Large Woody Debris and Salmonid Habitat in a Small Coastal British Columbia Stream

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Sections of a small coastal British Columbia stream that had previously been cleaned of large woody debris (LWD) were compared with sections where most debris was left and with others where debris had been relatively undisturbed for at least 40 yr. Three sections where debris had been removed had simple habitat that was less sinuous, wider, and shallower and had less pool volume and overhead cover than four sections with more complex habitat where debris was retained. Habitat in four relatively undisturbed sections was generally similar to complex sections. Most pools in all sections were scour or plunge pools formed by LWD or large roots oriented perpendicular to the flow or angled downstream. Standing crop (kolograms per hectare) and individual weights of age 1+ and older coho salmon (*Oncorhynchus kisutch*) and cutthroat trout (*O. clarki*) were significantly greater ($P < 0.02$) in complex than in simple sections. Biomass of age 1+ and older salmonids was closely related to section pool volume ($r^2 = 0.92$, $P = 0.0006$). Projections based on this model and average habitat conditions suggest that during 1990 a total of 8.0 kg of salmonid biomass, 5 times the current standing crop, was forgone in the 332-m simple reach due to prior debris removal.

Des segments d'un petit cours d'eau côtier de la Colombie-Britannique dans lesquels on a récemment retiré les gros débris de bois ont été comparés à des segments où la plupart des débris ont été laissés en place, et à d'autres dont les débris n'ont pour ainsi dire pas été touchés depuis au moins 40 ans. Par rapport à quatre segments où les débris n'ont pas été retirés et présentant un habitat complexe, trois segments dont les débris n'ont pas été retirés et présentant un habitat complexe, trois segments dont les débris avaient été retirés présentaient un habitat simple, moins sinueux, plus large, moins profond et ayant un volume de fosses et un couvert végétal plus faible. L'habitat dans quatre segments relativement peu perturbés était généralement semblable à celui des segments à habitat complexe. La plupart des fosses dans tous les segments étaient des fosses creusées par affouillement ou par une chute d'eau attribuables à la présence de gros débris de bois ou de grosses racines perpendiculaires au sens d'écoulement ou formant un angle ouvert vers l'aval. La biomasse totale (kilogrammes par hectare) et les poids individuels des saumons cohos (*Oncorhynchus kisutch*) et des truites fardées côtières (*O. clarki*) d'âge 1+ et plus dans les segments complexes étaient supérieurs ($P < 0,02$) à ceux mesurés dans les segments à habitat plus simple. La biomasse des salmonidés d'âge 1+ et plus était fortement corrélée au volume total des fosses des segments ($r^2 = 0,92$, $P = 0,0006$). Les prévisions fondées sur ce modèle et sur les conditions moyennes des habitats laissent entendre qu'au cours de 1990, la biomasse de salmonidés dans le segment simple de 332 m a été réduite de 8,0 kg, ce qui représente 5 fois la biomasse totale actuelle, après qu'on y ait retiré des débris.

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Large woody debris (LWD) that enters forested streams plays important roles in shaping channel morphology (Keller and Swanson 1979; Bisson et al. 1987; Robison and Beschta 1990a, 1990b). Channels shaped and maintained by LWD in turn form the habitat templet (Southwood 1977) to which salmonids and other aquatic biota in Pacific Northwest streams have evolved (Sullivan et al. 1987).

Human activity in the riparian forest frequently reduces the amount of LWD that enters or persists in stream channels. This occurs either indirectly by deforesting the riparian zone that is the source of LWD, or by direct removal of debris from streams. Both are especially detrimental in streams near urban areas where standing dead trees are removed due to the perceived hazard to human life and property, and fallen debris is more or less continuously removed for firewood or "cleaned up" for misguided aesthetic reasons. This cumulative debris removal is expected to greatly alter channel morphology and the biotic processes that depend on it.

We studied the role of LWD in forming salmonid habitat in a stream that traverses second-growth forest near the city of Vancouver, British Columbia. Our primary hypothesis was that sections where debris had been removed would have fewer pools and harbor fewer salmonids compared with those left uncleaned.

Study Area

The Musqueam–Cutthroat Creek system (Fig. 1), adjacent to the city of Vancouver, British Columbia, drains a 730-ha watershed that is underlain by glacial till and sediments of marine origin (Armstrong 1956; Anonymous 1981). Both

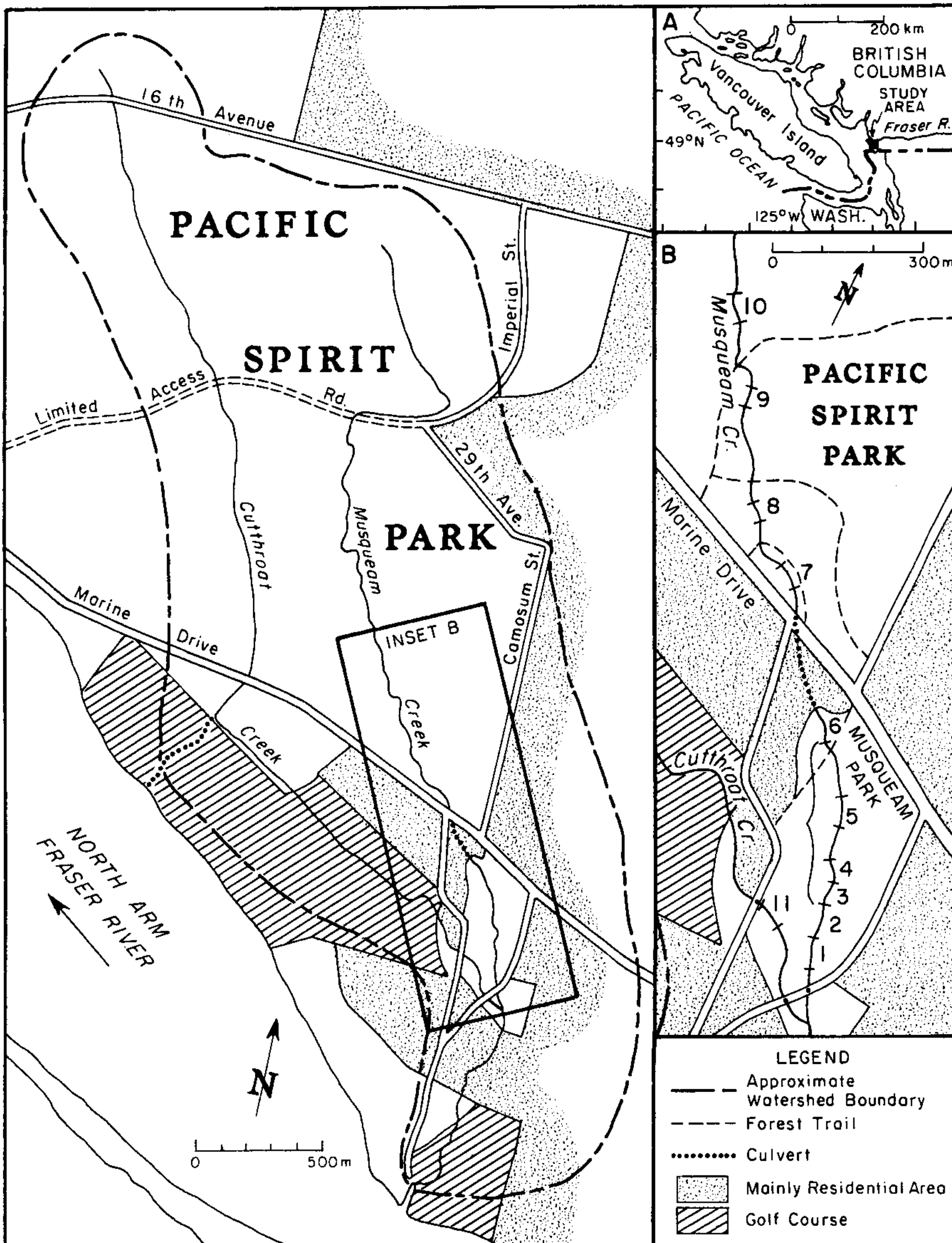

FIG. 1. The Musqueam–Cutthroat Creek watershed. Stippling indicates lands that are mainly residential, and hatching shows golf courses. Inset A shows the location of the study area near Vancouver, British Columbia, and inset B shows the study sections in Pacific Spirit Park and Musqueam Park. The bracket in Musqueam Park shows the reach where LWD was removed. Long culverts beneath Marine Drive are probably impassable to all fish, and the culvert immediately upstream from section 11 is probably impassable to all but adult coho salmon (see text).

streams arise in bogs on the uplands (130 m above sea level) and originally downcut through 30-m-high coastal cliffs to a tidal marsh. Discharge varies from maxima in fall or winter that reach 6.5 $m^3 \cdot s^{-1}$ (Anonymous 1981) to late summer minima as low as 0.0002 $m^3 \cdot s^{-1}$ (Fausch 1990; Heggenes et al. 1991). Water temperatures range from about 1 to 20°C, with lower summer maxima in upstream reaches.

The streams are some of the last in the greater Vancouver area that support salmon or trout (Harris and Proctor 1989). Populations in the reaches studied are dominated by coastal cutthroat trout (*Oncorhynchus clarki clarki*) and juvenile coho salmon (*O. kisutch*). Western brook lamprey ammocoetes (*Lampetra richardsoni*) were abundant in section 1 (Fig. 1B), and a few prickly sculpin (*Cottus asper*) were also captured there.

Original vegetation was dominated by old-growth Douglas-fir (*Pseudotsuga menziesii*), western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and red alder (*Alnus rubra*). The region was selectively logged periodically from 1886 to 1950 (Norris 1973). No large slash fires occurred and little fire history is known. After 1912 the uplands became part of the University of British Columbia Endowment Lands forest, formally established in 1925. Recently, much of this area has been redesignated as Pacific Spirit Park. The land surrounding the high-gradient reach of Musqueam Creek downstream became Musqueam Park in the 1920s.

Urbanization near the downstream reaches of Musqueam and Cutthroat creeks has increased since the 1960s. Long steep culverts (279 m, 2.6–4.3% slope on Musqueam Creek) constructed beneath Marine Drive during the 1970s probably are impassable to fish, and another on Cutthroat Creek downstream from Marine Drive probably limits upstream passage of all but adult coho salmon (Fausch 1990). Only very small populations of resident cutthroat trout persist upstream from Marine Drive (Northcote and Hartman 1988; T. G. Northcote and K. D. Fausch, pers. obs.).

Cutthroat Creek was diverted into a tributary of lower Musqueam Creek during golf course construction several decades ago. Floods and base flows throughout the watershed have been made more extreme by lawn irrigation and tile and storm drainage associated with residential development. During spring and summer 1990, dissolved ions, heavy metals, and nutrients were generally 1.3–15 times higher downstream from Marine Drive than upstream due to drainage from roads and suburban lands, but no dissolved concentrations were high enough to pose known hazards to salmonids (Fausch 1990).

The second-growth forest upstream from Marine Drive has been relatively undisturbed since at least about 1950. In contrast, although 25–50 m of riparian forest remains along either side of the 541 m of stream that traverses Musqueam Park, most LWD was removed from the middle 332 m during park maintenance in the 1960s and 1970s (T. G. Northcote, pers. obs.). Leaning or fallen trees throughout the park are often removed to reduce hazards to park visitors.

Methods

We chose eleven 45- to 70-m stream sections (Fig. 1) to contrast LWD and fish habitat in the relatively undisturbed Pacific Spirit Park forest (PSP) with that in Musqueam Park sections downstream that had been either cleaned of LWD (simple) or not cleaned (complex). We also compared fish populations in the simple and complex sections, all of which held both cutthroat trout and juvenile coho salmon. Fish were not sampled in PSP sections because few occurred there.

Four PSP sections, located in the 1200 m of Musqueam Creek upstream from Marine Drive, were randomly chosen within four relatively homogeneous reaches delineated by forest trails. Each section began at a randomly selected distance from an adjacent trail, except in the most downstream reach (section 7) where only one 50-m length had relatively undisturbed wood debris. In Musqueam Park, three simple sections (3, 4, and 5) were located in the 332-m midreach that had been cleaned of most debris, and three relatively complex sections were located upstream (6) and downstream (1 and 2) of these (Fig. 1). A fourth complex section (11) was in lower Cutthroat Creek near its confluence with Musqueam Creek. All sections had similar flows (0.0015 $m^3 \cdot s^{-1}$) when habitat and LWD were mapped and measured during 8–22 June 1990 (Fausch 1990). Angling was prohibited in Musqueam Park, and no evidence of angling was found in any of the reaches studied.

We analyzed differences in habitat, LWD, and fish populations among simple, complex, and PSP sections using a random-effects one-way analysis of variance (ANOVA), which is based on the assumption that the three types of sections were a random sample of more such types (Sokal and Rohlf 1981). Although not strictly true, we selected this analysis because inferences based on random-effects ANOVA are more conservative than for fixed effects, where the investigator purposely manipulates variables (e.g. LWD) to set up treatments. Furthermore, after completing the ANOVA, we calculated multiple comparisons among pairs of means using Bonferroni t-tests, while controlling experimentwise error rate at P = 0.05, which is also a conservative procedure.

Salmonid Habitat

In each stream section, wetted and bankfull widths were measured at transects perpendicular to flow, spaced at 1-m intervals in pools and at 2- or 3-m intervals in runs and riffles. The 3-m interval was used in the simple sections because most habitat consisted of long runs. Depth was measured at 0.5-m intervals along transects, beginning 0.25 m from the right stream bank facing downstream. The first transect was at half the transect interval from the downstream end of each habitat type, so depth measurements were assumed to represent conditions in cells 0.5 m wide and 1–3 m long.

Total length of each habitat unit (riffle, run, pool) was measured along the stream centerline. Pools were classified as scour, plunge, dammed, or backwater pools after Bisson et al. (1982) and the maximum depth measured. Length of undercut bank and overhanging log and rock cover that could conceal a 150-mm-long salmonid from overhead view was measured for each section. Structures that were at least 15 cm wide (10 cm for undercut banks, due to blind end), had a least 15 cm of water beneath them, and were no more than 15 cm above the water surface were included. In early August 1990 when surface flow had ceased in the PSP reach of Musqueam Creek, all pools in the most downstream 770 m were classified as before and their volumes and maximum depths measured.

The six sections in Musqueam Park were mapped with compass and tape using the deflection-angle-traverse method (Orth 1983). Section sinuosity was calculated from the maps as the distance along the centerline divided by the distance along a straight line between the section ends. Section gradients were determined by surveying with a level and leveling rod.

Large Woody Debris and Riparian Stands

The dimensions and orientation of all pieces of LWD (≥1 m long, ≥10 cm mean diameter) that were at least partially within or above the bankfull channel were measured for each section, and in the reaches between sections in Musqueam Park. Habitat in the 19 m downstream from section 1 had been modified and was not included. The total length of each LWD piece, the length within or above the bankfull channel (hereafter termed within bankfull channel), and the diameters at each end and at the channel margins were measured using a tape and tree calipers. Pieces of debris that formed pools were related to habitat measurements.

Volumes were calculated for individual pieces of debris ≥2 m long by assuming cylindrical shape and using length and average diameter (Lienkaemper and Swanson 1987). The volume of debris within the bankfull channel and the total debris volume were determined for each section. Biomass within the bankfull channel was estimated from an average conifer wood density of 0.40 $Mg \cdot m^{-3}$ (Harmon et al. 1986) because relatively little debris in channels was hardwood. Mean diameters and lengths of debris were calculated for each section using geometric means because of skewed distributions (Bilby and Ward 1989). Mean volume was calculated as a cylinder with geometric mean diameter and length.

In addition to total and bankfull LWD volume and biomass, we also calculated the number and within-channel volume of pieces that directly influenced channel morphology. We used our maps and field notes for the sections in Musqueam Park to identify only those pieces that deflected flow and caused scour or fill at flows of bankfull or less, or supported stream banks so that pools could form. We thus eliminated pieces suspended above the channel at bankfull flow or lying loose within the channel (often parallel to flow and along the bank) and not causing scour at any flow.

The diameter at breast height (DBH at 137 cm above the ground) and distance from the stream bank of each tree and stump within 30 m of the channel (Murphy and Koski 1989) throughout the 541-m Musqueam Park reach were measured to estimate future (and past) riparian sources of LWD. Each tree and stump ≥20 cm DBH was identified to species and measured with a steel diameter tape.

Fish Populations

Fish populations in the seven simple and complex sections downstream from Marine Drive were measured between 5 and 12 April 1990 before most age 1+ and older coho salmon had smolted. Flow was low and water temperatures ranged from 8 to 11°C, so electrofishing was effective and fish mortality low. Salmonid abundance was estimated by three- or four-pass removal electrofishing with a Smith-Root Type VIII A backpack electrofishing unit operated at 250–850 V. Voltage was increased in deep pools. The unit delivered square-wave pulsed DC via a 15-cm-diameter wand-mounted ring anode and a 20 × 30 cm metal screen cathode that trailed behind the operator, who also carried a net.

Section ends were blocked with fine-meshed seines (≤6.4 mm), and the bottom was lined with gravel or cobble to ensure population closure. The downstream block net of section 6 was removed by adolescents before the second pass but was reinstalled within 20 min, after which work continued. All habitat in each section was carefully electrofished with the same effort on each pass, an important assumption of removal estimators (Riley and Fausch 1992). Work was scheduled so that 1–2.5 h elapsed between passes.

Fish from each pass were retained in separate buckets and later anesthetized (2-phenoxyethanol), measured (total length, TL), and weighed (nearest 0.1 g, Ohaus model C300 electronic balance). Weights of age 1+ and older salmonids from two sections were estimated from species-specific length–weight regressions based on all weighed fish because of a balance malfunction. The weight of one other cutthroat trout that exceeded the 300-g balance capacity was similarly estimated.

Population estimates were calculated using the maximum-likelihood generalized removal estimator of Otis et al. (1978) via the computer program CAPTURE (White et al. 1982). Log-based confidence intervals (Burnham et al. 1987, p. 212) were calculated to ameliorate the slight negative bias and low coverage normally associated with intervals for this estimator (Riley and Fausch 1992). Separate population estimates were calculated for age 1+ and older coho presmolts (>60 mm TL) and cutthroat trout (>70 mm). Section biomass was calculated as the product of the population estimate and mean weight for each species. Confidence intervals were determined using a finite population correction based on numbers of fish weighed. Recently emerged age 0 coho averaged only 36–38 mm TL during this period (n = 24–50 per section for five sections that had age 0 fish). Their abundance was not estimated due to low capture efficiency and to prevent high mortality.

Results

Salmonid Habitat

The simple and complex sections in Musqueam Park differed markedly in sinuosity, pool volume, bankfull width, depth, and overhead cover for fish provided by undercut banks and overhanging logs (Table 1). The three sections with simple habitat had lower sinuosity, were wider and shallower, and had little cover for fish when compared with the four complex sections. Pools made up 9–25% of the total volume at base flow in the simple sections but were 61–69% of volume in the complex sections. Differences in percent pool volume (arcsine square-root transformed), width, depth, and cover were significant ($P < 0.05$ experimentwise error rate) when tested using Bonferroni t-tests for unequal variance, after one-way random-effects ANOVA.

The four randomly chosen PSP sections upstream of Marine Drive also had deep and relatively complex habitat. Pools comprised much of the total volume (44–58%), channels were narrower and deeper than in most downstream sections, and overhead cover was plentiful. The decrease in width, increase in depth (compared with simple sections only), and change in pool volume were significant, but the increase in overhead cover was not because of high variation. Much of the variation was due to section 7 which was wider and shallower than the other PSP sections, probably due to water and sediment contributed by an intermittent tributary entering immediately upstream. Although decreased width in sections 8–10 upstream may have been partially due to lower bankfull flows, increased depth was probably due to more stable banks and more LWD (see below).

Large Woody Debris

Total abundance and volume of LWD and estimated biomass within the bankfull channel were variable and similar for the simple and complex reaches in Musqueam Park, but generally greater in PSP sections (Table 2). For example, sections in the simple and complex reaches had 3–30 pieces per 100 m of stream whereas the upstream PSP sections had 26–60 pieces per 100 m. None of the differences in total debris abundance, volume, or biomass was significant by ANOVA due to high variance, although the difference in abundance between the PSP and complex sections was nearly so (P = 0.0525).

TABLE 1. Characteristics of physical habitat in simple, complex, and the relatively undisturbed PSP sections of Musqueam and Cutthroat creeks, June 1990. Weighted means and standard errors (SE, n = total sample size) were calculated for bankfull widths and depths, based on the proportion of section length (for width) and area (depth) made up by each habitat type. Significant differences ($P \leq 0.05$ experimentwise error rate, Bonferroni t-tests) among reaches for means of four habitat variables are denoted by different letters. Means followed by the same letter are not significantly different.

Section	Sinuosity	Gradient (%)	Length (m)	Volume (m^3)	% pool Area	% pool Volume	Mean bankfull width (m) (SE, n)	Mean depth (cm) (SE, n)	Overhead cover ($m \cdot 100\ m^{-1}$)
Simple: Musqueam Park									
3	1.03	1.9	53	9.1	7	19	5.3 (0.38, 18)	6.2 (0.42, 103)	5.7
4	1.03	1.5	45	6.1	11	25	5.1 (0.50, 19)	6.4 (0.33, 90)	2.0
5	1.07	4.1	53	6.2	4	9	5.8 (0.29, 19)	4.8 (0.27, 95)	1.7
Mean						17.7 a	5.4 a	5.8 a	3.1 a
Complex: Musqueam Park									
1	1.24	2.1	70	14.6	43	64	3.4 (0.16, 45)	10.2 (0.51, 177)	22.7
2	1.29	1.5	69	13.0	35	61	3.6 (0.17, 45)	10.3 (0.48, 165)	14.3
6	1.37	4.0	51	9.0	42	62	3.1 (0.18, 34)	9.2 (0.48, 145)	23.9
11	—[a]	3.1	53	13.7	45	69	3.5 (0.24, 32)	12.5 (0.69, 159)	17.2
Mean						64.0 b	3.4 b	10.6 b	19.5 b
Undisturbed: Pacific Spirit Park									
7	—	1.2	48	8.3	27	46	3.0 (0.17, 29)	11.5 (0.63, 88)	11.3
8	—	0.6	46	11.7	27	44	2.4 (0.08, 27)	16.4 (0.95, 91)	20.2
9	—	0.7	48	12.7	43	51	1.9 (0.07, 31)	16.8 (0.87, 94)	37.1
10	—	0.5	48	13.4	44	58	2.2 (0.16, 33)	20.0 (0.87, 100)	36.7
Mean						49.7 c	2.4 c	16.2 b	26.3 ab

[a]Indicates that no map was drawn, so sinuosity could not be estimated.

The number of pieces of LWD that directly influenced channel morphology was greater in complex sections (except section 2) than in simple ones. However, the total volume of these pieces that was within the bankfull channel was variable within reaches, and neither difference was significant due to high variability ($P > 0.05$ by t-test for unequal variance). In sections 2, 3, 4, 5, 5–6, and 6, ≥63% of this volume was contributed by one large piece of LWD. Geometric mean LWD diameters, lengths, and calculated mean volumes were also variable and similar among the three reaches, except that the most upstream PSP section had primarily long pieces of debris of moderate diameter.

The distribution of LWD lengths in all sections was skewed toward short pieces (Fig. 2), although PSP sections had a higher percentage of longer pieces than those downstream. Overall, 36% of 104 LWD pieces in PSP sections were ≥8 m whereas only 19% of 85 pieces in the simple reach and 2% of 57 pieces in the complex reach of Musqueam Park were this long.

How important was LWD in forming pools? The majority of both number and volume of pools was formed either by LWD or large root masses of standing trees or stumps. In all, 72% of pool volume in the seven simple and complex sections downstream from Marine Drive (reaches combined to increase sample size) and 80% of pool volume in PSP sections were formed by these two agents (Table 3). In the PSP sections, most volume was contributed by lateral scour pools around LWD or large roots (76% of total) whereas in the downstream sections, about 40% of the pool volume formed by debris was from plunge pools, perhaps due to generally higher gradient. Neither dammed nor backwater pools contributed substantial volume in either reach. Lateral scour pools around boulders or beneath undercut banks supported by roots of shrubs or grasses were also important in both reaches, making up about 20% of the volume in each. Percentages of pools by number were similar to that by volume.

Maximum depths of pools were greater in PSP sections, even though the channel cross-sectional area was smaller and gradient lower there, probably due to more LWD and more stable banks. Pools in PSP sections averaged >40 cm deep whereas only plunge pools formed by LWD in the downstream reach were this deep on average, even though habitat in both reaches was measured at the same base flow.

By early August when surface flow had ceased upstream of Marine Drive, maximum depths had declined an average of 19 cm (SE = 4.9) in 9 of 12 pools in sections 7–10 that were measured in mid-June (the other three were dry). For the 20 pools that remained in the entire lowermost 770 m of the reach at this low flow, 96% of the volume was in pools formed by LWD or large roots, of which 81% consisted of lateral scour pools and 15% plunge pools. Maximum depths ranged 30–52 cm in 11 of the 18 pools formed by LWD, even though flow had ceased.

Most of the debris that formed pools downstream from Marine Drive was oriented perpendicular to the channel (59% was 90°; Fig. 3). Most of the debris forming pools in the PSP sections was oriented either perpendicular or angled downstream (86% was 90–135°).

Riparian Sources of Large Woody Debris

The stand of trees within 30 m either side of Musqueam Creek in Musqueam Park was dominated by relatively young, small trees (Fig. 4). Most were <70 cm DBH, and only 5 of the 583 trees ≥20 cm DBH were >100 cm in diameter. In

TABLE 2. Characteristics of LWD (≥10 cm in diameter and ≥2 m long) in simple and complex reaches, and the relatively undisturbed PSP sections of Musqueam and Cutthroat creeks, June 1990. Number of pieces and volume of debris that directly influenced channel morphology are referred to as "channel." Geometric means of length, diameter, and mean volume per piece were calculated due to skewed distributions (see text). Volumes were summed for individual pieces of debris, based on lengths within the bankfull channel and on total length. Biomass within the bankfull channel was based on average conifer density of 0.4 $Mg \cdot m^{-3}$ (Harmon et al. 1986). Significant differences ($P < 0.05$ experimentwise error rate, Bonferroni t-tests) among reaches for means of five debris characteristics are denoted by letters. Means followed by the same letter are not significantly different.

Section	Pieces·100 m^{-1}		Geometric mean			Volume ($m^3 \cdot 100\ m^{-1}$)		Bankfull biomass
	All	Channel	Diameter (m)	Length (m)	Volume (m^3)	Channel	Total	($Mg \cdot ha^{-1}$)
				Simple: Musqueam Park				
3	11	4	0.37	6.0	0.65	4.6[a]	19.9	67
4	16	4	0.30	6.9	0.48	9.0[a]	15.3	83
4–5	30	0[b]	0.20	5.8	0.18	0.0	13.4	36
5	11	2	0.24	3.5	0.15	1.3	3.2	19
5–6	15	5	0.23	4.9	0.21	2.8	16.0	—[c]
Mean	16.6 a	3.0 a				3.5 a	13.6 a	51.2 a
				Complex: Musqueam Park				
1	20	17	0.41	3.0	0.39	10.7	11.2	133
2	3	1	0.25	3.9	0.20	1.2	1.5	15
6	16	16	0.43	3.7	0.55	15.2	45.0	190
11	13	9	0.32	3.9	0.30	3.2	6.7	42
Mean	13.0 a	10.7 a				7.6 a	16.1 a	95.0 a
				Undisturbed: Pacific Spirit Park				
7	60	—[d]	0.19	6.3	0.18	—[d]	25.4	142
8	26	—	0.29	3.7	0.24	—	16.6	74
9	40	—	0.32	5.9	0.48	—	45.9	448
10	42	—	0.27	12.6	0.69	—	85.0	274
Mean	42.0 a[e]						43.2 a	234.5 a

[a]A large percentage (65% in section 3, 80% in section 4) of "channel" volume was contributed by one large piece of LWD that had little effect on flow.

[b]An additional eight pieces (12 per 100 m) of new, broken red alder LWD were wetted and eight more were suspended above the channel. All affected channel morphology little, and none was stable.

[c]Biomass could not be estimated because section area was not measured.

[d]Neither the number nor volume of pieces that influenced channel morphology could be calculated for PSP sections (see text).

[e]Differences between the number of LWD pieces in simple and PSP sections ($P = 0.08$) and complex and PSP sections ($P = 0.0525$) were significant at $P < 0.10$.

contrast, 17 fir and 11 cedar stumps of 100–240 cm DBH remained from the original stand, 6 of which were >200 cm.

Fir and hemlock were relatively more abundant and hardwoods (primarily red alder) less abundant adjacent to the complex sections than to the simple ones. This may be partly due to steeper, drier slopes near several complex sections and partly due to a narrower riparian strip that supported primarily alder on one side of the simple midreach of Musqueam Park.

If half of the conifers >20 cm DBH now growing within 30 m of the stream eventually fell across or into the channel and remained there for 100–200 yr, as has been estimated elsewhere in the Pacific Northwest (Murphy and Koski 1989), debris loads would be 37 pieces per 100 m of stream in the complex reach and 21 pieces per 100 m in the simple reach (based on total trees divided by reach lengths). These estimated conifer loads are probably conservative, given slope and other factors that bias fall direction toward the stream (Van Sickle and Gregory 1990), yet are relatively high compared with those now present in most of Musqueam Park (Table 2; 80% of pieces in section 4–5 were alder). The debris load estimate for the complex reach is similar to the average for PSP sections where debris has presumably been disturbed little during the last 40 yr.

Salmonid Populations

Mosts age 1+ and older salmonids that could be captured by electrofishing were removed from each section in three or four removal passes (Table 4). The generalized removal estimator indicated that 58–95% ($\bar{x} = 78\%$) of the fish remaining were captured on each pass. As a result, standard errors of estimates were low, and the lower 95% confidence limit, total number of fish captured, and population estimate were equal for all cases. For 11 of 14 estimates the upper confidence limit was only zero or one fish more than the estimate.

Estimates and upper confidence limits probably slightly underestimate true population size either because capture probabilities decline for fish remaining (Bohlin and Cowx 1990) or because some fish cannot be sampled by electrofishing. Simulations indicate that the former bias is probably 5% or less for the range of capture probabilities reported here (Riley and Fausch 1992). Biomass estimates are precise because the entire

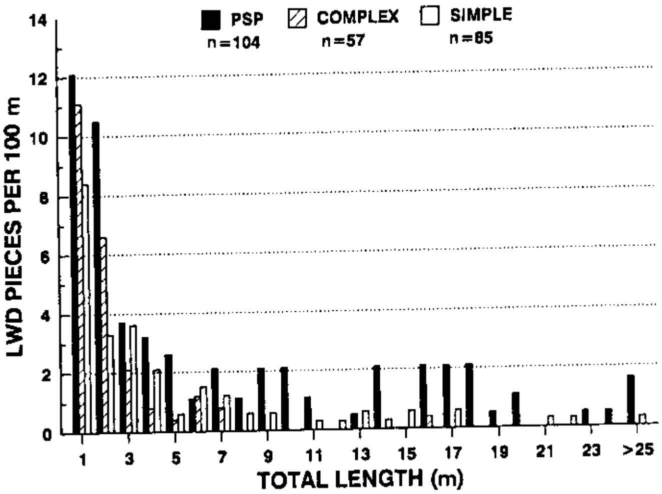

FIG. 2. Frequency of LWD pieces per 100 m of stream by 1-m length classes in PSP, complex, and simple sections of Musqueam and Cutthroat creeks. The total number of pieces measured in each reach is shown.

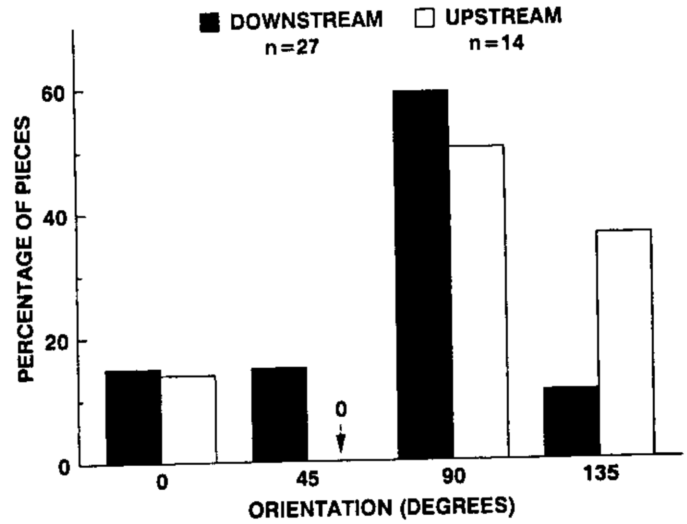

FIG. 3. Orientations of pieces of LWD that formed pools in four sections upstream and seven section downstream from Marine Drive. Orientation classes consisted of 45° quadrants centered around the bearing shown, with 0° referring to debris with tips pointing straight upstream. Debris oriented in analogous, but opposite, quadrants (e.g. centered at 135 and 225°) was combined for each class.

TABLE 3. Characteristics of pools of four types (after Bisson et al. 1982) created by LWD and other agents in reaches downstream and upstream of Marine Drive. Data for the seven simple and complex sections in the downstream reach were combined to increase sample size. Percentages of total pool volume (% *V*) and total numbers (% *N*) for each reach (*n* = sample size) and mean (SE) and range of maximum pool depths are shown.

	Downstream		Upstream	
Pool type	LWD or roots	Boulders, POM,[a] or other	LWD or roots	Boulders, POM,[a] or other
Scour				
% *V*	38	19	76	20
% *N*	39	25	67	25
Max. depth	28.1 (3.28)	27.5 (1.47)	51.3 (5.56)	45.7 (3.18)
Range	19–76	18–33	30–78	42–52
Plunge				
% *V*	29	8	4	0
% *N*	18	7	8	0
Max. depth	41.1 (5.24)	34.0 (7.23)	44 (—)	—
Range	21–64	22–47	44	—
Dammed				
% *V*	1	0	0	0
% *N*	2	0	0	0
Max. depth	23	—	—	—
Range	23	—	—	—
Backwater				
% *V*	4	0	0	0
% *N*	9	0	0	0
Max. depth	14.8 (5.88)	—	—	—
Range	1–28	—	—	—
Total				
% *V*	72	28	80	20
% *N*	68	32	75	25
n	30	14	9	3
Volume (m^3)	26.0	10.0	18.2	4.4

[a]Fine particulate organic matter (POM) included woody debris <10 cm in diameter or <1 m long.

estimated population was captured and weighed, except when the balance malfunctioned. Because on average about 80% of the fish in each section were captured on the first pass, and most of the rest retreated beneath cover, few fish probably escaped during the brief loss of the block net in section 6. If fish were lost, estimated numbers and biomass would be slightly less than, and capture probabilities slightly greater than, the true values for this section.

Cutthroat trout populations consisted primarily of fish <200 mm long (see also Northcote and Hartman 1988; Heggenes et al. 1991), except in the Cutthroat Creek section where 7 of 30 trout were >200 mm and none was smaller than 120 mm. All but two salmonids in this section were captured in a large deep pool formed at the outlet of a culvert, which had 2.7 m of wide undercut bank. Four of the largest trout bore finclips or scars from tags probably applied when the fish were captured in Musqueam Park by previous investigators (Heggenes et al. 1991), which suggests that these fish may have been anadromous. Upstream movement of cutthroat was probably limited by the 31-m culvert because calculated velocities were $>1.2\ m \cdot s^{-1}$ at depths ≥15 cm, and the outlet dropped approximately 30 cm at low flow (Fausch 1990).

Standing crop of age 1+ and older salmonids was low (10–25 $kg \cdot ha^{-1}$) in the three simple sections and much higher (93–200 $kg \cdot ha^{-1}$) in the four complex sections ($P < 0.02$ by *t*-test for unequal variance). Although the simple sections held small numbers of age 1+ cutthroat (estimated 70–125 mm from length–frequency histograms) and coho presmolts and relatively large numbers of age 0+ coho (K. D. Fausch, pers. obs.), no older cutthroat (>125 mm) were captured there. Mean weights (grams) of age 1+ and older cutthroat trout and coho salmon were significantly greater in complex than in simple sections (cutthroat (mean (SE)), 48.5 (6.27) versus 10.4 (1.03), $P = 0.0001$; coho, 10.2 (0.34) versus 8.5 (0.38), $P = 0.0012$ by *t*-test).

Relationships among Fish Biomass and Habitat

Pool volume, section volume, mean depth, and length of overhead cover were all strongly and significantly intercorre-

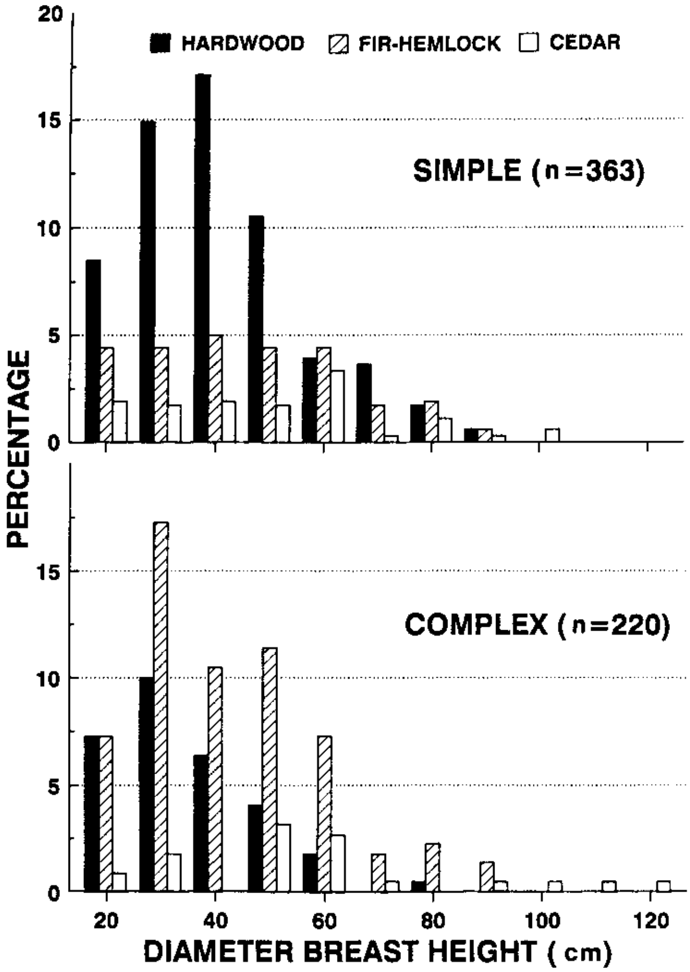

FIG. 4. Distribution of DBH of all trees ≥20 cm DBH within 30 m either side of Musqueam Creek in Musqueam Park, adjacent to the 332-m simple reach and the 209-m complex reach. Hardwoods include predominantly red alder, but also broadleaf maple (*Acer macrophyllum*) and a few western white birch (*Betula papyrifera*). The total number of trees measured adjacent to each reach is shown.

lated (r = 0.79–0.97, $P < 0.05$ for six pairs) for the seven sections downstream from Marine Drive where fish were sampled, which reflects the strong association between these variables and LWD. Because variance in biomass of age 1+ and older salmonids increased at higher values of these habitat variables (e.g. Fig. 5), we calculated correlation and regression coefficients after transforming both biomass and habitat variables using logarithms. Less stringent transformations were not sufficient to stabilize variance.

Total biomass of age 1+ and older salmonids was strongly correlated with all four habitat variables (r = 0.85–0.96, $p < 0.01$), but was most strongly associated with pool volume and depth ($r = 0.96$, $P < 0.01$ for both). Coho biomass was most strongly associated with overhead cover ($r = 0.92$, $P < 0.01$) and cutthroat biomass with mean depth ($r = 0.93$, $P < 0.01$), although both were also strongly correlated with pool volume (r = 0.88 and 0.90, $P < 0.01$).

Because correlations between salmonid biomass and pool volume were most consistent among species, we calculated the following linear model after transforming the data:

$$\text{Log}_{10} \text{ salmonid biomass (kg)} = -0.7044 + 0.9687 \log_{10} \text{pool volume } (\text{m}^3)$$
$$(r^2 = 0.92, P = 0.0006, \text{SE}_{\text{intercept}} = 0.0882, \text{SE}_{\text{slope}} = 0.1268).$$

The error in measuring pool volume was small (estimated <0.25 m^3), so no correction was made for possible bias in the slope (Snedecor and Cochran 1967).

It is possible that a few large cutthroat captured in Cutthroat Creek were anadromous fish unable to ascend the culvert, although Heggenes et al. (1991) found that few trout in Musqueam Park moved more than 50 m during winter through late summer. This may, however, partially account for the higher biomass in section 11 compared with others with complex habitat (Fig. 5).

The relationship between biomass and pool volume is nearly linear because the exponent of the power function we fit (equivalent to the slope after logarithmic transformation) is close to 1. This assumption seems biologically reasonable, although we have no data for sections with intermediate pool volume to substantiate it. Finally, we caution against using this equation to predict salmonid biomass in other similar streams, or in this stream during other years, without validating it (cf. Fausch et al. 1988).

Discussion

Our results indicate that LWD in Musqueam Creek plays a critical role in creating and maintaining pools which, in turn, provide important habitat for salmonids. Sections that had been cleaned of woody debris had little pool volume (Table 1) and harbored few age 1+ and older salmonids (Table 4) whereas those where debris was left had much greater pool volume and salmonid biomass (Fig. 5).

Large Woody Debris and Pool Formation

Recent research has established the importance of LWD in shaping channel morphology and forming pools in Pacific Northwest streams (Bisson et al. 1987; Bilby and Ward 1989; Robison and Beschta 1990a, 1990b). These studies indicate that most pools are formed by LWD (Andrus et al. 1988) and that debris removal triggers changes that lead to wide, shallow channels with little pool volume at low flows (Bilty 1984; Bisson and Sedell 1984; Heifetz et al. 1986), similar to those we found in the cleaned reach of Musqueam Creek.

We found clear differences between simple and complex sections in sinuosity, width, depth, pool volume, and overhead cover for fish (Table 1), but differences in LWD were more subtle. Total LWD abundance, volume, and biomass within the bankfull channel were variable and the range of values generally similar between simple and complex reaches, although most values were lower than for undisturbed PSP reaches (Table 2). Similarly, when only debris that influenced channel morphology and flow during bankfull or lower discharge was included, LWD volume was variable and similar in simple and complex sections.

However, the clearest difference was that complex sections (except section 2) had more pieces of debris that influenced channel morphology than simple sections. This is perhaps also the best measure of "effective" debris because small streams are incapable of moving pieces of even moderate diameter (approximately 30 cm) if they are long enough to be stable (Keller and Swanson 1979; Bilby and Wasserman 1989; Robison and Beschta 1990a, 1990b), making debris volume less relevant. Moreover, relatively few pieces of LWD in each complex section accounted for most of the pool volume. Of the 6–11 pools in each of the four complex sections, the two largest in each made up 46–75% of pool volume. All were formed by

TABLE 4. Population estimates for age 1+ and older coho salmon and cutthroat trout in seven simple and complex sections of Musqueam and Cutthroat creeks during 5–12 April 1990. Estimates of population size ($\hat{N}$) and probabilities of capture ($\hat{p}$) were calculated using the generalized removal estimator in the program CAPTURE (White et al. 1982). In all cases, the number of fish captured in all passes was used as the lower 95% confidence limit (CI) because it exceeded the calculated lower limit.

Section	Species	$\hat{p}$	$\hat{N}$ (CI)	Biomass (g) (±CI)	Standing crop (kg·ha^{-1})
			Simple		
3	Coho	0.78	29 (29–30)	233[a]	16.3
	Cutthroat	0.77	11 (11–12)	118[a]	8.3
	Total			350[a]	24.6
4	Coho	0.75	12 (12–13)[b]	104 ± 9	9.9
	Cutthroat	0.89	8 (8–8)	105 ± 3	10.1
	Total			209 ± 12	20.0
5	Coho	0.60	3 (3–5)[b]	39 ± 18	3.1
	Cutthroat	0.69	11 (11–13)[b]	90 ± 13	7.1
	Total			129 ± 31	10.1
			Complex		
1	Coho	0.82, 0.58[c]	75 (75–78)	693 ± 30	55.9
	Cutthroat	0.80, 0.75[c]	15 (15–15)	456 ± 11	36.8
	Total			1149 ± 41	92.7
2	Coho	0.75, 0.71[c]	60 (60–61)	479[a]	38.0
	Cutthroat	0.72, 0.78[c]	25 (25–26)	791[a]	62.9
	Total			1270[a]	100.9
6	Coho	0.87	27 (27–28)	410 ± 8	41.9
	Cutthroat	0.95	22 (22–22)	1260 ± 5	128.7
	Total			1671 ± 13	170.6
11	Coho	0.89	17 (17–17)[b]	249 ± 4	22.6
	Cutthroat	0.86	30 (30–31)	1954 ± 34	177.2
	Total			2203 ± 38	199.7

[a]Weights of some (section 2) or all (section 3) fish were estimated by species-specific length–weight regressions based on fish captured in all sections, so no standard errors for biomass could be calculated.

[b]The chi-square test in CAPTURE detected declining capture probability after the first pass ($P <$ 0.20), so these three-pass population estimates and confidence intervals probably underestimate the true population size slightly (Riley and Fausch 1992). However, in all cases, either no fish were captured on the third pass or no fish were captured on the second pass and only one on the third pass, so most fish were probably captured.

[c]Four passes were completed for sections 1 and 2, which allows calculating a different capture probability for the first pass versus subsequent passes and produces a more accurate estimate.

LWD or tree roots >10 cm in diameter, except in section 6 where both were formed by scour beneath undercut banks, in one case combined with a plunge pool at the culvert outlet. Andrus et al. (1988) also found that pools in a coastal Oregon stream were formed by relatively few influential pieces of debris and proposed that beyond some threshold, factors other than the abundance of debris control pool formation. We cannot explain the lack of debris in section 2, although we suspect that the channel may have been formed by previous debris, now rotted away or incorporated into the bed or banks.

Our analysis of pool-forming agents also highlights the importance of LWD. Most pools, and most pool volume, in reaches throughout the Musqueam Creek system were scour or plunge pools formed by LWD or large tree roots (Table 3; see also Bilby and Ward 1989). Heifetz et al. (1986) and Andrus et al. (1988) also reported that 70–75% of pools were formed by LWD. Of debris that formed pools, most was oriented either perpendicular to the flow or angled downstream (Fig. 3), a conclusion also reached by Bilby and Ward (1989) for streams of similar size in foothills of the Cascade Mountains in Oregon. Natural distributions of LWD in small streams may be skewed toward perpendicular because trees rooted farther away from channels can intersect them only in this orientation (cf. Robison and Beschta 1990a).

Large Woody Debris Volume

Bankfull channel debris volume and biomass were generally low in Musqueam Park (Table 2). Most of the volume was contributed by one large piece in six of nine sections where it was calculated. In contrast, the average bankfull biomass for sections in the PSP reach was similar to values measured in similar biomes. Harmon et al. (1986) reported biomass averaging 270 Mg·ha^{-1} (SE = 53, maximum 670 Mg·ha^{-1}) for nine streams 11–20 m wide in Sitka spruce (*Picea sitchensis*) and western hemlock forests of coastal British Columbia and averages of 252 Mg·ha^{-1} (SE = 25, maximum 550 Mg·ha^{-1}) for 25 streams <10 m wide in Douglas-fir forests of Oregon's Cascade Mountains, both based on the same wood density we used.

We suspect that debris volumes are low in Musqueam Park because the small amount of standing or fallen debris that might

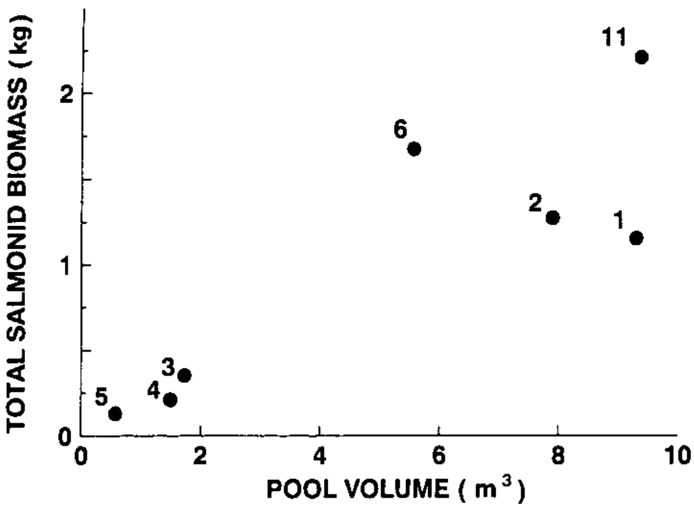

FIG. 5. Total biomass of age 1 + and older salmonids as a function of pool volume for seven sections of Musqueam (sections 1–6) and Cutthroat (section 11) creeks sampled in April 1990 (see Fig. 1). Ninety-five percent confidence intervals for biomass are smaller than the points in each case and are given in Table 4.

enter the stream is periodically removed for safety or aesthetic reasons, even that adjacent to complex sections. As a result, the framework of debris left from the preharvest stand that forms pools and binds habitat together has largely rotted and broken into small pieces (Fig. 2) and soon will collapse and wash away. Other investigators predict that LWD reaches a minimum approximately 100 yr after clearcut in Pacific Northwest streams (Harmon et al. 1986; Murphy and Koski 1989), but even this amount probably far exceeds the LWD left in Musqueam Creek after cleaning. When the remnants of original debris wash away, pool volume will be at its lowest ebb, so debris inputs or other habitat enhancement measures (e.g. Ward and Slaney 1979) are needed now if habitat for age 1 + and older cutthroat and overwintering juvenile coho is to be maintained.

It is also clear that the lack of debris in simple sections is not due primarily to differences in riparian sources. Although conifers are relatively more abundant adjacent to the complex reach (Fig. 4), crude estimates indicate that debris would be more abundant in both simple and complex reaches if none had been removed. A more sophisticated model of future debris inputs is available (Van Sickle and Gregory 1990) but is beyond the scope of this study.

Pools as Salmonid Habitat

Although previous research has shown a direct link between LWD and channel morphology, our knowledge of the importance of pools to salmonids is less complete. Several investigators proposed that pool volume and overhead cover, both formed by debris, provide important overwinter habitat for juvenile coho salmon (Hartman 1965; Bustard and Narver 1975a; Bisson et al. 1985, 1988) and cutthroat trout (Glova 1986). Both have been implicated in models that predict coho salmon abundance or biomass from pool and/or debris volume (Nickelson et al. 1979; Tschaplinski and Hartman 1983; Murphy et al. 1986). Experiments in laboratory (Hartman 1965) and artificial channels (Bustard and Narver 1975b; McMahon and Hartman 1989) also showed the importance of pools with complex habitat to overwintering coho salmon.

Despite these field observations and small-scale experiments, few investigators have conducted field experiments to measure salmonid populations in sections where debris was removed versus control reaches. Moreover, in all such experiments know to us the treatment was a combination of both canopy and debris removal. For example, Bisson and Sedell (1984) and Murphy et al. (1985) reported that salmonid biomass was higher in sections adjacent to clearcuts that had been cleaned of logging slash than in those next to old-growth, but effects of reduced canopy on light, temperature, and primary and secondary production were inseparable from the effects of debris removal on channel morphology (cf. Murphy et al. 1981, 1986; Hawkins et al. 1983). In both cases, the clearcut sections produced primarily age 0 salmonids due to known or suspected higher primary and secondary production, but harbored few age 1 + and older parr due to lack of pools with complex cover. Murphy et al. (1985, 1986) found that reaches where buffer strips were left adjacent to clearcuts, which often had more debris and pool volume, held more coho and steelhead parr than sections adjacent to clearcuts where some LWD generally had been removed from the channel.

We also found that age 1 + and older cutthroat and coho presmolts were larger and more abundant in sections with complex habitat (Table 4), which supports the hypothesis that more salmonid smolts are produced from such habitat. Moreover, although many age 0 coho were captured in three sections with simple habitat, none held fish older than age 1 +. Tschaplinski and Hartman (1983) reported that during the first autumn freshet, most age 0 coho emigrated from sections in Carnation Creek that had little LWD (see also Bisson et al. 1985; Johnson et al. 1986; Murphy et al. 1986), which provides a mechanism to explain these results. Pools formed by LWD also provided the only habitat capable of supporting age 2+ and older cutthroat trout during extreme low flows of late summer (K. D. Fausch and T. G. Northcote, pers. osbs.).

Although we chose sections to contrast the effects of long-term debris removal in Musqueam Creek, we were unable to fully randomize treatments to sections or to employ a paired design. The most important consequence is that we cannot rule out the possibility that difference in some other environmental factor, such as gradient, caused the lower biomass in the mid-reach of Musqueam Park that was cleaned. This lack of randomly assigning treatments to sections is a form of pseudoreplication (Hurlbert 1984). The overriding effect of some other factor seems unlikely, however, given the overall similarity in gradient and other feature among sections. Moreover, the complex sections were interspersed upstream and downstream of the simple reach and in a tributary, and we made conservative statistical inferences, both of which strengthen our conclusions that salmonid habitat and biomass were greater in complex sections.

Salmonid Production Forgone

The outcome of cleaning woody debris from stream channels is that much fish habitat is lost as channel morphology becomes simple, and much fish production is subsequently forgone. The overall effects are likely to be more drastic after relatively complete debris removal, such as occurred in Musqueam Creek, compared with removing only new slash and debris as is currently practiced after logging (Bisson et al. 1987). Even the latter can cause modest but significant declines in salmonid production (Dolloff 1986; Elliott 1986) which may, however, be ameliorated by increased stream temperature and light (Hawkins et al. 1983; Bisson and Sedell 1984; Hartman et al. 1987).

Our data allow us to make a preliminary estimate of the salmonid production forgone during 1990 in the 332-m reach of Musqueam Park with simple habitat, as a result of prior stream cleaning. Based on average conditions in the four complex sections, one would expect this simple reach to be 26% longer due to increased sinuosity created by LWD (Table 1) and to contain 0.13 m^3 of pool volume per metre of stream. The resulting 55.0 m^3 of pools would have produced 9.6 kg of salmonid biomass (age 1+ and older), if our model is accurate. This exceeds the 1.6 kg of biomass estimated for the simple reach, based on similar assumptions about current conditions, by 5.0 times.

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