Influence of Cover Complexity and Current Velocity on Winter Habitat Use by Juvenile Coho Salmon (*Oncorhynchus kisutch*)[1]

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Winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) varied with cover type and flow level in outdoor stream channels. Cover utilization and the number of fish remaining in stream channels increased significantly as cover complexity increased. Most fish emigrated during a simulated freshet unless the most complex cover (low velocity, shade, and wood debris combined) was available. At both high and low flows, emigration occurred primarily during the rapid decline in light levels at twilight. Most coho formed aggregations beneath cover, exhibiting feeding and aggression at temperatures as low as 2.5°C. We conclude that (1) social interactions, in concert with habitat features, influence the abundance of coho salmon within specific stream habitats in winter, and (2) structural complexity of wood debris is an important consideration for management practices designed to protect or enhance winter habitat for this species.

L'habitat utilisé en hiver par les saumons cohos juvéniles (*Oncorhynchus kisutch*) variait en fonction du type de couvert et du débit dans les chenaux extérieurs. L'utilisation du couvert et le nombre de poissons restant dans les cheneaux augmentait nettement en fonction de la complexité du couvert. La plupart des poissons émigraient pendant une crue simulée à moins de disposer du couvert le plus complexe (faible vitesse, ombre et débris de bois combinés). Que le débit soit fort ou faible, l'émigration se produisait surtout pendant la rapide baisse de l'éclairement au crépuscule. La plupart des cohos se tenaient en groupe sous le couvert, présentant des comportements d'alimentation et d'agression à des températures pouvant descendre jusqu'à 2,5°C. Nous en concluons que 1) les interactions sociales, combinées aux caractéristiques de l'habitat, influent sur l'abondance du saumon coho dans certains habitats lotiques précis en hiver et que 2) la complexité structurale des débris de bois est un aspect important à considérer dans les pratiques de gestion visant à protéger ou à améliorer l'habitat hivernal de cette espèce.

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Over the past decade, the behavior and ecology of stream-dwelling salmonids during winter has received considerable attention. High mortality rates and different, often more restrictive, habitat requirements during winter (e.g. Mason 1976; Rimmer et al. 1984; Cunjak and Power 1986) have emphasized the importance of this season to salmonid management. Because the quality and quantity of cover appears to be a major factor governing overwinter survival (e.g. Hunt 1969; Mason 1976; Tschaplinski and Hartman 1983), research has focused on defining winter cover requirements.

For juvenile coho salmon (*Oncorhynchus kisutch*), large wood debris provides a major component of winter cover (Hartman 1965; Bustard and Narver 1975a; Tschaplinski and Hartman 1983; Heifetz et al. 1986). Wood debris is thought to provide protection from predators during this period of low water temperatures, and from downstream displacement from high velocities by frequent and at times severe winter freshets that characterize coastal systems (Hartman 1965; Bustard and Narver 1975a). Recent studies have documented that (1) higher numbers of coho salmon remain within accumulations of wood debris after winter freshets than in other types of stream habitats (Tschaplinski and Hartman 1983), (2) the number of overwintering coho salmon is positively correlated with the volume of debris (Tschaplinski and Hartman 1983; Martin et al. 1986), and (3) the number of overwintering coho is low in stream reaches where debris abundance has been reduced by debris removal associated with streamside logging (Tschaplinski and Hartman 1983; Murphy et al. 1986) or other disturbance (Martin et al. 1986).

Although previous studies have established the importance of debris in providing winter cover for coho salmon, the characteristics that determine its suitability have not been clearly defined. The objective of this study was to examine selection of various cover types by coho salmon. The effects of high current velocities on cover selection were also examined, because population declines during winter have often occurred in conjunction with freshets (Mason 1976; Tschaplinski and Hartman 1983).

Materials and Methods

Test Channels and Fish

Experiments were conducted in outdoor stream channels that allowed fish either to become residents or emigrate in response

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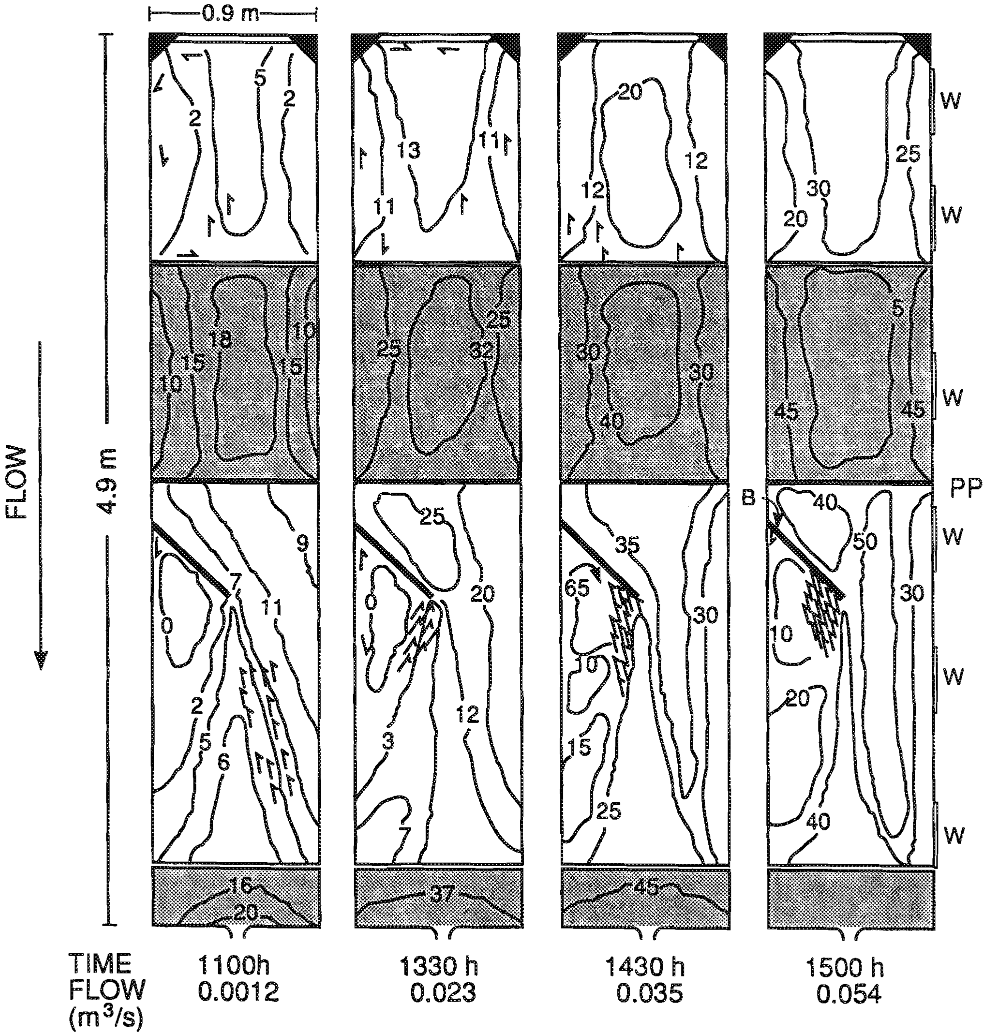

FIG. 1. Stream channel dimensions and representative distribution (arrows) of coho salmon in relation to velocity isopleths (cm/s) before (1100 h) and during (1330, 1430, 1500 h) a simulated freshet in stream channels having a baffle cover structure. PP = plunge pool at pool–riffle interface, W = windows. Shaded sections = riffles, unshaded = pools.

to manipulations of cover features and current velocity. The pair of channels (each $4.9 \times 0.9 \times 0.6$ m) (Fig. 1) was constructed adjacent to Dicks Creek, a tributary of Carnation Creek, a small stream located on the west coast of Vancouver Island (see map, Bustard and Narver 1975a). Channels contained a gravel (2–6 cm in diameter) substrate and two alternating sequences of pools (depth 23.5 cm) and riffles (depth 6.4 cm). A flume carried water from Dicks Creek to a common header box, and water flow into each channel was controlled by boards in the header box and the flume. A dam located at the outlet of Dicks Lake, 1 km upstream from the channels, allowed us to release large quantities of water into the channels to simulate a freshet. A 0.6-cm-mesh screen was placed at the upstream end of the channels to prevent fish from entering the header box. Emigrating fish were captured in a net positioned at the downstream end.

Wild coho used in experiments were captured during December 1985 from the Sarita River (2 km south of Carnation Creek) with baited minnow traps. Fish were held in outdoor tanks supplied with a constant flow of Dicks Creek water and fed frozen euphausids daily. One hour prior to tests, coho were mildly anesthetized in a 2-phenoxyethanol solution and their fork length was measured to the nearest millimetre. At least 1 wk elapsed prior to re-use of fish in experiments.

Cover × Flow Experiments

Four types of cover and two levels of flow were used to test winter cover use. In order of increasing complexity, cover types were:

(A) No cover: channel lacked any in-stream or overhead cover.

(B) Baffle: low velocity refuge as provided by a submerged log was simulated by a 25 × 45 cm plywood sheet attached at a 45° angle to the side of the channel in the upstream half of the second pool.

(C) Baffle/shade: an undercut bank providing both overhead shade and low velocity refuge was simulated by extending a 36×91 cm plywood sheet extending downstream from the top of the baffle, and positioned 5 cm above the water surface.

(D) Baffle/shade/simulated root mass: a debris jam providing low velocity refuge, shade, and a complex of interstitial spaces was simulated by placing a 25 × 36 × 91 cm 'root mass' (six alternating layers of 3–6 cm diameter limbs) beneath the baffle/shade structure.

The two flow levels used in experiments were "low flow" and "high flow," the latter simulating the rising flow pattern of a freshet. During low flow, mean bottom velocity was 15 cm/s in riffles and 3.5 cm/s in pools when no cover (cover type A) was present. During a simulated freshet, mean bottom velocity was 60 cm/s in riffles and 28 cm/s in pools at maximum flow (Fig. 1). Velocity was measured 5 cm above the substrate at three points along six equidistant transects across each channel with a Gurley pygmy current meter. Low and high flows corresponded to average bottom velocities determined from measurements made along pool and riffle transects of Carnation Creek when discharge at the main hydrological weir was at base winter low (0.23 m^3/s) and during a small-magnitude freshet (2.26 m^3/s), respectively. Winter flows in Carnation Creek fluctuate widely and rapidly from about 0.2 m^3/s up to 64.9 m^3/s; annual peak winter flows averaged 35 m^3/s from 1971 to 1986 (Tschaplinski and Hartman 1983; Hetherington 1988).

During each 46-h trial, the type of cover in the experimental channels was the same. At 1100 h on day 1 of an experiment, 20 coho ranging in fork length from 54–77 mm ($\bar{x} = 64.6$ mm) were added to each channel. For the first 24 h, rear exits were blocked and low flows were maintained in both channels to allow fish to acclimate. At 1100 h on day 2, rear exit screens were removed, and fish had the choice of remaining in or leaving channels over the next 22 h. In one channel, low flow was maintained for the remainder of the trial. In the other, fish were exposed to a simulated freshet (high flow) by increasing the release of water from the header box every 30 min from 1300 to 1500 h (Fig. 1). Maximum discharge was then maintained for the remainder of the trial (18 h). At 0900 h on day 3, channels were drained and remaining fish counted and measured.

Two trials of this procedure were performed for each of the four different combinations of cover. The relatively short test period (46-h) was considered representative of the patterns of residency, emigration, and habitat use exhibited by coho over longer periods since fish readily acclimated to experimental conditions (see below). In a more direct test of this assumption, Taylor (1988) found that, over a 1-mo observation period, microhabitat use by coho in laboratory stream channels remained stable after as little as 24 h. The low variation in patterns of cover use and emigration in our experiments lent additional support to our assumption.

Trials were run from 15 December 1985 to 5 March 1986. Fish were not artificially fed during experiments. Natural insect drift entered channels from Dicks Creek. Drift net samples taken from the flume indicated the amount of drift available during an experiment was low. Water temperatures ranged from 2.0 to 8.3°C, but were usually 5–6°C; temperature extremes never exceeded 1.8°C during an experiment. During the winter high flow period in Carnation Creek (October–March), average daily temperatures ranged from 2–9°C and were usually 4–6°C (Bustard and Narver 1975a; Brown and McMahon 1988). Bustard and Narver (1975a) found that cover-seeking behavior of juvenile coho salmon during this period was most pronounced at temperatures <7°C. Moderate increases in turbidity occurred in stream channels during high discharge (actual levels not measured), but declined to a level where an observer could easily see across the channel within 1 h after maximum flow was attained (1600 h).

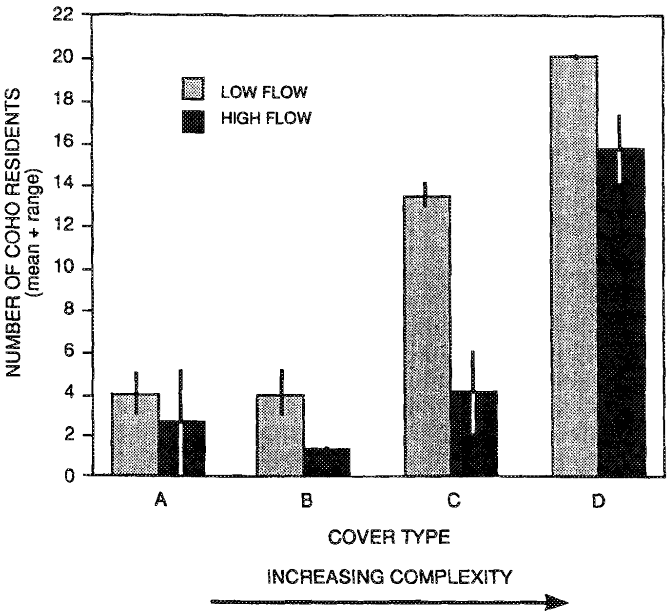

FIG. 2. Mean number (± range) of juvenile coho salmon remaining in stream channels with cover × flow combinations (A) no cover; (B) baffle; (C) baffle/shade; and (D) baffle/shade/root mass.

Fish were observed through slits in black plastic curtains covering six windows located along one side of each channel. Fish appeared to readily acclimate to experimental channels. Fright responses (rapid swimming, rapid breathing, tight grouping, and bleached coloration) subsided within 1 h and normal feeding and aggressive behaviors occurred within 6 h of release. After this 6-h period, observations of cover use, feeding, and aggression were made at least once each morning and afternoon along the length of each channel.

Cover use was defined as the percent of fish in the channel occurring within 15 cm behind or under a cover structure. Cover use was based on observations of ≥15 fish; fish numbers varied due to emigration. Use of cover at high flow was determined during the 2-h period of flow increase. Use of cover by coho inhabiting the darkened shade or simulated root mass cover structures was determined by subtracting the number of fish away from cover from the total number of fish present.

Rates of feeding were determined by counting the number of feeding acts and rates of aggression by counting the number of aggressive acts (nipping, chasing, lateral display, sensu Hartman 1965) observed in groups of 3–15 fish for 10 min during low-flow conditions. Feeding rates of coho in groups of less than three fish were not counted since feeding tended to be sporadic and variable among individuals and hence did not accurately reflect trends in feeding of the entire group of coho inhabiting a channel. Observations of feeding and aggression of fish occupying the shade or simulated root mass cover structures were made on fish occurring along the edge of cover.

Fish behavior was monitored during simulated freshets and their distribution was recorded at least every 30 min during daylight hours. Emigrants were removed from nets and measured at least hourly from 1200–2000 h (every 15 min during periods of high emigration) and again at 0900 h the next morning. Timing of emigration in relation to time of sunset, sunrise, and twilight was calculated from the Nautical Almanac (Anonymous 1986) corrected for the latitude and longitude of Carnation Creek (48°55′N, 125°00′W).

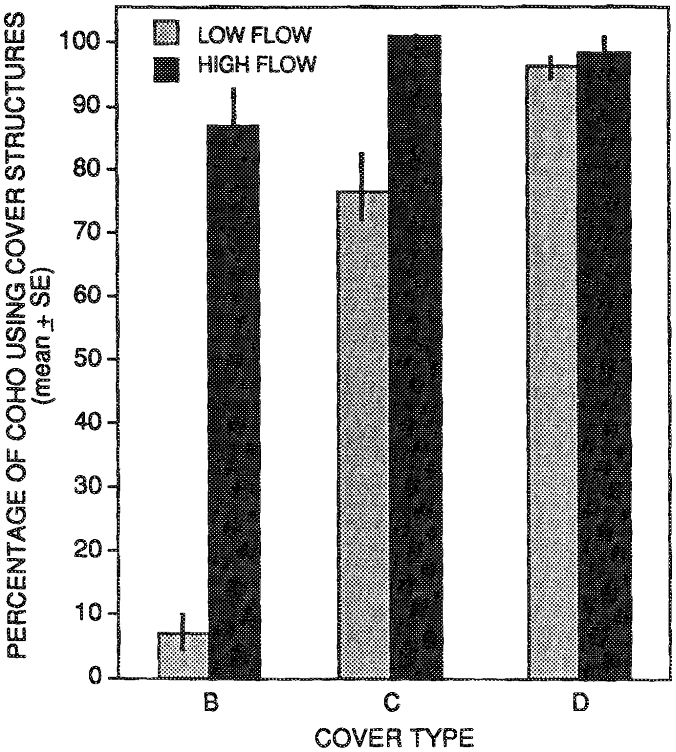

FIG. 3. Mean percentages (±SE) of coho salmon using cover types (B) baffle; (C) baffle/shade; and (D) baffle/shade/simulated root mass at low and high flows.

Results

The number of coho remaining in stream channels (Fig. 2) varied significantly among cover types (Friedman's two-way ANOVA, Zar 1984; $\chi_r^2 = 11.37$, $p<0.01$) and flow levels ($\chi_r^2 = 7.0$, $p<0.01$). During low flow trials, less than five coho remained in channels when no cover or a baffle was present. The number of residents increased markedly with the addition of overhead shade. When the root mass was added, all 20 fish introduced at the start of the experiment remained in the channels. Further, few coho remained in channels during a freshet unless the baffle/shade/root mass structure was present. Pairwise comparisons of each cover × flow treatment demonstrated that, at both high and low flows, significantly more coho remained in channels during trials with the root mass than when other cover types were available (Fig. 2; Duncan's multiple range tests on ranked data, $p<0.05$).

Coho behavior and distribution also varied with cover type and flow. At low flow, during trials with either no cover or a baffle present, coho occurred in front or rear pools in aggregations of >15 individuals, where water velocity was 2–7 cm/s; no fish were observed in riffles and only a few were observed in the lee of the baffle where velocity was near zero (Figs. 1 and 3). When overhead shade was added, coho use of the cover structure increased significantly (arcsine transformation of percentages, $t = 9.21$, $df = 18$, $p<0.001$). Cover use increased significantly again when the baffle, shade, and simulated root mass were combined ($t = 2.47$, $df = 18$, $p<0.05$) (Fig. 3). At low flow, therefore, increased use of cover was accompanied by an increase in the number of fish remaining in channels. Cover use was similar when channels were closed (during acclimation) or open to emigration (t-tests, $p>0.3$).

As water velocity was increased during a simulated freshet, use of cover also increased (Figs. 1 and 3). During no cover trials, coho oriented downstream in the plunge pool at maximum flow, but had difficulty maintaining position in the turbulence, and most fish later emigrated from the channel. During trials with a baffle or a baffle/shade structure, fish formed a tight group that swam against the eddy behind the baffle (Fig. 1). Bottom velocity at this location averaged 10 cm/s at maximum flow; however, high turbulence made it difficult for coho to maintain position. In contrast, the addition of a simulated root mass to the baffle/shade structure provided an effective refuge from high velocity and turbulence. At maximum flow, water velocity in the downstream half of the cover structure was 14 cm/s, but velocity and turbulence directly behind the baffle was near zero.

Emigration occurred predominantly during twilight (Fig. 4). Seventy-five percent of the total number of coho emigrating from channels during a freshet and 61% of the total emigrating from channels with low flow did so during the period of rapidly decreasing light intensity from 30 min before to 60 min after sunset; an additional 23% of coho emigrating from channels with low flow left early the next morning. This emigration pattern was consistent throughout the experimental period, despite a progression in the time of sunset of ~90 min.

Physical displacement of coho by high current velocities did not appear to be the primary cause of emigration during simulated freshets. During a freshet, coho maintained their position in the lee of a baffle or in the plunge pool, but as light levels decreased they swam higher in the water column and then were swept downstream. Only 17% of all emigrants from high flow channels (18 of 105) left channels during the ~4 h period of high flow before sunset (Fig. 4) and only four fish were found impinged on the rear screen that covered most of the downstream end of the channels. Few fish left channels during the ~2 h period of higher turbidity following the increase in flows (Fig. 4).

Feeding and aggression occurred during all trials and were observed at temperatures as low as 2.5°C. Neither rates of feeding (means = 1.4–4.7 acts per 10 min; Kruskal–Wallis one-way ANOVA, $H = 2.38$, $P = 0.49$) nor aggression (means = 0.6–1.2 acts per 10 min; $H = 1.79$, $P = 0.41$) differed significantly between trials with different cover types. Aggression was less pronounced and less frequent than that reported at higher temperatures (Hartman 1965; Glova 1986), occurring most frequently when one to two fish excluded all others from territories established during brief (<30 min) feeding bouts at the interface of fast and slow currents near the edge of cover. When the root mass was present, coho were evenly distributed within the structure ~15–20 cm apart and defended small areas around these sites primarily by erecting the dorsal fin whenever another fish swam close by, and occasionally by nipping or chasing intruders.

Size differences between residents and emigrants were not significant in most trials (Table 1). Residents tended to be smaller than emigrants in trials lacking the root mass and larger than emigrants when the root mass was present, but in only three trials were differences statistically significant. The four coho found impinged on the rear screen during a freshet were all in the smallest 5-mm size range used, suggesting that small coho were most susceptible to downstream displacement.

Discussion

Structurally complex accumulations of large wood are an important component of winter habitat for juvenile coho

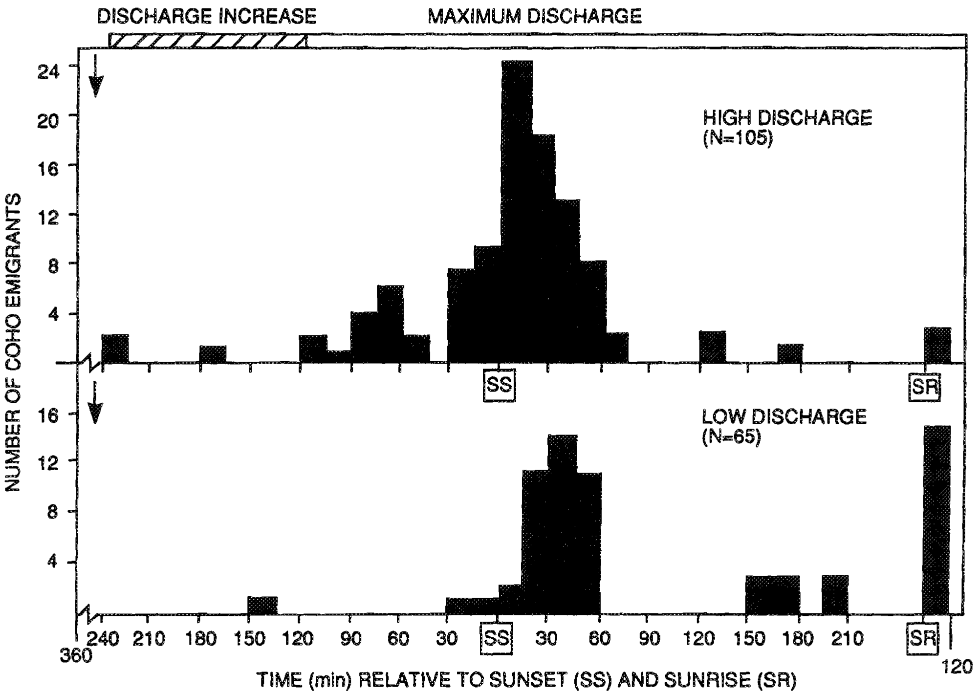

FIG. 4. Number of coho salmon emigrating from stream channels in relation to time of day during both high- and low-flow trials. Data combined for the eight trials at each flow level (N = total number of emigrants). Vertical arrow indicates when rear exit screens were removed.

TABLE 1. Mean lengths and differentes (t-test) between mean lengths of resident and emigrants coho salmon in cover × flow experiments (number of fish in parentheses). Initial refers to fish introduced into stream channels at the start of the experiment.

Cover[a] × flow[b] treatment	Mean fork length (mm)			t
	Initial	Residents	Emigrants	
A × LF	62.8	56.0 (3)	63.8 (17)	2.45[c]
	66.1	61.0 (5)	66.8 (15)	−1.57
A × HF	62.8	— (0)	62.8 (20)	—
	66.1	65.8 (5)	66.3 (15)	−0.15
B × LF	63.1	58.0 (3)	66.3 (17)	2.16[c]
	68.5	65.8 (5)	69.6 (15)	−1.14
B × HF	63.8	53.0 (1)	63.8 (19)	—
	66.0	64.0 (1)	66.0 (19)	—
C × LF	63.1	64.3 (13)	61.6 (7)	+0.43
	66.5	64.6 (14)	70.7 (6)	2.15[c]
C × HF	63.3	59.5 (2)	64.8 (18)	−1.09
	66.4	63.8 (6)	67.0 (14)	−1.07
D × LF	66.8	66.8 (20)	— (0)	—
	66.1	66.1 (20)	— (0)	—
D × HF	65.9	66.4 (14)	65.0 (6)	+0.33
	66.0	66.6 (17)	62.0 (3)	+1.15

[a] A = no cover, B = baffle, C = baffle/shade, D = baffle/shade/root mass.

[b] LF = low flow, HF = high flow.

[c] $p < 0.05$.

salmon. The results of our experiments support previous field and experimental studies which demonstrated that during winter coho occupy pools and undercut banks containing large wood or root wads and are generally absent from main-channel habitats lacking such cover (Bustard and Narver 1975a,b; Tschaplinski and Hartman 1983; Heifetz et al. 1986; Brown and McMahon 1988). Our study demonstrated that coho abundance increased as cover complexity increased, with only the most complex structure supporting significant numbers of fish during simulated freshets. As in studies of cover selection in brown trout (*Salmo trutta*; Hartman 1963), we found that the most suitable winter cover for coho combined all three environmental features of low velocity, shade, and three-dimensional complexity.

Cover requirements of coho during winter differ from, and are generally more restrictive than those during summer. In summer, coho occupy a wide range of stream habitats, including pools, side channels, glides, and the edges of riffles (Bisson et al. 1982; McMahon 1983; Murphy et al. 1986). Current velocity is often considered the primary variable governing microhabitat selection by salmonids during summer (e.g. Shirvell and Dungey 1983; deGraaf and Bain 1986). We found that slow current velocities are important to coho in winter habitat selection, but only when in conjunction with cover that provides shade and three-dimensional complexity (see also Bustard and Narver 1975a). The preference by coho for shade during winter contrasts sharply with Ruggles' (1966) findings that the number of resident coho decreased by nearly 50% during summer when overhead shade was added to his experimental channels. Such a response may be related to a general increase in photonegative behavior among salmonids during winter (Bustard and Narver 1975a; Cunjak 1988).

Shifts into high cover, low velocity microhabitats during winter appear to be characteristic of many stream-dwelling salmonids (Chapman and Bjornn 1969; Bustard and Narver 1975a; Rimmer et al. 1984; Cunjak and Power 1986). Types of cover utilized as overwintering habitat vary depending on species, fish size, temperature, and hydrologic regime (Bustard 1986; Cunjak and Power 1986). In addition to their use of large woody debris as winter habitat, coho also overwinter in lakes and in off-channel ponds, swamps, sidechannels, and tributaries (Peterson 1982a, 1982b; Swales et al. 1988; Hartman and Brown 1988). In these habitats, too, coho are found in close association with woody debris or other types of complex cover such as emergent vegetation.

We observed two behaviors in coho that would minimize displacement during winter freshets. First, there was a strong preference for structurally complex cover; second, as velocities increased, coho shifted to the lowest-velocity microhabitats available and then emigrated (chiefly during twilight) from areas that failed to provide shelter from high turbulence. Movements of coho from sites lacking wood into areas having suitable winter habitat have been described for a number of streams coincident with declining temperatures and increasing flows in autumn (e.g. Peterson 1982a, 1982b; Tschaplinski and Hartman 1983; Brown and McMahon 1988). Emigration from these areas during twilight may serve to decrease mortality from visual predators during shifts in habitat (Helfman 1981a).

In coastal streams, these behaviors are undoubtedly important for survival of young coho during winter when freshets are common and swimming abilities are reduced. Based on data from Glova and McInerney (1977), we calculated that at 3°C the critical swimming speed of coho 60-mm long is 22 cm/s, ~50% less than that at summer temperatures (18–23°C). Bottom velocity in open pools and riffles in Carnation Creek commonly exceeds this level even during relatively small freshets (e.g. 2.26 m^3/s). Both this study and that of Tschaplinski and Hartman (1983) indicate that debris serves to dissipate the energy of flowing water and create pockets of shelter from high current velocities. In a recent analysis of pool-forming features in various coastal streams in Oregon, Kaufmann (1987) found that the size of pools and the volume of low velocity zones present at high flows was positively related to the structural complexity of debris.

Use of structurally complex cover by coho salmon during winter is likely also to minimize predation risk (Werner et al. 1983). A. Dolloff's (U.S. Forest Service, Blacksburg, VA 24061, pers. comm.) recent count of 230 juvenile coho salmon and Dolly Varden charr (*Salvelinus malma*) otoliths in one river otter scat collected next to a beaver pond in southeast Alaska points to the potentially high predation rates on coho during winter. The preference of coho for shade as shown in our study may also minimize predation by providing camouflage and by enhancing detection of predators (Helfman 1981b).

Although aggression diminishes in winter and coho commonly form aggregations under cover (Hartman 1965; Mason 1965; Glova 1986, this study), we found that coho continue to exhibit agonistic behaviors. High structural complexity of wood debris may serve an additional function of reducing the frequency of agonistic interactions by increasing the visual isolation of individual fish (Dolloff 1986). This may explain the significant increase in numbers of coho of all sizes remaining in stream channels when the root mass was added to the baffle/shade cover structure.

The results of our experiments emphasize the importance of protecting and/or enhancing the structural complexity of wood debris for proper management of coho salmon habitat. The abundance and structural integrity of wood debris can be substantially reduced after streamside logging, stream cleaning, and other forest management practices (Bisson et al. 1987). In Carnation Creek, stream reaches impacted by logging had 93% less wood volume and a 75% fewer overwintering coho than nonimpacted reaches (Tschaplinski and Hartman 1983; Brown and McMahon 1988). Since accumulations of large wood remain low for at least 50 yr after debris loss (Grette 1985; Martin et al. 1986; Andrus et al. 1988), winter habitat for coho salmon in the mainchannels of debris-impoverished streams is likely to be reduced for many decades. Winter habitat for coho can best be maintained during and after logging by leaving wood debris in the stream and ensuring its continued recruitment by leaving buffer strips of trees along streambanks (Tschaplinksi and Hartman 1983; Heifetz et al. 1986). Protecting clumps of trees along certain stream sections could increase the possibility that natural processes of windthrow and bank undercutting introduce wood into the channel in multiple configurations (Sedell et al. 1984; Bisson et al. 1987).

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