TIMBER HARVEST TRANSFORMS ECOLOGICAL ROLES OF SALMON IN SOUTHEAST ALASKA RAIN FOREST STREAMS

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Abstract. Although species commonly modify habitats and thereby influence ecosystem structure and function, the factors governing the ecological importance of these modifications are not well understood. Pacific salmon have repeatedly been shown to positively influence the abundance of benthic biota by annually transferring large quantities of nutrients from marine systems to the nutrient-poor freshwaters in which they spawn. Conversely, other studies have demonstrated that salmon can negatively influence the abundance of freshwater biota, an effect attributed to bioturbation during upstream migration and nest construction. The factors determining which of these contrasting ecological effects predominates are unknown, including how human activities, such as land use, influence ecological responses to salmon. We sampled a key basal food resource, sediment biofilm, in seven southeast Alaskan streams impacted to varying degrees by timber harvest. Biofilm abundance (measured as chlorophyll *a* and ash-free dry mass) was positively related to timber-harvest intensity prior to salmon arrival. However, during the salmon run, an inverse relationship emerged of more abundant biofilm in less-harvested watersheds. Among-stream variability in biofilm response to salmon was largely explained by sediment particle size, which was larger in less-harvested watersheds. Collectively, these results suggest that, by altering stream sediment size, timber harvest transformed the dominant effect of salmon from nutrient enrichment to physical disturbance, thus modifying nutrient linkages between marine and freshwater ecosystems.

Key words: Alaska, USA; context dependency; disturbance; epilithon; Oncorhynchus *spp.; resource subsidy; salmon-derived nutrients; stream ecosystem; Tongass National Forest.*

INTRODUCTION

Species influence the structure (Wright et al. 2006) and function (Taylor et al. 2006) of most, if not all, ecosystems through modifications of the abiotic environment. The diverse mechanisms through which species perform such modifications are well documented (e.g., Jones et al. 1994: Table 1), but the factors that govern their overall ecological importance remain poorly understood. A prime example of species that modify their abiotic environment can be found in salmon-bearing freshwaters of the northern Pacific Rim. During spawning runs, Pacific salmon (*Oncorhynchus* spp.) transport large quantities of nutrients to typically nutrient-poor freshwater ecosystems (Gende et al. 2002, Schindler et al. 2003). Evidence suggests that the ecosystems receiving these annual resource subsidies benefit through increased nutrient availability that can stimulate the abundance, biomass, and growth of biota (Chaloner et al. 2004, Schindler et al. 2005), leading many to conclude that salmon-derived nutrients are important for maintaining ecosystem productivity (Willson et al. 1998, Schindler et al. 2003). However, other studies have shown that rather than having a strictly positive influence on resident biota, salmon can function

as important agents of disturbance by scouring stream sediments during upstream migration and nest (redd) excavation, thereby reducing the abundance of benthic organisms (Minakawa and Gara 1999, Moore et al. 2004, 2007). The factors that determine whether salmon function primarily as sources of nutrient enrichment or as agents of disturbance have not been identified, nor has research considered how human alterations of stream habitats influence these two contrasting roles in ecosystems.

Researchers have recently proposed that the abiotic environment is an important determinant of how organisms modify, or engineer, their environment (Moore 2006, Wright and Jones 2006, Hastings et al. 2007), although demonstrations of such "context dependency" remain rare (but see Villenave et al. 1999, Wright et al. 2006). Extending the concept of context dependency to salmon–benthos interactions, the heterogeneous physical environment (Townsend 1989) may explain the inconsistent salmon effects that have been documented among streams (e.g., Chaloner et al. 2004). Moreover, human activities alter the physical stream environment and could modify how organisms, such as salmon, influence stream ecosystems.

One human activity with profound impacts on physical stream environments is timber harvest, which often alters hydrologic regimes (Wright et al. 1990), reduces quantities of large wood (Cordova et al. 2007,

TABLE 1. Characteristics of the seven study streams on Prince of Wales Island, Alaska, USA.

Stream name	Latitude (N)	Longitude (W)	Watershed area (km²)	Watershed harvested (%)	Baseflow discharge (m³/s)	Mean daily temperature (°C)	Maximum no. salmon counted†	Mean channel width (m)	Mean sediment size (mm)
Twelve Mile (TWE)	55°20′	132°43′	31.11	68.3	0.44	7.88 (2.83)	533	12.33 (3.64)	32.5 (37.3)
Slide (SLI)	55°44′	132°29′	25.96	57.9	0.25	10.08 (3.73)	24	9.78 (3.72)	118.4 (137.6)
Maybeso (MAY)	55°29′	132°40′	38.66	21.8	0.46	9.12 (2.77)	782	18.46 (4.62)	46.5 (32.1)
Dog Salmon (DOG)	55°19′	132°31′	37.31	14.4	0.49	10.67 (2.50)	316	11.81 (2.32)	93.5 (67.8)
Trocadero (TRO)	55°22′	132°50′	44.79	11.2	0.40	10.08 (2.12)	12	13.6 (4.35)	88.7 (79.3)
Indian (IND)	55°26′	132°42′	25.87	9.3	0.27	9.51 (3.16)	297	8.78 (3.83)	75.9 (78.4)
Nossuk (NOS)	55°42′	132°17′	19.52	5.4	0.39	12.01 (1.45)	101	9.95 (5.71)	91.6 (81.6)

Note: Where means are presented, standard deviations are included in parentheses.
† Salmon were counted in each stream reach on multiple dates, surveying 40% of the stream channel area.

Keeton et al. 2007), and increases width-to-depth ratios of stream channels (Hogan and Church 1989). Among the best documented impacts of timber harvest on streams is reduction in the size of stream sediments (Platts et al. 1989). While many studies have demonstrated that timber harvest can negatively influence salmon populations by altering juvenile rearing habitat (Burnett et al. 2007), none have determined whether timber harvest modifies the roles of adult salmon in stream ecosystems as sources of nutrient enrichment and sediment disturbance. Biofilms on stream sediments are important for the uptake and retention of salmon nutrients (Gende et al. 2002), and constitute a key basal food resource for stream ecosystems (Lamberti 1996). We measured biofilm biomass and chlorophyll *a* content before, during, and after the annual salmon run in seven southeast Alaska watersheds that span a wide range of timber harvest intensity. We hypothesized that in watersheds with less timber harvest, the dominant ecological response to salmon is nutrient enrichment, while physical disturbance dominates in watersheds with more timber harvest and finer sediments.

MATERIALS AND METHODS

Study sites

Our study was conducted in the Tongass National Forest on Prince of Wales (POW) Island in southeast Alaska, USA (Fig. 1). The Tongass National Forest is currently managed for multiple land uses, but historically timber harvest was of primary importance (U.S. Department of Agriculture, U.S. Forest Service 1997). Climate in this region is cool maritime with a mean annual air temperature of 7°C and annual precipitation of 250 cm (Barr and Swanston 1970). Forest type is predominantly coniferous temperate rain forest, largely composed of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*). Disturbed areas (e.g., harvested sites, riparian areas) are typically colonized by red alder (*Alnus rubra*). Salmon runs on POW are dominated by pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*), which occur in late summer, while other species are much less abundant or absent.

Seven streams on POW island were selected for the study, the watersheds of which have been subjected to varying levels of timber harvest, ranging from 5% to 68% of the watershed area upstream of our study reaches (data *available online*).[2] Additional criteria for inclusion of streams in our study were evidence of salmon runs, similar stream-channel morphology and slope, and similar size (Table 1). A 300-m reach was delineated within each stream, sufficient to encompass the predominant habitats present in each stream while reducing within-reach variability by avoiding major tributaries.

Sediment size

Mean sediment size for each stream was determined using a gravelometer (Bunte and Abt 2001). This apparatus is effective for particles ranging in size from 2 mm to 180 mm. For larger particles, a meter stick was used to determine size. Five sediment particles were randomly selected at intervals along a transect that was arranged perpendicular to the base-flow stream channel. This procedure was repeated every 10 m along the 300-m study reach of each stream to obtain a mean value of sediment size for each reach.

Stream water chemistry

Water samples (60 mL) were taken from each stream before (19–26 July), during (5–18 September), and after (5–13 October) the salmon run. To characterize the entire study reach, three replicate samples were taken at four locations that were equally distributed along the stream reach. After determination of dissolved nutrient concentration, data were pooled to obtain a mean value for each stream on each sampling date. In the field, water was filtered through a Whatman GF/F (0.7 μm) filter into polyethylene bottles for analysis of soluble reactive phosphorus (SRP), nitrate (NO_3^--N), and ammonium (NH_4^+-N), and stored frozen at −20°C prior to laboratory analysis. A Lachat QC8500 Flow Injection Autoanalyzer (Lachat Instruments, Loveland, Colorado, USA) was used to determine SRP with the ascorbic acid method and nitrate with the cadmium reduction method (American Public Health Association 1995). Ammonium concentration was determined on a Shi-

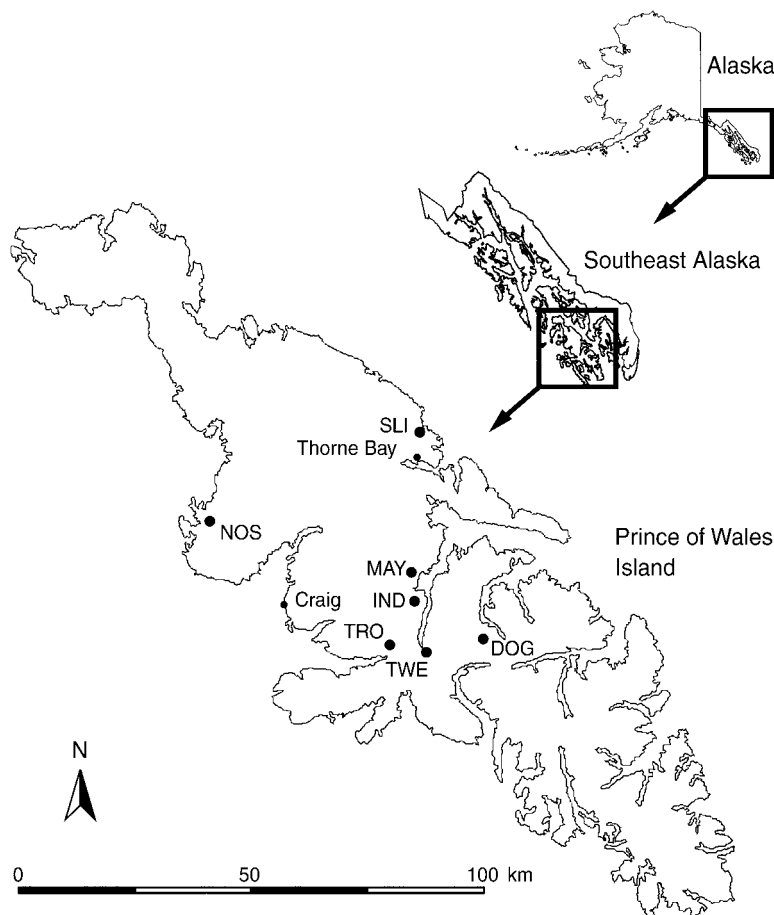2 ⟨http://gina.uas.alaska.edu/joomla/⟩

Fig. 1. Locations of the seven study streams on Prince of Wales Island, Alaska, USA. Complete site names are given in Table 1.

madzu UV-1601 spectrophotometer (Shimadzu Corporation, Columbia, Maryland, USA) using the phenol-hypochlorite method (Solorzano 1969, American Public Health Association 1995).

Biofilm

Sampling was conducted three times in each stream on approximately the same dates used for water chemistry (i.e., before, during, and after the salmon run). During each sampling, five individual rocks were haphazardly collected from three or four riffles distributed along the full length of the study reach. Biofilm was removed from the surface of each rock using a syringe–toothbrush sampler by scraping a known area (7.1 cm^2; Steinman et al. 2006). The biofilm slurry was filtered through a Whatman GF/F (0.7-μm) filter and stored at −20°C until analyzed. Each filter was analyzed first for chlorophyll a (chl a), and then for ash-free dry mass (AFDM) ($n = 15$–20 filters per stream, per sampling date). Chlorophyll a was extracted in 10 mL of ethanol at 4°C for approximately 12 h, and measured fluorometrically (after Sartory and Grobbelaar 1984). The AFDM of the remaining material was measured according to Steinman et al. (2006) after drying for a

minimum of 48 h at 60°C and ashing for 4 h at 550°C. Like the samples gathered for water chemistry determination, data from each stream on each date were pooled to obtain a mean value for each stream on each sampling date.

Statistical analyses

Repeated-measures analysis of covariance (rmAN-COVA) was used to assess the influence of timber harvest and salmon on sediment biofilm (chl a and AFDM). The percent timber harvest in each watershed was treated as a covariate, while sampling date relative to the salmon run (before, during, after) was the repeated measure. An interaction between sampling date and percent timber harvest was used as the basis to test for differences in the slope between timber harvest and biofilm among the three sampling dates. Similarly, rmANCOVA was used to examine the relationship between biofilm attributes and mean sediment size among sampling dates. Stream water nutrient concentrations were analyzed with rmANOVA with sampling date as the repeated measure. Linear regression was used to test for relationships between timber harvest and sediment size. SAS (Release 9.1; SAS Institute, Cary,
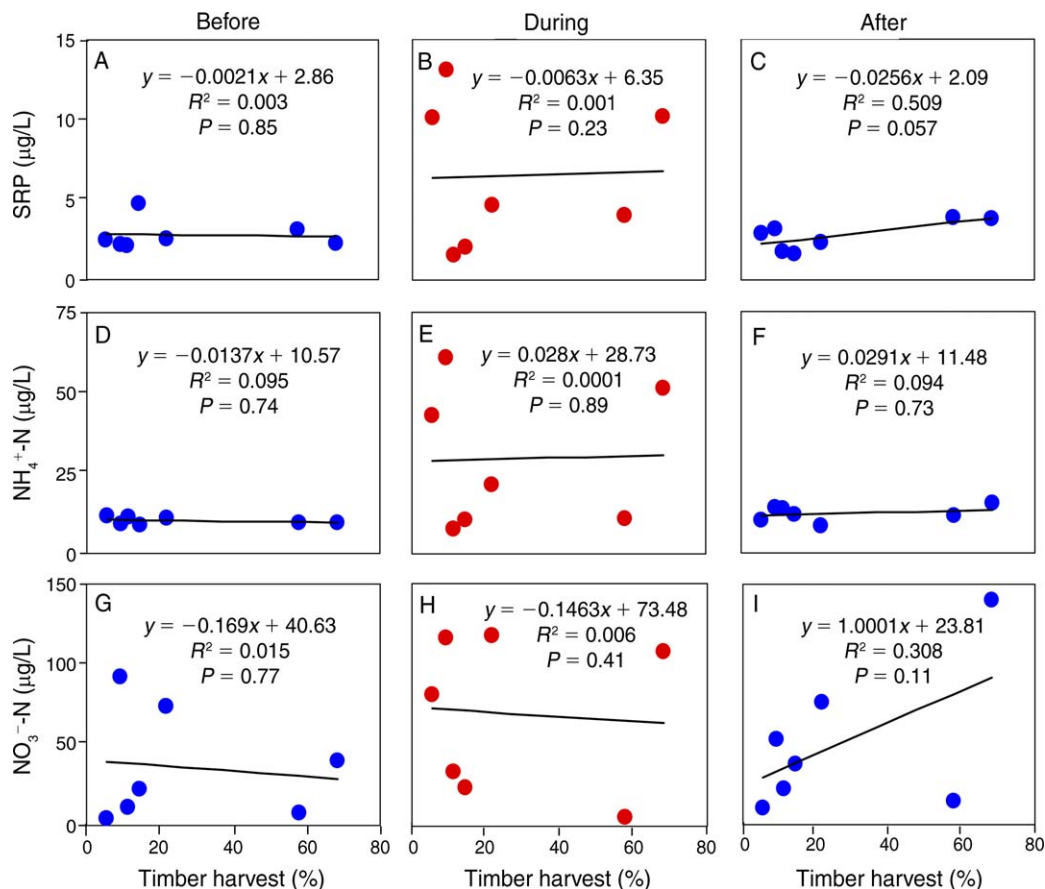
FIG. 2. Linear regressions between soluble reactive phosphorus (SRP), ammonium, and nitrate concentration and percent timber harvest before, during, and after the salmon run.

North Carolina, USA) was used to perform rmANCO-VA, and SYSTAT was used for regressions (Version 10; Systat Software, Richmond, California, USA). Outlier data points in regression models were identified when they had studentized residuals (Belsley et al. 2004) greater than 2.0 (Systat default value). A single outlier was identified and excluded from the regression of mean sediment size and percent timber harvest (studentized residuals = 2.4). For analysis of biofilm attributes and sediment size, data were normalized with natural-logarithm transformations.

<h2 style="text-align:center">RESULTS</h2>

Physical and chemical stream attributes

Mean sediment size across streams was negatively related to percent timber harvest ($R^2 = 0.82$, $P = 0.01$). Mean stream water concentrations of NH_4^+-N and SRP differed among sampling dates, with increases occurring during salmon runs (Fig. 2A–F; Table 2) whereas NO_3^--N did not differ among sampling dates (Fig. 2G–I; Table 2). No significant relationships were observed between mean concentrations of dissolved nutrients and percent timber harvest on any of the three sampling dates,

although there was a weak and marginally significant tendency of increasing SRP with increasing timber harvest following the salmon run (Fig. 2C).

Biofilm

The relationship between biofilm chl *a* and percent timber harvest strongly differed among the three sampling dates (i.e., before, during, and after the salmon run) as indicated by significant interaction between percent timber harvest and sampling date (Fig. 3A–C; Table 3). Prior to the salmon run, chl *a* concentration increased with percent timber harvest (Fig. 3A), but this relationship became negative during the salmon run (Fig. 3B), and no relationship was observed following the salmon run (Fig. 3C). Significant differences in mean chl *a* abundance were observed among the sampling dates, with an increase occurring during the salmon run. Percent timber harvest was not a significant covariate (Fig. 3A–C; Table 3).

Similar to chl *a*, the relationship between biofilm AFDM and percent timber harvest differed among the three sampling dates (Fig. 3D–F), as indicated by a significant interaction between percentage of timber

TABLE 2. Results of repeated-measures ANOVA performed on dissolved nutrient concentrations in the seven streams before, during, and after the annual salmon run ("Salmon," the repeated measure).

Effect	df	F	P
Ammonium			
Salmon	2, 18	4.84	0.021
SRP			
Salmon	2, 18	4.71	0.023
Nitrate			
Salmon	2, 18	1.07	0.365

Note: "SRP" is soluble reactive phosphorus.

harvest and timing of the sampling relative to the salmon run (Table 3). Prior to the salmon run, we observed a marginally significant positive relationship between the quantity of AFDM and percent timber harvest (Fig. 3D). This relationship became significantly negative during the salmon run (Fig. 3E), and no relationship was observed after the salmon (Fig. 3F). Significant differences in mean AFDM were not observed among the sampling dates (Table 3), and percent timber harvest was not a significant covariate (Table 3).

Biofilm and sediment interactions

The relationship between sediment size and AFDM differed among the three sampling dates, as indicated by a significant interaction between sediment size and sampling date (Table 4), whereas the relationship between chl *a* and sediment did not differ among dates (Table 4). Across the three sampling dates, sediment size was not a significant covariate with the abundance of either chl *a* or AFDM (Table 4). AFDM differed among the three sampling dates, whereas chl *a* did not (Table 4). When analyses were restricted to only the five streams that received substantial salmon runs, both AFDM and chl *a* differed among the three sampling dates (Table 5). Sediment size was a significant covariate with mass of chl *a*, but was not a significant covariate with AFDM (Table 5). For quantities of both AFDM and chl *a* there was significant interaction between timing of the sampling, relative to the salmon run, and sediment size (Table 5).

No relationship was observed between sediment size and chl *a*, either before ($R^2 = 0.26$, $P = 0.24$) or after the salmon run ($R^2 = 0.00$, $P = 0.89$). Similarly, no relationship was found between AFDM and sediment before the salmon run ($R^2 = 0.11$, $P = 0.46$) or after ($R^2 = 0.005$, $P = 0.95$). However, during the salmon run a significant positive relationship emerged between both chl *a* and sediment size ($R^2 = 0.59$, $P = 0.04$), and AFDM and sediment size ($R^2 = 0.68$, $P = 0.02$). To further assess the influence of salmon runs on the relationship between biofilm and sediment size, regressions were also performed on only the five streams that received significant salmon runs (i.e., Slide and Trocadero excluded, see Table 1). For this relevant subset of streams, during the salmon run, very strong relationships ($R^2 > 0.9$) were found between chl *a* and sediment size (Fig. 4A) and AFDM and sediment size (Fig. 4B).

DISCUSSION

Consistent with the results of previous studies, we observed highly variable biofilm responses to the arrival of salmon among our seven study streams. Previously
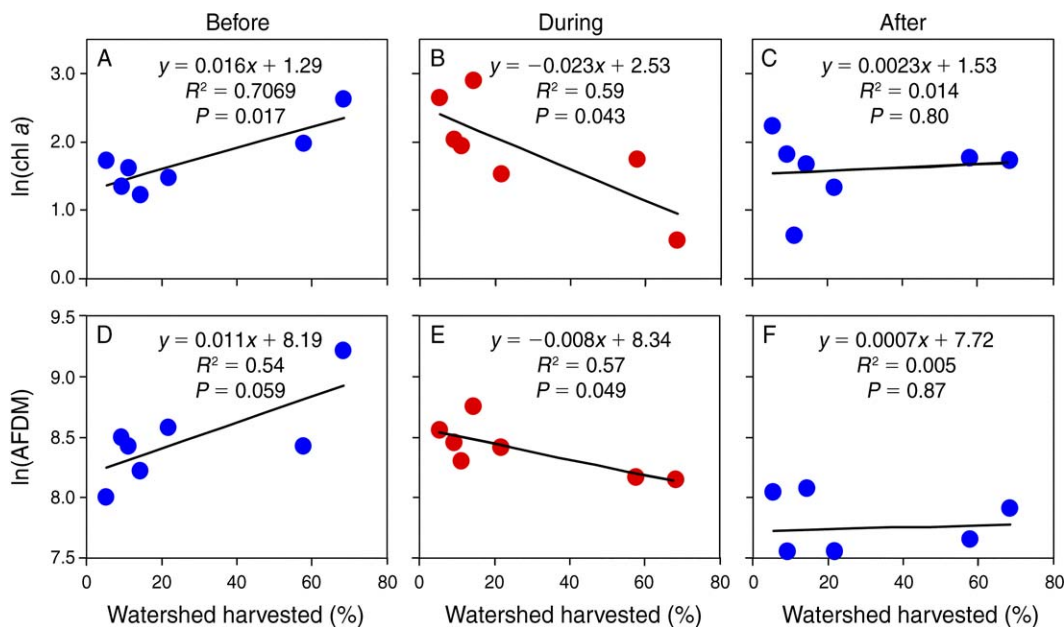

FIG. 3. Linear regression of biofilm chlorophyll *a* and ash-free dry mass, AFDM (both log-transformed), and the percentage of the watershed area that was harvested of its timber before, during, and after the salmon run.

TABLE 3. Results of repeated-measures ANCOVA on chlorophyll *a* and ash-free dry mass (AFDM) across a gradient of timber harvest ("Timber harvest," covariate), before, during, and after the salmon run ("Salmon," the repeated measure).

Effect	df	F	P
Chlorophyll *a*			
Timber harvest	1, 15	1.31	0.690
Salmon	2, 15	5.10	0.013
Timber harvest × salmon	2, 15	5.59	0.008
AFDM			
Timber harvest	1, 15	0.63	0.208
Salmon	2, 15	3.30	0.160
Timber harvest × salmon	2, 15	5.57	0.007

documented responses ranged widely from strong increases in biofilm AFDM and chl *a* (Chaloner et al. 2004), to no response to salmon (Mitchell and Lamberti 2005), to pronounced declines in these two biofilm attributes (Minakawa and Gara 1999, Moore et al. 2004). In our study, the positive effects of increased nutrient availability, as indicated by a ~200% increase in chl *a* during the salmon run relative to pre-salmon values, were restricted to streams in watersheds with low levels of timber harvest. Biofilm in streams within heavily harvested watersheds either did not respond to the salmon run (e.g., Maybeso), or in the case of the stream with the most heavily harvested watershed and finest sediments (Twelve Mile), exhibited a >400% decrease in chl *a* and AFDM during the salmon run relative to pre-run values. Thus, biofilm declined or did not change in heavily harvested sites during the salmon run, despite strong increases in dissolved nutrient concentrations, suggesting that any positive effects of these nutrients were more than countered by the bioturbation effects of migrating and spawning salmon. This idea is corroborated by our finding that during the salmon run, a large percentage of among-stream variability in biofilm abundance (~90%) was explained by the mean sediment size, which decreased with increasing timber harvest. An alternate explanation of the patterns we observed prior to the salmon run (i.e., higher chl *a* and AFDM in the harvested sites) is that nitrogen-fixing alder trees, which are more abundant in

TABLE 4. Results of repeated-measures ANCOVA on chlorophyll *a* and ash-free dry mass (AFDM) before, during, and after the salmon run ("Salmon," the repeated measure), treating the mean sediment size as a covariate in each of seven streams.

Effect	df	F	P
Chlorophyll *a*			
Salmon	2, 15	1.78	0.203
Sediment	1, 15	1.08	0.316
Salmon × sediment	2, 15	2.59	0.108
AFDM			
Salmon	2, 15	9.57	0.002
Sediment	1, 15	3.16	0.096
Salmon × sediment	2, 15	5.13	0.0200

TABLE 5. Results of repeated-measures ANCOVA on chlorophyll *a* and ash-free dry mass (AFDM) before, during, and after the salmon run ("Salmon," the repeated measure), treating the mean sediment size of each stream as a covariate in the five streams that received appreciable numbers of salmon.

Effect	df	F	P
Chlorophyll *a*			
Salmon	2, 9	5.34	0.046
Sediment	1, 9	13.36	0.002
Salmon × sediment	2, 9	9.95	0.005
AFDM			
Salmon	2, 9	2.01	0.19
Sediment	1, 9	12.61	0.003
Salmon × sediment	2, 9	18.25	0.0007

Note: Tocadero Creek and Slide Creek were excluded due to insufficient salmon numbers (see Table 1).

the harvested watersheds, provide a source of nitrogen that alleviates nutrient limitation such that salmon nutrients (at least N) no longer elicit a biofilm response. However, nutrient-diffusing substrates placed in the same seven streams prior to the salmon run indicate that nitrogen limitation of stream autotrophs is present
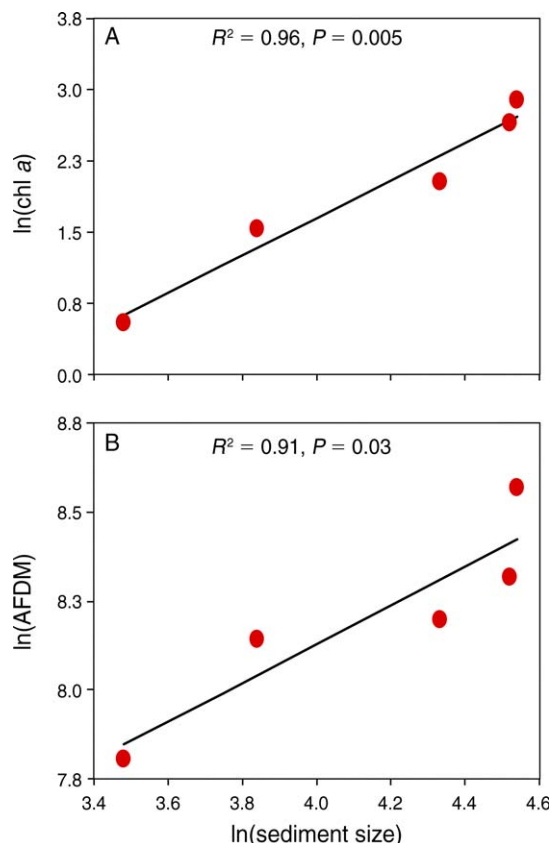

FIG. 4. Relationship of biofilm (A) chlorophyll *a* and (B) ash-free dry mass (AFDM) to sediment particle size during the salmon run for the five streams receiving significant salmon runs. Values have been log-transformed; original measurements were in mg/m^2 for chl *a* and AFDM, and mm for sediment size.
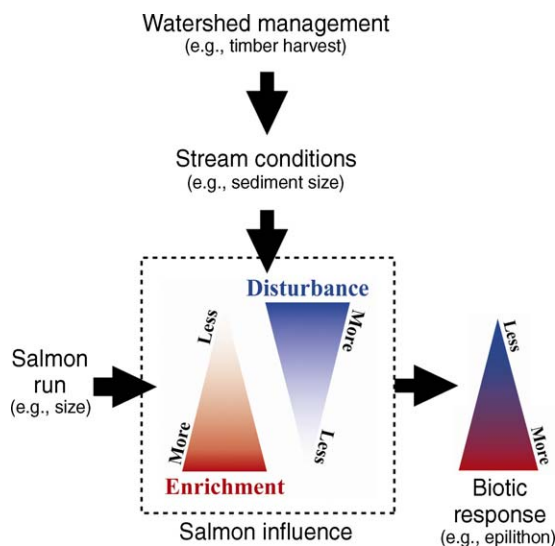
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Fig. 5. Conceptual model illustrating the interactions between watershed management and abiotic stream characteristics that govern the ecological influence of adult salmon, as sources of nutrient enrichment and agents of physical disturbance, on instream biota. Arrows indicate the path of influence.

irrespective of timber harvest (J. Rüegg, *unpublished data*). Collectively, our results from Southeast Alaska suggest that nutrient enrichment is the dominant role of salmon in the streams from unharvested watersheds but bioturbation is the dominant process in the finer sediments of streams within heavily harvested watersheds. These results demonstrate that human activities change the stream environment to the extent that the ecological roles of adult salmon are dramatically transformed.

Active management of species that modify their physical and chemical environment (i.e., ecosystem engineers) has been proposed as a means of restoring ecosystems (Byers et al. 2006). Similarly, some studies have advocated adding salmon nutrients (in the form of carcasses) or salmon nutrient substitutes to freshwaters with anthropogenically diminished salmon populations (see review by Compton et al. 2006). The goal of this restoration technique is to enhance the overall productivity of ecosystems with the intent of increasing juvenile salmon recruitment and survivorship (Ashley and Slaney 1997, Pearsons et al. 2007), thus restoring the flux of nutrients from marine to freshwater ecosystems. However, without specific knowledge of the factors controlling the ecological effects of salmon-derived nutrients, and given that the stream enrichment effects of salmon are variable across both time and space (e.g., Chaloner et al. 2004, 2007), the outcome of this stream restoration approach is uncertain. While high levels of spatial heterogeneity across and within streams pose a challenge for generalizing about the ecological role of salmon, knowledge of a few key environmental variables, such as sediment size and logging history, could provide a

powerful predictor of the responses to the addition of salmon nutrients.

The ecological function of adult salmon in streams has classically been considered from the perspective of resource subsidies in which salmon function as vectors of nutrients and other resources from marine to freshwater ecosystems (e.g., Willson et al. 1998). This perspective is now giving way to an emerging understanding that salmon have multifaceted roles in freshwater ecosystems. Our results show that the physical stream environment can determine whether the dominant role of salmon is nutrient enrichment or physical disturbance, and that this context dependency can be strongly influenced by human activities in the watershed (Fig. 5). While land use was responsible for altering the physical stream environment in our study, environmental conditions at even the most impacted sites are still well within the range typically encountered in unimpacted systems, suggesting that natural variation in stream attributes such as sediment size and amounts of large woody debris could result in a wide range of ecosystem responses to salmon runs. Thus, natural variability in the physical stream environment could explain why salmon disturbance was identified as the dominant process in some studies conducted in unimpacted streams (e.g., Moore et al. 2007), while salmon-derived nutrients stimulated the abundance of biota in other streams (e.g., Chaloner et al. 2004). We propose that a broader appreciation of both the physical context of the stream environment and the complex ecological roles of salmon will improve our understanding of how these unique fish affect stream ecosystems and ultimately contribute to better management of salmon and the watersheds in which they spawn.

LITERATURE CITED

American Public Health Association. 1995. Standard methods for the examination of water and waste water. 19th edition. American Public Health Association, Washington, D.C., USA.

Ashley, K. I., and P. A. Slaney. 1997. Accelerating recovery of stream and pond productivity by low-level nutrient enrichment. Pages 239–262 *in* P. A. Slaney and D. Zaldokas, editors. Fish habitat rehabilitation procedures. British

Columbia Ministry of Environment, Lands and Parks and Ministry of Forest, Vancouver, British Columbia, Canada.

Barr, D. J., and D. N. Swanston. 1970. Measurement of creep in a shallow, slide-prone till soil. American Journal of Science 269:467–480.

Belsley, D. A., E. Kuh, and R. E. Welsch. 2004. Regression diagnostics: identifying influential data and sources of collinearity. Wiley, Hoboken, New Jersey, USA.

Bunte, K., and S. R. Abt. 2001. Sampling frame for improving pebble count accuracy in coarse gravel-bed streams. Journal of the American Water Resources Association 37:1001–1014.

Burnett, K. M., G. H. Reeves, D. J. Miller, S. Clarke, K. Vance-Borland, and K. Christiansen. 2007. Distribution of salmon-habitat potential relative to landscape characteristics and implications for conservation. Ecological Applications 17:66–80.

Byers, J. E., K. Cuddington, C. G. Jones, T. S. Talley, A. Hastings, J. G. Lambrinos, J. A. Crooks, and W. G. Wilson. 2006. Using ecosystem engineers to restore ecological systems. Trends in Ecology and Evolution 21:493–500.

Chaloner, D. T., G. A. Lamberti, A. D. Cak, N. L. Blair, and R. T. Edwards. 2007. Inter-annual variation in the water chemistry and epilithon responses to Pacific salmon spawners in an Alaskan stream. Freshwater Biology 52:478–490.

Chaloner, D. T., G. A. Lamberti, R. W. Merritt, N. L. Mitchell, P. H. Ostrom, and M. S. Wipfli. 2004. Variation in responses to spawning Pacific salmon among three south-eastern Alaska streams. Freshwater Biology 49:587–599.

Compton, J. E., C. P. Andersen, D. L. Phillips, J. R. Brooks, M. G. Johnson, M. R. Church, W. E. Hogsett, M. A. Cairns, P. T. Rygiewicz, B. C. McComb, and C. D. Shaff. 2006. Ecological and water quality consequences of nutrient addition for salmon restoration in the Pacific Northwest. Frontiers in Ecology and the Environment 4:18–26.

Cordova, J. M., E. J. Rosi-Marshall, A. M. Yamamuro, and G. A. Lamberti. 2007. Quantity, controls and functions of large woody debris in Midwestern USA streams. River Research and Applications 23:21–33.

Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. BioScience 52:917–928.

Hastings, A., J. E. Byers, J. A. Crooks, K. Cuddington, C. G. Jones, J. G. Lambrinos, T. S. Talley, and W. G. Wilson. 2007. Ecosystem engineering in space and time. Ecology Letters 10:153–164.

Hogan, D. L., and M. Church. 1989. Hydraulic geometry in small, coastal streams—progress toward quantification of salmonid habitat. Canadian Journal of Fisheries and Aquatic Sciences 46:844–852.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

Keeton, W. S., C. E. Kraft, and D. R. Warren. 2007. Mature and old-growth riparian forests: structure, dynamics and effects on Adirondack stream habitats. Ecological Applications 17:852–868.

Lamberti, G. A. 1996. The role of periphyton in benthic food webs. Pages 533–572 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe, editors. Algal ecology in freshwater benthic ecosystems. Academic Press, San Diego, California, USA.

Minakawa, N., and R. I. Gara. 1999. Ecological effects of a chum salmon (Oncorhynchus keta) spawning salmon run in a small stream of the Pacific Northwest. Journal of Freshwater Ecology 14:327–335.

Mitchell, N. L., and G. A. Lamberti. 2005. Responses in dissolved nutrients and epilithon abundance to spawning salmon in southeast Alaska streams. Limnology and Oceanography 50:217–227.

Moore, J. W. 2006. Animal ecosystem engineers in streams. BioScience 56:237–246.

Moore, J. W., D. E. Schindler, J. L. Carter, J. Fox, J. Griffiths, and G. W. Holtgrieve. 2007. Biotic control of stream fluxes: spawning salmon drive nutrient and matter export. Ecology 88:1278–1291.

Moore, J. W., D. E. Schindler, and M. D. Scheuerell. 2004. Disturbance of freshwater habitats by anadromous salmon in Alaska. Oecologia 139:298–308.

Pearsons, T. N., D. D. Roley, and C. L. Johnson. 2007. Development of a carcass analog for nutrient restoration in streams. Fisheries 32:114–124.

Platts, W. S., R. J. Torquemada, M. L. Mchenry, and C. K. Graham. 1989. Changes in salmon spawning and rearing habitat from increased delivery of fine sediment to the South-Fork Salmon River, Idaho. Transactions of the American Fisheries Society 118:274–283.

Sartory, D. P., and J. U. Grobbelaar. 1984. Extraction of chlorophyll a from freshwater phytoplankton for spectro-photometric analysis. Hydrobiologia 114:177–187.

Schindler, D. E., P. R. Leavitt, C. S. Brock, S. P. Johnson, and P. D. Quay. 2005. Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska. Ecology 86:3225–3231.

Schindler, D. E., M. D. Scheuerell, J. W. Moore, S. M. Gende, T. B. Francis, and W. J. Palen. 2003. Pacific salmon and the ecology of coastal ecosystems. Frontiers in Ecology and the Environment 1:31–37.

Solorzano, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnology and Oceanography 14:799–801.

Steinman, A. D., G. A. Lamberti, and P. R. Leavitt. 2006. Biomass and pigments of benthic algae. Pages 357–379 in F. R. Hauer and G. A. Lamberti, editors. Methods in stream ecology. Elsevier, Amsterdam, The Netherlands.

Taylor, B. W., A. S. Flecker, and R. O. Hall. 2006. Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. Science 313:833–836.

Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. Journal of the North American Benthological Society 8:36–50.

U.S. Department of Agriculture, U.S. Forest Service. 1997. Tongass land management plan revision. Final Environmental Impact Statement, Region 10 (Alaska Region). U.S. Department of Agriculture Forest Service, Juneau, Alaska, USA.

Villenave, C., F. Charpentier, P. Lavelle, C. Feller, M. Brossard, B. Pashanasi, I. Barois, and A. Albrecht. 1999. Effects of earthworms on soil organic matter and nutrient dynamics. Pages 173–197 in B. P. Lavelle, P. Hendrix, C. Fragoso, and B. K. Senapato, editors. Management of tropical earthworm activities. CAB International, Wallingford, UK.

Willson, M. F., S. M. Gende, and B. H. Marston. 1998. Fishes and the forest. BioScience 48:455–462.

Wright, J. P., and C. G. Jones. 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. BioScience 56:203–209.

Wright, J. P., C. G. Jones, B. Boeken, and M. Shachak. 2006. Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. Journal of Ecology 94:815–824.

Wright, K. A., K. H. Sendek, R. M. Rice, and R. B. Thomas. 1990. Logging effects on streamflow: storm runoff at Caspar Creek in northwestern California. Water Resources Research 26:1657–166.

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