Dead Wood Dynamics in Stream Ecosystems[1]

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Abstract

Large woody debris (LWD: > 10 cm diameter and > 1 m in length) in stream channels of forested regions in North America is an essential ecosystem component. This article summarizes information from the literature on the spatial and temporal variability of LWD abundance, distribution and age; the processes of LWD delivery and elimination; and the influence of LWD on material retention, habitat formation, and productivity of streams. Examples are drawn mostly from the Pacific Coastal Ecoregion, but the fundamental principles learned from this region have application over the broad, forested regions of the Temperate Zone. Key studies show that LWD is an integral component of stream and river corridors, positively affecting material retention, habitat formation, and productivity. It is abundant in streams of all sizes flowing through forested regions, although the density and form of accumulation changes with forest type, landscape topography, and flow regime. The management implications of maintaining natural stream LWD dynamics are significant. Overall, LWD is a fundamental component of streams in many western states. This suggests that measures assuring a continued supply of LWD of appropriate size, volume, and species composition are essential for maintaining the long-term integrity of stream and river corridors.

Introduction

All stream and river ecosystems are intimately associated with the surrounding terrestrial landscape (Naiman and Bilby 1998, Naiman and Décamps 1997). One of the most obvious indications of this association is the abundance of large woody debris (LWD: > 10 cm diameter and > 1 m in length) in stream channels. LWD has a variety of controlling influences on lotic ecosystems, dictating channel form, providing sites for storage of organic matter and sediment, and modifying the movement and transformation of nutrients (Bisson and others 1987). It is well known that LWD influences the physical characteristics of streams, affecting the in-channel biological community (Bilby and Bisson 1998, Maser and Sedell 1994) as well as the dynamics of the riparian forest (Naiman and others 1998, 2000). Additionally, LWD on the riparian forest floor and in the channel provides habitat for many species of wildlife (Bartels and others 1985, Steel and others 1999).

Management of stream LWD is of increasing concern in forested regions. Woody debris in stream channels is dynamic, moving with floods and being replaced

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by trees captured mostly from adjacent riparian forests. Important, contemporary resource issues are related to the origin and maintenance of LWD in channels for habitat and to the production of adequate LWD from spatially restricted riparian zones being managed for other purposes. Even though considerable research has been conducted on LWD in the past three decades, a number of key issues (such as delivery rates and persistence) remain to be elucidated before a comprehensive LWD model can be constructed.

This article summarizes existing information on the spatial and temporal variability of LWD abundance, distribution, and age through drainage networks; the processes of wood delivery and elimination; and the influence of large wood on material retention, habitat formation; and productivity of stream ecosystems. Examples are drawn mostly from the Pacific Coastal Ecoregion of North America, but the fundamental principles learned from this region are applicable over the broad, forested regions of the Temperate Zone.

Abundance and Size

It is difficult to make quantitative comparisons of LWD abundance across the Pacific Coastal Ecoregion. In general, LWD abundance peaks in the southern end of the region and decreases toward the north *(table 1*; Harmon and others 1986). At one extreme, the LWD biomass in redwood-forested streams of California averages 74.2 kg/m^2, with highs of 180 kg/m^2 in certain reaches. At the other extreme, biomass in Sitka spruce-lined streams of southeast Alaska averages only 6.6 kg/m^2. As a whole, the Pacific Coastal Ecoregion has a higher abundance of LWD than other forested areas in North America (Harmon and others 1986). Nevertheless, in every case examined, LWD comprises > 90 percent of the standing stock of organic matter in the stream channel *(fig. 1)*.

The abundance of LWD in any watershed depends, in part, on channel size. Small channels tend to have more abundant LWD per unit area than large channels, since large channels have a greater capacity to transport wood (Bilby and Ward 1989, Swanson and others 1982). For example, LWD in first- and second-order streams may cover 50 percent of the channel, while the percentage declines by half or more in higher order streams (Anderson and Sedell 1979, Swanson and Lienkaemper 1978, Triska and others 1982). Abundance is influenced by channel type as well as by size *(fig. 2)*. LWD is reported to be twice as abundant in unconstrained channels with fine substrate than in constrained channels with bedrock and boulder substrate (Bilby and Wasserman 1989).

The abundance of LWD also depends on the surrounding riparian forest. LWD biomass is positively related to tree density in eastern Washington streams (Bilby and Wasserman 1989). Streams in coniferous forests have more LWD than streams in hardwood forests because conifers are usually larger and less easily transported (Harmon and others 1986). Similarly, streams in mature stands tend to have more LWD than streams in young stands where the riparian forest often is composed of small hardwoods (Bilby and Ward 1991, Grette 1985).

The average size of LWD, measured in length, volume or diameter, increases with channel size (Bilby and Ward 1989). Larger channels have a greater capacity to transport wood. Small pieces are flushed downstream, leaving mostly large debris.

Therefore, while abundance is lower in large channels, the average size of LWD pieces is greater.

Table 1—*Biomass of LWD in small streams (channel width <10m) flowing through undisturbed mature forests of the Pacific Coastal Ecoregion and other areas in North America (modified from Harmon and others 1986 and Bilby and Bisson 1998).*

Location	Primary tree species	Number of reaches inventoried	Average channel width	LWD biomass (kg/m^2)
Northern Rocky Mountains, Idaho	Pine (*Pinus* spp.)	3	4.4	2.2
White Mountains, New Hampshire	Red Spruce *(Picea rubens),* Eastern hemlock *(Tsuga canadensis)*	2	4.2	2.2
Northern Rocky Mountains, Idaho	Engelman spruce *(Picea engelmanii)*	2	3	2.8
Smoky Mountains, Tennessee	Mixed hardwoods	5	5.1	5
Smoky Mountains, Tennessee	Red spruce, balsam fir *(Abies balsamea)*	2	4.8	7.2
Southeast Alaska	Sitka spruce *(Picea sitchensis),* western hemlock *(Tsuga heterophylla)*	4	3.5	6.6
Coastal British Columbia	Sitka spruce, western hemlock	5	-	31.6
Cascade Mountains, Oregon	Douglas fir *(Pseudotsuga menziesii)*	24	3.5	34.7
Northern California	Coast redwood *(Sequoia sempervirens)*	8	6.8	74.2

Distribution

The distribution of LWD also depends on channel size (Bilby and Ward 1989, Swanson and others 1982). In small channels, LWD exhibits a random distribution reflecting the pattern and rate of LWD recruitment, since flows cannot normally move the debris *(fig. 2)*. In large channels, LWD is distributed in clumps, due to transport and subsequent aggregation. The clumps increase in size and decrease in frequency in a downstream direction (Bisson and others 1987, Swanson and others 1982). They are often located along the channel margin or on the inner banks of meander bends.

The distribution of LWD also depends on input processes. If the dominant process is bank undercutting of live trees or direct fall of dead trees, then distribution follows the patterns described above. If the dominant input process is episodic, such as debris flow, wind-throw, or flooding, then clumps of LWD are larger and less frequent than in streams without such inputs (Bisson and others 1987).

Figure 1—A) Plunge pool formed by LWD on the Kadashan River, Alaska. B) Episodic deposition of LWD after winter flooding on the South Fork of the Hoh River, Washington (photos by R. J. Naiman).

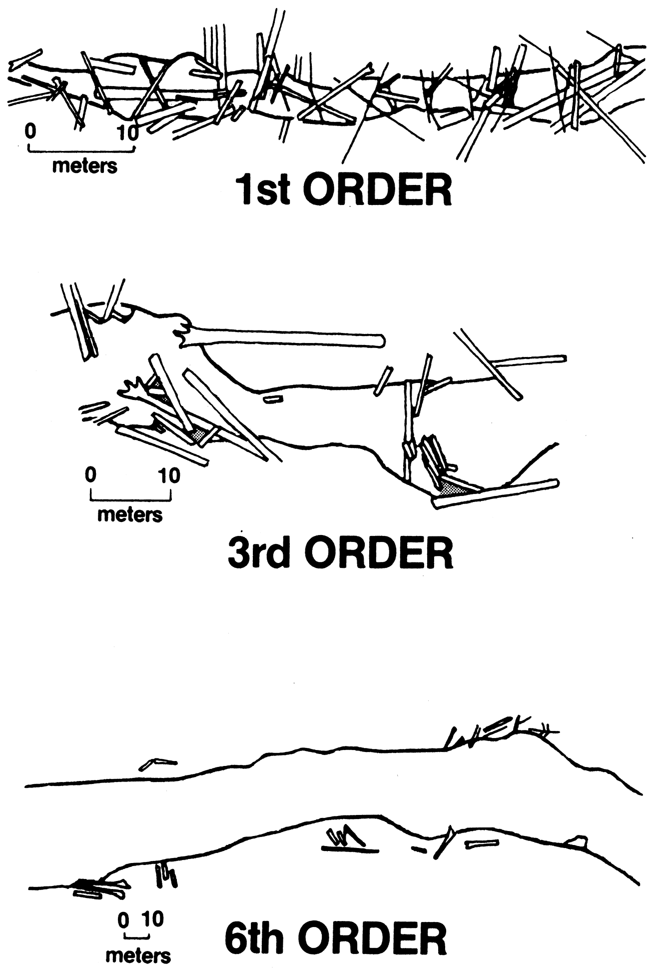

Figure 2—Typical distribution of LWD in channels of various size. Aggregation of wood increases with channel size and total wood abundance decreases. Figure based on maps of LWD from the McKenzie River, Oregon (modified from Swanson and others 1982).

Residence Time

LWD may reside in channels for decades to centuries or move unhindered downstream. Several regional studies have shown that LWD exposed to wetting and drying normally remains in the channel for 70-100 years, but many pieces appear to remain for several centuries to millennia (Hyatt and Naiman 2001; Murphy and Koski 1989; Swanson and Liekaemper 1978; Swanson and others 1984, 1976). Residence time of a particular piece of wood is influenced by many of the same environmental factors affecting LWD abundance and distribution: wood decay rate, extent of wood exposure, bed stability, channel morphology, flood intensity, and riparian forest composition.

The LWD decay rate may be of particular importance to the residence time. The decay rate is a function of stream temperature, wood chemistry, and surface area (Aumen and others 1983, Harmon and others 1986). For example, the estimated decay rate of old-growth conifer debris is 1 percent per year, but differences exist between species (Grette 1985). Of those species tested, Western red-cedar *(Thuja plicata)* decomposes most slowly, followed by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock *(Tsuga heterophylla)* (Anderson and others 1978). Red alder *(Alnus rubra)* decays fastest. LWD surface area affects the decay rate because microbial decomposition occurs from the surface inwards. Pieces with low surface area-to-volume ratios decay more slowly than those with high ratios (Bisson and others 1987). High lignin content also slows decay (Melillo and others 1982). Large pieces of debris are characterized by both a low surface area-to-volume ratio and a high lignin content, resulting in slow decay rates. Leachates from debris also may impede microbial decay.

The extent of wood exposure or burial is another critical determinant of LWD residence time. Wood buried in alluvium may have extraordinarily long residence times, facilitated by preservation from aerobic decomposition and shelter from transport processes. On the Queets River floodplain in Washington, buried LWD may persist for 3,000 years (Abbe and Montgomery 1996); LWD buried in a Tasmania floodplain dates back 17,000 years (Nanson and others 1995). Exposed LWD in the same systems resides for only a fraction of those times: several centuries on the Queets River and ~2000 years in Tasmania. Wood that is constantly submerged has a much slower rate of decomposition than those pieces that are repeatedly wetted and dried (Bilby and others 1999).

Riparian forest composition also plays an important role in the residence time of LWD. Coniferous debris persists longer than hardwood debris (Harmon and others 1986). Therefore, hardwoods may account for a larger fraction of the riparian forest than conifers but a smaller fraction of LWD in channels (Hyatt and Naiman 2001). On the Queets River, for example, the coniferous LWD resides on the channel surface for an average of 84 years (range: 1 to 1,400 years). Hardwoods have shorter residence times (normally < 50 years) than conifers, suggesting that hardwoods disappear more easily than conifers. Since the Queets River experiences extreme floods, most wood (regardless of species) is expected to be exported downstream, piled on the banks, or buried within a few decades after input. Only a few pieces remain on the channel surface for centuries (Hyatt and Naiman 2001). Further, LWD from mature stands persists longer than LWD from younger stands where the wood is typically shorter, smaller in diameter, more easily broken, and less easily anchored (Maser and others 1988).

Origin and Input Rates

Processes of Wood Delivery to Streams

Mechanisms of wood delivery to streams range from processes that provide wood predictably through time to relatively rare, episodic events that generate large quantities of wood in a very short period of time (Keller and Swanson 1979). Perhaps the most predictable wood input mechanism is tree mortality related to stand development and succession. Rate of LWD input to the channel due to mortality varies as a function of tree species and successional stage of the riparian stand. In the Pacific Coastal Ecoregion, red alder is a common early successional species in riparian areas. This species has a relatively short life span, beginning to senesce and contribute LWD to the channel approximately 60 years after stand establishment (Grette 1985). Shade-tolerant conifers, such as western red-cedar or western hemlock establish in the alder understory, then occupy the site and contribute wood to the channel as a result of stem suppression. The rate of wood delivery to the channel from the developing conifer stand is dependent on the density of seedlings established beneath the alder overstory. The success of conifer seedling establishment is related to the proximity of a seed source (Beach 1998) and the abundance of large wood on the riparian forest floor, which serves as a germination site (Thomas and others 1993). Rot and others (2000) found evidence that suppression and successional development continued to play a role in contributing LWD to stream channels in stands up to 300 years old in the western Cascade Mountains of Washington. In stands > 300 years old, mortality of larger trees due to disease and wind-throw became the dominant process delivering wood to channels.

Relatively rare, severe disturbances, including windstorms, fire or flood, can add massive amounts of wood to the channel network (Harmon and others 1986). Avalanches, landslides, and debris torrents transport wood from hill slopes through headwater tributary channels and deposit the wood and associated sediment in downstream reaches (Keller and Swanson 1979). Severe windstorms can deliver large amounts of wood to streams, the amount delivered depending on wind direction relative to the channel, soil moisture, tree species, and a number of other interrelated factors. Fire occurrence varies as a function of aspect, elevation, and other factors. However, fires recur in most western forests at intervals ranging from decades to more than 1,000 years (Agee 1988). Wood abundance in channels increases rapidly after a fire as the standing-dead trees fall (Benda and others 1998). Very severe floods also add large amounts of wood to channels through accelerated bank cutting and transport of wood stored on the floodplain into the channel (Keller and Swanson 1979). This mechanism of input tends to be particularly prevalent in large channels with extensive floodplains.

The relative importance of input mechanisms varies by stream size and watershed characteristics. In gentle terrain, where landslides or avalanches are rare, trees growing along the channel network generate nearly all wood delivered to the stream (Murphy and Koski 1989). In unstable landscapes, however, landslides and resultant debris torrents make significant contributions of LWD to channels. From 10 percent to over 50 percent of the wood in fish-bearing stream reaches in several watersheds of the Oregon Coast Range is generated by landslides that initiate debris torrents in low-order stream channels. The relative importance of wood delivery process also varies with valley form. Wind-throw is the primary mechanism of wood delivery to tightly constrained channels with erosion-resistant banks (Andrus 1998, Swanson and others 1982). In unconstrained stream reaches, undercutting of trees by bank erosion becomes a more important input mechanism. In unconstrained channel reaches in southeast Alaska under-cutting of the stream bank produces over 40 percent of the wood (Murphy and Koski 1989).

After a vegetation-removing disturbance, the length of time needed for the riparian area to begin producing LWD of sufficient size to be retained in the channel will vary with the size of the stream. Larger streams require larger pieces of wood (Bilby and Ward 1989). Thus, it takes a longer period of time for input of stable LWD to resume (Beechie and others 2000). Logged riparian areas along third-order channels on the Olympic Peninsula in Washington did not begin to contribute wood until 60 years after harvest (Grette 1985). Bilby and Wasserman (1989) suggest that streamside vegetation must be at least 70 years old to provide stable material to streams wider than 15 m in southwestern Washington.

The zone from which LWD is supplied to the channel varies as a function of the species composition and age of the riparian trees (Beechie and others 2000, McDade and others 1990). In general, most wood input to channels from stream-adjacent tree fall originates in a zone with a width equivalent to the height of the tallest trees growing along the stream. The probability of a tree within this tree-height zone entering the stream when it falls decreases with distance from the channel edge *(fig. 3;* Andrus 1998, McDade and others 1990, Van Sickle and Gregory 1990). Riparian zones with taller trees will deliver a higher proportion of LWD from a greater distance from the channel. However, even in areas supporting very tall trees, 70 to 90 percent of the input of LWD occurs within 30 m of the channel edge (Beechie and others 2000, McDade and others 1990). Steep stream-adjacent hill slopes or prevailing wind direction can alter the probability of wood delivery with distance from stream channels and cause a higher proportion of delivery to occur from greater distance than would be the case with random direction of fall (Steinblums and others 1984).

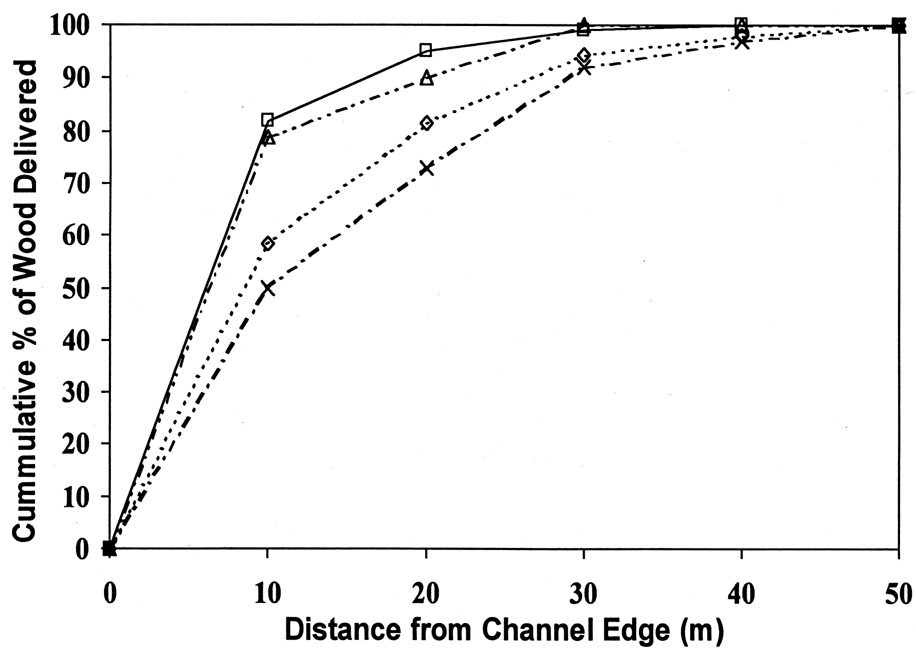

Figure 3—Cumulative percentage of LWD delivered to stream channels as a function of distance from the channel edge for streams flowing through different forest types: Δ = hardwood stands in western Oregon (McDade and others 1990); □ = old-growth conifer stands in southeastern Alaska (Murphy and Koski 1989); ◊ = mature conifer stands in western Oregon (McDade and others 1990); X = old-growth conifer stands in western Oregon (McDade and others 1990, VanSickle and Gregory 1990).

Models of Wood Input to Streams

Numerous models of wood delivery from riparian stands to stream channels have been developed recently (Andrus 1998, Bilby and Wasserman 1989, Kennard and others 1999, Van Sickle and Gregory 1990). Most models have attempted to predict the amount of wood delivered from buffer strips of varying width, which is a topic of considerable controversy in the ongoing efforts to formulate forest practices rules. These models have helped frame the regulatory discussions associated with this issue. The general structure of all these models is similar. All include a component that models forest stand growth and mortality. The output from the stand growth model is used to estimate the number and sizes of falling trees. The probability of a fallen tree entering the channel is estimated from a simple geometric model assuming random fall direction or from empirical data on probability of stream entry with distance from the channel. Input rates are coupled with an estimate of wood depletion rate from the channel to determine standing stock.

Many of the assumptions incorporated into these models clearly indicate a need to interpret the output carefully (Kennard and others 1999). All the wood input models include assumptions about tree growth rate and mortality rate, longevity of wood in the channel, and fall direction of trees, which can greatly influence the estimates of wood abundance in the channel. Nearly all the models treat tree fall and depletion of wood from the channel as constant processes, ignoring episodic disturbances. It is often assumed that the projected mortality rate of riparian trees due to suppression is an adequate surrogate for tree-fall rate. This assumption ignores the fact that most tree-fall is caused by relatively rare disturbance events such as windstorms, floods, or fires. Similarly, wood output from a stream reach is greatly influenced by floods; a factor not accounted for by the models. All these models acknowledge that the probability of a fallen tree intersecting the channel decreases with distance from the channel edge, but most assume that the probability of direction of fall for a tree is random (Kennard and others 1999, Van Sickle and Gregory 1990). However, empirical data on probability of fall direction indicates that the chance of a tree falling toward the channel is considerably greater than the chance of falling in another direction (Andrus 1998). In addition, none of the wood input models addresses delivery from sources other than riparian tree-fall. These assumptions may render the projections of wood abundance unrealistic. Despite these shortcomings, the models have proved useful in making relative comparisons of wood production among various riparian management approaches (Beechie and others 2000).

In-stream Retention of Matter

Physical Aspects

LWD, through its impacts on channel morphology and hydraulics, affects the accumulation of mineral and organic particles. Woody debris increases pool frequency and size (Robison and Beschta 1990), forms and stabilizes gravel bars (Abbe and Montgomery 1995, Fetherston and others 1995, Lisle 1986a), and increases channel width and complexity by increasing the number of meanders and backchannels (Cherry and Beschta 1989, Swanson and Lienkaemper 1978). The higher hydraulic roughness associated with LWD reduces flow velocities (Buffington and Montgomery 1999, Lisle 1986b, Maser and others 1988). The influence of LWD on channel networks and matter retention depends on stream size and gradient, flow regimes, and LWD residence time. The greatest impacts occur on small streams at low flow and immediately after wood emplacement as channel dimensions adjust to the new flow regimes (Nanson and others 1995).

Sediment Retention and Pool Formation

The relative importance of LWD in material retention decreases with increasing channel size (Bilby and Bisson 1998, Bilby and Ward 1989, Montgomery and Buffington 1998). In small streams (up to about third order), single large pieces of debris, or accumulations of small pieces anchored by a large piece, form small waterfalls by obstructing flow. This creates a plunge pool downstream of the debris. Sediments deposit upstream of the LWD and along the margins of the plunge pool *(fig. 4;* Heede 1972, Montgomery and Buffington 1998). Pools also are associated with eddies behind LWD and other structures located at the channel margin. These eddy pools and backwaters provide critical habitat for fish and other aquatic organisms.

LWD is the major factor influencing pool formation in small plane-bedded and step-pool channels (Montgomery and Buffington 1998). Bilby (1984) noted that > 80 percent of the pools in a small stream in southwest Washington are associated with wood. Likewise, 80 percent of the pools in a series of small streams in Idaho result from LWD obstruction (Sedell and others 1985). Furthermore, pools occupy only 4 to 11 percent of the surface of streams in British Columbia containing little wood, whereas pools occupy 27 to 45 percent of the stream surface in nearby streams with abundant wood (Fausch and Northcote 1992). Removal of woody debris from stream channels resulted in decreasing pool frequency and volume (Bilby and Likens 1980).

In small streams, the formation of pools by LWD creates frequent but small depositional sites. In streams flowing through mature forests in western Washington, 39 percent of the LWD pieces in channels < 7 m wide create sites of sediment deposition (Bilby and Ward 1989), and 16 percent of the streambed in channels < 5 m wide are covered by sediments associated with LWD (Bilby and Ward 1991). Nevertheless, high gradients, steep banks, and step-pool morphology limit the size of depositional areas in small streams. In addition, short-lived debris dams in small streams often form pools that break up before the storage capacity is filled (Lisle 1986b). Sediments stored at low flow are then released during high flow events. Pool volume can be maintained by the rapid turnover of debris.

In large streams, the position of LWD strongly influences the size and location of pools (Bisson and others 1987). In these systems, most LWD is oriented downstream by powerful streamflow, which favors formation of backwater pools along margins of the mainstem. In secondary channels, however, LWD can remain perpendicular to the main flow as it does in small channels. LWD functions to reduce bed shear stress downstream, or between the LWD and the stream bank, but only the largest woody structures actually generate depositional areas in large rivers. For example, only 19 percent of the LWD was associated with sediment accumulation in channels > 10 m wide (Bilby and Ward 1989), and the depositional area created by LWD covered only 2.5 percent of the streambed in channels 15 m wide (Bilby and Ward 1991).

Unusually large woody aggregations in wide channels create infrequent but substantial areas of sediment deposition. Depositional areas may occur in the middle or along the margins of the channel, creating gravel bars that grow in size with accumulation of additional debris and coarse sediment. These gravel bars are colonized by pioneer vegetation that contributes to bar stabilization and additional material accumulation (Abbe and Montgomery 1996, Fetherston and others 1995).

Measurement of sediment transport before and after experimental removal of woody debris from streams has demonstrated the critical role of LWD in sediment routing and storage. In seven small Idaho streams, 49 percent of the sediment was stored by LWD (Megahan 1982). Removal of wood from a 250 m stream reach in Oregon released 5,250 m^3 of sediment (Beschta 1979). In northern California, after removal of redwood LWD from a 100 m stream reach, 60 percent of stored sediment was mobilized by winter high flows (MacDonald and Keller 1983). The stability and storage capacity of debris are enhanced by the presence of branches and roots, which anchor the debris and serve to trap and consolidate sediments and particulate organic matter (Triska and Cromack 1980).

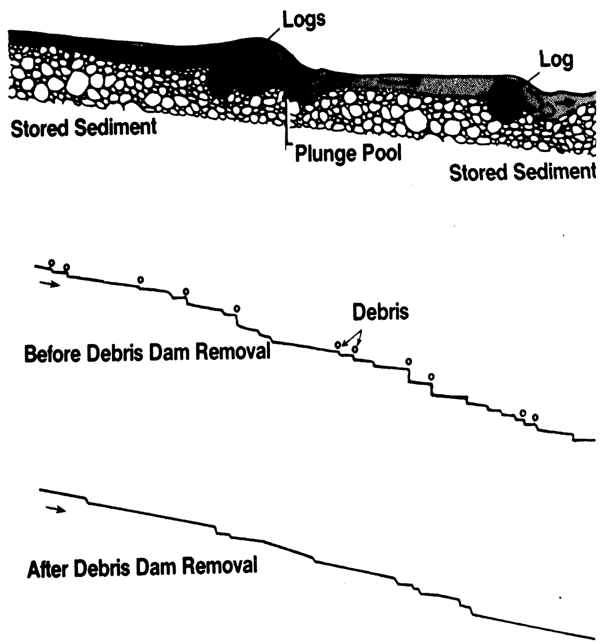

Figure 4—Stepped longitudinal profile consisting of stored sediment, LWD, and plunge pool (redrawn from Keller and Swanson 1979). Bottom: Effects of woody debris removal on the longitudinal profile of a small stream (after Bilby and Likens 1980).

Particulate Organic Matter Storage

The importance of LWD in retaining organic matter depends on the size of the organic particles. The storage of coarse particulate organic matter (CPOM: 1 mm to 10 cm diameter) such as leaves, needles, or twigs is strongly influenced by the abundance of LWD in reaches of the McKenzie River in Oregon *(fig. 4;* Naiman and Sedell 1979). The presence of LWD doubles the amount of stored coarse organic matter compared to reaches without LWD (Trotter 1990). Removal of LWD from a second order channel in New Hampshire was responsible for a dramatic 138 percent increase in the export of CPOM (Bilby and Likens 1980). In this watershed 75 percent and 58 percent of the total stored organic matter in, respectively, first and second order channels were associated with LWD (Bilby and Likens 1980). Additionally, in streams where salmon spawn, salmon carcasses represent an important input of organic matter. LWD helps to retain and accumulate carcasses, increasing their availability for consumers (Cederholm and others 1989).

Fine particulate organic matter (FPOM: < 1 mm diameter) is stored in depositional sites and backwater areas formed by LWD and in accumulations of CPOM associated with LWD. FPOM storage capacity depends on stream power and is greatly increased when shear stress and velocity are reduced by LWD. Removal of LWD from the second order New Hampshire channel was responsible for a 632 percent increase in the export of FPOM (Bilby and Likens 1980). Conversely, LWD additions increase the storage of particulate organic matter in streams. The mass of particulate organic matter increased from 88 to 1,568 g/m^2 after addition of LWD to three reaches in southern Appalachia streams. Without LWD most of this organic matter would have been transported downstream (Wallace and others 1995).

By regulating organic matter and sediment transport, LWD also influences nutrient movement through drainages. LWD removal from the small stream in New Hampshire resulted in a 144 percent increase in the export of 12 elements. Most of this increase was due to elevated export of particulate matter, which increased 446 percent (1,450 to 9,150 kg) after wood removal *(table 2;* Bilby 1981). Aluminum, iron, and manganese showed the greatest elevation in export rates after LWD removal (> 500 percent increase). These elements are transported almost entirely in particulate form. The release of phosphorus is also greatly increased by LWD removal (382 percent increase). Since phosphorus is a key nutrient for ecosystem function, LWD removal may have undesirable effects on downstream aquatic ecosystems (Likens 1972). LWD has less influence on dissolved matter, which displayed a small increase (6 percent) after wood removal (4,060 to 4,290 kg), mostly due to an increase in dissolved carbon export (18 percent). In fact, addition of wood to the stream may contribute to dissolved organic matter release by slowing decomposition. LWD may also affect the rate of nutrient removal from stream water by influencing microbial uptake rates (Wallace and others 1995).

Riparian Habitat

Habitat Formation

LWD plays a key role in the creation of riparian habitat in rivers. The process involves the accumulation of individual pieces of LWD into distinctive types of jams (Abbe and others 1993, Nakamura and Swanson 1993). Pieces usually embed parallel to the direction of flow with their roots oriented upstream. They originate from the largest of the channel-margin trees (Abbe and Montgomery 1996), effectively reducing the width of flow. Once the width of flow decreases, other pieces accumulate and jams begin to form. Jams then form bars and, eventually, bars form islands or floodplains where vegetation establishes, initiating forest succession. The resulting riparian habitat may persist for centuries before being removed by floods or other disturbance processes.

Table 2—*Estimated export of various elements from a 175m reach of a second order stream in the White Mountains of New Hampshire before and after removal of LWD (modified from Bilby 1981).*

Element	Total export (kg/year)		Increase without LWD (pct)	Particulate matter export for each element (kg)		Dissolved fraction for each element (kg)	
	With LWD	Without LWD		With LWD	Without LWD	With LWD	Without LWD
Si (silica)	710	2,350	231	295	1,930	415	420
Al (aluminum)	84.7	554	554	84.7	554	0	0
Fe (iron)	32.5	213	555	32.5	213	small	small
Ca (calcium)	275	331	20	10.2	65.5	264.8	265.5
Na (sodium)	152	225	48	13.1	85.9	138.9	139.1
K (potassium)	63.3	212	235	26.9	175.7	36.4	36.3
Mg (magnesium)	66.5	110	65	7.9	51.7	58.6	58.3
Mn (manganese)	1.1	6.99	536	1.1	6.99	small	small
P (phosphorus)	1.1	5.27	382	0.8	4.99	0.3	0.28
S (sulfur)	389	392	0.8	0.6	3.8	388.4	388.2
C (carbon)	791	1,940	145	233	1,280	558	660
N (nitrogen)	57.5	72.7	26	3.4	18.5	54.1	54.2
Total Export	5,510	13,440	144	1,450	9,150	4,060	4,290

Two types of LWD jams are responsible for the creation of riparian habitat (Abbe and Montgomery 1996). Channel-margin jams form when two or more pieces of wood lodge parallel to the flow on a point bar and amass a perpendicular stack of LWD. In contrast, a mid-channel jam forms when single pieces of wood lodge parallel to the flow and gather perpendicular and obliquely oriented pieces of LWD sequentially *(fig. 5)*. Both types of jams reduce the flow velocity nearby, creating areas of low shear stress upstream and downstream where deposition of sediment and organic matter creates bars (Fetherston and others 1995).

Two types of bars arise from the two types of jams, causing different effects on the local channel geomorphology (Abbe and Montgomery 1996). Channel-margin jams form bars downstream that merge into and extend the existing floodplain. These bars alter geomorphology by limiting erosion on the outside of meander bends. Mid-channel jams form elliptical bars downstream, diminishing channel migration in the area. As mid-channel bars grow, sediment height exceeds the water level and islands emerge.

The deposition of sediment and organic matter by which bars form provides the substrate and nutrients needed for vegetation establishment. Colonization proceeds by predictable patterns based on bar type (Abbe and Montgomery 1996). Riparian vegetation on channel-margin bars is typically of a uniform age class. On mid-channel bars, however, colonization progresses downstream over time as the island grows, creating a profile of decreasing age. In either case, colonization stabilizes bars and increases deposition, further increasing the size of the island and providing new sites for establishment of vegetation (Naiman and others 2000).

Riparian habitat associated with LWD may persist for long periods. Individual islands formed from mid-channel bars eventually may merge with each other or the bank (Fetherston and others 1995). This process can result in patches of late-successional forest surrounded by young riparian vegetation. In fact, some forest patches associated with LWD on the Queets River are > 300 years old, whereas the rest of the riparian zone is often < 100 years old (Abbe and Montgomery 1996). Thus, LWD creates hydraulic refuges, or sites of long-term stability in the midst of a habitat characterized by disturbance.

The creation and disintegration of riparian habitat is ongoing. Riparian habitat associated with LWD may be removed by sufficient disturbance. Hillslope or fluvial disturbances, such as landslides and flooding, break up LWD jams and redistribute bars within the channel. Riparian trees from the bars are recruited to the channel as LWD, and the cycle of habitat formation begins again.

Impacts on Riparian Forest Diversity

Floristically and structurally, the most diverse vegetation in forested watersheds, is associated with the riparian area (Naiman and others 1998, 2000). Efforts have been made to quantify riparian diversity along various streams from California to Alaska. In general, species diversity decreases laterally from the active channel to the hill slope. High diversity in the active channel and nearby floodplain is caused by the large variety of landforms, microclimates, and vegetative age classes created and maintained by a complex disturbance regime (Gregory and others 1991, Pollock and others 1998).

LWD increases riparian diversity by increasing the variety of landforms, microclimates, and age classes in the riparian zone. LWD heightens the variety of landforms and microclimates by adding structural heterogeneity to floodplains (Bilby and Bisson 1998). The variety of age classes is augmented through its role as a stabilizing force, allowing for old-growth patches within more dynamic stands. On cobble bars, LWD encourages the successful establishment of deciduous trees, such as red alder, by providing safe moisture-laden sites for germination and early growth. In later successional stages, LWD aids conifer establishment in the same way within an otherwise deciduous area. For example, in riparian forests of the Oregon Coast Range, 80 percent of all conifer regeneration occurs on decomposing logs (Thomas and others 1993). Similar trends exist on the Hoh River floodplain in Washington, where more than 90 percent of western hemlock and Sitka spruce *(Picea sitchensis)* seedlings establish on downed wood (McKee and others 1982). LWD also aids conifer establishment by providing a microsite with limited competition from forest floor plants (Harmon and Franklin 1989) as well as by elevating seedlings above floods while offering moisture during annual summer droughts.

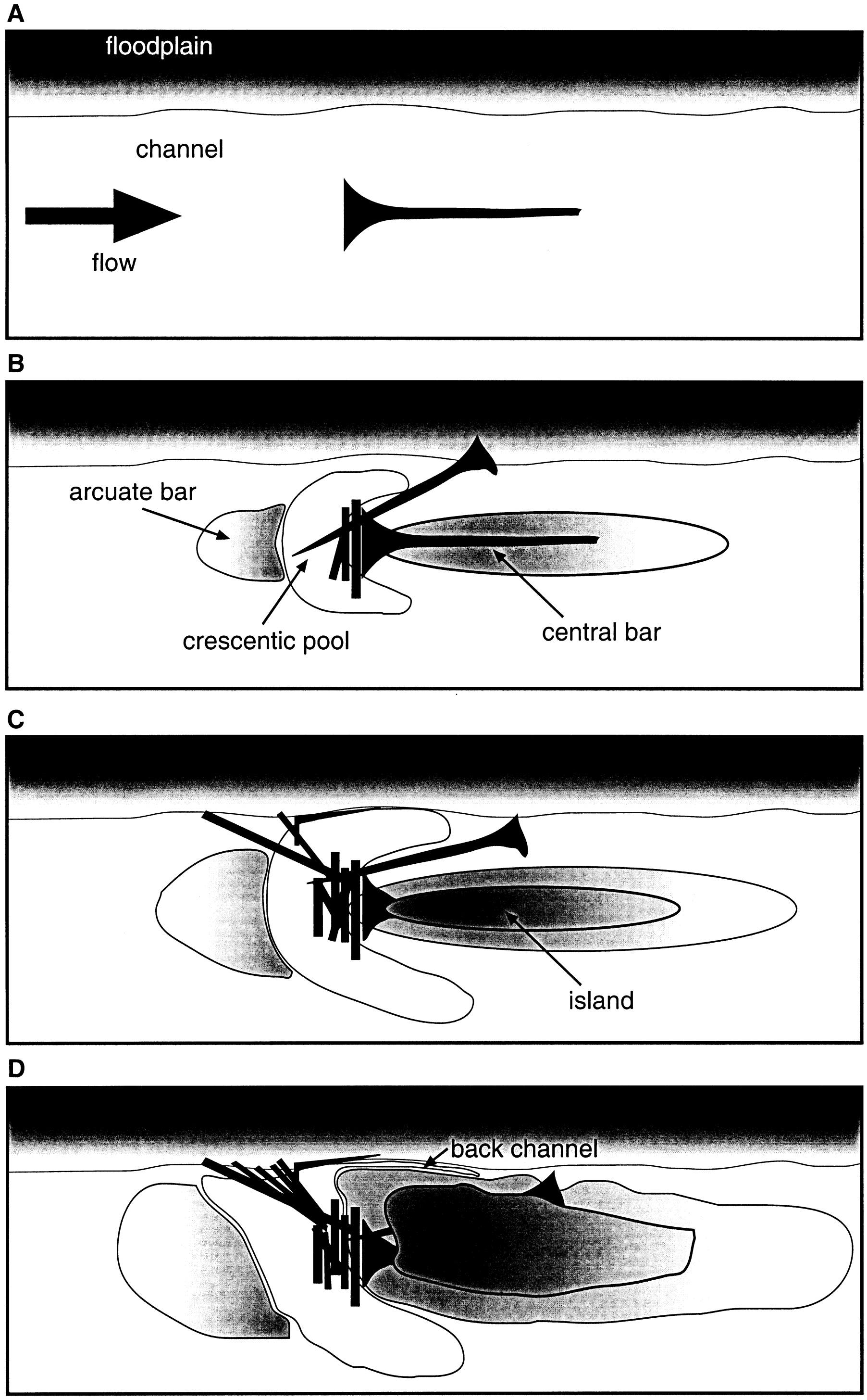

Figure 5—Morphological stages in alluvial topography associated with construction of a woody debris (bar-apex) jam. (a) Deposition of an especially large tree with the root wad intact. (b) Formation of a coarse gravel bar upstream, a crescent-shaped pool immediately upstream of the root wad, and a downstream central bar of finer sediments along the axis of the tree. (c) Island development along the central bar. (d) Integration into the broader floodplain (modified from Abbe and Montgomery 1996).

Impacts on Riparian Wildlife

The presence of LWD in riparian forests impacts the wildlife community, yet the specific processes linking LWD to riparian wildlife are far from being fully understood. There are surprisingly few studies examining the importance of LWD to riparian wildlife even though nearly two-thirds of wildlife species make significant use of river corridors sometime during their life cycles. Many wildlife food resources (i.e., insects, fungi, and seeds) are concentrated in and around LWD (Mason and Koon 1985). LWD also provides shelter from predators and environmental extremes. Small mammals and birds use LWD piles for perching, food, and cover. Summer temperatures inside debris piles are significantly cooler, and the diversity of small mammals doubles when LWD is present (Steel and others 1999). Finally, LWD influences the community composition of riparian wildlife by directly affecting the structure and composition of vegetation in different successional stages (Kelsey and West 1998).

Effects on System Productivity

Invertebrate Productivity

Increased Food Availability

Streams in the Pacific Northwest are typically oligotrophic, depending on the influx of terrestrial and marine nutrients to maintain productivity (Bilby and Bisson 1998). Terrestrial nutrients enter the stream as leaves, needles, and twigs, and as dissolved nutrients in subsurface water, while marine nutrients are transported into stream systems by spawning salmonids.

LWD traps and retains particulate organic material and creates pools in which organic matter settles during low flows, allowing the material to be utilized within the stream channel by a variety of organisms (Bilby and Bisson 1998, Gregory and others 1987). For example, marine-derived nutrients from salmon carcasses are an important source of nitrogen, and possibly phosphorus, for juvenile coho salmon *(Oncorhynchus kisutch)* and aquatic invertebrates, except shredders (Bilby and others 1996, Helfield and Naiman 2001). Cederholm and others (1989) found that LWD retained 60 percent of the tagged salmon carcasses in several Washington streams. Likewise, leaves and needles are preferentially consumed and fragmented by shredding invertebrates, producing finer particles that are eaten by collector/gatherers (Bilby and Bisson 1998). As a result, invertebrate production is often highest in areas with plentiful particulate organic matter (Gurtz and Wallace 1984, Huryn and Wallace 1987, Richardson 1991, Smock and others 1989).

Increased Habitat Quality

Habitat formed by and comprised of LWD contributes substantially to invertebrate production in streams. LWD provides stable substrate, which is used by invertebrates for filter-feeding, oviposition, burrowing during rearing, attachment during rearing, and as pupation sites (Harmon and others 1986). Experimental additions of LWD to a southern Appalachian stream resulted in a 24-fold increase in invertebrate production (Wallace and others 1995). In a southeastern coastal stream, woody habitat had the highest invertebrate production per unit surface area, highest species richness, and greatest invertebrate biomass when compared to sandy and muddy substrates (Benke and others 1985). In two headwater streams on the coastal plain in Virginia, invertebrate densities in woody debris dams were at least 10 times greater and biomass was more than 5 times greater than in sandy sediments (Smock and others 1989). Invertebrate density and biomass in reference stream reaches were correlated with organic matter storage in woody debris dams. Experimental increases in dam abundance augmented organic matter storage and invertebrate abundance.

Shifts Toward Productive Taxa

LWD also increases invertebrate production in streams by shifting the invertebrate community structure toward more productive taxa. Invertebrate communities associated with habitat created by LWD tend to be more productive (P) per unit biomass (B). Wallace and others (1995) attributed increased P:B ratios following LWD addition to shifts in collector biomass toward small, multivoltine taxa, shifts in the shredder biomass toward short-lived, univoltine taxa, and shifts in predator biomass from fewer semivoltine taxa to greater biomass in univoltine dipteran taxa *(fig. 6)*. In a Virginia stream, the proportion of invertebrate biomass comprised of shredders increased in response to experimental addition of woody debris dams (Smock and others 1989).

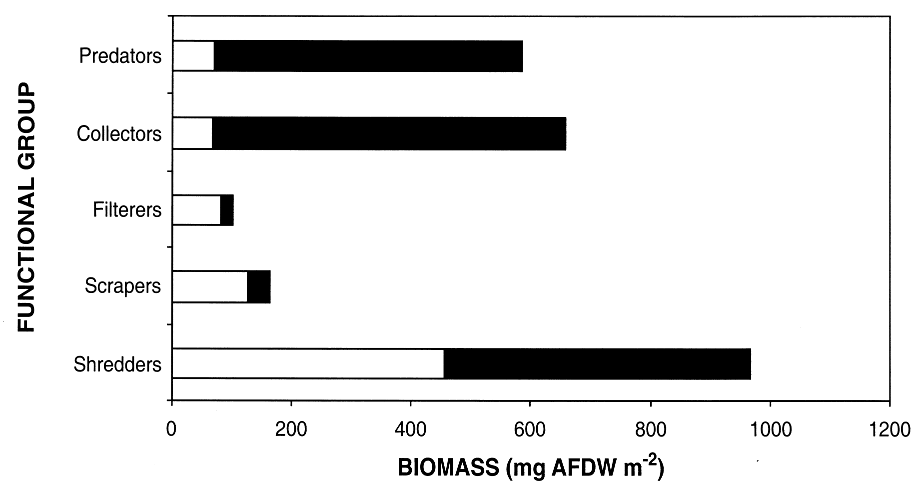

Figure 6—Biomass of invertebrate functional feeding groups at channel cross sections before LWD addition (□) and after LWD addition (■) in a southern Appalachian stream (data from Wallace and others 1995).

Fish Productivity

Increased Food Availability

By increasing prey availability, LWD contributes substantially to enhancing fish production. Bilby and Bisson (1987) found that coho salmon production (as indicated by growth) was related to food availability in several western Washington streams. In a southeastern coastal stream, > 60 percent of the prey biomass for four of eight recreationally important species and 78 percent of the biomass of drifting invertebrates were associated with wood, which represented only 4 percent of the total habitat surface area (Benke and others 1985).

Increased Habitat Quantity and Quality

LWD creates and maintains lateral habitat (backwater pools, side-channels, and eddies) by adding structural and hydraulic diversity near stream margins. The abundance of cutthroat trout *(Oncorhynchus clarki)* fry is proportional to the area of lateral habitat in streams (Moore and Gregory 1988a). LWD removal reduces the quantity of lateral habitat, reducing the population size of juvenile cutthroat trout (Moore and Gregory 1988b).

LWD also plays a critical role in the creation and maintenance of pool habitat in the Pacific Northwest. Pools are preferred by juvenile coho salmon and by adult cutthroat trout and steelhead *(Oncorhynchus mykiss*; Bisson and others 1982). This is because the fish seek energetically profitable positions in a stream, where the metabolic cost of maintaining a position in the current is lower than the energetic benefit of greater prey availability (Fausch 1984). Fausch and Northcote (1992) found that adult salmonid biomass in small coastal streams in British Columbia is strongly correlated with pool volume and depth. Murphy and others (1986) observe that densities of Dolly Varden *(Salvelinus malma)* parr are related directly to the volume of woody debris in Alaskan streams, while coho salmon parr density is best described by pool and debris volume, which also are related directly.

Deep pools formed by LWD further contribute to fish productivity by providing critical refuge and cover. Pools created by LWD provide refuge from extreme flows, which reduce salmonid recruitment (Connelly 1997, Fausch and Northcote 1992, Latterell and others 1998, McMahon and Hartman 1989). During winter freshets in Carnation Creek, British Columbia, stream reaches with deep pools and stable woody debris retained more coho salmon than reaches without those characteristics (Tschlapinski and Hartman 1983). Deep pools created by LWD also may provide thermal refuge, increasing over-winter and over-summer survival. Deep pools provide considerable protection from terrestrial and aquatic predators (Harvey and Stewart 1991). In Carnation Creek, British Columbia, juvenile coho salmon abundance was positively correlated with the volume of LWD that provided cover and refuge all year (Hartman and others 1996).

Several studies have documented that removal of LWD from the stream channel reduces pool volume and salmonid production. Fausch and Northcote (1992) estimated that effects of LWD removal on pool volume in a stream in southern British Columbia reduced salmonid biomass by 500 percent *(fig. 7)*. Much of this reduction may be due to the depleted carrying capacity of streams in winter, a critical period for salmonid survival (Murphy and others 1986). Removal of woody debris from a stream in Alaska decreased mean Dolly Varden population biomass from 12.5 to 3.9 g/m^2 and length from 106 to 79 mm, probably from a progressive loss of large fish (Elliott 1986). Likewise, the abundance and production of coho salmon and Dolly Varden were reduced by woody debris removal from two streams in southeast Alaska, despite the use of conservative removal techniques (Dolloff 1986). Taking an opposite approach, the addition of LWD to reaches of the Chehalis River, Washington, increased pool area as well as coho smolt yield and abundance of winter populations of juvenile coho (Cederholm and others 1997).

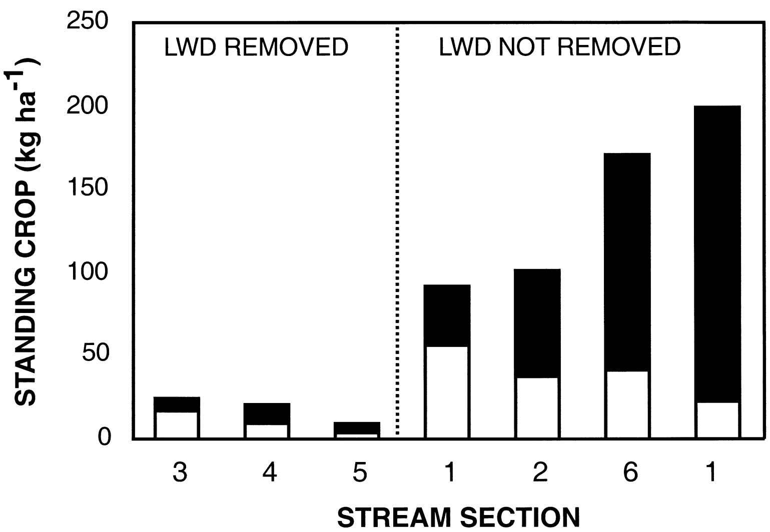

Figure 7—Standing crop of age 1+ and older coho salmon (□) and coastal cutthroat trout *(Oncorhynchus clarki clarki)* (■) in southern British Columbia stream reaches (data from Fausch and Northcote 1992)

Habitat complexity appears to contribute to salmonid production. By increasing pool volume and structural complexity, LWD encourages habitat partitioning and reduces competitive interactions among sympatric species (Reeves and others 1997). Adult cutthroat trout and juvenile coho salmon are larger and more abundant in stream sections with complex habitat (Fausch and Northcote 1992). Coho salmon abundance increases with cover complexity, suggesting that streams with little woody debris have limited over-winter habitat for survival (McMahon and Hartman 1989).

Woody debris in streams also increases fish production by slowing the downstream transport of spawning substrate. House and Boehne (1989) observed that experimental addition of LWD to a channel, previously cleaned of woody debris, increased spawning gravel area from 4 m^2/100 m to 102 m^2/100 m. Subsequently, estimated coho salmon redd abundance increased from 3 to 25/100 m. The combined effects of LWD addition resulted in a 272 percent increase in coho salmon densities over untreated sites.

Conclusions

LWD is an integral component of stream and river corridors, positively affecting material retention, habitat formation, and productivity. It is abundant in streams of all sizes flowing through forested regions, although the density and form of accumulation changes with forest type, landscape topography, and discharge regime. Unfortunately, factors influencing input and depletion rates of LWD to streams from riparian zones at contrasting points in the drainage network remain poorly known. A portion of the LWD remains as an ecologically important component of the system for many centuries, while the other portion disappears in a few decades.

The management implications of this understanding of LWD dynamics are significant. LWD is very important for the long-term integrity of stream and river corridors. In many western states, this means maintaining a continued supply of LWD of appropriate size, volume, and species composition. Management actions may include larger and more widespread riparian buffers, regulations preventing LWD removal from riverine floodplains or the removal of dead and dying trees in riparian zones, and additions of LWD to channels previously cleaned. In combination, these and other thoughtful management actions will ensure the continued supply and abundance of LWD and, by doing so, maintain the long-term productivity of stream and river corridors.

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