

## Research Article

# Effects of spawning salmon on dissolved nutrients and epilithon in coupled stream-estuary systems of southeastern Alaska

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**Abstract.** Spawning migrations of Pacific salmon (*Oncorhynchus* spp.) represent a significant nutrient pulse to freshwater ecosystems of southeastern Alaska. These salmon-derived nutrients (SDN) can be transported by streamflow from spawning reaches of streams to estuaries, where their fate and significance have not been studied. Such estuaries represent an important aquatic ecotone in southeastern Alaska, especially for juvenile salmonids. We sampled dissolved nutrients and epilithon (i.e., benthic algae attached to rocks) before, during, and after salmon runs in three Alaskan streams and their associated estuaries. Salmon runs increased streamwater fluxes of dissolved ammonium and soluble reactive phos-

phorus to estuaries by 30–350% and 14–130%, respectively, depending on the stream and period. Although epilithon chlorophyll *a* and biomass increased in streams in response to SDN, epilithon did not increase in associated estuaries. We suggest that salmon spawner disturbance during estuary redd-building, invertebrate grazing, physical transitions from summer to fall, and nutrient influx from nutrient-rich tidal flow may have limited epilithon growth responses to SDN in estuaries. Although estuaries receive a significant flux of SDN flushed downstream from freshwaters, epilithon does not measurably respond to this nutrient enrichment from spawning salmon.

**Key words.** Pacific salmon; salmon-derived nutrients; estuaries; streams; water chemistry; epilithon.

## Introduction

The movement of material from donor to recipient ecosystems (or ecosystem resource subsidies, after Polis et al., 1997) is especially relevant to ecotones that are transitional interfaces between ecosystems (Odum, 1971). For stream ecosystems, the riparian-aquatic interface can strongly influence in-stream structure and function and has been the focus of

important conceptual developments in stream ecology (Vannote et al., 1980; Wallace et al., 1999). Estuaries represent another potentially important interface for flowing waters that stream ecologists rarely consider. Stream and riparian productivity can influence downstream estuarine areas, which are ecotones between freshwater and marine ecosystems, through the downstream transport of terrestrial and freshwater material and resources (Murphy, 1984; Jauquet et al., 2003; Jonsson and Jonsson, 2003). Estuaries also provide a physical conduit for the upstream movement of organisms and materials (Pringle, 2003).

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Migrations of anadromous fish provide a dramatic example of an upstream-vectored resource subsidy between marine and freshwater ecosystems. Throughout the northern Pacific Rim, millions of Pacific salmon (*Oncorhynchus* spp.) return to their natal streams to spawn and die, bringing with them many thousands of tons of salmon-derived nutrients (SDN) to freshwater and terrestrial environments. Spawning salmon also release stored nutrients, including SDN from previous spawning events, through streambed disturbance by swimming and redd construction (Gende et al., 2002). Because Pacific Northwest freshwaters are generally considered oligotrophic, with limited availability of nitrogen (N), phosphorus (P), or both elements (Ashley and Slaney, 1997), salmon nutrients could be important for freshwater productivity (Gende et al., 2002; Naiman et al., 2002). Juvenile Pacific salmon are thought to outmigrate to the northern Pacific Ocean because freshwaters are generally less productive than the marine environment (Gross et al., 1988; Thorpe, 1994).

Over the past decade, studies of the influence of spawning salmon on freshwater and adjacent terrestrial ecosystems have revealed great complexity in the responses of ecosystems to spawning salmon (see reviews by Gende et al., 2002; Naiman et al., 2002). Both nutrients and disturbance imparted by spawning salmon have been shown to influence freshwater and terrestrial ecosystems through many food web pathways (e.g., Chaloner et al., 2002; Bilby et al., 2003), although the context can determine whether fertilization or disturbance effects predominate (Tiegs et al., 2008). One such pathway in aquatic ecosystems is via the uptake of dissolved nutrients by epilithon, which is the community of algae, bacteria, and other microbes attached to inorganic substrates (Lamberti, 1996). Autotrophs and heterotrophs in the epilithon contribute to the transfer and retention of allochthonous carbon and nutrients (Pringle et al., 1986). Thus, nutrient uptake and retention by epilithon could be important for the incorporation and export of SDN in fresh waters.

Nutrient uptake and retention is, in part, determined by the capacity of an ecosystem to use those nutrients. Systems that accrue a large biomass typically can process more nutrients than systems lacking biomass (Mulholland et al., 1994). Estuaries, which are defined as inlets of the sea that reach into a river valley as far as the upper limit of tidal rise (Fairbridge, 1980), are especially productive aquatic environments, particularly for microbial processes such as denitrification (Murphy, 1984). However, twice daily these systems undergo a periodic 'famine' in which the tide recedes and areas formerly inundated with predominantly salt water are exposed to the air or

covered by relatively fresh water from upstream (Correll, 1978), which is considered to be nutrient-poor compared with marine water (Schlesinger, 1997). Nutrient pulses during these periods, such as the downstream export of SDN from salmon migrations, may serve as an additional and potentially significant nutrient input for epilithon in estuaries.

Estuaries also are important habitats during parts of the salmon life cycle, as Pacific salmon pass through estuaries at least twice during their life cycle – during outmigration as juvenile smolts and when returning to spawn as adults (Thorpe, 1994). Estuaries can strongly influence the life history and development of juvenile salmonids (Thorpe, 1994), which use estuaries to forage, seek refuge from predators, and shift osmoregulation from freshwater to more saline environments (Thorpe, 1994; Magnusson and Hilborn, 2003). The intriguing possibility exists that food webs in estuaries, particularly benthic producers such as epilithon, are influenced by SDN from inflowing rivers, which may, in turn, benefit juvenile salmon. For example, juvenile salmon may consume invertebrates that graze benthic producers fueled by SDN. Benthic primary producers in estuaries may be an important repository for SDN given their contribution to overall estuary productivity; Hopkinson et al. (1999) found that a significant amount of the metabolism in one estuary was from the benthos.

The northern Pacific Rim region, including southeastern Alaska, is characterized by coastlines of thousands of islands and mountainous topography, resulting in thousands of streams and estuaries that harbor juvenile salmon populations. The topography means that many of these streams have relatively short freshwater reaches in which salmon can spawn (e.g., below waterfall barriers), thereby reducing stream length available for SDN uptake and retention. If in-stream SDN uptake is limited, coupled with increased discharge from seasonal storm runoff and benthic disturbance by salmon that accompany spawning runs, substantial export of salmon material and stored nutrients downstream to estuaries and the nearshore coastal area could result. Few studies have explicitly considered the influence of SDN on the productivity of the estuarine environment and how SDN may serve to link the stream-estuary ecotone. Mitchell and Lamberti (2005) studied one Alaskan stream and estimated that 46–60% of the SDN produced by the summer salmon run was exported to the estuary, but they did not directly sample the estuarine environment nor consider the potential ecological effects of this downstream flux of nutrients.

The objective of our study was to quantify the transport of SDN from three southeastern Alaskan streams to their estuaries and to determine the

influence of SDN on the growth of epilithon in both habitats. To do so, we assessed over time the effects of spawning salmon on dissolved nutrient chemistry and epilithon accrual in three streams with short spawning reaches and their associated estuaries. We hypothesized that the flux of SDN would increase longitudinally from stream to estuary during salmon runs because of a loading effect of nutrients from live and dead salmon with proximity to the estuary, coupled with limited in-stream capacity to take up those nutrients also contributing to the longitudinal increase in nutrients. Our specific hypotheses were that (1) salmon spawners would increase dissolved nutrient concentrations in spawning reaches of streams, (2) short spawning reaches and limited nutrient uptake by epilithon would result in substantial SDN export to estuaries, and (3) these salmon nutrients would stimulate epilithon growth in both streams and their estuaries.

## Materials and methods

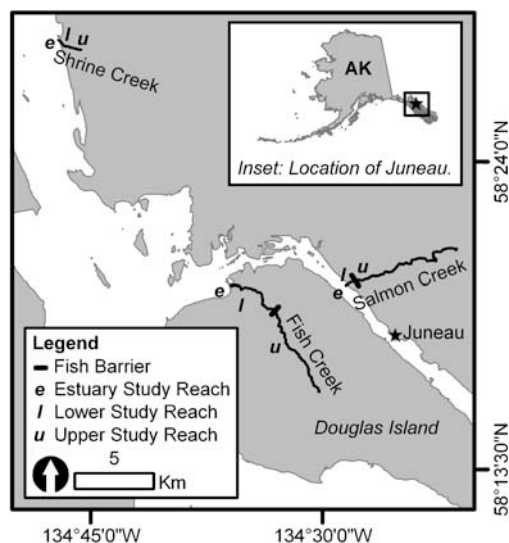
### Study sites

We studied three 3<sup>rd</sup> to 4<sup>th</sup>-order streams near Juneau in southeastern Alaska in July–September 2003 (Fig. 1). Fish Creek, Salmon Creek, and Shrine Creek all have similar physical characteristics (Table 1). Southeastern Alaska is characterized by temperate rainforest with a maritime climate of cool winters and wet summers. Mean monthly air temperatures range from  $-6^{\circ}\text{C}$  to  $17^{\circ}\text{C}$  and average annual precipitation is 137 cm, mostly as rainfall (NOAA, 2004). The study streams and associated estuaries were typical of those

found in southeastern Alaska, including upstream reaches that did not receive salmon migrations, typically because a waterfall blocked upstream migration. Downstream reaches and estuaries of all three streams have long received spawning runs of salmon, likely for the past 2000–3000 years since the Little Ice Age (Bethers et al., 1995). All three streams have natural late-summer runs of pink (*O. gorbuscha*) and chum (*O. keta*) salmon (Table 2) and also receive some stray salmon from hatcheries or from stock enhancement programs (Bethers et al., 1995).

The estuaries of the three study streams can be classified as drowned-river valley estuaries, which were created by the flooding of river valleys after the last ice age (Fairbridge, 1980). Estuary sampling was conducted at spring tides, which produce the greatest tidal fluctuation (Palmer, 1973). Samples were taken at low tide in the residual freshwater flow to minimize the influence of marine water on samples and to allow easier access to the estuary benthos. The amount of time that the estuaries spent at or below the Mean Low Water limit, or the lower extent of the tidal range and exposed to air, was calculated using NOAA tidal data to determine the amount of time estuaries were inundated by ocean water (NOAA, 2003). We used the average of all low water heights as a conservative estimate of low tide since tidal information was not available for our individual study estuaries. Low water height in the Juneau area, measured at its lowest point, was 1.5 to 3 m below mean sea level. Since all streams we studied were within 25 km of each other, it is reasonable to assume that these estimates are valid for all sites. The estuaries were estimated to be under marine water approximately 522 hours (or 21.75 days) during the month of July before the salmon run, 516 hours (or 21.5 days) during the month of August during the salmon run, and 519 hours (or 21.63 days) during the month of September after the salmon run. The actual amount of time spent under marine water at our estuary sampling locations is likely to be much less, however, particularly in upper sampling sites closer to the stream.

The relatively small sizes and shallow depths of the estuaries (Table 1) allowed for representative sampling of surface water chemistry and epilithon. Sampling locations were established in 3–5 similar riffles in freshwater reaches (lower and upper) and 3–5 similar locations with riffle attributes (at low tide) in estuary reaches. Sample locations, depending on reach length, ranged in intervals from 50–250 m apart in the estuary, lower reach, and upper reach of Fish Creek (the largest stream), 30–100 m apart in the reaches of Salmon Creek, and 25–65 m apart in the reaches of Shrine Creek (the smallest stream).



**Figure 1.** Location of study streams near Juneau, southeastern Alaska.

**Table 1.** Characteristics of the three study streams and their associated estuaries.

Stream	Barrier <sup>b</sup> (km)	Discharge <sup>a</sup> (m <sup>3</sup> s <sup>-1</sup> )	Water temperature <sup>a</sup> (°C)	Substrate size <sup>a,c</sup> (mm)	Oxygen <sup>a</sup> (mg·L <sup>-1</sup> )	Canopy cover <sup>a,d</sup> (%)	Estuary conductivity <sup>a</sup> (µS)	Estuary depth at low tide <sup>a</sup> (m)	Total estuary area <sup>c</sup> (km <sup>2</sup> )	Approximate reach area (m <sup>2</sup> )		
										Estuary	Lower	Upper
Fish Creek	4	1.1 (0.4–4.0)	11.8 (8.5–15.9)	125 (8–353)	10.1 (6.4– 12.5)	39 (0–57)	4410 (37–8300)	0.2 (0.0–0.4)	0.4	8458.9	60894.5	2343.3
Salmon Creek	0.5	1 (0.3–2.8)	11 (9.4–13.4)	99 (23–233)	10.4 (8.0– 11.8)	60 (0–70)	2977 (49–14410)	0.2 (0.0–0.3)	0.3	3339.5	2929.6	955.0
Shrine Creek	NA	0.5 (0.1–3.5)	11.2 (9.4–14.2)	83 (30–149)	10.2 (9.1– 12.3)	73 (0–84)	2996 (60–14410)	0.1 (0.0–0.3)	0.1	335.2	396.0	359.5

<sup>a</sup>Mean and (range) during study<sup>b</sup>Distance from saltwater<sup>c</sup>Dominant size class within the study reaches<sup>d</sup>Estimated using a spherical densitometer<sup>e</sup>Estuary surface area measured from USGS 1:25000 contour maps**Table 2.** Densities of live spawners and carcasses during and after the salmon runs in the lower reaches of the study streams.

Stream	Pacific salmon species <sup>a</sup>	Spawner densities <sup>b,c,d</sup> (fish·m <sup>-2</sup> ) During salmon run	
		Live fish	Dead carcasses
Fish Creek	CH, CK CO, PK	0.2 (0.0)	0.0 (0.0)
Salmon Creek	CH, CO PK	1.0 (0.2)	0.1 (0.0)
Shrine Creek	CH, PK	0.5 (0.2)	0.4 (0.2)

<sup>a</sup> CH, chum (*Oncorhynchus keta*); CK, chinook (*O. tshawytscha*); CO, coho (*O. kisutch*); PK, pink (*O. gorbuscha*)<sup>b</sup> Estimated using methods according to Chaloner et al. (2004)<sup>c</sup> Mean and (range) during study<sup>d</sup> After salmon run, no fish or carcasses were observed

In all streams, discharge was measured biweekly at one site in a riffle of the lower freshwater reach using the velocity-area method (Gore, 2006). Discharge for use in calculating nutrient flux values at each sampling location and time (cf. Wold and Hershey, 1999) was estimated by multiplying the average water velocity measured at each time in the lower freshwater reach by the active stream channel width and depth measurements of each sampling location. However, we acknowledge that water velocity may have varied among sampling sites of each stream, which could have influenced our final calculations of nutrient flux described below.

### Stream water chemistry

At each sampling location, three replicate water samples were collected in July before salmon spawning, in August during peak spawner abundance, and in September after salmon spawning (for a minimum of n = 9 per reach per sampling period). All water samples were filtered through Whatman® GF/F membrane filters and frozen at -20°C until analyzed. Ammonium (NH<sub>4</sub><sup>+</sup>-N) was measured using the fluorometric technique (Holmes et al., 1999). Nitrate (NO<sub>3</sub><sup>-</sup>-N) was measured using a Dionex ion chromatograph with an AS14A anion column (USEPA, 1993). Soluble reactive phosphorus (SRP) was measured spectrophotometrically using the ascorbic acid method with a 10-cm path-length cell (APHA, 1999). Dissolved organic carbon (DOC) was measured using a Shimadzu 5000A carbon analyzer in water samples acidified to a pH of 2–4 (Sharp et al., 1993). In flowing waters, flux can be calculated as the product of concentration x discharge (Tank et al., 2006). We calculated nutrient flux values so that (1) dilution from variable discharge at each sampling site and time would not confound results, and (2) estimates of nutrient load transported between sites could be made. Flux was calculated by

multiplying the concentration of a specific nutrient (e.g.,  $\text{NH}_4^+\text{-N}$ ,  $\text{NO}_3^-\text{-N}$ , and SRP measured as  $\mu\text{g L}^{-1}$  and DOC measured as  $\text{mg L}^{-1}$ ) by the discharge estimated for each sampling location on a specific date (measured as  $\text{L s}^{-1}$ ) (see also methods in Vanni et al., 2001; Tomer et al., 2003; Mitchell and Lamberti, 2005).

### Epilithon standing crop

Epilithon was sampled from rocks haphazardly collected from stream and estuary sites. Sampling locations and dates were the same as those for water chemistry. At each location, five rocks (average diameter range, 8–12 cm) were removed from erosional habitats. A syringe-toothbrush sampler was used to scrub a round divot ( $7.5 \text{ cm}^2$ ) from the surface of each rock (see Steinman et al., 2006). Because estuary rocks were too irregular to sample effectively with the syringe-toothbrush sampler, rocks were returned to the laboratory in individual bags and the entire rock surface was scrubbed with a toothbrush. Rock surface area was estimated by weighing the amount of aluminum foil needed to wrap each rock without overlap (Steinman et al., 2006). Epilithon slurry was filtered onto pre-ashed and pre-weighed Whatman® GF/F filters, and chlorophyll *a* and ash-free dry mass (AFDM) were measured sequentially. Chlorophyll *a* was extracted with 90% buffered acetone for 24 hours at  $4^\circ\text{C}$ , measured spectrophotometrically, and corrected for phaeopigments using the trichromatic method (APHA, 1999). AFDM of the same sample was measured according to Steinman et al. (2006).

### Statistical analyses

Differences in response variables among reaches and sampling times were analyzed using a 2-way ANOVA with bootstrap resampling (Efron, 1990; Fisher and Hall, 1990), with reach and time as the fixed effects and blocked by stream ( $n = 3$ ). Reaches (stream above salmon barrier, stream below salmon barrier, estuary) and sampling times (before, during, or after the salmon run) were considered to be sufficiently independent to warrant statistical analysis via ANOVA, although we acknowledge that some longitudinal and temporal dependence may exist, especially for water chemistry between the stream salmon reach and the estuary. To minimize this dependency, we resampled the actual data using the bootstrapping method, in which mean values were resampled according to the total sample size and repeated to generate confidence intervals for each mean (see Crowley, 1992). In all analyses, a significant Reach x Time interaction term suggests that reaches responded differently to periods of salmon influence. Data were analyzed using SPSS

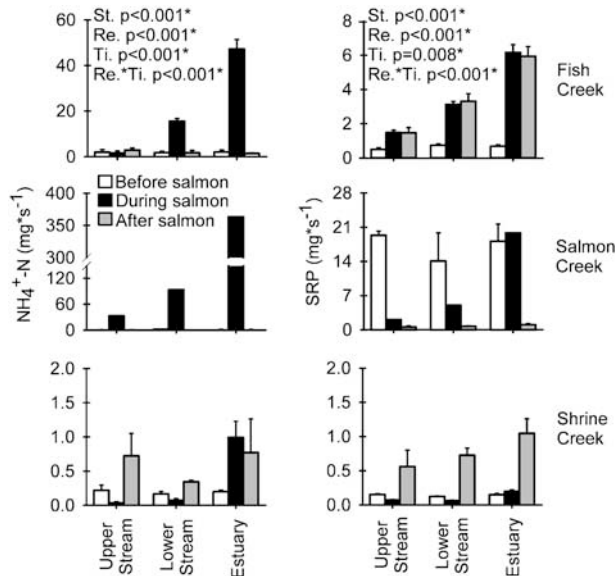
11.5 (SPSS Inc., Chicago, IL) and SYSTAT 12 (SPSS Inc., Chicago, IL). Data that violated the assumptions of ANOVA were transformed prior to analysis (log, square, or reciprocal, as appropriate). When examining the overall results of the model, a sequential Bonferroni technique (Dunn-Šidák method) was used to limit our procedure-wise error rate (Sokal and Rohlf, 1995).

## Results

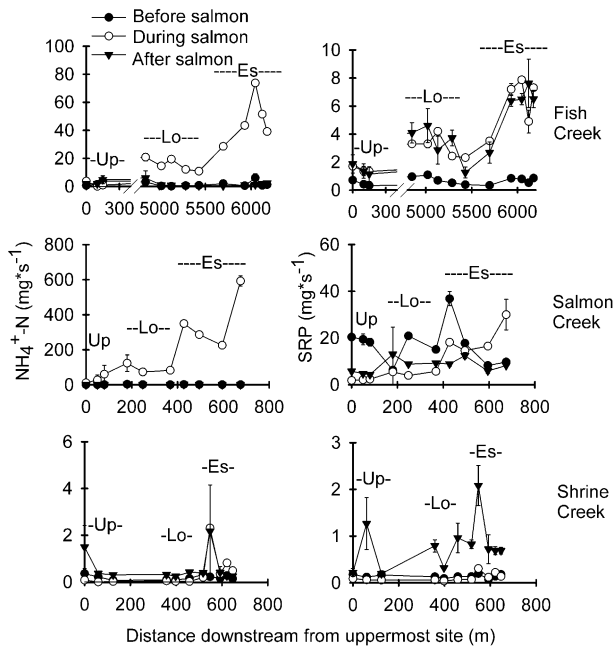
### Streamwater chemistry

Fluxes of ammonium ( $\text{NH}_4^+\text{-N}$ ) and soluble reactive phosphorus (SRP) increased in the estuaries of all three streams during or after the salmon run (Fig. 2), and in some cases during both periods (e.g., SRP in Fish Creek). These flux values correspond to increases in  $\text{NH}_4^+\text{-N}$  concentrations from 1–2  $\mu\text{g L}^{-1}$  before the salmon run to approximately 40–300  $\mu\text{g L}^{-1}$  during the salmon run in estuary reaches, depending on the stream, and increases in SRP concentrations from approximately 2–4  $\mu\text{g L}^{-1}$  before the salmon run to 4–19  $\mu\text{g L}^{-1}$  during the salmon run. In the lower stream spawning reaches, however, we did not see consistent responses in  $\text{NH}_4^+\text{-N}$  and SRP fluxes to the presence of salmon spawners (Fig. 2). Fluxes of  $\text{NH}_4^+\text{-N}$  increased in Fish Creek and Salmon Creek during the salmon run, but did not increase in Shrine Creek. Fluxes of SRP increased during and after the salmon run in Fish Creek, but changed only slightly in Salmon Creek at those times. SRP flux in Shrine Creek was relatively consistent among reaches throughout the study period. Overall, the magnitude of  $\text{NH}_4^+\text{-N}$  and SRP flux increase in estuaries was much larger than the increase in fresh water. Fluxes of  $\text{NO}_3^-\text{-N}$  and DOC did not appear to be affected by salmon spawners in any stream at any location or time.

The longitudinal flux of  $\text{NH}_4^+\text{-N}$  increased dramatically with distance downstream during the salmon run in Fish Creek and Salmon Creek, but increased only modestly in Shrine Creek at a single estuarine site (Fig. 3). Furthermore,  $\text{NH}_4^+\text{-N}$  fluxes in the estuaries of Fish and Salmon creeks were 2–3× greater than fluxes in the lower reaches during the salmon run. In Fish Creek, SRP flux increased longitudinally during and after the salmon run, and fluxes in the estuary were ~1.5× greater than fluxes in the lower stream reach. SRP flux increased longitudinally during the salmon run in Salmon Creek, but SRP levels were comparable to before and after the salmon run. In downstream reaches of Shrine Creek, SRP flux increased appreciably only after the salmon run. However, this pattern also was apparent in one site in the upstream reach.



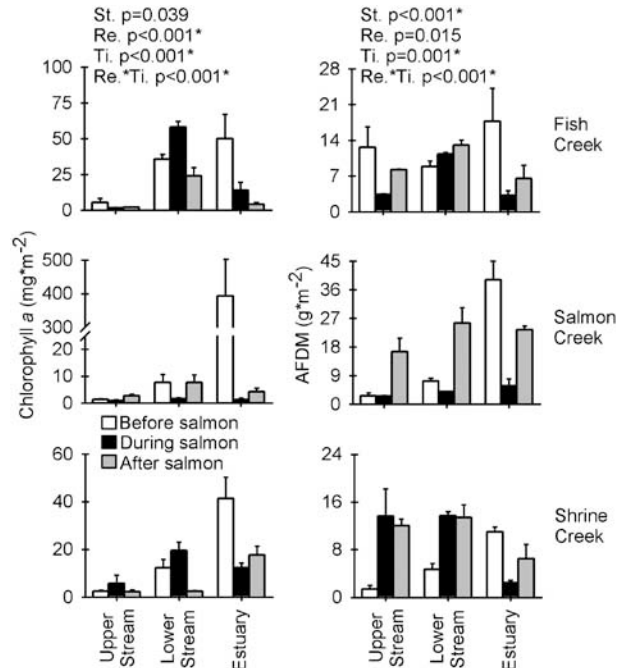
**Figure 2.** Mean (+SE) flux of surface water ammonium ( $\text{NH}_4^+\text{-N}$ ) and soluble reactive phosphorus (SRP) in Fish Creek, Salmon Creek, and Shrine Creek before, during, and after the salmon run. St indicates stream, Re indicates reach, and Ti indicates time. Asterisks indicate significance after sequential Bonferroni correction (Dunn-Šidák method).



**Figure 3.** Longitudinal trends (mean  $\pm$  SE) of surface water ammonium ( $\text{NH}_4^+\text{-N}$ ) and soluble reactive phosphorus (SRP) flux in Fish Creek, Salmon Creek, and Shrine Creek before, during, and after the salmon run. Up indicates the location of the upper stream reach, Lo indicates the location of the lower stream reach, and Es indicates the location of the estuary

### Epilithon standing crop

Epilithon chlorophyll *a* and ash-free dry mass (AFDM) were highest in the estuaries of all three



**Figure 4.** Mean (+SE) epilithon response as chlorophyll *a* and ash-free dry mass (AFDM) of epilithon in Fish Creek, Salmon Creek, and Shrine Creek before, during, and after the salmon runs. St indicates stream, Re indicates reach, and Ti indicates time. Asterisks indicate significance after sequential Bonferroni correction (Dunn-Šidák method).

streams before the salmon run, but greatly declined during the salmon run and did not recover to pre-salmon levels (Fig. 4). After the salmon run, chlorophyll *a* increased in the estuaries of Salmon Creek and Shrine Creek to levels greater than during the salmon run, but not to levels observed before the salmon run. AFDM showed a similar pattern of decline and recovery as chlorophyll *a*. In lower stream reaches, chlorophyll *a* increased during the salmon run in Fish Creek and Shrine Creek, but declined in Salmon Creek (Fig. 4). AFDM increased during the salmon run in the lower stream reaches, except in Salmon Creek, and maintained those levels or further increased after the salmon run.

## Discussion

### Salmon spawner influence on nutrient fluxes in streams and estuaries

Our results correspond with previous studies of salmon streams that have reported significant salmon-induced increases in  $\text{NH}_4^+\text{-N}$  and SRP, but not in  $\text{NO}_3^-\text{-N}$  and DOC, in the presence of salmon carcasses in some streams (Jauquet et al., 2003; Chaloner et al., 2004; Johnston et al., 2004; Mitchell and Lamberti, 2005; Chaloner et al., 2007; Moore et al., 2007). In all

three estuaries studied, we also documented salmon-induced increases in  $\text{NH}_4^+$ -N and SRP, but not in  $\text{NO}_3^-$ -N or DOC. When observed, increases in  $\text{NH}_4^+$ -N and SRP in the estuaries were significantly larger than increases found in freshwater spawning reaches, including fluxes of  $\text{NH}_4^+$ -N and SRP that were 1.5–3× greater in the estuaries of some streams than in freshwater during the salmon run, which suggests a cumulative downstream effect of salmon spawners (Mitchell and Lamberti, 2005; Moore et al., 2007). In addition, decomposing carcasses tended to accumulate in downstream areas, especially in the estuaries of these short streams, and, coupled with direct spawning and carcass decomposition in these downstream areas, may have resulted in further nutrient release. Several other studies have reported that salmon nutrients were exported from streams during the salmon run (Johnston et al., 2004; Mitchell and Lamberti, 2005), and ours was the first study to add statistical rigor to these patterns by assessing multiple reaches and estuaries in multiple streams.

These fluxes were not long lasting or were variable for particular nutrients studied. For example, we observed a dramatic increase in  $\text{NH}_4^+$ -N during the salmon run in Fish and Salmon creeks followed by its rapid decline after salmon spawners were gone. This decline likely occurred because  $\text{NH}_4^+$ -N is the main form of nitrogen excreted by metabolizing live fish (Hargreaves, 1998). SRP also did not respond as consistently to the presence of spawning salmon as did  $\text{NH}_4^+$ -N in freshwater and estuaries, although a general pattern of downstream increase was apparent. In Fish Creek, SRP remained elevated in the spawning reach and estuary after the salmon run, likely due to phosphorus release from the bones of decomposing fish carcasses and release of stored P from the stream bed as a result of spawner swimming and redd construction (Gende et al., 2002; Mitchell and Lamberti, 2005; Moore et al., 2007). Additionally, the flux of SRP in Shrine Creek increased longitudinally downstream in the spawning reach and estuary after the salmon run, indicating that stored P from the stream bed may have been released (Moore et al., 2007). However, other non-salmon nutrient sources, such as fall leaf inputs (Meyer and Tate, 1983; Mitchell and Lamberti, 2005), may have contributed to these elevated SRP levels, as SRP was elevated in one site in the upper reach of Shrine Creek after the salmon run. Inconsistent patterns in SRP in the study reaches also may have been linked to factors affecting epilithon growth and overall P availability in streams, such as preferential incorporation of P by primary producers including epilithon, given the elevated N:P ratios in freshwater as a result of the presence of N-fixing red alder (*Alnus rubra*) (Naiman et al., 2002). Such

inconsistencies highlight the complexity of biogeochemical cycling in both streams and estuaries, particularly in how SDN may fit within the many factors affecting nutrient movement and sequestration.

High N:P ratios, indicative of P limitation, are generally thought to be found in freshwaters, compared to low N:P ratios, indicative of N limitation, which are generally found in saline waters (Schlesinger, 1997). In the study streams, N:P ratios generally decreased in all streams from upper freshwater reaches to lower freshwater reaches to estuaries. However, fluxes of  $\text{NH}_4^+$ -N were much larger in estuary reaches than in freshwater reaches, indicating a cumulative delivery of N from salmon (both from export and local inputs) that, coupled with unchanging fluxes of  $\text{NO}_3^-$ -N, may have tempered N limitation in the estuary reaches during the salmon run. Changes in surface water salinity, in which increased salinity has been linked to increased flux of  $\text{NH}_4^+$ -N from estuary sediments (Hopkinson et al., 1999), also do not appear to have driven the increase in flux of  $\text{NH}_4^+$ -N we found during the salmon run in the estuaries, as discharge did not vary greatly between reaches at each sample time (i.e., no dilution or concentration of salinity in the estuary sample sites compared to upstream freshwater sites, given that we sampled the estuaries in residual freshwater at low tide). Estuaries also receive large influxes of marine water with higher nutrient concentrations than freshwaters. Data on nutrient concentrations of marine water in southeastern Alaska are limited, but one study found average concentrations of  $\text{NO}_3^-$ -N,  $\text{NH}_4^+$ -N, and phosphate ( $\text{PO}_4^{3-}$ ) to be approximately  $341 \mu\text{g L}^{-1}$ ,  $24 \mu\text{g L}^{-1}$ , and  $114 \mu\text{g L}^{-1}$ , respectively, in nearshore marine water samples taken in the vicinity of our study estuaries (Orsi et al., 2000). The marine concentrations of  $\text{NO}_3^-$ -N and  $\text{PO}_4^{3-}$  were much higher than we found in freshwater and estuaries before and during the salmon runs. However, concentrations of  $\text{NH}_4^+$ -N in freshwater and estuaries at low tide did exceed the marine concentration during the salmon run. While salmon may have increased  $\text{NH}_4^+$ -N concentrations in estuaries relative to marine water, the biological importance of this salmon nutrient input may have been limited, given the already abundant and more consistent nutrient sources from marine water and estuarine processes.

#### **Salmon spawner influence on epilithon in streams and estuaries**

Responses in epilithon biomass in streams and estuaries to salmon spawners were quite variable within and across the study streams. Previous studies have found differing responses of epilithon to the presence of salmon spawners, with some studies

showing increased epilithon (e.g., Wipfli et al., 1999; Mitchell and Lamberti, 2005) and others showing reduced epilithon in salmon streams (e.g., Peterson and Foote, 2000; Moore et al., 2004). In our study, epilithon biomass in spawning reaches generally increased during the salmon run, but the magnitude of this increase varied among study streams. Although nutrients (N, P) were probably replete during the salmon run, epilithon responses to SDN may have been linked to irradiance, disturbance, and grazing. Average canopy cover in our study streams varied from 40–70%, and when coupled with declining light levels in late summer, could have limited epilithon growth, particularly in Shrine Creek, which had the highest level of canopy cover. Sediment disturbance from late-season floods (e.g., Wellnitz and Rader, 2003) and salmon spawning activity (e.g., Peterson and Foote, 2000), coupled with invertebrate grazing (e.g., Wipfli et al., 1999), also may have limited epilithon accrual in the freshwater reaches of our study streams and resulted in the variability apparent between streams.

Before salmon spawners arrived, epilithon biomass was higher in the estuaries compared to stream reaches, which is consistent with other studies of benthic production (Murphy, 1984) and not surprising given the higher nutrient concentrations in nearby marine ecosystems (Orsi et al., 2000). Contrary to our expectations, however, epilithon biomass declined in the estuaries when salmon spawners arrived. This reduction may reflect seasonal and environmental changes, such as declining light (e.g., Hill, 1996), increasing discharge (e.g., Peterson, 1996), and declining water temperature (e.g., Whitton, 1975); these changes are also experienced by the stream. In addition, dissolved oxygen and temperature did not vary substantially over the total sampling period. Physical disturbance of the sediments by adult salmon during swimming and reproduction (e.g., Peterson and Foote, 2000) may be particularly intense in the estuarine interface. All salmon must pass through estuaries to reach their freshwater spawning habitats, and several species will even spawn in estuaries (Thorpe, 1994), imparting substantial sediment disturbance. Pink salmon, the most abundance salmon in our study streams, are particularly prone to spawning at the stream-estuary interface (Morrow, 1980). Such disturbance by spawners was evident in the estuaries we studied (A. D. Cak, personal observation). Estuaries also serve as transitional holding areas for spawning salmon during their upstream migration, and thus sediments may be subject to additional disturbance from bidirectional swimming during tidal change. Finally, invertebrate grazing on SDN-influenced epilithon may be intense during the salmon run

(e.g., Wipfli et al., 1999). Several studies have documented increased abundance of invertebrates with addition of SDN (Wipfli et al., 1999; Gende et al., 2002; Naiman et al., 2002) that also may have led to decreases in epilithon in estuaries.

## Conclusions

Spawning migrations of Pacific salmon can alter the fluxes of important dissolved nutrients in streams and their estuaries. However, this large flux of nutrients was not accompanied by a consistent or immediate response in epilithon, as we observed significant variation between streams and their associated estuaries, as well as among streams. Although ‘bottom-up’ effects of salmon-derived nutrients have been shown to strongly influence freshwater food webs, a similar effect on estuarine benthic autotrophs was not evident in our study. As transitional habitats, estuaries are dynamic environments that are strongly influenced by both tidal fluctuations that daily replenish nutrients from nutrient-rich marine water and biogeochemical processes within estuarine sediments. Therefore, although estuaries are clearly important to the salmon life cycle by providing both rearing habitat and a physical link between spawning streams and the marine environment, an ecological reliance upon salmon nutrients does not appear to be likely.

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