North American Journal of Fisheries Management 29:702–714, 2009
American Fisheries Society 2009
DOI: 10.1577/M08-144.1

[Article]

Salmon Carcass Movements in Forest Streams

BURKE STROBEL*[1]
U.S. Forest Service, Pacific Northwest Research Station, Corvallis, Oregon 97331, USA

DANIEL R. SHIVELY
U.S. Forest Service, Mt. Hood National Forest, Sandy, Oregon 97055, USA

BRETT B. ROPER
U.S. Forest Service, Forest Sciences Laboratory, Fish and Aquatic Ecology Unit, Logan, Utah 84321, USA

Abstract.—The movements of salmon carcasses over time were studied in two forest streams in the context of a large-scale salmon carcass supplementation program. The objectives were to assess both the level of treatment after stream flows had displaced carcasses and to evaluate whether the magnitude of carcass movements outside of a given reach could be predicted. The movements of hand-placed, radio-tagged salmon carcasses were studied and compared with those of flagged carcasses dropped by helicopter. Repeated surveys showed that, in both streams, radio-tagged carcasses moved, on average, only a short distance, even after high-flow events, the maximum observed movement being 1.14 km after 77 d. In-channel wood and slow-water habitats contributed most to the retention of carcasses. The amount of wood that was incorporated into jams of medium and high complexity (including accumulated pieces of small wood) was the best predictor of the proportion of carcasses that would be retained within a given length of stream, whereas the amount of pool habitat contributed to a lesser degree. A particular high-complexity debris jam, however, confounded the use of hand-placed carcasses to predict the distribution of movements of helicopter-dropped carcasses by retaining almost all carcasses that encountered it. As in other studies, our results demonstrate the importance of wood in retaining salmon carcasses and show that complexity in the form of branches and accumulated small wood makes wood jams effective carcass collectors.

Nutrient availability plays an important role in determining the productivity of aquatic systems (Ashley and Slaney 1997). A source of stream nutrients that has received considerable attention is the carcasses of spawned-out Pacific salmon (Wipfli et al. 1998, 1999; Bilby et al. 1998). Because many salmon are anadromous and semelparous, their life history provides a mechanism for transporting nutrients derived in marine environments to freshwater systems (Willson and Halupka 1995; Stockner and Ashley 2003).

Declining salmon populations throughout much of the Pacific Northwest have resulted in fewer spawning fish and, therefore, lesser amounts of marine-derived nutrients being transported to freshwater systems. Schoonmaker et al. (2003) estimates that the combined biomass of runs of all salmon species currently are approximately 12% of historical levels (1880–1920) for Oregon and 10% for Washington. Historical records indicate that, by 1880, salmon runs in the Columbia River system were already experiencing a sharp decline, presumably due to overharvest (summarized in Cramer and Associates 2001). A negative feedback between fewer carcasses and lower productivity, leading to fewer carcasses in the future, has even been suggested as being one of the factors that may suppress salmon recovery (Gresh et al. 2000).

One technique used to increase nutrient availability in streams where escapement has been low relative to historical levels is the placement of postspawned salmon carcasses from hatcheries. The degree of benefit to be derived from treating streams with hatchery salmon carcasses has been related to the quantity of carcasses used (Bilby et al. 2001; Michael 1998). Higher carcass loading seems to be associated with greater biological benefits, although both mesocosm experiments (Wipfli et al. 2003; Wipfli et al. 1999) and stable isotope analyses (Bilby et al. 2001) suggest that this relationship eventually reaches a saturation point and levels off. Use of salmon carcasses, however, also has drawbacks, especially in streams associated with residential or recreational areas. Homeowners living adjacent to or downstream of treated streams might protest to the odor or the sight of decaying salmon carcasses. Dogs may be exposed to

---

* Corresponding author: burke.strobel@ci.portland.or.us
[1] Present address: Portland Water Bureau, Portland, Oregon 97204, USA.

Received June 25, 2008; accepted October 27, 2008

elevated risk of salmon poisoning. Downstream systems may already exceed water quality standards for the nutrients provided by carcasses. Such a problem would probably occur in areas where treatment occurs upstream of agriculture and urbanization. Carcass decay could also lower dissolved oxygen levels, impacting fish assemblages. For these reasons, the states of Oregon and Washington have imposed limits on the quantity of carcasses that can be placed in streams per unit of stream length or area. In Oregon that limit is 705 kg of wet carcass weight per stream kilometer. In Washington the limits, as of 2001, vary with species carcass size: 0.15 kg/m^2 of stream surface (based on bank-full widths) for coho salmon *Oncorhynchus kisutch* and steelhead *O. mykiss*; 0.78 kg/m^2 for pink salmon *O. gorbuscha*, sockeye salmon *O. nerka*, and chum salmon *O. keta*; and 0.39 kg/m^2 for Chinook salmon *O. tshawytscha*.

To maximize the benefits of supplementation with hatchery salmon carcasses, managers may want to treat streams with as large a quantity of carcasses as is allowed. The level of treatment ultimately attained by restoration projects depends, in part, on the loss of carcasses to downstream displacement. The degree to which the potential negative effects listed above can be mitigated is also directly impacted by the degree to which carcasses are transported downstream. Studies have indicated that in some systems hand-placed carcasses are largely retained in the vicinity of the treatment, traveling only tens of meters (e.g., Cederholm et al, 1989). In other systems carcasses can be transported up to several kilometers (Glock et al. 1980). Additionally, significant quantities of salmon carcass material can be removed from streams by avian and mammalian scavengers (Cederholm et al. 1989). Although movement and removal of carcasses are natural phenomena, they affect the effectiveness and social acceptance of carcass additions as a management tool.

The primary goal of this study was to determine, in the context of a large-scale salmon carcass- enrichment restoration project, the degree to which carcasses might be washed out of treatment streams or treatment reaches. Specific objectives included determining whether and to what degree application rates would have to be increased to achieve a desired level of treatment and investigating what physical factors contributed to the retention of salmon carcasses. Although rates of scavenging of hatchery carcasses is also an important piece of information when determining or predicting levels of treatment for a restoration project, it was beyond the scope of this study to predict the proportion of carcasses that might be expected to be lost in this way. Nonetheless, observed rates of scavenging are included.

Study Site

The study was conducted in a single reach of two streams in northwest Oregon: Camp Creek and the Clear Fork Sandy River (Figure 1). Both reaches are low-gradient, moderately sized streams (Table 1). Both streams lie within the Sandy River basin, a tributary to the Columbia River. These streams are located within 50 km of Portland, Oregon, a major metropolitan area with a population exceeding 1.5 million people.

Historically, these streams supported naturally spawning populations of salmon and trout, including coho salmon, Chinook salmon, steelhead, and cutthroat trout *O. clarkii*. In recent years, no coho salmon spawning has been found within Camp Creek, but Clear Fork Sandy River continues to support spawners, though in numbers considerably below historical levels. There is evidence of sporadic use of Clear Fork Sandy River by Chinook salmon spawners. Both streams have resident cutthroat trout populations and support remnant steelhead runs. Current numbers of spawning salmonids are estimated to be only 10–25% of those occurring in 1890, a population which at that time was already reduced by decades of intensive harvest (PGE 1998).

Both streams occur within watersheds primarily managed by the U.S. Forest Service. The main management activities that have occurred within these watersheds have been timber harvest and road building. In Camp Creek, some summer residences are also present downstream of the study area. Both streams were treated with salmon carcasses as part of a large-scale restoration project seeking to enhance productivity in a number of streams in the Sandy River basin and neighboring Clackamas River basin. Treatment with salmon carcasses in Camp Creek, as well as other streams included in the restoration project, avoided stream reaches with homes, unless homeowners consented. Several streams included in the restoration project also flow into larger waterways from which water is withdrawn for human consumption and where elevated nutrient levels and potential associated algal blooms were of concern.

Methods

On November 20, 2001, Camp Creek and the Clear Fork Sandy River were supplemented with coho salmon carcasses from the Oregon Department of Fish and Wildlife Sandy Fish Hatchery (Sandy, Oregon). This was near the end of the wild coho spawning run, which typically occurs in October and November. Carcasses were estimated to weigh approximately 4 kg

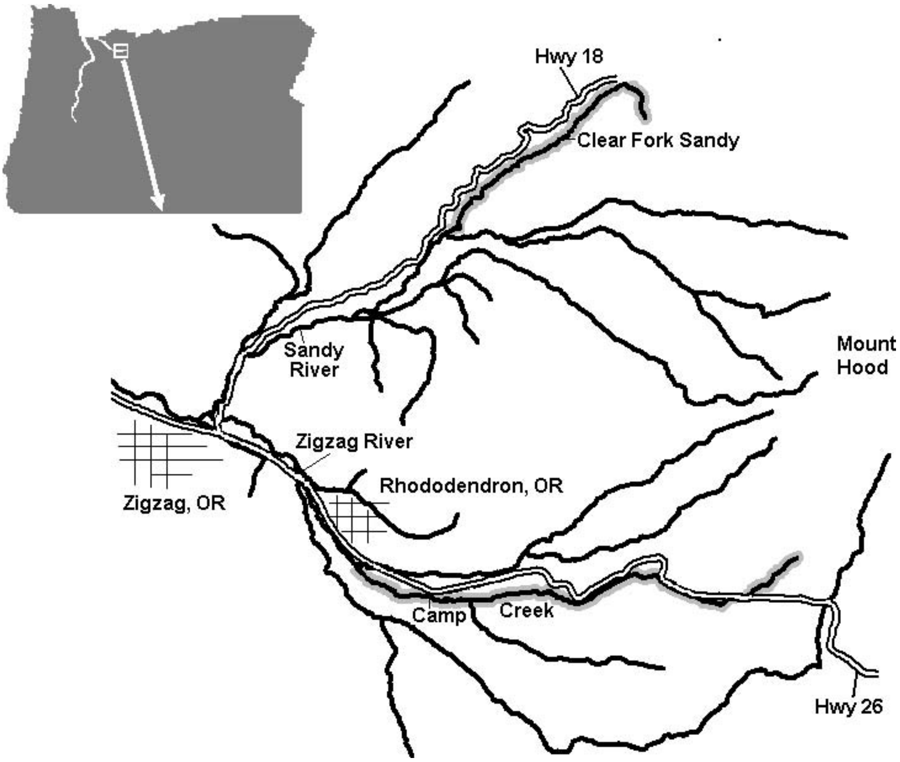

FIGURE 1.—Locations of the two streams in northwestern Oregon—Clear Fork Sandy River and Camp Creek (shaded)—where salmon carcass supplementation was studied.

and measure about 64 cm fork length; their sex ratio was roughly 50:50. A small portion of the females had their eggs removed at the hatchery. The majority of females contained their full compliment of eggs. The salmon were killed 2 weeks before distribution and kept in storage at 1.5°C. Some decay had occurred before carcasses were placed in study streams. The number of carcasses that could be placed in each stream was determined by preexisting Oregon Department of Environmental Quality regulations, allowing a maximum of 705 kg per linear stream kilometer. This treatment level resulted in 0.12 kg/m^2, as averaged over 1.6 km in Camp Creek and 0.09 kg/m^2 in the Clear Fork Sandy River. Because of the large number of carcasses, placement in streams was facilitated by the use of a helicopter that dropped carcasses while flying down the center of the channel.

TABLE 1.—Stream characteristics and channel variables within the study reaches that could affect carcass retention, as assessed in two streams in northwestern Oregon. Discharge was measured at the end of the study period (February 19, 2002); CHCMC is combined high-complexity and medium-complexity units.

Variable	Camp Creek	Clear Fork Sandy River
Watershed area (ha)	2,519	2,089
Wetted width (m)	8.0	8.2
Gradient (%)	4	3
Discharge (m^3/s)	1.20	0.93
Pool length (m/km)	265	327
Pool area (m^2/km)	2,213	1,693
Large wood pieces/km	145	98
Large wood units/km	75	67
High-complexity units/km	13	31
CHCMC units/km	42	56
Spannning units/km	33	4

One day after the aerial introduction of carcasses, 97 additional carcasses (50 in Camp Creek and 47 in Clear Fork Sandy River) tagged with American Telemetry Systems (ATS) radio transmitters with unique frequencies were placed in each stream. A transmitter was attached to carcasses with baling wire wrapped around the spine and inserted into the body cavity. Each carcass was measured (fork length) and marked with both yellow and orange flagging labeled with the corresponding transmitter's frequency. Initially carcasses with transmitters were evenly spaced along a 100-m transect within each stream. Carcasses were haphazardly thrown into the stream every 2 m, neither

TABLE 2.—Dichotomous key to classification of complexity of large wood units found in streams.

Key	Description	Complexity category (or continue to)
1a	Large wood unit incorporates four or more pieces of large wood interacting within bank-full width.	High
1b	Large wood unit incorporates fewer than four pieces of large wood interacting within bank-full width.	(Go to 2)
2a	Large wood unit incorporates at least 0.3 m^3 of small wood, including branches and roots.	High
2b	Large wood unit collecting less than 0.3 m^3 of small wood, including branches and roots.	(Go to 3)
3a	Large wood unit incorporates three pieces of large wood and (or) at least 0.15 m^3 of small wood, including branches and roots.	Medium
3b	Large wood unit incorporates one or two pieces of large large wood and less than 0.15 m^3 of small wood, including branches and roots.	Low

targeting nor avoiding specific eddies or pieces of large wood. Tagged carcasses were interspersed with carcasses dropped by helicopter. To facilitate mapping carcass movements, each stream was flagged at 25-m intervals (following Cederholm et al. 1989) from the mouth to the upstream extent of tagged carcass placements. Exact locations were determined by measuring their distances (nearest meter) from these flagged interval-breaks. Measurements were made from channel center to channel center.

We intended to locate and map salmon carcasses on a weekly basis in both creeks from November 27, 2001, to January 2, 2002, but difficult access due to heavy snowfall restricted the number of surveys that could be conducted on Clear Fork Sandy River to three (December 11 and 20, 2001, and January 2, 2002). An additional survey was completed in Camp Creek on February 5, 2002, to determine if fish had continued to be displaced downstream after 2 months in the stream. During these surveys, efforts were made to visually locate all fish with transmitters. In some cases this was impossible because carcasses were buried in log jams or were not visible because of water depth or clarity. In these cases, carcass locations were estimated. When a carcass was found, the stream attribute responsible for the individual carcass retention (e.g., wood, boulder, shallow riffle, slow water of pools or stream margins) was noted. Scavenged carcasses were no longer considered to be fluvially transported. If a salmon carcass had been dragged up on the stream bank or into the riparian area and scavenged, its location and fate were noted.

A staff-gauge that incorporated a magnet and float for measuring maximum stage height was placed near the mouth of each stream. Stage height and maximum stage height since last survey were recorded at the time of each survey. Actual discharge at the gauge sites was only measured once, so gauge values are a surrogate of discharge instead of actual stream discharge.

The location and complexity of large wood within each reach were described and mapped using the same flagged 25-m intervals that were established to measure carcass locations. Streams were surveyed in the early summer of 2002, and each piece of large wood (diameter $\geq$ 30 cm at 4 m from the base, length $\geq$4 m) was mapped, counted, and given an individual identifying number. A separate identifying number was also given to large wood units, which we defined as one or more pieces of large wood in physical contact with each other and interacting as one piece. In some cases, large wood units were identified that contained no wood of sufficient size to receive an individual piece number, but consisted of large accumulations of smaller debris that together were of significant volume ($\geq$0.3 m^3 or the approximate volume of the minimum size of large wood). Each large wood unit was characterized by its complexity (high, medium, or low) and position within the channel (right bank, left bank, middle, or spanning). The complexity of a large wood unit was defined according to the quantity of large and small pieces of wood that the large wood unit had collected (Table 2). High-complexity large wood units occurred when several pieces of wood interacted to create a debris jam with a relatively large amount of interstitial spaces. They typically included several points at which smaller debris was observed to be accumulating, and this smaller debris generally contributed to collecting further debris. Medium-complexity large wood units incorporated some smaller wood, creating a limited amount of interstitial spaces. Attached branches and roots were considered to be acting as small wood and often contributed to the complexity of both high-complexity and medium-complexity large wood units. Low-complexity large wood units consisted of one to three pieces of large wood, without branches, that had collected little or no small wood. Volumes of small wood were estimated in the field.

The downstream displacement of carcasses was evaluated by considering the effects of carcass length, channel characteristics (e.g., the number and surface area of pools and the frequency and complexity of wood features), and the amplitude and timing of flows. The effects of flow on carcass movements were

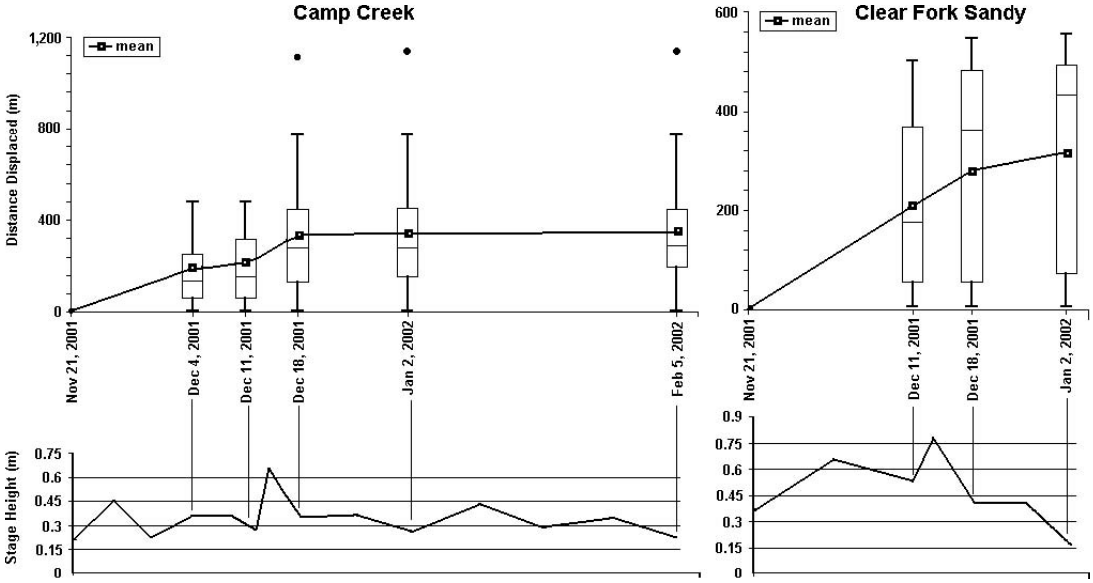

FIGURE 2.—Distribution of radio-tagged coho salmon carcasses over time juxtaposed with stage height for Camp Creek and Clear Fork Sandy River. The spatial distribution of carcasses on each date is represented by box-and-whisker plots, the center lines indicating the medians, the dark squares the means, the boxes SDs, and the whiskers ranges. The data include only those tags that were found during each survey (22 in Camp Creek and 20 in Clear Fork Sandy River). A survey on November 27 was omitted because too few carcasses were located.

analyzed by regressing average distance moved against stage height. The distance that carcasses moved from the previous survey was regressed on carcass length.

All-possible-variables regressions were performed to determine which retention elements or combination of retention elements were the best predictors of the proportion of carcasses entering a given stream segment that would be retained. Each stream was divided into 50-m segments, beginning immediately below the 100-m reach in which carcasses were initially placed. The quantities of various retention elements that could be derived from the stream surveys were summarized for each segment. The dependent variable for the individual regressions was the proportion of carcasses entering a given 50-m segment that was retained within that segment. This proportion represents an estimate of the probability of an individual carcass being caught and retained in the stream segment. Independent variables included the number of pieces of large wood, number of large wood units, number of high-complexity units, the number of combined high-complexity and medium-complexity (CHCMC) units, number of units that span the active channel, number of high-complexity units that span the channel, total length of pool habitat, and total surface area of pool habitat. Any model that included two or more collinear variables was discarded. The maximum number of variables any acceptable model could include, therefore, was two: one characterizing large wood and one quantifying pool habitat. The only stream segments considered in the analysis were those that were entered by at least five carcasses. All proportion data were arcsine transformed. The model with the highest R^2 value was chosen from among those that were significant at $\alpha = 0.1$).

The role of complexity of debris jams was evaluated using the chi-square statistic to assess whether complex features captured carcasses at significantly higher rates than less complex features. The chi-square analysis was repeated to assess whether individual wood pieces captured carcasses at significantly higher rates when incorporated in complex features as opposed to pieces incorporated in less complex features.

We developed a simple model using the movements of radio-tagged carcasses to predict the proportion of carcasses expected to move from a reach of a given length. The model was intended to help estimate the actual carcass density in treatment stream reaches after flows displace carcasses downstream. The accuracy of the model's predictions was tested by flagging an additional 200 salmon carcasses, mixing them with the unflagged carcasses, and dropping half of them by helicopter on November 20, 2001, at each of two separate locations in Clear Fork Sandy River, down-

TABLE 3.—Downstream distribution of all relocated radio-tagged coho salmon carcasses in Camp Creek and Clear Fork Sandy River at each survey date; N is the number of carcasses relocated on a given survey.

Statistic	Nov 27	Dec 4	Dec 11	Dec 18–20	Jan 2	Feb 5
Camp Creek						
N	31	49	49	37	41	35
Distance displaced (m)						
Mean	184	179	192	374	322	316
Median	130	135	143	342	266	268
Range	636	807	807	1,211	1,251	1,131
Maximum	647	811	811	1,215	1,255	1,136
Clear Fork Sandy River						
N			32	25	22	
Distance displaced (m)						
Mean			224	310	339	
Median			190	394	464	
Range			535	540	548	
Maximum			543	548	556	

stream of the reach where the radio-tracking study occurred. One location (upper reach) was in a reach that appeared to be similar to and was approximately 0.5 km downstream from the radio-tag study location. The second location (lower reach) was at the beginning of a lower-gradient reach containing more large wood. Different colors of flagging were used at each drop site. On December 4, 2001, a survey was conducted from the mouth of Clear Fork Sandy River to above the upper extent of where flagged carcasses were dropped by helicopter. Flagged carcasses were located visually and assigned, by color, to the 25-m interval in which they were found. We intended to conduct further surveys for flagged carcasses but were prevented from doing so by limited resources and heavy snowfall.

Results

Movements of Radio-Tagged Carcasses Placed by Hand

In Camp Creek all 50 radio-tagged fish were found at some point during follow-up surveys. In contrast, 40 of 47 radio-tagged fish in Clear Fork Sandy River were relocated; 22 carcasses were located during every survey, except on November 27 in Camp Creek, and 20 were located during every survey in Clear Fork Sandy River. The carcasses that were consistently relocated were used to characterize carcass movements over time (Figure 2).

The mean distance carcasses were displaced tended to increase with an apparent, though statistically insignificant, decreasing trend over time in both streams ($P_{\text{Camp}} = 0.11$, $P_{\text{Clear Fork}} = 0.18$; Figure 2). The range of radio-tagged carcasses in Camp Creek increased over time because many carcasses were retained near the upstream end of the study reach, and others continued to be displaced downstream (Table 3). In Clear Fork Sandy River the range remained static because a combination of slow water and a debris jam at 550 m captured nearly all carcasses that traveled that far. The mean and the median, however, shifted downstream over time as carcass movement continued within the first 550 m.

The movements of carcasses since the previous survey could not be predicted by stage height, as evaluated by simple linear regression ($R^2_{\text{Camp}} = 0.37$, $P = 0.28$; $R^2_{\text{Clear Fork}} = 0.25$, $P = 0.66$). In Camp Creek, for instance, little movement took place after the highest flow, even though subsequent high-flow events occurred (Figure 2), and the distance a carcass moved downstream could not be predicted by carcass fork length for any survey in either stream (linear regression: range of P-values = 0.19–0.99 for Camp Creek and 0.48–0.9 for Clear Fork Sandy River).

TABLE 4.—Categories of factors that retain salmon carcasses.

Retention category	Explanation
Wood	Caught in, on, or under large and small wood.
Boulder	Caught on or under large or small boulders.
Wood + boulder	Caught in a combination of wood and boulders, both playing a role in carcass retention.
Slack water	Carcass not caught but settled out, including slow margin-water, pools, pocket-pools behind large wood or boulders, etc.
Slack + buried	Carcasses in slack water that were commonly buried gradually over time.
Buried	Carcass buried in substrate.
Stranded	Left above waterline by receding high flows.
Roots	Caught in roots along bank, usually where undercut.
Shallow riffle	Found in moving water so shallow that it was pinned by its own weight to the substrate.
Riparian vegetation	Caught in branches or stems of vegetation growing along banks.

TABLE 5.—Percent by stream category of coho salmon carcasses retained in Camp Creek and Clear Fork Sandy River, 2001–2002. The numbers of radio-tagged carcasses are given in parentheses beneath the dates.

	Camp Creek						Clear Fork Sandy River		
Retention category	Nov 27 (31)	Dec 4 (46)	Dec 11 (46)	Dec 18 (34)	Jan 2 (41)	Feb 5 (33)	Dec 11 (33)	Dec 20 (18)	Jan 2 (19)
Wood	39	46	48	59	68	55	58	89	84
Boulder		7	13	6	18	21	9		
Wood + boulder	13	4	4	6	6				
Slack water	35	35	24	18	21	18	24	6	5
Slack + buried	3			6					
Buried					3	3		6	11
Stranded			2		3				
Roots	3	2	2	3			3		
Shallow riffle	6	4	4						
Riparian vegetation		2	2	3	3	3	6		

Factors Contributing to Carcass Retention

In both streams, carcasses were retained by a variety of physical factors, which we divided into 10 general categories (Table 4). Large wood and boulders both functioned to retain carcasses in two ways: (1) carcasses were impinged or snagged on the upstream side, or (2) they settled out in the slack water created under or behind large wood and boulders. We treated these two types of retention separately. Carcasses that settled out in the slack water behind boulders and debris jams were grouped with those retained by all slack-water conditions.

Radio-tagged carcasses were not retained equally across categories (χ^2, $P < 0.0001$ for all survey dates in both streams). The percentage of relocated carcasses retained by each category was generally highest for wood (39–68% in Camp Creek, 55–68% in Clear Fork Sandy River) followed by slack water (18–35% in Camp Creek, 5–24% in Clear Fork Sandy River; Table 5). The role of wood was compounded by the fact that many pools and pocket pools contributing to the slack-water values were created by large wood.

No attempt was made to quantify the relative rate at which carcasses encountered factors that could retain them. We did, however, explore the relative ability of each category to retain carcasses over time (Tables 6, 7). Every radio-tagged carcass that was located during two consecutive surveys was categorized as having moved between one survey and the next or not moved (retained). No category was significantly better than another at retaining carcasses over time in either stream (chi-square: $P = 0.21$ to 0.7659). The same was true when comparing wood with all other categories combined (chi-square with Haber correction: $P = 0.21$ to 1.0).

Channel Variables Affecting Carcass Retention

The reaches of Camp Creek and Clear Fork Sandy River in which the study was conducted both had instream gradients of 3%, but differed in a number of other respects (Table 1). Pools formed a higher proportion of habitat, by length, in Clear Fork Sandy River. Camp Creek, however, owing to its greater pool widths, had more pool habitat by area. Large wood loads, overall, were higher in Camp Creek, both in terms of individual large pieces and large wood units. Clear Fork Sandy River, however, had a much higher

TABLE 6.—Numbers of radio-tagged coho salmon carcasses relocated during the next survey and the percent (in parentheses) that had moved by the time of that survey, by retention category, Camp Creek, 2001–2002.

Retention category	Number and (percent)				
	Nov 27	Dec 4	Dec 11	Dec 18	Jan 2
Wood	12 (42)	20 (15)	18 (61)	18 (17)	17 (12)
Boulder		3 (33)	4 (75)	2 (50)	6 (50)
Wood + boulder	4 (25)	2 (0)	2 (50)	2 (50)	2 (50)
Slack water	11 (55)	16 (31)	7 (57)	5 (0)	4 (25)
Slack + buried	1 (100)			1 (0)	
Buried					1 (0)
Stranded					1 (100)
Roots	1 (0)	1 (0)	1 (100)		
Shallow riffle	2 (100)	2 (50)	1 (100)		
Riparian vegetation		1 (0)	1 (0)	1 (0)	1 (0)

TABLE 7.—Numbers of radio-tagged coho salmon carcasses relocated during the next survey and the percent (in parentheses) that had moved by the time of that survey, by retention category, Clear Fork Sandy River, 2001.

Retention category	Number (percent)	
	Dec 11	Dec 18
Wood	15 (53)	9 (22)
Boulder	3 (33)	
Wood + boulder		
Slack water	4 (100)	1 (0)
Slack + buried		
Buried		1 (0)
Stranded		
Roots		
Shallow riffle		
Riparian vegetation	1 (100)	

proportion of medium-complexity and high-complexity large wood units. Of the large wood pieces in the Camp Creek study reach 73% were restoration logs (i.e., logs artificially placed in the streambed in the early 1990s to create fish habitat, not for the purpose of retaining carcasses). In the Clear Fork Sandy River study reach, only 14% of the large wood pieces were placed as restoration logs.

The total number of CHCMC units appeared most frequently from survey to survey as a predictor of how effective a given 50-m segment of Camp Creek would be at retaining carcasses that drifted into it (Table 8). The addition of pool surface area or pool length improved the models to some degree (explaining an additional 2–13% of variability). An exception was the data from the December 18 survey. The variability in these data, which were collected immediately following a large freshet, was best explained by the frequency of complex debris jams that spanned the full channel. After 2 weeks had passed, however, CHCMC units were again the best predictor of retention rates. Additional variables explained more of the observed variability, but none did so consistently or to a great extent. All regressions except for the December 4 survey were significant at $P \geq 96\%$. No model, however, was very effective at predicting the proportion of carcasses a given stream segment might be expected to retain.

For the first and last surveys in the Clear Fork Sandy River, the number of pieces of large wood was the best predictor of how effective a given 50-m segment of the stream would be at retaining carcasses (Table 8). For the December 20 survey, the total length of pool habitat in each segment explained more of the variability than any other retention element. This survey occurred immediately after a large freshet. The regressions were statistically significant ($P \geq 90\%$) but failed to explain the majority of observed variability.

Effects of Wood Complexity

High-complexity large wood units captured carcasses at significantly higher rates than lower-complexity units in both Camp Creek and Clear Fork Sandy (chi-square: $P \leq 0.004$ for all dates). There was no confounding trend in the ratio of high-complexity to lower-complexity large wood units along the length of the survey reaches. In Camp Creek, large wood units of both medium-complexity and high-complexity captured significantly more carcasses than simple features early in the season ($P \leq 0.004$ for December 4 and 11, 2001), but these results shifted over time as carcasses were dislodged from medium-complexity units but were retained by high-complexity units ($P < 0.001$ for December 18, 2001, and January 2 and February 5, 2002). In Clear Fork Sandy River, high-complexity units captured significantly more carcasses than both

TABLE 8.—Variables that best predict the proportion of coho salmon carcasses entering a given 50-m reach that will be retained in Camp Creek and Clear Fork Sandy River. Abbreviations are as follows: PA = pool area, PL = pool length, M + C = combined number of medium-complexity and high-complexity (CHCMC) large wood units, SC = number of high-complexity large wood units that span the channel, WD = number of pieces of large wood, and RMSE = root mean square error. Power is the estimated probability of incorrectly concluding that there is no relationship between the indicated variables and the proportion of carcasses retained.

Survey	Variable(s)	R^2	RMSE	P	Power
Camp Creek					
Dec 4, 2001	M + C, PA	0.43	13.32	0.04	0.6
Dec 11, 2001	M + C, PL	0.44	10.48	0.02	0.8
Dec 18, 2001	SC	0.17	13.95	0.017	0.74
Jan 2, 2002	M + C	0.35	12.35	0.002	0.99
Feb 5, 2002	M + C, PA	0.22	6.95	0.0006	1.00
Clear Fork Sandy River					
Dec 11, 2001	WD	0.23	22.97	0.02	0.71
Dec 20, 2001	PL	0.07	26.7	0.09	0.41
Jan 2, 2002	WD	0.34	17.36	0.04	0.62

TABLE 9.—Percentages of coho salmon carcasses aerially dropped in Camp Creek and Clear Fork Sandy River that were estimated to have been lost in 2001–2002 (i.e., carried by the current beyond the 1.6-km river segment [L in equation 1] they were dropped in), assuming carcasses were evenly spread over the 0.4-km-long drop segment (S in equation 1); D is the distance (in SDs) of the downstream end of reach L from the average point of origin (0.5S).

Variable	Nov 27	Dec 4	Dec 11	Dec 18	Jan 1	Feb 5
Camp Creek						
Percent lost	0.6	0.9	1.3	6.9	7.4	7.6
D	2.51	2.39	2.24	1.48	1.46	1.43
Clear Fork Sandy River						
Percent lost			1.7	5.7	6.6	
D			2.11	1.58	1.51	

low-complexity and medium-complexity units ($P \leq 0.002$ for December 18, 2001, and January 2, 2002).

The interpretation of these results was somewhat confounded by the fact that complex debris jams tend to incorporate more large pieces of wood than simpler ones. To assess whether wood pieces captured more carcasses per piece of large wood when incorporated in a more complex wood feature than in a simple one, the above chi square analysis was repeated using the number of wood pieces incorporated in large wood units at each level of complexity (rather than the number of units) to determine expected values. In Camp Creek, the strength of the relationship was reduced. On December 4, 2001, wood pieces incorporated into medium-complexity units and high-complexity units still captured carcasses at significantly higher rates than did low-complexity units (chi-square: $P = 0.025$), and subsequently, high-complexity units captured carcasses at significantly higher rates than low-complexity units and medium-complexity units ($P = 0.033$ on December 18, 2001, $P = 0.048$ on January 2, 2002, and $P = 0.052$ on February 5, 2002). On December 11, 2001, the results were not significant. In Clear Fork Sandy River the relationship was generally insignificant, primarily because the large majority of pieces in the entire survey reach (75%) were incorporated in high-complexity units.

Predicting Carcass Movements

Aerial salmon carcass treatments of streams in the fall of 2001 were conducted in 1.6-km reaches, but carcass distribution was limited to stream lengths of 0.4 km or less. Because the maximum movement of a radio-tagged carcass in this study was approximately 1.3 km, it is possible that some carcasses could move outside of an established 1.6-km reach, even if carcasses were dropped in the upper 0.4 km of the reach.

We estimated the loss of carcasses to a given reach, as follows (Table 9):

$$D = [\log_e(L - 0.5S) - X]/\text{SD}, \qquad (1)$$

where L is the lineal stream length of a given reach, S is the lineal stream length to which carcasses were directly applied (or subreach), X is the mean of the $\log_e$ transformed movement distances observed in Camp Creek and Clear Fork Sandy at the time of each survey (and SD is their standard deviation), and D is the distance of the downstream end of reach L to the average point of origin or 0.5S (in standard deviations). The Z distribution can then be consulted to estimate the proportion of carcasses lost out of reach L. We assumed that 0.5 of subreach S represents the average starting point of carcasses and that the application subreach was at the upstream end of reach L. The actual proportion of carcasses leaving reach L was expected to more closely resemble the predicted proportion as the numbers of carcasses approached infinity. The results would only apply to channel types similar to those in which the study took place.

Movements of Flagged Carcasses Dropped by Helicopter

Flagged carcasses, which were mixed with unflagged carcasses and dropped by helicopter into two separate reaches (upper and lower) of Clear Fork Sandy River during the restoration project, were used to test the validity of equation (1). In each reach, the drop area (S) was 300 m long, and the stream length between the upstream end of the upper reach and the upstream end of the lower reach was 700 m long, which represented the reach length (L) in equation (1).

The two reaches into which each group of carcasses (100 flagged carcasses in each reach) were dropped differed in gradient and amount of large wood and pool habitat. The upper reach was similar to the reach in which the radio-tracking study took place, both in average gradient (3%) and amount of large wood (6.6 versus 6.0 pieces/50 m, respectively; t-test, $P = 0.71$); however, there were significant differences: less main-stem pool habitat, in terms of both percent of length (respectively, 16.1% versus 34.6% per 50 m; heteroscedastic t-test on arcsine-transformed values: $P = 0.02$) and percent surface area (14.1% versus 32.5%

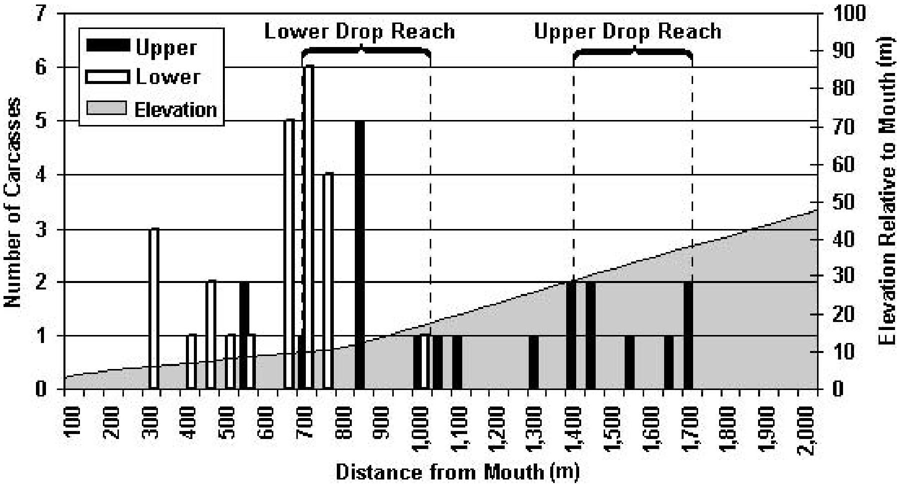

FIGURE 3.—Numbers of flagged coho salmon carcasses relocated 2 weeks after being dropped by helicopter into two separate 300-m subreaches (upper and lower) of Clear Fork Sandy River, along with the elevation change with respect to the distance from the stream mouth.

per 50 m; $P = 0.01$). The lower reach, compared with the radio-tracking reach, had a lower gradient (1%) and significantly more large wood (respectively, 16.6 versus 6.0 pieces per 50 m; *t*-test: $P = 0.0005$) and main-stem pool habitat, in terms of both percent length (55.9% versus 34.6% per 50 m; heteroscedastic *t*-test on arcsine-transformed values: $P = 0.01$) and percent surface area (55.7% versus 32.5% per 50 m; $P = 0.008$).

Of the 100 carcasses that were dropped by helicopter into the upper reach, 24 were located at the time of the survey and 9 (45%) had moved beyond *L* (i.e., the defined 700-m reach length for that drop). This compares with a prediction of 2 carcasses (12%), using average distance moved and standard deviation from the December 11 survey. Of the 100 carcasses that were dropped by helicopter into the lower reach, 24 were relocated and none had moved beyond the 700-m *L* that drop. This compares with the prediction of 3 carcasses, using average distance moved and standard deviation from the December 4 survey. Carcasses from the upper reach were dispersed over 1,150 m, extending into the lower reach, whereas carcasses in the lower reach were confined to their 700-m segment (Figure 3).

Scavenging

Rates of scavenging were higher on Clear Fork Sandy (26%) than on Camp Creek (16%). Nine radio-tagged carcasses were found scavenged on December 11, one on December 18, and three on January 2. No radio-tagged carcasses were found scavenged on Camp Creek until January 2, when five were located in the riparian area. The later onset of scavenging of radio-tagged carcasses in Camp Creek corresponds to observations of scavenging of nontagged carcasses, which was first noticed in January. Three more scavenged carcasses were found on Camp Creek in February.

Discussion

As in studies from the Olympic Peninsula (Cederholm and Peterson 1985; Cederholm et al. 1989) and the Cascade Range (Minakawa and Gara 2005) in Washington, we found salmon carcasses to not disperse great distances downstream, even during high-flow events. The tendency of forest streams to retain salmon carcasses contributes to the probable effectiveness of anadromous runs at delivering marine-derived nutrients into freshwater ecosystems. Median carcass movements, however, in Camp Creek after 70 d were more than 5 times those observed in Olympic Peninsula streams at 37–118 d and were 9 times for Clear Fork Sandy River after 36 d (Cederholm et al. 1989). Average carcass movements were from 9 to 17 times greater, respectively, than those observed after 32–46 d in Cascade Range streams (Minakawa and Gara 2005). We collected large wood data according to U.S. Forest Service Region 6 criteria. These data were not comparable to the large wood information reported in either Washington study. Stream gradients were also not reported for either of the above Washington studies, so the reasons behind the differences in observed carcass movements could not be fully explored. Carcasses drifted farther in Clear Fork Sandy River than in Camp Creek, despite Clear Fork Sandy River having more high-complexity wood features and pool habitat by length than Camp Creek. The Camp Creek study reach has a slightly lower gradient than the Clear Fork Sandy River reach, which may help explain differential carcass retention. Furthermore, Camp Creek had had more pool habitat by area than Clear Fork Sandy River, and medium-complexity and high-complexity wood features in Camp Creek also incorporated more individual pieces of wood, many more of which spanned the entire channel. Carcass distributions were skewed toward shorter distances throughout the survey period in Camp Creek and initially in Clear Fork Sandy River, as observed in streams in the Olympic Peninsula (Cederholm et al. 1989). Although in the Cascade Range, Minakawa and Gara (2005) found that a significantly higher proportion of carcasses were retained by wood as the season progressed, we did not find that in our two streams.

Johnston et al. (2004) addressed the effects of carcass movements in several Canadian streams by examining the loss of carcasses from a given reach over time, which they characterized using an exponential loss model. They did not follow the movements of individual carcasses, but looked for downstream carcass accumulations and measured carcass decay. They determined that decay was probably the primary cause of carcass disappearance, not carcasses being washed downstream. In contrast, water-flow displacement of carcasses in our study streams (comparably sized stream segment) was a significant cause of carcass loss. For the first survey (November 27), the average instantaneous carcass removal rates, as related to downstream movement out of a 192-m stream reach immediately downstream of where carcasses were initially placed, were 0.0362/d in Camp Creek and 0.0179/d in Clear Fork Sandy River. The instantaneous carcass removal rate was calculated using a derivation of the exponential loss model from Johnston et al. (2004): $k_p = -\log_e(C_t/C_i)t$, where k_p is the instantaneous removal rate, C_i is the initial number of carcasses, and C_t is final number of carcasses after t days. Instantaneous removal rates were calculated for survey date and then averaged. Johnston et al. (2004), using nonlinear least squares, calculated an average instantaneous loss rate of 0.0388/d due to all factors combined, including decay for three reaches ranging in length between 115 and 192 m. Unlike scavenging and decay, the loss of carcasses due to downstream displacement is contingent on the length of reach being evaluated. The average instantaneous carcass removal rate in Camp Creek dropped to 0.0028/d when the study reach was tripled to 600 m. No carcasses moved that far in Clear Fork Sandy River. Downstream loss of carcasses was probably greater in our study streams because of lower proportions of pool habitat (half as much by length) and large wood densities that were one-fifth to one-sixth those of the Canadian study streams.

Our study also experienced a high-flow event, which resulted in the furthest movements of carcasses observed during our study. In larger rivers, high-flow events can contribute to salmon carcasses moving up to 12 mi (Glock et al. 1980). Cederholm et al. (1989) also found that carcasses moved up to twice as far during freshets as under low-flow conditions, although the median movement they observed (66 m) was only a fraction of that observed in our study. Higher flows than those experienced in Camp Creek and Clear Fork Sandy River during our study occur in most years and, in fact, a higher flow occurred 2 months after the end of the study. Typically, the highest flows occur during late autumn or winter, often when coho salmon carcasses would still be present. In snowmelt-driven streams, where the highest flows tend to occur during the spring, most salmon carcasses would be largely decayed before high flows washed them downstream.

Scavenging removed far more carcasses from each treatment reach than downstream transport. All scavenged carcasses that were located, however, were found within a few meters of the stream, and their nutrients may have still found their way into the stream over time. A large amount of evidence of scavenging by coyotes was seen in both streams. Mountain lion tracks were seen along Clear Fork Sandy River near carcasses, though no direct evidence of scavenging by mountain lions was apparent. Mink and otters are also present in both watersheds and are suspected scavengers. Scavenging rates were highest in Clear Fork Sandy River, where there were no summer homes or adjacent roads. Scavenging rates would probably be even higher in more remote streams. Radio-tagged carcasses mingled with much larger numbers of other carcasses dropped by helicopter, so the observed scavenging rates are assumed to be representative of the overall rates in these two streams during the study. The rate of scavenging in a given stream, however, is likely to vary as a function of the number of carcasses, the number of scavengers, and time. Large numbers of carcasses may overwhelm scavengers (Cederholm et al. 1989), but predictably high numbers of carcasses may lead to greater abundance of scavengers, either in the short term, through animals becoming aware of the resource, or the long term, through increased reproductive rates. Smaller, shallower streams might also be expected to have higher scavenging rates than larger, deeper streams because terrestrial scavengers would be able to more easily retrieve submerged carcasses. The total rate of removal of salmon carcasses from Camp Creek and Clear Fork Sandy River were in the range described by Johnston et al. (2004) for inland British Columbia streams (10–35%) but were well below that observed by Cederholm et al. (1989) in coastal streams of the Olympic Peninsula, Washington (40%), where black bears *Ursus americanus* are plentiful.

Channel features contributing to carcass retention were varied, but large wood incorporated in complex debris jams played a dominant role. Large wood catches carcasses moving in the current and creates slow-water areas where carcasses settle out. Small wood (i.e., too small to be included in most regional survey protocols) was a vital component of debris jams. Accumulations of sticks and small branches provided a large quantity of points that carcasses could catch on and slowed down currents moving through debris jams.

The quantity of pieces of wood or large wood units, however, was a poor predictor of how many carcasses would be retained within a given interval of stream, though a significant relationship generally existed in both Camp Creek and Clear Fork Sandy River (as in Cederholm et al. 1989). The reason for this appears to be that, whereas certain high-complexity debris jams captured the majority of carcasses, many others caught none. Fallen trees with branches spanning the majority of the stream channel appeared to be particularly effective at capturing both carcasses and small wood.

Naturally occurring wood in debris jams appeared to be more effective at retaining carcasses than wood placed for restoration purposes. Restoration wood typically has a large diameter and few to no branches. In Camp Creek and Clear Fork Sandy River, restoration logs appeared to be relatively ineffective at capturing either carcasses or smaller wood pieces. They generally captured carcasses at points where they had been cabled together, or attached to boulders, or where large pools were created by sill logs. Managers concerned with carcass retention or small wood retention should leave branches attached to project wood to whatever degree is practical or, otherwise, design restoration structures with retention of carcasses and small wood in mind. Complex wood structures also provide improved cover for fish by creating a variety of slow-water interstitial spaces.

High salmon carcass retention rates in Camp Creek and Clear Fork Sandy River precluded the need to increase application rates to attain a desired level of treatment. Movement of carcasses into areas where they were not desired, such as reaches adjacent to summer homes, was also determined to be minimal. The precise magnitude of carcass movements, however, proved to be unpredictable. The carcass movements on which the Clear Fork Sandy River model was based were heavily influenced by the presence of a single debris jam that collected almost all carcasses that encountered it. The presence of such debris jams confounds the prediction of the distribution of carcass movements. Streams with high wood loads, however, should generally have relatively high numbers of wood features with characteristics necessary for retaining carcasses. Differences in the amount of in-stream wood, pools, gradient, and the disproportionate influence of unique individual features may all contribute to differences in the ability of streams and reaches to retain carcasses. The model for Clear Fork Sandy River underestimated the movement of carcasses in a reach similar to that in which the model parameters were derived and overestimated movements in a reach where gradient was lower and in-stream wood and pool habitat were more common. Several carcasses from the upper reach also moved downstream and were retained in the lower reach, which had a low gradient. It is likely that these carcasses would have moved even further, if the lower reach had the same gradient and lesser in-stream wood loads of the upper reach. Visual surveys for marked carcasses, such as the one conducted for carcasses dropped by helicopter in Clear Fork Sandy River, however, are probably also biased towards locating fish that move further. The most visible marked carcasses are probably the most mobile ones, whereas those caught deep in debris jams would be harder to locate (unless radio-tagged).

Carcasses of naturally spawned salmon may respond differently to flows than those placed by hand or by helicopter. Dying salmon may move into areas of slack water, where their carcasses may be less susceptible to being washed downstream but, concurrently, more susceptible to removal by scavengers (Cederholm et al. 1989). Regardless, if a wild-spawner's carcass starts moving with flowing water, it would be subject to the same factors as a supplemented carcass, (e.g., wood quantity and complexity, amount of pool habitat, and stream gradient).

If salmon runs can be rebuilt, they will produce the same odors, pathogen issues, and potential water quality impacts as those of rotting supplemented carcasses. Even though the public may be willing to accept that price for recovering the species, the public may be less willing to accept those negative aspects when carcass supplementation is used as an interim restoration measure. Aquatic resource managers who place salmon carcasses will often want to know how many carcasses are likely to be washed downstream to more populated areas. Managers may also need to know what level of treatment they obtained within treated stream segments after carcasses have been removed by high flows and scavengers. To enhance effectiveness, managers may even decide to add wood to streams for the express purpose of slowing the loss of carcasses. Streams with lower gradients, more pool habitat, and higher wood levels, especially complex debris jams that span part or all of the channel width, are likely to retain a larger proportion of salmon carcasses than streams with higher gradient and less pool habitat and wood. Our results indicate, however, that it will be difficult to predict carcass retention rates with a great deal of accuracy. In-stream wood structures that are designed to help retain carcasses should incorporate complexity, such as branches, roots, or small wood, and will be most effective if they span most or all of the channel and are placed in pools.

Acknowledgments

We are grateful to David Saiget for leading the field effort in the Clear Fork Sandy River and Robin Miranda, Mark Schoenborn, Dean Thomas, Loren Meager, and Fran Gray for assisting in field surveys. Thanks to Jim Muck, Dave Liscia, Russ Plaeger, and members of the Sandy River Basin Watershed Council, who helped distribute tagged salmon carcasses. The Oregon Department of Fish and Wildlife and the U.S. Fish and Wildlife Service also deserve gratitude for providing and helping to transport carcasses to refrigeration trailers and for assisting with helicopter operations. Ken Ashley assisted in the planning phase. Gordie Reeves and three anonymous reviewers provided helpful comments on the initial drafts.

References

Ashley, K. I., and P. A. Slaney. 1997. Accelerating recovery of stream, river, and pond productivity by low-level nutrient replacement. Chapter 13 *in* P. A. Slaney and D. Zaldokas, editors. Fish habitat rehabilitation procedures. British Columbia Ministry of Environment, Lands, and Parks and Ministry of Forests Watershed Restoration Technical Circular 9.

Bilby, R. E., B. R. Fransen, J. K. Walter, C. J. Cedarholm, and W. J. Scarlett. 2001. Preliminary evaluation of the use of nitrogen stable isotope rations to establish escapement levels for Pacific salmon. Fisheries 26(1):6–14.

Bilby, R. E., B. R. Fransen, P. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 55:1909–1918.

Cederholm, C. J., D. B. Houston, D. L. Cole, and W. J. Scarlett. 1989. Fate of coho salmon (*Oncorhynchus kisutch*) carcasses in spawning streams. Canadian Journal of Fish and Aquatic Sciences 46:1347–1355.

Cederholm, C. J., and N. P. Peterson. 1985. The retention of coho salmon (*Oncorhynchus kisutch*) carcasses by organic debris in small streams. Canadian Journal of Fisheries and Aquatic Sciences 42:1222–1225.

Cramer and Associates. 2001. Documentation of existing and historic habitat and native and introduced fish in the Clackamas Basin. Final report prepared for Portland General Electric, Portland, Oregon.

Glock, J. W., G. Hartman, and L. Conquest. 1980. Skagit River chum salmon carcass drift study. Seattle City Light Department, Seattle.

Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An estimation of historic and current levels of salmon production in the northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. Fisheries 25(1):15–21.

Johnston, N T., E. A. MacIsaac, P. J. Tschaplinski, and K. J. Hall. 2004. Effects of the abundance of spawning sockeye salmon (*Oncorhynchus nerka*) on nutrients and algal biomass in forested streams. Canadian Journal of Fisheries and Aquatic Sciences 61:384–403.

Michael, J. H., Jr. 1998. Pacific salmon spawner escapement goals for the Skagit River watershed as determined by nutrient cycling considerations. Northwest Science 72(4):239–248.

Minakawa, N., and R. I. Gara. 2005. Spatial and temporal distribution of coho salmon carcasses in a stream in the Pacific Northwest, USA. Hydrobiologia 539:163–166.

PGE (Portland General Electric). 1998. Salmon and steelhead runs and related events of the Sandy River basin: a historical perspective.

Schoonmaker, P. K., T. Gresh, J. Lichatowich, and H. D. Radtke. 2003. Past and present Pacific salmon abundance: bioregional estimates for key life history stages. Pages 33–40 *in* J. G. Stockner, editor. Nutrients in salmonid ecosystems: sustaining production and biodiversity. American Fisheries Society, Symposium 34, Bethesda, Maryland.

Stockner, J. G., and K. I. Ashley. 2003. Salmon nutrients: closing the circle. Pages 3–15 *in* J. G. Stockner, editor. Nutrients in salmonid ecosystems: sustaining production and biodiversity. American Fisheries Society, Symposium 34, Bethesda, Maryland.

Wipfli, M. S., J. P. Hudson, and J. P. Caouette. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 55:1503–1511.

Wipfli, M. S., J. P. Hudson, J. P. Caouette, and D. T. Chaloner. 2003. Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. Transactions of the American Fisheries Society 132:371–381.

Wipfli, M. S., J. P. Hudson, D. T. Chaloner, and J. P. Caouette. 1999. Influence of salmon spawner densities on stream productivity in Southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 56:1600–1611.

Willson, M. F., and K. C. Halupka. 1995. Anadromous fish as keystone species in vertebrate communities. Conservation Biology 9:489–497.