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THE EFFECT OF WOOD AND TEMPERATURE ON JUVENILE COHO SALMON WINTER MOVEMENT, GROWTH, DENSITY AND SURVIVAL IN SIDE-CHANNELS

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ABSTRACT

In British Columbia, side-channels have been built to compensate for lost salmonid habitat. Most are structurally simple with little in-stream wood; however, they support high densities of juvenile coho salmon. We longitudinally divided in halves the top 100 m of two dead-end artificial side-channels, one side-channel with low winter water temperatures (surface-fed) and one with relatively higher water temperatures (groundwater-fed), closed the downstream end of each side-channel with two-way traps, and treated only one half of each channel with bundles of wood. Trapped fish were marked daily and coho salmon movement, growth and smolt output were monitored for two years. Wood addition increased juvenile coho winter carrying capacity and spring smolt output only in the 'colder' surface-fed side-channel. In contrast, in the groundwater-fed side-channel, with relatively higher water temperatures, the wood treatment slightly reduced the channel's carrying capacity and the spring output of coho salmon smolts. Copyright © 2003 John Wiley & Sons, Ltd.

KEY WORDS: instream wood; coho salmon; smolt production; winter survival; off-channel habitat

INTRODUCTION

In the Pacific Northwest, the flow of coastal rivers closely reflects the precipitation regime. Thus, streams and rivers have reduced flows during summer and experience relatively high but fluctuating flows during the fall and winter. As channel flow increases in the fall, so does the number of juvenile coho salmon (*Oncorhynchus kisutch*) moving from main-stem river habitats into alcoves or side-channels to avoid being displaced by water currents into unfavourable areas (Cederholm and Scarlett, 1982; Peterson 1982a; McMahon and Hartman, 1989; Swales and Levings, 1989; Nickelson *et al.*, 1992a). In fact, even modest increases in water discharge make many individuals move downstream (Giannico and Healey, 1998) and relocate into sheltered habitats well before the occurrence of scouring freshets (Tschaplinski and Hartman, 1983). In their winter nursery habitats, coho salmon often seek refuge in accumulations of in-stream wood and beneath undercut banks (Bustard, 1973; Bustard and Narver, 1975).

Seasonal habitat shifts may allow fish to conserve energy and, therefore, increase their chances to survive a period of the year that is characterized by frequent peaks in stream flow, reduced water temperatures and scarce food. Under such circumstances, groundwater-fed side-channels and ponds become refuges for juvenile coho salmon because the relatively stable water flow, higher temperatures and invertebrate production of these habitats allow fish to continue foraging and even growing during winter (Peterson, 1982a,b; Brown, 1985).

In many coastal watersheds of the Pacific Northwest, off-channel habitat availability and quality seem to impose a bottleneck on coho salmon production (Mason, 1976; Nickelson *et al.*, 1992a; Solazzi *et al.*, 2000). The mountain headwaters and foothill reaches of most coastal streams tend to run through deep ravines and

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gullies that constrain channel movement and, therefore, limit the development of off-channel fish habitat. In contrast, the broad low valley reaches of many of these streams offered abundant off-channel fish nursery habitat in the past. However, the availability of secondary channels, riverine ponds and wetlands has been markedly reduced during the last century by the cumulative impacts of a broad variety of human activities (i.e. gravel extraction, forestry, agriculture, hydroelectric projects, urban sprawl, etc.; Henderson, 1991; Hicks *et al*., 1991; Slaney *et al*., 1996).

The response to this gradual loss of nursery habitat in coastal watersheds has been the active restoration and construction of numerous side-channels, ponds and wetlands during the last two decades. In southwestern British Columbia, the first excavations and expansions of groundwater-fed side-channels were carried out during the late 1970s by the Canadian Department of Fisheries and Oceans (DFO) to increase the availability of chum salmon (*Oncorhynchus keta*) spawning beds. These early spawning side-channels were several hundred metres long and had relatively uniform depth and width, coarse gravel substrates, and rock-armoured banks. Because they were groundwater fed, these side-channels had stable and 'silt-free' year-round flows, relatively cool summer temperatures and ice-free winters (Sheng *et al*., 1990). It was not until coho salmon stocks began to decline in the 1990s that the DFO, often in partnership with other organizations, started restoring and building more structurally complex side-channels for this species to use as both spawning and nursery habitats (Sheng *et al*., 1990). Thus, simple channels were modified or replaced by series of interconnected side-channels and ponds with abundant in-stream wood (i.e. logs and root wads) and boulders. Such an emphasis on habitat structural complexity, however, seems to have diverted attention away from the importance of water temperature for fish growth and survival. A higher proportion of new side-channels are river-water fed rather than groundwater fed, suggesting an oversight of the fact that surface-fed systems experience large fluctuations in both water temperature and flow which may negatively affect juvenile coho salmon growth and survival (Sandercock, 1991).

Some researchers have suggested that freshwater production of coho salmon is primarily controlled by the amount of available winter habitat (Mason, 1976; Hartman *et al*., 1996; Solazzi *et al*., 2000). This idea of a winter 'bottleneck' to freshwater production (Mason 1976; Nickelson *et al*., 1992a,b) is supported by studies that found no correlation between spring smolt abundance and number of fry present the previous summer (Holtby and Hartman, 1982; Lestelle *et al*., 1993). Although there is evidence that off-channel habitats provide refuge to juvenile coho salmon from adverse hydrologic conditions or predators during winter (Cunjak, 1996), little is known about the combined effects that water temperatures and in-stream wood have on smolt production. Therefore, in this study we examined how juvenile coho salmon respond, in terms of winter movement, growth, density and survival, to two different combinations of winter temperature regimes, cover treatments and early fall fish densities in artificial side-channels.

MATERIALS AND METHODS

Study sites

Two artificial side-channels were used in this study: Upper Paradise (UP), in the Cheakamus River, and Upper Mamquam (UM), in the Mamquam River. These rivers are part of the Squamish River watershed, which flows into Howe Sound, southwestern British Columbia (Figure 1).

Both side-channels have an upstream dead-end that is fed by springs and subsurface water flow from the nearby river. They are connected to the main stem of the river only by their downstream ends. UP is 420 m long and, on average, 5.90 m wide and 0.45 m deep; UM is 360 m long and has an average width of 6.18 m and an average depth of 0.53 m. Both were excavated almost parallel to the rivers they connect to, have little or no gradient, and the fluvial deposits exposed during excavation constitute their gravel substrates. The banks are armoured with boulders (i.e. rip-rap), 0.30–0.50 cm in diameter, to approximately 0.50 m above the water level. Each side-channel receives a different proportion of groundwater and water from the river through subsurface flow and, as a result, their winter water temperatures differ. UP, largely groundwater fed, is warmer during winter (mean December–March water temperature = 5.9 °C, 1996/97; 6.2 °C, 1997/98) than UM, which is mainly fed by surface water (mean December–March water temperature = 3.3 °C, 1996/97; 3.9 °C,

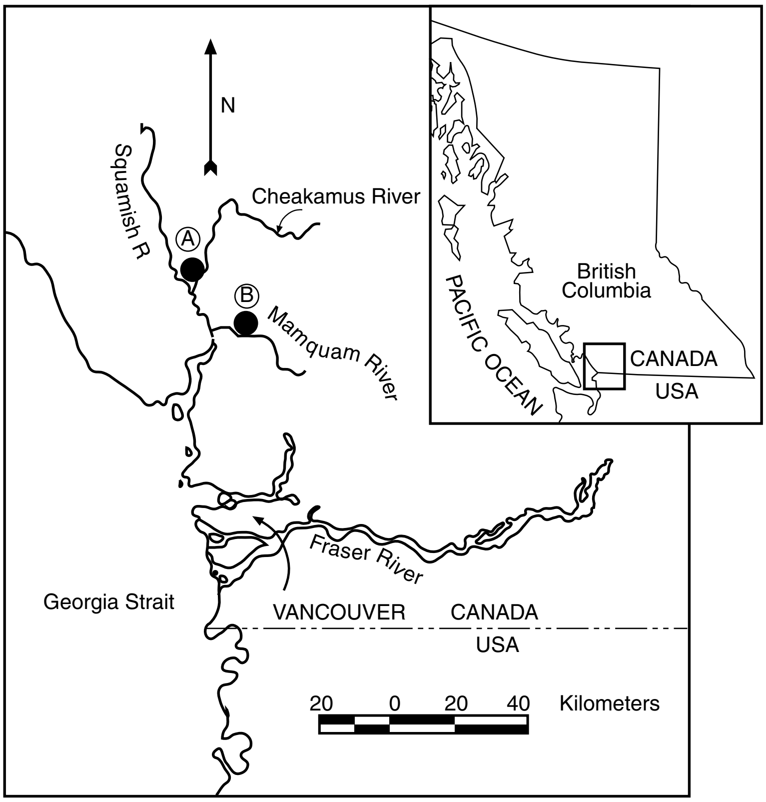

Figure 1. Map of the location of Upper Paradise (A) and Upper Mamquam (B) side-channels in the Cheakamus and Mamquam watersheds respectively

1997/98). Water discharges are similar in both side-channels and during 1996–98 ranged from 0.07 $m^3 s^{-1}$ in summer to 0.11 $m^3 s^{-1}$ in winter. Water samples (three replicates each time) were taken from both side-channels in December, March and June, and showed no significant differences in nutrient concentrations. Nitrate concentrations averaged 0.444 ppm (SE < 0.001) in UP and 0.466 ppm (SE $= 0.005$) in UM ($t = -0.29$, df $= 16$, $p = 0.774$). Orthophosphate concentrations averaged 0.052 ppm (SE $= 0.001$) in UP and 0.054 ppm (SE $= 0.001$) in UM ($t = -0.870$, df $= 16$, $p = 0.397$).

Coho and chum salmon were the two most abundant species in these side-channels. Steelhead trout (*Oncorhynchus mykiss*), cutthroat trout (*O. clarkii*), Dolly Varden char (*Salvelinus malma*), sculpins (*Cottus* spp.) and suckers (*Catostomus* spp.) were present but in extremely low abundance.

The pattern of movement of juvenile coho salmon in the upper sections of these side-channels was monitored during two consecutive years using two-way fish counting fences. In each side-channel, a 100 m long 'experimental' section was fenced off. The lower end of each section was closed with a V-shaped, 2 mm mesh, fish counting fence (labelled A in Figure 2). Each fence was built using 3 m long and 1 m high fence panels made of galvanized hardware-cloth framed with 2 × 4 wooden boards. A 50 cm wide clear plastic 'skirt' was stapled along the bottom board. These panels were buried 20 cm deep in the substrate and their plastic skirts were stretched in a downstream direction under the gravel to prevent fish from passing under the counting fence. In UP, the upper end of the 'experimental' section corresponded to the dead end of the channel. In UM, the upper end of the experimental arena, which was approximately 150 m downstream from the dead end of the channel, was closed off with a transversal 2 mm mesh fence. Each experimental section was longitudinally divided into two equal halves with a divider made of geotextile (Amoco 1199) material held in place using vertical 2 × 2 wooden posts (B in Figure 2). Both the geotextile divider and the wooden posts were buried 45 cm deep in the substrate to keep fish from moving between the side-channel halves.

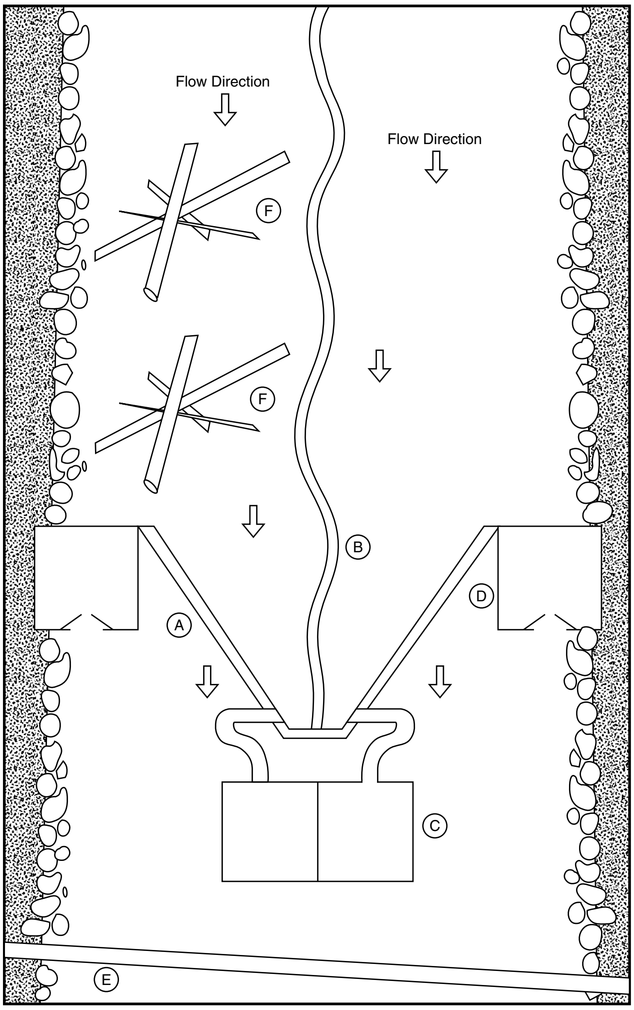

Figure 2. Diagram of fish counting fence and geotextile divider in a side-channel. A = fish counting fence; B = longitudinal divider; C = downstream fish trap; D = upstream fish trap; E = spawner stop fence; F = bundles of wood

Each counting fence included one downstream fish trap box (divided into two separate holding chambers; C in Figure 2) and two upstream fish trap boxes (for right and left halves of the side-channel; D in Figure 2). The right and left holding chambers of each downstream trap were respectively connected to the right half and left half of the fish fence by means of a flexible plastic pipe (diameter 0.20 m). These double-chambered trap boxes allowed fish emigrating from one half of the experimental section to be kept separate from fish leaving the other half until after they could be handled and released downstream from the fence.

The upstream trap boxes were placed between the side-channel banks (one on the right bank and the other on the left) and the upstream end of the V-shaped fence. Any spaces between the sides of these trap boxes and the bank boulders of the side-channel or the fence frames were sealed with wire mesh and geotextile material to prevent fish from entering or leaving the experimental sections without first entering the traps. A spawner stop fence (with chain link mesh; E in Figure 2) was placed in each side-channel approximately 10 m downstream from the counting fence to prevent spawners from entering and altering the experimental set-up.

One half of each side-channel was randomly chosen and treated with wood, whereas the other half remained untreated (control). Dense bundles of wood were used as treatment (F in Figure 2). Each bundle (diameter 1.20 to 1.60 m) consisted of one large alder root wad and 20 alder or willow branches (cross-section 4 to

8 cm) tied with nylon rope. The wood-treated half of each side-channel received twenty of these bundles. They were placed 4 m apart and anchored to bank boulders and trees by nylon ropes.

Experimental manipulations

Two experimental trials were carried out, one from November 1996 to August 1997 and one from November 1997 to August 1998. Because juvenile coho salmon early fall densities in both side-channels were much higher during the 1996–97 trial than during the 1997–98 trial we analysed the results from both trials separately. Thus, juvenile coho salmon early fall abundance became an additional treatment in our manipulations to water temperature and in-stream cover.

At the beginning, fish densities in each side-channel and trial were equal on both side-channel halves. The counting fences were used to estimate juvenile salmon migration rate in and out of the side-channels. All fish caught at the fences were anesthetized with CO_2 (dissolving one teaspoonful of 'Bromoseltzer'® in 4 litres of water), weighed to the nearest 0.01 g, measured to the nearest 0.1 mm in fork-length, and batch marked using a fluorescent dye injected into the fins using a high-pressure inoculation gun (Biomark Ltd). These marks were used to distinguish among the following four fish groups in each side-channel: immigrants to control side, emigrants from control side, immigrants to wood-treated side and emigrants from wood-treated side. Sets of four new marks were used every week to allow the reconstruction of fish movement patterns at weekly intervals (e.g. differences in time of channel residence and emigration timing) and to estimate differences in growth and survival.

The average intrinsic growth rate for all fish entering each side-channel half in late fall (November for UM and December for UP) and leaving that half in May was estimated using the following formula:

$$\frac{\log_e W_2 - \log_e W_1}{t_2 - t_1} \times 100$$

where W_1 is the average weight of all fish moving into the experimental arena in late fall, W_2 is the average weight of the subset of those immigrants who survived and were recaptured when they left the side-channel the following spring, and $t_2 - t_1$ is the number of days between mid-November and mid-May for UM or mid-December and mid-May for UP.

Treatment effect on fish winter survival was estimated using the relative index of treatment-dependent survival. This index was calculated for each trial, side-channel and treatment dividing the number of fish leaving a side-channel half between April and May carrying November/December marks (recaptures) by the number of fish that were initially marked moving into that side-channel half between November and December. Both survival rates and indices of treatment-dependent survival were useful for revealing trends, but because these values were not based on measures of individuals no estimates of variability around them were obtained.

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) in the experimental side-channel sections. Every month, fish were caught using minnow traps (6 mm mesh) baited with preserved salmon roe. Ten traps were evenly distributed throughout each side-channel half and left for approximately 18 h. Captured fish were fin-clipped for temporary identification and different clip marks were used every month. Every two months, fish densities were monitored in the middle and lower sections of these side-channels to detect possible differences with the experimental sections.

Age analysis

During the 1997–98 trial juvenile coho salmon were aged using two different methods: size of individuals of known age (late fall/early winter, only in UM) and scale analysis (spring in both channels). Several individuals carrying marks from the previous year were trapped at UM's counting fence between November and January. The lower 95% confidence limits estimated on the mean weight and mean fork length of these fish were used to set the cut-off value of weight and length between age 0+ and 1+ coho salmon.

The following spring, smolt aging was done based on the analysis of scale samples taken from 100 randomly selected individuals (25 fish from UP and 75 from UM). A subset of these scales was sent to the Fish Aging Laboratory of the DFO's Pacific Biological Station (Nanaimo, British Columbia) for age verification.

RESULTS

In both trials general fish movement patterns were similar in both side-channels, with fish activity increasing in late fall/early winter and in spring. During January, February and March very little fish movement was detected at the counting fences. Most juvenile coho salmon leaving the experimental sections in spring showed the changes of pigmentation associated with smolting.

Abundance and density

1996–1997 trial. The numbers of juvenile coho salmon handled at the counting fences between November and June were 1726 for UP and 1268 for UM. Fish densities were similar in both side-channels in November (Figure 3A and B) and decreased progressively between November and May. A similar reduction in fish densities over the winter was observed in the low and middle sections of the side-channels. In the warmer groundwater-fed UP, the control and wood-treated halves showed similar declines in fish densities (Figure 3A), whereas in colder surface-fed UM, the decrease in densities was 50–60% greater in the control half than in the wood-treated half between January and May (see estimated densities with 95% confidence limits, Figure 3B).

1997–1998 trial. Only 344 juvenile coho salmon moved through UP's counting fence between November and June (an 80% reduction from the previous year). The reduction in juvenile coho salmon numbers was less noticeable (20%) in UM, where 1013 fish were handled at the counting fence.

The lower numbers at the fences were closely matched by declines in fish densities. UP showed an 80% reduction in coho salmon densities from 1996–97, but no significant differences in fish densities between side-channel halves (Figure 3C). Juvenile coho densities went down by approximately 20% in UM compared to 1996–97 (Figure 3D). As fish numbers decreased, estimated densities were higher in the wood-treated half than in the control half; however, these differences were not significant (see 95% confidence limits, Figure 3D).

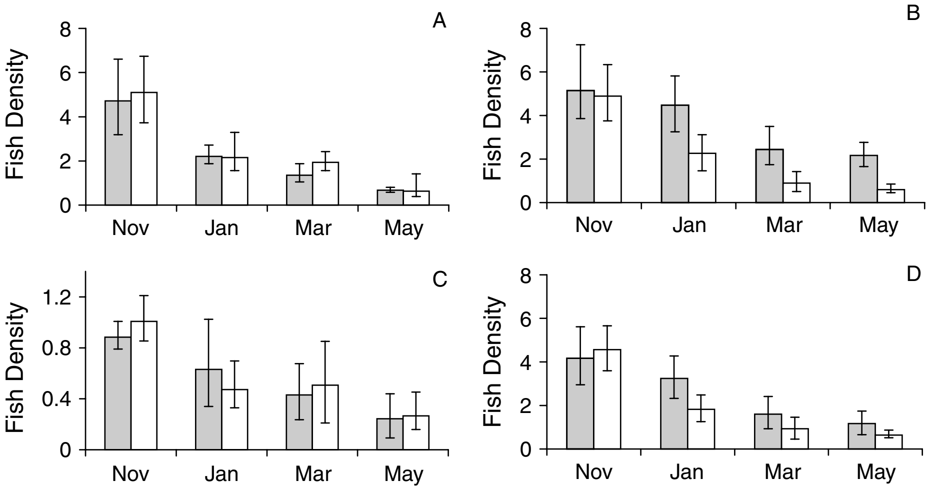

Figure 3. Monthly estimated densities of juvenile coho salmon during the 1996–97 trial (A = UP, B = UM) and the 1997–98 trial (C = UP, D = UM). Vertical bars indicate 95% confidence limits. Note smaller scale use for (C). Shaded bars = wood-treated half; White bars = control half

Movement and migration

1996–1997 trial. Between November and January, 213 juvenile coho salmon entered the control half of groundwater-fed UP while only 140 entered the wood-treated half. In the same period, 156 fish moved out of the control half (40% of them marked as recent immigrants) and 121 moved out of the wood-treated half (21% of which had entered that section a few days earlier; Figure 4A). Unmarked fish moving downstream were long-term side-channel residents (or immigrants to the side-channels before the completion of counting fences). Although the number of long-term residents that moved out of the experimental section between November and January was almost the same for both halves of UP (control = 94 fish, wood = 96 fish), the percentage of fish displaced in relation to the number of recent immigrants was higher in the wood-treated half (79%) than in the control (60%).

Spring smolt emigration from the control half (522 individuals) was only 6% higher than from the wood-treated half (492 individuals). Smolt output per square metre was 1.74 and 1.64 respectively.

In the surface-fed UM, 60% more juvenile coho entered the half treated with wood (328 fish) than the control half (132 fish) from November to January. In this period, approximately 38% more fish moved out of the control half (143) than out of the wood-treated half (88) (Figure 4B). In addition, almost 24% (32) of the fish that entered the control half and only 8% (25) of those that entered the wood-treated half during late fall/early winter left within a few days.

The number of long-term residents that emigrated (or were displaced) from the experimental area between November and January was higher for the control (111 fish) than for the wood-treated half (63). The percentage of displaced long-term residents in relation to the number of recent immigrants was also higher in the control half (84%) than in the wood-treated half (19%).

Smolt emigration did not begin until April (one month later than in the 'warmer' side-channel), reached a peak in May and continued well into the summer. Smolt yield was 102% higher from the wood-treated half

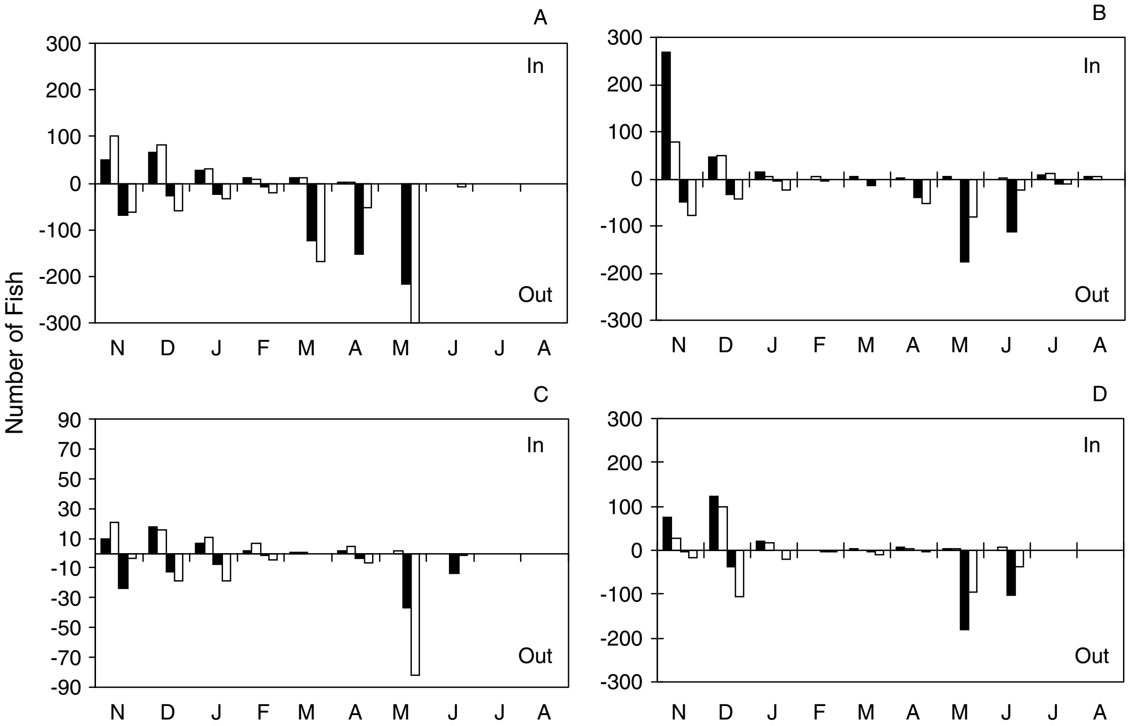

Figure 4. Number of juvenile coho salmon moving in and out of the experimental channel sections during the 1996–97 trial (A = UP, B = UM) and the 1997–98 trial (C = UP, D = UM). Black bars = wood-treated half; White bars = control half

(352 individuals) than from the control half (174 individuals) of UM. Smolt output per square metre was 1.17 and 0.58 respectively.

1997–1998 trial. The abundance of juvenile coho salmon in groundwater-fed UP during this trial was low. Between November and January, a few more individuals (48) entered the control half than the wood-treated half (35). During those three months, 42 fish moved out of the control half and 45 left the half treated with wood (Figure 4C). Approximately 33% (14 individuals) of the fish leaving the control half and 11% (5 individuals) of those moving out of the wood-treated half were recent immigrants; the rest were long-term residents. The percentage of resident fish that moved downstream in relation to the number of immigrants was higher in the wood-treated half (114%) than in the control half (58%).

Forty per cent fewer juvenile coho salmon emigrated from the wood-treated half of UP (56 fish) than from the control half (91 fish). The output of smolts per square metre was 0.19 for the half with wood and 0.30 for the control half.

Between November and January, in surface-fed UM 34% more juvenile coho salmon entered the wood-treated half (218) than the control half (143), whereas approximately 71% more fish emigrated from the control half (143) than from the half treated with wood (42) (Figure 4D). Among the emigrants, 11% (16 individuals) of those moving out of the control half and 33% (14 individuals) of the ones leaving the wood-treated half were recent immigrants. The number of long-term residents leaving the control half (127 individuals) was higher than in the wood-treated half (28 individuals). The percentage of emigrating long-term residents in relation to the number of immigrants was higher (39%) in the wood-treated half than in the control half (20%).

The number of smolts leaving the half treated with wood was almost twice as high (287) as for the control half (150). Output was 0.96 smolts/m^2 from the wood-treated half and 0.5 smolts/m^2 from the control half.

Survival, growth and age composition

Although the values of the relative index of survival for juvenile coho salmon varied widely between both side-channels and from year to year, they were consistently higher in the wood-treated side (UM: 1996–97 = 0.08, 1997–98 = 0.28; UP: 1996–97 = 0.20, 1997–98 = 0.26) than in the control side (UM: 1996–97 = 0.01, 1997–98 = 0.15; UP: 1996–97 = 0.07; 1997–98 = 0.21). In both side-channels, survival rates were higher during the 1997–98 trial (a relatively mild winter) than during the 1996–97 trial (a cold winter).

For each year, juvenile coho salmon growth rates between fall and spring were consistently higher in the wood-treated halves of the side-channels (UM: 1996–97 = 0.34, 1997–98 = 0.66; UP: 1996–97 = 0.44, 1997–98 = 0.47) than in their control halves (UM: 1996–97 = 0.23, 1997–98 = 0.54; UP: 1996–97 = 0.40, 1997–98 = 0.39).

1996–1997 trial. In UP, fish size differed between halves of the side-channel and between immigrants and emigrants from November to January (Figure 5A). The mean weight of juvenile coho salmon in the control half (3.68 g, SE = 0.08) was significantly higher ($t = 5.475$, df = 530, $p < 0.001$) than in the wood-treated half (3.02 g, SE = 0.09). However, in both halves immigrants were significantly heavier than emigrants (control: immigrant mean weight 4.14 g, SE = 0.11; emigrant mean weight 3.22 g, SE = 0.10; $t = -6.275$, df = 330, $p < 0.001$; wood-treated half: immigrant mean weight 3.51, SE = 0.12; emigrant mean weight 2.61 g, SE = 0.11; $t = -5.289$, df = 198, $p < 0.001$). Mean smolt weight did not differ ($t = 1.775$, df = 290, $p = 0.077$) between side-channel halves in March (control = 2.92 g, SE = 0.09; treated half = 2.69 g, SE = 0.08). In April and May, however, smolts leaving the wood-treated half (mean weight 4.63 g, SE = 0.18) were heavier ($t = -3.512$, df = 722, $p < 0.001$) than those emigrating from the control half (mean weight 4.19 g, SE = 0.09). Comparisons based on fish fork lengths showed the same trends.

In UM, fish size did not differ between treatments or between immigrants and emigrants (mean weight of fish in all groups 2.63 g, SE = 0.13; mean length 6.0 cm, SE = 0.19) from November to January (Figure 5B). In January, however, one unusually large individual (weight 16.01 g, fork length 10.9 cm) increased the mean size of immigrants to the wood-treated side. In February and March, no clear differences in size were observed between emigrants and immigrants except for one large individual (weight 8.23 g, fork length 9.4 cm) that left the wood-treated half. Smolt size did not differ between side-channel halves in April or May (Figure 5B). However, in June smolts from the control half of UM (mean weight 4.99 g, SE = 0.36)

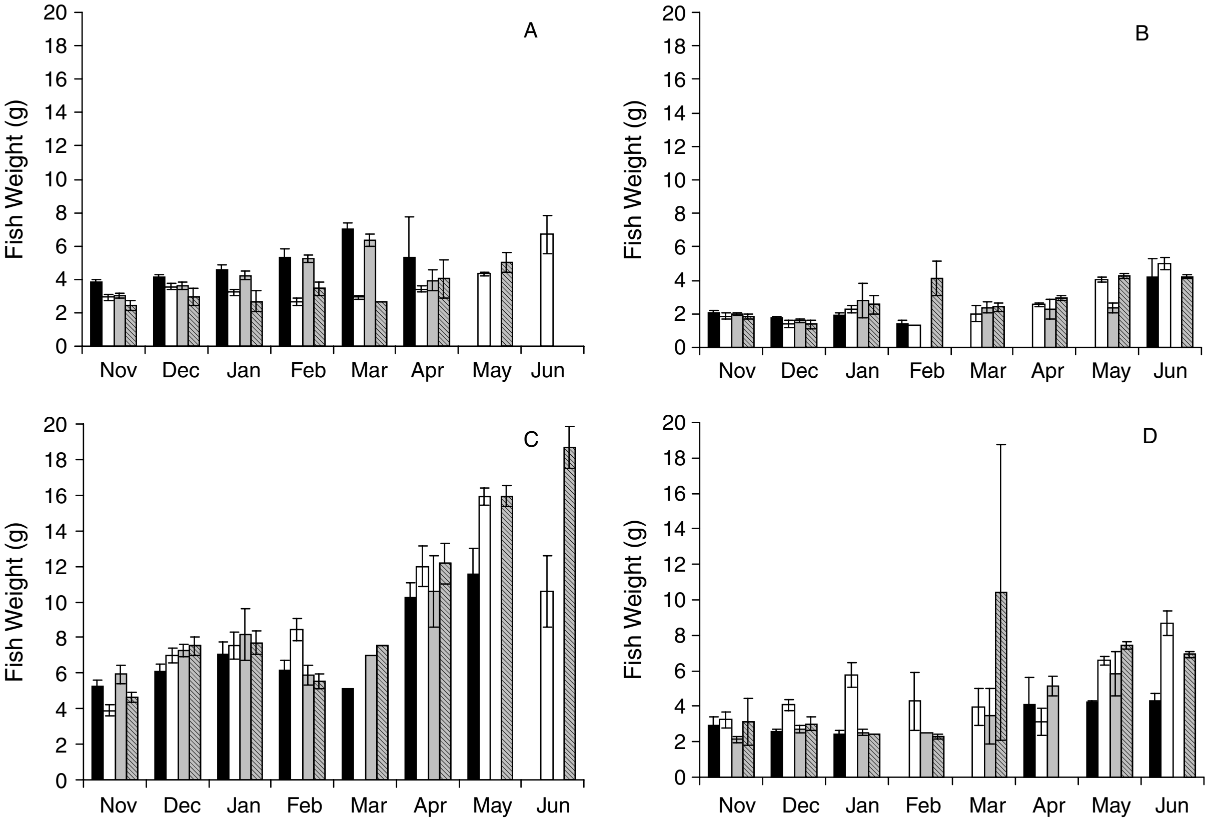

Figure 5. Mean weight of juvenile coho salmon trapped at counting fences during the 1996–97 trial (A = UP, B = UM) and the 1997–98 trial (C = UP, D = UM). Vertical lines indicate 2 SE

were heavier (t = 2.592, df = 137, p = 0.010) than those from the wood-treated half (mean weight 4.20 g, SE = 0.12).

1997–1998 trial. Between November and January, there were no differences (t = −0.208, df = 168, p = 0.835) in fish mean weight between both halves of UP (control = 6.39 g, SE = 0.25; treatment = 6.46 g, SE = 0.25). Neither were there significant differences (t = −1.154, df = 179, p = 0.475) in the mean weight of immigrants (5.95 g, SE = 0.28) and emigrants (6.46 g, SE = 0.42) (Figure 5C).

In April, there was no significant difference in mean weight (t = 2.131, df = 15, p = 0.159) between emigrants (12.05 g, SE = 1.12) and immigrants (10.36 g, SE = 1.39). The treatment did not affect smolt size until June, when smolts leaving the wood-treated half (mean weight 18.72 g, SE = 1.18) were significantly heavier (t = 2.144, df = 14, p = 0.026) than those moving out of the control half (mean weight 10.59 g, SE = 2.03) (Figure 5C).

In UM, there were significant differences (t = 3.86, df = 567, $p < 0.0001$) in juvenile coho mean weight between channel halves (control = 3.41 g, SE = 0.16; treated half = 2.59 g, SE = 0.13) from November to January if 33 age 1+ individuals were included in the sample. This difference was not observed when only age 0+ individuals were included (t = 1.97, df = 538, p = 0.059). Although the mean weight of emigrants (3.88 g, SE = 0.22) was higher than that of immigrants (2.53 g, SE = 0.10), this difference was not significant due to relatively large standard errors caused by the presence of the larger age 1+ individuals (Figure 5D).

Scale analyses were carried out only during this second trial. Size variation among groundwater-fed UP salmon was relatively low compared to surface-fed UM, and only one smolt in UP was age 2+. In UM, 16 coho salmon were identified as age 1+ during late fall/early winter because they had marks from the 1996–97 trial. They were bigger (mean weight 12.22 g, SE = 1.10, 95% confidence limits = 3.35; mean fork length 9.38, SE = 0.26, 95% confidence limits = 1.05) than other individuals handled between November and January at the counting fence. Seventeen additional individuals were classified as age 1+, based on their weights and fork lengths, increasing the total number of fish in this age class to 33. They represented 17.8% of the juvenile coho salmon trapped at the fence between November and January. The analysis of scales sampled in the spring, combined with the use of fork length and weight cut-off values, allowed us to estimate that 20 smolts (4.7% of the UM smolts) were, by then, age 2+ (same cohort as those classified during the previous winter as 1+).

DISCUSSION

Both cover availability and winter water temperatures affected juvenile coho salmon winter survival, growth and ultimately smolt production in artificial side-channels. In both trials, the presence of wood in the surface-fed side-channel, UM, not only increased the retention of juvenile coho during late fall and early winter but increased carrying capacity between January and May (based on density estimates) and doubled spring smolt output. In contrast, in the groundwater-fed system, the addition of wood reduced late fall and early winter fish retention capacity, did not change January–May carrying capacity and decreased somewhat the spring output of smolts. These results were consistent for both trials and independent of juvenile coho salmon abundance early in the fall.

The addition of wood seems to have increased the rates of winter growth and survival of juvenile coho salmon in both the groundwater and the surface-fed side-channel. However, the use of cover structures by juvenile coho salmon during winter was different in both systems. In the groundwater-fed side-channel, fish were regularly seen feeding away from cover, whereas in the surface-fed unit, with the exception of the few individuals that were trapped, no fish were observed until the spring. This suggests that juvenile coho salmon remained under cover during the day and fed at night in the colder surface-fed side-channel. Because these side-channels did not differ visibly in morphology, water discharge or nutrient concentrations, we concluded that their differences in fish activity and cover use may have been caused by their dissimilar water temperatures. Shifts in diel activity patterns from predominantly diurnal to predominantly nocturnal has been observed in Atlantic salmon (*Salmon salar*), brown trout (*Salmon trutta*) and rainbow trout (*Oncorhynchus mykiss*) (Heggenes *et al*., 1993; Riehle and Griffith, 1993; Fraser *et al*., 1995; Bremset, 2000) when temperatures decline. Different water temperatures may cause these contrasting behaviours because fish may have different levels of vulnerability to diurnal endothermic predators, whose movements are not slowed down at low temperatures (Metcalfe *et al*., 1999).

It is possible that such differences in levels of fish activity could be attributed also to differences in prey availability between both side-channels. Although we did not assess benthic productivity we assumed it was similar in both side-channels because Decker (1999), who examined benthic invertebrate community composition in eight similar channels in the area (including UP, used in our study), found that side-channels like ours with the same nutrient concentrations had similar levels of benthic invertebrate biomass regardless of water temperatures. Therefore, if differences in prey abundance were not causing the different activity patterns we observed in fish, temperature-mediated changes in benthic invertebrate diel movement may be an alternative explanation to the observed differences in fish behaviour. Such diel synchronicity with drifting invertebrates was observed in Atlantic salmon feeding at night in subarctic rivers (Amundsen *et al*., 2000) in response to low water temperatures.

The fact that juvenile coho winter survival was higher in the presence of wood provides further support to the notion that predation rather than starvation may be the leading cause of mortality in these artificial side-channels. Peterson (1982a) found predation to be the main cause of winter mortality for juvenile coho salmon residing in riverine ponds. It is not clear, however, why the estimated increase in winter survival translated into a higher spring smolt output from the wood-treated half only in the surface-fed side-channel. Such a difference suggests that in the side-channel with low water temperatures the availability of cover was critical for the young salmon to survive during the early spring period. Shelter from predation may have been particularly important in the cold environment because as temperatures decrease the movement of fish becomes slower (Rimmer *et al.*, 1985). Considering the relatively slow and regular discharge of the side-channels, it is unlikely that wood was used as a current shelter by the fish in the way it has been observed in main-stem river habitat (McMahon and Hartman, 1989; Shirvell, 1990; Nickelson *et al.*, 1992a).

Considering that our fences were not located at the mouth but on the upper portion of the channels, the possibility remains that our results may not entirely reflect the pattern of fish movement and size distribution for the entire channels. However, this is unlikely because fish trapping carried out downstream of the fences did not reveal major differences with the control halves of our experimental sections in terms of overall fish abundance, activity and size.

The general findings of Sheng *et al.* (1990) regarding the utilization of artificial side-channels by juvenile coho salmon were confirmed by our study. This species uses side-channels as nursery habitat throughout the year and displays a markedly seasonal pattern of movement, as revealed by the few juvenile salmon handled at the fences during summer and most of winter, and the hundreds of individuals that moved both in late fall/early winter and in spring. The November–January movement was bidirectional (upstream and downstream), whereas the spring movement was predominantly downstream by emigrating smolts. However, the assumption of Sheng *et al.* (1990) that the fall immigration of large juvenile coho, presumably from the main stem of the river, resulted in the displacement of large numbers of relatively smaller long-term channel residents and a net reduction of fish in the channels was not supported by our study. Not only did more fish move upstream than downstream of the fences during late fall and early winter, resulting in a net increase of fish rearing densities, but there were no clear and consistent differences in size between immigrants and emigrants except during the first trial in the warmer side-channel, when immigrants were bigger than emigrants. Similar size between both types of 'movers' indicates that neither age nor social status is an important factor affecting movement by coho salmon in these side-channels. The fact that from 11 to 40% of the fall and early winter emigrants, depending on trial, were individuals that had recently entered the experimental sections, further suggests that habitat exploration, rather than displacement by dominant fish, was the main reason for movement in late fall and early winter. Similar exploratory behaviour was observed by Kahler *et al.* (2001) during summer in three Washington streams. They concluded that such habitat selection strategy seemed to increase the feeding opportunities of juvenile coho salmon because movers grew faster than sedentary individuals. During late fall and early winter this exploratory tendency may increase the chances of young fish to find suitable shelter to survive the winter.

In the surface-fed side-channel, a greater proportion of both residents and immigrants remained during the winter in the wood-treated half than in the control half. Our observations that fish were more sedentary in the structurally complex than in the simple habitats were consistent with those of Roni and Quinn (2001a), who found that juvenile coho salmon in artificial channels moved less often and shorter distances when wood was present.

As in other studies (Roni and Quinn, 2001b), fish size was inversely related to density and, therefore, during our first trial individuals were much smaller than during the second trial. Fish were larger in the warmer groundwater-fed system than in the colder surface-fed one. Fish in surface-fed UM also showed the greatest differences in body size. The largest fish were not necessarily main-stem immigrants but two-year-old individuals that may have stayed in the system for an additional year after failing to reach a smolting size threshold during their first year (Metcalfe, 1994).

The important role played by in-stream wood in enhancing salmonid habitat in natural streams has been documented by many studies (Bisson *et al.*, 1987; Hicks *et al.*, 1991; Roni and Quinn, 2001b). This study shows that the addition of wood may also increase coho salmon smolt production in artificial side-channels that are predominantly fed by surface waters. However, for groundwater-fed side-channels this is not the case. The benefits of higher water temperatures during winter seem to override any benefits that cover availability may have for juvenile coho salmon, to the extent that wood may be even slightly detrimental to their survival. Therefore, whenever possible, the use of groundwater in creating off-channel nursery habitat for salmonids may be more cost-effective than relying on sources of surface water and having to obtain, transport and place large amounts of wood to improve salmonid winter survival.

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