

Large Woody Debris and Salmonid Habitat in the Anchor River Basin, Alaska, Following an Extensive Spruce Beetle (*Dendroctonus rufipennis*) Outbreak

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Large Woody Debris and Salmonid Habitat in the Anchor River Basin, Alaska, Following an Extensive Spruce Beetle (*Dendroctonus rufipennis*) Outbreak

Abstract

A widespread and intense spruce beetle outbreak during the 1990s has killed most of the mature white spruce (*Picea glauca*) trees across many watersheds in south-central Alaska. To investigate the potential habitat impacts in a salmon stream, we characterized the current abundance and species composition of large woody debris (LWD), examined the linkages between LWD and salmonid habitat, and estimated changes in LWD abundance and associated pool habitat over time. LWD abundance was relatively low (97 pieces/km overall) and varied widely according to riparian vegetation typology, ranging from 15 pieces/km at sites with non-forested riparian zones to 170 pieces/km at sites adjacent to cottonwood forest. LWD provided significant fish cover in pools, especially in cottonwood forest stream reaches. LWD-formed pools were relatively rare (15% of total), but LWD abundance explained much of the variation in pool frequency ($r^2 = 0.86$ in spruce forest reaches) and in the proportion of pool habitats ($r^2 = 0.85$ in cottonwood forest reaches). We project the spruce beetle outbreak to result in a substantial net increase in LWD abundance over a 50-year span, peaking with 243% and 179% increases in LWD abundance for spruce forest and cottonwood forest stream reaches, respectively, in the year 2025. Concurrent with the peak in LWD abundance, our estimates show pool frequency in spruce forest reaches to reach 207% of current levels and the proportion of pools in cottonwood forest reaches to reach 167% of current levels, changes that correspond with substantially increased potential habitat for juvenile salmonids.

Introduction

The importance of large woody debris (LWD) in the formation and maintenance of salmonid habitat in streams has been well documented (Bisson et al. 1987). Pools (Fausch and Northcote 1992, Rosenfeld and Huato 2003), spawning gravel (Keller and Swanson 1979), and escape cover (Bisson et al. 1987) are created and maintained by LWD deposits. LWD also contributes to stream productivity as a macroinvertebrate substrate and food source (Anderson et al. 1984, Rinella and Feminella 2005) and through the retention of salmon carcasses (Cederholm et al. 1989) and other organic matter (Bilby and Likens 1980). Salmonid abundance is typically greater in streams

with more LWD (Bilby and Bisson 1998, Fausch and Northcote 1992) and decreases have been documented following wood removal from stream channels throughout the Pacific Northwest (Bilby and Bisson 1998).

Spruce beetles (*Dendroctonus rufipennis* Kirby, 1837) have caused extensive spruce mortality across western North America during the last two decades (Holsten et al. 1999), likely having widespread effects on in-stream LWD dynamics (Bragg 2000). Mature trees are most vulnerable to beetle attack (Doak 2004) and stand mortality can reach 90% (USDA Forest Service 1997). The intensity and magnitude of recent spruce beetle outbreaks have been linked to climatic warming and it is expected that outbreaks will spread and intensify in upcoming years (National Assessment Synthesis Team 2001). As such, studying how insect-caused deforestation affects stream habitats should be a priority; yet, to our knowledge, no field studies addressing this have been published.

A recent spruce beetle outbreak has killed an immense number of mature white spruce (*Picea*

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glauca [Moench] Voss) across south-central Alaska (Werner et al. 2006). The outbreak, persisting through the 1990s and peaking in 1996, resulted in spruce mortality across 1.19 million ha (Werner et al. 2006) and was the most extensive outbreak ever recorded in North America (National Assessment Synthesis Team 2001). The outbreak occurred during a period of high temperatures that were linked to increased winter survival and accelerated maturation rates (from 2 years to 1 year) for beetles and was augmented by drought-induced tree stress (Berg et al. 2006). The forests on the southern Kenai Peninsula were particularly hard hit, undergoing an 87% reduction in basal area of mature white spruce (Boucher and Mead 2006).

Kenai Peninsula streams are situated in a climate zone that is transitional between coastal rain forest and interior boreal forest. The riparian zones are not consistently forested throughout the watersheds; rather, they are a mosaic of forests, grasslands, shrublands, and non-forested wetlands. Few studies have examined the role of LWD in boreal streams (Clark et al. 1998, Liljaniemi et al. 2002, Mossop and Bradford 2004) and no research has investigated the extent to which LWD contributes to salmonid habitats in boreal/maritime transitional systems. This research seeks to improve our understanding of the potential habitat effects associated with a spruce beetle outbreak along some of the most productive salmon streams in Alaska.

Beetle-killed spruce trees will definitely constitute a flux of LWD to stream systems as boles are weakened by fungi and eventually break (Harmon et al. 2005), but it has been unclear if the net effect of the beetle outbreak will be a gain or loss of LWD in the upcoming decades. The main factors determining future LWD abundance in impacted streams will be the rate at which potential LWD-forming trees are regenerated in beetle-killed stands, the rate at which dead trees enter streams, and the rate at which instream LWD is removed from the system. A cumulative increase in LWD abundance would occur if regenerating trees mature before beetle-killed spruce is depleted from the stream (Bragg 2000).

Forest stands along the Anchor River, a productive salmon stream on the southern Kenai Peninsula, have been decimated by spruce beetles (61% mortality for trees >10 cm dbh [diameter at breast height]) yet, to date, only 10% of the

basin's snags have fallen (Boggs et al. 2008). As such, the timing of this study presented a unique opportunity to characterize the role of in-stream LWD prior to any sizable influx of beetle-killed trees while simultaneously making projections regarding the influx rates and effects of beetle-killed LWD. The goals of this study were to document the current abundance, species composition, and size distribution of LWD, to identify any associations between LWD and salmonid habitat, and to predict future changes in the abundance of LWD and associated habitat within the Anchor River. We conducted stream surveys to determine 1) the frequency and species composition of LWD in stream reaches adjacent to different riparian vegetation types, 2) the importance of LWD as in-stream fish cover, 3) the importance of LWD to pool formation, and 4) the contribution of beetle-killed spruce to the current load of Anchor River LWD. In addition, we developed a simple model to predict changes in LWD load and associated pool habitat over a 50-year span.

Methods

Study Area

This study was conducted in the Anchor River watershed, just north of Homer on the southern Kenai Peninsula, south-central Alaska. The Anchor River is a 5th-order peat wetland-supported system typical of non-glacial streams in the area. The watershed area is 583 km² and 185 km of anadromous fish streams support ecologically and economically important stocks of Chinook salmon (*Oncorhynchus tshawytscha* Walbaum, 1792), coho salmon (*O. kisutch* Walbaum, 1792), steelhead/rainbow trout (*O. mykiss* Walbaum, 1792), and Dolly Varden char (*Salvelinus malma* Walbaum, 1792) (Mauger 2005). The watershed drains westward into lower Cook Inlet and is bounded on the east by the subalpine Caribou Hills; the topography is gently rolling with wide river valleys and extensive wetlands. Elevation ranges from sea level to 600 m in the headwaters. The climate is transitional between continental and maritime and average precipitation is 64 cm, mostly occurring in late summer through fall (August to November; Mauger 2005). Maximum stream discharge occurs during this season and also during snowmelt and ice breakup (April and May); low flows occur during June and July (Mauger 2005). Watershed land uses include private and public

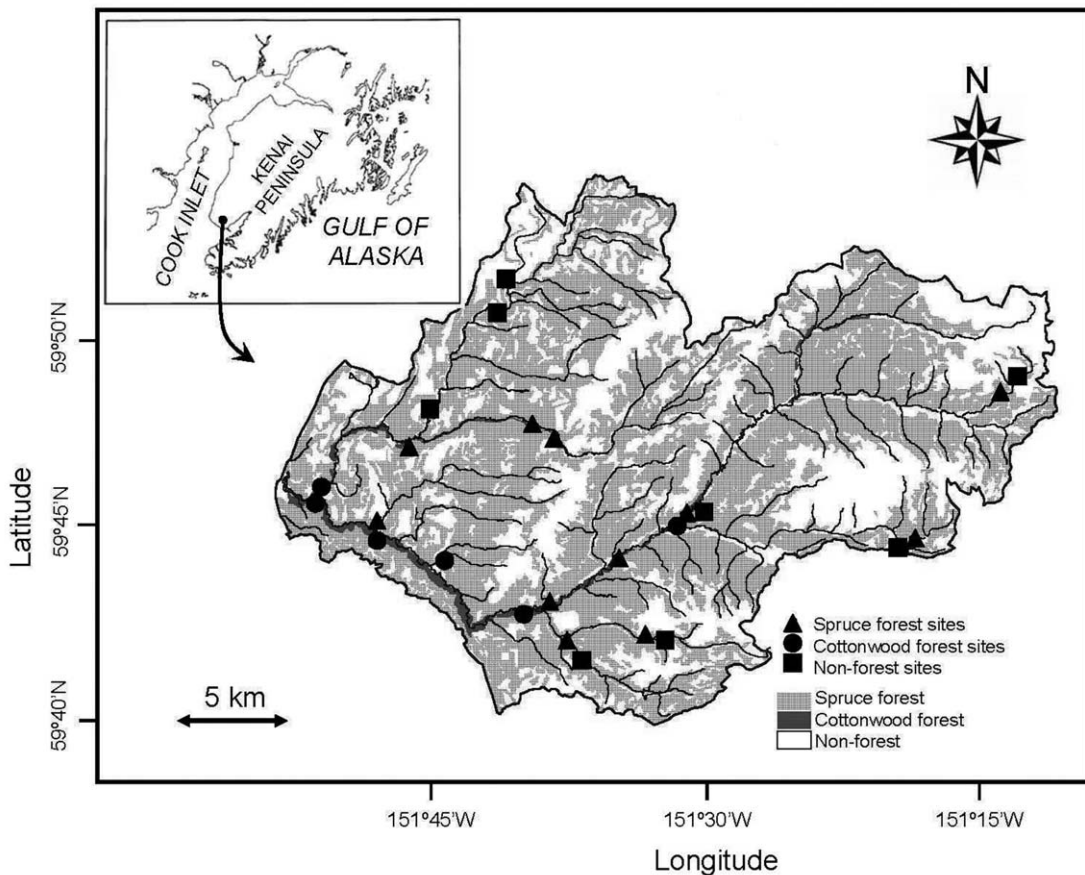


Figure 1. Distribution of dominant vegetation types and in-stream survey sites within the Anchor River basin, Alaska.

timberlands, road and trail networks, recreational and residential development, oil and gas fields, and gravel mines (Szarzi et al 2003).

We defined the LWD recruitment zone as a 30-m-wide band along each streambank since nearly all LWD originates from this area (Murphy and Koski 1989). The vegetation map by Greenberg and Rude (2003) identifies seven dominant vegetation types throughout the riparian zones of the Anchor River, although only four are common (Figure 1). Willow (*Salix* spp.) and grass (primarily bluejoint [*Calamagrostis canadensis* (Michx.) Beauv.]), combined into the non-forested vegetation type for this study, dominate some reaches in the upper half of the basin (1st- through 3rd-order reaches), making up 9% and 8% of the riparian zone, respectively. White spruce forest, comprising 52% of the riparian zone, is the most

common riparian vegetation type and is found throughout the watershed. Continuous bands of cottonwood forest (*Populus balsamifera* spp. *trichocarpa* [Torr. & Gray ex Hook.] Brayshaw) dominate the vegetation along the floodplain reaches of the lower valley floor (4th- and 5th-order reaches) for a total of 16% of the riparian zone. Although hybrid Lutz spruce (*Picea glauca* x *sitchensis*) were present in the study area, we considered them to be synonymous with white spruce due to the difficulty of distinguishing between these taxa in the field. The spruce forest was essentially a monoculture, but cottonwood stands contained a substantial number of spruce and lesser amounts of mountain alder (*Alnus tenuifolia* Nutt.).

Two large floods during the fall of 2002 undoubtedly influenced the abundance and

distribution of LWD in the Anchor River. We observed large LWD deposits and evidence of bank failure at some sites in the lower watershed, and the magnitude of flood disturbance appeared to increase in a downstream direction. However, pre-flood LWD data are lacking, making it impossible to quantify the influence of these events on LWD.

Site Selection

We focused our in-stream survey efforts on low-gradient, valley-floor streams because we expected these to be the most important in terms of salmonid habitat. Streams draining hillslopes were typically too steep and small to support extensive salmonid spawning or rearing habitat. Land ownership and accessibility also influenced our site selection process. We chose sites that were accessible from public roads or hiking trails or on private property

where access had been granted but sampling locations were at least 50 m from human influences such as trail crossings, road bridges or power lines. Hike-in sites were limited to day trips in order to maximize the number of sites surveyed. We stratified our in-stream sites according to the common riparian vegetation types (spruce forest, cottonwood forest, non-forested; Greenberg and Rude 2003) in order to extrapolate data from our sample reaches to the larger watershed. We sampled a total of 25 stream reaches throughout the Anchor River watershed (Figure 1, Table 1), allocating sites among the vegetation types roughly in proportion to their abundance within the watershed (n = 11 for spruce forest, n = 6 for cottonwood forest, n = 8 for non-forested). Our spruce forest sites coincided with some of those used by Boggs et al. (2008) for stand regeneration surveys.

TABLE 1. Descriptions of 25 Anchor River basin study reaches.

Site Name	Dominant vegetation type	Stream order ¹	Bankfull channel width (m)	Reach length (m)	Channel slope (%)
Beaver Creek	Spruce	2	2.9	181	1.5
Bridge Creek	Spruce	2	4.5	160	2
Gravel pit trib., S.F. Anchor R.	Spruce	2	4.2	365	1.5
Unnamed trib., S.F. Anchor R.	Spruce	1	2.0	150	2
North Fork Anchor River	Spruce	3	9.3	172	1.5
North Fork Anchor River	Spruce	3	9.2	160	1.5
North Fork Anchor River	Spruce	4	10.8	153	1
South Fork Anchor River	Spruce	4	19.0	220	1
South Fork Anchor River	Spruce	4	35.3	101	0.5
South Fork Anchor River	Spruce	4	20.0	279	1
Twitter Creek	Spruce	2	3.8	146	2
North Fork Anchor River	Cottonwood	4	12.5	269	1
South Fork Anchor River	Cottonwood	4	30.0	703	1.5
South Fork Anchor River	Cottonwood	4	28.7	314	1
South Fork Anchor River	Cottonwood	4	25.3	477	1.5
South Fork Anchor River	Cottonwood	4	25.3	206	1.5
South Fork Anchor River	Cottonwood	4	18.7	410	1.5
Beaver Creek	Non-forest	3	6.3	171	2
Bridge Creek	Non-forest	2	4.1	143	3.5
Unnamed trib., S.F. Anchor R.	Non-forest	1	3.9	188	1.5
Twitter Creek	Non-forest	2	2.8	153	4
Beaver Creek	Non-forest	2	2.2	155	0.5
Chakok River	Non-forest	3	7.4	301	0.5
Chakok River	Non-forest	3	6.1	160	1
Chakok River	Non-forest	3	2.4	201	1

¹Derived from 1:63,000 map

In-stream LWD and Habitat Survey

We conducted field surveys during the fall of 2004 and spring of 2005. Our sample reaches encompassed at least three riffle/pool sequences with a minimum reach length of 100 m. At each sample reach, we surveyed each piece of LWD (defined as any piece ≥ 10 cm in diameter and ≥ 2 m long; Bilby and Ward 1989) present in the bankfull channel. For each piece, we recorded the species (when possible to identify), length and dbh (or diameter at large end if rootwad was missing), and the source (e.g., bank erosion, beetle-killed, windthrow). We inferred the source of each spruce LWD piece based on the presence/absence of a rootwad and evidence of beetle galleries in the bole. Trees that have died due to beetle infestation typically develop a secondary fungal infection that weakens the bole and allows it to snap within a meter or so of the rootwad. As such, we classified LWD that showed beetle galleries and a snapped bole (i.e., no rootwad) as *beetle kill*. We assumed that such LWD pieces were recruited into the stream solely due to the beetle infestation. We classified LWD pieces with beetle galleries and an attached rootwad as *bank-eroded beetle kill*—these pieces had been recruited to the stream by bank erosion regardless of the fact that they were beetle-infested. We classified LWD with no beetle evidence as *bank eroded/windthrow* and we considered these pieces to have been recruited independently of the beetle outbreak.

In terms of salmonid habitat, we focused on the extent to which LWD was associated with pool quantity and fish cover. Although spawning habitat can be created by LWD (Keller and Swanson 1979), we found that deposits of gravel of a suitable size for salmonid spawning were ubiquitous in the Anchor River and that documenting the extent of spawning gravel coverage within stream reaches was subject to observer bias. For each pool in each sample reach, we measured surface area, maximum depth, and residual depth and recorded the formative agent (primarily LWD, boulders, and lateral scour). LWD and boulders cause pools to form in two basic ways. They can deflect or constrict stream flow which causes scouring of streambed or bank material or they can impound water (Buffington et al. 2002). For our purposes, lateral scour pools were those on the outside of stream bends that were not associated with any other formative agent. We took all

in-stream measurements from the bankfull level to account for fluctuating water levels and to allow among-site comparisons. For each pool we also indexed the areal extent of in-stream fish cover (e.g., LWD, boulders, overhanging streambank; see USEPA 2004). Cover classes were as follows: 0 = not present; 1 = $<10\%$ cover; 2 = $10\text{--}39\%$; 3 = $40\text{--}75\%$; and 4 = $>75\%$. We averaged the cover scores from each pool within a study reach, using the midpoint of the cover ranges to represent their respective cover classes, to give a score representative of the entire reach. For each reach we also quantified the areal percentage of pool habitat and the pool frequency (expressed as the number of pools per unit of stream length equal to the mean bankfull width) which allowed us to standardize pool frequency across streams of varying size.

We used nonparametric comparisons when possible because the skewed distributions and zero values in the data caused violations of parametric assumptions. We used nonparametric (Kruskal-Wallis) ANOVA (and post-hoc nonparametric multiple comparisons) to test for size differences among LWD species and to compare habitat attributes (LWD abundance, pool abundance, pool cover) among stream reaches in the three riparian vegetation types (spruce forest, cottonwood forest, non-forested). We used Pillai's trace MANOVA, a relatively robust parametric statistic (Zar 1999), to compare multiple responses (e.g., LWD species composition) among the vegetation types, followed by nonparametric ANOVAs when significant differences were indicated by a MANOVA. We used linear regression to test the relationship between LWD abundance and reach-wide measures pool habitat abundance (i.e., pool frequency and % pool). We used Statistica 6.0 with α of 0.05 for all analyses; results are summarized as mean \pm one standard deviation.

Results

LWD Abundance and Attributes

We surveyed 5.9 km of stream and a total of 575 LWD pieces for a basin-wide LWD abundance of 97 pieces/km in the Anchor River. Species of trees producing LWD included cottonwood, white spruce, mountain alder, paper birch (*Betula papyrifera* Marsh.), and willow. Cottonwood and white spruce accounted for 39% and 34% of the LWD pieces surveyed, respectively. Alder made

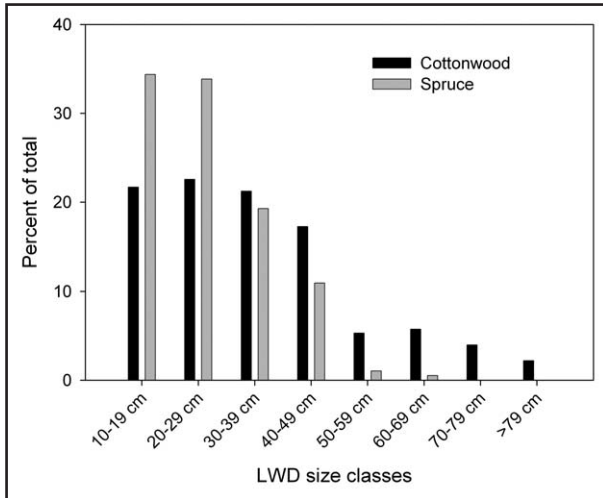


Figure 2 Diameter at breast height (dbh) frequency histograms for spruce and cottonwood LWD.

up 11% of the total and birch and willow each accounted for less than 1%. Fifteen percent of the LWD pieces were too decayed to identify. The two common LWD-forming species differed significantly in volume: spruce was $1.7 \pm 2.7 \text{ m}^3$ and cottonwood was $4.9 \pm 9.5 \text{ m}^3$ (ANOVA, $P < 0.001$; $n = 194$ and 225 , respectively). Spruce LWD ranged from 10 to 65 cm dbh and cottonwood LWD ranged from 10 to 145, but the majority of pieces were <49 cm dbh for both species (Figure 2).

Access constraints forced us to select sites that were often spatially clumped and/or on the same tributary system (Figure 1). This created potential for LWD inputs at some sites to drift to nearby downstream sites and, in turn, for data from such sites to be autocorrelated, even after controlling for forest type. Autocorrelation would cause over-estimation of power with our statistical procedures. To determine if this was the case, we used the abundance of each LWD species found at each site to calculate the Euclidian distance between all pairwise combinations of sites. This provided a similarity measure of distance between sites in terms of relative abundances of various LWD species. We then plotted the Euclidean versus geographic distances and looked for patterns in the data scat-

ter. No patterns were evident, suggesting independence among our sampling units.

The abundance of LWD in the Anchor River varied widely according to riparian vegetation typology, ranging from 15 pieces/km at sites with non-forested riparian zones to 170 pieces/km at sites adjacent to cottonwood forest (Figure 3). ANOVA indicated significant differences among vegetation types ($P = 0.003$) and a multiple comparisons test indicated that spruce forest and cottonwood forest sites had similar LWD abundance ($P = 0.61$) while non-forested sites had significantly lower LWD abundance than sites in spruce forest ($P = 0.048$) or cottonwood forest ($P = 0.003$) (Figure 3). MANOVA indicated differences in LWD species composition among the riparian vegetation types ($P = 0.002$) and follow-up ANOVAs indicated that spruce and cottonwood forest sites had statistically similar abundances of the various LWD taxa ($P > 0.05$), whereas the non-forested sites had significantly less cottonwood LWD than did cottonwood forest sites ($P = 0.004$) and non-forested sites had less unknown/other LWD than either spruce forest sites ($P = 0.011$) or cottonwood forest sites ($P = 0.044$) (Figure 3).

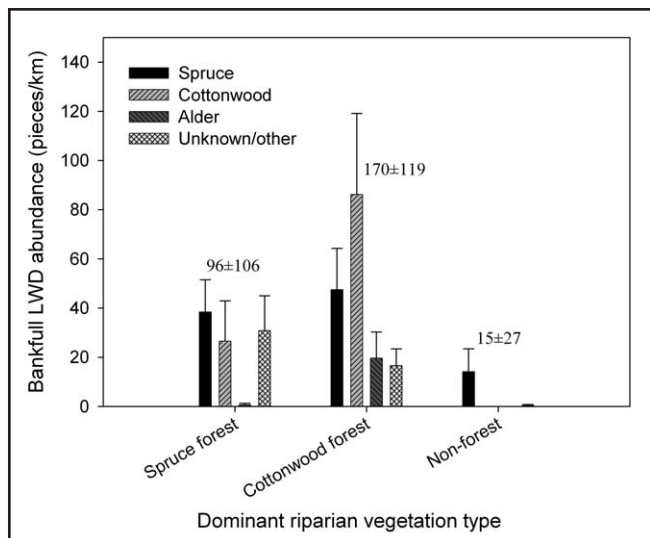


Figure 3. Mean + standard deviation LWD frequency by species (bars) and dominant riparian vegetation type (numerical text); total LWD, cottonwood LWD, and unknown/other LWD were significantly less abundant in non-forested stream reaches than in other stream reaches ($P < 0.05$).

The spruce LWD associated with the three riparian vegetation types showed similar composition in terms of source (i.e., beetle kill, bank-eroded beetle kill, bank-eroded; MANOVA, $P = 0.68$). Overall, spruce LWD was equally divided among the three sources: bank-eroded beetle kill comprised 28%, bank-eroded/windthrow comprised 36%, and beetle kill comprised 36% of the current spruce LWD.

LWD and Stream Habitat

We surveyed 155 pools during this study; of these, 71 were in spruce forest reaches, 21 were in cottonwood forest reaches, and 63 were in non-forested reaches. There was no difference among the overall pool cover scores for the riparian vegetation types (ANOVA, $P = 0.73$; $n = 11$ for spruce forest, $n = 6$ for cottonwood forest, $n = 8$ for non-forested; Figure 4). However, pool cover scores for constituent cover types (i.e., LWD and undercut bank) varied according to riparian vegetation type (MANOVA, $P = 0.047$; Figure 4). Follow-up ANOVAS showed that LWD provided more pool cover in cottonwood forest stream reaches than in non-forested stream reaches ($P = 0.01$; Figure 4). Additionally, cottonwood stream reaches had significantly less pool cover from undercut bank than did stream reaches in spruce forest ($P = 0.03$) or non-forested reaches ($P = 0.005$) (Figure 4).

To account for differences in stream size among our sites, we expressed pool frequency in terms of pools per unit of stream length equal to the channel width of the respective reach (i.e., pools/channel width). Overall, the pool frequency was 0.25 ± 0.20 pools/channel width and there was no significant difference in pool frequency among the riparian vegetation types (ANOVA, $P = 0.46$). Likewise, the proportion of pools attributed to any given formative agent (i.e., LWD, boulder, lateral scour) did not vary according to riparian vegetation type (MANOVA, $P = 0.36$; $n = 21$ for LWD, $n = 42$ for boulder, $n = 92$ for lateral scour). Lateral scour was the dominant pool forming process, forming 59% of all pools. Twenty-seven percent of pools were formed by boulders and LWD-formed pools were relatively rare, comprising 15% of all pools. Despite the overall infrequency of LWD-formed pools, pool frequency was positively correlated with

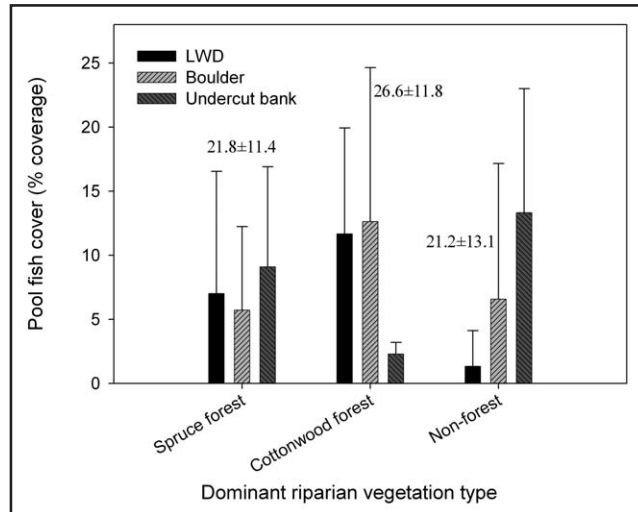


Figure 4. Mean + standard deviation pool fish cover by cover type (bars) and riparian vegetation type (numerical text); total pool cover did not significantly differ among the three vegetation types, LWD cover was significantly greater in cottonwood forest than in non-forested stream reaches, and undercut bank cover was significantly lower in cottonwood forest than in other stream reaches ($P < 0.05$).

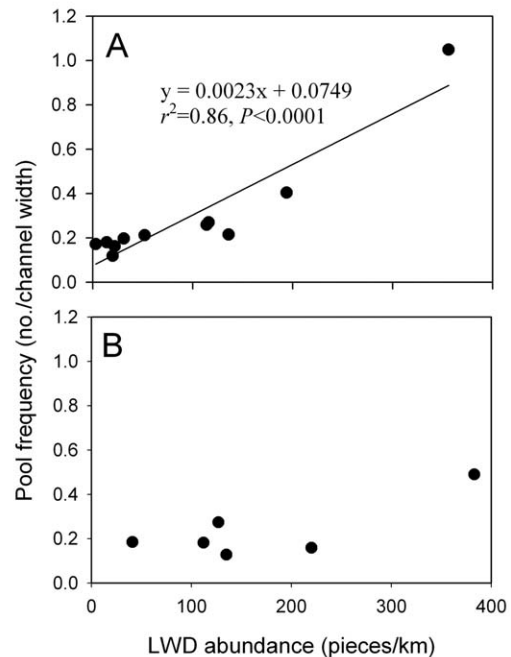


Figure 5. The relationship between LWD abundance and pool frequency for stream reaches in spruce forest (panel A) and cottonwood forest (panel B).

LWD abundance in spruce forest stream reaches ($P < 0.0001$; Figure 5A), however no significant

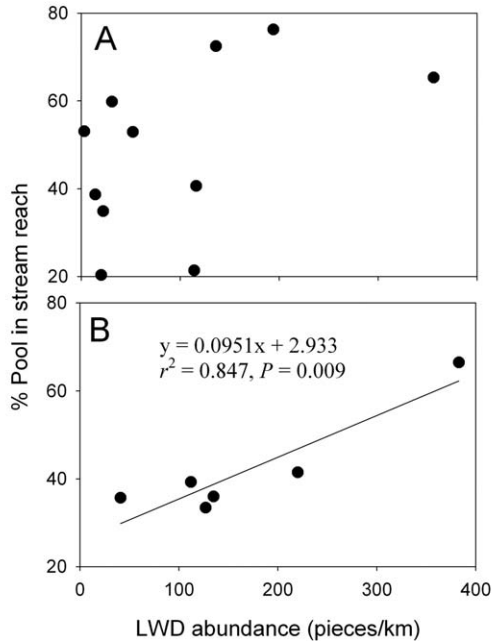


Figure 6. The relationship between LWD abundance and % pool in stream reach for stream reaches in spruce forest (panel A) and cottonwood forest (panel B).

trend occurred in the cottonwood forest reaches ($P = 0.066$; Figure 5B). The spruce forest site with highest LWD abundance and pool frequency (Figure 5A) was a 4th-order reach on the South Fork where 67% of pools were formed by LWD. Additionally, the areal percentage of the sample reach as pool habitat was positively correlated with LWD abundance in cottonwood forest sites ($P = 0.009$; Figure 6B); spruce forest reaches showed high percent pool at high LWD abundances but this trend was not statistically significant ($P = 0.12$; Figure 6A). The cottonwood forest site with the highest LWD abundance and pool area was a 4th-order reach on the South Fork. Although none of the pools in this reach were formed by LWD, scouring associated with LWD accumulations contributed considerably to the size of existing lateral scour pools. Across all forested sites, LWD abundance correlated with the percentage of pools that were formed by LWD ($P = 0.002$; Figure 7).

Discussion

LWD Abundance and Attributes

Our results indicate that LWD abundance and species composition in spruce and cottonwood

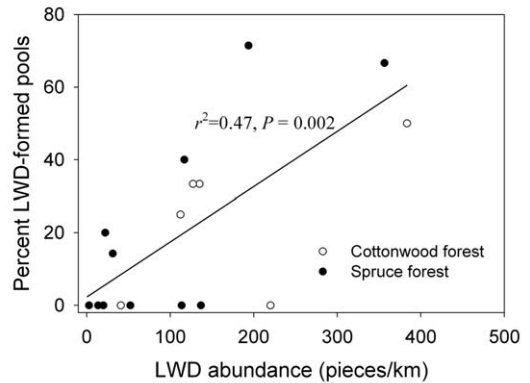


Figure 7. The relationship between LWD abundance and the percentage of pools formed by LWD.

forest reaches are comparable (albeit highly variable). Cottonwood LWD was substantially larger in volume than spruce and, all else being equal, cottonwood should be more effective at forming stream habitats (Buffington et al. 2002). However, this assertion must be made in the context that cottonwood stream reaches tended to have larger, less erodible substrates.

Our basin-wide LWD abundance estimate for the Anchor River (97 pieces/km) is less than the 133 pieces/km surveyed by Martin (2001) in the coastal coniferous forest south of Kachemak Bay, Alaska, and considerably lower than the 303 to 357 pieces/km measured at temperate rainforest sites in southeast Alaska. The Anchor River is farther north than the streams surveyed by Martin (2001) and our results are consistent with the northward decrease in LWD load observed across the Pacific Northwest (Bilby and Bisson 1998) and Alaska (Martin 2001). However, wood abundance in the Anchor River was typically much lower than that found further to the north in Yukon River tributaries draining boreal forest (Mossop and Bradford 2004).

In contrast to this study, where LWD abundance generally increased in a downstream direction, others have found LWD to be most abundant in headwater reaches. In heavily forested basins of western Washington, where large tree species like western redcedar (*Thuja plicata* Donn ex D. Don), Douglas fir (*Pseudotsuga menziesii* [Mirbel] Franco), and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) dominate the riparian zone, Bilby and Ward (1989) found LWD abundance to decrease in a downstream direction. They attributed

this pattern to the decreased power of headwater streams to move LWD, which accumulated more and, on average, smaller LWD than downstream reaches. A meta-analysis of 3793 western Oregon stream reaches yielded similar patterns (Wing and Skaugset 2004). The downstream increase in LWD abundance, along with the relatively low LWD abundance observed in the Anchor River, is obviously related to the patchiness of riparian forest in this area, where shrubs and grasses dominate a significant portion of the riparian vegetation in the upper watershed.

LWD and Stream Habitat

The scarcity of undercut bank fish cover in cottonwood stream reaches was likely related to differences in stream channel morphology associated with different riparian vegetation types. Cottonwood forest reaches had unconsolidated alluvial streambanks that resisted undercutting while spruce forest and non-forested reaches tended to have steep, vegetated streambanks that were susceptible to undercutting. Taken together our data show that, while LWD was not the dominant source of pool cover in any vegetation type, it did contribute somewhat to the available pool cover, particularly in cottonwood forest stream reaches.

The positive correlations between LWD abundance and pool frequency suggest that, despite the relative infrequency of LWD-formed pools, locally-abundant LWD contributed to pool formation, an assertion supported by the correlation between LWD abundance and the percentage of pools formed by LWD. As observed by Montgomery et al. (1995), increased LWD abundance was associated with increased pool-forming LWD pieces and, in turn, more pools. The significant relationship between LWD abundance and pool frequency in spruce forest sites and the lack thereof in cottonwood reaches may be related to differences in stream channel morphology within these vegetation types. Generally, spruce forest reaches were narrower and had finer substrates than cottonwood forest reaches and this would tend to make spruce forest reaches more amenable to the processes of LWD anchoring and substrate erosion necessary for LWD-associated pool formation. While LWD abundance did not correlate with pool frequency in cottonwood reaches, LWD abundance was associated with an increase in the proportion of pool habitat. This suggests that LWD was ineffective at creating pools in the larger substrates and wider

floodplain channels typical of cottonwood forest reaches but that the size of existing pools was increased by locally-abundant LWD.

Projected LWD and Pool Abundance

We developed a simple model to estimate the future LWD load in spruce forest and cottonwood forest stream reaches. It was impossible to make similar projections for non-forested sites due to the lack of LWD at many sites. We assumed that the non-beetle kill portion of the LWD pool was at equilibrium and held this constant over the 50-year span. We divided the current beetle-killed instream LWD (17 pieces/km) by the estimate of the percent of beetle-killed trees fallen to date (10%, Boggs et al. 2008) to yield an estimate of the total quantity of beetle-killed spruce expected to eventually enter the channel (170 pieces/km). These estimates were likely conservative since a considerable amount of LWD was deposited outside of the bankfull channel during the 2002 floods. We then derived an equation to estimate the timing of this flux based on the locally-derived approximations of spruce snag dynamics in Harmon et al. (2005):

$$(1) \quad LWD_t = LWD_f - LWD_f e^{-rt}$$

LWD_t = LWD abundance at year t , t = time in years, LWD_f = the total expected flux of beetle-killed LWD (170 pieces/km), and r = the annual rate (0.10) of snag failure. We assumed that there would be a 10-yr lag prior to any snags falling (Harmon et al. 2005) and we also assumed that all beetle-killed trees died in 1997, the weighted average year of Kenai Peninsula spruce mortality (USDA Forest Service and Alaska Department of Natural Resources 2005).

To account for the depletion of LWD after it enters the stream channel, we applied the exponential decay model from Murphy and Koski (1989)

$$(2) \quad LWD_t = LWD_0 e^{-kt}$$

where LWD_t = LWD abundance at year t , t = time in years, LWD_0 = the original LWD abundance, and k = a decay constant. Murphy and Koski (1989) provide empirically-derived decay constants from southeast Alaska streams that account for depletion due to decomposition, abrasion, and export and are based on different combinations of LWD size and stream channel form (channel typology followed Paustian et al. [1984]). We used decay

TABLE 2. Current and projected LWD abundance and pool frequency for Anchor River stream reaches in spruce forest and cottonwood forest.

	Year projected					
	2005	2015	2025	2035	2045	2055
LWD abundance in spruce forest stream reaches (pieces/km)	96	204	233	227	210	192
LWD abundance in cottonwood forest stream reaches (pieces/km)	170	277	304	296	277	259
Pool frequency in spruce forest stream reaches (pools/channel width)	0.30	0.54	0.61	0.60	0.56	0.52
Percent pool in cottonwood forest stream reaches	19	29	32	31	29	28

constants for the B3 and C1 channel types for spruce forest and cottonwood forest reaches, respectively. B3 were small, low-gradient channels (1–3% slope) in forested valleys with alluvium and bedrock substrates; C1 were large, alluvial channels on the valley floor (Murphy and Koski 1989). We averaged constants for the 10–30 cm and the 31–60 cm diameter classes to represent the size distribution of Anchor River LWD.

We applied the model at 10-year increments over a 50-year span and we project the spruce beetle outbreak to result in a substantial net increase in LWD abundance, peaking with 243% and 179% increases in LWD abundance for spruce forest and cottonwood forest stream reaches, respectively, in 2025 (Table 2). These findings are consistent with those of Bragg’s (2000) simulations which indicated a sharp increase in LWD delivery with peak channel loads occurring ~30 yrs after a spruce beetle outbreak.

We expect significant numbers of potential LWD-forming spruce to be regenerated along the Anchor River prior to the depletion of the expected pulse in beetle-killed LWD. Several studies from the Kenai Peninsula have indicated that seedling regeneration is adequate to restock beetle-killed stands (Davis et al. 2000, van Hees 2005, Boucher and Mead 2006), contrasting earlier observations that a lack of exposed mineral soil and competition with post disturbance colonizers like bluejoint grass may inhibit seedlings (Holsten et al. 1995). Most recently, Boggs et al. (2008) found abundant seedling regeneration in the Anchor River basin, observing that most seedlings had germinated on downed logs, as did Davis et al. (2000). We expect that many of these new seedlings, along with the larger residual spruce, will grow to LWD-forming size within 50 years. In the past, Anchor River basin spruce trees have reached 10 cm dbh within 50 years of age and 30 cm dbh within 100 years (on average) (Boggs et al. 2006) and growth of regenerating spruce will

likely be higher (e.g., 40% higher; Holsten et al. 1995) for several decades following the beetle outbreak due to a release in competition associated with canopy loss (Berg et al. 2006).

Considering the positive correlations between LWD and pool habitat documented in this study, it can be expected that the projected LWD increase will be accompanied by an increase in pool habitat. We used projected LWD abundance data and the regression equations given in Figures 5A and 6B to project pool frequency and percent pool in spruce and cottonwood stream reaches, respectively, over a 50-yr span. Concurrent with the peak in LWD abundance, our estimates show pool frequency in spruce forest reaches to reach 203% of current levels and the proportion of pools in cottonwood forest reaches to reach 168% of current levels (Table 2).

Management Considerations

Aside from changes in the abundance of LWD and associated pools, the spruce beetle outbreak could potentially alter salmonid habitat by indirect means. Changes in vegetation structure may alter the timing and volume of water yield through increases in snowpack quantity and/or evapotranspiration rates (Kostadinov and Mitrovic 1994, Zimmermann et al. 2000, Stottlemeyer and Troendle 2001). Also, increased sunlight penetration is inevitable, particularly in stream reaches flowing through spruce stands. Summer water temperatures in the Anchor River already reach levels potentially detrimental to salmonid health (i.e., 20 °C for 6 days during 2005; Mauger 2005), however we expect these high temperatures are related to the extensive low-gradient, non-forested streams and wetlands in the upper portion of the basin. Temperature and streamflow are regulated by a complex interaction of the above factors and it is difficult to foresee the extent to which such changes may occur. However, the extensive seedling germination and the ongoing regeneration of

the impacted stands (Boggs et al. 2008) along with rapid growth rates for surviving spruce (Berg et al. 2006) may foreshorten any impacts. We have not observed any obvious evidence of increased streambank erodability following spruce mortality, possibly due to soil stabilization by the thick understory of bluejoint grass, spruce seedlings, and other vegetation. As such, we don't expect to see significant changes in the sediment dynamics of the Anchor River.

A number of studies have linked LWD and pool habitat to increased numbers of rearing salmonids (Murphy et al. 1986, Bilby and Bisson 1998, Fausch and Northcote 1992). For example, Sharma and Hilborn (2001) found the density of pools in Washington watersheds to be strongly associated with coho smolt abundance ($r^2 = 0.85$) and Mossop and Bradford (2004) found juvenile chinook abundance in Yukon River tributaries to be correlated with LWD abundance. Stock-recruitment models suggest the Anchor River Chinook salmon population is at carrying capacity

(Nicky Szarzi, Alaska Department of Fish and Game, personal communication), indicating that smolt production is probably limited by in-stream habitat. Assuming that changes in streamflow, water temperature, or other unforeseen factors do not counteract the anticipated increases in pool formation and cover, it is conceivable that smolt production in upcoming years will increase as more beetle-killed spruce trees enter the stream.

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