Habitat selection by juvenile coho salmon in response to food and woody debris manipulations in suburban and rural stream sections

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Abstract: This study explored the effects of food and woody debris manipulations on the summer distribution of juvenile coho salmon (*Oncorhynchus kisutch*) in small suburban streams. To examine fish responses to these factors, three different experiments were carried out in modified sections of two streams. The results showed that the distribution of juvenile coho salmon in a stream section was primarily controlled by the availability and distribution of food among pools and by the presence and density of woody debris. Food, however, played a dominant role because the foraging quality of a pool not only affected the density of fish in it but also the response of those fish towards instream debris. In food-rich stream sections, low proportions of juvenile coho salmon occupied pools with dense woody debris in the spring, which changed towards late summer. In contrast, in food-poor reaches, high proportions of fish were found in pools with abundant debris in the spring. Pools that combined abundant food with sparse woody debris were the most favoured by the fish. It is important that salmonid habitat enhancement projects consider that open foraging areas interspersed with woody debris characterize the type of summer habitat that juvenile coho salmon prefer.

Résumé : La présente étude examine les effets de la manipulation des aliments et des débris ligneux sur la distribution d'été du saumon coho (*Oncorhynchus kisutch*) juvénile dans les petits cours d'eau suburbains. Pour étudier la réaction des poissons à ces facteurs, trois différentes expériences ont été effectuées dans des tronçons modifiés de deux cours d'eau. Les résultats ont montré que la distribution du coho juvénile dans un tronçon était principalement régie par la disponibilité et la distribution de la nourriture dans les fosses ainsi que par la présence et la densité des débris ligneux. Le facteur dominant était cependant la nourriture, car la qualité de l'alimentation dans une fosse influe non seulement sur la densité de poissons, mais également sur la réaction des poissons face aux débris ligneux du cours d'eau. Dans les tronçons riches en aliments, de faibles proportions de cohos juvéniles occupaient les fosses très denses en débris ligneux au printemps, situation qui allait changer vers la fin de l'été. Au contraire, dans les tronçons pauvres en aliments, de fortes proportions de poissons ont été trouvées dans les fosses ayant d'abondants débris au printemps. Les fosses qui présentaient à la fois beaucoup d'aliments et peu de débris ligneux étaient les plus appréciées par les poissons. Il est donc important que les projets de mise en valeur de l'habitat des salmonidés tiennent compte du fait que les aires d'alimentation découvertes parsemées de débris ligneux caractérisent le type d'habitat d'été que le saumon coho juvénile préfère.

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Introduction

In the Pacific Northwest, coho salmon (*Oncorhynchus kisutch*) find prime spawning and nursery habitat in small low-gradient coastal streams, with a large proportion of marginal areas, slow-flowing waters, and relatively equal proportions of alternating pools and riffles (Sandercock 1991). Juvenile coho salmon prefer pools to riffles and use instream structures, such as rocks and logs, as water current shelters to minimize the energy costs associated with maintaining position in the stream while feeding on drifting food (Mundie 1969; Fausch 1993). Logs (large woody debris (LWD)) increase pool frequency in both low- and moderate-slope stream reaches (Montgomery et al. 1995; Beechie and Sibley 1997), augment retention of sediments and particulate organic matter (Bilby 1981), and slow down the downstream migration rate of gravel (Montgomery et al. 1996).

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Instream woody debris, both large and brushy or fine (FWD), may increase not only the availability of fish food (Nielsen 1992) but also the structural complexity of fish habitat. Instream structures make fish less visible to predators (Helfman 1981), provide physical refuge from predation (Reinhardt and Healey 1997), and increase intraspecific visual isolation among competitors (Dolloff 1986). Visual isolation reduces aggressive interactions among competitors and may therefore increase the number of young fish occupying a given area (Bugert et al. 1991`; Fausch 1993).

The topographic, hydrologic, and climatic conditions that make certain watersheds suitable for coho salmon are also well suited for human settlement. As a result, coho salmon nursery habitat in many watersheds of southwestern British Columbia has been affected by both agriculture (Birtwell et al.1988) and urban development (Slaney et al. 1996). In those systems, loss of instream woody debris, through both direct removal and reduced recruitment, is perhaps one of the most pervasive alterations to salmonid habitat (Booth

1991). Managers have been trying to reverse this situation largely by means of instream debris placement projects. As a result, most habitat restoration projects are limited to the artificial installation of instream woody debris. Development of effective and efficient rehabilitation protocols depends in part on a clear understanding of how fish use such structures. However, there is no consensus in the literature on whether woody debris availability makes a stream reach more or less attractive to juvenile coho salmon during spring and summer. While some studies have found positive correlations between juvenile coho salmon and instream cover abundance (Dolloff 1986; Dolloff and Reeves 1990; Shirvell 1990), others have reported that the fish preferred to occupy open areas and showed no association with cover (Bugert and Bjornn 1991; Bugert et al. 1991; Spalding et al. 1995). Such contradictory results may be due to (*i*) the nature of the studies (i.e., descriptive versus experimental work), (*ii*) the type of system or habitat considered (i.e., small streams, artificial laboratory channels, or the mainstem of the river), (*iii*) the time of the year (early versus late summer), and (*iv*) the spatial scales considered (i.e., 40-m-long stream sections versus 1-m-long pools). Thus, the value of woody debris placement as a summer habitat enhancement technique remains somewhat controversial.

The objectives of this study were, first, to investigate the spatial distribution of juvenile coho in response to woody debris and food manipulations in stream habitat that has been altered by suburban residential development and farming activities and, second, to determine whether such responses change over time. To examine these responses, three different experiments were carried out in modified sections of two streams and were repeated throughout the summer. Two of these experiments (Experiments 1 and 3) evaluated the effects of woody debris and food on the spatial distribution of fish by manipulating woody debris and food abundance in the pools of an experimental stream section. The other experiment (Experiment 2) examined whether the spatial distribution of the fish was affected by woody debris density or type (LWD versus FWD) by placing logs in some stream pools and bundles of fine brushy debris in other pools.

Materials and methods

Study sites

Two of the three experiments were carried out in Spring Creek, Chilliwack, B.C., and the third one in Coghlan Creek, Langley, B.C. (Fig. 1). Both creeks run through agricultural land with interspersed residential areas and are characteristic of the type of habitat that wild juvenile coho salmon find on the rural–urban fringe of the Pacific Northwest.

Spring Creek originates at the base of Isar Mountain on the International Ridge of the Skagit Mountains and flows into Cultus Lake. The upper half of the stream, which runs through a golf course, has been cleared of riparian vegetation and is used by cutthroat trout (*Oncorhynchus clarki*). In contrast, the lower half, which is well shaded by the surrounding vegetation and has abundant overhanging cover and a mixed substrate of gravel and sand, is used by both cutthroat trout and chum salmon (*Oncothynchus keta*). Chum salmon spawn in early winter and their fry leave shortly after emergence, between March and April. Spring Creek had a coho salmon run that disappeared several years ago (D. Barnes, Cultus Lake Salmon Research Laboratory, 4222 Columbia Valley Highway, Cultus Lake, BC V2R 5B6, Canada, personal communication). The Canadian Department of Fisheries and Oceans presently stocks hatchery coho salmon fry into the lower half of the creek each spring. However, no adult coho salmon returns have been observed.

Water flow in Spring Creek remained relatively constant throughout the summer at 0.04 $m^3 \cdot s^{-1}$. Water temperature at the head spring was constantly 9°C but increased downstream. Daily water temperatures entering the experimental reach ranged from 12.3°C in May mornings to 22.9°C in August evenings.

The lower half of Spring Creek has a stairway-like aspect due to a series of low wooden weirs placed 20–50 m apart. The weirs create a series of waterfalls (20–40 cm high) that are separated by long pool/glide-like sections. The first glide immediately downstream from the golf course was used to build the experimental arena upstream from where the Department of Fisheries and Oceans had released coho salmon fry. This stream section was 20 m long and 4.5 m wide, and its upstream and downstream limits were set by 40-cm-high waterfalls. A net placed across the upstream waterfall prevented any of the fish used in the experiments from leaving this section. The downstream waterfall entered a fish trap box, which retained any fish trying to emigrate from the experimental section and blocked the upstream movement of other fish. The entire experimental section was longitudinally divided in half with a 2-mm-mesh fence to form two adjacent channels. Four pools and three riffles were constructed in each channel using large gravel and cobble. The pools were all similar, with a mean length of 4.1 m and a mean width of 2.0 m (mean area = 8.26 m^2). Their maximum depth was 0.5 m and their mean depth was 0.32 m. The dividing fence was partly buried in the substrate and was sealed to prevent fish movement between the two channels.

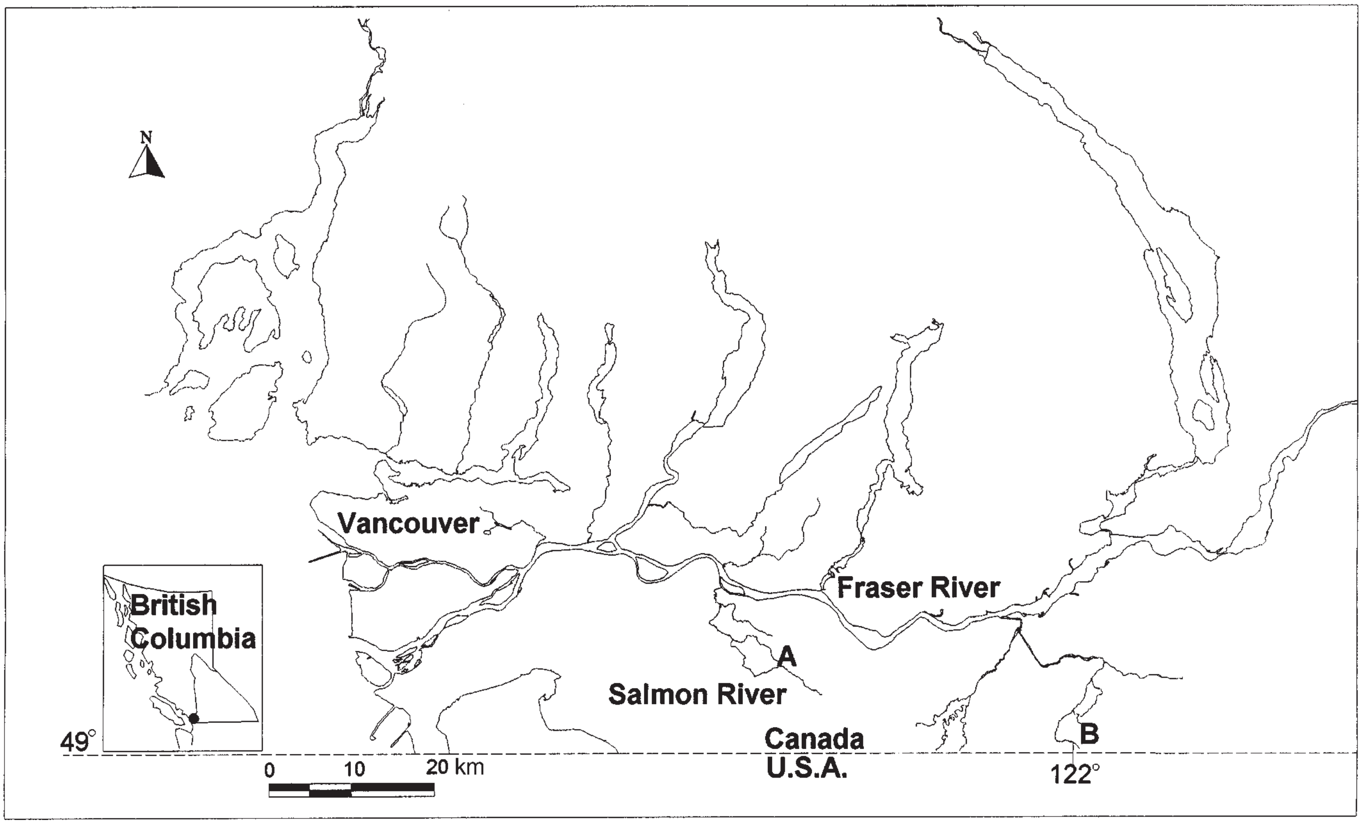
The site was considered ideal for food manipulations because invertebrate drift from the upstream golf course reach was very low. This was corroborated by drift and benthic samples. Four midwater drift samples were taken upstream from the experimental section on June 21, July 12 and 26, and August 11 using 1-m-long drift nets (200-µm mesh) with 5 × 15 cm mouths. After 24 h in the stream, the nets had no aquatic invertebrates and only a few terrestrial ones (mean = 2.25 insects per sample from orders Coleoptera, Diptera, and Hemiptera). Four benthic samples were taken at the same site using a 929-cm^2 Surber sampler with a 200-µm-mesh net. Two of those samples were taken on July 12 and the other two on July 26. These samples contained a few caddisfly (Trichoptera) larvae (mean = 1.62 larvae per sample) and a total of two worms (Annelida).

Coghlan Creek, the main tributary of the Salmon River, sustains a large coho salmon run and is also used by steelhead (*Oncorhynchus mykiss*) and cutthroat trout. Three sites near its headwaters were used as replicates for one of the experiments. In the summer of 1994, these sites had a mean flow of 0.06 $m^3 \cdot s^{-1}$ and their temperature ranged from 12.9 to 16.6°C (mean = 14.8°C). Two of the experimental sites, B and C, were 40 m apart in a shallow treeless ravine and lacked cover. The downstream site, C, was 19.5 m long and an average of 0.24 m deep and 3.4 m wide. The upstream site, B, was 18.6 m long and an average of 0.19 m deep and 2 m wide. A third site, A, was about 1 km further upstream. This site was 24.4 m long and averaged 0.35 m deep and 2 m wide. It was partially shaded by surrounding trees but did not have any instream cover. All three sites were glides with well-defined riffles at both ends. Three riffles of gravel and rocks about 1 m long and 0.03 m deep were constructed within each glide to create four pools of approximately equal size.

Experimental subjects

The fish used in Coghlan Creek were wild coho salmon from that creek, while in the Spring Creek experiments, coho salmon fry

Fig. 1. Locations of Coghlan Creek (A, within the Salmon River watershed) and of Spring Creek (B, within the Vedder–Chilliwack system) in the lower Fraser Valley.



from the Chilliwack River Hatchery were used. These fish were kept in an outdoor holding channel (0.9 m wide, 0.4 m deep, and 17.4 m long) at the Cultus Lake Research Laboratory (Department of Fisheries and Oceans) from April 1 until they were used for the experiments. During the holding period, handling was kept to a minimum. Food (ground freeze-dried shrimp (*Euphasia pacifica*)) was delivered into the holding channel by means of automatic feeders placed 3 m apart from each other. This created a low but regular prey input rate intended to resemble invertebrates falling from the overhanging vegetation. Fish were exposed to avian predators because of the uncovered holding channel. Predation shelters were provided by bundles of two dozen 0.5-m-long twigs placed at 1.5-m intervals in the channel, and most fish were observed to make use of them.

All fish used in these experiments were cold branded using brass-made brands cooled in a mix of acetone and dry ice (see Bryant et al. 1990). For the purpose of this study, fish marking was only used to distinguish recaptured experimental individuals from potential immigrants to the experimental sites. This was particularly relevant for the Spring Creek experimental section.

During the experimental trials, fish were exposed to predation. American dippers (*Cinclus mexicanus*), green-backed herons (*Butorides striatus*), and kingfishers (*Ceryle alcyon*) were observed at all locations. Cutthroat trout of a size that could predate upon juvenile coho salmon were found at the three Coghlan Creek sites but were excluded from the Spring Creek experimental section.

Experiment 1

This experiment was carried out in the Spring Creek split channel section and tested the response of fish to woody debris presence and density under high- and low-food channel conditions. It examined whether (*i*) juvenile coho salmon distribution among pools is affected by woody debris availability and density, (*ii*) food abundance (food versus no-food channels) alters fish response to woody debris and (*iii*) fish response to woody debris changes over the summer.

Woody debris treatment consisted of tree branches grouped in bundles. These bundles resembled some of the FWD commonly present in coho salmon nursery habitat. However, they represented a simple test model, since they could not simulate all the parameters of niche separation and stability of spatial definition provided by some of the naturally occurring debris. Each bundle was made of eight red alder (*Alnus rubra*) branches (0.5–1.5 cm thick and 1.2–1.5 m long, with numerous offshoots each) combined with a branch of Douglas-fir (*Pseudotsuga menziesii*) and one of western redcedar (*Thuja plicata*) 1–1.2 m long, both with foliage intact. All branches were tied together and anchored with rocks so they would not drift away. The sunken alder branches provided fish with instream cover, and the fan-shaped coniferous branches that spread on the water surface served as overhead cover.

Freeze-dried shrimp was used as food treatment and was delivered by means of automatic belt conveyor feeders placed on the channel riffles. For this experiment, food treatment was randomly assigned to only one of the two channels before the beginning of each trial. In the treated channel, each pool received 7.5 g of freeze-dried shrimp per day (approximately a rate of 15% of biomass of released fish). In both channels, all pools were treated with one of three different amounts of debris: none, sparse FWD (one bundle of branches), or dense FWD (three bundles). Before releasing fish in the channels and starting a new trial, debris treatments were randomly assigned to pools (one of them was repeated, at random, because there were four pools in each channel). The sparse FWD treatment introduced a low density of cover that could offer predation refuge and visual isolation from competitors but, at the same time, left a large proportion of the pool unobstructed. In contrast, cover occupied almost the entire pool in the dense FWD treatment, leaving no open foraging areas.

Each fish was only used in one trial. At the beginning of each trial, equal numbers of randomly chosen fish were released into the Spring Creek's channels and allowed 72 h to explore and redistribute themselves among pools. At the end of each 72-h-long trial, fish were removed from the pools using a pole seine until none were caught in two consecutive passes. Thereafter, any fish remaining in the pools were captured by electrofishing. To prevent fish from switching pools during seine passes, stop nets were placed on the riffles and at the downstream waterfall.

In the early summer trials (May 24 to June 27), 50 juvenile coho salmon (mean length = 4.32 cm, SD = 0.425, n = 200; mean weight = 1.03, SD = 0.318, n = 200) were released into each experimental pool per trial (total = 200 fish in each experimental channel). The number of fry released into each pool was sufficient to create a very high initial density (6 fish·m^{-2}), similar to early summer densities reported for some highly productive coho salmon streams in this part of the province (Ptolomy 1993). Under these conditions, a large proportion of juvenile coho salmon moved downstream and entered the fish trap as expected (see Chapman 1962). Ten trials were carried out for each food treatment. For the late summer trials (August 18 to September 9), the number of juvenile coho salmon released into the channels was reduced to 25. Because the fish were larger (mean length = 5.71 cm, SD = 0.467, n = 100; mean weight = 2.06 g, SD = 0.532, n = 100), this number gave a similar biomass per pool to that in the earlier trials (about 6.15 g·m^{-2}). Due to time constraints, the number of trials in this case was reduced to seven for each food treatment.

The design of this experiment corresponded to a split-plot factorial. Food was the main plot factor (with two levels: food versus no food) and woody debris was the subplot factor (with three levels: none, sparse, and dense). The experiment was replicated over time. Because the waterfall at the upper end of both channels seemed to attract fish into the upstream pools in the absence of treatments (see control experiment), analysis of covariance (ANCOVA) was used to separate the effect of this factor from those of food and woody debris on fish distribution. Two covariables were used: "distance" (between the centre of each pool and the upstream end waterfall) and "distance^2," because the control experiment revealed that a quadratic regression provided the best "fit" for predicting fish abundance based on pool distance to upstream waterfall.

Experiment 2

This experiment was carried out in the three Coghlan Creek sites and examined whether (*i*) juvenile coho salmon distribute among stream pools in response to woody debris density and type (LWD versus FWD) and (*ii*) fish response to woody debris changes over time.

Before beginning experimental trials, pools in each of the three sites were closed with nets (5-mm mesh) and all fish were removed by pole seining and electroshocking. Fish were counted and sorted by species into separate holding buckets. Besides coho salmon, three other species of fish were found: rainbow/steelhead trout, cutthroat trout, and threespine stickleback (*Gasterosteus aculeatus*). After removing the fish, different debris treatments were randomly assigned to pools.

Each of the four pools built at each site received one of the following debris treatments: no debris, sparse LWD, sparse FWD, or dense FWD. The LWD treatment consisted of two logs (diameter of at least 20 cm) forming a "Y" in the pool. The logs were anchored to the stream banks with nylon rope and were submerged under the weight of three boulders. Pools treated with sparse FWD received three bundles of branches, which were anchored to bank rocks with nylon rope. The bundles were made of eight red alder branches and one fan-shaped western redcedar branch, similar in dimensions to those used in Spring Creek. Pools treated with dense FWD were entirely covered with nine bundles.

After debris placement, all fish but juvenile coho salmon were returned to the pools from which they had been caught. At each site, juvenile coho salmon were divided into four equal groups to create equal densities in all pools. Fish were individually measured (June: mean length = 4.43 cm, SD = 0.578, n = 100; mean weight = 1.05, SD = 0.457, n = 100). Afterwards, each group of fish was randomly assigned to and released into one of the four pools. From 75 to 120 fish were released per pool, depending on the number of fish caught at each experimental site. Trials began in June, and fish at each site were sampled again in July and August (July: mean length = 4.78 cm, SD = 0.676, n = 100; mean weight = 1.39, SD = 0.655, n = 100; August: mean length = 4.93 cm, SD = 0.547, n = 100; mean weight = 1.36, SD = 0.486, n = 100). During each of these sampling times, cover treatments were randomly redistributed among pools before coho salmon were released back into the pool in which they were found. Thus, although the type of cover that coho salmon found in their pools may have changed, each individual found itself in the same pool that it had occupied just before sampling began.

This experiment had a randomized block design (blocks were monthly replications) with two factors (debris and site) and its data were examined using analysis of variance (ANOVA) (Hicks 1993). The effect of debris on fish distributions was also tested separately for each month using single-factor ANOVA.

Experiment 3

This experiment was carried out in the Spring Creek split channel and examined whether woody debris or food alone or the combination of both factors controls the distribution of juvenile coho salmon among pools.

Two treatments were used in it, food and FWD, and each treatment had two levels: food versus no food and dense FWD versus no debris. Each one of the four possible treatment combinations was randomly assigned to one of the four pools in each channel.

Floating shrimp were prevented from drifting between pools by means of small-mesh screens placed at the tails of the pools. The screens sat on wire legs above the substrate, leaving enough space for fish to swim underneath. Their mesh was cleaned every 8–10 h to keep it from clogging. However, although no evidence of overflow was ever found, the possibility of food drifting among pools remained. Twenty-five fish were released into each pool at the beginning of each trial. Eleven trials were completed between July 22 and August 11.

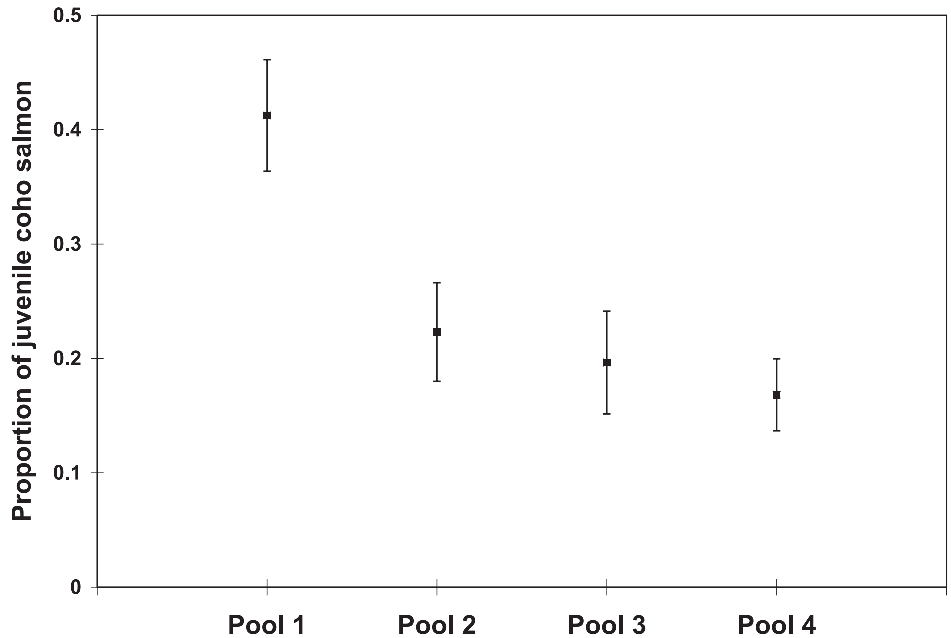
This experiment, with its two factors (debris and cover) and a randomized block (trial) design, was analyzed using ANCOVA. As in Experiment 1, distance and distance^2 to upstream end waterfall were the covariables used to adjust for the effect that the waterfall had on the distribution of fish. In contrast with Experiment 1, which could not test the effect of the interaction among treatments because woody debris was a "subtreatment " (subplot factor) applied to pools within food-rich or food-poor channels, this experiment examined the main effects of both woody debris and food as well as their interaction on fish distribution.

Control experiments

In the experimental section of Spring Creek, pool distance from upstream waterfall seemed to affect pool choice by fish. Therefore, a control experiment was used to examine how juvenile coho salmon distributed among pools in the absence of any experimental treatments. Fifty juvenile coho salmon were released per pool and their distribution was recorded 72 h later. This experiment was replicated 10 times. Six trials were carried out between July 1 and 11 and four trials between August 12 and 18.

This was a single-factor experiment with a randomized block (trial) design and was analyzed using ANOVA. The main factor

Fig. 2. Proportional distribution of juvenile coho salmon among control experimental channel pools. Squares are mean values and vertical lines represent ±2 SE.



was pool distance to upstream end waterfall. Based on Fig. 2, a quadratic model was chosen as a first approximation to predict "fish distribution" from pool distance. The ANOVA was performed on a model that partitioned pool distance into linear and quadratic components and the interaction term into distance by trial and distance^2 by trial. Its results confirmed that pool distance ($F = 44.14$, df = 1, $p < 0.001$) and pool distance^2 ($F = 9.93$, df = 1, $p = 0.011$) from upstream end waterfall affected fish distribution among pools. Therefore, both pool distance and pool distance^2 were used as covariables in the analyses of Experiments 1 and 3.

Because Chilliwack River hatchery fish were used in the Spring Creek experiments and wild fish were used in the Coghlan Creek experiment, another control test was carried out to determine whether juvenile coho salmon of those two stocks showed different habitat preferences in a common experimental channel.

An artificial outdoor channel at the Cultus Lake Research Laboratory was used for this test. The experimental channel was shaped as a "B" with a straight 10-m-long, 0.9-m-wide, and 0.05-m-deep riffle and two curved side pools (3 m long, 0.9 m wide, and 0.5 m deep) connected to it. The channel received Cultus Lake water and its temperature was maintained at 13°C. Pool water velocity was 1 $cm \cdot s^{-1}$, and riffle water velocity was 20 $cm \cdot s^{-1}$. A dense FWD bundle (of the type described earlier) was randomly assigned to one of the two pools at the beginning of each trial. Groups of 24 fish, either all hatchery or all wild in origin, were released into the pools (12 in each one) at the beginning of each trial and their final distribution recorded 72 h later. Every evening, from 7 to 9 p.m., 5 g of shrimp was delivered into each pool by means of automatic feeders. Ten replicates were obtained, five with each fish type, between August 9 and September 15.

The numbers of wild and hatchery fish found in each habitat type at the end of this experiment's trials were compared using a t test ($p = 0.05$), and no difference in pool choice was observed between these two types of fish in the artificial channel ($t = 1.45$, df = 8, $p = 0.176$).

Data analyses common to all experiments

All statistical analyses were carried out using SAS systems software (SAS Institute Inc. 1988).

In all experiments, except the control comparison between hatchery and wild fish, data were expressed as proportions (number of fish present in individual pool/total number of fish present in the channel) to compensate for different fish densities in early and late summer trials and among experimental sites. The Shapiro and Wilk test (W) (Zar 1984) was used to test departures from normality. Whenever interactions between factors were significant, the means of one of the factors were compared separately for each level of the other factor using Tukey's studentized range test, which controls for Type I experimentwise error rate (Zar 1984).

Results

The Shapiro and Wilk test indicated that data were normally distributed in all cases, and therefore, no transformations were applied.

Fish immigration into Spring Creek's experimental section was negligible and all fish caught at the end of each trial were those that had been released at the beginning of those same trials. Only two unmarked fish were found in this section during any of the experimental or control trials. In Coghlan Creek, fish marks showed that by late summer, 68.7% of the fish were occupying the same creek sections were they had been found in early June (Site A = 61.5%, Site B = 73.5%, and Site C = 71.2%).

Experiment 1

Choice of pool by young coho salmon was not significantly affected by either FWD ($F = 0.48$, df = 2, $p = 0.626$) or food treatments ($F = 0.03$, df = 1, $p = 0.865$) in early summer. In contrast, the interaction between both treatments had a significant effect on the distribution of the fish ($F = 3.37$, df = 2, $p = 0.050$), suggesting that fish responded in a different manner to woody debris presence and density depending on whether food was abundant in the channel or not. Higher proportions of fish occupied pools without FWD than pools with dense FWD in trials with food treatment; but without food, higher proportions of fish preferred pools with dense FWD to clear pools. The proportion of juvenile coho salmon found in pools with sparse FWD was the same under both food treatments (Fig. 3A).

In the late summer trials, woody debris also had a significant effect on fish distribution (F = 4.21, df = 2, p = 0.037), whereas food did not seem to influence fish behaviour (F = 0.001, df = 1, p = 0.976). The interaction between debris and food also had a marginally significant effect on fish distribution (F = 3.46, df = 2, p = 0.051) (Fig. 3B), but with an inverse trend in the proportion of fish choosing pools with either no debris or with dense FWD depending on food treatment.

Albeit always influenced by food abundance, woody debris density had a stronger effect on fish distribution in late summer than in early summer (Tukey's studentized range test; early summer trials: pools without debris and pools with sparse FWD were grouped together and pools with dense FWD were classified by themselves; late summer trials: pools without debris formed their own group and pools with FWD debris, both sparse and dense, were grouped together). This difference, however, seemed quantitative rather than qualitative. The main distinction was that, independently of food treatment, there were lower proportions of fish in pools without woody debris in late summer than earlier in the season. Otherwise, fish distribution among pools in response to debris and food treatments followed similar trends in both early and late summer trials (Fig. 3).

Experiment 2

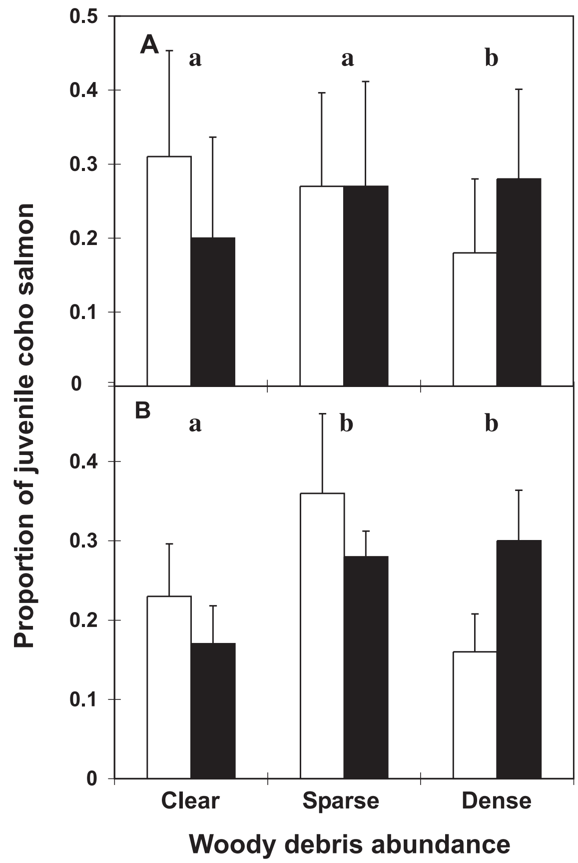
Combined data from all three Coghlan Creek sites for the months of June, July, and August showed that woody debris treatments had a significant effect on pool choice by juvenile coho salmon (F = 5.09, df = 3, p = 0.044). The interaction between debris and site was not significant (F = 1.08, df = 6, p = 0.424), indicating that fish response to debris treatments did not differ among experimental locations. The statistical model was expanded to include an estimate of the monthly replicate by woody debris interaction. This interaction was considered significant (F = 3.09, df = 6, p = 0.0514) and is supported by trends shown in Fig. 4.

Separate analyses by month showed changes in the effect of woody debris on fish pool selection. In June, debris did not affect fish distribution among pools (F = 0.81, df = 3, p = 0.525) whereas in July, it did have a significant effect on pool choice by fish (F = 13.72, df = 3, p = 0.002), with sparse FWD treated pools attracting a higher proportion of fish than the other pools (Tukey's studentized range test) (Fig. 4). In August, the effect of debris on fish distribution was also significant (F = 8.67, df = 3, p = 0.007) and fish were equally attracted to pools with sparse debris density regardless of debris type (Tukey's studentized range test combined sparse FWD and sparse LWD in one group and placed dense FWD and pools with no cover in another group) (Fig. 4).

Experiment 3

In this experiment, both food (F = 21.82, df = 1, p < 0.001) and the interaction between food and FWD (F = 5.19, df = 1, p = 0.049) had a strong effect on the distribution of juvenile coho salmon among pools. In contrast, FWD did not influence pool choice (F = 1.14, df = 1, p = 0.311). High proportions of young coho salmon were found in pools with food and low proportions in pools without food (Fig. 5), where Tukey's studentized range tests confirmed the difference between food and no-food treatments by classifying them separately. These results indicate that juvenile coho salmon responded primarily to food and that woody debris altered such response.

Fig. 3. Proportional distribution of Spring Creek coho salmon fry among channel pools receiving one of the following treatments: sparse FWD, dense FWD, or no woody debris. Channel treatments were food (open bars) or no food (solid bars) in (A) early summer and (B) late summer. Bars represent mean values and vertical lines represent 2 SE. Treatments with the same lowercase letters were classified in the same group with Tukey's test (α = 0.05).



Discussion

In suburban and rural streams, the summer distribution of juvenile coho salmon in salmon-bearing reaches is primarily governed by the abundance of food and their distribution among pools, by the presence and density of instream woody debris, and by hydrological features such as small waterfalls. Pool foraging quality affects not only the number of juvenile coho salmon that occupy a pool, but also the response of those fish towards instream debris. In a food-rich environment, the association between coho salmon and instream woody debris is low in May and June but increases as the summer progresses. In mid- to late summer, the presence of low to medium densities of woody debris (either

Fig. 4. Proportional distribution of Coghlan Creek coho salmon fry among pools that received one of the following treatments: no cover, sparse LWD, sparse FWD, or dense FWD. Bars represent mean values for three different experimental sites and vertical lines indicate 2 SE. Open bars, June; solid bars, July; stippled bars, August. Within each month, treatments with the same lowercase letters were classified in the same group with Tukey's test (α = 0.05).

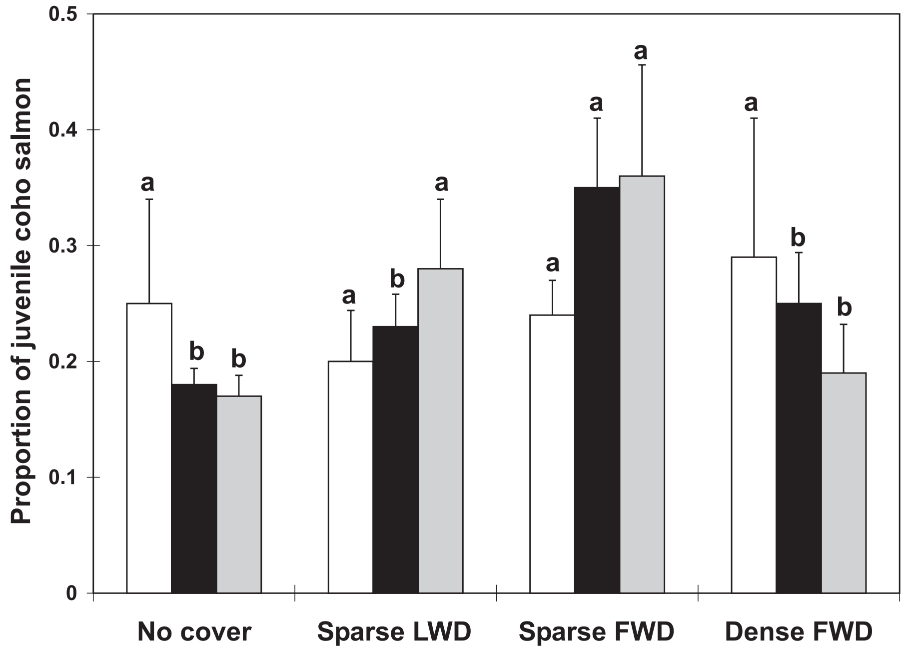
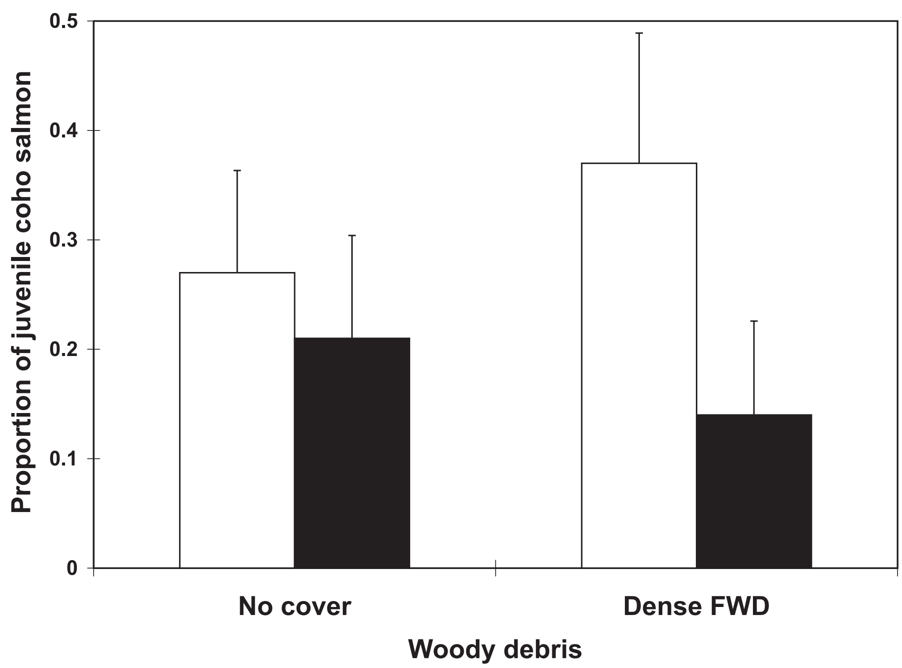


Fig. 5. Proportional distribution of Spring Creek coho salmon fry among pools receiving one of the following treatments: no cover and food, cover and food, no cover and no food, and cover and no food. Bars represent mean values and vertical lines represent 2 SE. Open bars, food; solid bars, no food.



large or fine) enhances the quality of stream pools as nursery habitat.

Food abundance alters the response of juvenile coho salmon to woody debris density, and this response changes over the summer months. Although fish responded to the presence of woody debris in different manners depending on food availability, pools with intermediate debris densities were chosen by relatively high proportions of individuals in most trials. Instead of always choosing pools with the highest density of debris to minimize predation risk, when food was abundant, most fish selected pools with either sparse FWD or no debris at all. This suggests that the young fish, when given the chance, tried to maximize their food intake rather than balance foraging opportunity with cover use. Gilliam and Fraser (1987) observed similar behaviour in creek chub (*Semotilus atromaculatus*) that spent a decreasing amount of time in a predation refuge (without food) as the food level increased in the unprotected environment. In the case of visual feeders, like coho salmon and other salmonids, it is likely that underwater structures may have a negative impact on their foraging efficiency that is strong enough to cause what appears to be risk-prone behaviour (Ware 1973).

The fact that in trials without food addition, the proportion of juvenile coho salmon found in pools with dense FWD was higher, largely at the expense of pools with no cover, further supports the idea that fish display risk-prone behaviour as long as it pays off (i.e., with higher food intake rate). Fish response to woody debris did not change markedly over time in the absence of food treatment. Most fish preferred pools with sparse or dense cover, both in early and in late summer. However, when food was added to the pools, fish response to FWD changed. In early summer, the young coho salmon preferred pools with sparse or no FWD, whereas in late summer, the majority of fish chose pools that offered sparse FWD. This difference in fish behaviour between May and August trials in Spring Creek could have been caused, at least in part, by the different length of holding channel residence experienced by the fish used in these trials. However, it is important to point out that wild fish in food-rich Coghlan Creek also showed an increased preference over time for pools with sparse woody debris, at the expense of pools without debris.

Woody debris type may influence fish pool selection. Juvenile coho salmon distributions in the experimental sites of Coghlan Creek were not affected by either debris density or debris type in June (early summer), but they were in July and August, when the young fish showed a preference for pools with sparse debris. In July, pools with sparse FWD attracted a greater number of fish than pools with sparse LWD, dense FWD, or no debris. By August, however, the fish did not seem to discriminate between debris types (fine versus large) as long as the pools offered both large open foraging areas and a low density of structures. Reasons for the brief preference for fine brushy cover over LWD are not immediately apparent but could have resulted from the experimental setup. For example, differences in invertebrate availability among microhabitats may have been induced by the type of debris.

Despite differences in fish origin (hatchery versus wild), stream productivity, and experimental setups, the observed distributions of fish among pools in response to woody debris treatment and their changes over time followed similar patterns in both creeks. The control test results also indicated comparable habitat preferences between fish from the two stocks used in this study.

The presence of food rather than cover seemed to be the preeminent factor determining juvenile coho salmon habitat preference. However, woody debris availability altered fish response to food. It is possible that woody debris affected the spatial distribution of coho salmon by hindering their ability to detect food (Giannico and Healey 1999), reducing aggressive interactions among competitors (Chapman 1962; Fausch 1993), and providing various risk–reward conditions (Dill and Fraser 1984).

Food predominance over cover in determining suitable salmonid nursery habitat has already been observed in other species. For example, Wilzbach (1985) found that food abundance was more important than cover in determining the abundance and microhabitat distribution of adult cutthroat trout in laboratory channels. This could explain why almost 70% of the coho salmon chose pools with food treatment. Among them, a slight majority preferred pools that also offered cover. The possibility that sparse cover would have been strongly preferred, as was observed in other experiments, also exists. Thirty percent of the fish occupied pools with scarce food for a variety of possible reasons (e.g., inadequate habitat sampling, displacement from more favourable sites by dominant individuals, avoidance of competition, and even the possibility that some shrimp could have drifted among pools, increasing the actual foraging value of the pools that did not receive food treatment). The fact that two thirds of these fish were in pools without cover suggests that many individuals gave priority to prey detection over predation-risk reduction (Reinhardt and Healey 1997). As Dill and Fraser (1984) observed, hungry coho salmon are prepared to take more risk and to continue foraging even when predators are sighted.

In the absence of food and debris, high proportions of fish moved into the upstream-end pool of each Spring Creek experimental channel. Such preference for pools with waterfalls could be attributed to (*i*) the cover generated by water turbulence and (or) (*ii*) the availability of fast-moving waters next to slow-moving waters, which offer the combination of foraging and resting patches that juvenile coho salmon seem to prefer (Fausch 1993).

These results may explain, at least in part, the conflicting reports in the literature about use of cover by coho salmon. Studies conducted in spring and early summer (Bugert and Bjornn 1991; Bugert et al. 1991; Spalding et al. 1995) did not find a preference for cover whereas those conducted later in the summer did (Dolloff 1986; Dolloff and Reeves 1990; Shirvell 1990). It is possible that this change in cover use over time can be induced, at least in part, by predation risk. Several studies have shown that juvenile coho salmon increase their use of cover after exposure to predation (Dill and Fraser 1984; Grand and Dill 1997; Reinhardt and Healey 1997). Furthermore, predation risk does not seem to elicit the same response in all individuals. Reinhardt and Healey (1997) observed that in the absence of predation, juvenile coho salmon distributed independently of cover, but after being exposured to a real or simulated predator, some individuals increased their use of cover whereas others changed their foraging strategies and moved away from bundles of FWD. In their study, the larger (presumably dominant) fish were more likely to seek cover (risk averse) in the presence of a predator; this created feeding opportunities in open areas for the smaller individuals that seemed prepared to risk exposure to predation. In this study, fish were exposed to wild predators in both the outdoor holding channel and the experimental stream sections. Therefore, it is possible that as size difference among individuals increased over the summer, different foraging strategies developed under predation risk, causing the observed seasonal changes in cover use. Unfortunately, this hypothesis could not be tested because neither the size nor the response to cover of individual fish was recorded in this study.

Increased preference for pools with woody debris is a behavioural change associated with the habitat shift that juvenile coho salmon undertake with the first fall freshets (Sandercock 1991). As water temperature falls below 4.5°C, the level of activity of coho salmon decreases markedly and they move closer to objects providing cover (Bustard and Narver 1975). By late August or early September, however, neither water flow nor water temperature had begun changing significantly to support the idea that fish had started to seek winter habitat in response to such environmental clues. If late summer reduction in invertebrates is what increases fish use of cover in preparation for less favourable winter conditions, only coho salmon in Coghlan Creek should have shown such behaviour. Fish response to woody debris in Spring Creek increased towards late summer, despite the fact that they were receiving the same food supplement as in early summer. The only environmental factor that changed in both experiments between early and late summer trials was the photoperiod, and it is possible that shorter days may increase fish association with cover in preparation for winter conditions (Bustard and Narver 1975). In addition, the larger body size of fish by the end of summer could account for increased risk aversion (Reinhardt and Healey 1997) and preference for pools with woody debris.

In many agricultural and suburban streams, where the natural supply of woody debris is limited, it is common practice to enhance salmonid habitat by adding LWD. When planning such projects, it is important to consider that high densities of woody debris in the stream channel can negatively affect juvenile coho salmon abundance just as its absence can. This study indicates that open foraging areas interspersed with woody debris (LWD and FWD) and small hydrological structures (waterfalls) characterize the summer habitat that juvenile coho salmon prefer. The artificial placement of woody debris may only increase salmonid densities in the treated sections due to fish immigration from other sections (Riley and Fausch 1995) and locally enhanced carrying capacity (Culp et al. 1996) but may not affect the size of the population in the entire stream during summer. However, fish winter survival, and therefore smolt production, may increase as a result of increased availabilty of instream woody debris (Quinn and Peterson 1996).

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