BIOTIC CONTROL OF STREAM FLUXES: SPAWNING SALMON DRIVE NUTRIENT AND MATTER EXPORT

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Abstract. Organisms can control movements of nutrients and matter by physically modifying habitat. We examined how an ecosystem engineer, sockeye salmon (*Oncorhynchus nerka*), influences seasonal fluxes of sediments, nitrogen (N), and phosphorus (P) in streams of southwestern Alaska. The purpose of this study was to investigate whether salmon act as net importers or net exporters of matter and nutrients from streams and how these roles change as a function of salmon population density. We measured discharge and concentrations of suspended sediments and total N and P every 7–14 days for up to four summers in 10 streams spanning a gradient in salmon densities. We statistically allocated whole-season fluxes to salmon activities, such as excretion and bioturbation, and to export by hydrologic discharge. In addition, we used counts of spawning salmon to estimate nutrient and matter imports by salmon to streams. Large seasonal pulses of suspended sediments, P, and N were associated with salmon spawning activities, often increasing export an order of magnitude higher than during pre-salmon levels. Years and streams with more salmon had significantly higher levels of export of sediments and nutrients. In addition, years with higher precipitation had higher background export of P and N. Salmon exported an average of the equivalent of 189%, 60%, and 55% of total matter, P, and N that salmon imported in their bodies. The relative magnitude of export varied; salmon exported more than their bodies imported in 80%, 20%, and 16% across all streams and years for sediments, P, and N, respectively. A bioassay experiment indicated that the P exported by salmon is directly available for use by primary producers in the downstream lake. These results demonstrate that salmon not only move nutrients upstream on large spatial scales via their migration from the ocean and subsequent death, but also redistribute matter and nutrients on finer spatial scales through their spawning activities.

Key words: Alaska, USA; bioturbation; disturbance; ecosystem engineer; excretion; marine-derived nutrients; mass balance; Oncorhynchus nerka; *redd; sockeye salmon; subsidy.*

INTRODUCTION

Availability of limiting nutrients and energy are controlled by cycling both within and across ecosystem boundaries (Vanni 2002, Polis et al. 2004). Fluxes of matter and nutrients across ecosystems are controlled by abiotic and biotic vectors (Polis et al. 1997, 2004). In streams, for example, water physically transports organic and inorganic particles and nutrients from upstream to downstream habitats (Hynes 1975, Vannote et al. 1980, Wipfli and Gregovich 2002, Stanford et al. 2005). Not surprisingly, hydrology often dominates downstream transport of phosphorus (P) (e.g., Meyers

and Likens 1979), nitrogen (N) (e.g., Bernhardt et al. 2005), and detritus (e.g., Fisher and Likens 1973).

Animals influence nutrient and matter movement in streams via several mechanisms. Consumers transport nutrients by ingesting them in one habitat and excreting, egesting, or dying in a different habitat (Polis et al. 1997, 2004, Vanni 2002). For example, fish migrations move nutrients upstream against the flow of water. Excretion of dissolved nutrients by fish and benthic invertebrates is often a large component of nutrient budgets (e.g., Hall et al. 2003, Hood et al. 2005). In addition, organisms influence the local transport of materials in streams through habitat modification (Moore 2006). For example, beaver dams increase sediment retention (Naiman et al. 1986), and activities of many animals reduce local sediment and carbon accumulation, such as benthic fishes (e.g., Power 1990, Flecker 1996, Taylor et al. 2006), shrimps (e.g., Pringle et al. 1999, Greathouse et al. 2006), and nest-digging salmon (e.g., Kondolf et al. 1993, Montgomery et al. 1996, Moore et al. 2004). While these ecosystem engineers have local impacts, it is poorly

understood how ecosystem engineers control nutrient and sediment fluxes across ecosystem boundaries.

One of the most remarkable examples of biotic control of ecosystem fluxes is that of Pacific salmon (*Oncorhynchus* spp.). Salmon influence ecosystem fluxes via two main mechanisms. First, and most widely recognized, Pacific salmon can transport vast quantities of nutrients and matter from oceans to freshwaters with migrations upstream, spawning, and death following the accumulation of >99% of their biomass in the ocean (Gende et al. 2002, Naiman et al. 2002, Schindler et al. 2003). As salmon spawn and die, they excrete dissolved nutrients (e.g., Mitchell and Lamberti 2005). Second, bioturbation by nest-digging salmon may influence fluxes of matter and nutrients. Salmon often spawn at high densities and dig large nests (Moore 2006). Disturbance from this nest digging suspends nutrient-rich sediments in the water column allowing subsequent downstream transport by water flow (Gottesfeld et al. 2004, Moore 2006). Therefore, salmon replenish upstream habitats by transporting materials in their bodies, but simultaneously redistribute nutrients and sediments downstream by disturbing stream beds. The nutrients and sediments stirred up or excreted by salmon will likely be transported to depositional reaches downstream or out of the stream ecosystem to downstream lakes or estuaries.

It remains unknown whether salmon act as net importers or net exporters of matter and nutrients from streams and how these roles change as a function of salmon population density. We examined the manner in which sockeye salmon (*Oncorhynchus nerka*) simultaneously modify fluxes of nutrients and matter into and out of Alaskan streams via (1) swimming upstream and dying and (2) disturbing benthic habitats during spawning. Through monitoring inputs and outputs of suspended sediments and nutrients of 10 streams with natural variation in salmon densities across four years, we show that spawning salmon drive export of nutrients and sediments. This illustrates how an ecosystem engineer can control ecosystem-scale fluxes of nutrients and matter. Our findings have specific application to understanding the role of Pacific salmon as dominant species in freshwater ecosystems and the subsequent application to restoration of streams with endangered salmon populations (Ruckelshaus et al. 2002).

METHODS AND MATERIALS

Study area and field methods

We examined the impacts of sockeye salmon on ecosystem fluxes of streams located within the Wood River drainage of southwestern Alaska, USA. This 300 000-ha river system is an important spawning and nursery system for anadromous sockeye in the Bristol Bay region. Approximately 1.0×10^6 sockeye spawn in the system each year (Alaska Department of Fish and Game, Division of Commercial Fisheries, *unpublished data*). Although timing varies among sites, sockeye spawning in the system starts in mid-July, peaks in August, and is nearly complete in September. Sockeye represent >99% of the spawning salmon in the study streams.

Seasonal fluxes.—We quantified the manner in which salmon altered seasonal movements of nutrients and matter by measuring ecosystem fluxes for up to four summers on 10 streams for a total of 30 stream/year combinations (Appendix A). Streams spanned a natural gradient in salmon densities (0–0.54 salmon/m²). We monitored fluxes from June to September in 2002–2005. This seasonal period spanned the bulk of the ice-free period and included times before, during, and after salmon spawning.

At each collection period (roughly every 7–14 days) and in each stream, we sampled duplicate suspended sediment concentration at stream outflows (immediately upstream of where the stream flows into lake) by filtering a known volume (up to 2 L) of subsurface stream water onto pre-weighed and pre-ashed 47 mm GF/F silica filters (pore size = 0.7 μm). Filters were frozen and transported to the laboratory where they were dried to a constant mass at 50°C and weighed. Concentration of suspended sediment was calculated as the final mass of filter and material, minus initial mass of individually weighed filter, divided by volume of water filtered. To obtain background suspended sediment concentrations, we collected stream water at the upper limits of the salmon spawning area for a subset of these sampling periods and processed them as described above.

We measured concentrations of total phosphorus (TP) and total nitrogen (TN) on the same dates. Unfiltered water was collected in acid-washed polyethylene bottles, frozen, and transported to the Marine Chemistry Laboratory at the School of Oceanography, University of Washington. Nutrient samples were digested by the persulfate method and analyzed colorimetrically on a Technicon model AAII auto-analyzer (duplicate samples; Bran Luebbe, Tarrytown, New York, USA).

Stream discharge was estimated using a combination of flow profiling using a flow meter (Hauer and Lamberti 1998) and stream-specific relationships between stream heights of established depth gauges and measured discharge. Discharge was estimated every 6.6 ± 4.8 d (mean ± SD). Our adaptive sampling strategy was driven by higher resolution sampling bracketing storms and the entry of salmon to streams to capture variation in fluxes. During each sampling period we calculated adult salmon densities, easily enumerated in our small streams (Appendix A). Salmon counts were converted to densities by using the known wetted area of available stream habitat.

Bioassay.—We used a bioassay experiment in a representative stream, Pick Creek, to assess the bioavailability of exported P for primary producers in downstream lakes. Previous studies have recognized that

in addition to soluble reactive P, variable amounts of particulate P are available for uptake (Ekholm and Drogerus 2003, Ellison and Brett 2006). We compared the capacity of TP in stream water to enhance lake phytoplankton growth compared to known amendments of orthophosphate, which is considered completely available for use by lake primary producers (Kitchell et al. 1999). This experiment was performed with stream water collected on 14 July, 25 July, and 20 August 2005, corresponding to before, during, and after salmon spawning. We added known concentrations of orthophosphate (0.1, 0.05, 0.001, 0.005 mg P/L final concentration) or stream water (50, 100, 250, 500 mL) to 1-L plastic cubitainers ($n = 3$ per treatment). We then filled these containers with lake water that had been filtered through a 120-μm filter to remove zooplankton grazers. We added N to all treatments to prevent N limitation by the primary producers (1.6 mg N/L final concentration), which corresponded to the Redfield ratio of N:P for the highest P treatment. Thus, for each experimental period, there were treatments of stock orthophosphate across a range of P concentrations, as well as stream phophorus across a range of P, and a control with no added P. After an incubation of 7 days at the thermocline of the lake (9 m depth), we filtered 900 mL of each container onto GF/C filters that were frozen and transported to the University of Washington for chlorophyll *a* analysis using fluorometry following solubilization in methanol (Marker et al. 1980). We calculated the starting concentrations of P and algae for each treatment based on the measured P and algal content of stream and lake water prior to incubation. We determined growth of algae in each treatment by subtracting "initial" from "final" pigment concentration.

Precipitation.—The relationship between total summer precipitation and cumulative summer export of nutrients and sediments was investigated using publicly available data from the National Climatic Data Center. For each year of our study we calculated total precipitation from May to September from the nearest weather station, in King Salmon, Alaska (~130 km distant).

Statistical analysis

SYSTAT 11.0 (Systat Software, San Jose, California, USA) was used for all analyses. We averaged duplicate samples of nutrients and sediment concentration. The coefficient of variation (CV) among replicates across streams was $28.3 \pm 18.4\%$, $7.67 \pm 4.08\%$, and $6.76 \pm 3.88\%$ for suspended sediments, TP, and TN, respectively. Due to the lower sampling intensity at upstream sites, we averaged concentrations for periods that corresponded to the period before and during salmon spawning for each stream.

Seasonal fluxes.—We investigated how stream discharge and salmon densities influenced the concentrations of TN, TP, and suspended sediments on a given date. We ran multiple regressions on TN, TP, and

suspended sediment for each stream, investigating the manner in which concentrations were influenced by discharge and salmon density.

Nutrient bioassay.—The relationship between P concentration and algal growth was examined for each time period and treatment (stock P vs. stream P) by fitting the Michaelis-Menten saturating relationship:

$$\text{Growth} = k \times \frac{\text{TP} - b}{\text{TP} - b + \left(\dfrac{k}{m}\right)}$$

where TP is total phosphorus (in micrograms per liter), growth is total algal growth (the sum of chlorophyll *a* and degradation pigments in micrograms per liter), *m* is the initial slope, *k* is the maximum growth, and *b* is the intercept to allow the lines to not be forced through the origin. Nonlinear function fitting was used to obtain confidence intervals around parameters.

Integrating fluxes across the entire season.—We estimated the fluxes of nutrients and sediments over the entire sampling season for each stream-year. In addition, we estimated how much of this export was attributable to salmon vs. hydrology. These estimations were performed using a combination of regression analyses and interpolation. For each stream, we developed general linear models with concentrations of nutrients and suspended sediments as the response variable and year and discharge as predictor variables, using only dates on which salmon were not present. Based on concentrations of nutrients and suspended sediments from non-salmon dates, we determined the statistical relationships between discharge and concentrations of nutrients and sediments. We used those parameters to estimate background concentrations of nutrients and matter for dates when salmon were present, in the theoretical absence of salmon. These concentrations were multiplied by flow on those days to estimate background export. Using linear interpolation, we estimated season-long total export (using measured data), discharge or background export (using estimated concentrations), and salmon-related export (difference between observed and estimated) of nutrients and suspended sediments. These flux estimates were normalized by stream area.

We also estimated how much matter and nutrients are transported into streams in salmon bodies. We used the annual spawning salmon counts of the University of Washington Alaska Salmon Program to estimate total sockeye returns. We assumed that the number of live plus dead salmon counted at the peak of spawning activity represented 75% of the total number of returning salmon (Quinn et al. 2003). Based on the numbers of returning fish, we estimated TN and TP content of carcasses using nutrient content data following Moore and Schindler (2004), mean adult sockeye mass of 1.8 kg, and an average 25% dry mass (Hendry and Berg 1999).
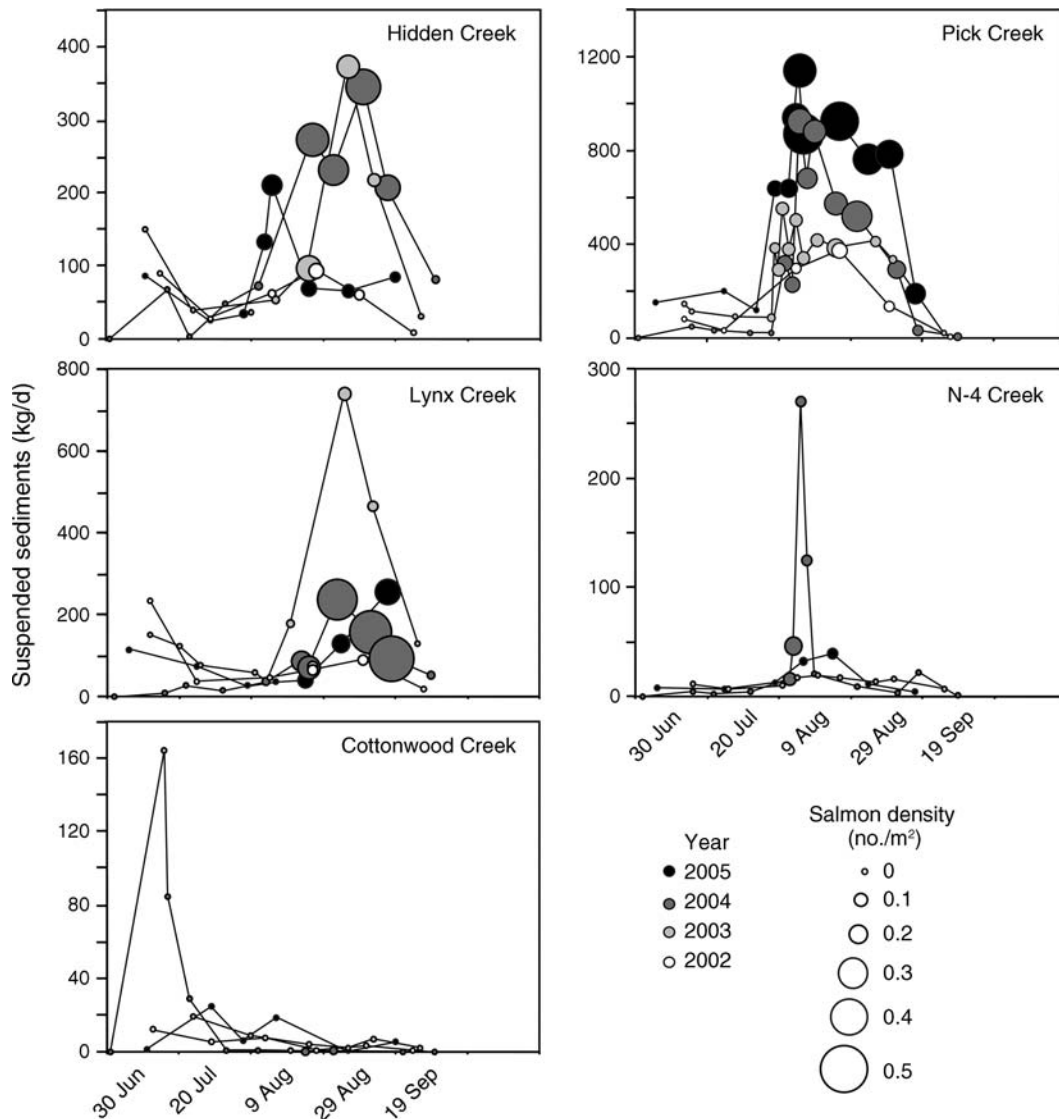
FIG. 1. Seasonal flux of suspended sediments (dry mass) from streams across all years. Shown are streams with three or more years of data. Circle size is proportional to the density of live sockeye salmon in the stream on the day of that sampling. The largest circles correspond to densities of 0.5 salmon/m^2, while the smallest circles represent 0.0 salmon/m^2. Symbol fill corresponds to year. Notice that the *y*-axes have different scales. We examined the impacts of sockeye salmon on ecosystem fluxes of streams located within the Wood River drainage of southwestern Alaska, USA.

Salmon density, stream, and precipitation were investigated as factors that could be controlling season-long fluxes of nutrients and sediments with a general linear model (GLM). If factors were significant, we ran post hoc regressions between the variables.

<center>RESULTS</center>

Background

Our sampling captured a broad range of salmon densities, ranging from 0 to 0.54 live salmon/m^2 (Appendix A). This range was obtained both among streams and among years for a given stream. For example, over the four years of this study, Pick Creek had a mean maximum live density of 0.38 fish/m^2,

representing a mean return of 6893 sockeye, while Cottonwood Creek had no or few fish, a mean maximum density of only 0.0029 fish/m^2, representing a mean return of only 4 sockeye per year. Although different streams had consistently higher or lower returns, there was substantial variability across years for a given stream. In general, flows were higher in the spring and decreased over the season. However, several years had storms that caused substantial late-season increases in discharge.

Seasonal export

Suspended sediments.—Sediment export from streams consistently and substantially increased as salmon

TABLE 1. Coefficients of determination (r^2) from linear regressions between flow (m^3/s) and salmon density (salmon/m^2) and concentrations (µg/L) of different materials in water from different streams at a given date.

Stream	Suspended sediments		Total phosphorus		Total nitrogen	
	Salmon	Flow	Salmon	Flow	Salmon	Flow
Bear	**0.554***(+)**	0.105	**0.479***(+)**	0.098	**0.286**(+)**	0.000
Cottonwood	0.000	0.078	0.000	**0.206**(−)**	0.000	0.006
Elva	0.179	0.000	0.039	0.000	0.000	0.000
Hansen	0.112	0.000	0.068	0.041	0.000	0.076
Hidden	**0.784***(+)**	0.009	**0.426***(+)**	0.003	**0.225**(+)**	0.000
Lynx	**0.277***(+)**	0.000	**0.524***(+)**	0.010	**0.120*(+)**	0.000
N-4	**0.112*(+)**	0.000	**0.097*(+)**	0.000	**0.124*(+)**	0.000
Pick	**0.653***(+)**	**0.107*(−)**	**0.669***(+)**	0.014	**0.316***(+)**	0.000
Whitefish	**0.815***(+)**	**0.203*(−)**	**0.673***(+)**	0.029	**0.311**(+)**	0.003
Yako	**0.628***(+)**	**0.248*(−)**	**0.290**(+)**	**0.285*(−)**	**0.328**(+)**	0.084

Notes: Significant relationships are indicated by boldface type. Direction of significant relationships is shown in parentheses. We examined the impacts of sockeye salmon on ecosystem fluxes of streams located within the Wood River drainage of southwestern Alaska, USA.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ for regression.

entered streams (Fig. 1). For example, in Pick Creek 2004, before salmon entered the stream, export averaged 24.7 kg/d. When salmon entered, export of dry matter increased to 318.8 kg/d within four days. As more salmon entered the stream to spawn, export increased and eventually peaked at 925.1 kg/d. This represents a 37-fold increase in export over mean spring pre-salmon export (Fig. 1), despite a decrease in stream discharge over the same period. Streams without salmon did not have this mid-season pulse in export (Fig. 1).

Within a given stream, annual variability in salmon returns led to corresponding variability in export of sediment (Fig. 1). For example, in N-4 Creek, export was low and constant throughout 2003, with only two sockeye seen. In contrast, in 2004, export was similarly low until >600 sockeye entered and initiated nest digging, driving a 50-fold increase in the export of sediment (Fig. 1). However, this increase in export was transient, probably driven by the rapid mortality of these salmon due to heavy predation by grizzly bears (*Ursus arctos*; 84% of sockeye were killed within three days).

Seasonal variability in both discharge and concentrations of suspended sediments drove seasonal patterns in export. The main factor that influenced sediment concentration was salmon density. For a given stream, suspended sediment concentrations were higher during higher salmon densities (Fig. 1, Table 1). Depending on the stream, salmon density explained up to 82% in the variance in particulate load and was a significant predictor in 7 out of 10 streams (Table 1). In general, discharge was not as strong a predictor of particulate load, but this varied across streams. There was a significantly negative relationship between discharge and particulate load in 3 out of 10 streams (Table 1). Before salmon spawned, suspended sediments were 56.2% ± 12.8% organic (mean ± SD across streams; Appendix B). During salmon spawning, the inorganic material increased in exported materials, with 47.2% ± 12.7% organic across all streams. This average decrease

across all streams was mostly driven by significant decreases in two streams with high salmon densities, Pick and Whitefish (Appendix B).

Phosphorus.—Across all streams, TP concentration was strongly correlated with suspended sediments ($r = 0.65$). In streams with salmon, peak P export occurred during salmon spawning (Appendix C). In streams without salmon, P export was highest during the spring when flows were highest. These seasonal patterns in P export were driven by a combination of seasonal discharge and seasonal differences in P concentrations. Salmon density was positively related to the concentration of P in 7 out of 10 streams and explained up to 67% of the variance, depending on stream (Table 1). Discharge was only a significant factor in 2 out of 10 streams, and in those streams higher discharge was associated with lower P concentrations (Table 1). For a subsample of streams in which water was also filtered prior to nutrient analyses, TP was composed of mostly dissolved forms prior to salmon spawning ($0.72 ± 0.13$; mean ± SD across streams of the proportion of nutrients that were dissolved; Appendix D). As salmon entered the streams to spawn, dissolved P became a smaller portion of TP in stream water ($0.64 ± 0.25$; Appendix D).

Nitrogen.—Total N concentrations were correlated with suspended sediment concentrations ($r = 0.38$). Like P, nitrogen export was also usually highest during salmon spawning. However, salmon spawning generally produced a lower magnitude mid-season pulse in export (Appendix E) as compared to suspended sediment and P, presumably due to higher levels of background watershed export. Salmon density explained up to 33% of the variance in N concentration of stream water and was a significant and positive factor in 7 out of 10 streams (Table 1). Discharge was not a significant predictor of N concentration in any stream (Table 1). Virtually all nitrogen both before and during salmon
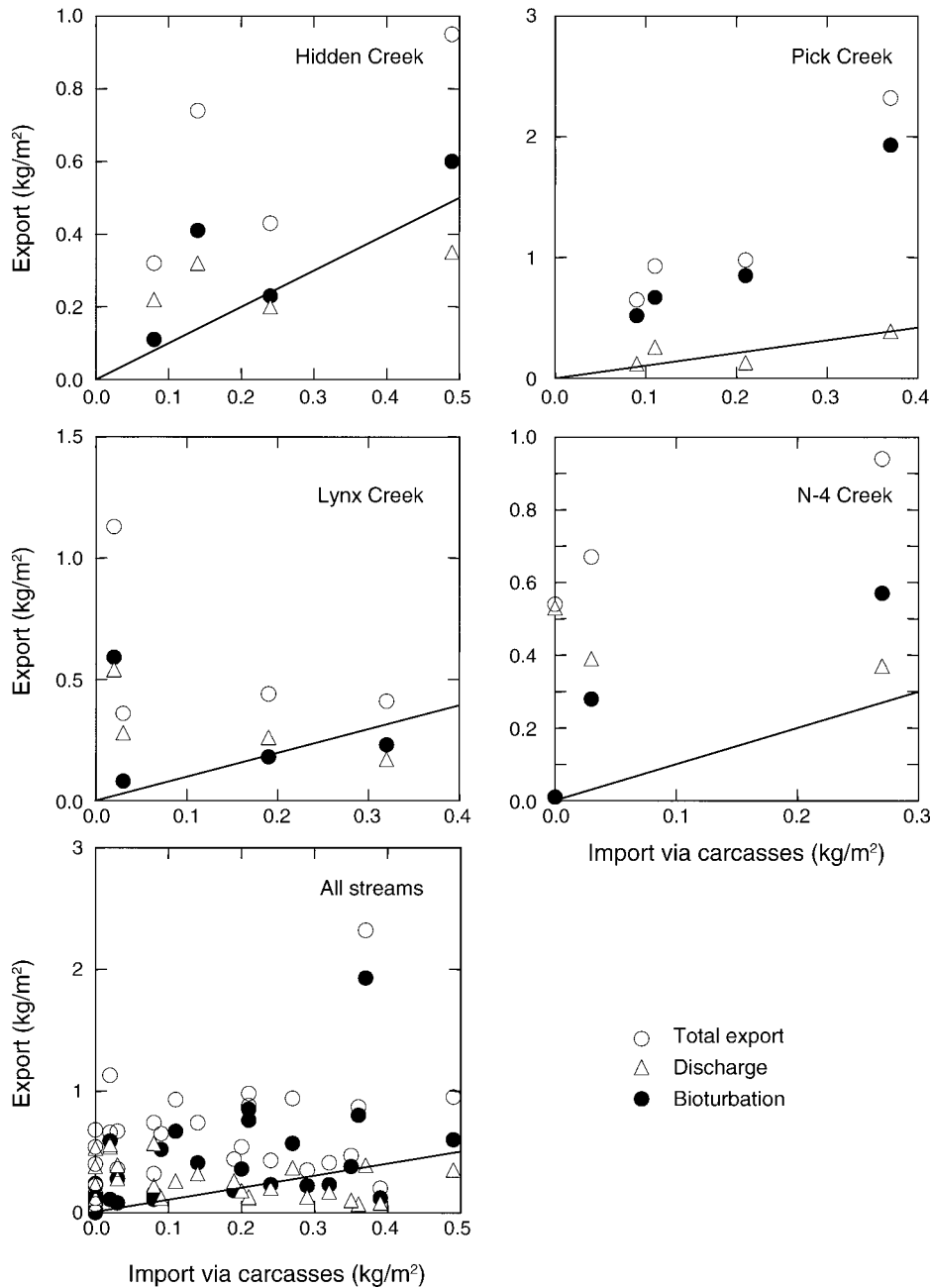
FIG. 2. Season-wide fluxes of total suspended sediments (dry mass). Each point represents the flux for a given year based on the integration over the entire sampling season, normalized by stream area. The three different symbols represent different fluxes, total export (open circles), export due to background discharge (open triangles), and export due to salmon activities, presumably due to nest digging by salmon (solid circles). Also shown is the 1:1 line, at which salmon import equals salmon export. Solid circles above this line represent stream-years during which salmon exported more than they imported.

spawning was in dissolved forms (proportion dissolved > 0.98; Appendix D).

Upstream nutrients and sediments.—Concentrations of nutrients and suspended sediments collected upstream of salmon spawning did not exhibit elevated concentrations during salmon spawning (Appendix F). In addition, upstream samples from before or during salmon

spawning were similar to samples collected from stream outflows before salmon spawning (Appendix F).

Integrating fluxes across the entire season

Suspended sediments.—Salmon density was strongly related to total export of sediments (Fig. 2). Salmon bioturbation contributed to greater export of suspended

TABLE 2. Results from linear regressions between import and export of sediments and nutrients integrated over the season.

Stream	n	Sediments		Phosphorus		Nitrogen	
		Slope	r^2	Slope	r^2	Slope	r^2
Hidden	4	1.283*	0.899	0.833**	0.928	0.737***	0.995
Lynx	4	0.873	0.242	0.595**	0.965	0.593**	0.989
N-4	3	2.199	0.885	0.742*	0.969	0.528	0.653
Pick	4	5.035***	0.987	1.021**	0.987	0.952*	0.872
All streams	31	1.890***	0.572	0.601***	0.749	0.550***	0.719

Notes: The line was forced through the origin (no salmon leads to no import or export). The slope of this line compares the relative magnitude of salmon-exported fluxes to salmon-imported fluxes.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ from regression.

sediments than background discharge in 16 of the 25 stream-years with salmon (Fig. 2). In 20 of 25 stream-years with salmon, salmon exported more sediments via bioturbation than total matter they imported as dry mass in their bodies (Fig. 2). In fact, over all streams and years, salmon exported almost two times more total matter than their bodies imported, demonstrated by the slope of the relationship between import and export being 1.89 (Table 2). Higher salmon returns corresponded with significantly higher bioturbation export of suspended sediments, both across all streams and years and within Pick and Hidden Creeks across years (Fig. 2, Table 2). Total summer precipitation was not a significant factor influencing total background export of sediments for any stream.

Phosphorus.—Total P export was controlled by the combination of precipitation and salmon activities. Salmon activities were a substantial component of P budgets, both in terms of import as well as export (Fig. 3). Over all stream and year combinations, salmon carcasses imported on average 2.1 g P/m² of streambed, but depending on stream and year, this ranged from 0.0 to 7.1 g P/m². Salmon exported slightly less, an average of 1.3 g P/m², ranging from 0 to 6.9 g P/m². Higher salmon returns corresponded with significantly higher salmon export of P, both across all streams and years, and within Pick, Hidden, Lynx, and N-4 Creeks (Table 2). Background export tended to be slightly higher than salmon-caused export, an average of 3.7 g P/m², ranging from 0.9 to 11.0 g P/m². Background export of P tended to be higher during years with higher precipitation (Fig. 4). Specifically, there were positive relationships between background export of P and precipitation for all streams with three or more years of data, but these relationships were insignificant with the exception of N-4 Creek ($r^2 = 0.99$, $P < 0.05$).

Salmon exported the equivalent of a substantial portion of the P that was imported in their bodies. In 5 out of the 25 streams that had spawning salmon, salmon actually exported more P from streams than they imported in their bodies. For example, in Pick Creek, salmon tended to export marginally more than they imported in their carcasses (Fig. 3, Table 2). Across all stream-years, salmon exported the equivalent of 60% of the P that they imported in their bodies.

Nitrogen.—Salmon activities also substantially influenced seasonal N budgets in streams (Fig. 5). Over all streams and years, salmon imported an average of 17.0 g N/m² in their bodies (0–57.2 g N/m², minimum–maximum) and exported 9.7 (0–52.2) g N/m². Background export dominated total export, averaging 137.5 (34.5–569.9) g N/m². Across all streams and years, salmon exported the equivalent of an average of 55% of the N imported by their bodies (Fig. 5, Table 2). This varied among streams. In Pick Creek for example, salmon export was 95% of imported N, but in Lynx they exported the equivalent of 59%. Salmon exported more N than they imported in 4 of the 25 stream-years with salmon returns. Background export of N tended to be higher during years with higher precipitation for all streams, and these relationships were marginally significant in Cottonwood and Hidden Creeks (results from regressions $r^2 = 0.80$, $P = 0.064$; $r^2 = 0.83$, $P = 0.052$, respectively; Fig. 4).

Bioassay of P availability

Phosphorus from stock solutions and stream water increased growth of primary producers in lake water. Orthophosphate additions increased algal growth, but in a saturating relationship (Fig. 6). Phosphorus in stream water during salmon spawning also increased algal growth, indicating that stream nutrients were biologically available. Parameter values of the model fits indicate that initial slopes were slightly different in the "during" treatment, suggesting that stock P is slightly but significantly more available than stream water during this time (Table 3). However, in the "after" treatment, the initial slopes were statistically indistinguishable (Table 3), evidence that the P in stream water was as bioavailable as the orthophosphate in the stock solution. In addition, stream water significantly increased the saturation point past that observed in the stock P treatments (Fig. 6, Table 3), suggesting that stream water added additional limiting elements to the incubation media, perhaps silica. Therefore we conclude that during much of the season nearly all of the P exported by spawning salmon is bioavailable.

Discussion

Previous research on salmon as nutrient vectors has focused on how anadromous and semelparous salmon transport nutrients and matter upstream to spawning habitats (Larkin and Slaney 1997, Gresh et al. 2000,
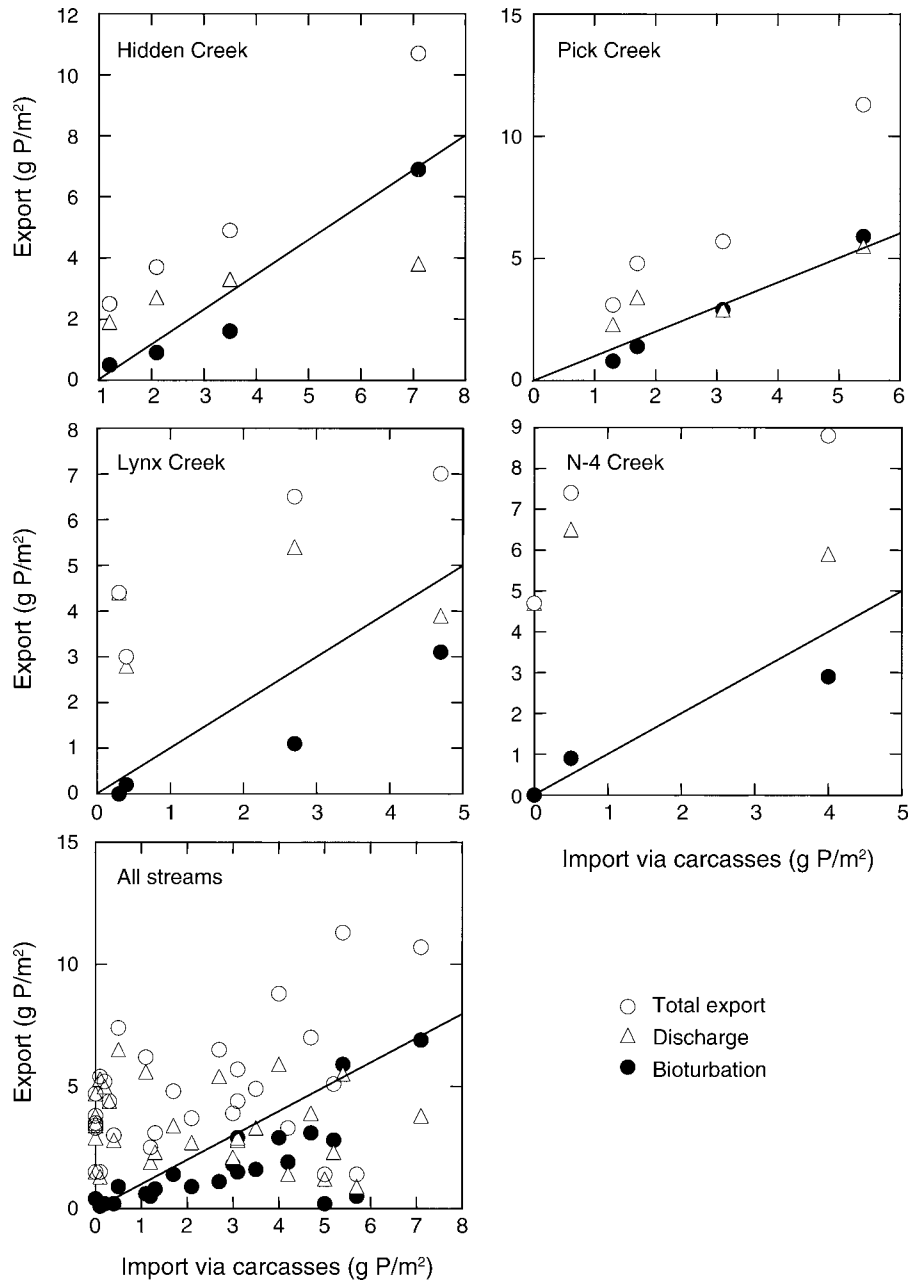
FIG. 3. Integrated season-wide fluxes of total phosphorus. Each point represents the size of a flux for a given year based on the integration over the entire sampling season, normalized by stream area. Symbols are the same as Fig. 2.

Gende et al. 2002, Naiman et al. 2002, Schindler et al. 2003). Our results confirm that salmon are significant components of nutrient and matter cycling of coastal freshwaters, but also suggest that previous views of salmon oversimplified their role as transporters of nutrients and matter. Indeed, on large spatial scales, salmon migrations import massive quantities of nutrients from marine ecosystems to coastal freshwater ecosystems (Larkin and Slaney 1997, Gresh et al. 2000, Moore and Schindler 2004, Helfield and Naiman 2006). Our novel finding was that at finer spatial scales, salmon

nest digging and excretion redistributes nutrients and matter within the larger watershed, moving these materials out of streams and into depositional environments such as lakes. Thus, salmon link oceans to lakes and streams via their migrations and link streams to lakes via their nest-digging and spawning activities.

Seasonal dynamics

Salmon drive seasonal dynamics of nutrient and suspended sediment export in streams used as spawning habitat. Export of nutrients and suspended sediments
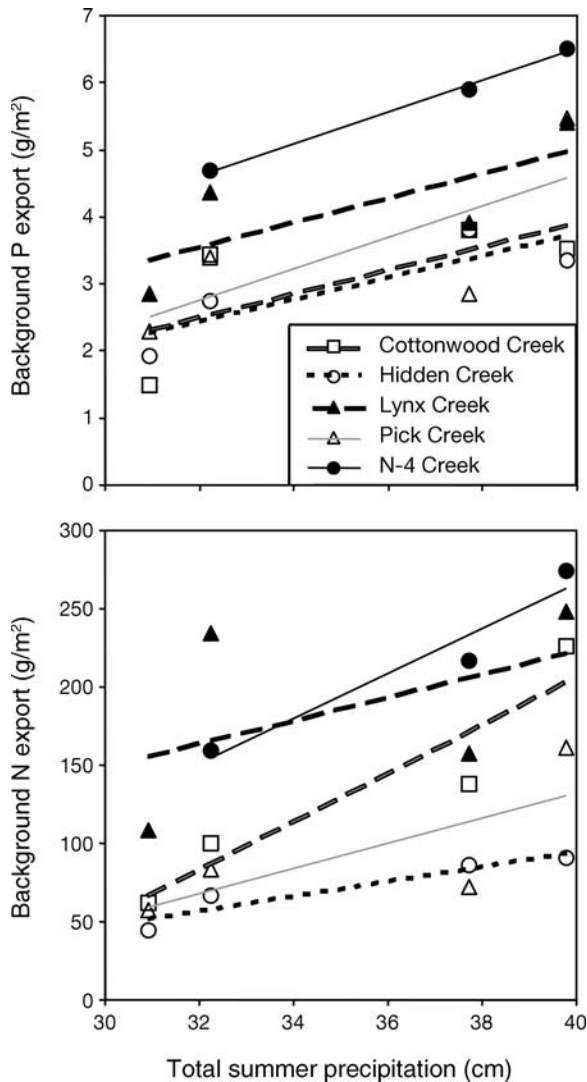
FIG. 4. Season-wide background fluxes of total phosphorus and total nitrogen that were not attributed to salmon activities for streams with three or more years of data, plotted as a function of summer-long precipitation. Lines represent best fits of linear regressions for each stream but do not convey significance (see *Results*).

consistently increased, often over an order of magnitude, when salmon entered the streams to initiate spawning (Fig. 1; Appendices C and E). The relative increase in export during salmon spawning differed among materials: salmon increased export of suspended sediments the most and increased export of N the least. Export of nutrients and sediments was consistently highest during salmon spawning in streams and years with high densities of salmon. In contrast, hydrology dominated export of nutrients and suspended sediments in streams without salmon; for example, higher export is associated with higher discharge in spring (Fig. 1).

Previous studies have observed substantial local increases in nutrient concentrations in stream water during salmon spawning (Bilby et al. 1996, Minakawa and Gara 1999, Chaloner et al. 2004, Mitchell and Lamberti 2005). Salmon could increase the concentrations of nutrients and suspended sediments in stream water during spawning via several possible mechanisms. (1) Salmon nest digging and bioturbation directly suspend nutrient-rich sediments in the water column where it is transported downstream. This bioturbation likely drives the dramatic pulse of sediment export during salmon spawning. It is also likely that bioturbation drives much of the observed export of P, as the proportion of particulate P increased during salmon spawning (Appendix D). However, this mechanism is likely unimportant for N export, as virtually all N is dissolved (Appendix D). Further, it should be noted that this nest digging has also been shown to increase the stability of the remaining substrate (Montgomery et al. 1996), which may decrease export of sediments during non-spawning periods. (2) Excretion of dissolved nutrients from gonadal tissue and dead and dying salmon likely contributes to elevated concentrations of nutrients during salmon spawning. Indeed, we observed significant correlations between salmon densities and stream N concentrations. This excretion is expected to produce a gradual increase in dissolved nutrients; Johnston et al. (2004) observed that carcasses lost 50% of their dry mass and N in about 20 days, while P in carcasses was more recalcitrant. (3) Salmon nest digging often scours or buries periphyton (Minakawa and Gara 1999, Moore et al. 2004), which take up dissolved nutrients. Thus, salmon may indirectly decrease dissolved nutrient retention. (4) It is possible that salmon nest digging increases the transfer of dissolved nutrients between the water column and benthic habitats. Previous studies have noted that bioturbation often increases nutrient transfer across the sediment–water interface by releasing dissolved nutrients trapped in sediment porewater (Vanni 2002). Depending on the nutrient, it is likely that a combination of all these mechanisms drives the seasonal pulse of nutrients and sediment export observed during salmon spawning. Regardless of the mechanism, salmon activities dramatically increased the rate of nutrient and sediment movement downstream. Thus, salmon spawning activities can control the seasonal patterns of material flux from streams to recipient lake ecosystems via multiple mechanisms.

Mass balance

Interpolation of measured fluxes suggests that salmon movement of nutrients and matter, both upstream and downstream, are major components of the sediment, P, and to a lesser extent, N budgets. In streams and years with high densities of salmon, we estimate that salmon are responsible for exporting up to 90% of all sediments estimated to leave streams during the summer season (Fig. 7). Salmon exported >50% of all the P that left streams with high densities of salmon (Fig. 7). Salmon
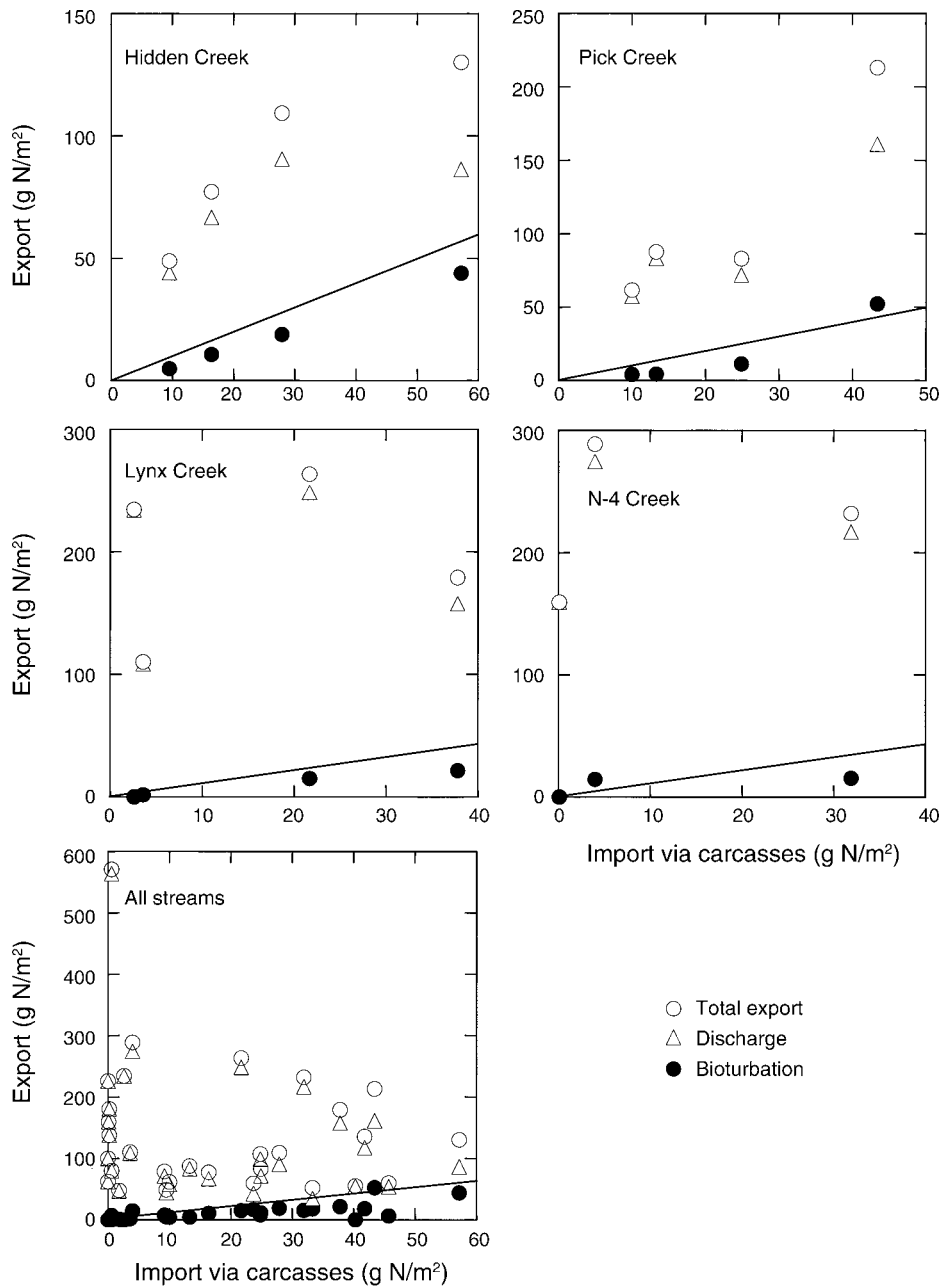
FIG. 5. Integrated season-wide fluxes of total nitrogen. Each point represents the size of a flux for a given year based on the integration over the entire sampling season, normalized by stream area. See Fig. 2 for an explanation of symbols.

are responsible for >30% of the exported N in streams and years with high densities of salmon (Fig. 7). In addition, across years within a given stream, higher salmon densities led to higher export of matter and nutrients (Figs. 2, 3, and 5). Thus, year-to-year variation in salmon abundance translates into interannual variability in export of nutrients. In addition, increased precipitation drives significant increases in interannual background export of N and P (Fig. 4).

The nutrients that salmon displace from streams subsequently get deposited in downstream lakes. P is generally the limiting nutrient for these lakes (D. E. Schindler and M. D. Scheuerell, *unpublished data*), similar to other lakes in the area (e.g., Goldman 1960). Our bioassay experiment indicated that P leaving streams during salmon spawning is highly available to primary producers in downstream lakes (Fig. 6), giving further support to previous observations that particulate
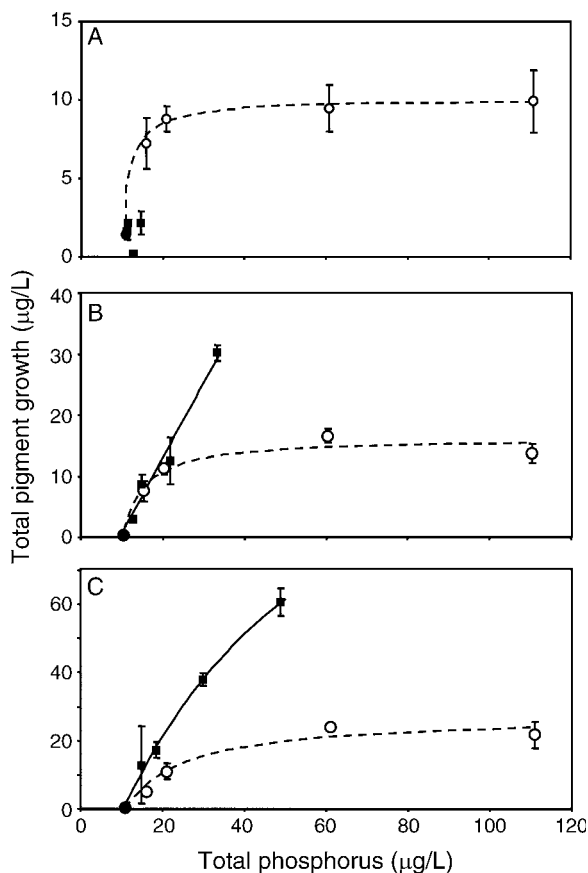
Fig. 6. Response of primary producers to stream and stock phosphorus (A) before, (B) during, and (C) after salmon spawning. Data presented are means ± SD ($n = 3$) of total pigment growth (chlorophyll a plus pheophyton) as a function of the calculated total P content of each treatment. Solid squares represent lake water fertilized with stream water, while open circles represent lake water fertilized with stock P. Lines are the best fit of the saturating relationship (see *Methods and materials* and Appendix F).

P can be biologically available (e.g., Ellison and Brett 2006). Thus, salmon move bioavailable nutrients out of streams. These exported nutrients fertilize primary producers in downstream lakes. Schindler et al. (2005) observed that productivity of Lake Nerka was responsive to changes in loading of salmon-derived nutrients. Brock et al. (2006) found that sediments were slightly enriched with the stable isotope ^{15}N around the mouth of Pick Creek, evidence of local deposition and retention
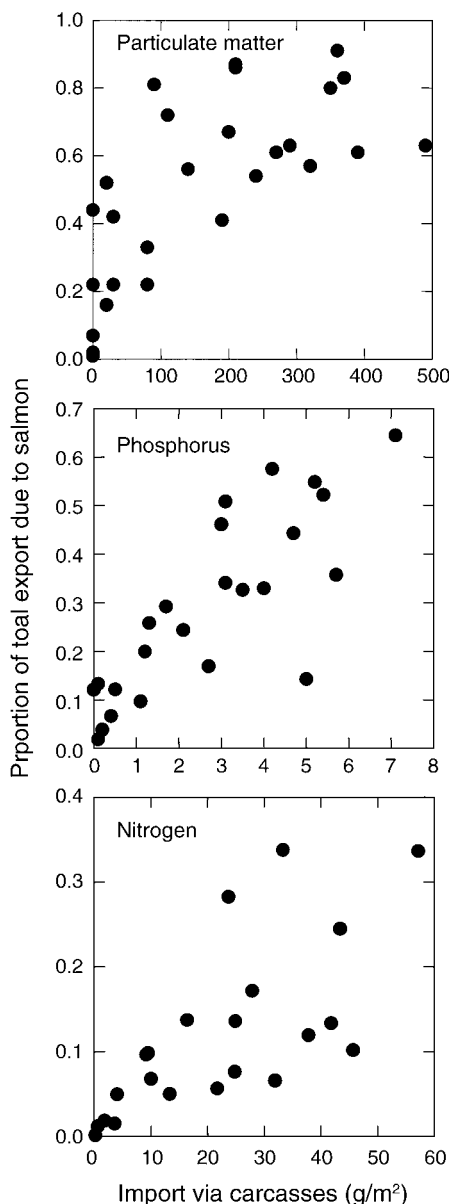

Fig. 7. Relative importance of bioturbation and other salmon activities (excretion) in export of nutrients and matter. Each point is a stream-year, the proportion of the total export that was attributed to salmon activities, plotted as a function of salmon density (import of nutrient and matter by carcasses).

Table 3. Fitted growth parameters of the bioassay experiment.

Treatment	Initial slope	Saturation	r^2
Before			
Stock	5.33 (0.29–10.37)	10.0 (8.72–11.4)	0.881
Stream	NS	NS	
During			
Stock	3.29 (1.75–4.71)	16.2 (14.2–18.2)	0.922
Stream	1.23 (1.05–1.41)	NS	0.953
After			
Stock	1.89 (0.74–3.02)	11.0 (9.1–12.9)	0.940
Stream	2.59 (1.57–3.61)	155.9 (52.0–259.7)	0.971

Notes: Data presented are best estimates of parameters and 95% confidence intervals for the saturating growth equation (see *Methods and materials* for a description of the equation). Parameters that were not significantly different from 0 or undefined are shown as NS (not significant).

of salmon-derived nutrients. However, beyond this local and minor enrichment there was little spatial heterogeneity, suggesting that most salmon-derived N mixes rapidly in the lakes' water column. Given that sockeye export massive quantities of bioavailable P from streams and that the majority of the spawning in the lake basins of this study occurs in tributaries (lakes Nerka and Aleknagik; Burgner et al. 1969), it is likely that the P exported by spawning salmon from streams substantially contributes to lake productivity, adding to the nutrient subsidies contributed by spawning on lake beaches.

Conservation implications

Salmon populations have drastically declined throughout their southern range due to a variety of anthropogenic impacts (Ruckelshaus et al. 2002). The loss of this once-dominant species has raised substantial concerns that coastal freshwaters have lost a critical source of nutrients (Stockner 2003). Restoration efforts have attempted to mimic the impacts that salmon runs have on streams by placing salmon carcasses or fertilizers in streams (Compton et al. 2006). For example, $>1.58 \times 10^5$ salmon carcasses have been placed in Oregon streams since 1995 (Compton et al. 2006). Numerous experiments have placed salmon carcasses in streams and monitored the bottom-up (fertilizing) impacts of salmon carcasses on streams (e.g., Wipfli et al. 1999). However, our study suggests that a stream filled with live nest-digging salmon and their eventual carcasses has much different nutrient and matter cycling, retention, and movement than a stream filled with only carcasses. If the objective of these restoration efforts is to replace the impacts that salmon runs have on stream ecosystem dynamics, such restoration efforts are misguided. Nutrient enrichment programs could easily over-apply fertilizers, leading to potentially damaging eutrophication (Compton et al. 2006), especially given our findings that live salmon export the equivalent of a substantial proportion of the nutrients they import.

In addition, export of suspended sediments by spawning salmon may improve stream conditions for incubating and young salmon. Fine sediments decrease survival of incubating eggs by decreasing interstitial water and oxygen flows (Tappel and Bjorn 1983). Fine sediments can also decrease habitat complexity and reduce the availability of edible prey, subsequently decreasing growth and survival of juvenile salmon (Suttle et al. 2004). Previous studies have shown that salmon nest digging can decrease local levels of fine sediments (Kondolf et al. 1993, Montgomery et al. 1996). Here we quantify for the first time the magnitude of the stream-wide export of fine sediments caused by salmon nest digging. Given that fine sediments reduce salmon survival and salmon reduce fine sediments, it is likely that salmon influence future population viability,

through habitat modification (Montgomery et al. 1996, Moore 2006).

Our study gives further support to the concept that organisms are important to nutrient and matter cycling and movement in stream ecosystems (Naiman and Décamps 1997, Vanni 2002, Baxter et al. 2005). Through habitat modification, ecosystem engineers can control ecosystem fluxes (Moore 2006). Previous studies have recognized the importance of detritivorous invertebrates in cycling nutrients and matter in streams (Cummins 1974, Covich et al. 1999). For example, Wallace et al. (1991) found that experimentally removing invertebrates that process organic matter dramatically decreased the export of fine organic particles. To our knowledge, ours is the first attempt to quantify how bioturbation by an ecosystem engineer contributes to nutrient and sediment fluxes on a watershed scale. We demonstrate that sockeye salmon, an ecosystem engineer, dominate fluxes, both imports and exports, of nutrients and matter from streams. Therefore, stream fluxes are not only influenced by abiotic drivers such as precipitation, but also by the migrations, life histories, and behaviors of the organisms that inhabit those streams.

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APPENDIX A

A table of relevant stream characteristics from different sampling years (*Ecological Archives* E088-080-A1).

APPENDIX B

A table of the proportion of organic matter of suspended sediments in stream water, for streams from different periods (*Ecological Archives* E088-080-A2).

APPENDIX C

A figure showing seasonal flux of P from streams across all years (*Ecological Archives* E088-080-A3).

APPENDIX D

A table of the proportions of total phosphorus and total nitrogen that are in dissolved form, for a subsample of streams (*Ecological Archives* E088-080-A4).

APPENDIX E

A figure showing seasonal flux of N from streams across all years (*Ecological Archives* E088-080-A5).

APPENDIX F

A table showing upstream and downstream concentrations of total nitrogen and total phosphorus (*Ecological Archives* E088-080-A6).