Juvenile coho salmon (*Oncorhynchus kisutch*) responses to salmon carcasses and in-stream wood manipulations during winter and spring

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**Abstract:** We investigated the growth rate, winter survival, presmolt size, and emigration timing of juvenile coho salmon (*Oncorhynchus kisutch*) in response to salmon carcasses and in-stream wood. Experimental trials were conducted during two consecutive years and pre-winter fish size and densities differed between years. Sixteen pens with emigration traps were built in a side-channel of the Mamquam River, British Columbia. Pens were randomly assigned salmon carcasses, in-stream wood, both carcasses and in-stream wood, or neither (control). Our first trial was conducted between December 1996 and August 1997 and the second between December 1997 and August 1998. Initial rearing densities and average individual body mass were 3.1 fish·m⁻² and 2.4 g, respectively, in the first trial and were 1.6 fish·m⁻² and 6.6 g, respectively, in the second trial. Results were influenced by both fish initial size and density. During the first trial (smaller-sized fish at high densities), salmon carcasses increased fish growth rates and presmolt size. Winter survival did not increase in response to any treatment; however, a pre-winter size-related survival pattern was observed during the first trial. During the second trial, (larger-sized fish at low densities), no treatment influenced fish growth rates or presmolt size but all treatments augmented fish survival.

**Introduction**

Juvenile coho salmon (*Oncorhynchus kisutch*) smolt output is largely dependent on winter nursery habitat. The availability of this type of habitat can constitute a “bottleneck” to coho salmon smolt production (Mason 1976; Nickelson et al. 1992a; Solazzi et al. 2000). Slow-flowing waters, deep pools, off-channel areas (i.e., side-channels, backwaters, and ponds), and in-stream structures such as fallen logs, root wads, and boulders appear to be critical to the young of this species (Bustard and Narver 1975; Peterson 1982; Swales and Levings 1989).

In many watersheds of the Pacific Northwest, reduced spawning by anadromous fish seems to have affected aquatic,
and even terrestrial productivity (Cederholm et al. 1999; Gresh et al. 2000). The delivery of nutrients by spawning salmon to Washington, Oregon, Idaho, and California watersheds is presently at about 6%–7% of historical levels (Gresh et al. 2000). Even in southern British Columbia, large reductions in nutrient delivery by salmon have occurred (Larkin and Slaney 1997). Such important losses of subsidies of marine-derived nutrients (i.e., nitrogen and carbon) are deemed to decrease the capacity of many freshwater habitats to support juvenile salmon and other aquatic biota (Bilby et al. 1998). Therefore, stream salmon carcass placement is promoted by stream restoration organizations based on the assumption that it should help compensate for the effects of declining postspawning salmon carcass availability.

Most studies on the fate of salmon carcasses in streams have focused on the incorporation pathways of marine-derived nutrients by primary producers and benthic macroinvertebrates (Wipfli et al. 1998; Chaloner and Wipfli 2002). However, the response of juvenile salmonids to indirect nutrient uptake or direct carcass consumption has received limited attention. Bilby et al. (2001) looked at the indirect uptake of marine-derived nitrogen and found that this element increases in juvenile coho salmon muscle tissue in direct proportion to the abundance of salmon carcasses and reaches a peak at densities of approximately 0.15 kg of carcass per square metre of streambed. More recently, Heintz et al. (2004) found that salmon carcass availability led to increased lipid reserves in juvenile coho salmon.

The effects of direct consumption of salmon eggs and (or) carcasses on juvenile salmonids have been examined in only three studies. The earliest, by Bilby et al. (1998), found that carcass availability caused a significant boost in juvenile coho salmon densities, body weight, and condition factor. The two more recent studies, those of Wipfli et al. (2003, 2004), reported that salmon carcass addition caused a significant boost in the growth rates, body mass, and production of cutthroat trout (Oncorhynchus clarkii) and juvenile coho salmon. Increased growth rates and large late-fall body mass in juvenile salmonids can significantly raise their odds of surviving winter (Holthby 1988; Quinn and Peterson 1996). Considering that juvenile coho salmon continue feeding at low water temperatures (Bustard and Narver 1975; Giannico and Healey 1998) and can even gain weight under winter conditions (Peterson 1982), it is possible that salmon carcasses and eggs contribute to increasing fish winter survival and smolt output as long as the winter carrying capacity of the system is not limited by availability of refuge (Armstrong and Griffiths 2001).

Juvenile salmon body size and growth rates have a strong influence on smolting rates and emigration timing. Thorpe (1986) reported that juvenile Atlantic salmon (Salmo salar) need to reach a minimum critical size by winter to “afford” smolting the following spring and that smaller individuals remained in freshwater for an additional year. In turn, among smolting individuals, body size is one of the factors determining emigration timing. Larger coho salmon have been observed to emigrate up to several weeks before peak dates for smolt output in the Keogh River (Irvine and Ward 1989). Thus, salmon carcass availability may potentially increase the proportion of juvenile coho salmon that smolt at age 1+ and affect their emigration timing by increasing winter growth rates and fish body size.

In late fall and winter, when freshet intensity and frequency increase in coastal streams, in-stream wood (often termed large woody debris) becomes particularly important to the young fish by offering not only predation refuge (Doloff 1993) but also protection from elevated water velocities (Nickelson et al. 1992b; Cederholm et al. 1997). Thus, winter refuge availability and the tendency to avoid sharing it with other individuals observed in some wild juvenile salmonids (Cunjak 1988; Armstrong and Griffiths 2001) may help define the winter carrying capacity of a stream reach because fish that fail to find shelter are likely to emigrate or be removed by predators (Gregory and Griffith 1996). This explains the frequently observed lower densities of juvenile salmonids in pools with scarce in-stream wood than in wood-rich pools (Nickelson et al. 1992b; Cederholm et al. 1997; Roni and Quinn 2001). During the spawning season, in-stream wood also contributes to retaining salmon carcasses and preventing stream currents from flushing them downstream (Cederholm et al. 1989), thus increasing the influence of carcasses on the food web.

This study examined whether salmon carcass availability, when in-stream wood is abundant, affects juvenile coho salmon winter growth, winter survival, presmolt size, and emigration timing. It also looked at the relationship between early-winter fish body size and emigration. Our predictions (hypotheses) were as follows: (1) salmon carcasses cause a longer-lasting increase in winter daily growth rates of coho salmon parr when in-stream wood is present than when it is absent, (2) the combination of carcasses and in-stream wood significantly increases coho salmon parr winter survival, (3) the combination of carcasses and in-stream wood significantly increases coho salmon presmolt size, (4) the early-winter body size of survivors to spring is larger than that of nonsurvivors, (5) the early-winter body size of coho salmon parr that emigrate in spring (presmolts) is larger than that of individuals that remain in the channel through the summer (residual fish), and (6) carcasses and in-stream wood significantly augment the proportion of early emigrants (by increasing fish body size).

Materials and methods

Study site

We carried out experiments in an artificial side-channel of the lower reaches of the Mamquam River, a tributary to the Squamish River, draining into Howe Sound in southwestern British Columbia (Fig. 1). The Upper Mamquam side-channel is 360 m long and runs parallel to the river. It was constructed in the 1980s as a spawning area for adult coho and chum salmon (Oncorhynchus keta); however, juveniles of both species occupy it for very different periods of time. Chum salmon fry are only present in the side-channel during a few days in late February and early March, whereas juvenile coho salmon are found in it throughout the year. Steelhead/rainbow trout (Oncorhynchus mykiss), cutthroat trout, Dolly Varden (Salvelinus malma), sculpins (Cottus spp.), and suckers (Catostomus spp.) are also present but in very low abundance (e.g., only one to four individuals of each species were captured while surveying the channel).
The Upper Mamquam side-channel has little or no gradient (0.005), and the fluvial deposits that were exposed during its excavation constitute its gravel substrate (average grain size 0.042 m). The channel’s banks are armored with boulders (i.e., rip-rap), 0.30–0.50 m in diameter, to approximately 0.50 m above the water level. The channel has an average width of 6.2 m and depth of 0.53 m. It only connects to the river through its downstream end, while its upstream end is closed and has a circular pond 12.5 m in diameter and a maximum depth of 1.75 m. A mix of groundwater and river water reaches the Upper Mamquam side-channel as subsurface flow and raises its winter water temperatures slightly above those in the adjacent river (Upper Mamquam December–March water temperature: mean = 3.36 °C, SD = 0.79 °C, and range = 2.33–3.88 °C in 1996–1997 and mean = 3.92 °C, SD = 0.63 °C, and range = 3.00–4.71 °C in 1997–1998; adjacent mainstem river December–March water temperature: mean = 2.31 °C, SD = 1.01 °C, and range = 1.56–4.02 °C in 1996–1997 and mean = 2.75 °C, SD = 0.93 °C, and range = 2.10–5.82 °C in 1997–1998). Water discharge in the Upper Mamquam side-channel was constant and ranged from 0.07 m$^3$s$^{-1}$ in summer to 0.11 m$^3$s$^{-1}$ in winter between 1996 and 1998. Water samples (three replicates each time) were taken in December, March, and June of each year. Nitrate concentrations averaged 0.466 ppm (SE = 0.005) and orthophosphate concentrations averaged 0.054 ppm (SE = 0.001).

We selected the top 100 m of the side-channel, downstream from the pond, for our experimental manipulations and closed it off with a transverse fence at the upstream end to prevent any fish in the pond from entering this section. The fence, which spanned the width of the channel, consisted of three 1 m × 3 m panels of galvanized hardware-cloth (2 mm mesh) framed with 0.05 m × 0.10 m × 3 m wooden boards. A 0.4 m wide clear plastic “skirt” was stapled along the bottom board of each fence panel. The panels were placed vertically with their bottom edges buried 0.20 m deep in the substrate, and their plastic skirts were spread underneath the gravel to prevent fish movement. All fish found in the experimental section were removed by means of a combination of repeated pole seining and electrofishing.

The pens were built with the same type of fence panels described above and arranged in eight pairs ($n = 16$) along the side-channel’s experimental section. Each pair of pens
was delimited by an upper and a lower fence running perpendicular to the banks of the channel parallel to each other and 6 m apart. These fences, which spanned the entire channel width, enclosed an area that was subsequently divided into two equal 3 m wide halves by means of a longitudinal midchannel fence. Thus, seen from above, the resulting fence configuration for each pair of pens resembled a letter “H” (Fig. 2). Each pair of pens was separated from the next one immediately downstream by a 6 m long “buffer” zone. As in the upstream fence, the pen panels were placed with their bottom edges buried 0.20 m deep in the substrate, and their 0.40 m wide clear plastic skirts were spread underneath the gravel in a downstream direction. Any spaces between the end of the cross-channel fences and the channel banks were sealed using hardware-cloth and geotextile material (Amoco® 1199).

Each pen had one downstream passageway that allowed fish to leave the pen and reach an “emigration” trap (Rubbermaid® container: 0.84 m long × 0.40 m wide × 0.45 m high). The mouth of this passageway was a clear plastic funnel glued with silicone by its broadest end (0.20 m diameter) to a similar-sized opening in the mesh of the fence. In turn, the funnel was connected to a 2 m long plastic pipe (0.08 m inner diameter), which led fish into the emigration trap. The end of the pipe, inside the trap, was fitted with a “one-way exit door” shaped like a cone made of three triangular clear acetate sheets (Fig. 2). This kind of conical fixture operated like a one-way valve that let fish into the trap but, once in the trap, did not allow them to return to the pen. To minimize the attractiveness of the outlet structures as predation shelters, both the funnel and the plastic pipe were of translucent plastic. The emigration traps were placed in the buffer zones between pen pairs (Fig. 2).

Experimental manipulations

We randomly assigned salmon carcasses or in-stream wood to four pens each (for a total of eight). The combination treatment (carcasses and in-stream wood) was randomly assigned to another four pens, and the remaining four pens did not receive any treatment and served as control. Pens treated with in-stream wood received a bundle made of a single red alder (Alnus rubra) log (0.30 m in diameter and 3.0 m long) covered with 40 alder twigs (0.03–0.06 m thick and 2.0–3.0 m long) and 10 western redcedar (Thuja plicata) branches (0.02–0.04 m thick and 1.5 m long). Those treated with carcasses received one chum salmon carcass per pen. Carcasses were cut into 0.10 m × 0.20 m pieces to keep bald eagles (Haliaeetus leucocephalus) from taking them and prevent juvenile coho salmon from using them as cover. All carcasses were collected from the lower portion of the side-channel, where wild chum salmon spawned between late November and early January and coho salmon between December and late January. The day before beginning the experiment, one large chum carcass (mean wet mass = 10 kg, SE = 019 kg) was placed into the appropriate pens. This represented a carcass wet mass of approximately 0.56 kg·m−2 per pen, which is equivalent to that used by Bilby et al. (1998) in one of their experimental streams and mimics the average carcass mass per streambed area observed elsewhere in the side-channel. Additional carcasses were stored in a freezer for later use. Carcasses were available for approximately 8 weeks in the side-channel; this was in part due to the relatively slow decomposition of carcasses under low temperatures but also to the arrival of late spawners whose carcasses lasted in some cases until early March. To match the natural availability of carcass remnants elsewhere in the channel, half a chum salmon carcass was added to the appropriate pens 1 month after the trials had begun.

Although not tested in a direct manner, we assessed the influence of early-winter average fish size and rearing densities on fish response to our treatments by running our trials over two consecutive years. During the first year, juvenile coho salmon were relatively small and reared at high densities, whereas in the second year, they were approximately three times larger and almost half as abundant.

Juvenile coho salmon captured with a pole seine in the lower section of the side-channel were used in this study. Once captured, fish were kept overnight in a holding pen that was partially submerged in the channel. The following day, captured fish were transported to a nearby hatchery for...
individual marking. Fish were rendered unconscious with CO₂ (dissolving one teaspoon of Bromoseltzer® in 4 L of water), weighed to the nearest 0.01 g, measured to the nearest 0.1 mm fork length, and individually marked using a modified high-pressure inoculation gun (Biomark Ltd.) that injected dye into the fins. The combination of four different fluorescent colours of dye and three fins (i.e., dorsal, caudal, and anal) made individual marking of fish possible. Fish were randomly assigned to the experimental pens before receiving their unique marks. Once marked, fish were held overnight in 16 small holding tanks (one for each pen) at the hatchery. The following day, they were examined to make sure marks were still visible and re-marked if necessary. Only 2%–3% of the fish needed to be re-marked. Afterwards, fish were transported in separate buckets to the side-channel and released into the pens.

The mark–recapture method and Petersen’s mark–recapture equation (Krebs 1989) were used to estimate juvenile coho salmon densities (and their 95% confidence limits) 50 m downstream of the pen locations. The area was blocked off with a pair of nets, and then, 10 minnow traps (6 mm mesh) baited with salmon roe were soaked overnight for two consecutive nights for the capture and recapture, respectively. Fish trapped during the first session had half of one pelvic fin clipped. Juvenile coho densities in the side-channel were 3.10 fish·m⁻² (95% confidence limits = 2.51 and 3.69) in December 1996 and 1.56 fish·m⁻² (95% confidence limits = 1.42 and 1.70) in December 1997. These natural densities were replicated in our experiments by releasing 55 fish in each pen on 23 December 1996 and 28 fish in each pen on 24 December 1997. Initial fish biomass per unit of area was lower at the beginning of the “high-density” 1996–1997 trial (7.41 g·m⁻²) than at the beginning of the “lower-density” 1997–1998 trial (10.35 g·m⁻²). This was due to the smaller initial size of coho in December 1996 (mean mass = 2.39 g, SE = 0.05 g, mean fork length = 5.1 cm, SE = 0.07 cm) than in December 1997 (mean mass = 6.64 g, SE = 0.15 g, mean fork length = 7.6 cm, SE = 0.05 cm).

After being released in the pens, fish were given 1 week to acclimatize to the conditions of the pens before the outlets were opened to allow “emigration”. General fish activity level and movement were recorded during 32 min long morning and afternoon observations (2 min per pen) carried out from the channel banks on the days the emigration traps were examined. We made the following three assumptions: (i) the persistence of high levels of fish activity and exploratory behaviour at low winter temperatures after 1 week of acclimatization was an indicator of unfavourable conditions in the experimental pens, (ii) individuals that were active and explored their surroundings could find the passageways to the emigration traps relatively easily, and (iii) the 2 m long emigration pipes, made of translucent plastic, did not offer fish protection from predation and constituted unsuitable zones for residency. Thus, one would expect that only true emigrants would be enticed to explore such areas and reach exits with one-way valves leading them into traps (Matter et al. 1989). Therefore, more fish should “emigrate” from pens lacking adequate cover and food than from those with in-stream wood and (or) salmon carcasses.

The downstream movement of juvenile coho salmon into the emigration traps was monitored three times a week from January to June. These fish were removed from the traps, identified by their marks, weighed to the nearest 0.01 g, measured to the nearest 0.1 mm fork length, and released in the side-channel downstream of our experimental section. Fish that entered the emigration traps between January and March were considered winter emigrants and those trapped between April and June spring emigrants. Fish that had not moved into the emigration traps by the end of June were considered summer residual individuals and were removed from the pens using minnow traps and electrofishing between July and mid-August. This allowed us to account for all surviving coho salmon that had not left the pens by the end of June, when movement into the traps ceased. Fish mortality of those individuals not accounted for was attributed to predation because the pens did not exclude avian or mammalian predators.

Growth of juvenile coho during the trials was examined in terms of changes in weight (mass gain) and in fork length. We calculated the percent daily (or instantaneous) growth rate for each fish as

\[
\begin{align*}
(1) & \quad \left( \log_e W_2 - \log_e W_1 \right) / t_2 - t_1 \times 100 \\
(2) & \quad \left( \log_e L_2 - \log_e L_1 \right) / t_2 - t_1 \times 100
\end{align*}
\]

where \( W_1 \) is the initial weight (g) and \( L_1 \) is the initial fork length (cm) when released into the experimental pens and \( W_2 \) is the final weight and \( L_2 \) is the final fork length at time of entering the emigration traps or when removed from the pens at the end of trials. The formulas’ denominators, \( t_2 - t_1 \), are the numbers of days between the releases and recaptures of fish (Ricker 1975).

**Statistical analyses**

Because fish size, fish stocking densities, and side-channel water temperatures differed between the winter of 1996–1997 and the winter of 1997–1998, data for these two trials were analyzed separately. We used an \( \alpha \) value of 0.05 in all tests and SAS systems software (SAS Institute Inc. 1988) for all of our analyses. We utilized normal probability plots of the residuals (also known as q-q-norm plots) (Kuehl 2000) derived from ANOVAs to examine departures from normality. Residual versus fit plots were used to determine whether our data met the assumption of homogeneity of variance. Before testing our various hypotheses, we investigated possible differences in the initial body mass and length of fish among the 16 pens using one-way ANOVAs with the 16 pens as the factor.

The first prediction was tested using three-way mixed-model ANOVAs, with pens also randomly nested within treatments, and season as the third factor. The response variable in this case was daily growth rate. When using mixed models, the expectations of the mean squares may show that the F statistics cannot be formed directly with the use of mean squares; in such cases, approximate F statistics were calculated. This caused the degrees of freedom associated with each mean square to be approximate and thus took on fractional values. The term “approximate F” is used because under these conditions, the underlying \( F_0 \) distribution is approximated (Kuehl 2000).

One-way general linear model ANOVAs, with the treatments carcass, wood, carcass plus wood, and control as four levels of a single factor, were used to test our second predic-
tion. In this case, the response variable was total number of survivors. To test our third prediction, we used two-way mixed-model ANOVAs, with pens nested as a random effect within treatments, and final size (body mass or fork length) of presmolt s as the response variable. Two-way general linear model ANOVAs were used to test our fourth prediction (factors survival status and pen, and response variable initial mass or fork length). Pen was used as the second factor in these two-way analyses to detect potential effects of individual pens on fish responses. Two-way general linear model ANOVAs were also used to test our fifth prediction (factors season of emigration and pen, and response variable initial mass or fork length), with pen as the second factor. Finally, three-way mixed-model ANOVAs, with repeated measures for winter, spring, and summer, were used to test our sixth prediction. The four factors were carcass (fixed), wood (fixed), season (fixed), and pen (random and nested within carcass and wood). The response variable was number of emigrants per season.

Results

The normal probability plots of the residuals indicated that our fork length data were normally distributed and did not need to be transformed. However, the fish mass data showed a positively skewed distribution and were logarithmically transformed before being used in any of our statistical analyses. The residual versus fit plots revealed that our data met the homogeneity of variance assumption. No significant differences were observed among the 16 experimental pens in either of the trials with regard to initial fish body mass (1996–1997 trial: \( F_{[15]} = 1.23, p = 0.239 \); 1997–1998 trial: \( F_{[15]} = 1.57, p = 0.084 \)) or initial fish fork length (1996–1997 trial: \( F_{[15]} = 1.50, p = 0.100 \); 1997–1998 trial: \( F_{[15]} = 1.45, p = 0.122 \)), thus confirming that all pens received groups of fish with equivalent initial mean sizes.

First prediction

A statistically significant “treatment and season” interaction effect was detected on fish daily growth rates during the first trial (Table 1). Specific contrasts showed that treatment effects on fish daily growth rates changed from one season to the next. For example, winter daily gain in body mass increased in response to both wood and carcasses combined and salmon carcasses alone (\( t_{[474]} = 2.22, p = 0.027 \) and \( t_{[474]} = 2.35, p = 0.019 \), respectively). In the spring, only the combination of wood and carcasses increased growth rates in body mass in a significant manner (\( t_{[474]} = -2.56, p = 0.011 \)). The results for daily growth rates in fork length showed the same patterns. In contrast, the daily growth rates of residual fish were not influenced by any of our treatments. During the second-year trial, which involved relatively larger fish, we failed to reject the null hypothesis regarding treatment effect on daily growth rates (Table 1). Only “season” had a statistically significant effect on fish growth rates (body mass: \( F_{[2]} = 38.22, p < 0.001 \); fork length: \( F_{[2]} = 17.82, p < 0.001 \)), and specific contrasts revealed that growth rates increased between winter and spring regardless of treatment (body mass: \( F_{[1]} = 59.07, p < 0.001 \); fork length: \( F_{[1]} = 26.07, p < 0.001 \)).

Second prediction

In the first trial, none of the treatments had a significant effect on fish survival, although fish had low body masses and occurred at high densities (Table 1). The percentage of fish that survived during this first trial ranged from a minimum average of 51% in control pens to a maximum average of 62% in pens with wood plus carcasses (Fig. 3a). However, in the second trial, when fish had high body masses and were at low densities, statistically significant differences among treatments were found (Table 1). Specific contrasts of the ANOVAs showed that the availability of salmon carcasses (\( t_{[1]} = -2.50, p = 0.028 \)), wood (\( t_{[1]} = -2.40, p = 0.033 \)) or the combination of carcasses and wood (\( t_{[1]} = -3.55, p = 0.004 \)) significantly increased fish survival during the second-year trial. Percent fish survival in pens receiving these two treatments combined was 59%, in those receiving only carcasses was 50%, and in those with only wood was 49%, while in control pens, it was 27% (Fig. 3b).

Third prediction

When early-winter juvenile coho salmon size was relatively small, during the first trial, we found a statistically significant treatment effect on both the final body mass and the length of presmolt s (Table 1). The specific contrasts of least square means revealed that the combination of carcasses and in-stream wood was responsible for these differences (body mass: \( t_{[12]} = -3.88, p = 0.002 \); fork length: \( t_{[12]} = -3.46, p = 0.005 \) (Fig. 4a). However, during the second trial, there were no statistically significant differences in the final body size of fish among treatments (Table 1) (Fig. 4b).

Fourth prediction

In the first trial, statistically significant differences in early-winter body size were detected between fish that survived winter and those that were presumed dead (Table 1). Winter survivors were heavier in December than fish that were not recaptured again and presumed dead (mean body mass = 2.65 g, SE = 0.07 g, mean fork length = 6.24 cm, SE = 0.05 cm and mean body mass = 2.06 g, SE = 0.04 g, mean fork length = 5.71 cm, SE = 0.07 cm, respectively). In the second trial, juvenile coho salmon were in general heavier at the start of the experiment than those tested the previous year (survivors mean body mass = 6.65 g, SE = 0.213 g, mean fork length = 7.58 cm, SE = 0.077 cm; dead or missing fish mean body mass = 6.64 g, SE = 0.216 g, mean fork length = 7.62 cm, SE = 0.068 cm), and in this case, no significant size differences were found in December between survivors and nonsurvivors (Table 1).

Fifth prediction

The early-winter size of emigrating presmolt s was significantly larger than that of residual individuals in the first trial (Table 1). The December mean body mass of spring emigrants was 2.74 g (SE = 0.083 g) and their mean fork length was 6.34 cm (SE = 0.059 cm), whereas the December mean body mass and fork length of the residual fish were 1.72 g (SE = 0.125 g) and 5.46 cm (SE = 0.106 cm), respectively. Because by the end of the second trial, residual fish remained only in a few pens, a t test on the December weight of spring emigrants versus residual fish was used to test the
fifth hypothesis instead of a two-way ANOVA. This test showed that during the second year, the slight difference in December size between emigrating presmolts and summer residual fish was not statistically significant (Table 1). The mean December body mass of presmolts was 6.46 g (SE = 0.231 g) and their mean fork length was 7.55 cm (SE = 0.080 cm), while the mean December body mass of residual

**Table 1.** Results of ANOVA and *t* tests.

<table>
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<tr>
<th>Prediction</th>
<th>Variable</th>
<th>Trial</th>
<th>df</th>
<th><em>F</em></th>
<th><em>t</em></th>
<th><em>p</em> (power of test)</th>
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<tr>
<td>1</td>
<td>Growth (mass)</td>
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<td>6</td>
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<td>Growth (mass)</td>
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<td>3</td>
<td>0.28*</td>
<td>—</td>
<td>0.838 (0.05)</td>
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<td>No. of survivors</td>
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<td></td>
<td>No. of survivors</td>
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<td>3</td>
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<td>3</td>
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<td>0.40*</td>
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<td>Final size (length)</td>
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<td>3</td>
<td>0.51*</td>
<td>—</td>
<td>0.685 (0.05)</td>
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<td>Initial length</td>
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<td>0.15</td>
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<td>0.702 (0.05)</td>
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<td>1</td>
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<td>—</td>
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</tr>
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<td>1</td>
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<tr>
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<td>0.45</td>
<td>0.652 (0.05)</td>
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<tr>
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<td>Emigrants per season</td>
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<td>2</td>
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<td>2</td>
<td>38.07</td>
<td>—</td>
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</tbody>
</table>

Note: Trial 1, 1996–1997; trial 2, 1997–1998. An asterisk indicates an approximate *F* value. The power of tests is provided only for tests that failed to reject the null hypothesis.

**Fig. 3.** Percentage of juvenile coho salmon in experimental pens that survived winter. The total percentage of survivors includes both spring emigrants and summer residual fish. (a) First trial; (b) second trial. Vertical error bars represent 2 SE. W + C, pens with wood plus carcass treatment.

**Fig. 4.** Final weight of spring emigrant and residual juvenile coho salmon from experimental pens. (a) First trial; (b) second trial. Vertical error bars represent 2 SE. W + C, pens with wood plus carcass treatment. Dissimilar scales on the vertical axes reflect interannual differences in fish size.
that these numbers were not affected by any of the pen treatments. Fish movement was limited during winter – early spring (January–April), and few juvenile coho salmon entered the emigration traps during that period (Fig. 5a). Emigration peaked between May and June (spring). No fish left the pens during July and August. The summer “residual” fish, which had to be removed by the end of August, represented approximately 8% of the initial number of fish that were released in the pens at the beginning of the trial. This was the only case in which the results of the second trial did not differ from those in the previous year. However, although season had a significant effect on number of emigrants (Fig. 5) and shows that these numbers were not affected by any of the pen treatments. The greater growth observed in pens that only received salmon carcasses, fish daily growth rates, although initially high, dropped once the carcasses were no longer available. The greater growth observed in pens that received the combined wood and carcass treatment suggests that the presence of in-stream cover somehow reduces fish energetic costs and thus enhances growth rates during late winter and early spring. This could be due to reductions in either predation pressure (Reinhardt and Healey 1999) or aggressive interactions among the young fish (Giannico and Healey 1999; Völlestad and Quinn 2003) or both. In-stream wood could not have played an important velocity shelter role in this study because water flow in the side-channel was very low.

None of our results support the second prediction that the combination of carcasses and in-stream wood would increase over-winter fish survival. However, there were important inter-annual differences in our findings. While during the 1996–1997 trial, none of the treatments (i.e., carcasses, in-stream wood, and carcasses and wood combined) had an effect on coho salmon parr over-winter survival rates, all of the treatments, not just carcasses plus wood, increased fish overwinter survival during the 1997–1998 trial. Having dissimilar fish sizes and densities between trials caused different responses to our treatments, and the combination of both small body mass and high densities in early winter seemed to have an overriding effect over other factors in terms of survival rates.

Our third prediction regarding salmon carcasses and in-stream wood increasing coho salmon presmolt size was also only confirmed during our first year trial, when fish were relatively small and densities high. However, the results of our second trial show that the final-size response of juvenile coho salmon to treatments was influenced by their early-winter size and rearing densities. Hence, when the average fish size was relatively large and densities high, none of the treatments affected presmolt size. Treatment effect may have been more difficult to detect in this trial because any spring growth spurt (percent mass gained per day) that took place was proportionately smaller in these large fish than in the small fish of the first trial.

We had anticipated, in our fourth prediction, a positive relationship between early-winter fish body size and survival, and this was observed during the first trial, in which the smallest individuals in that relatively small body size-class died in greater proportion than their larger counterparts regardless of treatment. Interference competition (Sutherland 1983) for resources (including space) under the crowded condition of the first trial may have exacerbated size-related mortality in all pens to a point where no treatment effect
could be detected. Conversely, during the second trial, with large coho salmon parr at low densities, no size-related mortality was detected, as all treatments increased the percentage of fish that survived winter.

Relationships between juvenile salmonid pre-winter size and winter survival are complex in nature and therefore not simple to predict. Results not only change with fish rearing densities but also respond to a range of other factors (both biotic and abiotic) that influence the intensity of selection pressures during the least favourable of all seasons. For example, Quinn and Peterson (1996) found that during a low-survival year, juvenile coho salmon that were larger than average by October had greater probability of surviving to smolt stage, and this was independent of habitat quality. This result contrasted sharply with the independence that they observed between fish fall size and winter survival during a subsequent high-survival year, when even fish from the smallest size-classes fared well. Quinn and Peterson (1996) did not mention differences in fish rearing densities and suggested that the higher winter discharge during the first year of their study may have accounted for some of the inter-annual variation they observed. Water temperature seems to have been similar during both years in their study creek, and they considered it too mild (consistently above 4 °C) to have induced thermal stress on the fish.

In our experimental reach, however, average water temperatures were well below 4 °C during both years and were particularly lower during the first year, with temperatures in January dropping to 2.33 °C and remaining low well into mid-February. Under these conditions, it is feasible that size-related fish survival, particularly for our experimental group with the smallest body size, could be attributed to the increase in metabolic efficiency that occurs with greater body mass at low water temperatures (Hunt 1969). The physiological advantages that relatively large early-winter body mass may give some individuals under crowded rearing conditions (i.e., high competitive pressure) could override some of the effects that cover and food have on their survival. Our smaller than average fish may have starved to death (Hunt 1969; Meyer and Griffith 1997), and the fact that salmon carcass availability, especially when combined with submerged wood, had no effect on their survival suggests that the growth path that they were on from before the experiments began could not be reversed by food availability later on in winter. Morgan and Metcalfe (2001) explained this as the result of “deferred costs of fall food shortages”. In their study, juvenile Atlantic salmon that had faced a food shortage during summer underwent delayed compensatory or “catch up” growth in late fall or early winter, but despite this spurt in growth, they remained at a physiological disadvantage compared with other fish in the long term. The salmon that were undernourished before winter suffered a persistent decline in body lipids, and their growth rates fell below those of the well-fed individuals between December and March (Morgan and Metcalfe 2001). It is possible that the size-dependent winter survival that we observed was the related outcome of previous restrictions in food access caused by, among other things, differences in the social status of fish (Metcalfe et al. 1990). The absence of such a size-dependent survival pattern during our second trial suggests that most fish in it may have been larger than a minimum threshold size at which low-temperature-induced physiological stress causes mortality. Furthermore, the good initial condition of these relatively large fish may have allowed them to use more efficiently any benefits derived from having access to food and cover in winter (Morgan and Metcalfe 2001).

Size-dependent shelter use also deserves consideration in the interpretation of our results, particularly because the proportion of individuals with access to shelter should have been lower under the crowded conditions of the first trial than in the second trial. It has been well established that juvenile salmonids consistently show a clear tendency to avoid sharing shelter with conspecifics (Cunjak 1988; Gregory and Griffith 1996; Armstrong and Griffiths 2001). Under high-density rearing conditions, one would expect the smallest fish to be displaced from shelters by the largest fish (Harwood et al. 2002; Orpwood et al. 2003), which could explain the observed size-related mortality if, for example, predators consistently captured fish that were not able to occupy shelters (Doloff 1993). Like in Quinn and Peterson’s (1996) study, size-selective predation may have had an influence on our results because pens were not designed to exclude predators (except for large fish that were removed from the experimental section). American dippers (Cinclus mexicanus) and minks (Mustela vison) were observed in or near the pens, whereas river otters (Lutra canadensis) and belted kingfishers (Ceryle alcincion) were known to be present in the area. Nevertheless, because fish survival was relatively the same across all pens regardless of treatment during the first trial and differed between the control and treatment pens during the second trial, it seems unlikely that access to predation shelter may have been a major factor in our results. Instead, thermal stress induced by the lower temperatures of the first trial on the smaller than average individuals within a cohort of small-bodied fish provides a better explanation for the observed size-related over-winter fish survival. Temperature-related physiological stress accounted for the lower winter survival rates Smith and Griffith (1994) reported for small Snake River rainbow trout compared with large ones, and this was the case even when protected from predators.

Results from the first trial confirmed our fifth prediction that early-winter body size of spring emigrants is larger than that of residual fish. This size difference at the beginning of the winter between regular 1-year-old smolts and residual coho suggests that there may be a minimum size for a successful smolt (Holtby et al. 1990), and unless fish reach such a threshold during a critical time window, they tend to remain in freshwater for an additional year (Thorpe 1986). The idea of such a threshold size may help explain the observed differences in percentage of residual fish between our two trials. Residual fish were twice as abundant at the end of our first trial, with relatively small fish, than at the end of the second trial, in which the average size of fish was larger.

Contrary to our sixth prediction, the timing of presmolt emigration was not affected by any of our treatments and was likely a response to season-related factors such as temperature and photoperiod (Saunders and Henderson 1970). Fish in our study showed emigration patterns and timing similar to those reported by Giannico and Hinch (2003) for this same side-channel and another one in a nearby system. Although during the first trial, there was a tendency for
some of the largest individuals to emigrate in mid- to late winter, emigration in earnest started in April and peaked in May in both of our trials. This tendency for the larger, and likely older, juvenile coho salmon to move downstream earlier than their smaller conspecifics was also observed by Irvine and Ward (1989) in the Keogh River, northern Vancouver Island. Giannico and Hinch (2003) concluded that the large-sized early emigrants were generally 2-year-old individuals that had probably been too small at the start of their first winter to afford the physiological costs of smolting (Thorpe 1986) and needed an additional year to reach a size that would improve their odds of ocean survival (Holtby et al. 1990). It is likely that in the present study, the 2-year-old coho salmon were the few that emigrated several weeks prior to most of the fish, which were 1 year old. Emigration only peaked after water temperatures rose above 4.5 °C in the springs of both 1997 and 1998. This observation was consistent with other studies of juvenile coho salmon winter activity (Bustard and Narver 1975; Giannico and Healey 1998).

Unlike other studies that reported effects of experimental-unit position (e.g., Spalding et al. 1995), we did not find evidence that any potential difference among pens, which were included as one of the factors in the analyses, biased our results. Although salmon carcass derived nutrients might have induced an increase in invertebrate numbers in our entire experimental reach (Wipfli et al. 1998; Chaloner and Wipfli 2002), this did not mask the strong positive effect that direct access to salmon flesh had on fish growth rates during the first trial. Fish were observed feeding on the available pieces of salmon carcass, and this significantly boosted the growth rates of most individuals. Bilby et al. (1998) showed that the salmon flesh and eggs consumed by young salmonids are readily assimilated. They calculated that the ratio of marine-derived nitrogen in muscle tissue ranged from 44.1% in coho salmon to 71.9% in age-1 steelhead that had access to carcasses compared to 16.6% and 36.3% in coho salmon and steelhead, respectively, from reaches without carcasses.

Densities of juvenile coho salmon in streams vary from year to year depending on adult escapement, early-life survival, and availability of nursery habitat. Likewise, the average body size of coho salmon parr will change on an annual basis in response to not only their rearing densities but also water temperature and food availability. In our study, the interannual differences in initial juvenile coho salmon densities and body size, which reflect that natural variation, have had marked effects on the results. Had the study been performed during only one of the two years, its findings would have been very different. A simple interpretation of a single year’s worth of data could have been that there was either a strong treatment effect or none at all. However, our results imply that the extent of the benefit that young coho salmon can derive from salmon carcasses varies with both their physiological and their rearing conditions.

Our mesocosm experiment allowed us to test specific factors in a setup that had many natural conditions (e.g., water temperature, photoperiod, and predation) while improving statistical power through replication. Although our results contribute to our understanding of coho salmon ecology, caution is required when they are extrapolated to natural systems (Warren and Davis 1971). However, it is important to highlight that our findings agree with those of earlier field- and enclosure-based studies (Bilby et al. 1998; Wipfli et al. 2003) regarding the important role that salmon carcasses play in increasing juvenile coho salmon winter growth and body mass. Furthermore, they reveal that wood availability may play an important role in extending over time the beneficial effects that carcasses have on fish daily growth rates.

When evaluating the role of salmon carcasses in feeding another generation of salmonids, it is important to consider not only the influence that in-stream habitat complexity may have on the final outcome but also that the effect of carcasses will differ from year to year depending on juvenile fish pre-winter body size and over-wintering densities. Under the experimental conditions of this study, small-sized juvenile coho salmon rearing at high densities derive benefits from salmon carcasses (in terms of both winter growth and presmolt size) that large-sized individuals at low densities do not. Historically, juvenile coho salmon were likely to occupy nursery habitats at higher densities than they do at present in the countless basins that have low adult escapement (Gresh et al. 2000). The prevailing rearing conditions of the past mean that summer feeding competition among salmon fry must have been intense, and as a result, the average prewinter salmon parr size should have been relatively small. Consequently, one may hypothesize that the influence of salmon carcasses on the next generation of salmon may have been greater in the past than it is today in many underseeded streams where large-sized salmon parr occur at low rearing densities. Although additional research is needed to investigate such a proposition, the potential benefits of salmon carcass placement projects should be considered within the ecological context of each individual watershed and cannot be regarded as the “silver bullet” of stream restoration.

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