

# Effects of food and cover on the growth, survival, and movement of cutthroat trout (*Oncorhynchus clarki*) in coastal streams

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**Abstract:** To examine the extent to which stream-resident coastal cutthroat trout (*Oncorhynchus clarki*) are limited by food and cover, we manipulated these two factors in a 2 × 2 design using enclosures containing 1-year-old trout in two streams. During summer, fish receiving food additions experienced an average growth rate of 1.73% body mass·day<sup>-1</sup> compared with a rate of 0.022 for unfed fish (ambient food supply only), indicating marked food limitation. The addition of cover decreased mortality by approximately 50% in one stream, but survival was high both with and without cover in the other. There was no interaction of food and cover on growth or survival. Emigration rates were low and were not strongly affected by either factor. We also used mark–recapture modeling to examine whether the 48% greater mass of fed fish at the end of the experiment improved survival over winter. Fed fish were still 46% larger than unfed fish by the next spring, but overwinter survival was not explained by body size. Our results show that, during summer, food availability can limit trout growth, and cover, by mediating predation, can limit survival.

**Résumé :** Afin de déterminer dans quelle mesure le gîte et la nourriture peuvent être des facteurs limitants pour les truites fardées côtières (*Oncorhynchus clarki*) habitant les cours d'eau de la côte, nous avons établi un plan d'expérience de type 2 × 2 pour manipuler ces facteurs dans des enclos contenant des poissons de 1 an dans deux cours d'eau. En été, les poissons qui ont reçu des suppléments de nourriture avaient un taux de croissance moyen de 1,73 % de la masse totale·jour<sup>-1</sup>, alors que les poissons qui n'ont eu accès qu'à la nourriture ambiante avaient un taux de 0,022, ce qui indique que la nourriture est un facteur limitant important. L'addition de gîtes a réduit la mortalité d'environ 50 % dans un des cours d'eau, mais, dans l'autre, la survie est restée élevée avec ou sans les gîtes additionnels. Il n'y a pas eu d'effet combiné de la nourriture et du gîte sur la croissance ou la survie. Les taux d'émigration étaient bas et n'étaient pas affectés ni par l'un, ni par l'autre des facteurs. Une modélisation de type marquage–recapture nous a permis de voir si la masse accrue de 48 % à la fin de l'expérience chez les poissons nourris en supplément augmentait leur survie en hiver. Les poissons nourris avaient une masse supérieure de 46 % à celle des poissons non nourris le printemps suivant, mais la survie à l'hiver n'était pas reliée à la taille des poissons. Nos résultats indiquent qu'en été la disponibilité de la nourriture peut limiter la croissance des truites fardées et que le gîte peut limiter la survie en affectant la prédation.

[Traduit par la Rédaction]

## Introduction

Resource availability has long been recognized as playing a central role in limiting, and possibly regulating, populations. Food and cover (i.e., a 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). Labora-

tory 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; Poff and Huryn 1998) or have manipulated only a single variable. Few field manipulations have incorporated proper controls and replication (except see Gowan and Fausch 1996), and none have addressed the precise interplay between these two factors, perhaps in part due to the logistic difficulties inherent in performing stream experiments. Thus, the relative values of food and cover, and how they interact to limit fish production, have not yet been well quantified.

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). Similar trends have been found in studies that have increased primary and secondary production through nutrient additions (e.g., Deegan and Peterson 1992; Slaney and Ward 1993). Cover

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**Table 1.** Comparison of stream characteristics, experimental details, and enclosure characteristics of East and Spring creeks.

	East Creek	Spring Creek
Stream characteristics		
Gradient of study reach (%)	1.9	1.8
Elevation (m)	154	160
Experimental details		
No. of replicates	12	4
Start date – end date	8 Aug. – 16 Sept.	28 Aug. – 16 Sept.
Duration (days)	40	20
No. of fish per enclosure	5	10
Mean temperature (°C)	15.1 (range = 12.6–17.2)	NA
Enclosure characteristics		
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 <sup>-1</sup> )	<0.14	<0.10
Substrate size (% distribution ± SE)		
Sand and silt (<2 mm)	6.3±1.3	70±10.8
Gravel (2–64 mm)	70.3±3.0	26.3±9.7
Cobble (64–130 mm)	22.3±3.7	3.75±1.3

**Note:** NA, not available (temperature logger in Spring Creek was lost); SE, standard error.

may influence survival by protecting fish from their predators and by providing refuge from high water velocities. Many studies have demonstrated a positive correlation between the abundance of salmonids and the amount of in-stream physical structure (e.g., Fausch et al. 1988; Roni and Quinn 2001). The association of fish with in-stream structure, however, may simply reflect habitat preferences and does not provide sufficient evidence that cover improves survival.

Previous experiments have provided insight into the role of food (Mason 1976) or cover (Gowan and Fausch 1996) separately but have only partially addressed the interaction of these resources (Wilzbach et al. 1986). Evidence of density dependence in individual growth rates (e.g., Jenkins et al. 1999) and increased growth and survival of salmon from direct addition of food (Mason 1976) provides strong support for a food-limitation hypothesis. Field and artificial stream experiments have reported conflicting results when testing for the effect of cover on survival (Lonzarich and Quinn 1995; Gowan and Fausch 1996) and growth (Harvey 1998; Sundbaum and Näslund 1998). Quantifying the effects of food and cover on growth, survival, and migration requires experimental manipulation in the field.

In addition, linking summer growth to other measures of individual performance, such as overwinter survival, may further clarify the role of summer resources for fish. A pattern of improved winter survival with increasing size has been found for several species of stream salmonids, including trout (e.g., Mason 1976; Hutchings 1994; Smith and Griffith 1994). Thus, factors limiting growth during summer may impact individuals and populations through both immediate and delayed mechanisms.

Resident (i.e., nonanadromous) coastal cutthroat trout (*Oncorhynchus clarki*) are common in small streams of the Pacific Northwest. We tested how and to what extent food, cover, and the interaction of the two affect cutthroat trout during summer. We experimentally manipulated the supply of food and cover within enclosures containing individually

marked trout in two natural streams. We predicted that (i) food addition would affect individuals primarily through increased growth, (ii) cover addition would primarily increase survival, and (iii) 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.

## Materials and 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 (Table 1), with unexploited populations of resident coastal cutthroat trout were selected that contained suitable reaches for installing experimental enclosures. 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

During August and September of 1997, we performed a factorial experiment in East and Spring creeks with two levels of food and cover. The four treatments were (i) control (no food or cover added), (ii) food addition, (iii) cover addition, and (iv) both food and cover added. Each treatment was

replicated four times (three in East Creek and one in Spring Creek). Groups of individually marked 1-year-old cutthroat trout were introduced into 9-m-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 a food and cover treatment. Due to the intensive setup necessary, we first installed enclosures in East Creek and began the experiment and then constructed the Spring Creek enclosures. This resulted in the experiment running for 40 days in East Creek and 20 days in Spring Creek (Table 1).

The food addition treatment consisted of live mealworms (larval *Tenebrio molitor*). Daily rations were 16% of the biomass of all fish per enclosure. In East Creek, we adjusted rations at the midpoint of the experiment to account for increased biomass due to fish growth. Food was dispensed over 12 h by automatic conveyor belt style feeders attached to the upstream fence of the enclosure. This slow, haphazard introduction of food mimics how fish would encounter natural prey falling from riparian vegetation. A cover structure consisted of a 25.4 cm × 2.54 cm × 1.8 m wooden plank tied to the top of two cinder blocks. In East Creek, each enclosure assigned a cover treatment received three plank – cinder block structures, and in Spring Creek, which at the time of setup was twice the wetted width, each received six. Fish readily used the structures as cover and as foraging stations throughout the experiment.

The reaches selected for enclosure locations were low in structural complexity and had relatively homogeneous widths and depths (Table 1). Although rarely necessary, any structure present, such as boulders or small wood, was removed. Two fences installed across the width of the stream enclosed each reach. Enclosure fences were 4-mm wire mesh attached to an 81.3-cm-high wooden frame supported by steel reinforcing rods, with the bottom board of each fence buried in the substrate. To control for differing light levels among enclosures, any shrubs overhanging the stream were tied back.

Each enclosure had an upstream and downstream emigration trap fitted onto the fences. Traps were 28 × 28 × 28 cm and had a 2-cm-wide v-notched entrance; two flexible plastic strips extended 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 marking and monitoring**

Baited minnow traps and some electrofishing were used to collect the study fish from their respective streams. Fork length (millimetres) and mass (nearest 0.01 g) were measured for all fish. Five size-classes of 1-year-old cutthroat trout were used: (i) 68–72, (ii) 73–76, (iii) 77–80, (iv) 81–84, and (v) 85–88 mm for East Creek and (i) 74–78, (ii) 79–82, (iii) 83–86, (iv) 87–90, and (v) 91–94 mm for Spring Creek. Aging was based on examined scales (data from 1973–1976 and 1983) and length–frequency histograms (data from 1997) of fish in East Creek (S. Hinch, K. Young, and T. Northcote, Department of Forest Sciences, University of British Columbia, Vancouver, BC V6T 1Z4, Canada, unpublished data). We attempted to match the density of fish in the enclosures to that of natural stream densities, approximately

0.49 fish·m<sup>-2</sup> (Young et al. 1999). 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 g in East Creek and from 3.66 to 7.55 g in Spring Creek. Fish were individually marked with unique combinations of colored latex dye injected into anal, caudal, and dorsal fins, and all adipose fins were clipped. Prior to the introduction of experimental fish, the enclosures were intensively trapped and electrofished to remove any unwanted fish.

Fish were sampled using minnow traps baited with salmon roe. Traps were set and checked daily for three consecutive days at the midpoint (East Creek only), end, and 1 week after the end of the experiment. Captured fish were anesthetized with carbon dioxide, weighed, measured, and released back into enclosures.

Relative growth rate (RGR) (percent change in body mass per day) for individuals was calculated as

$$(1) \quad RGR = [(final\ mass - initial\ mass)/(initial\ mass \\ \times\ no.\ of\ days\ between\ sampling)] \times 100$$

Most fish were in enclosures for several days before the experiment began, and some were not recaptured until several days after it had ended. We 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 to ensure conservative growth estimates. We 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.

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, individuals that emigrated on two or more consecutive days were returned to the enclosure but not remeasured.

To place growth of experimental fish in a natural context, we calculated growth rates for 14 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.

Drift nets with a mesh size of 250 µm were used to collect stream invertebrates in enclosures. Two out of three replicates of each treatment in East Creek were sampled midway and at the end of the experiment, and each enclosure in Spring Creek was sampled at the end of the experiment. Drift nets were set for a total of 3 h: 2 h before sunset until 1 h after sunset. Drift density was calculated as numbers per 100 m<sup>3</sup>.

### **Analyses**

To test for treatment effects on mean RGR, percent survival, and emigration, we used a randomized block analysis of variance (ANOVA), where stream was the blocking variable and replicates were nested within blocks and treatments (Table 2). This design created a sampling error term that was used to test for a block effect and block by treatment interactions.

To compare condition of fish among treatment groups, we used analysis of covariance (ANCOVA) with final mass as the dependent variable and final length as the covariate (both

**Table 2.** Mean square estimates of ANOVA for the 2 × 2 factorial experiment, randomized block design.

Source	df	df (calculated)	Sum of square	Mean square	Mean square estimate ( <i>F</i> value)
Block (random)	$n - 1$	$2 - 1 = 1$	$SS_{\text{BLOCK}}$	$MS_{\text{BLOCK}}$	$MS_{\text{BLOCK}}/MS_{\text{SE}}$
Treatment	$k - 1$	$4 - 1 = 3$	$SS_{\text{TREAT}}$	$MS_{\text{TREAT}}$	$MS_{\text{TREAT}}/MS_{\text{EE}}$
Food (fixed)		1	$SS_{\text{FOOD}}$	$MS_{\text{FOOD}}$	$MS_{\text{FOOD}}/MS_{\text{EE}}$
Cover (fixed)		1	$SS_{\text{COVER}}$	$MS_{\text{COVER}}$	$MS_{\text{COVER}}/MS_{\text{EE}}$
Food × Cover		1	$SS_{\text{F} \times \text{C}}$	$MS_{\text{F} \times \text{C}}$	$MS_{\text{F} \times \text{C}}/MS_{\text{EE}}$
Experimental error	$(n - 1)(k - 1)$	$(2 - 1)(4 - 1) = 3$	$SS_{\text{EE}}$	$MS_{\text{EE}}$	$MS_{\text{EE}}/MS_{\text{SE}}$
B × F		1	$SS_{\text{B} \times \text{F}}$	$MS_{\text{B} \times \text{F}}$	$MS_{\text{B} \times \text{F}}/MS_{\text{SE}}$
B × C		1	$SS_{\text{B} \times \text{C}}$	$MS_{\text{B} \times \text{C}}$	$MS_{\text{B} \times \text{C}}/MS_{\text{SE}}$
B × F × C		1	$SS_{\text{B} \times \text{F} \times \text{C}}$	$MS_{\text{B} \times \text{F} \times \text{C}}$	$MS_{\text{B} \times \text{F} \times \text{C}}/MS_{\text{SE}}$
Sampling error	$k \sum_{i=1}^n (r_i - 1)$	$4(1 - 1) + 4(3 - 1) = 8$	$SS_{\text{SE}}$	$MS_{\text{SE}}$	
Total	$\left( k \sum_{i=1}^n r_i \right) - 1$	$(4 \times 1 + 4 \times 3) - 1 = 15$	$SS_{\text{TOTAL}}$		

**Note:** Stream is the blocking factor, food and cover are treatments, and each treatment is replicated four times. Block (B) is a random factor, food (F) and cover (C) are fixed factors, and replicates are nested in blocks and treatments. *n*, no. of blocks; *k*, no. of treatments; *r*, no. of replicates.

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. We compared the initial size-class of survivors versus nonsurvivors and fish that emigrated versus those that did not. Mann–Whitney *U* tests were used for these tests because size-class data (i.e., 1, 2, 3, 4, or 5) were ordinal and not normally distributed. We further compared final condition and RGR of fish that emigrated versus those that did not using two-factor ANCOVA (as above) and ANOVA, respectively. In both the ANCOVA and ANOVA, the second factor was food treatment. When necessary, data were transformed (and noted in the results) to meet the assumptions of ANOVA.

Young-of-the-year and a few 1-year-old cutthroat that had either not been successfully removed from enclosures or entered during a high-water event midway through the experiment in East Creek (the experiment had not yet started in Spring Creek) were present in some enclosures prior to the introduction of the experimental fish. These 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 was emigration or growth rate affected by density of all fish in each enclosure (i.e., surviving experimental fish plus extra fish) (five analyses, ANCOVA, density covariate, all *p* > 0.05). Thus, we did not correct for density in the final analyses. No experimental fish were captured outside the enclosures during an intensive trapping session in East Creek after the high-water event.

We used the average of individual growth rates of fish in each enclosure as our response variable. However, not every fish was recaptured at the end of the experiment, and enclosures in each stream contained different numbers of fish initially. Enclosure means that are based on different numbers of fish could be biased if RGR is correlated with size of fish. Testing for this relation showed that growth rates were not

related to initial mass of fish (ANCOVA on log *x* + 1 transformed RGR, mass covariate  $F_{[1,64]} = 1.48, p = 0.23$ ; slope = −0.018). We also calculated growth for East Creek over the entire 40-day period, rather than presenting data on the first and last 20 days separately, as average growth rates were not significantly different for these two time periods (repeated-measures ANOVA, time  $F_{[1,8]} = 2.73, p = 0.14$ ).

**Winter sampling**

At the end of the summer experiment, the enclosure fences were removed, allowing the fish to disperse. We 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 downstream 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.

Traps were set 5 m apart, with an extra trap set every 15 m, 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 during October and November of 1997 and in January, February–March, April, and June of 1998. Sessions in Spring and East Creeks 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 one to three consecutive days, and traps were checked approximately every 24 h. Each captured animal was identified, measured, weighed, and returned to its point of capture. All fish had passive integrated transponder tags for individual identification implanted into the

body cavity upon first capture, as some of the latex marks were fading.

### Analysis

#### Growth

To test for differences in overwinter growth between fish that had or had not received food additions during the summer, we compared the mass of 26 experimental fish caught in September and again in April. As fish were no longer restricted to enclosures, each individual was considered a replicate. We compared mass and Fulton's condition factor (grams per cubic millimetre  $\times 10^{-5}$ ) (Ricker 1975) of fish in September and April by three-factor ANOVA after testing to ensure that condition did not increase or decrease as a function of fish length (Cone 1989). We did not use ANCOVA (as for condition analysis for the summer experiment) to test for differences in length–mass relationships because sample sizes were too low. 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.

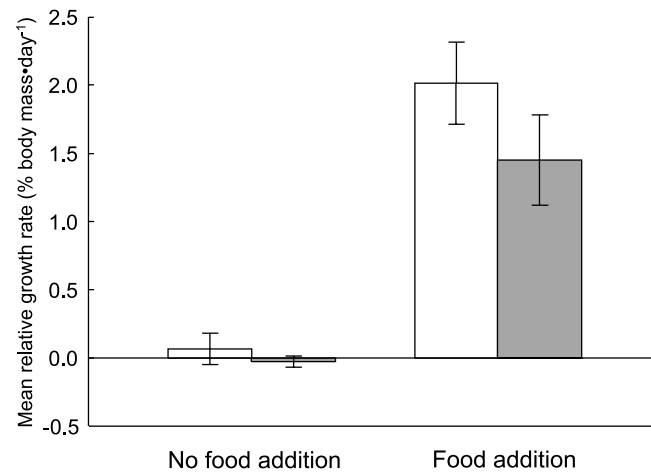
#### Survival

We used capture data from experimental fish for which we had measures of September mass 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 were pooled, with the assumption that no demographic changes had occurred over this short period. Analysis of capture–recapture data results in separate estimates of survival ( $\Phi$ ) and capture ( $P$ ) probabilities. Here, mortality reflects losses due to both death and emigration. We 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.

The 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 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, although some with a more complex or simpler structure were also fit. Covariate models were fit using the logit link, with survival or recapture expressed as a linear function of mass, 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). 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. We used a limited number of likelihood ratio tests to confirm results based on AIC. The overall goodness-of-fit of the global model was

**Fig. 1.** Mean relative growth rates of cutthroat trout in enclosures with and without food and cover ( $n = 4$  for all treatment combinations). Open bars represent no-cover treatments and solid bars represent cover treatments. Error bars are  $\pm 1$  SE.



checked using the  $\chi^2$  statistics of Test2 + Test3 described in Burnham et al. (1987). Program MARK (White and Burnham 1999) was used for model fitting and selection (based on AICc, a modification of AIC that corrects for bias related to sample size) and goodness-of-fit testing and to calculate the final maximum likelihood survival and recapture estimates.

## Results

### Summer experiment

Our initial level of cover added and stocking densities were based on the relative wetted widths of the two streams at the time of setup and our estimation of what their widths would be at summer low flow. By the time summer low flows were reached, Spring Creek was only about 1 m wider than East Creek. This resulted in cover treatments not being proportional (percent area in cover was 6.8 and 9.4% in East and Spring creeks, respectively) in the two streams and densities (about 0.25 and 0.34 fish·m<sup>-2</sup>) were below our projections. However, these differences should not be problematic because as noted earlier, growth was not related to density of fish, and stream was treated as a blocking factor and would thus control for such differences.

### Growth

Growth of trout was strongly influenced by food (ANOVA, food  $F_{[1,3]} = 34.76$ ,  $p = 0.01$ ); based on mean growth rates per enclosure, fish receiving food addition experienced 80 times higher growth rates than fish that did not receive food (Fig. 1). By the end of the experiment, the mean mass of fed fish was 71% higher than that of unfed fish in East Creek and 30% higher in Spring Creek (Table 3). Cover did not affect growth rates (cover  $F_{[1,3]} = 0.62$ ,  $p = 0.49$ ) and there was no interaction between treatments (food  $\times$  cover  $F_{[1,3]} = 0.04$ ,  $p = 0.85$ ). Growth also did not vary by stream (block  $F_{[1,8]} = 0.04$ ,  $p = 0.85$ ), nor were there stream by treatment interactions (all  $p > 0.05$ ).

**Table 3.** Initial and final size (mean ± SE) of cutthroat trout receiving different food treatments in East and Spring creeks.

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

**Note:** SE, standard error.

**Table 4.** Numbers (mean ± 1 SE (range)) of invertebrates collected during 3-h drift net samples in experimental enclosures in East and Spring creeks.

	East Creek, Aug.	East Creek, Sept.	Spring Creek, Sept.
<b>Aquatic</b>			
Diptera	49±23 (7–182)	28.3±5.3 (8–69)	23±2.0 (17–26)
Plecoptera	4.1±1.0 (1–8)	3.5±0.8 (1–9)	6.5±1.0 (4–9)
Trichoptera	3.7±1.4 (1–11)	5.9±1.8 (1–23)	5±1.1 (3–8)
Ephemeroptera	0.4±0.4 (0–3)	3±0.8 (0–7)	2.5±1.4 (0–5)
Other	4.7±1.4 (1–11)	8.8±2.6 (0–34)	8±1.6 (5–12)
<b>Terrestrial</b>			
	2.4±0.6 (1–4)	4.3±1.1 (0–12)	6±0.9 (4–8)
Drift density (no. per 100 m <sup>3</sup> )	340±68 (200–738)	292±30 (194–519)	284±18 (251–329)
<i>n</i>	7	8	4

**Note:** SE, standard error.

Although the RGRs of unfed fish were low and sometimes negative (mean ± 1 SE = 0.029 ± 0.05% body mass·day<sup>-1</sup>, *n* = 35), they were not different from those of free-ranging trout (0.147 ± 0.04, *n* = 14, *t* = -1.21, *df* = 47, *p* = 0.23). Further, the minimum growth rate of unfed fish was the same as that for free-ranging fish, suggesting that growth of unfed fish was within the range of what is naturally experienced. Although not significant, the mean growth of unfed fish was five times lower than that of free-ranging fish. Any enclosure effects are likely to have been equal across all treatments, however, and thus the magnitude of growth differences between fed and unfed fish would not be affected. Growth rates of fed fish were 12 times higher than those of free-ranging trout. Drift densities were similar among enclosures (Table 4) and comparable with densities typically found in other streams (100–1000·m<sup>-3</sup>) (Allan 1995).

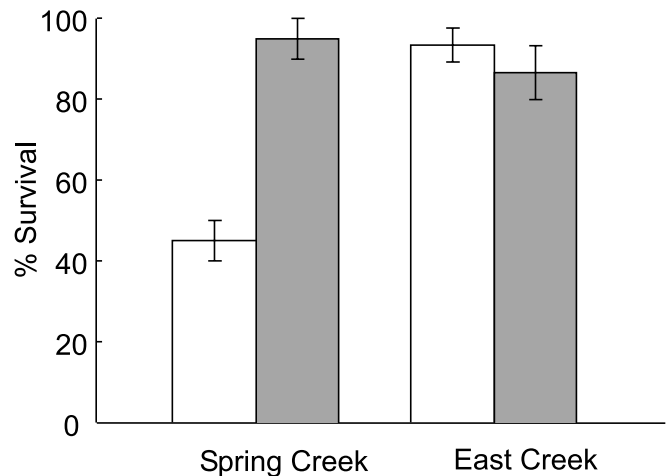
**Condition**

The elevation of the length–mass regression lines was different for fed and unfed fish only (ANCOVA, food *F*<sub>[1,3]</sub> = 83.39, *p* < 0.01) and the slopes of the regression lines were parallel (block × food × cover *F*<sub>[1,58]</sub> = 0.29, *p* = 0.96). Thus, fed fish were in better condition, weighing 13% more than unfed fish at any given length.

**Survival**

Survival of trout ranged from 40 to 100%, but was generally high, with the median survival within enclosures equaling 95%. Although the main effect of cover did not indicate an effect on survival, the block (i.e., stream) by cover interaction was significant. In East Creek, survival was high regardless of treatment. Spring Creek differed, in that survival

**Fig. 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). Open bars represent no-cover treatments and solid bars represent cover treatments. Error bars are ± 1 SE.

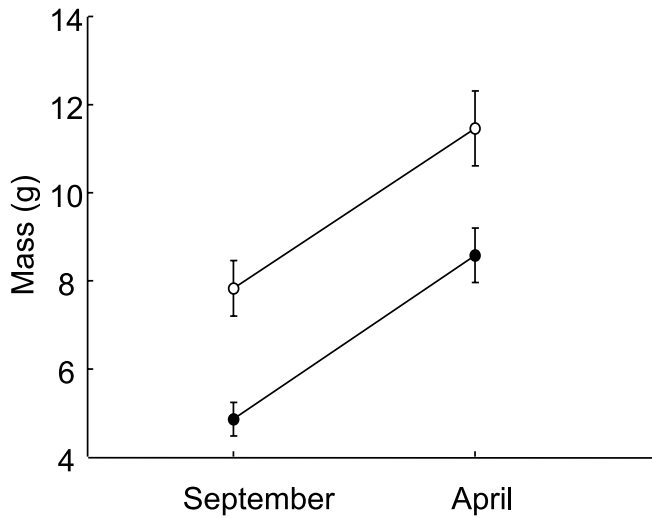


of trout in enclosures without cover was less than half that of trout with cover (ANOVA, block × cover *F*<sub>[1,8]</sub> = 10.32, *p* = 0.01) (Fig. 2). There were no other treatment effects on survival (all *p* > 0.05). The initial size of fish was not related to survival (Mann–Whitney *U* test, *Z* = -0.55, *p* = 0.58).

**Emigration**

Emigration was low during the experiment, with only 16 individuals out of 100 fish making a total of 29 moves into

**Fig. 3.** Comparison of mean mass of unfed (solid circles) and fed cutthroat trout (open circles) in fall and spring ( $n = 12$  for unfed trout and  $n = 14$  for fed trout). Error bars are  $\pm 1$  SE.



emigration traps. Of those moves, 25 were into downstream traps and four were into upstream traps. The mean number of times that fish emigrated per enclosure was not affected by either food or cover (ANOVA, food: mean  $\pm$  SE =  $2.75 \pm 1.11$ ,  $F_{[1,3]} = 0.64$ ,  $p = 0.49$ ; cover:  $2.75 \pm 0.63$ ,  $F_{[1,3]} = 1.34$ ,  $p = 0.33$ ). Emigration decreased to an average of  $0.50 \pm 0.50$  moves per enclosure with both food and cover present, but the decrease was not significant ( $F_{[1,3]} = 3.49$ ,  $p = 0.16$ ). Trends did not change when only one emigration event was counted per individual. Emigrants did not differ from nonmovers in initial size (Mann–Whitney  $U$  test,  $Z = -1.13$ ,  $p = 0.26$ ), final condition (ANCOVA, emigration  $F_{[1,69]} = 0.83$ ,  $p = 0.37$ ), or RGRs (ANOVA on  $\log x + 1$  transformed RGR, emigration  $F_{[1,69]} = 1.14$ ,  $p = 0.29$ ).

## Winter

### Growth

Fed fish maintained their size advantage by 46% over unfed fish during winter (ANOVA, food  $F_{[1,22]} = 6.27$ ,  $p = 0.02$ ; time  $F_{[1,22]} = 136.48$ ,  $p < 0.001$ ; stream and all interaction terms,  $p > 0.05$ ) (Fig. 3). By the spring, condition of fed fish (mean  $\pm 1$  SE =  $0.926 \pm 0.03$ ) had decreased to that of unfed fish ( $0.926 \pm 0.01$ ) (ANOVA on square-root-transformed condition factor, food  $\times$  time  $F_{[1,22]} = 6.72$ ,  $p = 0.02$ ).

### Survival

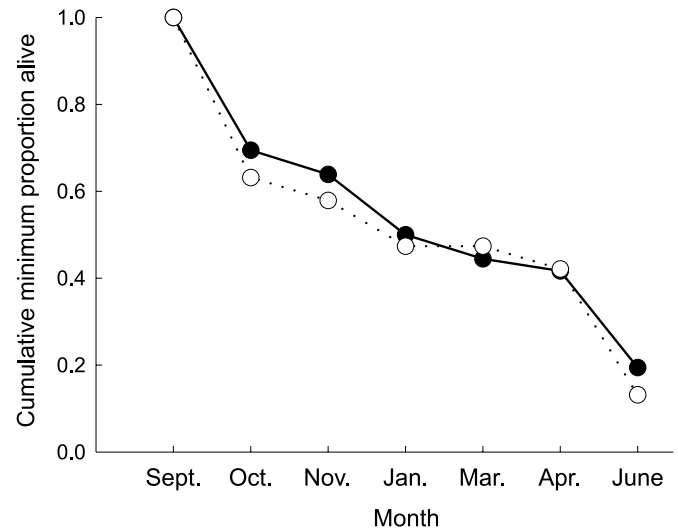
We had measures of September mass for 74 of the 100 experimental fish and thus used capture data from these 74 individuals for survival modeling. A total of 85 recaptures were made over winter. The global Cormack–Jolly–Seber model, which estimates a unique survival and capture probability for every time 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. Test power was low, however, because data were sparse.

**Table 5.** Best fitting survival and recapture models for size–survival analysis of experimental cutthroat trout over winter.

Survival $\Phi$	Capture $P$	No. parameters	AICc	$\Delta$ AICc	Deviance
<b>•</b>	<b><i>t</i></b>	<b>7</b>	<b>428.71</b>	<b>0.00</b>	<b>413.90</b>
<i>s</i>	<i>t</i>	8	430.75	2.04	413.70
<b>•+<i>m</i></b>	<i>t</i>	8	430.85	2.14	413.80
<b>•</b>	<i>t+m</i>	8	430.95	2.24	413.90
<i>s+m</i>	<i>t</i>	9	432.92	4.21	413.60

**Note:** Notation describes the factors and covariates that affect survival and capture probability: “*s*” indicates that the parameter varies between streams, “*t*” that the parameter varies among trapping sessions, and “•” that the parameter is constant between streams or over time. “+*m*” indicates that 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 stream (*s+m*) or at each time period (*t+m*). The best model is in bold. Modeling was performed using program MARK.

**Fig. 4.** Comparison of the cumulative minimum proportion of unfed (solid circles, solid line) and fed cutthroat trout (open circles, dotted line) present over time.



Of all of the models fit, model  $\Phi, P_t$ , had the lowest AICc, i.e., it was the most parsimonious model (Table 5). All other models had AICc values greater by at least 2.0. Selection of model  $\Phi_t$  indicates that none of the factors tested (stream, time, or the 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,  $\Phi_{+m}$ , had a very shallow 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. Under the best model, monthly recapture rates varied from 18 to 55%. Plotting the cumulative minimum proportion of unfed versus fed fish present over time illustrates no difference between the two groups (Fig. 4).

Two days of extra trapping in 140-m (East Creek) and 76-m (Spring Creek) sections immediately downstream of the study reaches during April captured no experimental fish. This suggests that emigration was minimal, although it is possible that fish had moved beyond this distance.

## Discussion

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, but there was no evidence that cover affected growth. The only cover effect was in Spring Creek, where mortality was substantially higher in the absence of cover. Although the effects of food and cover did not interact statistically, they do interact in a biological sense in that the highest biomass would occur under conditions of both high food and high cover availability. Fed fish were still larger than unfed fish by the following spring, but larger fall size did not appear to confer an advantage to fish in terms of overwinter survival.

### Food and growth

Several studies have inferred that food availability limits population densities and growth of 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. Our 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 underyearling coho salmon (*Oncorhynchus kisutch*) in enclosed reaches of a Vancouver Island stream and increased their biomass, through both increased growth and increased survival, by 2.5 times that of controls. Stimulating primary production by adding nutrients has resulted in increased growth rates (e.g., Deegan and Peterson 1992), individual size (e.g., Slaney and Ward 1993), and possibly density (Slaney and Ward 1993) of trout and salmon. Although the scale of our experiment was not ideal for measuring a survival effect of food, the large difference in growth between treatments indicates the potential for substantial fitness consequences and thus survival and population-level changes.

The extent to which fish are limited by food likely varies seasonally and spatially. Metabolic requirements, and thus food demand, of fish increase with temperature (Ursin 1979). During summer, warm temperatures, high fish densities as a result of new recruits, and reduced water volume increase the potential for food limitation. Late summer, the period when this study was conducted, appears to be a time when growth of stream trout is naturally quite low. For example, in three small Oregon streams, growth rates of 1-year-old cutthroat trout declined steadily over the summer and by August and September had reached levels similar to rates of unfed trout in this study (Lowry 1966). In an uncontrolled field setting, it is difficult to establish food limitation as the cause of low growth, since fish may, for example, feed very little in response to decreasing temperatures, even if food is available in excess (Jonsson et al. 2001). On a basic level, our experiment shows that fish are not incapable of high growth during this period but rather that they are in fact food limited. Numerous studies report low or negative growth of stream trout during summer (e.g., Cada et al. 1987; Ensign et al. 1990), which suggests that food limitation may be common across many populations of salmonid species. Generally, the potential for food limitation may be

greatest in cool, densely shaded streams, where light and low temperatures limit productivity (Hetrick et al. 1998), and (or) nutrient-poor waters. Food availability may set an upper limit on productivity (Richardson 1993), but it is important to note that other factors may curb 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, a number of fitness measures, such as the number or size of eggs produced by females, age of first reproduction, and overall survivorship, can be positively correlated with body size (Wootton 1990). 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 (e.g., 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, although not significant, points to this possibility.

### Cover and survival

We found no effect of cover on trout growth rates. Previous work on how cover affects growth has been equivocal. Experiments where fish have been enclosed have found increases (Sundbaum and Näslund 1998), decreases (Wilzbach et al. 1986), or no difference (Lonzarich and Quinn 1995; Spalding et al. 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 (e.g., Gowan and Fausch 1996; Harvey 1998). However, density-dependent growth may confound the outcome of such studies because the habitat manipulation often results in higher numbers of fish. How cover affects fish growth may depend on whether the structure acts as velocity refuge, visual isolation, or predation refuge to fish. Cover may enhance growth by providing favorable foraging sites, for example, 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). There may be a negative effect on growth, however, if heavy shading 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, season, and state-dependent differences among fish.

We 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, as 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. Predator sightings were not common, but 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 substrate size in East Creek may have provided fish with cover from predation even in the absence of the cover treatment.

The cover effect in Spring Creek contradicts 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 seminatural 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 (*Oncorhynchus mykiss*). Rosenfeld and Boss (2001) found that energetics alone explained selection of deep habitat (i.e., pools) by 1- to 2-year-old anadromous cutthroat trout, without having to invoke greater predation risk in shallow, riffle habitats. Research based in warm-water streams demonstrates very strong predator impacts, mediated by water depth (e.g., Power 1987). The role that predation plays in structuring fish populations in more northern temperate regions is less clear. Even though predators appeared uncommon in our study area, the chance arrival of a single predator in a situation where prey are vulnerable could cause very high mortality. A study of the relation between stream size or type, predator abundance, and prey behavior would help clarify the role of predators and (or) cover.

Our 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 (1996) 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 we found no evidence of this. Under high population densities, however, some individuals may be forced into suboptimal habitats by dominant conspecifics (e.g., Fausch 1984). 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). In situations such as these, cover could be naturally limiting to fish.

### Body size and overwinter survival

Previous studies of stream-resident trout have noted a positive relation between body size and survival over winter (e.g., 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. We did not find that September mass of individuals was a predictor of winter survival. In fact, monthly survival rate, estimated for all 100 experimental fish using program MARK, was nearly equal for summer (excluding "no-cover" treatment in Spring Creek, 96.7%) and winter (96.6%) (Boss 1999). Fed fish did, however, maintain their

size advantage over winter. That fed fish gained weight and simultaneously lost condition (i.e., grew longer) suggests that they converted energy into permanent somatic tissue rather than only using it in maintenance metabolism or temporary fat stores. Therefore, despite a lack of evidence for a survival benefit of increased size, fed individuals may have been able to allocate more energy into somatic tissue, earlier reproduction, higher fecundity, or securing 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 (e.g., Post and Evans 1989). The winter of this study was quite mild with relatively moderate rain events and temperatures. This may have minimized size-biased mortality. In addition, the trout continued to grow from September until November and thus may have reached a threshold where survival was no longer influenced by size.

Despite a longstanding interest in identifying limiting resources for fish, basic experimental tests have rarely been performed in the field. Manipulations like those used in this study can help identify the relative importance of limiting resources and how they interact. Our study demonstrated the separate effects of food and cover on trout growth and survival and the possible implications of differences in body size for fish.

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### References

- Allan, J.D. 1995. Stream ecology: structure and function of running waters. Chapman and Hall, London, U.K.
- Bjornn, T.C., and Reiser, D.W. 1991. Habitat requirements of salmonids in streams. *Am. Fish. Soc. Spec. Publ.* **19**: 83–138.
- Boss, S.M. 1999. Summer resource limitation and over-winter movement and survival of stream-resident coastal cutthroat trout. M.Sc. thesis, University of British Columbia, Vancouver, B.C.
- Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C., and Pollock, K.H. 1987. Design and analysis methods for fish survival experiments based on release-recapture. *Am. Fish. Soc. Monogr.* **5**.
- Cada, G.F., Loar, J.M., and Sale, M.J. 1987. Evidence of food limitation of rainbow and brown trout in southern Appalachian soft-water streams. *Trans. Am. Fish. Soc.* **116**: 692–702.
- Chapman, D.W. 1966. Food and space as regulators of salmonid populations in streams. *Am. Nat.* **100**: 345–357.
- Cone, R.S. 1989. The need to reconsider the use of condition indices in fishery science. *Trans. Am. Fish. Soc.* **118**: 510–514.

- Deegan, L.A., and Peterson, B.J. 1992. Whole-river fertilization stimulates fish production in an Arctic tundra river. *Can. J. Fish. Aquat. Sci.* **49**: 1890–1901.
- Elliott, J.M., and Hurley, M.A. 1998. Population regulation in adult, but not juvenile, resident trout (*Salmo trutta*) in a Lake District stream. *J. Anim. Ecol.* **67**: 280–286.
- Ensign, W.E., Strange, R.J., and Moore, S.E. 1990. Summer food limitation reduces brook and rainbow trout biomass in a southern Appalachian stream. *Trans. Am. Fish. Soc.* **119**: 894–901.
- Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Can. J. Zool.* **62**: 441–451.
- Fausch, K.D., Hawks, C.L., and Parsons, M.G. 1988. Models that predict standing crop of stream fish from habitat variables. U.S. For. Serv. Gen. Tech. Rep. PNW-GTR-213.
- Gowan, C., and Fausch, K.D. 1996. Long-term demographic responses of trout populations to habitat manipulation in six Colorado streams. *Ecol. Appl.* **6**: 931–946.
- Grand, T.C., and Dill, L.M. 1997. The energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*): ideal free distribution theory applied. *Behav. Ecol.* **8**: 437–447.
- Harvey, B.C. 1998. Influence of large woody debris on retention, immigration, and growth of coastal cutthroat trout (*Oncorhynchus clarki clarki*) in stream pools. *Can. J. Fish. Aquat. Sci.* **55**: 1902–1908.
- Hetrick, N.J., Brusven, M.A., Meehan, W.R., and Bjornn, T.C. 1998. Changes in solar input, water temperature, periphyton accumulation, and allochthonous input and storage after canopy removal along two small salmon streams in southeast Alaska. *Trans. Am. Fish. Soc.* **127**: 859–875.
- Hutchings, J.A. 1994. Age- and size-specific costs of reproduction within populations of brook trout, *Salvelinus fontinalis*. *Oikos*, **70**: 12–20.
- Jenkins, T.M., Jr., Diehl, S., Kratz, K.W., and Cooper, S.D. 1999. Effects of population density on individual growth of brown trout in streams. *Ecology*, **80**: 941–956.
- Jonsson, B., Forseth, T., Jensen, A.J., and Næsje, T.F. 2001. Thermal performance in juvenile Atlantic salmon, *Salmo salar* L. *Funct. Ecol.* **15**: 701–711.
- Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L., and *S. trutta* L.). *Inst. Freshwater Res. Drottningholm Rep.* **39**: 55–98.
- Keeley, E.R., and Grant, J.W.A. 1995. Allometric and environmental correlates of territory size in juvenile Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* **52**: 186–196.
- Lebreton, J.D., Burnham, K.P., Clobert, J., and Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**: 67–118.
- Lonzarich, D.G., and Quinn, T.P. 1995. Experimental evidence for the effect of depth and structure on the distribution, growth, and survival of stream fishes. *Can. J. Zool.* **73**: 223–2230.
- Lowry, G.R. 1966. Production and food of cutthroat trout in three Oregon coastal streams. *J. Wildl. Manage.* **30**: 754–767.
- Mason, J.C. 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. *J. Wildl. Manage.* **40**: 775–788.
- Mesick, C.F. 1988. Effects of food and cover on numbers of apache and brown trout establishing residency in artificial stream channels. *Trans. Am. Fish. Soc.* **117**: 421–431.
- Northcote, T.G., and Hartman, G.F. 1988. The biology and significance of stream trout populations (*Salmo* spp.) living above and below waterfalls. *Pol. Arch. Hydrobiol.* **35**: 409–442.
- Poff, N.L., and Huryn, A.D. 1998. Multi-scale determinants of secondary production in Atlantic salmon (*Salmo salar*) streams. *Can. J. Fish. Aquat. Sci.* **55**(Suppl. 1): 201–217.
- Post, J.R., and Evans, D.O. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. *Can. J. Fish. Aquat. Sci.* **46**: 1958–1968.
- Power, M.E. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. *In* Predation: direct and indirect impacts on aquatic communities. *Edited by* W.C. Kerfoot and A Sih. University Press of New England, Hanover, N.H. pp. 333–351.
- Richardson, J.S. 1993. Limits to productivity in streams: evidence from studies of macroinvertebrates. *In* Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. *Edited by* R.J. Gibson and R.E. Cutting. *Can. Spec. Publ. Fish. Aquat. Sci.* No. 118. pp. 9–15.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* No. 191.
- Roni, P., and Quinn, T.P. 2001. Density and size of juvenile salmonids in response to placement of large woody debris in western Oregon and Washington streams. *Can. J. Fish. Aquat. Sci.* **58**: 282–292.
- Rosenfeld, J.S., and Boss, S. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. *Can. J. Fish. Aquat. Sci.* **58**: 585–593.
- Slaney, P.A., and Ward, B.R. 1993. Experimental fertilization of nutrient deficient streams in British Columbia. *In* Le développement du Saumon atlantique au Québec: connaître les règles du jeu pour réussir. Colloque international de la Fédération québécoise pour le saumon atlantique, Québec, décembre 1992. *Edited by* G. Shooner and S. Asselin. Fédération québécoise pour le saumon atlantique (FQSA), 42B, rue Racine, Loretteville, QC G2B 1C6. Collection *Salmo salar* No. 1. pp. 128–141.
- Smith, R.W., and Griffith, J.S. 1994. Survival of rainbow trout during their first winter in the Henrys Fork of the Snake River, Idaho. *Trans. Am. Fish. Soc.* **123**: 747–756.
- Spalding, S., Peterson, N.P., and Quinn, T.P. 1995. Summer distribution, survival, and growth of juvenile coho salmon under varying experimental conditions of brushy instream cover. *Trans. Am. Fish. Soc.* **124**: 124–130.
- Sundbaum, K., and Näslund, I. 1998. Effects of woody debris on the growth and behaviour of brown trout in experimental stream channels. *Can. J. Zool.* **76**: 56–61.
- Ursin, E. 1979. Principles of growth in fishes. *Symp. Zool. Soc. Lond.* **44**: 63–87.
- White, G.C., and Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**(Suppl.): 120–138.
- Wilzbach, M.A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (*Salmo clarki*). *Can. J. Fish. Aquat. Sci.* **42**: 1668–1672.
- Wilzbach, M.A., Cummins, K.W., and Hall, J.D. 1986. Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. *Ecology*, **67**: 898–911.
- Wootton, R.J. 1990. Ecology of teleost fishes. Chapman and Hall, London, U.K.
- Young, K.A., Hinch, S.G., and Northcote, T.G. 1999. Status of resident coastal cutthroat trout and their habitat 25 years after riparian logging. *N. Am. J. Fish. Manage.* **19**: 901–911.