Relationship between Large Woody Debris Characteristics and Pool Formation in Small Coastal British Columbia Streams

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Abstract.—The characteristics and function of large woody debris (LWD) were measured in 41 small (1.2-11.2-m bank-full channel width), fish-bearing streams in coastal British Columbia to determine how total LWD abundance and the features of individual LWD pieces (diameter, length, orientation, and presence of a rootwad) influenced the effectiveness of pool formation. Pool spacing (the number of channel widths between channel-spanning pools) was a decreasing power function of total LWD abundance, but the relationship was relatively weak. Stratification of sites by channel gradient improved the model fit, steeper streams (≥2% gradient) having a significantly lower pool spacing than lower-gradient streams (< 2%). The proportion of LWD that formed pools increased from 6% for pieces with a diameter of 15–30 cm to 43% for pieces with a diameter of more than 60 cm. Large woody debris more than 60 cm in diameter formed a higher proportion of pools across all channel widths. A simple, size-structured model of LWD abundance in small streams suggests that loss of LWD larger than 60 cm in diameter will greatly decrease pool frequency across all channel widths but have the greatest impact on large streams. Models that estimate pool frequency based on total LWD abundance irrespective of size distribution may underestimate the impact of riparian management that reduces the number of larger-diameter trees recruiting to the stream channel.

Trees that fall into streams create pools when their trunks (large woody debris), either as individual pieces (Lisle 1986) or as logjams (Hogan 1986; Collins et al. 2002), form steps in the stream channel or deflect flow and cause bed scour. The role of large woody debris (LWD) as the major pool-forming agent in forested streams is well documented across a broad geographic range from the Pacific Northwest of the United States (Montgomery et al. 1995) to coastal Canada (Hogan 1986), the Rocky Mountains (Richmond and Fausch 1995), Europe (Gregory and Davis 1992), and Australia (Brooks and Brierley 2002). Only when the riparian forest is naturally absent (e.g., in deserts and grasslands) or subject to historic deforestation (much of Europe and eastern North America) or the channel structure is controlled by bedrock or boulders (typically at higher gradients; Church 1992) does LWD play a minor role in channel structure.

The general significance of LWD to fish habitat is now well established (Maser and Sedell 1994;

Bilby and Bisson 1998), and researchers have recently focused on developing quantitative LWDchannel structure relationships. These relationships are important for understanding how channel structure (e.g., pool frequency) will ultimately be affected by riparian management practices that alter LWD recruitment to the stream channel. For instance, both Montgomery et al. (1995) and Beechie et al. (2000) show that pool spacing (the distance between pools) decreases as a negative power function of LWD per linear meter of stream channel. Because pools are both important juvenile rearing (Lonzarich and Quinn 1995; Rosenfeld and Boss 2001) and overwintering (Nickleson et al. 1992) habitats for fishes in coastal streams, quantitative relationships between LWD loading and pool abundance are necessary for modeling the long-term effects of riparian management practices on fish habitat.

Most previous studies (e.g., Murphy and Koski 1989; Montgomery et al. 1995; Beechie and Sibley 1997) have focused on the relationship between total LWD abundance (i.e., the number of pieces per linear meter of stream channel) and channel structure. However, the characteristics of individual LWD pieces may also profoundly affect LWD

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function in small coastal streams, and models that use the average properties of LWD may generate inaccurate predictions if different types of LWD have different functional properties. Because LWD creates scour pools by locally reducing channel cross-sectional area, causing a deflection and acceleration of flow and local scour of the streambed (Lisle 1986; Abbe and Montgomery 1996), LWD diameter is a key feature influencing the effectiveness of pool creation. Bilby and Ward (1989) found that LWD size was positively correlated with pool size, and Beechie and Sibley (1997) also found that the minimum diameter required to create a pool increased with channel size. Quantifying these relationships is important, because LWD recruitment-channel structure models that account for the effect of LWD diameter on pool frequency may produce different predictions than models that treat source riparian trees of different diameters as equivalent in terms of the future probability of pool formation. This could be especially important when trying to predict the long-term effects of riparian management practices that alter both the size distribution and abundance of LWD recruiting to streams (e.g., Welty et al. 2002).

In this study, we consider how total LWD abundance and the characteristics of individual pieces affect LWD function in small coastal British Columbia streams. The specific objectives were (1) to assess how the characteristics of individual LWD pieces affect the likelihood of pool formation and (2) to test whether a model that incorporates the functional attributes of different sizeclasses of LWD generates different pool-spacing predictions than a simpler model based on total LWD abundance.

Methods

Study Sites

We assessed channel structure and LWD abundance in 41 small coastal streams (1.2-m to 11.2m bank-full channel width) containing coastal cutthroat trout *Oncorhynchus clarki clarki*. Coho salmon *O. kisutch* also occurred in most of these streams (Rosenfeld 2000; Rosenfeld et al. 2000). Streams were located on the west coast of Vancouver Island near the village of Tofino or on the Sechelt Peninsula of the mainland coast of British Columbia (Appendix 1). To ensure that sites were representative of the range of conditions available to cutthroat trout, streams were chosen to encompass a wide range of channel and basin gradients (0.5–10.4% and 1–66%, respectively) associated with high- and low-gradient topographies. Within these constraints, sites were selected primarily on the basis of logistics and ease of road or boat access. The 41 sites were distributed among 28 independent streams draining directly into the ocean, and 18 sites were located on separate tributaries of 5 of the larger streams. The sites were in predominantly forested watersheds with minimal urbanization and agriculture but some active or historic logging; although 4 sites had been clear-cut within the last 10 years, the remaining sites were old growth or second growth and none were visibly degraded by excessive sediment inputs, logging slash, or bank erosion. All sampling was done at summer base flow during June-September 1997 and 1998.

LWD and Habitat Survey

We inventoried LWD and measured channel characteristics over an average reach length of 35 bank-full channel widths at each site. Each channel (habitat) unit in the surveyed reach was classified as a pool (0% gradient, low current velocity, deep), glide (0-1% gradient, slow current velocity, minimal water surface turbulence), run (high current velocity, turbulent flow), riffle (1-3% gradient, high current velocity, water surface broken by protruding substrata, shallow), or cascade (>3% gradient, high current velocity, water surface broken by larger substrate particles), as described in Johnston and Slaney (1996) and Moore et al. (1997). If the channel unit was a pool, the pool-forming mechanism was recorded as boulder, LWD, bank, or free-form scour (Montgomery et al. 1995). Maximum wetted channel unit depth was measured at the thalweg, channel unit area was calculated as the length of the channel unit times the average channel unit wetted width, and the cover associated with LWD, undercut banks, and boulders was estimated as a percent of total surface area.

Channel units, including pools, were counted only when they spanned the entire width of the channel, so that secondary pools within larger channel units were not included as independent channel units. Our decision to exclude secondary pools was based on the desire to associate field estimates of fish abundance with different channel unit types (pools, riffles, runs, and glides) by stopnetting off individual channel units for multiplepass electroshocking depletions (Rosenfeld et al. 2000); this would not have been possible for secondary pools embedded within larger primary channel units, although visual counts in secondary pools may be possible in larger streams. This does not discount the importance of secondary pools as fish habitat or the role of LWD in their formation but rather reflects the logistic limitations on isolating fish at smaller habitat scales. We consider the implications of excluding secondary pools in the discussion.

The size and abundance of LWD (defined as wood greater than 15 cm in diameter and 1 m in length) was measured following the methodology outlined in Moore et al. (1997). Diameter was measured with a meter stick, and length was either measured with a meter stick or tape measure or visually estimated. Each piece of LWD was classified as having a rootwad present or absent and assigned to diameter and length classes. The diameter classes were 15-30, 30-60, 60-90, 90-120, and more than 120 cm and were based on the diameter of each piece in or over the active stream channel. To prevent overlap between classes, the lower bound was included in each class and the upper bound was not. For LWD with a rootwad, diameter was determined at approximate breast height (1.3 m) above the rootwad. Length classes were 1-3, 3-6, 6-9, 9-12, 12-15, 15-18, and more than 18 m (Moore et al. 1997); the total length of each piece was recorded as well as the length in or over the active (bank-full) channel. The angle of each piece of LWD with respect to the linear axis of the stream channel was estimated, the assigned values ranging from 0° (parallel to the stream channel) to 90° (at right angles to the stream channel).

The function of each piece of LWD was assessed with respect to its role in pool formation for 30 of the 41 sites. In accordance with the visual criteria described in Montgomery et al. (1995), a piece of LWD was classified as the primary agent in pool formation when it was clearly the primary structure deflecting flow and causing pool scour, when it was forming a step and plunge pool, or when it was the key member in a logjam causing pool formation.

The bank-full channel width at each site was calculated as the average of five measurements spaced approximately one channel width apart, where the location of the bank was identified based on the limit of permanently rooted vegetation.

Data Analysis

Effect of LWD abundance on pool frequency and quality.—Fish biologists and geomorphologists commonly express the relationship between LWD abundance and pool abundance in terms of pool spacing, where pool spacing is the average number of bank-full channel widths between pools (calculated as reach length in channel widths divided by the total number of pools in the reach). We modeled pool spacing as a negative power function of LWD abundance by back-transforming a regression of \log_{10} transformed pool spacing on \log_{10} transformed LWD/m, using a correction factor (CF = $e^{(MSE/2) \cdot 2.303}$, where MSE is the mean square error) for scaling back-transformed logarithmic values to arithmetic means (Sprugel 1983; Baskerville 1971). We also analyzed pool spacing as a function of LWD/m with streams stratified into two gradient classes (greater or less than 2%) to control for gradient-related differences in channel type that also affect pool spacing (Beechie and Sibley 1997). The relationship between LWD abundance and pool habitat as a percent of wetted surface area at base flow was also analyzed by modeling the percent pool area at each site (squareroot transformed to normalize residuals and equalize variance) as a linear function of LWD/m, channel width, and stream gradient. Only 37 sites could be used in this analysis because of missing data.

To determine whether pools that were formed by LWD scour differed in quality from pools formed by other mechanisms, we compared the average values of percent cover for fish, pool area, and maximum pool depth at the thalweg between LWD scour pools and pools formed by all other mechanisms in the same stream using a paired *t*test. Only 24 sites could be used in this analysis because of missing data and the absence of freeform pools at several sites. All data analyses were performed with PC SAS (SAS Institute 1989), and significance was assumed when P < 0.05.

Probability of pool formation.—We calculated the average long-term probability of a single piece of LWD forming a pool by dividing the number of LWD pieces that formed pools by the total number of LWD pieces per diameter class (i.e., as the proportion of pool-forming LWD pieces in each diameter class) for the subset of 30 sites where these data were collected. We modeled the probability of pool formation as a negative exponential function of channel width for each LWD diameter class to allow for differences in exponents between classes. The three largest diameter classes were combined into one diameter class of pieces greater than 60 cm in diameter because there were too few observations in the 90-120-cm and >120-cm diameter classes for meaningful analysis.

We used logistic regression, a technique for modeling the probability of a binary event (Tabachnik and Fidell 1996) as a function of independent predictor variables, to identify the factors influencing whether or not a piece of LWD would form a pool. We modeled the probability of pool formation as a function of LWD diameter, LWD length, presence of a rootwad, angle, channel width, and channel gradient (n = 1,704); channel gradient was subsequently dropped from the analysis because it was not significant at the 0.05 level. We also tested for changes in LWD function with stream size by including interaction terms between channel width and LWD diameter and length; when there was a significant interaction, we divided the data set at a threshold of one-half the maximum channel width and analyzed the smaller (<5.5-m channel width) and larger (\geq 5.5-m) streams separately.

Comparison of probability-based and regressionbased estimates of pool spacing.-Pool spacing (the inverse of pool abundance) can be estimated as a simple power function of total LWD abundance, as described above. By using total LWD abundance, this approach effectively treats all pieces of LWD as having an equal probability of forming pools, irrespective of LWD diameter or other attributes. The expected pool abundance in a reach of known length can also be estimated by multiplying the number of LWD pieces in each diameter class (15-30, 30–60, and >60 cm) by the average probability of pool formation for each diameter class (described above). Using this approach, pools per channel width (POOLPCW, the inverse of pool spacing) is calculated as follows:

$$POOLPCW = LWD_{15-30} \cdot CW \cdot P_{15-30} + LWD_{30-60} \cdot CW \cdot P_{30-60} + LWD_{>60} \cdot CW \cdot P_{>60}, \quad (1)$$

where the LWD terms are pieces of LWD/m for the three diameter classes, CW is one bank-full channel width, and the *P* terms are the probabilities that an individual piece of LWD will form a pool. Because this method disaggregates total LWD abundance into diameter classes that differ in their probability of pool formation, it may produce different predictions than the simpler method based on total LWD/m. We compared predicted pool spacing for the two methods for a hypothetical scenario with the largest diameter class of LWD removed, using values of LWD abundance that represent averages for our sites (0.181/m for the 15–30-cm diameter class, 0.182/m for 30–60-cm diameter class, and 0.06/m for the >60-cm di-



FIGURE 1.—Pool spacing as a function of the total abundance of large woody debris (LWD) per linear meter of stream channel. Diamonds represent data points, the middle line is the fitted power function, and the other lines are the upper and lower 95% confidence limits of the predicted means. One observation at high pool spacing is off the scale.

ameter class). Using an average diameter distribution for this exercise is reasonable because the LWD diameter distribution was unrelated to channel size (the correlations between channel width and the arithmetic and geometric mean LWD diameters were 0.08 (N = 41, P = 0.62) and 0.01 (N = 41, P = 0.95), respectively.

Results

Effect of LWD Abundance on Pool Frequency and Quality

Pool spacing (PS) decreased significantly (F =5.1; df = 1, 39; P = 0.03) as a power function of increasing LWD abundance (PS = $2.67 \cdot [LWD/$ m^{-0.33}; Figure 1). Although a great deal of the variance in pool spacing remains unexplained $(r^2 = 0.11)$, predicted pool spacing decreased from approximately 5 to 2.5 (i.e., pool abundance doubled) over the range of LWD abundance observed in this study. Inclusion of channel gradient as a class variable resulted in the equation PS = $3.40 \cdot (LWD/m)^{-0.25} \cdot (1 \text{ for a gradient } <2\%, 0.68)$ for a gradient >2%) and improved the model fit $(F = 7.3; df = 2, 38; P = 0.002; r^2 = 0.28);$ streams with a gradient greater than 2% had a significantly (P = 0.006) lower pool spacing than streams with lower gradients.

The (square-root-transformed) percent of wetted stream area that was pool habitat (PP) increased with LWD abundance and decreased with increasing channel width and gradient (PP = $[0.39 \cdot LWD/$ m - 0.03 · width - 0.021 · gradient + 0.67]²; F = 7.4; df = 3, 36; P = 0.0007; $r^2 = 0.40$). A significant positive interaction between LWD loading and channel width as predictors of percent pool habitat (F = 24.2; df = 1, 40; P = 0.0001;



FIGURE 2.—Probability that an individual piece of LWD will form a pool as a function of diameter. The circles represent the midpoints of the diameter classes (15-30, 30-60, 60-90, 90-120, and >120 cm); the error bars represent standard deviations.

 $r^2 = 0.38$ for log-transformed LWD/m) obscured the significance of other variables in multiple regression.

Pool-forming mechanism had a significant effect on indices of pool quality. Pools formed by scour associated with LWD were on average 9% deeper (t = 2.77; df = 23; P = 0.01) and had nearly twice as much instream cover (24% versus 13% of wetted surface area; t = 3.23; df = 23; P = 0.003) as pools formed by other mechanisms (boulder, bank, or free-form scour). However, the mean wetted surface area of non-LWD-formed pools was not significantly different from that of LWD-formed pools (t = -1.01; df = 23; P = 0.32).

Probability of Pool Formation

The average long-term probability of pool formation (the proportion of LWD pieces forming pools) increased with LWD diameter (Figure 2; F = 33.7; df = 2, 85; P = 0.0001), from 6% in the smallest (15-30-cm) diameter class to 42% for LWD greater than 60 cm in diameter; the probability of pool formation for LWD in diameter classes greater than 60 cm did not differ significantly. The probability of pool formation also decreased quickly with increasing stream width (Figure 3), particularly for the 15-30-cm and 30-60-cm diameter classes, but less so for the >60-cm diameter class for which data were also more variable because of fewer large LWD pieces. The declining probability of pool formation with increasing channel width was well described by negative exponential functions for the 15–30-cm (F = 20.2; df = 1, 30; P = 0.0001; $r^2 = 0.51$) and 30-60cm (F = 60.7; df = 1, 30; P = 0.0001; $r^2 = 0.50$) diameter classes, but not for the >60-cm diameter class (F = 1.32; df = 1, 30; P = 0.26; $r^2 = 0.05$). The average probability of LWD forming a pool was also a negative exponential function of channel width for all diameter classes combined ($P_{\text{all}} = 0.50 \cdot 2.71^{(-0.32 \cdot \text{width})}$; F = 80.5; df = 1, 30; P = 0.0001; $r^2 = 0.52$).

Logistic regression indicated that the probability of pool formation increased with LWD diameter, the presence of a rootwad, and LWD angle and decreased with increasing channel width (Table 1). LWD length was not a significant predictor of pool formation for the entire data set, but both length and diameter significantly interacted with channel width (Table 1). When the data set was split into small streams (channel width, <5.5 m) and larger streams (\geq 5.5 m), longer pieces of LWD were significantly more likely to form pools in larger channels but not in smaller ones.

The presence of rootwads had a large positive effect on the probability of pool formation. Forty percent of all LWD pieces with rootwads formed pools (or were key pieces in pool-formation), whereas only 16.3% of all pieces without rootwads formed pools (χ^2 = 44.9; df = 1, *P* = 0.0001). Based on frequency of occurrence in different angle classes, LWD was twice as likely to be oriented either parallel (0–15°) or perpendicular (75–90°) to the stream channel than at intermediate angles; the proportions in different angle classes (0–15°, 15–30°, 30–45°, 45–60°, 60–75°, and 75–90°) were, respectively, 0.22, 0.12, 0.15, 0.13, 0.12, and 0.26.

Comparison of Probability-Based and Regression-Based Estimates of Pool Spacing

For a scenario in which the largest (>60-cm) LWD diameter class was removed, the predictions of pool spacing based on the model relating pool spacing to total LWD/m (see above) were very different from predictions based on the model incorporating different probabilities of scour for different diameter classes as a negative exponential function of channel width (equation 1). When pool spacing was calculated as a simple function of total LWD/m, removing the largest diameter class (which represented on average only 14% of total LWD at each site) caused a small but consistent increase in pool spacing (Figure 4). When pool spacing was calculated based on the probability of scour of different diameter classes as a function of channel width, removing the largest diameter class led to predictions of a rapid increase in pool spacing at larger channel widths. Following the



FIGURE 3.—Probability of pool formation as a negative exponential function of bank-full channel width for LWD of the following diameters: (A) 15–30 cm ($P = 0.42 \times 2.71(^{-0.69 \cdot \text{width}})$), (B) 30–60 cm ($P = 0.57 \times 2.71(^{-0.33 \cdot \text{width}})$), and (C) >60 cm ($P = 0.56 \times 2.71(^{-0.07 \cdot \text{width}})$). Solid lines represent the fitted functions.

approach of Beechie et al. (2000), pool spacing was assumed to become asymptotic at a maximum of 15 channel widths, which is the approximate maximum pool spacing observed at intermediate stream gradients (Montgomery et al. 1995; Beechie et al. 2000).

Discussion

We found that LWD diameter was the most important factor influencing whether LWD was likely to form a pool. Previous research has also shown that larger wood is more likely to create pools (e.g., Ralph et al. 1994) or form key pieces in logjams (Collins et al. 2002), and Beechie and Sibley (1997) identified a minimum-diameter threshold (as a function of channel width) below which LWD was unlikely to initiate pool formation. The presence of a rootwad has also been observed to greatly increase the probability of a piece of LWD being a key member of a jam in larger rivers (Collins et al. 2002) and more than doubled the probability of LWD forming a pool in our small

TABLE 1.—Logistic regression coefficients for models predicting the probability of a single piece of large woody debris (LWD) forming a pool (or being the key member in a pool-forming jam) for all streams in the study (N = 32; 1,504 LWD pieces), for streams less than 5.5 m in channel width (N = 25; 938 LWD pieces), and for streams greater than 5.5 m (N = 7; 566 LWD pieces).

	All Streams		Streams <5 m		Streams ≥5.5 m	
Variable	Coefficient	Р	Coefficient	Р	Coefficient	Р
Diameter	0.022	0.0032	0.032	0.0001	0.047	0.0001
Length	-0.142	0.116 ^a	0.026	0.622 ^a	0.207	0.0024
Channel width	-0.566	0.0001	-0.430	0.0001	-0.237	0.0314
Rootwad	0.758	0.0001	0.680	0.0004	0.826	0.0004
Angle	0.014	0.0001	0.013	0.0001	0.018	0.019
Length \times channel width	0.039	0.0043				
Diameter \times channel width	0.0031	0.020				

a Not significant.

streams. Rootwads likely function to increase the probability of pool formation by anchoring LWD (Braudrick and Grant 2000) and, as with largerdiameter LWD, by providing a larger surface area for obstructing flow and forcing bed scour.

Our observation that LWD length was positively related to pool formation only in larger (\geq 5.5-mwide) channels suggests that short and long pieces are equally functional in small streams. In flume experiments, Braudrick and Grant (2000) also found that LWD stability was unaffected by length for pieces shorter than the channel width. Longer pieces in wider streams are more likely to create primary pools because they have a greater probability of being channel spanning and a lower probability of being transported downstream during floods (Bilby and Ward 1989).

We also found that the greater effectiveness of larger-diameter wood in forming pools persisted



FIGURE 4.—Modeled pool spacing plotted against channel width, where pool spacing was calculated as a power function of total LWD abundance (pool spacing = $2.67 \times (LWD/m)^{-0.33}$) either with all diameter classes included (triangles) or with the largest diameter class removed (diamonds). The solid circles show the pool spacing predicted by the diameter-specific probability model (equation 1 in text) with all diameter classes of LWD included; the open circles show the predicted pool spacing with the largest diameter class (>60 cm) removed.

even at relatively narrow channel widths. In contrast, the functionality in primary pool formation of LWD in the smaller (15–30-cm and 30–60-cm) diameter classes decreased quickly with increasing stream size. This pattern indicates that pool frequency is sensitive not only to total LWD abundance but also to the diameter distribution of the wood in the stream channel and source riparian zone.

The positive relationship between angle and probability of pool formation suggests that LWD is more likely to cause bed scour when perpendicular to the stream flow, which is consistent with previous observations that LWD becomes less functional when parallel to the stream bank (Hogan 1986; Ralph et al. 1994; Richmond and Fausch 1995). LWD that was nearly parallel or at right angles to the channel was overrepresented in our data, suggesting that fluvial forces preferentially rearrange LWD into these positions in smaller streams. This pattern is similar to that observed by Bilby and Ward (1989) and Richmond and Fausch (1995), except that they also found that the proportion of LWD oriented perpendicular to the channel declined with increasing stream size.

The pool spacing–LWD relationship derived for our streams had a somewhat lower slope (-0.25) and greater unexplained variance ($r^2 = 0.28$) than in previous studies (e.g., Montgomery et al. 1995: slope = -1.04, $r^2 = 0.85$; Beechie et al. 2000: slope = -0.78, $r^2 = 0.54$); this is probably due in part to our exclusion of secondary pools that were not channel spanning, which should reduce our estimates of pool abundance relative to those in other studies. The larger proportion of unexplained variance in our pool spacing–LWD relationship may also be related to the increased variation in LWD function associated with the greater range of gradients in our data set (0.5–12.3%) than in other studies. Although Montgomery et al. (1995) found that LWD appeared to decrease average pool spacing in step-pool channels, they excluded step-pool channels from their analysis because there was no clear functional relationship between LWD abundance and pool spacing in these steeper streams, where pool spacing tends to be lower (1-4 channel widths per pool) irrespective of LWD quantity. We included higher-gradient streams in our analysis because LWD (53% in jams, compared with 19% in jams for streams with a gradient less than 4%) were still responsible for 59% of the pool formation in our streams with gradients over 4%. Different studies have also used different criteria for identifying LWD (10 versus 15 cm minimum diameter, 1 versus 2 m minimum length), which may also contribute to differences in observed LWD-pool spacing relationships. In retrospect, we recommend that the minimum length and diameter of LWD be standardized to 1 m long and 10 cm in diameter when surveying smaller streams where LWD of these dimensions can significantly affect channel structure. We would also recommend that researchers measure continuous LWD dimensions rather than assigning LWD to broad diameter or length classes, since continuous measurements will permit development of more accurate relationships between LWD size and function.

An additional consequence of our choice to exclude non-channel-spanning pools was to underestimate the overall effect of LWD on channel complexity and fish habitat. While our analysis captured the gross effect of LWD on fish habitat, we clearly did not capture the functions that LWD has beyond the creation of primary pools, such as the creation of secondary (non-channel-spanning pools) in other channel unit types, the effect of LWD in providing cover in channel units other than pools, and the positive effect of LWD on stream productivity through retention of organic matter and fish carcasses. Because our analysis focused exclusively on primary channel unit formation, it should be viewed as extremely conservative (i.e., it will underestimate the aggregate effect of LWD loss on fish habitat and is not intended to discount the importance of these secondary effects). For instance, we observed that pools formed by LWD scour had greater depth and twice as much cover as free-form pools, indicating that LWD significantly increases pool quality as well as quantity. This is probaby a general effect of LWD across a broad range of stream sizes, since Abbe and Montgomery (1996) and Collins et al. (2002) also found that pools formed by LWD were deeper than free-form pools in Washington State rivers with channel widths on the order of 100 m. However, modeling the effects of LWD on pool frequency alone will not capture this effect.

Like Beechie and Sibley (1997), we found that the proportion of pool habitat at summer base flow increased as streams became smaller and that this was independent of LWD loading. A greater proportion of habitat as pool at summer low flow appears to be a general feature of smaller, lowgradient streams and may be one of the factors that contribute to their suitability as rearing habitat for juvenile salmonids. A higher proportion of pools may be related to the greater relative channel depth in small streams and the larger relative size of bed materials (cobble, boulders, and LWD; Church 1992) that obstruct flow. The ratio of average maximum pool depth to channel width decreased significantly with increasing channel width in our streams, supporting the argument that small streams are proportionally deeper than larger ones. Relatively larger substrate and deeper pools should contribute to greater overall channel roughness, providing greater habitat complexity for fish as well as lower mean water velocities at both high and low discharge. This is consistent with analysis by Statzner et al. (1988) that average water velocity decreases as streams become smaller. Collectively, the habitat features of greater relative pool area, channel complexity, and lower velocity may partly explain the tendency of many species of juvenile salmonids to rear at higher densities in smaller streams (e.g., Hartman and Gill 1968; Murphy et al. 1986; Rosenfeld et al. 2000).

Comparison of pool-spacing predictions between a model relating pool-spacing to total LWD abundance (irrespective of LWD diameter) and a model incorporating the increasing probability of larger-diameter LWD creating pools (equation 1) showed substantial differences. The diameterspecific probability model predicted a much larger decrease in pool abundance with the loss of largerdiameter LWD; however, this model probably overestimates pool spacing to some extent because it assumes that all pools are formed by LWD. In the absence of LWD, pools will form as a consequence of the natural tendency of streams to meander, with an average natural pool spacing of anywhere from 5-7 channel widths at low gradients (Leopold et al. 1964) to 10-15 channel widths at intermediate gradients (Montgomery et al. 1995; Beechie et al. 2000); however, these cited values are rough approximations and natural pool spacing will vary greatly within and between streams (Keller and Melhorne 1978; Knighton 1984). In our small coastal streams, an average of 33% of pools were free form or created by bank, boulder, or bedrock scour. Consequently, in the diameterspecific probability model the predicted pool spacing following the loss of large-diameter LWD (Figure 4; open circles) rises more steeply than it would if the presence of free-form pools were included, as they are by default in empirical LWD-pool spacing models; the true effect on pool spacing of losing the largest-diameter LWD probably lies somewhere between the two modeled scenarios.

Surprisingly, the diameter-specific probability model predicts that pool spacing will remain roughly constant over the 2–11.2-m channel width range for an average LWD diameter distribution. This is somewhat counterintuitive because the declining probability of pool formation for all LWD classes might be expected to increase pool spacing as streams become larger. Relatively constant pool spacing suggests that as streams increase in width the decreasing probability of scour for individual pieces is balanced by an increasing number of pieces of LWD per length of stream equivalent to one channel width.

Modeling and Management Implications

Most existing models relate pool spacing to the total quantity of LWD in the stream channel and ignore its diameter distribution. Although Beechie et al. (2000) used a minimum-diameter threshold relationship below which LWD is considered nonfunctional (Beechie and Sibley 1997), the default assumption remains that individual LWD pieces above this threshold have an equal likelihood of functioning in pool formation, which is not supported by our analysis. If the proportion of LWD of different diameters is constant across all sites, then modeling pool spacing as a function of total LWD abundance should be unbiased; however, if the diameter distribution of LWD under modeling scenarios differs substantially from those that were used to generate a pool spacing-total LWD relationship, projections of future channel condition will be unrealistic. Removing the large-diameter (>60-cm) LWD class (which contributes on average only 14% of total LWD) in a hypothetical management scenario (equivalent to high-grading larger riparian trees) resulted in a minimal change in pool spacing when pool spacing was calculated as a simple function of total LWD abundance. In contrast, the pool spacing predicted by the diameter-specific negative exponential probability

functions (equation 1) increased rapidly with channel width following the loss of larger-diameter LWD. These results indicate that models that ignore diameter-specific changes in the probability of scour may underestimate the impacts of removing larger-diameter LWD. Similarly, regional LWD benchmark loading targets for restoration and management that are based only on total abundance (e.g., Martin 2001) irrespective of LWD size distribution may not adequately maintain channel structure. To establish credible riparian management objectives and maximize the effectiveness of LWD entering the stream channel, future research and modeling must clarify how modifications of riparian forest diameter distributions (through selective harvest, thinning, etc.; Beechie et al. 2000) will affect future pool formation.

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References

- Abbe, T. B., and D. R. Montgomery. 1996. Large woody debris jams, channel hydraulics, and habitat formation in larger rivers. Regulated Rivers: Research and Management 12:201–221.
- Baskerville, G. L. 1971. Use of logarithmic regression in the estimation of plant biomass. Canadian Journal of Forestry Research 2:49–53.
- Beechie, T. J., G. Pess, P. Kennard, R. E. Bilby, and S. Bolton. 2000. Modeling recovery rates and pathways for woody debris recruitment in northwestern Washington streams. North American Journal of Fisheries Management 20:436–452.
- Beechie, T. J., and T. H. Sibley. 1997. Relationships between channel characteristics, woody debris, and fish habitat in northwest Washington streams. Transactions of the American Fisheries Society 126:217– 229.
- Bilby, R. E., and P. A. Bisson. 1998. Function and distribution of LWD. Pages 324–346 in R. J. Naiman and R. E. Bilby, editors. River ecology and management: lessons from the Pacific coastal ecoregion. Springer-Verlag, New York.
- Bilby, R. E., and J. W. Ward. 1989. Changes in the characteristics and function of woody debris with increasing size of streams in western Washington.

Transactions of the American Fisheries Society 118: 368–378.

- Braudrick, C. A., and G. E. Grant. 2000. When do logs move in rivers? Water Resources Research 36:571– 583.
- Brooks, A. P., and G. J. Brierley. 2002. Mediated equilibrium: the influence of riparian vegetation and wood on the long-term evolution and behaviour of a near-pristine river. Earth Surface Processes and Landforms 27:343–367.
- Church, M. 1992. Channel morphology and typology. Pages 126–143 in P. Calow and G. E. Petts, editors. The rivers handbook: hydrological and ecological principles. Blackwell Scientific Publications, Oxford, UK.
- Collins, B. D., D. R. Montgomery, and A. D. Haas. 2002. Historical changes in the distribution and function of large wood in Puget Lowland rivers. Canadian Journal of Fisheries and Aquatic Sciences 59:66– 76.
- Gregory, K. J., and R. J. Davis. 1992. Coarse woody debris in stream channels in relation to river channel management in woodland areas. Regulated Rivers: Research and Management 7:117–136.
- Hartman, G. F., and C. A. Gill. 1968. Distributions of juvenile steelhead and cutthroat trout (*Salmo gairdneri* and *S. clarki clarki*) within streams in southwestern British Columbia. Journal of the Fisheries Research Board of Canada 25:33–48.
- Hogan, D. L. 1986. Channel morphology of unlogged, logged, and debris torrented streams in the Queen Charlotte Islands. British Columbia Ministry of Forests, Land Management Report 49, Victoria.
- Johnston, N. T., and P. A. Slaney. 1996. Fish habitat assessment procedure. Watershed Restoration Technical Circular 8:95.
- Keller, E. A., and W. N. Melhorne. 1978. Rhythmic spacing and origin of pools and riffles. Geological Society of America Bulletin 89:723–730.
- Knighton, D. 1984. Fluvial forms and processes. Edward Arnold, London.
- Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. Freeman, San Francisco.
- Lisle, T. E. 1986. Stabilization of a gravel channel by large streamside obstructions and bedrock bends, Jacoby Creek, northwestern California. Geological Society of America Bulletin 97:999–1011.
- Lonzarich, D. G., and T. P. Quinn. 1995. Experimental evidence for the effect of depth and structure on the distribution, growth, and survival of fishes. Canadian Journal of Zoology 73:2223–2230.
- Martin, J. 2001. The influence of geomorphic factors and geographic region on large woody debris loading and fish habitat in Alaska coastal streams. North American Journal of Fisheries Management 21: 429–440.
- Maser, C., and J. R. Sedell. 1994. From the forest to the sea: the ecology of wood in streams, rivers, estuaries, and oceans. St. Lucie Press, Delray Beach, Florida.
- Montgomery, D. R., J. M. Buffington, R. D. Smith, K.

M. Schmidt, and G. Pess. 1995. Pool spacing in forest channels. Water Resources Research 31: 1097–1105.

- Moore, K., K. Jones, and J. Dambacher. 1997. Methods for stream habitat surveys. Oregon Department of Fish and Wildlife, Corvallis.
- Murphy, M. L., J. Heifetz, S. W. Johnson, K. V. Koski, and J. F. Thedinga. 1986. Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaskan streams. Canadian Journal of Fisheries and Aquatic Sciences 43:1521–1533.
- Murphy, M. L., and K. V. Koski. 1989. Input and depletion of woody debris in Alaska streams and implications for streamside management. North American Journal of Fisheries Management 9:427–436.
- Nickleson, T. E., J. D. Rodgers, S. L. Johnson, and M. F. Solazzi. 1992. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 49:783–789.
- Ralph, S. C., G. C. Poole, L. L. Conquest, and R. J. Naiman. 1994. Stream channel morphology and woody debris in logged and unlogged basins of western Washington. Canadian Journal of Fisheries and Aquatic Sciences 51:37–51.
- Richmond, A. D., and K. D. Fausch. 1995. Characteristics and function of large woody debris in subalpine Rocky Mountain streams in northern Colorado. Canadian Journal of Fisheries and Aquatic Sciences 52:1789–1802.
- Rosenfeld, J. S. 2000. Freshwater habitat requirements of anadromous cutthroat trout and implications for forestry impacts. Province of British Columbia, Fisheries Management Report RD 113, Victoria.
- Rosenfeld, J. S., and S. Boss. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. Canadian Journal of Fisheries and Aquatic Sciences 58: 585–593.
- Rosenfeld, J. S., M. Porter, and E. Parkinson. 2000. Habitat factors affecting the abundance and distribution of juvenile cutthroat trout (*Oncorhynchus clarki*) and coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 57:766– 774.
- SAS Institute. 1989. SAS/STAT user's guide, version 6. SAS Institute, Cary, North Carolina.
- Sprugel, D. G. 1983. Corrections for bias in logtransformed allometric equations. Ecology 64:209– 210.
- Statzner, B., J. A. Gore, and V. A. Resh. 1988. Hydraulic stream ecology: observed patterns and potential applications. Journal of the North American Benthological Society 7:307–360.
- Tabachnik, B. G., and L. S. Fidell. 1996. Using multivariate statistics. Harper Collins, New York.
- Welty, J. J., T. Beechie, K. Sullivan, D. M. Hyink, R. E. Bilby, C. Andrus, and G. Pess. 2002. Riaparian aquatic interaction simulator (RAIS): a model of riparian forest dynamics for the generation of larger woody debris and shade. Forest Ecology and Management 162:299–318.

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Appendix: Site characteristics

TABLE A.1.—Site and habitat characteristics of sampled streams.

UTM ^a coordinates			Site		Pool	Density/m ²	
(zone 10)		Bank-full					Coastal
East	North	width (m)	gradient (%)	LWD/m	spacing	Coho salmon	cutthroat trout
306687	5439675	1.68	2.0	0.27	3.02	2.22	0.23
306529	5440007	2.28	3.0	0.60	3.15	2.10	0.46
310600	5431700	11.20	0.5	0.60	4.03	0.33	0.10
305878	5441568	2.49	3.0	0.20	2.47	0.10	0.64
306615	5433600	5.50	0.6	0.66	2.45	0.23	0.08
307606	5432698	1.52	1.0	0.16	5.92	0.30	0.44
306450	5433435	1.18	5.0	0.48	4.28	0.95	0.00
296300	5452250	10.00	1.7	0.39	8.01	0.26	0.04
296800	5438850	3.98		0.28	4.52		
291700	5447500	4.90	1.4	0.39	2.54	0.38	0.18
292700	5447000	4.06	1.8	0.43	5.68	0.36	0.02
291700	5447500	4.00	1.4	0.23	3.31	0.43	0.24
297700	5453400	4.18	4.4	0.35	5.97	0.00	0.08
351100	5416300	5.83	2.3	0.78	2.75	0.40	0.20
373900	5475400	4.40	2.3	0.18	2.60	0.58	0.97
304800	5437200	1.64	1.0	0.40	4.10	1.78	0.22
308700	5440100	4.42	0.4	0.38	4.08	0.12	1.38
309400	5438150	4.52	2.2	0.28	6.94	0.29	0.98
309000	5440100	4.36	0.5	0.53	3.00	0.19	0.64
306000	5439500	2.40	1.0	0.49	5.28	0.19	0.27
449000	5477800	3.44	1.0	0.53	2.42	0.20	0.92
448800	5478400	3.38	1.0	0.44	4.41		
444000	5481500	2.22	2.5	0.21	3.66	0.05	0.99
429000	5497000	2.90	3.0	0.35	3.36	0.76	2.54
430200	5498800	3.00	1.0	0.20	3.84	0.76	0.71
460600	5498500	2.88	1.5	0.27	4.06	0.79	2.75
430700	5498700	1.96	1.2	0.31	3.32	0.92	1.93
445800	5483900	9.34	2.3	0.46	2.46	0.72	0.17
437400	5480700	2.94	0.9	0.30	4.90	1.13	0.81
442000	5484200	3.54	1.5	0.34	13.79	0.22	0.14
441800	5479800	5.62	2.6	0.15	3.54	0.81	0.15
307600	5432400	1.29		0.21	3.86		
307650	5432500	1.13		0.23	8.02		
307750	5432300	1.4		0.33	4.07		
310370	5455150	7.66	3.9	0.42	1.24	0.05	0.03
310640	5447600	4.0	12.3	1.27	2.26		
310750	5453300	6.85	2.5	0.42	1.94		
307600	5448850	2.48	8.0	1.10	2.40	0.00	0.59
307050	5448200	4.70	9.6	0.68	1.36	0.02	0.22
306850	5447700	3.32	10.4	0.65	2.78	0.10	0.14
464500	5480300	11.1	4.9	0.38	1.87		

^a Universal Transverse Mercator.