Habitat Associations of Juvenile Cutthroat Trout: Implications for Forestry Impacts

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ABSTRACT

Juveniles of sea-run coastal cutthroat trout (*Salmo clarki*) rear in small coastal streams for 2–3 years before migrating to the ocean to complete their life cycle. Associations of juveniles with different habitats (e.g., pools vs. riffles) and the effect of large woody debris (LWD) on channel structure were evaluated in order to assess the long-term impact of different riparian management practices on cutthroat populations. Cutthroat densities were highest in smaller streams (<4 m bankfull width), and smaller parr (0+ year-class) were typically associated with shallower hydraulic units, while parr >110 mm long (larger 1+ and 2+ year-classes) were usually found in pools. LWD was responsible for >50% of pool formation in most streams, including those classified as S4 (<1.5 m bankfull width) under the British Columbia Forest Practices Code. Pools formed by LWD scour were, on average, 10% deeper than pools formed by other mechanisms. This indicates that long-term depletion of LWD by removal of riparian forest has the potential to seriously reduce the capacity of smaller streams to support juvenile cutthroat.

Key words: channel structure, channel width, coho, cutthroat trout, large woody debris, *Oncorhynchus kisutch*, *Salmo clarki*.

Quantifying the habitat associations of a species is an essential step in defining ecological requirements and managing wild populations. Distribution and abundance of stream fish is closely linked to channel structure, since attributes of channel structure provide critical habitat for different species or life stages (Schlosser 1987). Structure in streams arises from both substrate heterogeneity and the natural tendency of running water to form pools, riffles, and meanders (Leopold et al. 1964), and is enhanced by the presence of obstructions such as large woody debris (LWD) and boulders, which cause flow convergence and scour (Lisle 1986).

Juveniles of anadromous coastal cutthroat trout (*Salmo clarki*), along with coho salmon (*Oncorhynchus kisutch*), rear in first to fourth order streams (Hartman and Gill 1967, Chamberlin et al. 1991), where channel structure, particularly that associated with LWD, plays an essential role in salmonid life history (Hartman et al. 1996). Scour created by LWD is a major pool-forming mechanism, and LWD may also provide an important refuge from predation. Side channels, backwaters, pools, and structure associated with LWD and rootwads provide critical overwintering and rearing habitat, by providing hydraulic refuges during winter floods (Bustard and Narver 1975*a*,*b*) and pool habitat during summer low flow.

Channel structure in small coastal streams is often significantly altered by both natural and anthropogenic processes. Land-use practices such as logging, agriculture, and urbanization can have pervasive effects on channel structure, ranging from increased sedimentation to bank instability and alteration of LWD input rates from the riparian zone. Smaller streams in particular may be severely impacted by logging because a greater proportion of the watershed may be cut at 1 time (Jones and Grant 1996), and because riparian regulations provide less protection for very small streams (e.g., the British Columbia Forest Practices Code requires no riparian buffers for streams <1.5 m bankfull width; Province of British Columbia 1995). Similarly, urban development is typically concentrated in valley bottoms, where small coastal streams are most abundant.

The overall project goal is to quantify cutthroat habitat relationships and develop predictive functions that can be

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used to model the effects of channel structure modifications on cutthroat distribution and abundance. Our initial objectives were to define the freshwater habitat associations of juvenile cutthroat both within and between streams, and to assess the role of LWD in the creation of cutthroat habitat.

METHODS

Study Sites

Forty-five sites on 44 streams with populations of anadromous coastal cutthroat trout were sampled at summer base flow during June–September 1997 and 1998. Coho parr were also present at 31 of the sites. Twenty-two stream sites were located on the Sechelt Peninsula of the lower mainland of British Columbia, 40 km NW of the city of Vancouver, within a 30-km radius of the town of Sechelt. The remaining 23 stream sites were located on the west coast of Vancouver Island, within a 30-km radius of the village of Tofino.

In order to represent the range of habitats used by anadromous cutthroat trout, sites were chosen to encompass a broad range of channel sizes (1.2–17.0 m bankfull width), logging histories (clearcut, second growth, and old growth), basin gradients (high or low), and channel complexity.

Data Collection

Fish were collected by triple-pass electroshocking of stop-netted sections using a backpack electrofisher, with voltage set between 300 and 500 volts to maximize capture efficiency while minimizing injury to fish. Shocked areas were left undisturbed for at least 45 minutes between passes, with the same shocking time (±10%) and operator during each pass. Stop-netted reaches were chosen to be representative of the average channel characteristics of the stream reach, and included 3–14 discrete hydraulic (channel) units. In order to assess associations of fish with discrete channel unit types, individual (contiguous) channel units were isolated using multiple stop-nets at 23 of the 45 sites sampled. All other sites were stop-netted at the upper and lower ends of the sample reach. Fish were anaesthetized using carbonated water, measured to the nearest mm, and weighted to the nearest 0.1 g after each pass, and released following completion of fish collection.

Canopy closure was visually estimated at each site; average site gradient was measured using a Sunnto clinometer; stream temperature was measured to the nearest degree C using an alcohol thermometer; and conductivity was measured to the nearest µSiemen with a hand-held meter (Cole-Parmer TDStestr-30). Sites were classified as either clearcut (logged within 15 yr), second growth (logged 15–100 yr ago), or old growth (unlogged or with minimal pre-industrial selective harvest), based on the age of the riparian forest and air photographs. Average channel structure was characterized by measuring habitat features over a reach length of 20 bankfull channel widths that included the electroshocked reach. Channel units were classified as pools (0% gradient, low current velocity, relatively deep), glides (0–1% gradient, flow, minimal water surface turbulence), runs (higher current velocity, turbulent flow), riffles (1–3% gradient, higher current velocity, water surface broken by protruding substrata, relatively shallow), or cascades (>3% gradient, higher current velocity, water surface broken by larger substrate particles), as described in Johnston and Slaney (1996) and Moore et al. (1997). Maximum depth, minimum depth (lower riffle crest if the channel unit was a pool), average width, and substrate composition (visually estimated in 5 size classes [fines: <2 mm; gravel: 2–64 mm; cobble: 64–250 mm; boulder: 250–4,000 mm; and bedrock: >4,000 mm]) were measured in each channel unit. If the channel unit was a pool, the pool-forming mechanism was also recorded as either boulder scour, LWD scour, bank scour, or free-form (Montgomery et al. 1995).

Data Analysis

Cutthroat and coho population size at each site was estimated from the removal data using the Schnute maximum likelihood procedure adapted to a 3-pass depletion (T. Johnston, B.C. Ministry of Fisheries, pers. comm.; Schnute 1983). Time constraints prevented a third pass at 2 of the sites, where populations were estimated using a Zippin removal estimate (Zippin 1958). Low fish numbers precluded depletion estimates of fish abundance for individual channel units. Numbers of fish collected in all 3 passes within a stop-netted channel unit were instead summed and divided by channel unit area to give minimum density estimates within individual channel units.

To assess the determinants of total cutthroat abundance at a site, cutthroat density was modelled (SAS General Linear Model procedure; SAS 1989) as a linear function of site (bankfull width, percent pool, channel type, dominant substrate class, b-axis of the largest particle moved by the channel; Province of British Columbia 1996) and drainage basin characteristics (high, medium, or low gradient) for the subset of 33 sites where all of these habitat factors were measured.

To define cutthroat habitat associations within a channel, juveniles were divided into 3 size classes for analysis (small: <80 mm; medium: 80–110 mm; and large: >110 mm). These groupings represent distinct classes in the size-frequency distribution of cutthroat collected from streams where individual channel units were stop-netted, and roughly correspond to 0+, 1+, and 1+ to 2+ or greater year-classes of fish. Selective use of different channel units as a function of maximum channel unit depth was evaluated by comparing observed frequency distributions for each size class with the

Table 1. Results of multiple regression of total cutthroat abundance versus habitat variables measured at sample sites (R^2 = 0.62, p = 0.001).

Source	Degrees of freedom (df)	Sum of squares (SS)	Mean sum of squares (MS)	*F* ratio	Probability (*P*)
bankfull width[a]	1	1.71	1.71	7.0	0.014 *
substrate	3	2.26	0.75	3.1	0.046 *
percent pool[b]	1	1.65	1.65	6.8	0.015 *
b-axis	1	1.62	1.62	6.7	0.017 *
basin gradient	2	2.19	1.10	4.5	0.020 *
error	24	5.83	0.24		
TOTAL	32				

[a] log-transformed
[b] arcsin (square root) - transformed

frequency distribution of maximum channel unit depth available in the environment (n = 188 individually stop-netted channel units). Significant deviation in maximum channel unit depth of occupied channel units relative to available channel units was evaluated using a chi-squared test.

Average density per channel unit type per site was calculated for the same subset of streams where individual channel units were stop-netted (n = 23). Preference for different habitats in terms of differences in densities of fish between channel unit types (for the 3 size classes of cutthroat) were evaluated using a 1-way ANOVA (n = 23) for the 3 different size classes. Only pool (n = 23), glide (n = 17), run (n = 5), and riffle (n = 20) channel unit types were included in the analysis, since cascades occurred too infrequently for meaningful analysis.

RESULTS

Total densities (per wetted area) of both cutthroat and coho juveniles were highest in smaller stream channels (Fig. 1). Maximum densities occurred in channels <4–5 m bankfull width.

Total cutthroat density was significantly related to channel bankfull width, dominant substrate size, percent pool in the electroshocked reach, b-axis of the largest particle moved at high flow, and basin gradient class (Table 1). These factors collectively accounted for 62% of the total variance in cutthroat abundance at 33 sites (P = 0.001).

Frequency of use of channel units of different maximum depth (deeper channel units tended to be pools, shallow ones were riffles, and runs and glides were intermediate in depth) was size-class dependent. Smaller cutthroat (<80 mm) used channel units of varying maximum depths roughly in proportion to their background availability (Fig. 2). Intermediate-sized cutthroat (80–100 mm) showed a disproportionately greater use of deeper channel units (Fig. 2; χ^2 = 28.2, P = 0.00), and larger cutthroat (>110 mm) showed strong selection for the deeper channel units (χ^2 = 27.9, P = 0.00).

Minimum density estimates of small cutthroat were not significantly different between channel unit types (Fig. 3), although densities were lowest in pools. Densities of intermediate-sized cutthroat trout were highest in pools and lowest in riffles (P = 0.04), and densities of larger cutthroat were also higher in pools than in riffles (P = 0.001). The apparent preference of cutthroat for pools was clearly size-related,

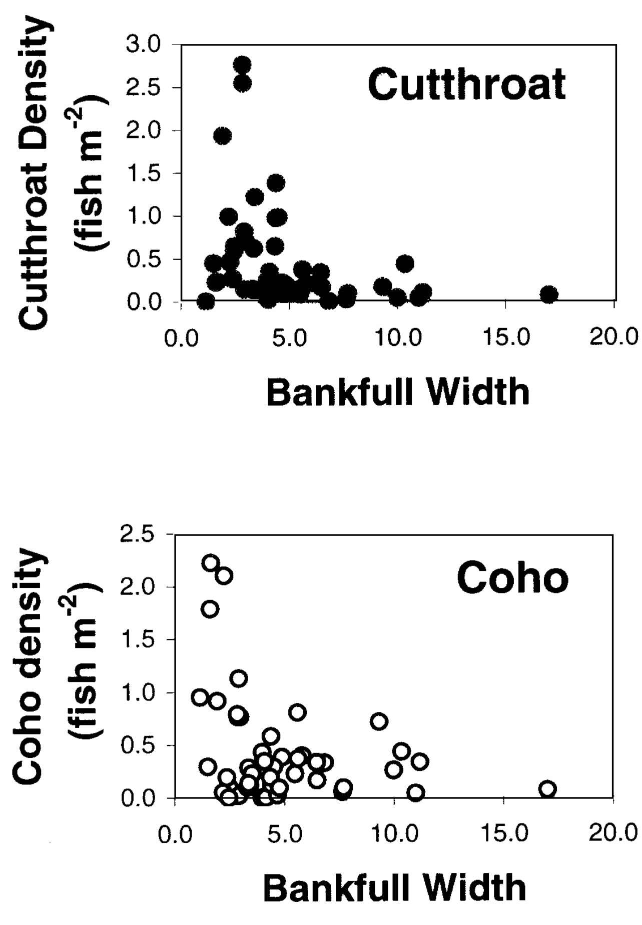

Figure 1. Density (per wetted stream area) of cutthroat trout and coho salmon juveniles as a function of bankfull channel width.

with densities of small, medium, and large size classes being, respectively, 0.7, 2.6, and 6.4 times greater in pools than in riffles. Coho also occurred in pools at densities 3 times greater than in riffles (Fig. 3).

The proportion of pools formed by scour associated with LWD was usually >50% across a wide range of channel widths (1.2–11.0 m; Fig. 4). Maximum channel depth was, on average, 10% deeper ($P = 0.005$) in pools that were formed by LWD scour (mean depth 38.8 cm) than in pools that were formed by other mechanisms (free-form meander, bank or boulder scour; mean depth 35.0 cm).

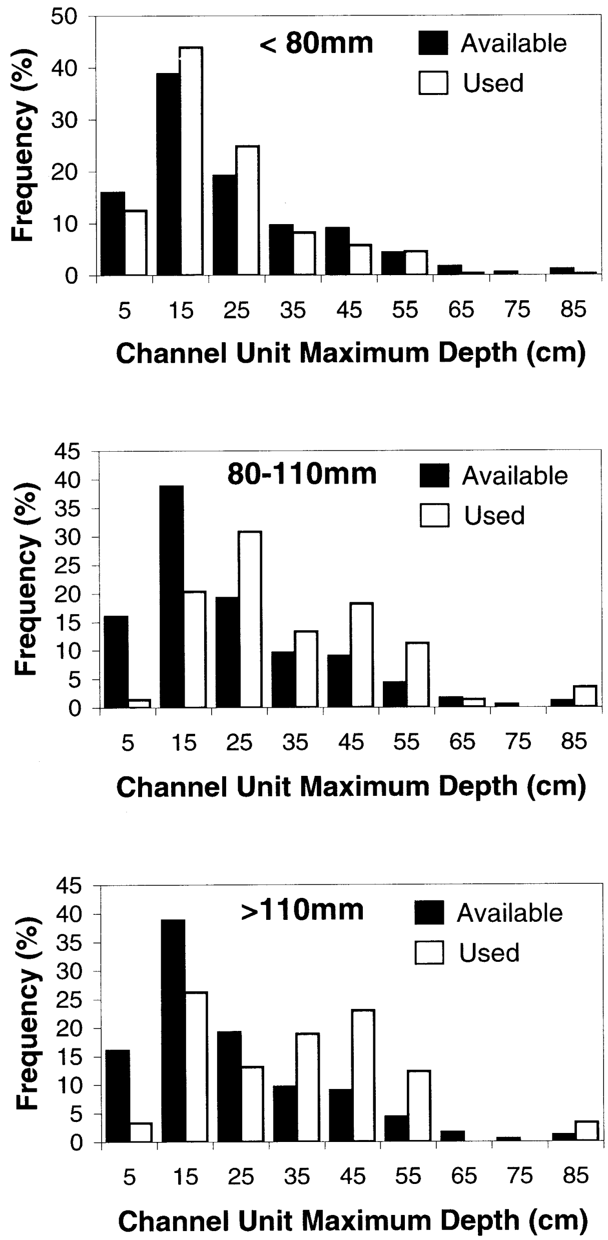

Figure 2. Frequency of occurrence of small (<80 mm; n = 686), medium (80–110 mm; n = 143), and large (>110 mm; n = 122 mm) cutthroat trout in channel units (n = 188) of different maximum depth.

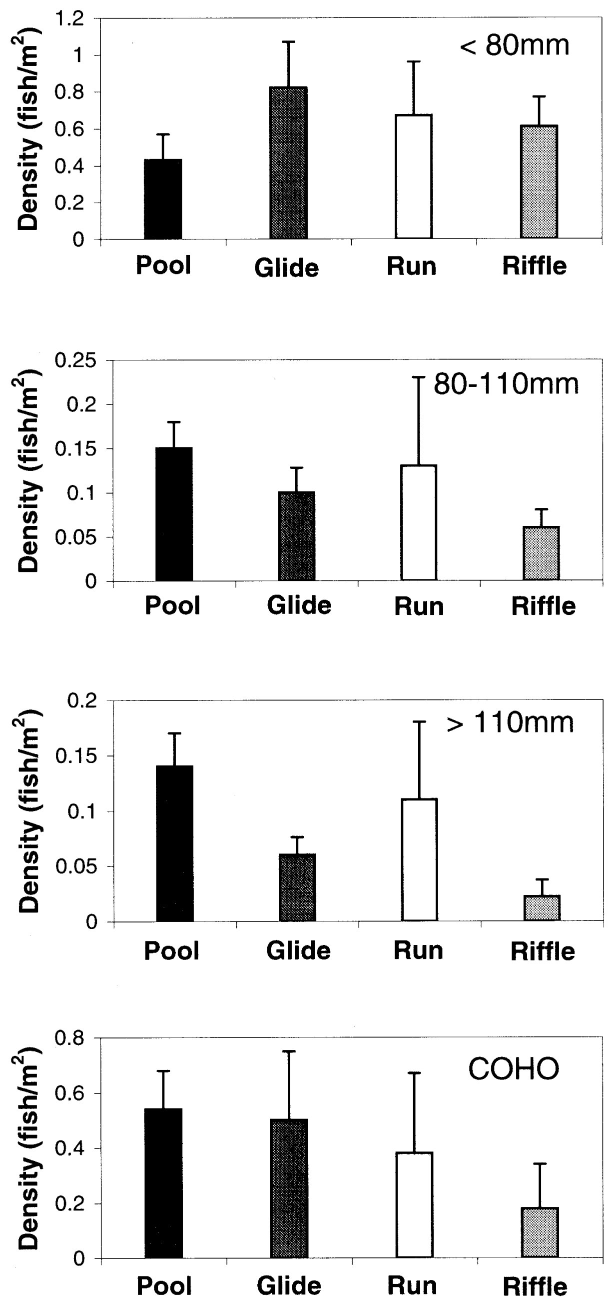

Figure 3. Density of small (<80 mm; n = 686), medium (80–110 mm; n = 143), and large (>110 mm; n = 122 mm) cutthroat trout and coho salmon juveniles in pools (n = 23 streams), glides (n = 17), runs (n = 5), and riffles (n = 20).

DISCUSSION

Juvenile cutthroat (and coho) were most abundant in smaller streams (<4 m bankfull width), which is consistent with previous observations of cutthroat ecology and distribution. Hartman and Gill (1967) found cutthroat to occupy smaller, low-gradient drainages in the lower Fraser valley, and De Leeuw and Stuart (1981) similarly observed highest densities of anadromous cutthroat in very small coastal streams (<3 m channel width).

Multiple regression analysis (Table 1) also indicates that cutthroat densities are significantly higher in lower gradient drainage basins with pool-riffle channel structure and gravel substrate. These streams typically occur in low gradient, alluvial, valley-bottom topography, areas that unfortunately are subject to the greatest impacts from logging, urbanization, and agriculture (Healey and Richardson 1996, Healey 1997). This pattern of human settlement has resulted in extensive degradation or loss of fish habitat, and the designation of anadromous cutthroat trout as a species with many stocks potentially at risk (Slaney et al. 1996).

The greater frequency of use (Fig. 2) and higher densities (Fig. 3) of larger-sized cutthroat (and coho) in deeper channel units is also consistent with previous observations of cutthroat habitat preference (Glova 1986). Larger cutthroat parr may avoid shallower channel units because of a higher vulnerability to predation (Harvey and Stewart 1991), higher energetic costs associated with holding in a swifter current (Facey and Grossman 1992), or because of a restricted visual field when feeding on drift in shallower turbulent water. Deeper channel units may provide greater cover associated with water depth or LWD, and have lower energetic costs, while providing a larger visual field for detecting prey items in the drift or on the water surface. Smaller cutthroat may be able to find suitable drift-feeding territories in shallower riffle or glide habitat, because of their smaller territory size (Grant and Noakes 1987) associated with a lower absolute food requirement relative to larger fish. Alternatively, the apparent lack of selection for pool habitat by smaller cutthroat may be driven by a high risk of predation in pools, since larger cutthroat will prey on smaller cutthroat as well as on coho parr.

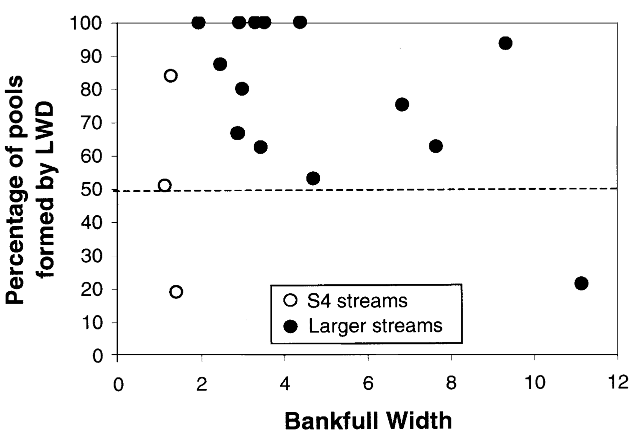

Figure 4. Percentage of pools formed by large woody debris as a function of bankfull channel width. S4 streams have a bankfull channel width of <1.5 m.

Because cutthroat parr rear for 2–5 years in coastal streams (Scott and Crossman 1973), the availability of deeper pool habitat for 1+ or 2+ year-class fish is the most likely habitat factor limiting freshwater productivity. This assumes that the streams preferred by cutthroat are not limited for spawning or young-of-the-year rearing habitat, which appears to be a reasonable assumption for lower-gradient (1–5%) gravel-cobble channels. Higher densities of coho in pools also indicates that the abundance of pool habitat may often be the most significant physical habitat factor limiting coho capacity as well.

There is a large amount of literature documenting the pervasive influence of LWD on channel structure (e.g., Bisson et al. 1987, Bilby and Ward 1989, Richmond and Fausch 1995), in particular the role of LWD in pool formation. Observations from our survey indicate that most of the pools in the sampled streams were formed by scour associated with LWD (Fig. 4). Although this does not demonstrate that pool frequency would be lower in the absence of LWD, it is consistent with other studies that have demonstrated an increase in pool frequency with higher LWD loading (Montgomery et al. 1995). Pools formed by LWD scour are also, on average, deeper than pools formed by other mechanisms, indicating that pools formed by LWD are of higher "quality"—assuming that greater depth and the presence of wood are reliable correlates of habitat quality to fish (e.g., Harvey and Stewart 1991). Small increases in pool depth may be very important for population persistence during episodic droughts with a long return period, when small coastal streams run dry and the entire freshwater population may be restricted to 1 or 2 deeper pools.

Although increased nutrients and decreased light limitation following logging may result in short-term increases in primary production, invertebrate production, and fish biomass (Murphy and Hall 1981, Murphy 1995), production usually declines to pre-disturbance levels following canopy closure (usually 10–15 years; Murphy and Meehan 1991). In many instances production will decline well below pre-disturbance levels if there has been significant degradation of channel structure, in particular excessive sedimentation (Hartman and Scrivener 1990) or loss of pool habitat.

Given that pools are likely to limit juvenile cutthroat (and coho) abundance in many small coastal streams, land management practices that reduce LWD input rates will lead to long-term reduction in habitat capacity as LWD in the channel decomposes without replacement (Murphy and Koski 1989). Channel structure in many coastal streams in British Columbia may continue to degrade over the next century, until clearcut riparian forests regrow and begin recruiting to the stream channel. In order to maintain undegraded channel structure, forested landscapes need to be managed so that LWD input rates approximate natural background inputs. Full riparian buffers will maintain LWD input rates from riparian (streamside) sources, which may be the major source of LWD to smaller, low-gradient streams. Other major sources of LWD include debris torrents from hillslopes (Hogan et al. 1998), and, potentially, S5 and S6 streams (fishless streams which require no riparian reserve zone under the B.C. Forest Practices Code) in coastal zones, where these tributary streams have the power to transport LWD downstream to fish-bearing reaches. Protecting and maintaining upslope sources of LWD may be equally or more important than maintaining riparian sources, depending on the relative importance of these different LWD sources for a given stream channel.

Our observations also indicate that LWD may be an equally important pool-forming mechanism in permanently wetted S4 streams (fish-bearing channels <1.5 m bankfull width), although our data set only includes 3 S4 streams (Fig. 4). Although the current British Columbia Forest Practices Code requires limited retention of riparian forest along S4 streams, and suggests retention of all conifer stems <30 cm DBH (diameter at breast height) in streams dependent on LWD to maintain channel processes, it is largely discretionary (Province of British Columbia 1995). Permanently wetted S4 streams (as opposed to smaller, seasonally dry ones) often constitute valuable rearing habitat for juvenile cutthroat trout and coho. Given that permanently wetted S4 streams are likely to provide as good habitat as S3 (1.5–5 m bankfull width) streams, and are likely to be partly dependent on LWD for pool formation, a largely intact riparian zone may be necessary to ensure long-term recruitment of LWD and maintenance of channel structure.

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LITERATURE CITED

Bilby, R. E., and J. W. Ward. 1989. Changes in characteristics and function of woody debris with increasing size of streams in western Washington. Trans. Amer. Fish. Soc. 118:368–378.

Bisson, P. A., R. E. Bilby, M. D. Bryant, C. A. Dolloff, G. B. Grette, R. A. House, M. L. Murphy, V. L. Koski, and J. R. Sedell. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. Pp. 143–190 *in* E. O. Salo, and T. W. Cundy, eds. Streamside management: forestry and fishery interactions. College of For. Resour., Univ. Washington, Seattle, WA.

Bustard, D. R., and D. W. Narver. 1975*a*. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 32:667–680.

_____, and _____. 1975*b*. Preferences of juvenile coho salmon (*Oncorhynchus kisutch*) and cutthroat trout (*Salmo clarki*) relative to simulated alteration of winter habitat. J. Fish. Res. Board Can. 32:681–687.

Chamberlin, T. W., R. D. Harr, and F. H. Everest. 1991. Timber harvesting, silviculture, and watershed practices. Pp. 181–205 *in* W. H. Meehan, ed. Influences of forest and rangeland management on salmonid fishes and their habitats. Amer. Fish. Soc., Bethesda, MD. Spec. Publ. 19.

De Leeuw, A. D., and K. M. Stuart. 1981. Small stream enhancement possibilities for sea-run cutthroat trout in the lower mainland and Sechelt peninsula. B.C. Minist. Environ., Victoria, BC. 100pp.

Facey, D. E., and G. D. Grossman. 1992. The relationship between water velocity, energetic costs and microhabitat use in four North American stream fishes. Hydrobiologia 239:1–6.

Glova, G. L. 1986. Interaction for food and space between experimental populations of juvenile coho salmon (*Oncorhynchus kisutch*) and coastal cutthroat trout (*Salmo clarki*) in a laboratory stream. Hydrobiologia 131:155–168.

Grant, J. W., and D. L. Noakes. 1987. A simple model of optimal territory size for drift-feeding fish. Can. J. Zool. 65:270–276.

Hartman, G. F., and C. A. Gill. 1967. Distributions of juvenile steelhead and cutthroat trout (*Salmo gairdneri* and *S. clarki clarki*) within streams in southwestern British Columbia. J. Fish. Res. Board Can. 25:33–48.

_____, and J. C. Scrivener. 1990. Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia. Can. Bull. Fish. Aquatic Sci. 223:148.

_____, _____, and M. J. Miles. 1996. Impacts of logging in Carnation Creek, a high-energy coastal stream in British Columbia, and their implications for restoring fish habitat. Can. J. Fish. Aquatic Sci. 53 (Suppl. 1):237–251.

Harvey, B. C., and A. J. Stewart. 1991. Fish size and habitat depth relationships in headwater streams. Oecologia 87:336–342.

Healey, M. C. 1997. Prospects for sustainability: final report, Fraser Basin Ecosystem study. Westwater Research Center, Vancouver, BC. 91pp.

_____, and J. S. Richardson. 1996. Changes in the productivity base and fish populations of the lower Fraser River (Canada) associated with historical changes in human occupation. Arch. Hydrobiol. Suppl. 113:279–290.

Hogan, D., S. A. Bird, and S. Rice. 1998. Stream channel morphology and recovery processes. Pp. 77–96 *in* D. L. Hogan, P. J. Tchaplinski, and S. Chatwin, eds. Carnation Creek and Queen Charlotte Islands fish/forestry workshop. Crown Publishers, Victoria, BC.

Johnston, N. T., and P. A. Slaney. 1996. Fish habitat assessment procedure. Queen's Printer, Victoria, BC. Watershed Restoration Tech. Circ. 8:95.

Jones, J. A., and G. E. Grant. 1996. Peak flow responses to clear-cutting and roads in small and large basins, western Cascades, Oregon. Water Resour. Res. 32:959–974.

Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. W. H. Freeman, San Francisco, CA.

Lisle, T. E. 1986. Stabilization of a gravel channel by large streamside obstructions and bedrock bends, Jacoby Creek, northwestern California. Bull. Geol. Soc. Amer. 97:999–1011.

Montgomery, D. R., J. M. Buffington, R. D. Smith, K. M. Schmidt, and G. Pess. 1995. Pool spacing in forest channels. Water Resour. Res. 31:1097–1105.

Moore, K., K. Jones, and J. Dambacher. 1997. Methods for stream habitat surveys. Oregon Dep. Fish and Wildl., Corvalis, OR. 45pp.

Murphy, M. L. 1995. Forestry impacts on freshwater habitat of anadromous salmonids in the Pacific Northwest and Alaska: requirements for protection and restoration. National Oceanic and Atmospheric Admin., Silver Spring, MD. 156pp.

_____, and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Can. J. Fish. Aquatic Sci. 38:137–145.

_____, and K. V. Koski. 1989. Input and depletion of LWD in Alaska streams and implications for streamside management. North Amer. J. Fish. Manage. 9:427–436.

_____, and W. R. Meehan. 1991. Stream ecosystems. Pp. 17–46 in W. R. Meehan, ed. Influences of forest and rangeland management on salmonid fishes and their habitats. U.S. Dep. Agric., Bethesda, MD.

Province of British Columbia. 1995. Riparian management area guidebook. Victoria, BC. 68pp.

_____. 1996. Channel assessment procedure field guidebook. Victoria, BC. 95pp.

Richmond, A. D., and K. D. Fausch. 1995. Characteristics and function of large woody debris in subalpine Rocky Mountain streams in northern Colorado. Can. J. Fish. Aquatic Sci. 52:1789–1802.

SAS Institute. 1989. SAS/STAT user's guide, Version 6. SAS Institute, Carey, NC.

Schlosser, I. J. 1987. A conceptual framework for fish communities in small warmwater streams. Pp. 17–24 *in* W. J. Matthews and D. C. Heins, eds. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman, OK.

Schnute, J. 1983. A new approach to estimating populations by the removal method. Can. J. Fish. Aquatic Sci. 40:2153–2169.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Board Can., Ottawa, ON. Bull. 184.

Slaney, T., K. Hyatt, T. Northcote, and R. Fielden. 1996. Status of anadromous salmon and trout in British Columbia and Yukon. Fisheries 21:20–35.

Zippin, C. 1958. The removal method of population estimation. J. Wildl. Manage. 22:82–91.