Summer Distribution, Survival, and Growth of Juvenile Coho Salmon under Varying Experimental Conditions of Brushy Instream Cover

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Abstract.—Woody debris is an important feature of streams, and its presence and abundance have been correlated with the abundance, growth, and survival of juvenile salmonids. To investigate the proximate mechanisms linking brushy woody debris to salmonid fishes, we determined, over a 1-month period in summer, the spatial distribution of juvenile coho salmon Oncorhynchus kisutch introduced into an outdoor experimental stream containing riffle-pool units that had one of four different levels of instream brushy-debris complexity. We then equalized the fish density in each unit and monitored fish growth and survival over a 15-week period. Coho salmon distribution, growth, and survival varied greatly but were not consistently related to the complexity of brushy debris.

Streams in unlogged, forested watersheds are characterized by abundant woody debris (Bilby and Ward 1989, 1991). As a result of the removal of mature streamside forests and regrowth dominated by alder, the amount and character of woody debris in streams that drain managed forests often differ from that in unmanaged forests (Bisson et al. 1987). Other practices, such as stream cleaning and log handling (Sedell et al. 1991), as well as storm-related debris flows, have also contributed to the loss of woody debris from streams. The effects of woody debris reduction on streams have been substantial. Large material can affect the stream's depth, flow, and the routing of sediment and finer organic material (Elliott 1986; Bisson et al. 1987; Andrus et al. 1988; Bilby and Ward 1989, 1991; Carlson et al. 1990). Smaller brushy debris may trap fine sediment, provide cover from predators, and visually isolate salmonids from each other, which may affect levels of aggression (Mesick 1988; Dolloff and Reeves 1990).

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Field studies often relate the density of juvenile stream-dwelling salmonids to the presence of woody debris (e.g., Dolloff and Reeves 1990; Bugert et al. 1991), to pools or hydraulic conditions associated with large pieces of wood (e.g., Bisson et al. 1988; Shirvell 1990; Taylor 1991; Fausch and Northcote 1992), or to food resources associated with woody debris (Nielsen 1992). However, it is not always clear whether the wood has affected the survival of fish or their distribution. Laboratory studies have demonstrated that salmonids, particularly coho salmon Oncorhynchus kisutch, show an affinity for pools (Bugert and Bjornn 1991; Taylor 1991) or complex cover (McMahon and Hartman 1989), but the link between these responses and survival in the field is weak. Although loss of woody debris from streams may reduce the abundance of juvenile salmonids (Elliott 1986; Dolloff 1986), growth and production, particularly in summer, may also be strongly influenced by temperature (Holby 1988), prey populations (Murphy et al. 1986; Bilby and Bisson 1987, 1992), fry density, freshets, and interactions among these factors (e.g., Scrivener and Andersen 1984).

Woody material is related to the ecology of juvenile stream-dwelling salmonids in complex ways (Bisson et al. 1987; Hartman et al. 1987). Only large woody material will structure the stream and form pools, but both large and smaller brushy wood may provide protection from predators, though this has not been clearly demonstrated (Bisson et al. 1987). To the extent that woody material provides relief from predation, it may enable fish to spend more time pursuing prey or allow them to forage more effectively (Dill 1983; Metcalfe et al. 1987; Angradi 1992). In-stream structure may also create velocity patterns that provide energetically efficient foraging stations for salmonids (Fausch 1984, 1993), and wood need not be very large to affect local velocities. Woody ma-
material may also be related to prey abundance and growth (Nielsen 1992).

Thus, woody debris may directly affect fish behavior and population characteristics and indirectly affect fish by altering stream channels. The relative importance of the effects of woody debris may vary with its size and characteristics (McMahon and Hartman 1989; Fausch 1993). Time of year strongly affects salmonid affinity for cover. Coho salmon, for example, are much more attracted to cover in winter than in summer (Bustard and Narver 1975; Murphy et al. 1986; Taylor 1988), coincident with a general tendency to seek off-channel rearing areas (Bustard and Narver 1975). Within species, age may affect cover use. Juvenile Dolly Varden Salvelinus malma and coho salmon showed increasing affinity for deep water and cover as they grew (Dolloff and Reeves 1990). Finally, there are important differences among salmonid species in their responses to cover (Bustard and Narver 1975; Bisson et al. 1988; Taylor 1988, 1991; Dolloff and Reeves 1990; Bugert and Bjornn 1991; Fausch 1993).

To clarify the role of brushy woody debris in the summertime ecology of juvenile coho salmon, we conducted experiments in seminatural experimental stream channels. We tested the hypotheses that fish distribution, growth, and survival are affected by the complexity of brushy material in otherwise similar, unstructured pools. We first conducted a fish distribution experiment, allowing fry to move throughout two channels with riffle-pool units that differed in debris complexity. We then isolated the units, equalized the densities of fry, and conducted a growth and survival experiment.

Methods

Experiments were conducted in a seminatural experimental stream receiving water from Big Beef Creek in Kitsap County, Washington (average flow at the inlet 0.02 m$^3$/s). During the experiment, groundwater and additional water from springs emanating from the hillside increased stream flow to an average of 0.05 m$^3$/s at the outlet. The experimental stream was 34 m long, 9 m wide, and divided longitudinally to create two parallel channels, designated A and B. Each channel consisted of seven riffle-pool units, designated 1–7 from upstream to downstream. The riffles were 2.4 m wide, 1.8 m long, and 0.05 m deep, and they flowed into 3 × 3-m pools with a maximum depth of 0.5 m. The substrate was gravel similar in size to that in Big Beef Creek (geometric mean diameter, 35 mm). The seven units in each channel could be separated by screens set on wooden sills or left open to permit fish movement between units. However, fish could not move from one stream channel to the other.

The canopy and streamside vegetation were composed of red alder Alnus rubra, western redcedar Thuja plicata, and salmonberry Rubus spectabilis. Canopy closure (measured with a spherical densiometer) averaged greater than 90% for all pools. All food came from natural aquatic and terrestrial production. Drifting aquatic invertebrates were sampled six times from each pool with a 1-m long by 0.5-m wide drift net with 240-μm mesh placed at the bottom of the riffle at dusk and removed 3 h later. Water depth and velocity were measured at the net openings at the beginning and end of each sampling period. Qualitative samples of terrestrial invertebrates were taken during 3-h periods with 36 × 23-cm pans (containing water and a detergent surfactant to prevent insects from escaping) placed on stakes above the surface of the pool, 10 cm downstream of the riffle. Water temperature was recorded and averaged with a data logger every 30 min in 10 of the 14 units.

Douglas fir “Christmas trees,” rather than large, channel-forming debris, were used as replicable debris to simulate tree tops or material left after logging operations. The needles were removed from the trees, and they were sheared in half along the long axis and cut to a length of 1.5 m from the natural top. The trees were then modified to create four different degrees of cover complexity (Figure 1). In the “simple” treatment, all the branches were removed from the tree, leaving only a trunk that tapered from a diameter of about 10 cm to a spike. In the “half-complex” treatment,
branches were alternately removed or retained every 15 cm up the trunk. In the “complex” treatment, all branches (except those on the sheared side) were left on, and in the “double-complex” treatment, two complex trees were stacked and tied together. One treatment tree was staked into each pool 0.5 m below the tail of the riffle and 2 cm below the water surface. The sheared side faced upward so that no branches extended above the water; no other cover was present in the units. Treatment types were randomly assigned to the stream channel units.

To initiate the fish distribution experiment, we collected 807 newly emerged coho salmon fry (mean size of a subsample of 60 on May 8 was 43.6 mm total length and 1.02 g) from Big Beef Creek from April 23 to May 8, 1991. We released 52 or 53 fry into each unit, except that the uppermost unit in each stream channel received an additional 32 fry to ensure adequate colonization of all treatment units after the anticipated downstream distribution of fry. Live boxes were installed below the bottom units to trap out-migrant fry. Eighteen fry emigrated between May 6 and 11 and were placed in the uppermost unit of their stream channel. The decision to return these fish to the stream was based on the concern that high rates of emigration or mortality might result in inadequately populated units for experimental design and statistical analyses, once the redistribution period had ended. However, only one other fry was trapped and relocated upstream during the remainder of the experiment. The distribution experiment ended on May 22; barriers were placed between all units and the fry were removed, counted, and sorted into 5-mm size-classes.

On May 23, we placed 56–57 coho salmon fry (mean size, 48.2 mm and 1.26 g) from the distribution experiment in each of the 14 units for the growth and survival experiment. All fry were measured, and equal numbers from each size-class were placed into each unit. Unlike the distribution experiment, screened barriers prevented movement between units. On September 3, all fish were removed from the units, measured, and weighed. A few juvenile sea-run cutthroat trout *O. clarki* colonized the stream channels during the growth and survival experiment. These cutthroat trout were initially much smaller than the coho salmon (they apparently entered the units through the mesh screen), but by the end of the experiment they were comparable in size to the coho salmon. Accordingly, our analysis of density-related growth of coho salmon included the cutthroat trout, but they were excluded from our computation of survival rates. Finally, daytime observations of predation were made from a blind situated at the downstream end of the stream on 36 occasions (154 h total) during the growth and survival experiment.

### Results

At the end of the distribution experiment, 788 of the 807 fry stocked were recovered; their density varied among units (*χ^2* = 31.78 and 62.64 for channels A and B, respectively; df = 6; *P* < 0.001 in both cases; Table 1). The densities of fry in the four treatments were also significantly different (*χ^2* = 15.70, df = 3, *P* < 0.001). Units with simple brushy debris had higher-than-average density (68.5 fry per unit), but densities in the other treatments were similar (50.7, 54.7, and 49.5 fry per unit in the half-complex, complex, and double-complex treatments, respectively). The high average density observed in simple treatments may have been partly related to the locations of those units; units at the top of one channel and the bottoms of both channels had higher than expected densities, and two of these were simple units.

In the growth and survival experiment, fry sur-
Table 2.—Survival and final weights (mean starting weight, 1.26 g) of coho salmon fry in experimental riffle–pool units, which are grouped by treatment type (see Table 1).

<table>
<thead>
<tr>
<th>Unit</th>
<th>Number of fry</th>
<th>Mean coho salmon weight (g)</th>
<th>Coho salmon biomass (g)</th>
<th>Number of cutthroat trout</th>
<th>Total biomass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Stocked</td>
<td>Recovered</td>
<td>Percent survival</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A4</td>
<td>56</td>
<td>47</td>
<td>83.9</td>
<td>3.3</td>
<td>154.0</td>
</tr>
<tr>
<td>A7</td>
<td>57</td>
<td>47</td>
<td>82.5</td>
<td>3.4</td>
<td>162.0</td>
</tr>
<tr>
<td>B1</td>
<td>56</td>
<td>36</td>
<td>64.3</td>
<td>4.9</td>
<td>174.8</td>
</tr>
<tr>
<td>B6</td>
<td>56</td>
<td>41</td>
<td>73.2</td>
<td>3.4</td>
<td>141.3</td>
</tr>
<tr>
<td>Total</td>
<td>225</td>
<td>171</td>
<td>76.0</td>
<td>3.7</td>
<td>632.1</td>
</tr>
</tbody>
</table>

**Simple brushy debris**

| A3   | 56            | 35                          | 62.5                   | 4.6                       | 160.9            | 165.5            |
| B2   | 57            | 36                          | 63.2                   | 4.9                       | 174.9            | 174.9            |
| B7   | 56            | 46                          | 82.1                   | 3.2                       | 147.0            | 206.3            |
| Total| 169           | 117                         | 69.2                   | 4.1                       | 482.8            | 546.7            |

**Half-complex brushy debris**

| A5   | 56            | 44                          | 78.3                   | 3.3                       | 145.7            | 154.2            |
| B4   | 56            | 38                          | 67.9                   | 3.8                       | 144.0            | 149.4            |
| Total| 168           | 118                         | 70.2                   | 3.7                       | 437.9            | 506.3            |

**Complex brushy debris**

| A2   | 56            | 51                          | 91.1                   | 3.0                       | 150.9            | 167.8            |
| A6   | 57            | 48                          | 84.2                   | 3.3                       | 158.9            | 167.8            |
| B3   | 56            | 39                          | 69.6                   | 4.8                       | 188.1            | 188.1            |
| B5   | 56            | 39                          | 69.6                   | 4.1                       | 160.1            | 160.1            |
| Total| 225           | 177                         | 78.7                   | 3.7                       | 658.0            | 683.8            |
| Overall total | 787       | 583                         | 74.1                   | 3.8                       | 2,210.8          | 2,390.4          |

Coho salmon growth in the units was comparable to that observed for free-ranging coho salmon in Big Beef Creek that season. The experimental fry averaged 3.8 g on September 2 and fry in the creek averaged 4.2 g on October 5 (N = 717; Peterson and Quinn, unpublished data). Growth varied among units, final mean weights ranging from 3.0 to 4.9 g (Table 2). Weights of individual coho salmon varied in units within treatments (F = 16.39, P < 0.001) and among treatments (F = 3.52, P = 0.015). However, growth variation among treatments was not related to the degree of cover complexity (mean fry weights: simple, 3.7 g; half-complex, 4.1 g; complex, 3.7 g; double-complex, 3.7 g). Growth was negatively related to coho fry density (Spearman's rank correlation, ρ = -0.853, P < 0.001), consequently the variation in coho salmon biomass among units (141.3–188.1 g) was less than the variation in mean fry weight (1.33-fold versus 1.63-fold).

The mean number of cutthroat trout was 3.5 per unit, and only two units held more than 5 (13 and 19 cutthroat trout). The abundance of cutthroat trout showed no pattern with respect to cover complexity. They grew to an average of 3.7 g and were a substantial component of the fish biomass in the two units where they were numerous. However, analysis of total fish density and coho salmon biomass showed the same density-dependent pattern indicated by analysis of coho salmon density alone (Spearman's rank correlation, ρ = -0.842, P < 0.001; Figure 2).

Daytime peak temperatures rose from about 10 to 12°C during the distribution experiment and from 12 to 20°C during the growth and survival experiment. Temperatures in the units followed similar diel and seasonal patterns, but the lowermost unit in channel A tended to be 1–2°C cooler than the upstream units. However, temperatures in
the units seemed to play no role in distribution or growth. The dry weight of invertebrate drift did not differ between the two channels (t-test, \( P = 0.76 \)) or among units (analysis of variance, \( P = 0.62 \)). Qualitative assessment of invertebrate fall-in indicated that this food resource was also similar among units.

Three avian predators were seen at the stream during the 154 h of observations. Belted kingfishers \( Ceryle alcyon \) made 10 strikes on coho salmon fry in the channel, and at least 3 were successful. A green-backed heron \( Butorides striatus \) was seen on two occasions and eight fry were killed. Two visits by great blue herons \( Ardea herodias \) were observed, but no attacks took place. This species is common in the area but was more often seen in the estuary downstream from the stream.

**Discussion**

We found no evidence that coho salmon fry were attracted to brushy debris, nor did the presence of brush influence survival or growth. Temperature and food abundance were similar among units and hence can be ruled out as factors that might have confounded or biased the results (Wilzbach 1985). The woody debris typically described in field studies is larger than that used in this experiment. Attraction to such large material may reflect the ability of wood to structure the flow, depth, and productivity of stream habitats more than the affinity of coho salmon for woody debris per se or any benefits in growth or foraging efficiency associated with the wood. Shirvell (1990) concluded that the velocity refuge provided by woody structures was the primary factor determining the location of coho salmon and steelhead \( Oncorhynchus mykiss \). Average velocities in our pools (about 15 cm/s) may have been too low for the debris to have served as velocity refuges.

In addition to the relatively small size of the wood and low water velocity in the experimental stream, the results were probably influenced by the season. The affinity of coho salmon for woody debris increases in winter (Bustard and Narver 1975; Heifetz et al. 1986; Murphy et al. 1986; Taylor 1988), and our experiments were carried out in summer. Moreover, attraction to cover seems to increase as coho salmon grow (e.g., Dolloff and Reeves 1990), and our experiments were initiated early in their first year. It is also possible that the experimental units did not accurately mimic natural conditions, so that aberrant growth and survival rates invalidated the results. However, coho salmon growth in the treatment units was comparable to that observed in free-ranging coho salmon in Big Beef Creek that season. We observed density-dependent growth in the treatment units, which indicated competition for food, but we have evidence of this in Big Beef Creek as well. Densities in the treatment units (4.6 fry/m² pool) were higher than those generally observed in Puget Sound streams during the summer (e.g., Nielsen 1992).

The survival rate of 74% from 23 May until 2 September may also be higher than might be expected in natural streams. However, there was significant predation; successful attacks by kingfishers and green herons were observed, and other predators (great blue herons, river otters \( Lutra canadensis \), raccoons \( Procyon lotor \), and common mergansers \( Mergus serrator \)) were seen near the experimental channels during the summer. The 154 h of observation constituted approximately 10% of the daytime period (given about 15 h of daylight per day) during the 103 d of the study. The 11 successful attacks observed, if expanded 10-fold, accounted for over half the 204 fish that disappeared during the study. Undoubtedly some predation occurred at night and during crepuscular periods when no observations were made.

That mortality was unaffected by cover complexity must be interpreted in the context of the size and configuration of the pools (50 cm deep).
The affinity of coho salmon for pools (e.g., Bisson et al. 1988; Bugert et al. 1991; Taylor 1991) suggests that we might have detected changes in distribution, survival, or both had the pools been shallower. Subsequent experiments with 50- and 25-cm pools indicated that coho salmon distribution and survival were strongly influenced by an interaction between depth and cover (Lonzarich 1994). Moreover, Atlantic salmon _Salmo salar_ and brook trout _Salvelinus fontinalis_ were attracted to overhead cover in shallow (24–29-cm) pools, but not in deep (43–50-cm) pools (Gibson and Power 1975).

Brushy debris in the experimental channels (and natural streams) may be relatively ineffective in providing escape refuge from the most common predators we observed. The nature of attacks by belted kingfishers and herons (surprise and stealth, respectively) may make them difficult for stream fishes to prevent. Angradi's (1992) experiments with rainbow trout indicated that threats from avian predators resulted in only a brief suspension of feeding, followed by the rapid resumption of normal behavior and no net loss of food intake. The survivorship benefits associated with wary behavior and maintenance of a feeding station near cover may be outweighed by the inferior growth opportunities, relative to feeding stations in more open areas of the stream. Fish predators, on the other hand, may pose a more constant threat, and cover may play a different role for small fish in the presence of piscivores (Billby and Fraser 1987; Angradi 1992). In light of these experiments, our results indicate that the major benefit to coho salmon of woody debris in streams is pool development, which small brushy material cannot produce.

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NOTES


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