT

by

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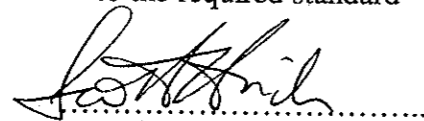
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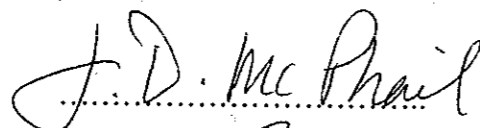
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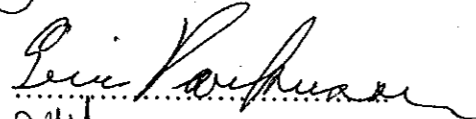
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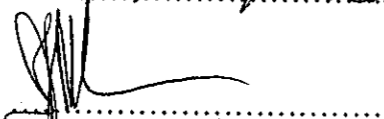
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ABSTRACT

To what extent are salmonids limited by food and cover in streams? To answer this question, I conducted a summer field experiment to test the effects of food and cover on growth, survival and emigration of coastal cutthroat trout (*Oncorhynchus clarki clarki*). Resources that affect summer growth can further influence individuals if body size is linked to other aspects of fish ecology, such as over-winter survival. Thus, I also examined whether size at the end of the experiment improved survival over winter.

Using a 2x2 factorial design, I manipulated food and cover in stream enclosures containing individually marked trout replicated in two streams. To address how summer growth affects over-winter survival, I monitored the released experimental fish throughout autumn and winter.

During summer, fish receiving food additions experienced growth rates 80 times higher than those of unfed fish, indicating marked food limitation. The absence of cover additions increased mortality by approximately 50% in one stream, but had no effect in the other. Emigration was not strongly affected by either factor. Over-winter survival was not explained by body size. Fed fish were still larger than unfed fish by the next spring.

Using capture-recapture methods, I further investigated relations between body size and movement, survival and growth during winter for the general population in each stream. Movement during winter was not related to body mass or condition. Survival increased over the size range of the smallest fish, and then gradually decreased as mass increased for larger individuals. On average, growth was positive during winter and relative growth was not related to mass during the coldest part of winter (November to January). This pattern of growth suggests the size-based mortality may not have been due to energetic stress.

My results show that during summer, food can limit trout growth, and cover, by mediating predation, can limit survival. How summer growth, or body size in general, affects winter ecology may depend on environmental factors. Size-related movement may be uncommon in winter if temperatures minimize aggression and food demand. Strong positive relationships between body size and winter survival might not be expected when warm temperatures preclude winter starvation, if predator abundance is low, and when low discharge minimizes mortality related to flooding or habitat limitation.

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CHAPTER 1. The effects of food and cover on the growth, survival and movement of cutthroat trout in coastal streams.

INTRODUCTION

Populations can exhibit pronounced temporal and spatial variability. Identifying factors that exert the greatest influence on population production and loss, and how they act to cause these changes, is a primary goal of ecology. Resource availability has long been recognized as playing a central role in limiting, and possibly regulating, populations. Several studies have pointed to this role in populations of mammals (e.g. Hubbs and Boonstra 1997), invertebrates (e.g. Richardson 1991), birds (e.g. Watson et al. 1984), and fish (e.g. Mason 1976). Experimental manipulations, such as these, are the best way to identify the relative importance of limiting resources, and how they interact.

Food and cover (i.e., habitat feature that provides protection from predators, competitors, or unfavorable environmental conditions) are often cited as critical resources for stream-dwelling salmonid fishes. Both are thought to strongly influence patterns of individual survival, growth and habitat selection, and hence, population abundance or biomass (Chapman 1966, Bjornn and Reiser 1991, Hicks et al. 1991). Laboratory studies have demonstrated how the availability of food and cover can mediate foraging rate-predation risk trade-offs (e.g. Grand and Dill 1997) or rates of emigration (Wilzbach 1985, Mesick 1988). However, most field studies that have linked food or cover to demographic measures are correlative (see Fausch et al. 1988, and Poff and Huryn 1998), or have manipulated only a single variable. Few field manipulations (e.g. Gowan and Fausch 1996b) have incorporated proper controls and replication; none have addressed the precise interplay between these two factors. Thus, the relative value of food and cover, and how they interact to limit fish production, has not yet been well quantified.

Cover may influence survival by protecting fish from their predators and by providing refuge from high water velocities. Many studies have demonstrated positive correlations between the abundance of salmonids and the amount of in-stream physical structure (e.g. Fausch and Northcote 1992). However, the association of fish with in-stream structure may simply reflect habitat preferences and does not provide sufficient evidence that cover improves survival. Further, cover use, and thus the relative benefit of

cover, varies among species (e.g. Fausch 1993). Higher survival of fish from more physically complex stream reaches (Quinn and Peterson 1996) and semi-natural stream channels (Lonzarich and Quinn 1995) suggests a fitness benefit does exist in being associated with cover. Yet several studies have failed to find a direct link between survival and cover in the field (e.g. Spalding et al. 1995, Gowan and Fausch 1996b). The relationship between cover and growth is also unclear. Cover may positively affect growth by creating hydraulic conditions favorable for foraging (Fausch 1984) or by visually isolating individuals from conspecifics (Sundbaum and Näslund 1998) and predators. Alternatively, overhead cover may reduce foraging efficiency by impairing detection of prey (Wilzbach et al. 1986).

Food limitation of stream salmonids has been inferred from several lines of indirect evidence. Positive correlations between food supply and fish abundance, biomass, or growth rates during summer have been commonly noted (e.g. Wilzbach et al. 1986, Ensign et al. 1990, Bilby and Bisson 1992). Similar trends have been found in studies that have increased primary and secondary production through nutrient additions (Warren et al. 1964, Johnston et al. 1990, Deegan and Peterson 1992). Evidence of density-dependence in individual growth rates further supports a food-limitation hypothesis (e.g. Bilby and Bisson 1987, Hume and Parkinson 1987, Jenkins et al. 1999). Finally, Mason (1976) demonstrated increased growth and survival of juvenile coho salmon (*Oncorhynchus kisutch*) by directly increasing food supply. Because body size is closely linked to many aspects of fish ecology (see Wootton 1990), even small variations in individual growth may have significant consequences for fitness. One such relation thought to be relevant to stream salmonids is the relation between size and over-winter survival. A pattern of improved survival with increasing size has been found for several species (Hunt 1969, Holtby 1988, Hutchings 1994, Smith and Griffith 1994, Quinn and Peterson 1996). Thus, factors limiting growth during summer may influence individuals and populations through both direct and indirect mechanisms.

Quantifying the effects of food and cover on growth, survival, and migration requires experimental manipulation in the field. Previous experiments have provided insight into the role of food (Mason 1976) or cover (Gowan and Fausch 1996b)

separately, but have only partially addressed the interaction of these resources (Wilzbach et al. 1986). In addition, linking summer growth to other measures of individual performance, such as over-winter survival, may further clarify the role of summer resources to fish. Coastal cutthroat trout (*Oncorhynchus clarki clarki*) are common in small streams of the Pacific Northwest (Trotter 1989). Resident (i.e., non-anadromous) cutthroat often complete their entire life history within relatively short reaches of stream. Thus, the availability and distribution of resources may strongly influence trout at both individual and population levels.

I tested how and to what extent food, cover, and both food and cover, affect resident cutthroat trout during summer. I experimentally manipulated the availability of food and cover within enclosures containing individually marked trout in two natural streams. I predicted that food addition would affect individuals primarily through increased growth, while cover addition would primarily increase survival; both would decrease emigration. To determine whether differences in body size (in this study, due to experimentally altered phenotypes) result in differential growth or survival over winter, experimental trout were recaptured over winter following their release from enclosures. I predicted the probability of surviving over winter would be positively related to the size of fish at the end of the summer experiment.

METHODS

Study area

Research was conducted at the Malcolm Knapp Research Forest (49°16'N, 122°34'W) within the Coastal Western Hemlock (*Tsuga heterophylla*) biogeoclimatic zone of British Columbia, Canada. Two streams, East Creek and Spring Creek, with unexploited populations of resident coastal cutthroat trout were selected that contained suitable reaches for installing experimental enclosures (Table 1.1). Resident cutthroat trout are the only species of fish within the study reaches. East Creek is a second order stream and is a tributary to Spring Creek, a third order stream; the study reaches were separated by approximately 0.5 km of stream.

The surrounding western hemlock, western redcedar (*Thuja plicata*), and Douglas-fir (*Pseudotsuga menziesii*) forests were harvested for the second time in the mid-1970s and replanted with Douglas-fir. The current streamside forest is dominated by Douglas-fir, with sparse red alder (*Alnus rubra*), salmonberry (*Rubus spectabilis*), and western redcedar in riparian zones.

Summer experiment

Experimental design

During August and September of 1997, I performed a factorial experiment in East and Spring Creeks with two levels of food and cover. The four treatments were: 1) control (no food or cover added), 2) food addition, 3) cover addition, and 4) both food and cover added. Each treatment was replicated four times (Table 1.1). I introduced groups of individually marked, one year old cutthroat trout into 9 meter long, enclosed reaches of stream. Enclosures were randomly assigned treatments within each stream, except in one case where a single enclosure, with a 40 cm deep undercut bank, was restricted to either a cover, or food and cover, treatment. The experiment ran for 40 days in East Creek and 20 days in Spring Creek (Table 1.1).

The food addition treatment consisted of live mealworms (larval *Tenebrio molitor*). Daily rations were 16% of the mean biomass of all fish per enclosure. In East Creek, I adjusted rations at the mid point of the experiment to account for increased biomass due to fish growth. Food was dispensed over 12 hours by automatic, conveyor belt-style feeders attached to the upstream fence of the enclosure. This slow, haphazard introduction of food mimics how natural prey falling from riparian vegetation would be encountered by fish. A cover structure consisted of a 10"x1"x6' wooden plank resting on two cinder blocks. Planks were sprayed with non-toxic brown paint to make them appear more natural. In East Creek, each enclosure assigned a cover treatment received three plank-cinder block structures, and in Spring Creek, which was wider (Table 1.1), each received six. Fish readily used the structures as cover and as foraging stations throughout the experiment.

I selected reaches for enclosure locations that were low in structural complexity and that had relatively homogeneous widths and depths (Table 1.1). Though rarely necessary, any structure present, such as boulders or small wood, was removed. Reaches were bounded by two fences installed across the width of the stream. Enclosure fences were 81.3 cm high, with 4 mm wire mesh attached to a wooden frame. Approximately 15 cm of each fence was buried in the stream substrate and, where needed, sandbags were stacked between the end of the fence and the stream bank. To control for differing light levels among enclosures, any riparian shrubs overhanging the stream were tied back.

Each enclosure had an upstream and downstream emigration trap fitted onto the fences. Traps were 28cm x 28cm x 28cm, and had a 2 cm wide v-notched entrance; two flexible plastic strips extended out from both sides of the v and met at the center of the entrance. Fish could exit the enclosure into a trap, which then held the fish until checked. Fish may have been able to escape from the traps back into enclosures. Emigration was still a relevant measure because ability to escape traps should be independent of treatment.

Fish marking and monitoring

Baited minnow traps and some electrofishing were used to collect the study fish from their respective streams. Fork length (mm) and mass (nearest 0.01g), were measured for all fish. Five size classes of one year old cutthroat trout were used (mm):

1. East Creek: (i) 68-72, (ii) 73-76, (iii) 77-80, (iv) 81-84, (v) 85-88
2. Spring Creek: (i) 74-78, (ii) 79-82, (iii) 83-86, (iv) 87-90, (v) 91-94.

I attempted to match the density of fish in the enclosures to that of natural stream densities, approximately 0.49 fish/m² (Young et al. in press). Each enclosure received a single fish of each size in East Creek, and two fish of each size in Spring Creek. Initial mass ranged from 2.89 to 7.11 grams in East Creek and 3.66 to 7.55 grams in Spring Creek. Fish were marked using unique combinations of colored latex dye injected into anal, caudal and dorsal fins. As insurance against any potential loss of dye markings, all experimental fish had adipose fins clipped. Prior to the introduction of experimental fish, the enclosures were intensively trapped and electrofished to remove any unwanted fish.

I sampled fish by setting four minnow traps baited with salmon roe in each enclosure for three consecutive days. Captured fish were anesthetized with carbon dioxide, weighed, measured, and released back into enclosures. Trapping took place in East Creek on August 25-27, September 14-16 and September 21-23 and in Spring Creek on September 14-16 and September 21-23.

Emigration traps were checked daily for fish. Emigrants were weighed, measured, and then released at the center of the enclosure reach. To minimize handling stress, any individuals that emigrated on two or more consecutive days were not re-measured.

I calculated relative growth rates (% change in body mass/day) for individuals as:

$$(1) \text{ relative growth rate (RGR)} = [(\text{final mass} - \text{initial mass}) / (\text{initial mass} * \# \text{ days between sampling})] * 100.$$

Most fish were in enclosures for several days before the experiment began, and some were not recaptured until several days after it had ended. To be conservative in my growth estimates, I used the actual number of days between sampling in calculations rather than back-calculating initial and final mass to the start and end date of the

experiment. I estimated survival as the percentage of fish from each enclosure that were caught at the end of the experiment, or at any point during winter sampling.

I used drift nets with a mesh size of 250 μm to collect stream invertebrates in enclosures. Samples were taken on August 22nd and September 6th in East Creek and on September 6th in Spring Creek. I randomly selected two out of three replicates of each treatment in East Creek for drift sampling, and sampled each enclosure in Spring Creek. Drift nets were set for a total of 3 hours - 2 hours before sunset until 1 hour after sunset. Drift density was calculated as numbers/100 m^3 .

Analysis

To test for treatment effects on mean relative growth rate, % survival, and emigration, I used a randomized block ANOVA, where stream was the blocking variable, and replicates were nested within blocks and treatments. This design created a sampling error term that was used to test for a block effect and block by treatment interactions (Appendix 1).

To compare condition of fish among treatment groups, I used analysis of covariance with final mass as the dependent variable and final length as the covariate (both variables were log transformed). This fits a regression relationship of length and mass for each treatment group, and tests if length-mass relationships differ among groups.

One might ask whether individuals that survived or emigrated differed in any way from those that died or did not move. I compared the initial size class of survivors versus non-survivors, and fish that emigrated versus those that did not, using Mann-Whitney U tests. Mann-Whitney U tests were used because size class data (i.e., 1, 2, 3, 4, or 5) were ordinal, and not normally distributed. I further compared final condition and relative growth rate of fish that emigrated versus those that did not using two-factor ANCOVA (as above), and two-factor ANOVA, respectively. In both the ANCOVA and ANOVA, the second factor was food treatment.

When necessary, data were transformed (and noted in results) to meet the assumptions of analysis of variance. All transformations resulted in normalized distributions and homogenous variances.

Winter sampling

Sampling protocol

At the end of the summer experiment, all of the enclosure fences were removed and the fish allowed to disperse. I performed multiple capture-recapture sessions for the experimental fish over winter using baited minnow traps. Trapping took place in the general vicinity of and extended beyond where the enclosures had been located. In Spring Creek, the trapping reach (total length 113 m) was bounded upstream by a steep increase in gradient, and downstream by a road culvert. Culverts set both the up and down-stream trapping limits on East Creek (total length 448 m). While deterrents to movement existed at all of the reach boundaries, the upstream culvert on East Creek was likely the only true barrier to emigration; immigration could potentially occur at all boundaries.

Traps were set approximately 5 meters apart, with an extra trap set every 15 meters, along the length of the stream reach. Traps were set in the same locations for every trapping session, and sampled a variety of habitat types.

Six trapping sessions were conducted after the summer experiment. Sessions took place in October and November of 1997, and in January, February/March, April and June of 1998. Sessions in Spring and East Creek were separated by 0, 8, 3, 3, 1, and 0 days, respectively. To simplify analysis, the sessions were treated as if they had taken place concurrently in each stream. Sessions lasted 1-3 consecutive days, and traps were checked approximately every 24 hours. Each captured animal was identified, measured, weighed, and returned to its point of capture. All fish had PIT (passive integrated transponders) tags implanted into the body cavity upon first capture as some of the latex marks were fading. PIT tags allow for individual identification of fish; previous studies have found no negative effects of PIT tags on growth or survival of cutthroat trout (Harvey 1998) or juvenile coho salmon (Peterson et al. 1994).

Analysis

Growth

To test for differences in over-winter growth between fish that had or had not received food additions during the summer, I calculated growth rates for 26 experimental fish caught in September and again in April. Because fish were no longer restricted to enclosures, each individual was considered a replicate. Stream (East or Spring) and food treatment (fed or unfed) were entered as fixed factors into a two-factor ANCOVA on relative growth rates. Mass was used as a covariate. I compared mass and Fulton's condition factor ($g/(mm)^3 \cdot 10^5$) (Ricker 1975) of fish in September and April by three-factor ANOVA. Stream (East or Spring) and food treatment (fed or unfed) were fixed, between group factors, and time (September or April) was a repeated measure factor. I did not use ANCOVA (see condition analysis for summer experiment) to test for differences in length-mass relationships because sample sizes were too low. Cone (1989) suggested that comparing Fulton's condition factor among groups can be problematic if condition increases or decreases as a function of fish length. I tested for this relation with regressions of condition factor versus length for each food treatment pooled across streams, and for each stream pooled across food treatment; none of the slopes differed from zero (all $p \gg 0.05$).

Survival

I had measures of September mass for 75 of the 100 experimental fish. I used capture data from these 75 individuals to examine the relationship between fall size and survival. For the purposes of capture-recapture analysis, the data from all days within a trapping session are pooled, with the assumption that no demographic changes have occurred over this short period. Analysis of capture-recapture data results in separate estimates of survival (Φ) and capture (P) probabilities. Here, mortality reflects losses due to both death and emigration. I estimated monthly survival by first fitting a series of biologically realistic survival-recapture models. The best model was then selected based on the principle of parsimony. The set of models was created by: 1) defining a global, or most parameterized model, 2) reducing the global model by alternately removing sources

of variation from capture and survival model structure, and 3) modeling survival and/or capture probabilities as logistic functions of individual fall mass.

My global model, $\Phi_{s*t} P_{s*t}$, allowed survival and capture rates to differ over time (t) and between streams (s), i.e., the time-dependent Cormack-Jolly-Seber (CJS) model applied to each site. Notation follows that of Lebreton et al. (1992), where factors can be combined additively (+, parallel on the logit scale) or interactively (*). The mass-dependent models were based primarily on the structure of the best model from step 2 above, though some with both a more complex or simpler structure were also fit (see Appendix 2 for details on model selection). Covariate models were fit using the logit link with survival or recapture expressed as a linear function of mass (m), i.e., probability = $b_0 + b_1(\text{mass})$.

The best model was selected according to the Akaike Information Criterion (AIC) (Lebreton et al. 1992, Burnham and Anderson 1992). AIC selects the most parsimonious model by compromising between simple model structure with good precision but high bias, and complex model structure with low bias but poor precision. The model with the lowest AIC represents the best compromise between bias and precision. I used a limited number of likelihood ratio tests to confirm results based on AIC. The overall goodness-of-fit of the global model was checked using the chi-squared statistics of Test2+Test3 described in Burnham et al. (1987). I used program MARK (White and Burnham 1999) for model fitting and selection (based on AICc, a modification of AIC that corrects for bias related to sample size), goodness-of-fit testing, and to calculate the final maximum likelihood survival and recapture estimates.

RESULTS

Summer experiment

Not all fish were successfully removed from the enclosures prior to the introduction of the experimental fish. Young-of-the-year and a few one-year old cutthroat that had either not been initially removed from enclosures, or had entered during a high water event midway through the experiment, were present. Extra fish were taken out of enclosures when captured. Emigration, growth rate, and survival were not affected by the density of extra fish (corrected for the amount of time in enclosure), nor were emigration or growth rate affected by density of all fish in each enclosure (i.e., surviving experimental fish, plus extra young-of-the-year and one-year old fish) (five analyses, ANCOVA, density covariate, all $p > 0.05$). Thus, I did not correct for density in the final analyses. No experimental fish were captured outside of the enclosures during an intensive trapping session after the high water event.

I averaged the individual growth rates of fish in each enclosure. This simplified the analysis because I had not recaptured every fish at the end of the experiment, and enclosures in each stream contained different numbers of fish initially. However, it also results in the enclosure averages being unequally weighted (i.e., enclosure means are based on different numbers of fish). This would bias the mean value for an enclosure if fish of different sizes differed in their growth rate. I tested for this relation and found growth rates were not related to initial mass of fish (ANCOVA on log+1 transformed RGR, mass covariate $F_{1,64} = 1.48$, $p = 0.228$; Slope = -0.018).

Drift densities were similar among enclosures (Table 1.2), and comparable to densities typically found in other streams (100-1000/m³) (Allan 1995).

Emigration

Emigration was low during the experiment, with fish making a total of 29 moves into emigration traps. Of those moves, 25 were into downstream traps and 4 were into upstream traps. Only 16 individuals out of 100 experimental fish were responsible for all of the movements. The mean number of times fish emigrated per enclosure was not

affected by either food or cover (two-factor randomized block ANOVA, food: mean \pm SE = 2.75 ± 1.11 , $F_{1,3} = 0.64$, $p = 0.482$; cover: 2.75 ± 0.63 , $F_{1,3} = 1.34$, $p = 0.331$).

Emigration decreased to an average of 0.5 ± 0.5 moves per enclosure with both food and cover present, but the decrease was not significant ($F_{1,3} = 3.49$, $p = 0.159$). Results did not change when only one emigration event was counted per individual. Emigrants did not differ from non-movers in initial size (Mann-Whitney U test, $Z = -1.13$, $p = 0.259$), final condition (two-factor ANCOVA, emigration $F_{1,69} = 0.83$, $p = 0.366$) nor relative growth rates (two-factor ANOVA on log+1 transformed RGR, emigration $F_{1,69} = 1.14$, $p = 0.289$).

Growth

Growth of trout was strongly influenced by food (two-factor randomized block ANOVA, food $F_{1,3} = 34.76$, $p = 0.01$); fish receiving food addition experienced 80 times higher growth rates than fish that did not receive food (Figure 1.1). By the end of the experiment, the mean mass of fed fish was 71% higher than unfed fish in East Creek, and 30% higher in Spring Creek (Table 1.3). Cover did not affect growth rates (cover $F_{1,3} = 0.62$, $p = 0.489$) and there was no interaction between treatments (food \times cover $F_{1,3} = 0.04$, $p = 0.854$). Growth also did not vary by stream (block $F_{1,8} = 0.04$, $p = 0.847$), nor were there any stream by treatment interactions (all $p > 0.05$).

To place growth of experimental fish in a natural context, I calculated growth rates for several free-ranging, marked fish in East Creek. The free-range fish were within the initial size class limits of the experimental fish. Growth rates were calculated over a minimum of 20 days during the same time period as the experiment. Although the relative growth rates of unfed fish were low and sometimes negative (mean \pm 1SE = 0.029 % body mass/day ± 0.05 , $n = 35$), they were comparable to those of free-ranging trout (0.147 ± 0.04 , $n = 14$, $t = -1.21$, $df = 47$, $p = 0.230$). Growth rates of fed fish were 12 times higher than those of free-ranging trout.

Condition

The elevation of the length-mass regression lines was different for fed and unfed fish only (food $F_{1,3} = 83.39$, $p = 0.003$) and the slopes of the regression lines were parallel (block x food x cover $F_{1,58} = 0.29$, $p = 0.956$). Fed fish were in better condition, weighing 13% more than unfed fish at any given length.

Survival

Survival of trout ranged from 40-100%, but was generally high, with the median survival within enclosures equaling 95%. The exception to this was in Spring Creek, where survival of trout in enclosures without cover was less than half that of trout with cover (Figure 1.2; block x cover $F_{1,8} = 10.32$, $p = 0.012$). In East Creek, survival was high regardless of treatment. There were no other treatment effects on survival (all $p > 0.05$). The initial size of fish was not related to survival (Mann-Whitney U test, $Z = -0.55$, $p = 0.582$).

Winter

Growth

Over winter, relative growth rate tended to decrease for larger individuals (Figure 1.3). Because unfed fish were smaller than fed fish, it was necessary to include mass as a covariate (two-factor ANCOVA, mass covariate, log transformed $F_{1,21} = 4.97$, $p = 0.037$). For a given mass, there were no differences in relative growth between unfed and fed fish (Figure 1.3; food $F_{1,21} = 2.68$, $p = 0.116$). Fish in East Creek tended to grow more than those in Spring Creek (stream $F_{1,21} = 3.87$, $p = 0.063$). On average, growth rates of fish in East Creek were 1.33 times higher than in Spring Creek (adjusted means).

Fed fish maintained their size advantage over unfed fish during winter (Figure 1.4; three-factor ANOVA on log transformed September and April mass, food $F_{1,22} = 7.13$, $p = 0.014$; repeated measure (time) $F_{1,22} = 1468.41$, $p < 0.001$; stream and all interaction terms, $p > 0.05$). By spring, condition of the two groups of fish had converged (Figure

1.5; three-factor ANOVA on square-root transformed condition factor, food x repeated measure (time) $F_{1,22} = 6.72, p = 0.017$).

Survival

The global CJS model, which estimates a unique survival and capture probability for every time period for each stream, appeared to be a good fit (East Creek $\chi^2_{10} = 3.44, p = 0.97$; Spring Creek $\chi^2_5 = 4.92, p = 0.43$; Total $\chi^2_{15} = 8.35, p = 0.91$). A probability of < 0.05 would indicate a poor fit. However, test power was low because data were sparse.

Of all the models fit, model $\Phi \cdot P_t$ had the lowest AICc, i.e., it was the most parsimonious model (Table 1.4, Appendix 2). All other models had AICc values at least two greater. Selection of model $\Phi \cdot$ indicates that none of the factors I tested - stream, time, or fall mass of fish - explained a significant amount of variation in survival. Likelihood ratio tests also indicated no effect of these factors. The best mass model, $\Phi_{\cdot+m}$ had a slope of -0.034 (on the logit scale), contrary to the predicted positive relationship between survival and size. Replacing the mass covariate with length or condition factor showed similar results.

Given that mass did not significantly influence survival, I did the analysis using all 100 experimental fish to get an overall survival estimate. I treated the start of the summer experiment in East Creek as the initial release of all fish. This added one more time period to the capture-recapture analysis. Rather than grouping fish by stream, which was not significant in the preceding analysis, I used the no cover treatment fish from Spring Creek as one group, and all other fish as a second group. This allowed me to verify the cover effect from the summer experiment. Also, the increase in sample size results in a gain in precision on the final estimates. The modeling procedure was the same as described previously, but without any mass-dependent models. I attempted to model time variation in capture rates as a function of mean water temperature during trapping and sampling effort using the logit link.

The global CJS model using all experimental fish showed a good fit to the data (Spring Creek - no cover $\chi^2_4 = 1.16, p = 0.88$; All others $\chi^2_{15} = 11.03, p = 0.75$; Total $\chi^2_{19} = 12.19, p = 0.88$). Model $\Phi_{g1, \cdot 2-7} P_{\text{temp+eff}}$ was selected as the final model, although

models $\Phi_{g1, \bullet 2-7} P_{\text{temp+eff}}$ and $\Phi_{g1, \bullet 2-7} P_t$ were also ranked highly (Table 1.5). Under model $\Phi_{g1, \bullet 2-7}$, survival varied by group (g) during the first time interval (1) (i.e., cover effect from summer experiment) but was constant (\bullet) between groups and among time periods over the rest of the sampling period (2-7).

The summer experiment survival estimates from capture-recapture for Spring Creek fish without cover (60%) and for all other fish (97%) are somewhat higher than, but consistent with, the return rate calculation used in the analysis of variance (45% and 91%, respectively) (Table 1.6). Over winter, monthly survival was 96% (Table 1.6). In other words, 73% of fish alive in September survived until June. Mean temperature and trapping effort explained the variation in capture rates. Model $P_{\text{temp+eff}}$ expressed capture rates as the additive effect of temperature and effort, where capture was positively related to both temperature and effort. Capture rates varied from a low of 0.18 to a high of 0.88, based on the equation $\log_e(P/1-P) = -3.997 + 0.215(\text{mean temperature}) + 0.0038(\text{trapping effort})$ (Table 1.6). The fit of the final model $\Phi_{g1, \bullet 2-7}, P_{\text{temp+eff}}$ was good ($\chi^2_{39} = 33.64, p = 0.713$). I conducted two days of extra trapping in 140m (East Creek) and 76m (Spring Creek) sections immediately downstream of the study reaches during April; no fish from the summer experiment were captured, suggesting emigration was minimal.

DISCUSSION

My results show that food and cover can limit the growth and survival of cutthroat trout during summer. As predicted, food was the dominant factor acting on trout growth, while cover acted through an effect on survival. Trout growth was clearly food-limited. Growth rates of fed fish were 80 times higher than for unfed fish, resulting in the mean mass of fed fish being 71% and 30% higher than unfed fish in East and Spring Creeks, respectively. I found no evidence that cover affected growth. Rather, the only cover effect was in Spring Creek, where mortality was substantially higher in the absence of cover. The effects of food and cover did not interact statistically (i.e., where the overall effect of both increasing food and cover would be greater than the sum of their effects separately). They do interact in a biological sense, however, in that the highest biomass would occur under conditions of both high food and cover availability. Though fed fish were still larger than unfed fish by the following spring, larger fall size did not appear to confer an advantage to fish in terms of over-winter survival.

Cover and survival

I found a direct link between cover and summer survival of trout. Interestingly, the absence of cover increased mortality in one stream, but had no effect in the other. All summer mortality was likely from predation, since the streams were near base-flow, no fish were found dead against enclosure screens, and the fish showed no signs of stress or disease during handling. This suggests that there may have been a difference in predation pressure between streams. Variation in predation intensity among streams is undoubtedly common in nature, but difficult to quantify. Though predator sightings were not common, a great blue heron (*Ardea herodias*) was observed at Spring Creek and on a few occasions a weasel (*Mustela* sp.) at East Creek. Also, larger gravel size in East Creek may have provided fish with cover from predation even in the absence of the cover treatment.

Another important factor to consider is season. In winter, many salmonids display an increased affinity for protective cover (e.g. Cunjak and Power 1986, McMahon and

Hartman 1989). Such behavior presumably improves survival by reducing exposure to dangers such as ice, high water velocities, and predators. Growing evidence supports this view. For example, Quinn and Peterson (1996) found winter survival of juvenile coho salmon was positively related to the habitat complexity of the stream reach they occupied. Thus, cover may play a stronger role in fish survival during winter.

My results in Spring Creek contradict previous studies that have found no strong relation between salmonid survival and physical structure during summer. Spalding et al. (1995) found significant avian predation on juvenile coho salmon in semi-natural stream channels, but mortality was not related to the complexity of brushy debris treatments. Similarly, Lonzarich and Quinn (1995) found that cover in the form of depth, rather than physical structure, was most important in determining patterns of survival for juvenile coho salmon and steelhead trout (*Oncorhynchus mykiss*). Research based in warm-water streams demonstrate very strong predator impacts, mediated by water depth (Power 1987, Harvey and Stewart 1991). The role predation plays in structuring fish populations in more northern temperate regions is less clear. I suggest that an experiment manipulating both cover and predators, or a large-scale predator exclusion would help clarify the role of predators and/or cover.

My results show that cover can improve survival when emigration is restricted. Under natural conditions, fish may choose to leave habitats low in cover to reduce predation risk. Indeed, in a large-scale experiment, Gowan and Fausch (1996b) found that only movement, not survival, of resident trout was affected by habitat manipulation. Artificial stream channel experiments sometimes find increased emigration under low cover conditions (Mesick 1988), although I found no evidence of this. However, under high population densities, some individuals may be forced into suboptimal habitats by dominant conspecifics (Hughes 1992). Also, it is not uncommon for fish to become isolated in pools during summer low flow in small streams (e.g. Northcote and Hartman 1988, Northcote 1992). In situations such as these, cover could be naturally limiting to fish.

I found no effect of cover on trout growth rates. Previous work on how cover affects growth has been equivocal. Experiments where fish have been restricted to

reaches have found increased (Sundbaum and Näslund 1998), decreased (Wilzbach et al. 1986), or no difference (Spalding et al. 1995, Lonzarich and Quinn 1995, this study) in growth in response to cover. Field manipulations where fish are free to move have generally found no effect of cover on growth (Saunders and Smith 1962, Boreman 1974, Moore and Gregory 1988, Gowan and Fausch 1996b, Harvey 1998). However, the results of such studies may be confounded by density-dependent growth effects, because the habitat manipulation often results in higher numbers of fish. How cover affects fish growth may depend on whether the structure functions as velocity refuge, visual isolation, or predation refuge to fish. Cover may enhance growth by providing favorable foraging sites, e.g. low-velocity positions next to swifter currents (Fausch 1984). Further, cover may reduce exposure to competitors and predators, allowing fish more time to forage and decreasing energy expenditure related to aggressive interactions (Sundbaum and Näslund 1998). However, there may be a negative effect on growth if cover reduces a fish's ability to detect or catch its own prey (Wilzbach et al. 1986). The relative importance of each function, and thus the net effect of cover, will likely vary by species (Fausch 1993), season, and state-dependent differences among fish (Grand 1999). Further work on the function of cover under various conditions will be necessary to better predict how fish growth will respond.

Food and growth

Several studies have inferred that food limits stream salmonids. These studies are often based on observations of density-dependent growth, positive correlations between food availability and fish growth or abundance, and response of fish to nutrient enhancement. My results confirm observations from correlative and nutrient addition studies, and show that food limits cutthroat trout growth in small, coastal streams. Mason (1976) also directly manipulated food supply to fish in enclosed reaches. In his study, supplemental feeding increased the biomass of underyearling coho salmon by 2.5 times that of controls in a Vancouver Island stream. The higher biomass of fed salmon was a result of both increased growth and survival. Stimulating primary production by adding nutrients has resulted in increased growth rates (Warren et al. 1964, Deegan and Peterson

1992) and individual size (Johnston et al. 1990, Slaney and Ward 1993) of trout and salmon. Of these studies, only Slaney and Ward (1993) reported a suggested increase in density. Though I found no survival effect of food, the scale of my experiment may have been inappropriate for measuring such a response.

The extent to which fish are limited by food likely varies seasonally and spatially. Metabolic demands, and thus food demand, of fish increase with temperature (Ursin 1979). During summer, warm temperatures and high fish densities resulting from new recruits increase the potential for food limitation. Experiments over a minimum of one year would be necessary to properly test this. Trends in the abundance of invertebrate prey are difficult to generalize, but also likely fluctuate seasonally, as well as unpredictably. Prey densities in this study were typical of streams (Allan 1995). The low growth rates of the unfed trout are similar to rates reported for other stream trout during summer. For example, summer growth rates of age one and two rainbow and brown (*Salmo trutta*) trout in Appalachian streams were lower (and often negative) than winter growth rates (Cada et al. 1987). Ensign et al. (1990) calculated energy intake of brook (*Salvelinus fontinalis*) and rainbow trout during summer to be below levels necessary for maintenance metabolism. Further, growth of cutthroat trout held in enclosures in a forested section of an Oregon stream ('forested control' enclosures from Wilzbach et al. 1986) was less than 0.05 % body mass/day on average, similar to growth of unfed fish in this study.

As energy sources and temperatures change along the length of a stream (Vannote et al. 1980), so will the extent of food limitation to fish. In small, closed canopy streams, light and low temperatures limit photosynthesis (McIntire 1975, Ulrich et al. 1993) and much of the energy comes from terrestrial sources, such as leaf litter (e.g. Fisher and Likens 1973). Streams with higher light levels receive more energy from primary production of aquatic macrophytes or algae (Minshall 1978). Work by Bilby and Bisson (1992) suggests that fish are more dependent on food derived from in-stream plant production. Thus, the potential for food limitation may be greatest in cool, densely shaded streams, and/or nutrient-poor waters. Although food availability may set an upper limit on productivity (Richardson 1993), it is important to note that other factors may

truncate production before food limitation occurs. Availability of spawning habitat, appropriate summer and winter habitats, predators, and temperature can all act, and potentially interact, to affect production.

Food limitation at the individual level does not necessarily mean that food is also limiting population growth. Nevertheless, body size is related to a number of fitness measures in organisms with indeterminate growth (Peters 1983, Kirkpatrick 1984). Thus, individual growth may be linked to population growth in several ways. For salmonids, the number or size of eggs produced by females (Beacham and Murray 1993), age of first reproduction (Hutchings 1993), and overall survivorship (Wootton 1990) can be positively correlated with body size. These factors could affect the numerical growth rate of populations. This may be particularly relevant for resident populations where population regulation can occur at adult stages (Elliott and Hurley 1998). Further, both food and cover can affect territory size of salmonids. Higher food levels tend to result in smaller territory sizes (Slaney and Northcote 1974, Keeley and Grant 1995), as does cover by increasing the degree of visual isolation (Kalleberg 1958). Thus, more fish can occupy a given area. In this study, the trend for decreased emigration in the presence of both food and cover points to this possibility.

Body size and over-winter survival

Previous studies of stream-resident trout have noted a positive relation between body size and survival over winter (Hunt 1969, Hutchings 1994, Smith and Griffith 1994). Size-biased survival is thought to arise because smaller individuals are more susceptible to winter stresses (e.g. depletion of energy reserves, displacement by high water velocities, competition for limited winter habitat) or are subject to size-selective predation (see Table 2.4). I did not find that September mass of individuals was a predictor of winter survival. Fed fish did, however, maintain their size advantage over winter. Therefore, although there was no evidence for a survival benefit of increased size, fed individuals may have benefited through the opportunity to allocate more energy into earlier reproduction, higher fecundity, or secure the best habitats.

The magnitude of the size-survival relation, and winter survival in general, may be affected by the severity (e.g. temperature, flood events) and duration of winter (Hunt 1969, Post and Evans 1989). The winter of 1997-1998 was quite mild with relatively moderate rain events and temperatures. This may have minimized size-biased mortality. Indeed, one striking finding of this study is that monthly survival estimates were nearly equal for summer ('all others' group, 96.7%) and winter (96.6%).

The conclusion that size did not affect survival appears somewhat contradictory to evidence in favor of a positive relation for small sizes of trout in the general population (see Chapter 2). The analysis for the general population was based on mass in October or November; September mass was used in the analysis for experimental fish. Since trout still experienced growth from September until November, the experimental fish were probably at a size by October/November where the relation between survival and size was relatively flat (Chapter 2). Thus, mass later in the fall may be a better predictor of over-winter survival.

Conclusions

In this study, food had a relatively greater influence on trout growth, and cover a relatively greater influence on survival. The effects of food and cover were additive; given these results, the highest growth rates and numbers of fish should occur under conditions of high food and cover availability. The difference in size between fed and unfed fish at the end of the experiment was greater for East Creek fish than for Spring Creek fish, and mortality also differed between streams. I suggested these differences were due primarily to a later start date in Spring Creek and different predation pressure or substrate size in the two streams. Other factors, such as innate behavioral and growth differences of fish or different stream widths (and thus size and shape of enclosures), also could have contributed to the between-stream trends. Larger fall size did not improve winter survival of trout, possibly due to mild winter conditions, which resulted in high survival of both fed and unfed fish. Fed fish maintained their size advantage over winter and thus likely experienced other advantages (e.g. increased fecundity, competitive ability) related to size.

Experimental manipulations of food and habitat over larger spatial and temporal scales are necessary to fully assess population level responses. In fact, the relative influence of each factor might change seasonally. Food limitation is likely to be most pronounced during the summer growing season. In winter, however, cover availability maybe more important as fish seek refuge from adverse environmental conditions. This study highlights the complexity of factors influencing trout production: food, cover, predation and body size may all contribute to observed patterns of growth, survival and movement.

Table 1.1. Comparison of stream characteristics, experimental details, and enclosure characteristics of East Creek and Spring Creek.

	East Creek	Spring Creek
<i>Stream characteristics</i>		
Gradient of study reach (%)	1.9	1.8
Elevation (m)	154	160
<i>Experimental details</i>		
# Replicates	3	1
Start Date	8 Aug 97	28 Aug 97
End Date	16 Sept 97	16 Sept 97
Duration	40 days	20 days
# of fish per enclosure	5	10
Mean Temperature (°C)	15.1 (range=12.6-17.2)	N/A
<i>Enclosure characteristics</i>		
Mean Wetted Width(m) (mean ± SE)	2.24 ± 0.05	3.25 ± 0.29
Mean Depth (cm) (mean ± SE)	12.09 ± 0.22	15.5 ± 1.44
Velocity (m/s)	< 0.14	< 0.10
Substrate Size (% distribution ± SE):		
Sand and Silt (< 2 mm)	6.3 ± 1.3	70 ± 10.8
Gravel (2mm - 64mm)	70.3 ± 3.0	26.3 ± 9.7
Cobble (64mm - 130mm)	22.3 ± 3.7	3.75 ± 1.3

Table 1.2. Numbers of invertebrates collected during 3 hour drift net samples in experimental enclosures in East Creek and Spring Creek. Values are mean \pm 1SE (range).

	East Creek, August	East Creek, Sept.	Spring Creek, Sept.
<i>Aquatic</i>			
Diptera	49 \pm 23 (7-182)	28.3 \pm 5.3 (8-69)	23 \pm 2.0 (17-26)
Plecoptera	4.1 \pm 1.0 (1-8)	3.5 \pm 0.8 (1-9)	6.5 \pm 1.0 (4-9)
Trichoptera	3.7 \pm 1.4 (1-11)	5.9 \pm 1.8 (1-23)	5 \pm 1.1 (3-8)
Ephemeroptera	0.4 \pm 0.4 (0-3)	3 \pm 0.8 (0-7)	2.5 \pm 1.4 (0-5)
Other	4.7 \pm 1.4 (1-11)	8.8 \pm 2.6 (0-34)	8 \pm 1.6 (5-12)
<i>Terrestrial</i>	2.4 \pm 0.6 (1-4)	4.3 \pm 1.1 (0-12)	6 \pm 0.9 (4-8)
Drift Density (# per 100m ³)*	340 \pm 68 (200-738)	292 \pm 30 (194-519)	284 \pm 18 (251-329)
n	7	8	4

* Water depths used in calculating volume of water filtered were estimated following drift sampling in September.

Table 1.3. Initial and final size (mean \pm SE) of cutthroat trout receiving different food treatments in East Creek and Spring Creek.

	Initial			Final		
	<i>n</i>	Length (mm)	Mass (g)	<i>n</i>	Length (mm)	Mass (g)
<i>East Creek</i>						
No food added	30	78.2 \pm 1.0	4.61 \pm 0.18	25	79.2 \pm 1.1	4.48 \pm 0.21
Food added	30	77.9 \pm 1.0	4.46 \pm 0.17	25	89.8 \pm 1.7	7.65 \pm 0.47
<i>Spring Creek</i>						
No food added	20	84.1 \pm 1.2	5.36 \pm 0.23	11	85.0 \pm 2.2	5.70 \pm 0.47
Food added	20	84.4 \pm 1.3	5.53 \pm 0.25	13	89.2 \pm 1.5	7.38 \pm 0.37

Table 1.4. Best fitting survival and recapture models for size-survival analysis of experimental cutthroat trout over winter. Notation describes the factors and covariates that affect survival and capture probability: “s” indicates that the parameter varies between streams, “t” the parameter varies among trapping sessions, and “•” the parameter is constant between streams or over time. “+m” indicates the parameter was modeled as a linear function of mass (m), parameter = $b_0 + b_1(m)$, where curves are fit with common slopes but different intercepts for each for each stream (s+m), or at each time period (t+m). Modeling was performed using program MARK. See also Appendix 2.

Survival Φ	Capture P	# Parameters	AICc	Δ AICc	Deviance
•	t	7	428.71	0.00	413.90
s	t	8	430.75	2.04	413.70
•+m	t	8	430.85	2.14	413.80
•	t+m	8	430.95	2.24	413.90
s+m	t	9	432.92	4.21	413.60

Table 1.5. Best fitting survival and recapture models using data from all experimental cutthroat trout in East Creek and Spring Creek over winter. Notation describes the factors and covariates that affect survival and capture probability: “g1, •2-7” indicates that survival varies between groups, “g”, (i.e., Spring - no cover fish and all other fish) during the first interval, “1”, and is constant, “•”, between groups and among time periods from the 2nd to 7th intervals, “t” that the parameter varies among trapping sessions, and “temp” and “eff” that capture is modeled as an additive (+) or interactive (*) logit function of stream temperature and trapping effort. Modeling was performed using program MARK. See also Appendix 2.

Survival Φ	Capture P	# Parameters	AICc	Δ AICc	Deviance
g1, •2-7	temp+eff	6	633.58	0.00	117.91
g1, •2-7	temp*eff	7	634.14	0.56	116.36
g1, •2-7	t	10	634.40	0.82	110.18
g1, t2-7	t	14	639.78	6.20	106.76
g	t	9	644.88	11.30	122.83

Table 1.6. Monthly survival and recapture rates for all experimental cutthroat trout in East Creek and Spring Creek over the winter of 1997-1998. Estimates are for the model $\Phi_{g1, \bullet 2-7} P_{temp+eff}$ and were calculated by program MARK. 95% confidence intervals are $\pm 1.96*SE$.

	Estimate	SE
<i>Survival</i>		
Spring - no cover (1 st interval)	0.602	0.104
All others (1 st interval)	0.967	0.026
Monthly rate, all fish (2 nd - 7 th interval)	0.966	0.020
<i>Capture Rates</i>		
September	0.876	0.039
October	0.222	0.033
November	0.292	0.033
January	0.179	0.031
February	0.215	0.032
April	0.339	0.034
June	0.226	0.054

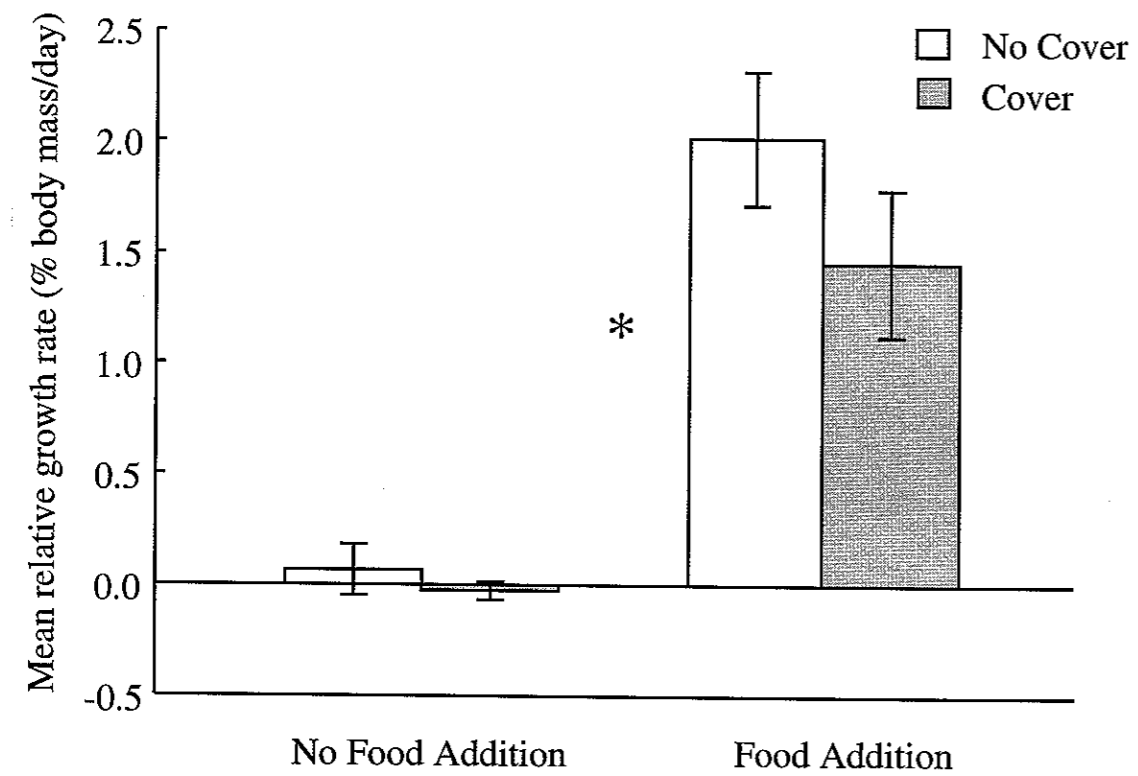


Figure 1.1. Mean relative growth rates of cutthroat trout in enclosures with and without food and cover ($n = 4$ for all treatment combinations). Error bars are $\pm 1SE$. * ($p < 0.05$) (2-factor randomized block ANOVA)

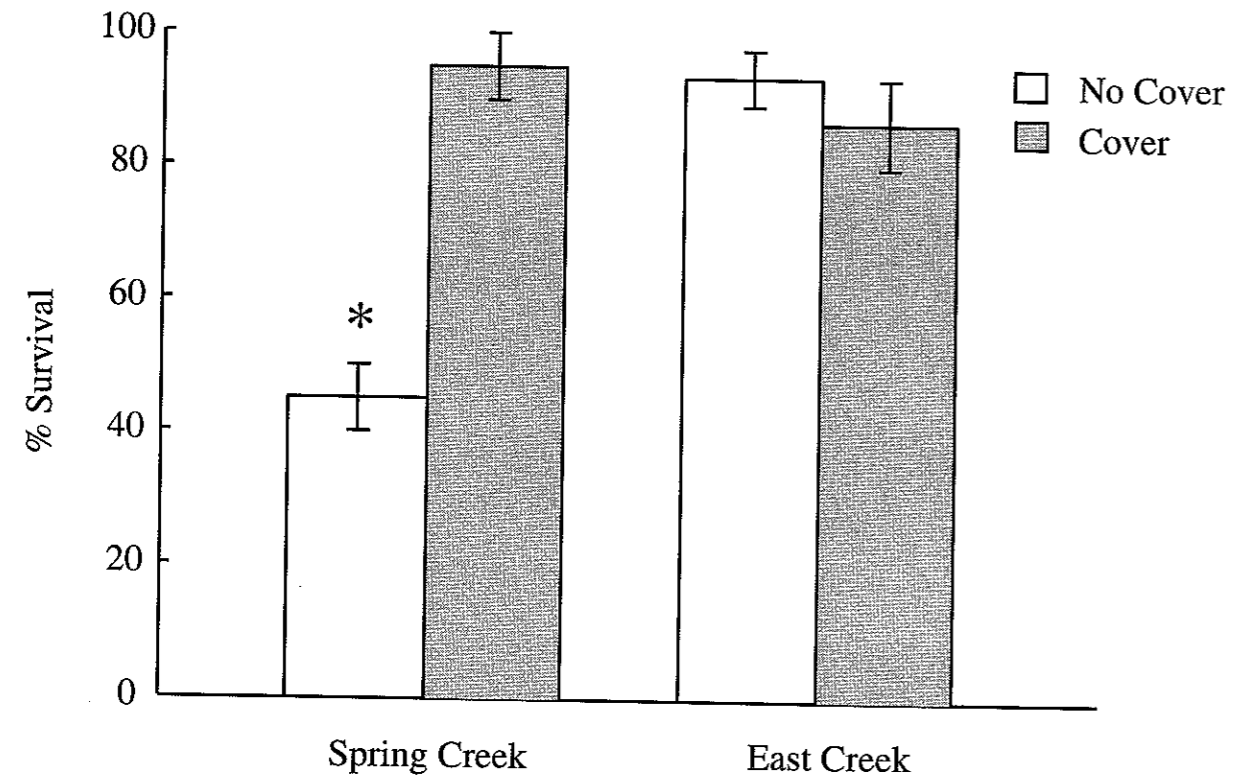


Figure 1.2. Mean survival of cutthroat trout in Spring Creek and East Creek enclosures with and without cover addition ($n = 2$ for Spring Creek treatments, and $n = 6$ for East Creek treatments). Error bars are $\pm 1SE$. * $p < 0.05$ (2-factor randomized block ANOVA)

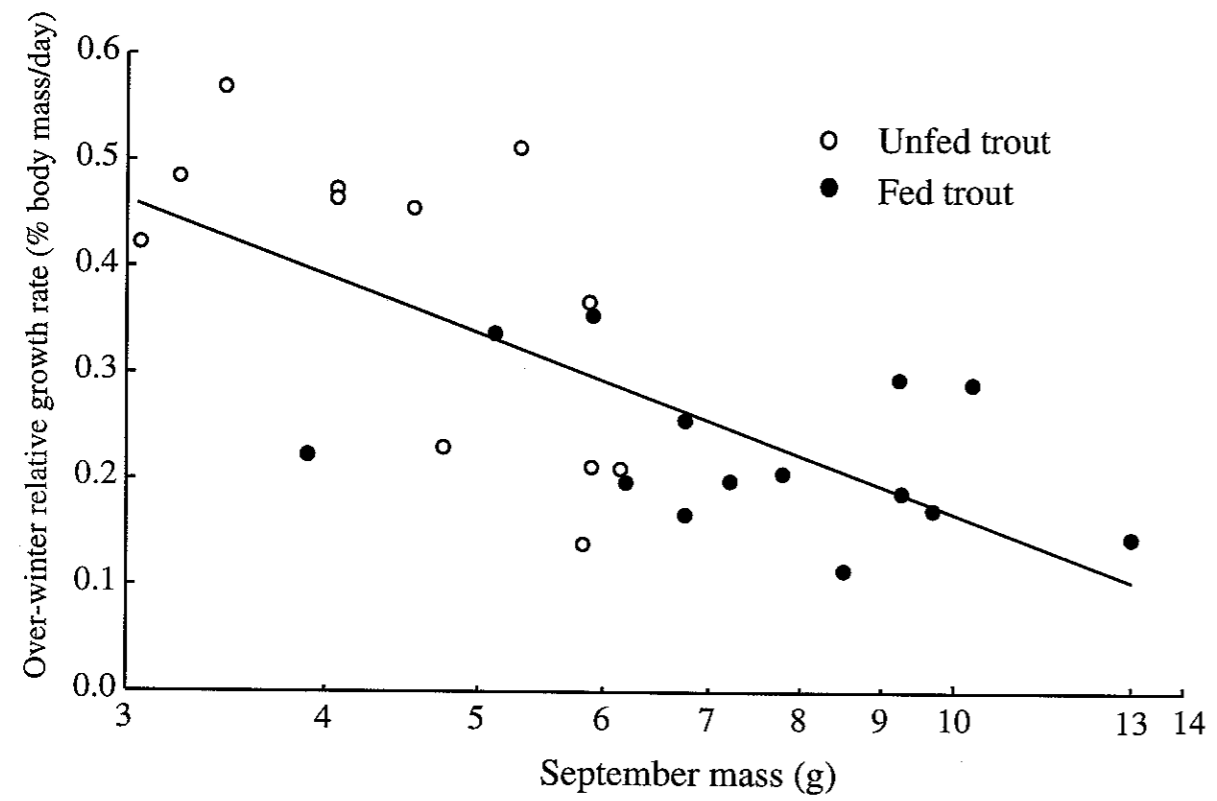


Figure 1.3. Relationship between relative growth rates over winter (from September to April) and September mass of unfed and fed cutthroat trout ($n = 12$ for unfed trout, and $n = 14$ for fed trout). Note logarithmic scale on x-axis. The relationship is described as relative growth rate = $0.73 - 0.57 \cdot \log$ september mass.

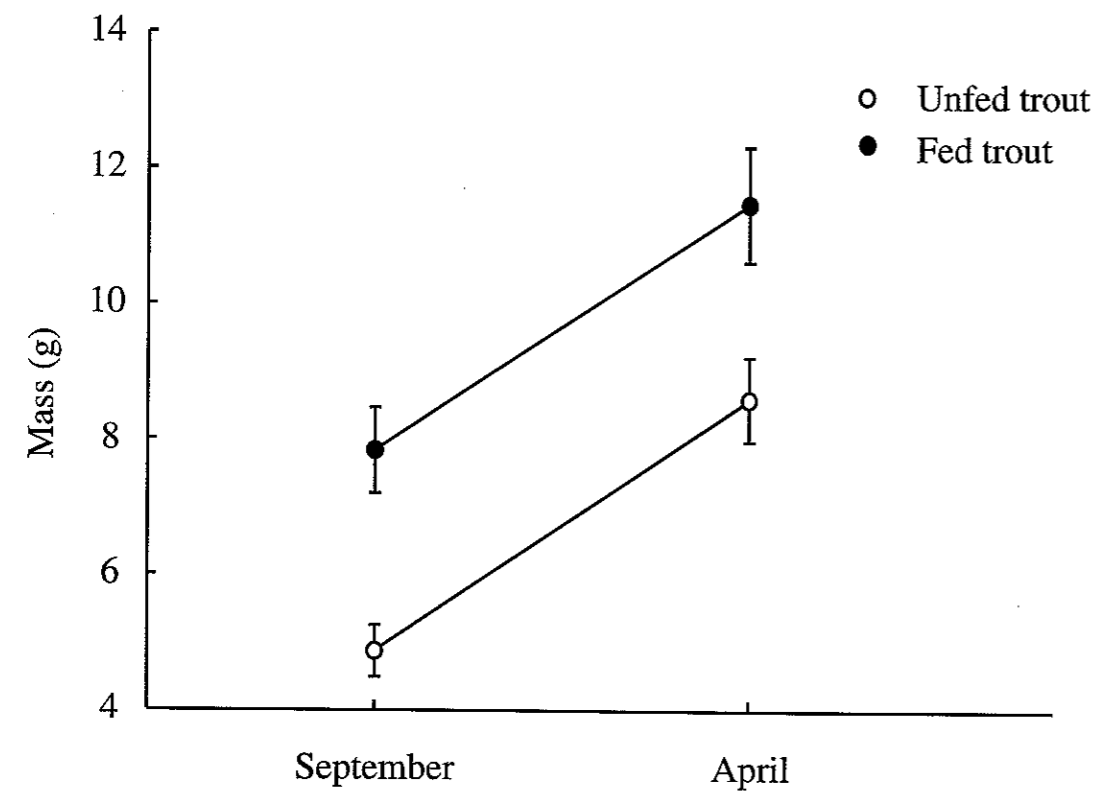


Figure 1.4. Comparison of mean mass of unfed and fed cutthroat trout in fall and spring ($n = 12$ for unfed trout, and $n = 14$ for fed trout). Error bars are $\pm 1SE$.

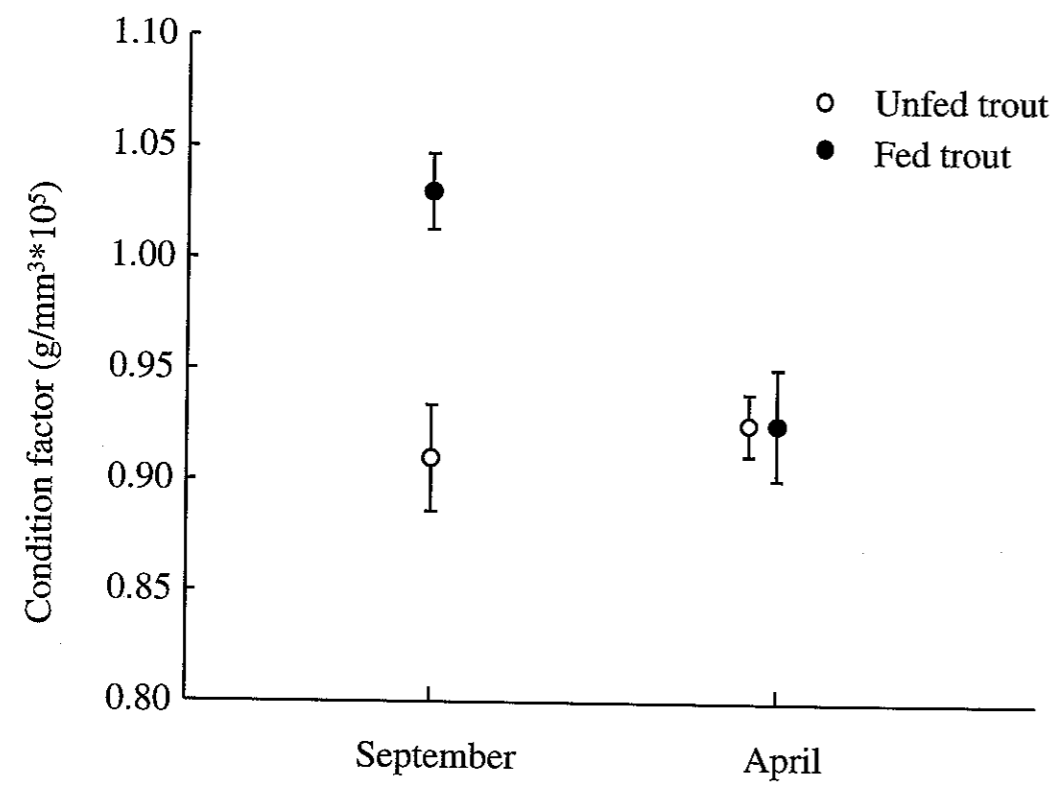


Figure 1.5. Comparison of mean Fulton's condition factor of unfed and fed cutthroat trout in fall and spring ($n = 12$ for unfed trout, and $n = 14$ for fed trout). Error bars are ± 1 SE.

CHAPTER 2. Winter movement, survival and growth of stream-resident cutthroat trout.

INTRODUCTION

Variation in individual traits of organisms can influence their behavior (e.g. Werner and Anholt 1993) and affect the demography of populations (Kirkpatrick 1984, Werner and Gilliam 1984). Thus, studies that relate individual traits to measures of individual performance or behavior (e.g. survival, growth, movement) can provide insight into the links between individual and population level processes. Body size is recognized as one of the most influential traits (Peters 1983), particularly for organisms with indeterminate growth, such as fish (Wootton 1990).

For stream dwelling salmonids, body size has been linked to many aspects of their ecology, including survival over winter (Hunt 1969, Holtby 1988, Hutchings 1994, Smith and Griffith 1994, Quinn and Peterson 1996). Adverse environmental conditions are usually blamed for high winter mortality often observed for stream fish. Low temperatures can slow digestion to the point where fish must metabolize energy reserves (Cunjak et al. 1987). Reduced swimming speed of fish at low temperatures (Brett et al. 1958) may put fish at a greater risk of predation or reduce their foraging success rate. Ice formation or freshets can displace or injure fish, especially if protective habitat is limiting (Cunjak et al. 1998). Smaller fish may be particularly susceptible to these perils and, as a consequence, experience higher mortality rates. Studies that relate survival over winter to body size typically focus on fish entering their first winter and seek to explain variation in recruitment between years. It is still unclear whether older age classes show size-survival relations over winter comparable to those of young-of-year fish, or whether it is even a common pattern of survival among different species and populations of stream salmonids (Burrows 1993).

Body size may also affect the movements of stream fish. Large individuals may need to forage over larger areas to meet resource requirements. Alternatively, smaller, sub-dominant fish may show more movement as they are displaced by larger or healthier individuals. There is evidence for both increased (e.g. Gowan and Fausch 1996a) and decreased (e.g. Bachman 1984) movement with increasing body size in trout. However,

these studies, like many studies of stream salmonids, took place during summer. There is a paucity of data on whether, or to what extent, similar patterns occur during winter.

Coastal cutthroat trout (*Oncorhynchus clarki clarki*) are a common inhabitant of Pacific Northwest streams (Trotter 1989). Several studies of stream-resident cutthroat trout have focused on defining winter habitat preferences (Bustard and Narver 1975, Heggenes et al. 1991, Griffith and Smith 1993, Brown and Mackay 1995, Jakober et al. 1998).

Information on individual patterns of survival, growth, or movement over winter are less common. The exception is data on winter movement of radiotagged trout (Brown and Mackay 1995, Jakober et al. 1998, Young 1998), but these data are limited to the largest-sized animals.

Here, I describe survival, movement, and growth of age 1+ resident cutthroat trout during one winter and relate each measure to fish size. I predicted that over-winter survival would be an increasing function of fish mass and, if winter conditions are more energetically stressful for smaller fish, relative growth rate should also be positively related to mass. Further, movement of trout should be negatively related to size if based solely on dominance hierarchies, but positively related if based on resource requirements. Finally, I predicted that fish that move would be in poorer condition than those that did not move.

METHODS

Study sites, trapping and handling protocol are the same as for experimental fish over winter described in Chapter 1. The openings of the minnow traps were expanded slightly to allow for capture of large fish. During trapping, all fish greater than one year old (determined by size-class histograms) were marked using PIT tags (see Chapter 1). Temperature data recorders in each stream took hourly readings. Hourly temperatures were averaged to obtain mean daily temperatures.

Movement

I used data from recaptured fish to calculate distances moved. For any fish caught in more than one location during a multi-day trapping session, its first location of capture during that session was used to calculate distance moved. I described movement patterns in three ways for each stream: 1) the distance between each point of capture (hereafter distance between captures) in either an upstream (+) or downstream (-) direction. Here, more than one movement per fish is counted if a fish was recaptured in more than two sessions. 2) net and total distance, in meters, moved by each fish. Net distance is the distance between first and final capture locations. Total distance is the sum of the absolute values of all movements made by an individual fish. 3) net and total number of habitat units moved (how many units fish change between). Also, I tested whether total distance moved was related to the mass of fish in each stream using rank correlation (regression was not used because data were non-normal with heterogeneous variances and not improved by transformation). Finally, I compared the condition of fish that changed habitat units to fish that did not, and fish that moved more than three habitat units to those that moved three or fewer. These analyses were done using analysis of covariance, where the dependent variable was mass (log transformed) and the covariate was length (log transformed). This fits a regression relationship of length and mass for each treatment group, and tests if length-mass relationships differ among groups.

During January, four adult trout (150mm - 168mm) had radiotags surgically implanted (using modified methods of Young 1995). Fish were located daily. I

calculated 'home range' (distance between furthest upstream and downstream points) and net distance moved for radiotagged fish, measured as meters and number of habitat units.

Growth

To look at over-winter growth, I calculated relative growth rates for fish caught in two consecutive time periods. I then plotted the average growth rate of fish from each stream for each time period. I tested relative growth rate as a function of mass using linear regression for the November to March period, pooled across streams.

Population estimates

I estimated population size in November for each stream using program CAPTURE (White et al. 1982). CAPTURE can provide closed population estimates under several models that assume time, behavior, or individual heterogeneity effects in capture probabilities. It was clear from inspection of the data that some animals were more likely than others to be recaptured within a session. Thus, I used the jackknife estimator under the heterogeneity model to estimate population size.

Survival

I used data from fish caught in either the October or November trapping sessions, including any experimental fish, to examine the relationship between fall size and survival. I used the mass of each individual in October or November as a covariate in the capture-recapture analysis. Rather than counting October and November as separate trapping sessions, I pooled the two sessions, treating them as one initial release. The June trapping session described in chapter 1 was specifically targeting experimental fish, and thus is not included in this analysis. Model selection followed the procedures outlined in chapter 1 (see also Appendix 3), starting with a stream and time dependent CJS model. The mass functions include: 1. probability = $b_0 + b_1(m)$, and 2. probability = $b_0 + b_1(m) + b_2(1/m^2)$, where m is mass. The first function fits a linear relationship and the second assumes a non-symmetrical curvilinear relationship.

I used data from all fish caught and marked over winter, not just those caught in the fall, to derive monthly winter survival rates. Model selection began from the time dependent CJS model with five trapping sessions (October, November, January, February/March, and April).

RESULTS

The temperature recorder in Spring Creek was lost and replaced in March. During the time that temperatures are available for both streams, temperatures in East Creek were higher on average than in Spring Creek, 8.6°C versus 7.9°C, respectively (Figure 2.1).

Movement

A total of 349 trout were tagged during the October, November, January, and February/ March sessions. In East Creek, 209 trout were tagged and 185 recaptures were made, representing 127 individuals. In Spring Creek, 140 trout were tagged, and 92 recaptures were made representing 65 individuals. Because capture-recapture methods tend to underestimate movement (Gowan and Fausch 1996a,b), it is important to understand what fraction of the population the recaptured individuals represent. Here, inferences are based on the 61% of marked fish that were recaptured in East Creek, and the 46% in Spring Creek. Survival estimates (see survival section and Table 2.3) indicated that, in any given month, in East Creek 87% and in Spring Creek 78% of marked fish present in the previous month were alive and present in the sampling reach.

In East Creek, distance between captures ranged from a maximum downstream movement of 304.6 m to a maximum upstream movement of 305.7 m (Figure 2.2). The modal distance between captures in East Creek was 0 m, but the mean, 5.68 m, showed a tendency toward upstream movement. The smaller range of movement in Spring Creek reflects that it was a shorter study reach (Figure 2.2). In Spring Creek, distance between captures ranged from 65.2 m downstream to 74.4 m upstream. Modal distance between captures in Spring Creek was the <0 to -5 m division, although mean distance between captures, 4.31 m, was in an upstream direction. Movement was common for recaptured fish: only 20% of East Creek fish and 9% of Spring Creek fish did not move (Figure 2.3). Much of the small scale net and total distance measured, however, represented movement within a habitat unit (compare 0 m bars in Figure 2.3 to 0 habitat unit bars in Figure 2.4); 30% of fish in both streams were recaptured within the same habitat unit. Most movement (56% in East Creek, 72% in Spring Creek) appeared to be in the >0 to 35m

range, though greater distances, particularly in East Creek, were not uncommon (24% >35m) (Figure 2.3).

For radiotagged trout, home ranges during January until the end of April were 0, 42, 130, and 295 m; expressed in habitat units, ranges were 0, 9, 23, and 33 habitat units. Net distances moved were 0, 15, 94, and 230 m. Net number of habitat units moved were 0, 4, 21, and 26.

Total distance moved was not correlated with size of fish in either stream (Figure 2.5; rank correlation, East Creek, mass Spearman $r = 0.039$, $p = 0.664$; Spring Creek, mass Spearman $r = 0.052$, $p = 0.683$). Similarly, the condition of fish that moved was not lower than that of fish that did not move. This was true when comparing between fish that stayed in one habitat unit versus fish that changed units (ANCOVA, move $F_{1,187} = 1.56$, $p = 0.214$), or when comparing fish that moved three or fewer habitat units versus those that moved more than three units (Figure 2.6; ANCOVA, move $F_{1,187} = 3.46$, $p = 0.064$; stream, slopes, and all other interaction terms for both analyses $p > 0.05$). Note that variances for log transformed length and mass were not homogeneous.

Growth

Trout in both streams had positive growth rates, on average, throughout winter and spring (Figure 2.7). Growth rates were lowest from November to March, and highest from March to June (Figure 2.7). Growth was generally higher in East Creek than in Spring Creek. Though some fish lost wet mass from November to January, changes in mass were variable and not related to size of fish in November (Figure 2.8; linear regression, mass $r^2 = 0.063$, $p = 0.128$).

Population estimates

The Spring Creek age 1+ population was estimated at 135 ± 11.37 (SE) individuals. This is equivalent to a density of 0.34 fish m^{-2} of wetted width (CI: 0.29 - 0.40). The East Creek estimate was 188 ± 13.27 (SE) age 1+ fish, or 0.19 fish/ m^{-2} (CI: 0.16 - 0.21).

Survival

Tests indicated the global model $\Phi_{s*t} P_{s*t}$, where monthly survival and capture rates can vary over time and between streams, was a good fit (East Creek $\chi^2_2 = 1.464$, $p = 0.481$; Spring Creek $\chi^2_2 = 0.000$, $p = 1.000$; Total $\chi^2_4 = 1.464$, $p = 0.833$). The model with the lowest AICc was $\Phi_{s+cm} P_t$ (Table 2.1): survival varied as a function of stream and fish mass (subscripted 'cm' for curvilinear mass function), and recapture varied as a function of time. Under this model, survival increased steeply over the size range of the smallest fish, then gradually decreased as fish mass increased (Figure 2.9). In East Creek, the survival-mass relation was described by the equation $\log_e(\Phi/1-\Phi) = 2.61 - 0.053(\text{mass}) - 19.3(1/\text{mass}^2)$ and in Spring Creek by the equation $\log_e(\Phi/1-\Phi) = 1.88 - 0.053(\text{mass}) - 19.3(1/\text{mass}^2)$. Because data were quite limited, confidence intervals around the curves were wide. Survival estimates based on splitting fish into three size groups, where sample sizes among groups were similar, showed the same increasing then decreasing trend in both streams (East Creek, Φ 3-9g = $0.84 \pm 0.03(\text{SE})$, 9-15g = 0.89 ± 0.03 , >15g = 0.76 ± 0.05 ; Spring Creek, Φ 3-7g = 0.70 ± 0.06 , 7-11g = 0.80 ± 0.04 , >11g = 0.62 ± 0.07). Nevertheless, the steepest part of the size-survival curve (i.e., less than 5 grams) was based on data from very few fish. Thus, to be conservative, I make inferences about survival only for fish above 5 grams. The change in AICc between the best model and the two next best models, $\Phi_{s*cm} P_t$ and $\Phi_{s+lm} P_t$, is less than two. Thus, these two models should be considered as reasonable alternatives to model $\Phi_{s+cm} P_t$ (Figure 2.9). When either condition factor or length were used as the covariate, models were ranked in the same order as the mass dependent models, and the slopes of the covariate models showed similar trends.

The starting model for deriving general over-winter estimates was a good fit (East Creek $\chi^2_8 = 5.290$, $p = 0.726$; Spring Creek $\chi^2_7 = 6.938$, $p = 0.435$; Total $\chi^2_{15} = 12.228$, $p = 0.662$). The final model was $\Phi_s P_t$, with constant survival within streams (s) and time-dependent (t) capture (Table 2.2). Monthly survival was 87% for East Creek fish and 78% for Spring Creek (Table 2.3), equivalent to 43% and 23% survival from October to April. The fit of the final model was good ($\chi^2_{23} = 20.976$, $p = 0.583$).

Two days of extra trapping for emigrants in April captured one marked fish in East Creek, and four in Spring Creek. Based on the April capture rate, I estimated only two fish in East Creek and six fish in Spring Creek had emigrated into the area sampled ($\# \text{ marked in reach} = \# \text{ captured in reach} / \text{April recapture rate}$). Including the emigrants in survival analysis as having been captured in April increases the East Creek monthly survival rate to 88% and Spring Creek to 81%.

DISCUSSION

Cutthroat trout movement was not related to individual traits such as body size or condition over winter. Winter survival, however, appeared to vary with body size. Growth was generally positive during winter, and was not related to mass over the November to January interval. These patterns of growth suggest that the size-biased survival cannot be attributed to energetic declines. Here, I discuss the role of body size in the winter ecology of trout, with respect to the potential mechanisms leading to size-based relationships.

I had predicted that movement would show either a positive or negative relationship with body size. Interestingly, this was not the case. My expectation was based on two possible scenarios. First, larger size generally confers dominance in stream salmonids (Kalleberg 1958; Fausch 1984, Hughes 1992), thus smaller individuals may move more as they are displaced by larger fish. Alternatively, movement may be related to the resource requirements of individual fish. Since large fish have greater absolute resource needs (e.g. food, space), larger fish might be expected to move more in order to find habitats that meet those requirements. A third hypothesis, combining both scenarios, further predicts that movement is related to body condition: fish in poor condition would not only need to move more to garner resources, but would also be subject to displacement by healthier individuals. Also contrary to my predictions, I found that fish that moved were in similar condition to those that did not move.

Previous studies have provided support for all three hypotheses. Most commonly, larger and/or fish in poor condition have shown the most movement (Shetter 1968, Gowan and Fausch 1996a), although Bachman (1984) reported smaller home ranges for larger trout. These studies differ from mine, however, in that they involve larger sizes of fish, and often larger spatial and/or temporal scales. Further, most work has been conducted during summer or could not differentiate seasonal movement. The fact that my study was conducted over winter may therefore explain why I found no relation between size and movement. Low temperatures, rather than food, probably limit growth during winter (Cunjak et al. 1987, Elliot et al. 1995), thus minimizing the need to move to