

Carcass Addition Does Not Enhance Juvenile Salmonid Biomass, Growth, or Retention in Six Northwestern California Streams

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Abstract.—Fisheries managers commonly consider the addition of salmon carcasses when seeking to enhance salmonid populations. However, the range of environmental conditions under which the technique is effective remains poorly defined. We addressed this issue by measuring the effects of wintertime addition of salmon carcasses on the biomass, growth, and retention of juvenile salmonids in an experiment that included two study reaches within each of six northwestern California streams. In the first 2 years of the study, half of the streams received carcasses in both study reaches; in the subsequent 2 years, we added carcasses only to the downstream reach in all six streams. For juvenile salmonid biomass, growth, and retention, the change in carcass distribution did not affect general patterns in the relationship of the upstream and downstream reaches within streams. Artificial addition of salmon carcasses during winter in streams similar to those we studied appears unlikely to benefit juvenile salmonids in the short-term; management alternatives focused on increasing escapement should probably take priority.

Fisheries managers seeking to benefit depleted anadromous salmonid populations commonly consider adding salmon carcasses to streams. The idea deserves consideration because current delivery of marine-derived nutrients to freshwater ecosystems via salmon carcasses is at a fraction of historical rates in many drainages (e.g., Gresh et al. 2000), even as the out-migration of salmonid smolts continues to export nutrients from freshwater ecosystems (Scheuerell et al. 2005). Many studies provide isotopic evidence that carcass nutrients are incorporated into freshwater and riparian ecosystems (e.g., Chaloner et al. 2002; Hicks et al. 2005; Merz and Moyle 2006). In addition, some reach- and smaller-scale experiments (Bilby et al. 1998; Wipfli et al. 2003; Williams et al. 2009) provide evidence that carcass addition can increase the density or growth of salmonids.

However, observations from a variety of studies

suggest that carcass addition should be carefully evaluated before implementation. Documented benefits to fish have covered relatively short periods of a few months or less (Bilby et al. 1998; Wipfli et al. 2003; Williams et al. 2009). Salmon eggs appear to be more valuable than somatic tissue from carcasses as a diet item for juvenile fish (Scheuerell et al. 2007). Artificially placed carcasses may not increase use of marine-derived nutrients (Shaff and Compton 2009) or may have modest effects in comparison with large, natural runs of salmon (Janetski et al. 2009). Addition of carcasses may increase the risk of introducing diseases (Compton et al. 2006). Carcass effects are likely to vary depending on features of the physical setting and disturbance regime (Tieggs et al. 2008). Additional observations on the effects of added carcasses across a greater variety of physical settings are needed.

We first explored the effects of carcass addition on juvenile salmonids in northwestern California streams in a 2-year experiment that also included manipulation of the riparian canopy (Wilzbach et al. 2005). The previous experiment revealed that canopy removal enhanced juvenile salmonid biomass but that carcass addition had little or no effect on juvenile salmonid biomass, growth, or retention. The design of that experiment, however, yielded a more powerful test of the canopy removal effect than the carcass addition effect. In the present study, we sought to more effectively test the carcass addition effect in the same study streams by altering the experimental design and extending the experiment for another 2 years.

Methods

Study sites.—The study was conducted in six second- to third-order coastal streams in northwestern California: two tributaries of the lower Klamath River (Tarup and Tectah creeks) and four tributaries of the lower Smith River (Peacock, Little Mill, Savoy, and South Fork Rowdy creeks). Catchment areas were 3.4–7.9 km², and bank-full widths were 3.8–8.6 m at the study sites. Nutrient concentrations were low and

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relatively homogeneous among streams on four dates from January to June 2002 (overall mean [\pm SE] concentrations [$n = 48$ for all]: nitrate = 0.27 ± 0.02 mg/L; total nitrogen = 0.35 ± 0.02 mg/L; total phosphorus = 9.05 ± 0.36 μ g/L). Hill slopes were covered by 30–60-year-old coniferous forest (coast redwood *Sequoia sempervirens*, Douglas-fir *Pseudotsuga menziesii*, and Sitka spruce *Picea sitchensis*). Red alder *Alnus rubra* dominated the riparian zones of all six streams. Fish assemblages at the study sites were dominated by juvenile steelhead *Oncorhynchus mykiss*. We selected study sites to occur just above the upstream limits of anadromous salmon to avoid any rapid export of carcass addition effects by emigrating juvenile salmon (see Wilzbach et al. [2005] for more details on the study streams).

Phase 1.—The first phase of the experiment included carcass addition and canopy opening in a split-plot design, with two levels (treatment and control) for each factor. To allow randomization while avoiding any within-stream confounding of carcass treatments, we assigned carcass treatments at the stream scale and canopy treatments at the reach scale. In all six streams, two 100-m study reaches were separated by 150–200 m of stream. In three streams, both study reaches received carcasses at an average rate of 0.94 kg/m^2 (wetted area). This exceeds the carcass loading used in several previous studies that detected salmonid responses to carcass addition (0.56 and 0.62 kg/m^2 : Bilby et al. 1998; 0.83 kg/m^2 : Wipfli et al. 2003; 0.2 kg/m^2 : Williams et al. 2009). The loading we used also exceeds that which maximized uptake of marine-derived nitrogen by coho salmon *O. kisutch* parr (Bilby et al. 2001) in Washington streams. Hatcheries on the Smith and Klamath rivers provided carcasses for study streams in their respective drainages. We staked carcasses to the streambed with rebar to enhance retention. Only 3 of 243 anchored carcasses in the first year of the study showed evidence of vertebrate scavenging over a 10-week period. Carcasses were distributed throughout the study reaches in areas where natural carcass deposition would have occurred. The canopy removal treatment consisted of cutting all standing hardwoods within 20 m of the stream on both sides of the channel. A low density of small conifers remained in canopy removal reaches, but they did not affect stream shading. Randomization of the canopy treatments resulted in canopy removal in the downstream reach of four streams and the upstream reach of two streams. Predictably, because of natural variation among streams, this design led to a stronger estimate of the canopy and canopy \times carcass effects than the carcass effect. For example, in the analysis of

total salmonid biomass, the mean square error used to test the carcass effect was about four times larger than the mean square error used to test the canopy and canopy \times carcass effects.

Phase 1 included canopy removal in December 2001 and carcass additions in January 2002 and 2003. We sampled fish by multiple-pass electrofishing in October 2001 before any experimental manipulations and sampled again in June and October of 2002 and 2003. Fish biomass data recorded after experimental manipulations were expressed as the difference in biomass from the October 2001 values. All juvenile salmonids larger than 70 mm fork length (FL) were implanted with passive integrated transponder (PIT) tags on all sampling dates except June 2003 so that within-reach retention and growth of tagged individuals could be compared among treatments. We quantified growth using specific growth rate (G):

$$G = [(\log_e W_t - \log_e W_0) / t] \times 100,$$

where W_t is final mass (g), W_0 is initial mass, and t is the growth period (d).

Canopy removal enhanced total salmonid biomass in phase 1, but carcass and canopy \times carcass interaction effects on biomass were not detected. Individual growth also varied among treatments. On two out of three sampling dates that provided results for growth, canopy removal had a greater positive effect on growth in the absence of salmon carcasses. In one case (June 2002), growth was similar for fish from open-canopy reaches in the presence and absence of carcasses; in the second case (October 2002), growth was particularly high in open-canopy reaches in the absence of carcasses. The treatments did not yield detectable variation in tagged fish retention, which was low over winter (12% and 18%) and modest over summer (June–October 2002; 51%).

Phase 2.—In the second phase of the experiment, we altered the assignment of carcass treatments to reaches by placing carcasses in the downstream reach of all six streams in January 2004 and January 2005 instead of placing carcasses in both reaches of three streams as was done in phase 1 (Table 1). This change resulted in the addition of carcasses for the first time to the downstream study reaches of three streams and the elimination of carcass addition to the upstream reaches of the other three streams. The change removed among-stream variation as a source of error in our analysis of carcass effects. In all six streams, any effect of carcass addition should be reflected in a change in the relationship between downstream and upstream reaches in 2002–2003 versus 2004–2005. Note that this approach to estimating a carcass effect in phase 2

TABLE 1.—Treatment history for the 12 reaches used in an experiment on the effects of riparian canopy removal and salmon carcass addition on juvenile salmonid biomass, growth, and retention in six northwestern California streams.

Creek	Reach	Canopy treatment	Carcass treatment	
			Phase 1 (2002–2003)	Phase 2 (2004–2005)
Mill	Upper	Control	Control	Control
	Lower	Removal	Control	Added
Savoy	Upper	Control	Control	Control
	Lower	Removal	Control	Added
Tectah	Upper	Control	Control	Control
	Lower	Removal	Control	Added
Peacock	Upper	Control	Added	Control
Rowdy	Lower	Removal	Added	Added
	Upper	Removal	Added	Control
	Lower	Control	Added	Added
Tarup	Upper	Removal	Added	Control
	Lower	Control	Added	Added

assumes the absence of a canopy \times carcass interaction. Particularly for salmonid biomass, the results of phase 1 provide support for this assumption.

Field methods remained consistent between the two phases of the experiment. The biomass density of added carcasses was similar in all 4 years, and the sources of carcasses were the same. Fish in the 12 study reaches were sampled by electrofishing in the fall and spring of 2002–2005; all fish larger than 70 mm FL received PIT tags (except in June 2003).

Analyses.—We considered the inspection of graphical results to be a reasonable approach to data analysis in this case as a meaningful carcass addition effect should yield, in most or all streams, a change in the relationship between reaches in 2002–2003 versus 2004–2005 that favors the downstream reach in the latter 2 years. We also conducted statistical analyses that provided an overall evaluation of before–after, control–impact comparisons for all six streams: a two-way analysis of variance was performed on the relationships between reaches, with before–after the change in experimental design and stream as factors. The relationships between upstream and downstream reaches were generally expressed as differences; we also used ratios to further explore some possible responses to carcass addition. This analytical approach assumes that the absolute value of any effect caused by carcass addition is equal to that of carcass removal. For the analysis of individual growth, we included season as a factor because of obvious growth differences in fall–spring versus spring–fall periods. Low retention of juvenile salmonids between sampling periods led to low sample sizes for mean growth within reaches. We selected three fish as a minimum sample size for inclusion of mean growth data for a given combination of reach and sampling period.

Results

Total salmonid density did not respond consistently across streams to the change in carcass distribution over the last 2 years of the experiment (Figure 1). Whereas statistical analysis suggested variation among streams in the response to the change in carcass distribution (stream \times carcass interaction term: $F_{5,36} = 2.35$, $P = 0.06$ for differences; $F_{5,36} = 3.71$, $P < 0.01$ for ratios), none of the streams exhibited a large, positive effect of carcass addition. A main effect of carcasses was not detected ($F_{1,36} = 1.04$, $P = 0.31$ for differences; $F_{1,36} = 0.01$, $P = 0.90$ for ratios). Two streams that originally received carcasses in both upstream and downstream reaches exhibited patterns that suggested a carcass effect in one (but not both) of the ways we expressed relations between upstream and downstream reaches. The difference between upstream and downstream reaches did not change dramatically after carcass addition to the upstream reach was stopped in Peacock Creek, but the downstream : upstream ratio was consistently higher. This pattern was caused by similar declines in biomass (g/m^2) in the two reaches during phase 2. Conversely, while the difference between downstream and upstream biomass in Rowdy Creek changed in favor of the downstream reach after carcass addition to the upper reach was stopped, the downstream : upstream ratio remained consistent. This pattern resulted from a greater reduction in biomass in the upstream reach compared with the downstream reach. These two instances of small changes consistent with a carcass effect must be placed in the context of the lack of any such changes in the four other streams.

Although the overall consistency in results for juvenile salmonid biomass between phase 1 and phase 2 of the experiment suggests the absence of a carcass effect, it also indicates the persistence of a canopy

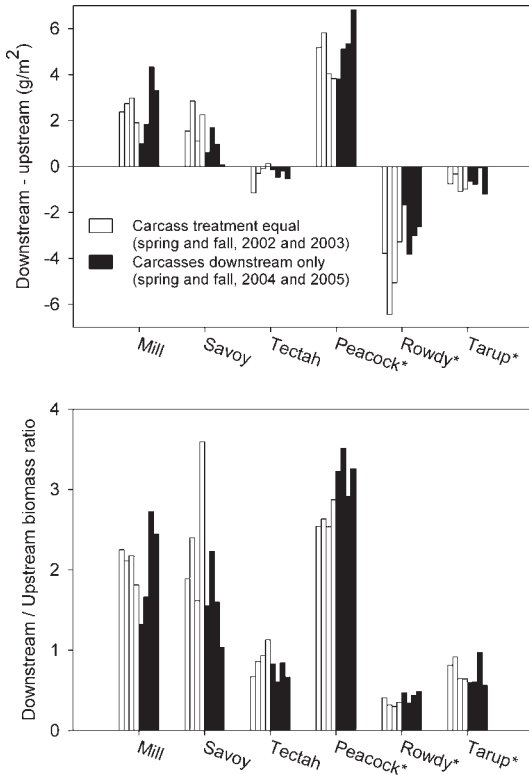


FIGURE 1.—Juvenile salmonid biomass during a 4-year experiment on the influence of salmon carcass addition in northwestern California streams (upper panel: biomass difference between reaches; lower panel: biomass ratio). For each creek, the four open bars indicate results for spring and fall sampling in the first 2 years of the experiment, when upstream and downstream reaches received the same carcass treatment (see Table 1); shaded bars reflect results for spring and fall sampling in the second 2 years, when carcasses were added to only the downstream reach. Bars for a given creek are in chronological order from left to right (e.g., open bars begin with spring 2002 and end with fall 2003). Asterisks indicate creeks that received carcasses in both reaches during the first 2 years. All data for the first 2 years are from Wilzbach et al. (2005).

effect. For all eight samples over 4 years, the change in biomass difference between reaches from premanipulation values indicated a positive effect of canopy removal, both where the canopy was removed from the downstream reach (Mill, Savoy, Tectah, and Peacock creeks) and where it was removed from the upstream reach (Rowdy and Tarup creeks).

Differences in juvenile salmonid growth between upstream and downstream reaches varied among streams, but the change to downstream-only carcass addition did not consistently affect the relationship between reaches or suggest variation in carcass effects

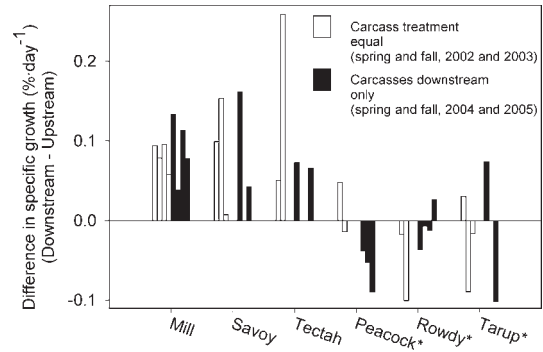


FIGURE 2.—Difference in juvenile salmonid specific growth rates between downstream and upstream reaches during a 4-year experiment on the influence of salmon carcass addition in northwestern California streams. For each creek, open bars indicate results for spring and fall sampling in the first 2 years of the experiment, when upstream and downstream reaches received the same carcass treatment (see Table 1); shaded bars show results for spring and fall sampling in the second 2 years, when carcasses were added to only the downstream reach. Asterisks indicate creeks that received carcasses in both reaches during the first 2 years.

among streams (Figure 2; stream \times carcass interaction term: $F_{5,20} = 0.95$, $P = 0.47$; carcass effect: $F_{1,20} = 0.24$, $P = 0.63$). Unfortunately, low recapture rates and our failure to tag fish in June 2003 limited the number of observations available for evaluating individual growth. The constraint that estimates of reach-specific growth for a given sampling date must include at least three fish limited the data set for growth to 33 of 48 possible comparisons between reaches. Although mean sample size for the calculation of reach-specific growth on a given sampling date averaged 15 fish, 13 of the 33 values are based on five or fewer fish.

Results for juvenile salmonid retention also did not suggest a consistent effect of carcass addition (Figure 3; carcass effect: $F_{1,36} = 1.29$, $P = 0.26$), although the pattern from one of the six streams suggested a positive effect of carcasses (stream \times carcass interaction term: $F_{5,36} = 2.16$, $P = 0.08$). Retention data for Peacock Creek revealed a relative increase downstream after carcass addition in the upstream reach was stopped. However, the change in the experimental manipulation coincided with a loss of pool habitat in the upstream reach.

Discussion

Although the change in experimental design between the first and last 2 years of the experiment improved our ability to detect effects of carcass addition, altering the pattern of carcass addition failed to reveal any consistent influence of carcasses on juvenile salmonid

biomass, growth, or retention in the six study streams. Thus, carcass addition on a limited spatial scale appears unlikely to significantly benefit salmonids on a within-year time scale in streams similar to those we studied. Of course, this experiment leaves open the possibility of benefits on different spatial and temporal scales. Low retention of juvenile salmonids on the 100-m scale raises the possibility that use of longer reaches would increase the probability of detecting carcass addition effects in the study streams. Bilby et al. (1998) observed positive effects of carcass addition on the density and growth of juvenile salmonids in two third-order Washington streams by adding carcasses over 500-m stream reaches, although the observed density and growth increases peaked sharply during the time carcasses were present in the streams. Our 4-year experiment also cannot address the possibility of longer-term benefits to fish (e.g., via effects on riparian vegetation; Helfield and Naiman 2001).

Several specific features of our experiment and the study streams probably contributed to the lack of a carcass effect on salmonid density, growth, and retention. The carcasses we added did not contain eggs. The provision of eggs may have been critical in several studies on carcass addition that showed benefits for juvenile salmonids (e.g., Bilby et al. 1998; Wipfli et al. 2003; Lang et al. 2006). Also, we timed carcass addition to match the life history of the dominant salmon runs in the region, which meant that we added carcasses when streamflows were high and water temperatures were low (i.e., when retention and demand for nutrients might be minimal). Downstream transport of whole carcasses was not a major issue because we anchored them to the stream bottom. However, June and November measurements of nitrogen and phosphorus uptake lengths in our study reaches (B. H. Hill, U.S. Environmental Protection Agency, unpublished data) indicate that most of the dissolved nutrients from the added carcasses would not have been retained within the reaches (average nitrogen uptake length [13 observations] = 75 m; average phosphorus uptake length [12 observations] = 500 m). Uptake lengths in the study streams are similar to those reported for other coastal streams in northwestern California (Hill et al. 2010). Previous research has revealed positive responses by primary producers, benthic invertebrates, and fish to carcasses, carcass analogs, and other forms of added nutrients (e.g., Johnston et al. 1990, 2004; Kohler et al. 2008). However, in streams such as those we studied, wintertime addition of nutrients appears unlikely to benefit fish unless the nutrients are in a form that fish are likely to consume directly (i.e., salmon eggs).

Similar to the initial (phase-1) results (Wilzbach et

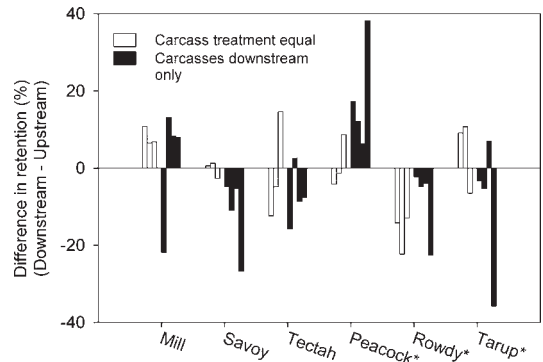


FIGURE 3.—Differences between downstream and upstream reaches in retention of tagged juvenile salmonids from one sampling period to the next during a 4-year experiment on the influence of salmon carcass addition in northwestern California streams. For each creek, open bars represent sampling conducted in the first 2 years of the experiment, when upstream and downstream reaches received the same carcass treatment (see Table 1; data shown for June 2002, October 2002, and June 2003 only; no data are available for October 2003 because fish were not tagged in June 2003); shaded bars show results for spring and fall sampling in the second 2 years, when carcasses were added to only the downstream reach. Asterisks indicate creeks that received carcasses in both reaches during the first 2 years.

al. 2005), the results of phase 2 of this experiment provide evidence of a positive effect of riparian canopy removal on juvenile salmonid biomass. Our results parallel observations by Hawkins et al. (1983) of higher abundances of both fishes and riffle invertebrates in low-canopy sites compared with high-canopy sites in coastal streams of Oregon and northwestern California. Specific features of our study streams are probably also important for the canopy result. Study reaches from which riparian red alder was removed nevertheless received substantial input of deciduous leaf litter from upstream. Deciduous leaf litter may be important in trophic pathways leading to fish (Allan et al. 2003). Also, canopy removal did not cause biologically significant changes in water temperature in the study streams.

In light of evidence that nutrients from artificially placed salmon carcasses may not increase utilization of marine-derived nutrients by juvenile salmonids (Shaff and Compton 2009) or may not increase juvenile salmonid density or growth (present study), management actions that facilitate escapement of spawning salmon (e.g., harvest restrictions) seem to offer the most straightforward way to benefit salmonid populations in some regions. Bilby et al. (1998) and others have made the point that carcass addition does not replace the ecological functions of spawning salmon.

Addition of carcasses without eggs denies juvenile salmonids an extremely valuable diet item that is available to them during natural spawning (Scheuerell et al. 2007; Moore et al. 2008). Also, carcass addition does not duplicate the role of spawning salmon as agents of physical disturbance. Spawning may provide short-term benefits to juvenile salmonids by enhancing invertebrate drift (Peterson and Foote 2000; Scheuerell et al. 2007) without causing long-term reductions in the biomass of benthic invertebrates (Moore and Schindler 2008; their Figures 4 and 5). The activities of spawning salmon also can increase the export of fine sediments from streams (Moore et al. 2007), with possible benefits for the survival of eggs (Reiser and White 1988) and juvenile salmonids (Suttle et al. 2004; Harvey et al. 2009).

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References

- Allan, J. D., M. S. Wipfli, J. P. Caouette, A. Prussian, and J. Rodgers. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. *Canadian Journal of Fisheries and Aquatic Sciences* 60:309–320.
- Bilby, R. E., B. R. Fransen, P. A. 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.
- Bilby, R. E., B. R. Fransen, J. K. Walter, C. J. Cederholm, and W. J. Scarlett. 2001. Preliminary evaluation of the use of nitrogen stable isotope ratios to establish escapement levels for Pacific salmon. *Fisheries* 26(1):6–14.
- Chaloner, D. T., K. M. Martin, M. S. Wipfli, P. H. Ostrom, and G. A. Lamberti. 2002. Marine carbon and nitrogen in southeastern Alaska stream food webs: evidence from artificial and natural streams. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1257–1265.
- Compton, J. E., C. P. Andersen, D. L. Phillips, J. E. Brooks, M. G. Johnson, M. R. Church, W. E. Hogsett, M. A. Cairns, P. T. Rygielwicz, 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.
- Gresh, T., J. A. 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.
- Harvey, B. C., J. L. White, and R. J. Nakamoto. 2009. The effect of deposited fine sediment on summer survival and growth of rainbow trout in riffles of a small stream. *North American Journal of Fisheries Management* 29:434–440.
- Hawkins, C. P., M. L. Murphy, N. H. Anderson, and M. A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. *Canadian Journal of Fisheries and Aquatic Sciences* 40:1173–1185.
- Helfield, J. M., and R. J. Naiman. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. *Ecology* 82:2403–2409.
- Hicks, B. J., M. S. Wipfli, D. W. Lang, and M. E. Lang. 2005. Marine-derived nitrogen and carbon in freshwater-riparian food webs of the Copper River Delta, south central Alaska. *Oecologia (Heidelberg)* 144:558–569.
- Hill, B. H., F. H. McCormick, B. C. Harvey, S. L. Johnson, M. L. Warren, and C. M. Elonen. 2010. Microbial enzyme activity, nutrient uptake and nutrient limitation in forested streams. *Freshwater Biology* 55:1005–1019.
- Janetski, D. J., D. T. Chaloner, S. D. Tiegs, and G. A. Lamberti. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. *Oecologia (Heidelberg)* 159:583–595.
- 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.
- Johnston, N. T., C. J. Perrin, P. A. Slaney, and B. R. Ward. 1990. Increased juvenile salmonid growth by whole-river fertilization. *Canadian Journal of Fisheries and Aquatic Sciences* 47:862–872.
- Kohler, A. E., A. Rugenski, and D. Taki. 2008. Stream food web response to a salmon carcass analogue addition in two central Idaho, USA streams. *Freshwater Biology* 53:446–460.
- Lang, D. W., G. H. Reeves, J. D. Hall, and M. S. Wipfli. 2006. The influence of fall-spawning coho salmon (*Oncorhynchus kisutch*) on growth and production of juvenile coho salmon rearing in beaver ponds on the Copper River Delta, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 63:917–930.
- Merz, J. E., and P. B. Moyle. 2006. Salmon, wildlife, and wine: marine-derived nutrients in human-dominated ecosystems of central California. *Ecological Applications* 16:999–1009.
- Moore, J. W., and D. E. Schindler. 2008. Biotic disturbance and benthic community dynamics in salmon-bearing streams. *Journal of Animal Ecology* 77:275–284.
- 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 (Washington, D.C.)* 88:1278–1291.
- Moore, J. W., D. E. Schindler, and C. P. Ruff. 2008. Habitat saturation drives thresholds in stream subsidies. *Ecology (Washington, D.C.)* 89:306–312.
- Peterson, D. P., and C. J. Foote. 2000. Disturbance of small-stream habitat by spawning sockeye salmon in Alaska.

- Transactions of the American Fisheries Society 129:924–934.
- Reiser, D. W., and R. G. White. 1988. Effects of two sediment size-classes on survival of steelhead and Chinook salmon eggs. *North American Journal of Fisheries Management* 8:432–437.
- Scheuerell, M. D., P. S. Levin, R. W. Zabel, J. G. Williams, and B. L. Sanderson. 2005. A new perspective on the importance of marine-derived nutrients to threatened stocks of Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences* 62:961–964.
- Scheuerell, M. D., J. W. Moore, D. E. Schindler, and C. J. Harvey. 2007. Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. *Freshwater Biology* 52:1944–1956.
- Shaff, C. D., and J. E. Compton. 2009. Differential incorporation of natural spawners vs. artificially planted salmon carcasses in a stream food web: evidence from ^{15}N of juvenile coho salmon. *Fisheries* 34:62–72.
- Suttle, K. B., M. E. Power, J. M. Levine, and C. McNeely. 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. *Ecological Applications* 14:969–974.
- Tiegs, S. D., D. T. Chaloner, P. Levi, J. Ruegg, J. L. Tank, and G. A. Lamberti. 2008. Timber harvest transforms ecological roles of salmon in southeast Alaska rain forest streams. *Ecological Applications* 18:4–11.
- Williams, K. L., S. W. Griffiths, K. H. Nislow, S. McKelvey, and J. D. Armstrong. 2009. Response of juvenile Atlantic salmon, *Salmo salar*, to the introduction of salmon carcasses in upland streams. *Fisheries Management and Ecology* 16:290–297.
- Wilzbach, M. A., B. C. Harvey, J. L. White, and R. J. Nakamoto. 2005. Effects of riparian canopy opening and salmon carcass addition on the abundance and growth of resident salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 62:58–67.
- 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.