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Pacific salmon effects on stream ecosystems: a quantitative synthesis

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Abstract Pacific salmon (*Oncorhynchus* spp.) disturb sediments and fertilize streams with marine-derived nutrients during their annual spawning runs, leading researchers to classify these fish as ecosystem engineers and providers of resource subsidies. While these processes strongly influence the structure and function of salmon streams, the magnitude of salmon influence varies widely across studies. Here, we use meta-analysis to evaluate potential sources of variability among studies in stream ecosystem responses to salmon. Results obtained from 37 publications that collectively included 79 streams revealed positive, but highly inconsistent, overall effects of salmon on dissolved nutrients, sediment biofilm, macroinvertebrates, resident fish, and isotopic enrichment. Variation in these response variables was commonly influenced by salmon biomass, stream discharge, sediment size, and whether studies used artificial carcass treatments or observed a natural spawning run. Dissolved nutrients were positively related to salmon biomass per unit discharge, and the slope of the relationship for natural runs was five to ten times higher than for carcass additions. Mean effects on ammonium and phosphorus were also greater for natural runs than carcass additions, an effect attributable to excretion by live salmon. In contrast, we observed larger positive effects on benthic macroinvertebrates for carcass additions than for natural runs, likely because disturbance by live salmon was absent. Furthermore, benthic macroinvertebrates and biofilm associated with small sediments (<32 mm) displayed a negative response to salmon while those associated with large sediments (>32 mm) showed a positive response. This comprehensive analysis is the first to quantitatively identify environmental and methodological variables that influence the observed effects of salmon. Identifying sources of variation in salmon–stream interactions is a critical step toward understanding why engineering and subsidy effects vary so dramatically over space and time, and toward developing management strategies that will preserve the ecological integrity of salmon streams.

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Introduction

The ability of organisms to modify habitats and transfer nutrients between ecosystems has been demonstrated across diverse taxa and environments (e.g., Thayer 1979; Flecker 1996). Two theoretical constructs used to describe these interactions are, respectively, ecosystem engineering and resource subsidies. Ecosystem engineers are organisms that modify the physical habitat (Jones et al. 1994), and resource subsidies refer to nutrients and energy transferred by organisms among spatially disparate ecosystems (Polis

et al. 1997, 2004). The effects that such organisms have on ecosystems are highly variable across space and time (Jones et al. 1997; Vanni et al. 2004; but see Marczak et al. 2007), and ecologists have long been faced with the challenge of accounting for variability in biotic–abiotic interactions (Menge and Sutherland 1987; Levin 1992). Here, we assess the roles of Pacific salmon (*Oncorhynchus* spp.) as ecosystem engineers and resource subsidies in stream ecosystems, and explore how environmental and methodological factors modulate observed variability in their ecological influence.

The varying role of Pacific salmon as ecosystem engineers and providers of resource subsidies has been demonstrated repeatedly over the last two decades (e.g., Bilby et al. 1996; Mitchell and Lamberti 2005). A number of studies focus on ecosystem engineering by adult salmon during redd construction (e.g., Moore et al. 2004; Moore 2006), while others emphasize the ability of salmon to subsidize, or enrich, the nutrient budgets of stream ecosystems by transferring nutrients from the marine environment (Gende et al. 2002; Schindler et al. 2003; Willson et al. 2004). Both roles are ecologically important. Disturbance during redd construction can reduce the abundance of benthic organisms (e.g., Minakawa and Gara 1999; Peterson and Foote 2000; Moore et al. 2004), as well as increase sediment export from watersheds (e.g., Hassan et al. 2008). Marine-derived nutrients delivered by salmon, which accrue 99% of their body mass in the ocean, constitute an influx of hundreds of metric tons of nitrogen and phosphorus to nutrient-poor systems (Gresh et al. 2000). Nutrients delivered by salmon can increase the abundance and growth rates of aquatic biota several fold (e.g., Wipfli et al. 2003; Chaloner et al. 2007). While salmon clearly function as ecosystem engineers and resource subsidies in streams, variability among studies in the magnitude and direction of effect toward disturbance or enrichment remains largely unexplained.

The environmental and methodological factors that govern observed salmon effects are largely unknown, although recent evidence suggests that variability in the ecosystem physical and biological context may be important. For example, a number of studies suggest that discharge, water temperature, sediment size, and salmon density can influence the overall salmon effect (Chaloner et al. 2007; Moore et al. 2007; Tiegs et al. 2008). In addition, the influence of methodological factors, such as the artificial addition of salmon carcasses compared with the observation of natural salmon runs, has previously been alluded to (e.g., Wipfli et al. 1998) but never quantified. Thus, despite some advances, the effects of salmon on stream ecosystems remain difficult to predict, as suggested by the contrasting effects that salmon reportedly have on streams.

Inconsistent results among studies have been reconciled to some degree by qualitative reviews (e.g., Willson et al. 1998; Naiman et al. 2002); however, a quantitative literature synthesis of the effects of salmon on streams is lacking. Quantitative data synthesis, or meta-analysis, provides a powerful tool for combining the results of independent studies, allowing broad, statistically supported conclusions to be drawn regarding overall treatment effects, as well as identifying key sources of variability in the magnitude of effects (Arnqvist and Wooster 1995; Gurevitch and Hedges 2001). Meta-analysis offers clear advantages for advancing understanding of salmon–stream interactions because individual studies are generally conducted over a limited geographic area and have low replication and power, while qualitative reviews lack statistical support (cf. Langellotto and Denno 2004). Thus, meta-analysis can move beyond previous qualitative reviews (e.g., Gende et al. 2002; Naiman et al. 2002; Schindler et al. 2003) and site-specific studies (e.g., Chaloner et al. 2007; Tiegs et al. 2008) of salmon effects on streams by quantifying the magnitude of difference in effects for difference response variables and factors while encompassing the entirety of Pacific salmon research.

We conducted a meta-analysis of the relevant salmon literature to evaluate the influence of salmon on different components of stream ecosystems and to quantify the importance of methodological and environmental factors. We define methodological factors as study conditions controlled by investigators, and environmental factors as parameters that define the physical and biological context of the locale in which the study was conducted. For methodological factors, we hypothesized that variation in the salmon treatment effect would be linked to (1) geographic location, (2) type of control (i.e., before-treatment controls, upstream controls, and nearby, non-salmon stream controls), and (3) method of salmon treatment (i.e., carcass additions vs natural salmon runs). For environmental factors, we hypothesized that the salmon effect would be mediated by (4) salmon biomass, (5) stream discharge, (6) salmon species, (7) mean sediment size, (8) water temperature, and (9) channel gradient. Finally, based on these analyses, we identify knowledge gaps that may help direct future research and discuss how our results contribute to the concepts of ecosystem engineering and ecosystem resource subsidies.

Methods

Data collection

Studies measuring the ecological responses of stream ecosystems to spawning salmon were identified using Web of Science (http://apps.isiknowledge.com), Google Scholar (www.scholar.google.com/), and the literature

cited sections of relevant review articles (Willson et al. 1998; Cederholm et al. 1999; Gende et al. 2002; Naiman et al. 2002; Schindler et al. 2003) and books (Groot and Margolis 1991; Stockner 2003; Quinn 2005). The search was intended to be comprehensive, and included literature from peer-reviewed journals, symposia, theses, dissertations, and government reports published between 1970 and June 2007 (with the exception of Tiegs et al. 2008, a draft of which was available to us before publication). The literature search produced 37 relevant studies, which includes 31 peer-reviewed journal articles, five theses, and one report (Supplement 1). These studies were conducted in the United States, Canada, and Japan, and collectively reported data for 79 streams [see electronic supplementary material (ESM) S2].

Three criteria for inclusion of studies were used to minimize the number of confounding ecological and methodological factors. First, the analysis was confined to studies within the native range of Pacific salmon (Fig. 1). Second, only research conducted in streams or rivers was included; studies measuring the ecological effects of salmon on lentic (i.e., lakes or ponds) or riparian ecosystems were excluded since the relatively low number of studies conducted in these habitats limits their usefulness in a formal meta-analysis. Third, the analysis was restricted to studies measuring changes in dissolved nutrient concentrations of stream water, biomass or abundance of aquatic biota, and/or ^{13}C and ^{15}N stable isotopic enrichment, which is considerably higher in salmon tissue than in freshwater-

or terrestrial-derived energy sources (e.g., Chaloner et al. 2002). These response variables were commonly reported and collectively provide a robust measure of stream ecosystem responses to salmon (sensu Bilby et al. 1996; Wipfli et al. 1998). Studies that reported only total nitrogen or total phosphorus in stream water were excluded because different forms (e.g., ammonium and nitrate) of these two elements have very different biogeochemical attributes (Vitousek et al. 1997).

Data extraction

Mean, standard deviations, and sample sizes for control and treatment groups were recorded for each stream in each study (after Gurevitch et al. 1992; Langellotto and Denno 2004). The control was defined as the stream reach or artificial channel lacking salmon in either space or time, and the treatment as the reach or channel having salmon. For time series data, the maximum difference between the control and treatment was used in analyses. Multiple sampling dates (i.e., observations taken on more than one occasion both before and during the salmon treatment) were treated as replicates when no error was reported for single sampling dates. When multiple streams were reported in a study, or when a stream was evaluated for multiple years, these were treated as independent units because of the substantial spatial and temporal variation found in the abiotic and biotic factors that influence salmon effects (e.g., Chaloner et al. 2004, 2007). For example, if a

Fig. 1 Native distribution of Pacific salmon and locations of each stream used in the meta-analysis. *Circled regions* represent the four geographic clusters identified by this analysis: (1) Japan, (2) Southwest/Central Alaska, (3) Southeast Alaska/Northern British Columbia, and (4) Pacific Northwest
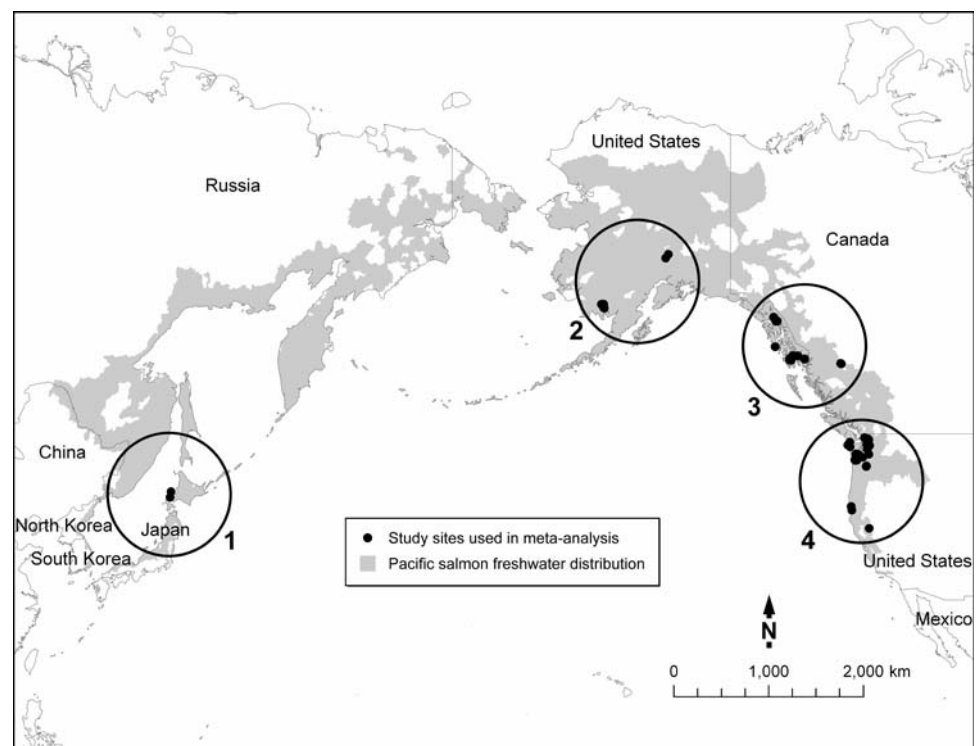
study sampled two streams each for 2 years, we considered these to be four independent units. Each unit, or stream-year, was analyzed only once. To test the validity of this approach we also performed the meta-analysis after pooling temporal replicates from the same stream, which may reduce the degree of non-independence among experimental units.

For each stream, data were extracted for nine independent variables and ten dependent variables according to availability; individual studies generally contained far less than the maximum number of 19 variables. The three independent variables related to methodology were categorical: study location, type of control, and method of salmon addition. Four location categories were defined using cluster analysis (see "Data analysis"). Three types of controls were defined: the stream reach before the presence of salmon, an upstream reach without salmon (i.e., above a barrier to salmon migration), or a nearby stream that did not receive salmon. Method of salmon addition was defined as either a natural salmon run containing live adult salmon (natural treatment), or the artificial addition of salmon carcasses to a stream or artificial channel that did not contain live adult salmon (artificial treatment). Artificial carcass additions were analyzed separately from natural runs to partition the effects attributable solely to nutrient enrichment from those related to the effects of natural salmon runs, which include both nutrient enrichment and substrate disturbance.

The six remaining independent variables were environmental factors: salmon biomass (kg/m^2), stream discharge (m^3/s), salmon species, mean sediment size (mm), mean water temperature (°C), and channel gradient (%). These variables were treated as continuous except for mean sediment size, which was treated as a categorical variable. When not explicitly reported in the study, salmon biomass was calculated using stream area, salmon abundance, and average mass for the dominant salmon species present (from Behnke 2002). When multiple measures of salmon biomass were reported, the peak value was used. Discharge was typically reported as a mean value for the duration of the study (e.g., mean autumn discharge). For regressions involving dissolved nutrient concentrations, salmon biomass was divided by discharge to account for dilution effects. Salmon biomass and salmon biomass per unit discharge were natural log transformed for regression analysis. Salmon species had seven categories: pink (*O. gorbuscha*), sockeye (*O. nerka*), chum (*O. keta*), coho (*O. kisutch*), chinook (*O. tshawytscha*), masu (*O. masou*), and mixed (two or more species present). Salmon species was considered as an independent variable only for studies of natural salmon runs (i.e., equal effects were assumed for artificial carcass treatments using different species). Sediment size was divided into two categories: small pebble–

gravel (<32 mm) and large pebble–cobble (>32 mm). Sediments size was treated as a categorical variable because for pink and sockeye salmon, the two predominant species across studies used in the analysis, spawning occurs primarily in sediments smaller than 32 mm (Kondolf and Wolman 1993), and because sediment size is often reported according to the categorical Wentworth scale (Wentworth 1922). The analysis using sediment size as the independent variable was performed only for studies of natural salmon runs.

The influence of salmon on stream ecosystems was assessed for ten dependent variables: dissolved concentrations of ammonium (NH_4^+), nitrate (NO_3^-), soluble reactive phosphorus (SRP), and organic carbon (DOC), biofilm chlorophyll *a* (chl *a*) and ash-free dry mass (AFDM), benthic macroinvertebrate density or biomass, stream-resident fish growth or condition factor, and $\delta^{13}C$ and $\delta^{15}N$ of biofilm, macroinvertebrates, and stream-resident fish. Since the different metrics (e.g., density, biomass, and condition factor) reported for macroinvertebrates and fish are unlikely to respond identically to salmon, the effect sizes reported in this analysis should be interpreted as a reflection of the general response of these organisms to salmon (see Gurevitch and Hedges 2001).

Data analysis

Effect size was computed using the log response ratio (*L*), which is defined as the natural log (ln) of the treatment mean (X_{trt}) divided by the control mean (X_{ctl}): $L = \ln(X_{trt}/X_{ctl})$ (Hedges et al. 1999). The magnitude and direction of *L* indicate whether the treatment had a positive ($L > 0$) or negative ($L < 0$) effect on the response variable. For example, $L = 1.1$ represents a threefold increase in response to the treatment. The log response ratio was chosen over other metrics of effect size because response ratios more closely reflect ecological significance by measuring the proportional increase (or decrease) induced by the treatment (Hedges et al. 1999). Response ratios, however, are inappropriate for calculating the effect size of stable isotope data because δ values can be positive or negative, i.e., a proportion cannot be calculated. We therefore used Hedge's *d* to measure the effect of salmon on isotopic enrichment (Hedges and Olkin 1985). Hedge's *d* is defined as the difference in mean between the treatment and control groups divided by the pooled standard deviation (s_p): $d = [(X_{trt} - X_{ctl})/s_p] \times J$ (Hedges and Olkin 1985), where *J* is an adjustment for bias due to small sample size ($J = 1 - 3/[4(n_{trt} + n_{ctl} - 2) - 1]$ where n_{trt} is the treatment group sample size and n_{ctl} is the control group sample size).

A two-step approach was used to assess the geographic distribution of the studies included in our analyses. First,

ArcGIS (ArcGIS 9.2, ESRI, Redlands, CA) was used to plot the study site locations using the latitude and longitude of each stream. The Average Nearest Neighbor tool was used to determine if the spatial arrangement of study sites exhibited clustering. Second, K-mean cluster analysis, which assigns data points to clusters by minimizing the distance among data points within clusters, was used to confirm the assignment of each study to its respective cluster (SPSS 11.5, SPSS, Chicago, IL). Salmon distribution meta-data were obtained from the Wild Salmon Center and Ecotrust (Portland, OR, www.stateofthesalmon.org/sosdb.asp).

Cumulative effect sizes were calculated in a hierarchical manner (after Gurevitch et al. 1992; Marczak et al. 2007), with individual effect sizes weighted according to the error and sample size reported in each study (Gurevitch and Hedges 2001). We first determined the effect size for all response variables combined, then for individual response variables, and finally for each category under each categorical independent variable (Gurevitch and Hedges 2001). Bootstrapping (10,000 iterations) was used to estimate 95% confidence intervals (CI) for mean effect sizes. Heterogeneity tests were used to determine the partitioning of variation between (Q_b) and within (Q_w) each category for each independent variable, analogous to one-way ANOVA among- and within-group sum of squares. Significant Q_w values indicate unexplained heterogeneity within response measures of the salmon treatment effect, suggesting that alternative models using different independent variables may better describe the variability in the data. We therefore interpreted significant Q_b accompanied by non-significant Q_w to indicate that the designated categories effectively explained the variation in effect size—i.e., no further breakdown of categories was necessary. For the continuous independent variables, we used weighted least-squares regression to test for relationships with each response variable (Rosenberg et al. 2000). Since the homogeneity statistic Q is used in meta-analysis to describe the partitioning of variance rather than sum of squares, we calculated an r^2 equivalent, which we refer to as Q^2, equal to $Q_{regression}/Q_{total}$ (M.S. Rosenberg, personal communication). We tested for differences in slope between regressions for different categories (e.g., method of carcass addition) using Student's t test (after Zar 1999). All other calculations were performed using the random effects model implemented in MetaWin v2.1.4 (Sinauer Associates, Sunderland, MA).

Results

Cumulative effect sizes

For all response variables combined, except isotopes, salmon had a positive overall effect (cumulative effect size
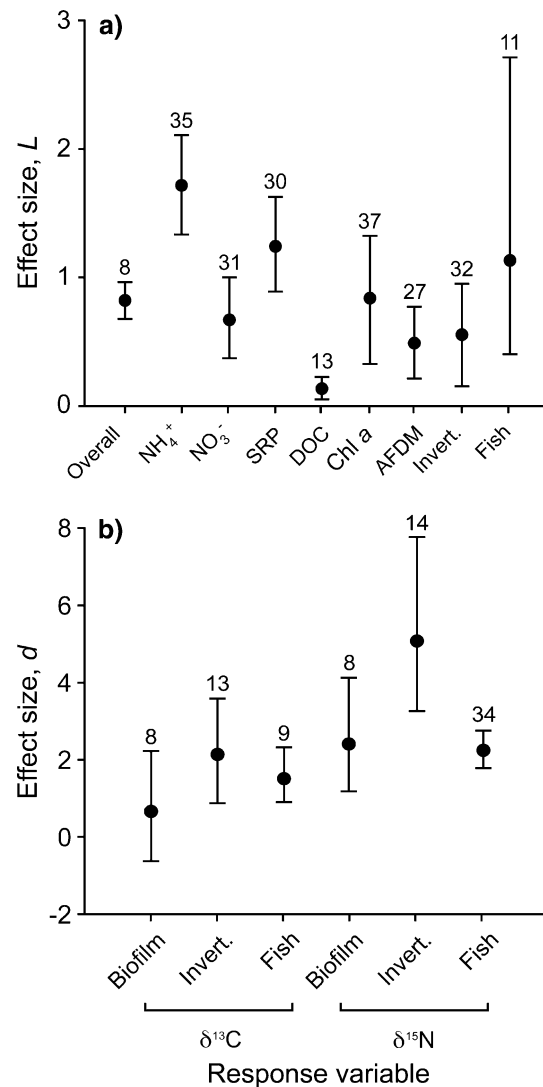

Fig. 2 Effect of salmon on streams (mean effect sizes ± 95% CI) for **a** all eight response variables combined (overall), water chemistry [ammonium (NH_4^+), nitrate (NO_3^-), soluble reactive phosphorus (SRP), and organic carbon (DOC)], benthic organisms [biofilm chlorophyll a (chl a), ash-free dry mass (AFDM), macroinvertebrates], stream-resident fish, and **b** isotopic enrichment of biofilm, macroinvertebrates, and fish with ^{13}C and ^{15}N derived from salmon. Sample sizes (n of streams) are given above each response variable

0.82, 95% CI = 0.68–0.96, Fig. 2). However, the magnitude of the response to spawning salmon differed strongly depending on the response variable measured ($Q_b = 235.6$, $P < 0.001$). Mean cumulative effect sizes for specific response variables differed markedly, ranging from 0.14 for DOC to 1.72 for NH_4^+ (Fig. 2). Cumulative effect sizes for stable isotopes were all significantly greater than zero, with a generally higher accumulation of salmon-derived nitrogen than carbon by stream biota and a higher assimilation of salmon material by macroinvertebrates than by biofilm or fish (Fig. 2).

Mean effect sizes were similar when the analysis was conducted using pooled temporal replicates from the same stream, the one exception being SRP, which had an effect size of 0.74 compared to 1.24 when stream-years were treated independently. This could be an indication that the study by Chaloner et al. (2007), which reports six years of data for one stream, has a disproportionately strong influence on mean effect size for SRP. However, only 10% of the streams included in the analysis were temporally replicated and they did not change the overall trends revealed by the results.

Methodological factors—location, experimental design, and method of carcass addition

Study streams exhibited a nonrandom distribution within the range of Pacific salmon (Z-score = 16.73, $P = 0.01$, Fig. 1). Four clusters of streams were identified based on geographic proximity: Japan, Southwest/Central Alaska (AK), Southeast AK/Northern British Columbia (BC), and Pacific Northwest [including Washington (WA), Oregon (OR), and Northern California (CA)]. Significant heterogeneity (Q_b) among the four clusters was found for all response variables except NO_3^-, DOC, and AFDM (see ESM S3). For NH_4^+, SRP, chl a, and fish, Q_b was accompanied by non-significant Q_w, suggesting that the influence of salmon on these response variables differs among geographic regions.

The magnitude of the salmon effect depended upon the type of control used and whether the salmon treatment was natural or artificial. Control type explained a significant portion of the variation in effect size for NO_3^-, AFDM, and fish (see ESM S3). For NO_3^- and AFDM, non-significant Q_w indicated that effect size was explained by different types of controls. Q_w for fish was significant, indicating that a significant portion of variability in effect size remained unexplained after accounting for different controls. Studies using upstream reaches as the control had an average effect size of −0.02 for NO_3^- (95% CI = −0.09–0.06, $n = 10$), compared with an effect size of 1.11 when samples gathered prior to the salmon treatment were used as the control (95% CI = 0.79–1.48, $n = 23$). For AFDM, the opposite trend was detected—studies with upstream controls had an average effect size of 1.07 (95% CI = 0.75–1.40, $n = 14$) and those with before-treatment controls had an effect size of −0.01 (95% CI = −0.39 to 0.32, $n = 11$).

The two categories of natural and artificial salmon treatment differed in effect size only for macroinvertebrates ($Q_b = 17.7$, $P < 0.001$; $Q_w = 91.8$, $P < 0.001$), with a larger effect detected for artificial salmon treatments (i.e., carcass additions). However, a trend towards larger effect sizes for natural salmon treatments than for artificial salmon treatments was evident for two water chemistry
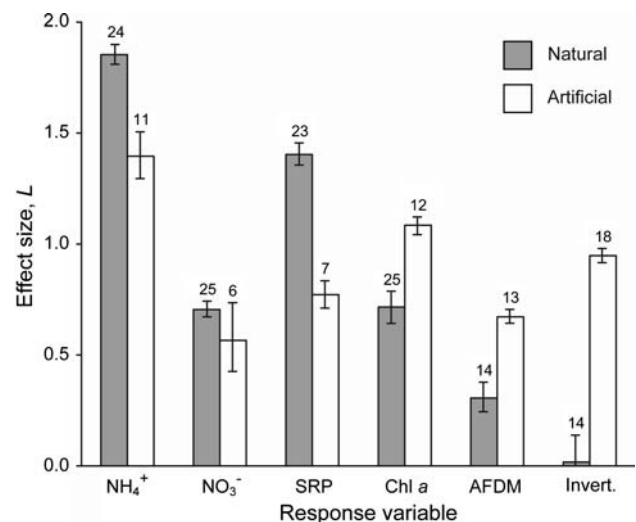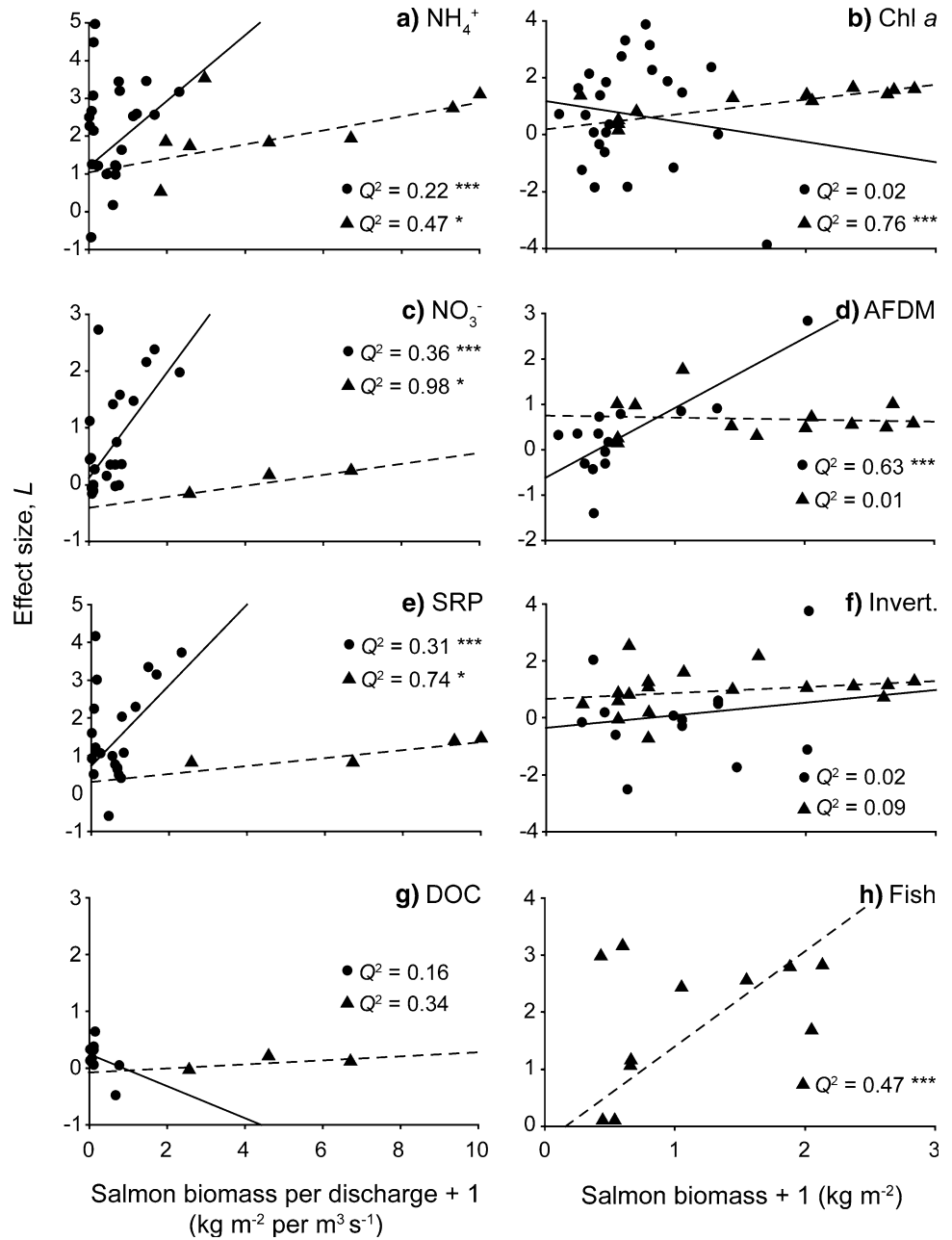

Fig. 3 Comparison of effect sizes (mean ± SE) for natural spawning runs (*Natural*) and carcass addition experiments (*Artificial*) for different response variables. Sample sizes are given above *bars*

variables—NH_4^+ and SRP (Fig. 3). This trend is notable since the average salmon dose (before natural log transformation) was much higher for studies using artificial treatments than for studies using natural treatments—i.e., doses were over 3,200× and 6,600× greater for NH_4^+ and SRP, respectively. If salmon loadings were comparable between artificial and natural treatments, a significant difference would likely have been observed. An opposite trend from water chemistry was observed for the three benthic response variables—chl a, AFDM, and macroinvertebrates, which had lower effect sizes in systems where live salmon were present. Regression slopes between effect size and salmon biomass differed depending on whether the salmon treatment was artificial or natural for five dependent variables: NH_4^+ ($t_{21,6} = 2.06$, $P < 0.05$), NO_3^- ($t_{21,1} = 2.14$, $P < 0.05$), SRP ($t_{20,2} = 3.25$, $P < 0.005$), chl a ($t_{23,10} = 3.81$, $P < 0.001$), and AFDM ($t_{12,11} = 3.61$, $P < 0.002$) (Fig. 4).

Environmental factors—salmon biomass, discharge, salmon species, and sediment size

The observed salmon effect on several stream response variables was driven by salmon biomass, discharge, salmon species, and/or mean sediment size. Salmon biomass per unit discharge was positively related to NH_4^+, NO_3^-, and SRP (Fig. 4). Furthermore, salmon biomass and chl a were positively related for studies where salmon carcasses were artificially added, and between salmon biomass and AFDM and macroinvertebrates during natural spawning runs, although these last two relationships were driven by outliers (Fig. 4). For DOC and isotopes, no relationship was found with salmon biomass. Salmon species accounted for

differences in effect size for NO$_3^-$ ($Q_b = 27.8$, $P < 0.001$; $Q_w = 51.7$, $P < 0.001$), SRP ($Q_b = 21.1$, $P < 0.001$; $Q_w = 41.8$, $P = 0.003$), and macroinvertebrates ($Q_b = 13.9$, $P < 0.001$; $Q_w = 31.0$, $P = 0.001$); however, in each case salmon species was confounded with other factors. For instance, for NO$_3^-$ the difference between sockeye and mixed species was roughly proportional to the difference in average biomass ($L_{sockeye}$:$L_{mixed} = 4.4$, biomass$_{sockeye}$: biomass$_{mixed} = 5.8$), and for SRP biomass was considerably higher for sockeye ($L_{sockeye}$:$L_{mixed} = 2.5$, biomass$_{sockeye}$: biomass$_{mixed} = 6.6$). For macroinvertebrates, mean effect size for chum and sockeye was considerably smaller than for mixed species and corresponded with a marked difference in

mean sediment size [$L_{chum} = -1.55$, $L_{sockeye} = -0.38$, $L_{mixed} = 0.68$; sediment$_{chum} = 32$ mm (reported for only one study), sediment$_{sockeye} = 23$ mm, sediment$_{mixed} = 161$ mm]. Effect sizes for chl *a* ($Q_b = 16.4$, $P < 0.001$; $Q_w = 27.1$, $P = 0.25$) and macroinvertebrates ($Q_b = 14.7$, $P < 0.001$; $Q_w = 33.9$, $P < 0.001$) were typically negative in habitats consisting of small-pebble and gravel sediments and positive in large-pebble and cobble habitats (Fig. 5). The likelihood that the differences in effect size between substrate categories were confounded by salmon biomass was considered to be low due to high within-category variability in biomass. Significance could not be evaluated for AFDM because of inadequate sample size. No relationship
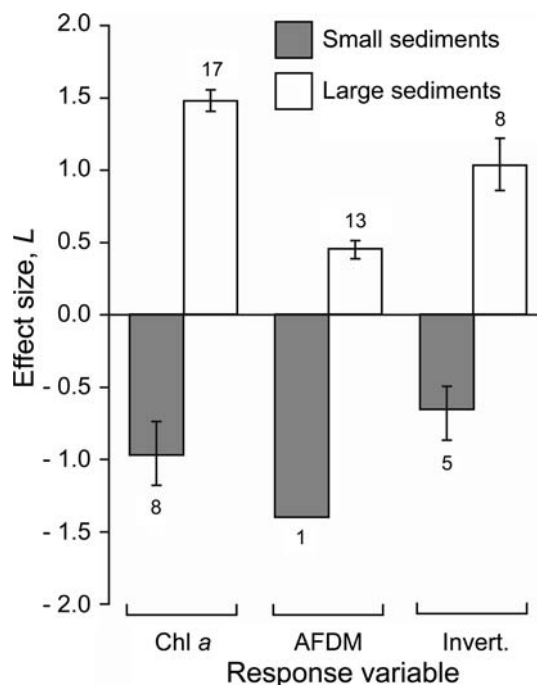
Fig. 5 Comparison of effect sizes (mean $\pm$ SE) measured on small (<32 mm) and large (>32 mm) sediments for chl a ($P < 0.001$), AFDM, and macroinvertebrate ($P < 0.001$) response variables. Sample sizes are given above/below *bars*

was detected between effect size and water temperature or channel gradient.

Discussion

By describing how methodological and environmental factors influence variability in reported salmon effects, our meta-analysis provides a more nuanced, integrative understanding of the complex interactions among salmon, stream food webs, and the physical environment. We found that variation in study design, including method of salmon treatment and type of control, as well as variation in salmon biomass, stream discharge, and sediment size can influence the direction and magnitude of the salmon effect. Given these sources of variability, the mean effect sizes generated by our analysis could be misleading if considered independently of the variability among streams and the context under which studies are conducted. For example, mean effect sizes may be biased towards enrichment effects (i.e., positive effects) because a large number of studies were conducted under conditions where disturbance (i.e., negative effects) is less likely, such as with large sediments or after carcass additions. Here we attempt to tease apart the sources of variation in salmon effects on different streams in different years, and discuss the implications of this analysis for salmon research and aquatic ecology.

Methodology of salmon experiments—when are observations realistic?

Since scientific knowledge reflects observations made in conjunction with experimentation, variability attributed to different methodologies has important epistemological implications for ecology. Experimental design can influence the outcome of ecological experiments (Diamond 1986; Lamberti and Steinman 1993; Osenberg et al. 1999), and researchers have even alluded to this issue in salmon studies (e.g., Wipfli et al. 1998). However, previous discussions of salmon study design have failed to consider the magnitude of difference among different methodologies. For example, results may differ when using only a temporal control (i.e., before salmon run observations) rather than both temporal and spatial (i.e., observations upstream of a barrier to salmon) controls. Also, more nutrients may be released by live salmon than by an equal mass of carcasses that have been artificially added to a stream.

We found that two methodological factors influence the outcome of salmon studies—type of control and method of salmon treatment (i.e., live fish vs carcasses). Several study designs have been used in salmon stream research, some with a single type of control and others with a combination of controls (e.g., Peterson and Foote 2000; Mitchell and Lamberti 2005). The discrepancy in effect size that we found for NO_3^- and AFDM among control types suggests that investigators should use a combination of spatial (e.g., upstream of a barrier) and temporal (e.g., before the salmon run) controls to reveal confounding effects that may occur over space and time (e.g., Chaloner et al. 2007). For instance, NO_3^- concentrations can increase in autumn independent of the salmon run, and AFDM appears to be lower upstream of barriers and often does not change within a reach upon the arrival of salmon. Thus, without spatial and temporal controls (e.g., upstream of a barrier to salmon), apparent treatment effects may be incorrectly attributed to salmon. While positive results from experimental additions of salmon material (e.g., Wipfli et al. 1999; Wilzbach et al. 2005, and unpublished data) lead us to doubt that salmon indeed have no effect on NO_3^- and AFDM, our results suggest that effects may differ substantially depending on the use of spatial or temporal controls (e.g., Chaloner et al. 2007). Accounting for both temporal and spatial variation inherent in the system increases confidence in attributing apparent treatment effects to the presence of salmon.

The method of salmon treatment was also an influential component of study design. One factor potentially contributing to the disparity among studies is that the majority of carcass addition experiments used larger amounts of salmon material than reported in studies of natural salmon runs. Some artificial salmon treatments, for instance, had dosages (biomass per unit discharge) over 1,000 times

those reported in natural systems. This difference in dosage is driven by studies involving carcass additions to artificial stream channels, which have very low flows relative to natural streams and thus very high concentrations of salmon material per unit discharge. Interestingly, effect sizes for carcass addition studies were never substantially greater than for natural salmon runs, suggesting an upper limit to the rate of nutrient mineralization and subsequent uptake and incorporation by aquatic organisms (cf. Wipfli et al. 1999, 2003; Bilby et al. 2001; Chaloner et al. 2002), as well as a higher potency for live salmon than for carcasses.

Artificial addition of carcasses to natural streams and artificial channels is a common approach for evaluating enrichment effects by salmon (e.g., Wipfli et al. 1998, 2003). However, we found that carcasses do not accurately mimic natural salmon runs. For example, behaviors associated with live salmon, such as waste excretion and substrate disturbance, are absent when carcasses are added to a stream (Lackey 2003; Moore et al. 2007). On average, we found that live salmon increase NH_4^+ and SRP concentrations by 50 and 90% more, respectively, than carcasses alone, presumably due to the direct excretion of nitrogen by live fish (Vanni 2002). By contrast, carcass additions increase chl a, AFDM, and macroinvertebrate abundance by 50, 60, and 200% more, respectively, than natural salmon runs, presumably due to the lack of spawner disturbance. Thus, the outcome of salmon studies appears to vary depending on whether the salmon treatment was with carcasses or live fish. The underlying cause for the differences in effect between carcasses and live fish, however, is driven by the interaction of live salmon with their environment.

Biological and physical context drives the magnitude of the salmon effect

Our analysis offers a quantitative explanation for how nutrient dynamics are influenced by salmon abundance and stream discharge. Live salmon and carcasses positively influence NH_4^+ and phosphorus concentrations in the water column, and, with the exception of DOC, the slopes of each relationship are significantly greater for studies of live salmon runs. Live salmon have 5×, 10×, and 10× greater influence on NH_4^+, NO_3^-, and SRP, respectively, than carcasses alone, presumably due to excretion and mineralization by live fish (Vanni 2002). Interestingly, relationships were not detected between effect size and biomass alone, but when effect sizes were plotted against biomass per unit discharge significant relationships emerged. Thus, effects of salmon spawners on dissolved nutrients decrease or increase with a respective rise or fall in discharge.

Variability in effect size for different salmon species was difficult to assess because of confounding factors, such as salmon biomass and sediment size. Mean effect size and

biomass for NO_3^- and SRP were both higher for sockeye than for mixed species, but since no prior research has indicated that these species differ in nutrient excretion, differences in biomass seems a more likely explanation for these contrasting effects. Similarly, mean effect size and sediment size for macroinvertebrates were both higher for mixed species than for sockeye, suggesting that differences in effect may be attributable to sediment size rather than salmon species. Many of the studies included in our analysis were dominated by runs of either pink or sockeye salmon. Since pink and sockeye are of similar size and spawn in relatively high densities (Quinn 2005), it is not surprising that no convincing differences in effect were detected among salmon species. By contrast, runs dominated by generally larger species, such as chinook salmon, that spawn at much lower densities and prefer larger sediments for spawning (Kondolf and Wolman 1993) may have less of a nutrient influence and more of a disturbance influence than smaller salmon species.

The response of benthic organisms to spawning salmon appears to be driven largely by substrate composition rather than salmon biomass. Our results support the contention of Tiegs et al. (2008) that sediment size is a significant determinant of ecological responses in salmon streams. The preference of salmon for gravel to pebble-sized sediments for spawning is a likely explanation for why those sediments showed the strongest disturbance effects. Since sediment size preference varies among salmon species (Kondolf and Wolman 1993), the size range of sediments experiencing disturbance effects will also vary by salmon species. In our analysis, small sediments (<32 mm) likely exhibited disturbance effects because the two predominant salmon species, pink and sockeye, are relatively small-sized and prefer to spawn in small sediments. In contrast, larger-sized sediments, such as large pebbles or cobbles, are disturbed in streams with runs dominated by larger species such as chum and chinook salmon (Kondolf and Wolman 1993). Thus, although we were unable to satisfactorily assess the influence of salmon species due to confounding factors, existing evidence suggests that disturbance effects on benthic organisms likely vary with salmon species.

Our meta-analysis allows for the effects of salmon on benthic organisms living in different sized sediments to be quantified and contrasted. In stream reaches dominated by small sediments, salmon decreased biofilm chl a and macroinvertebrate levels by 65 and 45%, respectively, whereas in habitats containing large sediments chl a and macroinvertebrates increased by 425 and 275%, respectively. While large particles remain relatively undisturbed, small gravels are actively shifted by salmon during migration and nest construction, causing scour and reducing organism abundance. Thus, activities that modify

substrate composition, such as flow regulation or timber harvest (Poff et al. 1997; Tiegs et al. 2008), could indirectly alter the response of benthic communities to spawning salmon.

Similar to dissolved nutrient concentrations, the growth and condition factor of stream-resident fish appear to be driven by the amount of salmon material. Unfortunately, the results of our analysis for resident fish are limited to carcass additions due to the lack of research on the response of resident fish to salmon during natural spawning runs; data from the few studies that examined fish responses to natural spawning runs did not meet our criteria for inclusion in the analysis (e.g., Bilby et al. 1996; Eastman 1996; Peterson and Foote 2000; Scheuerell et al. 2007). Regarding the effects of carcass additions, however, the positive response of resident fish is likely due to direct ingestion of salmon material and possibly through increased invertebrate production induced by salmon, although this remains uncertain (Gende et al. 2002). We also speculate that during natural spawning runs, resident fish may have a greater opportunity to capture prey due to macroinvertebrate dislodgement by spawning salmon (cf. Bilby et al. 1998; Peterson and Foote 2000). However, these conceptual explanations for how resident fish respond to salmon remain largely unverified by data, and constitute one of several critical knowledge gaps in salmon research.

Future directions and challenges in salmon research

Our literature search and synthesis revealed several specific research topics that, if addressed, will improve our understanding of the ecological effects of salmon and the relative role of physical and biological components of streams. First, research regarding the response of stream-resident fish to natural salmon runs is lacking, which is significant given that resident fish are often considered a benefactor of salmon-derived nutrients (Wipfli et al. 2003) and are a major focus of federal and state management agencies. Second, we found no relationship between salmon biomass and response variables at low doses of salmon material (0.1–1.0 kg/m^2), suggesting some uncertainty about the ecological influence of small salmon runs. Conversely, isotopic enrichment is positively related to salmon biomass at low doses (Bilby et al. 2001), suggesting that additional research may help to clarify the relationship between low levels of salmon biomass and the stream response variables considered here. The notions of a downward salmon 'spiral' when runs decline (i.e., enrichment is insufficient to sustain juveniles) could be tested under these conditions. Third, potentially important physical features of streams, namely large wood and canopy cover, have rarely been quantified in salmon studies (but see Ambrose et al. 2004). Large wood should enhance salmon carcass retention in streams, thereby increasing local nutrient provision from carcasses (Cederholm et al. 1989; Minakawa and Gara 2005). Alternatively, canopy cover could dampen the effects of nutrient enrichment by salmon if light limits algal growth (Wilzbach et al. 2005). Fourth, research has been conducted in less than one-third of the 66 ecoregions spanned by Pacific salmon (Augerot 2005), leaving ample opportunity to further investigate the effects of salmon on streams under different environmental contexts. Understudied regions include vast areas of BC, northwestern AK, and eastern Russia. Fifth, impacts on lotic systems where Pacific salmon have been introduced (e.g., Laurentian Great Lakes, South America) remain largely unexplored, despite the high potential for impacts by these non-native ecosystem engineers on native communities (Crawford 2001; Crooks 2002). Sixth, the influence of salmon material on basic ecosystem functions, such as organic matter decomposition, nutrient uptake rates, and stream metabolism, remains largely unstudied (Naiman et al. 2002). Finally, the vast majority of salmon studies considered just one or two streams and spanned only 1 or 2 years. Spatially and temporally robust studies of salmon effects in streams are needed because changes in certain environmental variables, such as nutrient loading, climate change, and land use change, may take place at the scale of decades or even centuries (Stockner and MacIsaac 1996; Krümmel et al. 2005).

Ecological implications: salmon as ecosystem engineers and resource subsidies

Our analysis provides quantitative evidence that Pacific salmon simultaneously function as ecosystem engineers and ecosystem resource subsidies in the streams in which they spawn. The salmon effects on streams revealed by our analysis are similar in magnitude to effects previously reported for subsidy inputs from terrestrial habitats to streams and from aquatic habitats to islands and riparian forests (Marczak et al. 2007). Salmon research, however, has generally been biased against the detection of disturbance effects (Moore et al. 2004), and methodological and environmental factors can play important roles in determining variability in the overall effect. Methodological and environmental factors likewise may bias the reporting of subsidy effects in other ecosystems, especially where organisms also disturb habitats. For example, nesting activities of seabird colonies and alteration of plant communities by large flocks of geese could be considered engineering effects, although these organisms have typically been viewed chiefly as resource subsidies (Polis and Hurd 1995; Kitchell et al. 1999). Similarly, some well-known ecosystem engineers, such as beaver and prairie dogs (Naiman et al. 1988; Whicker and Detling 1988; Wright and Jones 2004; Alba-Lynn and

Detling 2008), may simultaneously transport resources, such as vegetation, from one ecosystem to another. If Pacific salmon are any indicator, the observed effects of these and other ecosystem engineers and resource subsidies on their surroundings are likely to vary with environmental conditions and study design. Salmon exemplify how observations of biotic–abiotic interactions are influenced by environmental and methodological context, and such influences must be understood to properly manage a species and inspire effective policy.

The roles that salmon play in regulating natural ecosystem function have significant management implications. Salmon provide a critical link between marine and freshwater ecosystems (Willson et al. 2004), and restoring this link is a key objective for restoration ecologists (Naiman et al. 2002). Salmon declines alter natural ecosystem function by limiting the availability of dissolved nutrients (Lackey 2003), sometimes referred to as 'cultural oligotrophication' (Stockner et al. 2000). To reverse the consequences of diminished nutrient, salmon carcasses and carcass analogs designed to mimic salmon resource inputs have been added to streams (e.g., Compton et al. 2006; Kohler et al. 2008). However, our analyses suggest that artificial carcass additions do not mimic natural salmon runs for two reasons. First, carcasses generally provide less NH_4^+ and SRP per unit mass than live fish, indicating that to simulate the enrichment effects of a natural salmon run more analog mass should be added than existed in the former salmon run. Second, carcass and analog additions lack disturbance effects, which dislodge benthic macroinvertebrates and potentially provide food for stream-resident fish. Thus, artificial carcass and analog additions can restore some degree of nutrient enrichment, but fall short of restoring the patterns of disturbance, nutrient enrichment, and behavioral interactions provided by natural salmon runs.

Conclusion

Our meta-analysis revealed that the physical stream environment, including discharge and sediment size, is a key determinant of how salmon influence stream ecosystems. In addition, the outcome of salmon stream research appears to vary with the response variable measured and whether the study was observational (i.e., a natural salmon run) or manipulative (i.e., carcass addition). We propose a conceptual model for salmon research in which the physical environment and experimental methodology together influence the context of a given study (Fig. 6). The context determines the observed effects of salmon, which can range along a gradient from enrichment to disturbance. Factors such as climate, land use (e.g., timber harvest), hydrology, and commercial fishing (Groot and Margolis 1991;
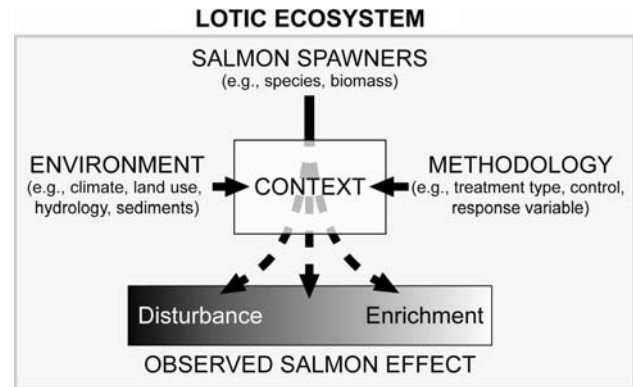

Fig. 6 Conceptual diagram depicting how the observed salmon effect on benthic communities in river systems is influenced by the context of individual studies

Oswood 1997; Finney et al. 2000; Tiegs et al. 2008) may indirectly influence the effect of salmon on streams by altering the context. Our model fosters a more complete understanding of the ecological role of salmon in streams and provides a framework for improving our understanding of the interaction of ecosystem engineers and resource subsidies with their surrounding environment.

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