



Salmon-derived nutrient and organic matter fluxes from a coastal catchment in southeast Alaska

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Abstract

1. Salmon are important vectors for biogeochemical transport across ecosystem boundaries. Here we quantified salmon contributions to annual catchment fluxes of nutrients (N and P) and organic matter (C, N, and P) from a forested catchment in coastal southeast Alaska.
2. Concentrations of ammonium and soluble reactive phosphorus increased by several orders of magnitude during spawning and were significantly correlated with spawning salmon densities. Nitrate concentrations increased modestly during spawning and were not significantly correlated with salmon densities. Salmon had a modest legacy effect on inorganic N and P as evidenced by elevated streamwater concentrations past the end of the spawning period.
3. Dissolved organic carbon concentrations did not respond to the presence of salmon; however, concentrations of dissolved organic nitrogen and phosphorus showed a significant positive relationship to salmon densities. Changes in spectroscopic properties of the bulk streamwater dissolved organic matter pool indicated that streamwater dissolved organic matter became less aromatic and biolabile during spawning.
4. On an annual basis, salmon were the dominant source of streamwater fluxes of inorganic nutrients, accounting for 92%, 65%, and 74% of annual streamwater fluxes of ammonium, nitrate, and soluble reactive phosphorus, respectively. In contrast, fluxes of organic matter were dominated by catchment sources with salmon accounting for <1% of the annual catchment flux of dissolved organic carbon and 12% and 15% of the annual fluxes of dissolved organic nitrogen and phosphorus respectively.
5. These findings indicate that, in small coastal catchments, salmon can be a quantitatively important source of dissolved streamwater nutrients with implications for productivity in downstream estuarine ecosystems.

KEYWORDS

biogeochemistry, catchment, nutrients, organic matter, Salmon

1 | INTRODUCTION

Migratory animals can transport organic matter and nutrients across ecosystem boundaries, thereby influencing the productivity and structure of recipient ecosystems (Nelson & Reynolds, 2015; Polis, Anderson, & Holt, 1997). These biogeochemical subsidies are particularly important to oligotrophic ecosystems, such as when nutrients are transported from the ocean to desert islands (Spiller et al., 2010) or temperate forested streams (Richardson, Zhang, & Marczak, 2010). Pacific salmon (*Oncorhynchus* spp.) are effective vectors for biogeochemical transport across ecosystem boundaries because the annual migration of salmon moves large quantities of marine-derived nutrients (MDN) from marine to freshwater ecosystems (Chaloner, Lamberti, Cak, Blair, & Edwards, 2007; Mitchell & Lamberti, 2005; Tiegs et al., 2009). However, these MDN inputs vary greatly across space (Janetski, Chaloner, Tiegs, & Lamberti, 2009) and time (Fellman, Hood, Edwards, & D'Amore, 2008) making it challenging to understand the significance of these nutrient subsidies for seasonal and annual ecosystem processes at the catchment scale (Holtgrieve & Schindler, 2011).

Salmon release nutrients, particularly ammonium ($\text{NH}_4\text{-N}$) and soluble reactive phosphorus (SRP), to streams via endogenous excretion across gill membranes and leaching from gametes and decomposing carcasses (Gende, Edwards, Willson, & Wipfli, 2002). The resulting increase in streamwater nutrient concentrations has been shown to be proportionate to salmon density (Levi et al., 2011; Tiegs et al., 2011). Marine-derived nutrients can be incorporated into aquatic food webs by direct consumption of salmon carcasses by invertebrates and fish (Chaloner, Martin, Wipfli, Ostrom, & Lamberti, 2002) or uptake of nutrients by benthic bacterial communities (Rex & Peticrew, 2008) and epilithon (Chaloner et al., 2007). In freshwater ecosystems, this nutrient subsidy can significantly increase biofilm and macroinvertebrate productivity (Johnston, MacIsaac, Tschaplinski, & Hall, 2004; Tiegs et al., 2009; Verspoor, Braun, Stubbs, & Reynolds, 2011; Wipfli, Hudson, & Caouette, 1998), although this increased productivity can be offset to some extent by physical disturbances associated with spawning salmon (Janetski et al., 2009; Verspoor, Braun, & Reynolds, 2010). Growth rates for juvenile salmonids (Wipfli, Hudson, Caouette, & Chaloner, 2003) and bird densities in estuarine bird communities (Field & Reynolds, 2011) can also be enhanced by salmon nutrient subsidies.

In addition to inorganic nutrients, salmon carcasses also release dissolved organic matter (DOM) to streams and influence concentrations of dissolved organic forms of C, N, and P (Collins, Moerke, Chaloner, Janetski, & Lamberti, 2011; Hood, Fellman, & Edwards, 2007). These organic subsidies alter the chemical quality of the bulk streamwater DOM pool during spawning because salmon-derived DOM is enriched in amino acids and low in aromatic, lignin-rich material typical of plant-derived DOM (Fellman, D'Amore, Hood, & Boone, 2008; Hood et al., 2007). From an ecological standpoint, organic matter that is high in proteinaceous material is more readily metabolized by freshwater and estuarine microbial communities (Fellman, Hood, & Spencer, 2010).

The annual salmon migration is a quantitatively important source of nutrients to coastal catchments in Alaska (Cak, Chaloner, & Lamberti, 2008; Tiegs et al., 2011). For example, Moore et al. (2007) found that, during spawning, the magnitude of nutrients imported by salmon was correlated with catchment export of total N and P, with salmon accounting for as much as 35–65% of stream fluxes of total N and P, respectively. However, the relative proportion of salmon-derived nutrients in the annual nutrient budgets of catchments is still not well understood because MDN studies have generally not been performed on an annual timescale in a basin-wide context where other catchment nutrient sources are considered (e.g. Tiegs et al., 2011). The extent to which MDN impact the speciation (organic versus inorganic) of catchment nutrient fluxes is also unknown. Without salmon, streamwater fluxes of N from forested catchments are typically dominated by organic N (e.g. Campbell et al., 2000), leaching losses of which are not subject to the tight biotic controls that limit the movement of inorganic N across the terrestrial-aquatic interface. Failure to examine MDN inputs together with other catchment inputs limits our ability to understand the ecosystem significance of either source and the extent to which spawning salmon influence the export of riverine nutrients and organic matter to estuarine ecosystems.

This study evaluated the importance of salmon-derived material in the overall catchment export budget for nutrients and organic matter from a forested catchment in coastal southeast Alaska. We sampled streamwater for dissolved C, N, and P in an upstream reference reach (above barrier waterfalls) and downstream salmon-bearing reach of Peterson Creek to quantify the contribution of salmon-derived nutrients to annual biogeochemical export from the catchment. We further used spectroscopic indices (UV absorbance and fluorescence index) to evaluate changes in the chemical quality of streamwater DOM associated with inputs of salmon-derived DOM to Peterson Creek. Our goal was to assess the extent to which spawning salmon alter seasonal and annual catchment biogeochemical fluxes to coastal ecosystems. Our hypothesis was that salmon-derived nutrients were the dominant contributor to annual catchment fluxes of inorganic N and P, whereas catchment sources such as vegetation and organic soils were the dominant source of organic species exported in streamwater. Our findings allow us to evaluate how MDN impact catchment biogeochemical fluxes in a region that currently supports healthy runs of Pacific salmon and is undergoing climate-driven changes in coastal catchment hydrology (Shanley et al., 2015).

2 | METHODS

2.1 | Site description and study design

Streamwater was collected from Peterson Creek, located about 30 km north of Juneau, southeast Alaska (Figure 1). The Peterson Creek catchment is located on the northern fringe of the perhumid coastal temperate rainforest that extends from British Columbia to the northern Gulf of Alaska. The study area has a maritime climate

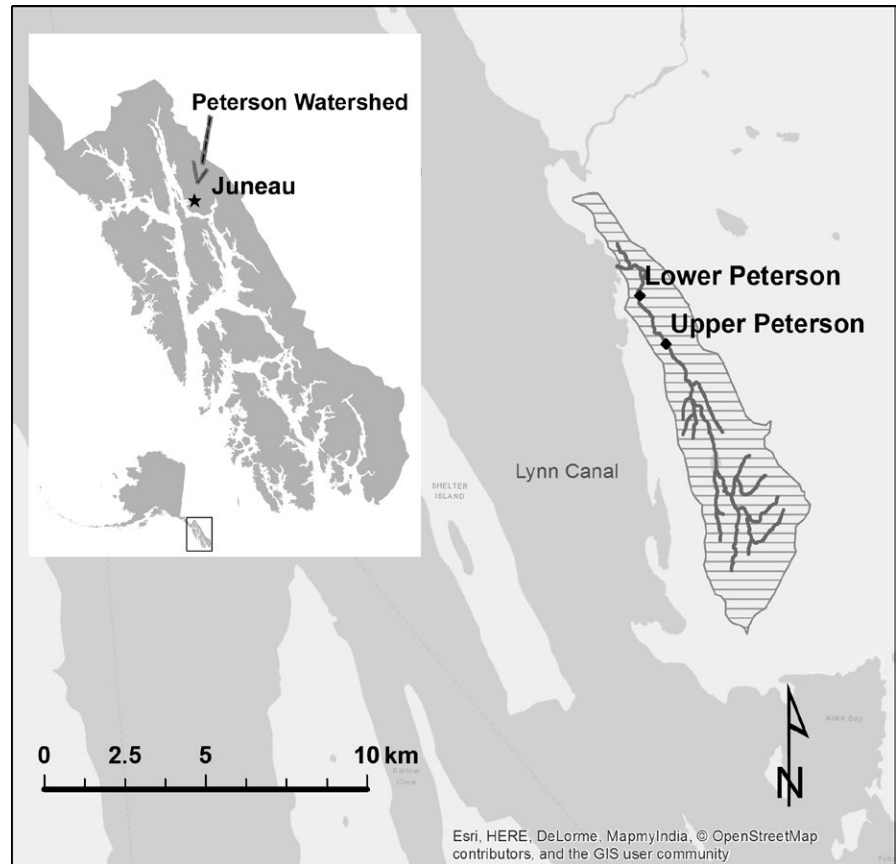


FIGURE 1 Map showing the location of the study sites in the Peterson Creek catchment near Juneau, Alaska

with mild winters and cool, wet summers. Peterson Creek is a low gradient stream with 34% of its 25 km² catchment area covered by wetlands, resulting in streamwater concentrations of dissolved organic carbon (DOC) that typically exceed 5 mg C/L throughout the year (Hood et al., 2007). The lower reaches of the catchment are uplifted marine terraces with some colluvial and alluvial sediments and are dominated by a mixed coniferous forest of *Picea sitchensis* and *Tsuga heterophylla*. Mean daily streamflow ranges from 0.1 to >12 m³/s and typically peaks during the autumn rainy season.

Streamwater was collected from a lower and upstream site on Peterson Creek (Figure 1). The upstream site (upper Peterson) is above a natural barrier waterfall that prevents the upstream migration of spawning salmon. The downstream site (lower Peterson) receives large salmon runs that typically occur from mid-July through mid-September. The barrier waterfall allows a direct comparison between the upstream and downstream reaches, a commonly used study design for evaluating the effects of spawning salmon on stream ecosystems (e.g. Mitchell & Lamberti, 2005; Chaloner et al., 2007).

Peterson Creek receives annual anadromous runs of coho (*Oncorhynchus kisutch*), pink (*Oncorhynchus gorbuscha*), and chum salmon (*O. keta*). Spawning usually begins in mid-July and extends through September with a peak in August. Previous estimates of spawning density in Peterson Creek range from 0 to 0.53 fish/m² in 2001 (Mitchell & Lamberti, 2005), with wet mass for the total run (all species) estimated at >200,000 kg over multiple years (Bethers, Munk, & Seifert, 1995). During this study, spawning salmon were

first observed at the lower Peterson site on the 13 July sampling date and the majority of carcasses were washed downstream from the site by early September (Figure 2). However, the largest spawning densities were observed at lower Peterson between 27 July and 19 August.

2.2 | Field and analytical laboratory methods

Streamwater samples were collected at both sites once or twice per month outside of the spawning season. During spawning, streamwater samples were collected at lower Peterson approximately three times per week on the same day that salmon counts occurred. Streamwater was sampled once per week at the upper Peterson site. Three replicate water samples were collected and filtered in the field through pre-combusted Whatman GF/F glass-fibre filters (nominal pore size 0.7 µm). All water samples were stored in the refrigerator in high-density poly-ethylene bottles, and laboratory analyses occurred within 1 week of collection.

Concentrations of DOC and total dissolved N (TDN) were analysed by high-temperature catalytic oxidation on a Shimadzu TOC/TN-V analyser with a lower detection limit of 0.3 mg C/L for DOC and 0.1 mg N/L for TDN. Ion chromatography (Dionex ICS-1500 and 2500) was used to measure NH₄-N (lower detection limit of c. 5.0 µg N/L) and NO₃-N (lower detection limit of c. 2.0 µg N/L). Dissolved organic N (DON) was calculated as the difference between TDN and dissolved inorganic N (DIN = NH₄-N + NO₃-N). Soluble reactive

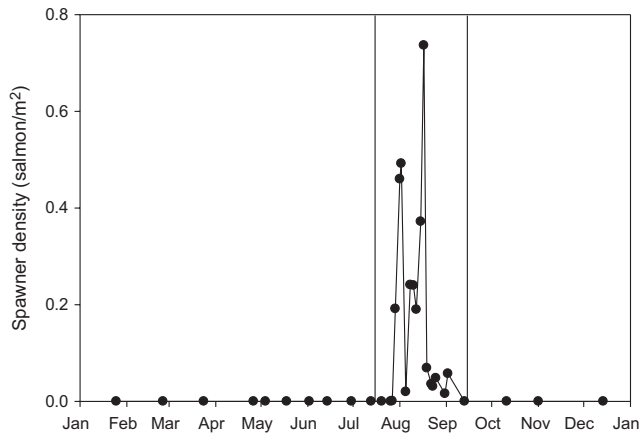


FIGURE 2 Time series of salmon densities (salmon m^{-2}), mainly as pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon, for lower Peterson Creek during the entire sampling period. Solid lines indicate the time period when salmon-derived C, N, and P fluxes were calculated

phosphorus was measured using the ascorbic acid method (Murphy & Riley, 1962) with a 10 cm quartz flow-through cell (lower detection limit of 0.5–1.0 μg P/L). Total dissolved phosphorus (TDP) was measured using a persulfate digestion combined with the ascorbic acid method (Valderrama, 1981), and dissolved organic phosphorus (DOP) was calculated as the difference between TDP and SRP.

The specific UV absorbance of DOC ($SUVA_{254}$), an indicator of aromatic C content, was measured on streamwater samples using a Genesis spectrophotometer at 254 nm (Weishaar et al., 2003). In general, $SUVA_{254}$ values in surface waters typically range from 2 to 5, corresponding to an aromatic C content of 15–35%. The fluorescence index (FI) was measured on a fluoromax-3 (Jobin Yvon Horiba) fluorometer, as the ratio of emission intensities at 470 nm and 520 nm produced at excitation 370 nm (Cory & McKnight, 2005). High FI values (1.7–1.8) indicate that DOM derived from salmon or algal/bacterial leachate and low values indicate that DOM derived from terrestrial plant and soil organic matter (Cory & McKnight, 2005; Hood et al., 2007; McKnight et al., 2001).

Spawning salmon density was estimated by visually counting the number of live salmon and carcasses within a fixed stream reach (50 m^2) following the procedures described in Chaloner et al. (2004). Adult spawners were estimated from two separate, demarcated reaches near the lower Peterson sampling site. Spawning salmon were visually counted approximately twice per week during the July through September spawning period. To estimate streamflow, we conducted manual measurements of streamflow across a range of stream stage to develop a stage-streamflow relationship. Stream stage was continuously measured using a stilling well equipped with a pressure transducer, and the rating curve was applied to estimate streamflow from stage.

2.3 | Catchment fluxes

We used a direct comparison of concentrations at the lower and upper Peterson sites to calculate salmon and non-salmon fluxes of

DOC, N, and P from the Peterson Creek catchment for the period 1 January 2005 to 31 December 2005. We used FLUXMASTER (Schwarz, Hoos, Alexander, & Smith, 2006) to calculate a non-salmon catchment flux using the concentration data from the upper Peterson site. The FLUXMASTER model relates the logarithm of nutrient concentration to the logarithm of daily streamflow and includes sine and cosine functions to account for seasonal patterns in nutrient concentrations. The additional seasonal terms were only included when they were statistically significant beyond the regression of the measured concentrations and streamflow. Daily fluxes are calculated as the product of the estimated daily concentration and measured daily streamflow. To calculate the salmon-derived nutrient fluxes, we subtracted the upstream from the downstream concentrations during the roughly 2-month period when salmon were present in the stream (13 July to 14 September) to generate a salmon-derived nutrient and DOC concentration (Figure 2). Salmon-derived nutrient concentrations were then used to calculate a salmon-derived flux using the sample–discharge interpolation method of Hinton, Schiff, and English (1997). The standard deviation for monthly and annual salmon-derived nutrient fluxes was calculated by taking the square root of the average of the sample variances.

2.4 | Data analyses

We used multiple, two-sample *t*-tests assuming unequal variances to compare C, N, and P concentrations between the upstream and downstream reach both during and outside the spawning salmon period to assess the influence of spawning salmon on stream biogeochemistry in the downstream reach. Since multiple *t*-tests were performed, a Bonferroni correction was used and α was set to 0.008. Linear regression was used to assess the relationship between C, N, and P concentrations and spot measurements of spawning density. If necessary, data were log transformed to satisfy the basic assumptions of regression analyses. All statistical analyses were performed in SPSS software.

3 | RESULTS

3.1 | Streamwater concentrations of C, N, and P

Streamwater concentrations of inorganic N and P species were low to below detection at both lower and upper Peterson outside the 2-month period when spawning salmon were present (Figure 3a–c). Discharge had little to no impact on NH_4 -N and SRP concentrations; however, concentrations of NO_3 -N increased during snowmelt in early May (Figure 3a–c). Concentrations of NH_4 -N and SRP increased by several orders of magnitude at the lower Peterson site during spawning but did not show a corresponding increase at the upper site above the fish barrier (Figure 3a,c). Concentrations of NO_3 -N also increased by up to an order of magnitude at the lower side during spawning, although modest increases in NO_3 -N concentrations were also seen at the upper site during this period (Figure 3b). For both NH_4 -N and SRP, streamwater concentrations

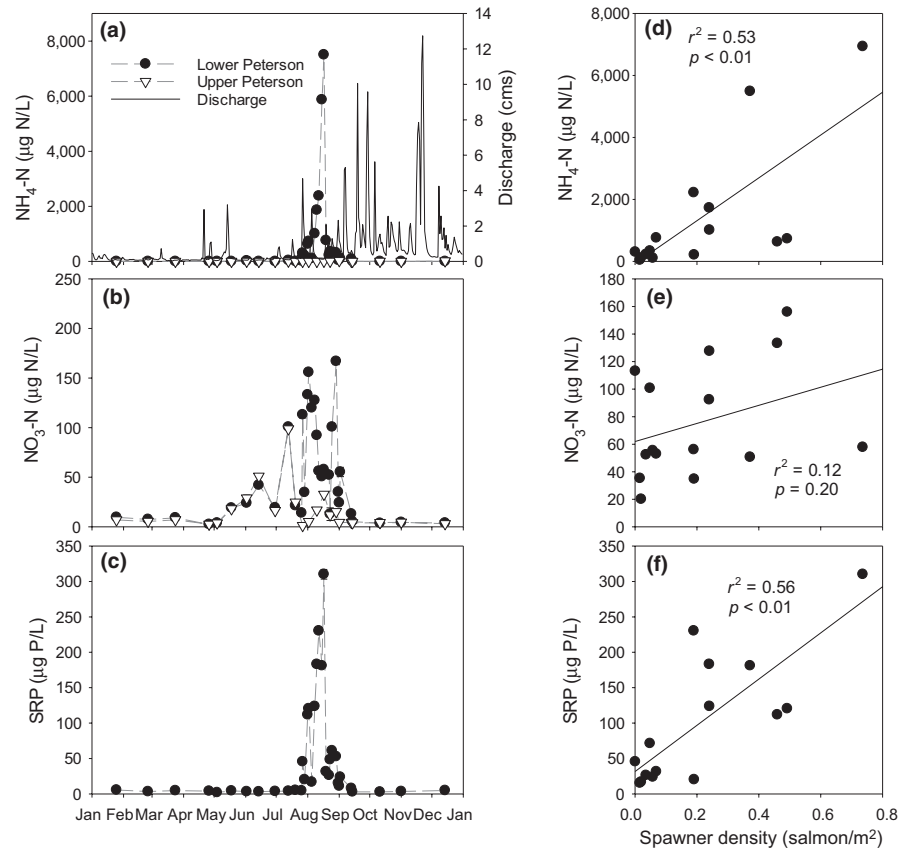


FIGURE 3 Mean (± 1 SE) streamwater concentrations of (a) ammonium ($\text{NH}_4\text{-N}$), (b) nitrate ($\text{NO}_3\text{-N}$), and (c) soluble reactive phosphorus (SRP) for lower (salmon influenced) and upper (above barrier falls) Peterson Creek, mean daily discharge (panel a only) and the relationship between salmon carcass density and streamwater concentrations of (d) $\text{NH}_4\text{-N}$, (e) $\text{NO}_3\text{-N}$ and (f) SRP for lower Peterson Creek during the year-long sampling period. Note difference in scale for $\text{NH}_4\text{-N}$

TABLE 1 Mean (± 1 SE) of surface water concentrations for Peterson Creek for the reach below (lower Peterson) and above (upper Peterson) the barrier waterfall during 2005

	Lower Peterson Non-spawning period	Upper Peterson Non-spawning period	Lower Peterson Spawning period	Upper Peterson Spawning period
$\text{NH}_4\text{-N}$ ($\mu\text{g N/L}$)	5.5 (2.3)	3.4 (1.7)	1,084.7 (416.1)	6.7 (3.8)
$\text{NO}_3\text{-N}$ ($\mu\text{g N/L}$)	35.7 (12.9)	19.5 (12.7)	70.5 (9.6)	23.6 (18.3)
SRP ($\mu\text{g P/L}$)	4.0 (3.5)	2.8 (0.2)	83.0 (19.0)	2.6 (0.2)
DOC (mg C/L)	6.8 (0.8)	7.4 (0.8)	12.1 (0.5)	12.9 (0.8)
DON (mg N/L)	0.2 (0.1)	0.2 (0.1)	1.2 (0.3)	0.2 (0.1)
DOP ($\mu\text{g P/L}$)	9.0 (1.2)	8.7 (0.8)	40.9 (10.1)	9.8 (1.4)
TDN (mg N/L)	0.2 (0.1)	0.2 (0.1)	2.3 (0.8)	0.3 (0.1)
TDP ($\mu\text{g P/L}$)	13.1 (1.2)	11.9 (0.8)	123.9 (28.4)	12.4 (1.3)

$\text{NH}_4\text{-N}$, ammonium; $\text{NO}_3\text{-N}$, nitrate; SRP, soluble reactive phosphorus; DON, dissolved organic nitrogen; DOP, dissolved organic phosphorus; DOC dissolved organic carbon; TDN, total dissolved N; TDP, total dissolved P

at the lower site were significantly correlated with densities of spawning salmon (Figure 3d,f), whereas $\text{NO}_3\text{-N}$ was not correlated with spawning density (Figure 3e). During the spawning period, there were significant differences in streamwater concentrations of $\text{NH}_4\text{-N}$ ($t_{21} = 2.08$, $p < 0.001$) and SRP ($t_{21} = 2.08$, $p < 0.001$) but not $\text{NO}_3\text{-N}$ ($t_{16} = 2.12$, $p = 0.025$), between upper and lower Peterson (Table 1). Outside of the spawning period, there were no significant difference between streamwater concentrations of $\text{NO}_3\text{-N}$ ($t_{21} = 2.08$, $p = 0.392$), $\text{NH}_4\text{-N}$ ($t_{20} = 2.09$, $p = 0.474$) and SRP ($t_{17} = 2.11$, $p = 0.146$) between the two reaches. Interestingly,

concentrations of SRP ($t_3 = 5.86$, $p = 0.01$) and $\text{NO}_3\text{-N}$ ($t_3 = 5.22$, $p = 0.03$) were higher in salmon-impacted lower Peterson in the 3-month period immediately following spawning (October–December). However, for both analytes the absolute magnitude of the difference in concentration between the sites was relatively small ($<10 \mu\text{g/L}$).

Concentrations of DON and DOP in the lower reach increased substantially during spawning, although the increase was less pronounced than for inorganic forms of N and P (Figure 4a,b). Concentrations of DOC varied seasonally, with

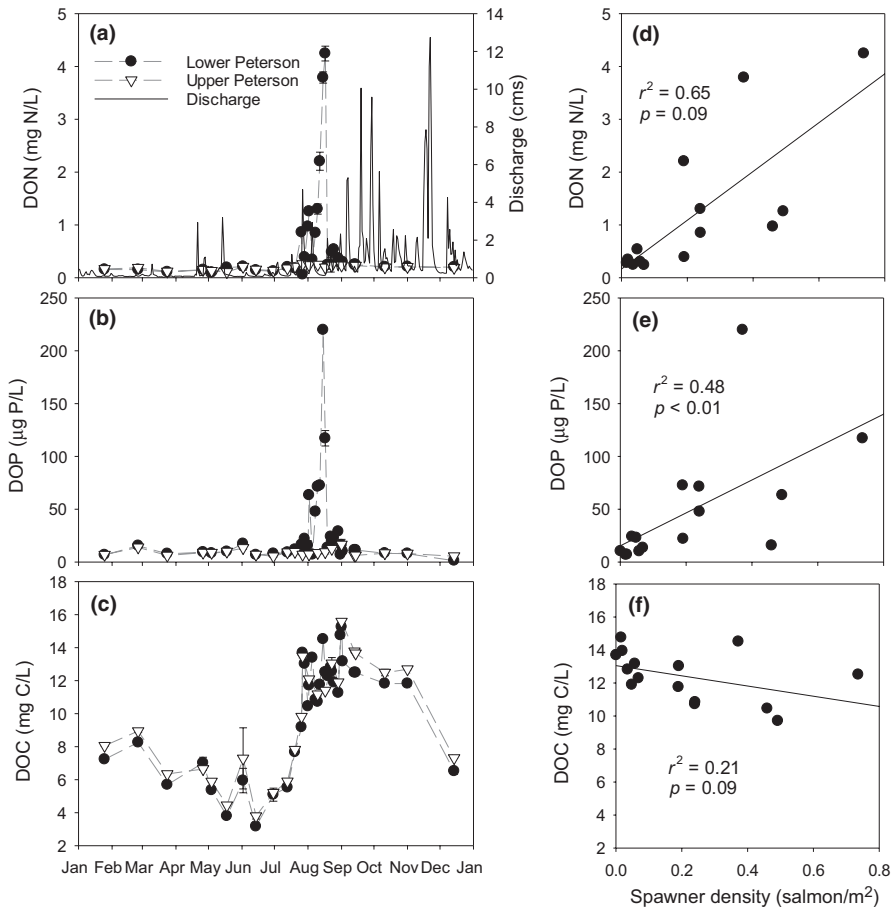


FIGURE 4 Mean (± 1 SE) streamwater concentrations of dissolved organic (a) nitrogen (DON), (b) phosphorous (DOP), and (c) carbon (DOC) for lower (salmon influenced) and upper (above barrier falls) Peterson Creek, mean daily discharge (panel a only) and the relationship between salmon carcass density and streamwater concentrations of (d) DON, (e) DOP and (f) DOC for lower Peterson Creek during the year-long sampling period. Note difference in units for DOP

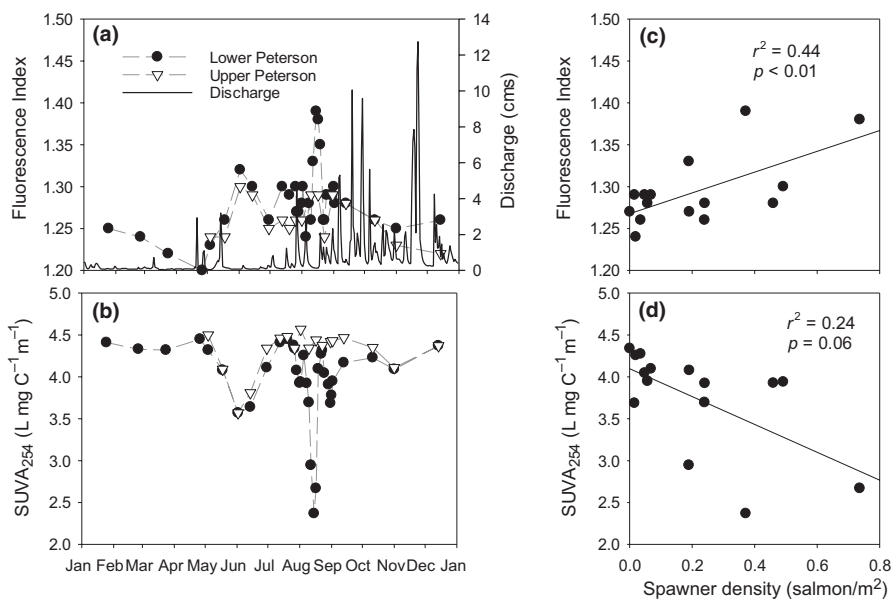


FIGURE 5 Streamwater (a) fluorescence index (FI) and (b) specific UV absorbance of dissolved organic carbon (SUVA₂₅₄) values for lower (salmon influenced) and upper (above barrier falls) Peterson Creek, mean daily discharge (panel a only) and the relationship between salmon carcass density and values of (c) FI and (d) SUVA₂₅₄ for lower Peterson Creek during the year-long sampling period

higher concentrations during summer and autumn, but demonstrated little difference between the upstream and downstream sites over the whole sample period (Figure 4c). Concentrations of DON and DOP were significantly related to salmon densities during spawning, while DOC concentrations showed no relationship to salmon densities (Figure 4d,e). Overall, there was no

significant difference between dissolved organic C, N, and P at the upper and lower Peterson sites during the non-spawning period (all $t_{19} > 2.07$, $p > 0.59$); During the spawning period, there was still no significant difference between organic C ($t_{21} = 2.14$, $p = 0.817$), N ($t_{21} = 2.08$, $p = 0.023$), and P ($t_{21} = 2.08$, $p = 0.014$) concentrations between the two sites; however, concentrations of DON and

DOP were 4–5 \times higher in the salmon-bearing reach compared to the non-salmon reach (Table 1).

Although DOM concentrations were not significantly impacted by spawning salmon, the spectroscopic characteristics of the bulk streamwater DOM pool did show a marked change during spawning. Outside of the spawning season, the fluorescence index for DOM was below 1.3 at both the upper and lower Peterson (Figure 5a), which is consistent with a catchment soil organic matter source of DOM (Fellman, D'Amore, et al., 2008). During the spawning season, FI values increased by >0.15 at the lower site, indicating a higher proportion of DOM derived from autochthonous sources such as salmon and algal material within the bulk streamwater DOM pool (Hood et al., 2007). Similarly, the $SUVA_{254}$ values for DOM decreased from c. 4 to as low as 2.4 at the lower site during spawning (Figure 5b). Overall, FI and $SUVA_{254}$ values in lower Peterson were significantly correlated to spawning density suggesting salmon-derived DOM significantly impacts the spectroscopic composition of the DOM pool in lower Peterson Creek (Figure 5c,d).

During the spawning period, total dissolved N increased tenfold whereas total dissolved P increased $>5\times$ (Table 1). The speciation of both TDN and TDP also shifted from being predominantly in the organic form ($>95\%$ for DON and 76% for DOP) outside of spawning to predominantly in the inorganic form (52% for DIN and 67% for SRP) during spawning. This shift in speciation was largely driven by pronounced increases in streamwater NH_4-N and SRP during spawning.

3.2 | Dissolved organic matter and nutrient fluxes from salmon and catchment sources

Streamwater fluxes of dissolved inorganic N and P were dominated by salmon-derived nutrients exported out of the catchment during the spawning period (July–early September; Figure 6a–c). This was particularly true for NH_4-N and SRP for which 92 and 74% of the respective annual fluxes were derived from salmon (Table 2). Background catchment fluxes of NO_3-N were comparatively higher, but salmon-derived NO_3-N still accounted for 65% of the annual catchment flux of NO_3-N (Table 2). Dissolved organic C, N, and P

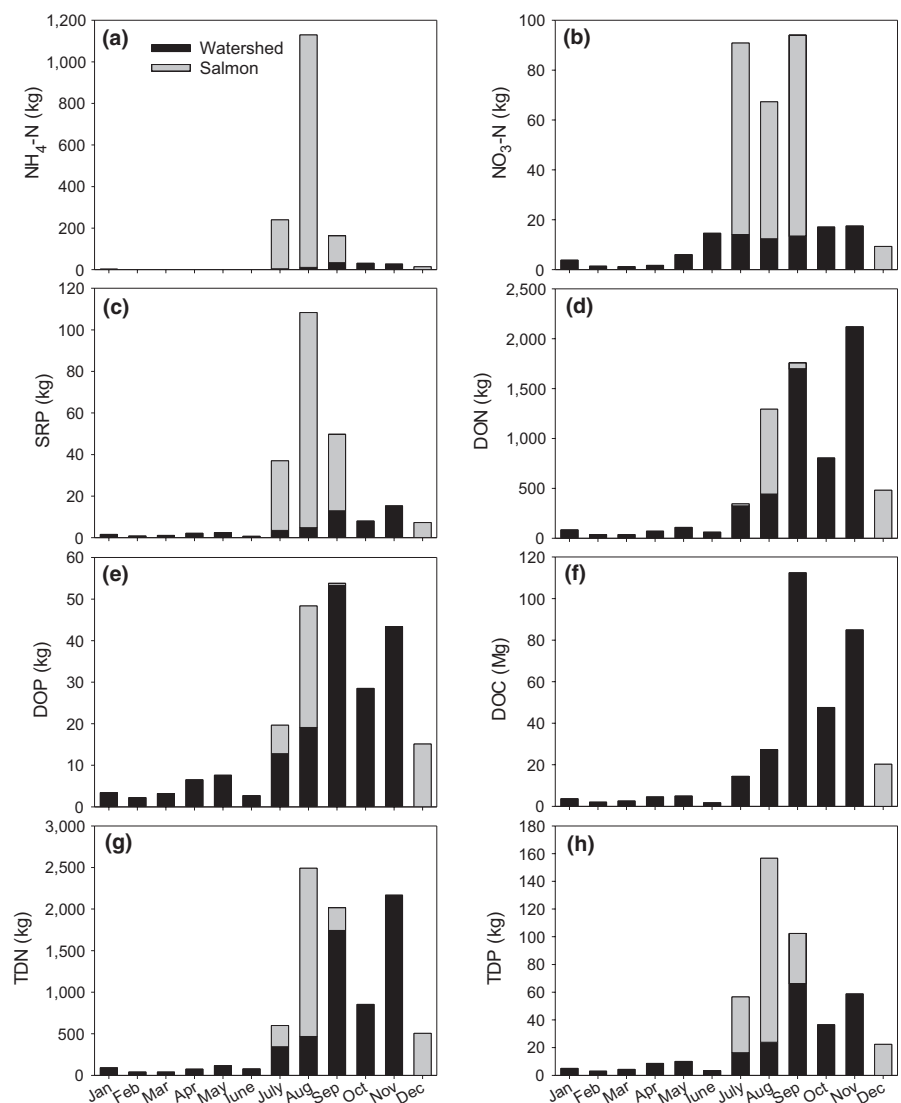


FIGURE 6 Monthly catchment and salmon fluxes (kg) of (a) ammonium (NH_4-N), (b) nitrate (NO_3-N), (c) soluble reactive phosphorus (SRP), (d) dissolved organic nitrogen (DON), (e) dissolved organic phosphorous (DOP), (f) dissolved organic carbon (DOC), (g) total dissolved N (TDN), and (h) total dissolved P (TDP) in Peterson Creek. Note the difference in units for DOC (Mg)

	Non-salmon flux, kg/year	Salmon flux, kg/year	Catchment flux, kg/year	% Salmon-derived
NH ₄ -N	126 (633)	1,485 (28)	1,611	92
NO ₃ -N	113 (211)	212 (7)	325	65
SRP	61 (12)	174 (3)	235	74
DOC	325,461 (56,885)	717 (53)	326,178	<1
DON	6,277 (758)	855 (19)	7,132	12
DOP	197 (47)	35 (1)	232	15
TDN	6,516 (2,355)	2,552 (40)	9,068	28
TDP	258 (44)	209 (3)	467	45

NH₄-N, ammonium; NO₃-N, nitrate; SRP, soluble reactive phosphorus; DON, dissolved organic nitrogen; DOP, dissolved organic phosphorus; DOC dissolved organic carbon; TDN, total dissolved N; TDP, total dissolved P

fluxes were dominated by catchment sources, although salmon contributions to streamwater DON and DOP fluxes were substantial during the salmon runs (Figure 6d–f). Annually, salmon-derived N and P accounted for <20% of streamwater DON and DOP fluxes, while salmon-derived C resulted in <1% of the catchment DOC flux (Table 2).

Fluxes of total dissolved N and P from Peterson Creek were partially to largely derived from salmon during July–September when salmon were present (Figure 6g,h). On an annual basis, salmon accounted for 28% of the catchment flux of TDN and 45% of the catchment flux of TDP (Table 2). The speciation of total dissolved N and P fluxes was similar, with organic N (85%) and organic P (76%) accounting for the bulk of the annual fluxes of TDN and TDP.

4 | DISCUSSION

4.1 | Streamwater nutrient concentrations

The presence of salmon in Peterson Creek significantly influenced streamwater inorganic N (as NH₄-N) and P (as SRP) concentrations, which is consistent with previous studies in Alaska (Chaloner et al., 2004, 2007; Hood et al., 2007; Mitchell & Lamberti, 2005; Moore et al., 2007), British Columbia (Johnston et al., 2004), and the Great Lakes (Collins et al., 2011), as well as a meta-analysis of data from studies in the U.S.A., Canada, and Japan (Janetski et al., 2009). The fact that streamwater concentrations of NH₄-N and SRP were strongly positively correlated with spawning salmon density in Peterson Creek indicates that spawners were a quantitatively significant source of these nutrients. However, NO₃-N, which is not directly released from salmon like NH₄-N and SRP, showed a comparatively muted increase during spawning and was not significantly correlated with spawning density. The observed increases in streamwater NO₃-N concentrations when fish were present were probably a result of nitrification of salmon-derived NH₄-N, delays in which may have contributed to observed short-term nutrient legacy patterns where low salmon densities were associated with elevated NO₃-N concentrations (Levi et al., 2011).

TABLE 2 Annual catchment (± 1 SE) and salmon nutrient (inorganic and organic species of N and P) and DOC fluxes (± 1 SE) in Peterson Creek

Unlike for inorganic N and P, there was no significant difference in DOC concentrations between the upper and lower Peterson sites when salmon were present. This finding is consistent with previous studies showing that spawning salmon are not a strong control on streamwater DOC concentrations in forested catchments (Chaloner et al., 2007; Hood et al., 2007; Mitchell & Lamberti, 2005; Sarica, Amyot, Hare, Doyon, & Stanfield, 2004). The lack of correlation between streamwater DOC and spawner densities also implies that the strong seasonal variation in DOC at both lower and upper Peterson was driven by catchment sources of DOC rather than by inputs of salmon-derived DOM. Salmon contributions to dissolved organic forms of N and P in streamwater have rarely been investigated and we found that, unlike for DOC, salmon densities had a strongly positive correlation with streamwater concentrations of DON and DOP.

The salmon-driven changes in streamwater concentrations of inorganic N and P that we observed were larger in magnitude than previous studies that used salmon carcass additions to the stream and thus did not include nutrient and organic matter released from live fish (Claeson, Li, Compton, & Bisson, 2006; Wipfli et al., 1998). This is consistent with a meta-analysis of data from 79 streams showing that the slope of the relationship between dissolved N and P fish biomass/unit discharge was 5–10 \times higher for natural fish runs compared to carcass additions due to nutrient excretion by live salmon (Janetski et al., 2009). Similarly, streamwater concentrations of inorganic N and P were found to be far more tightly correlated with live salmon densities compared to salmon carcasses in streams on Prince of Wales Island in Alaska (Levi et al., 2011; Tiegs et al., 2011). The strong relationship between dissolved inorganic N (mainly NH₄-N) and spawning salmon density in our study and others suggests that in-situ sensors that continuously monitor streamwater concentrations of inorganic N could be a useful tool for estimating temporal changes in the total density of salmon within a particular stream reach.

In temperate forested ecosystems minimally impacted by anthropogenic nutrient inputs, streamwater N and P export are typically dominated by DON and DOP because inorganic N and P are strongly retained within terrestrial ecosystems (Perakis & Hedin, 2001). Background concentrations of inorganic N and P in Peterson

Creek were consistently low ($<10 \mu\text{g/L}$) before the spawning season, but the presence of fish resulted in a shift from organic to inorganic N and P species, particularly $\text{NH}_4\text{-N}$ and SRP. These speciation changes are illustrated by ratios of DIN to DON in streamwater, which shifted from 0.2 before the spawning season to 1.0 during the spawning season. The average SRP:DOP similarly increased from 1.1 to 2.0 before and during spawning. The speciation of streamwater N and P that we documented during the spawning season approaches that of urban and agricultural catchments where inorganic forms of N and P dominate the streamwater nutrient pool (Seitzinger, Harrison, Dumont, Beusen, & Bouwman, 2005; Stanley & Maxted, 2008).

The spectroscopic changes in the DOM pool that we observed during spawning are consistent with the observed increases in concentrations of DON and DOP during spawning and indicate that DOM derived from salmon is less aromatic and more N- and P-rich compared to DOM from background catchment sources. The decrease in the SUVA of streamwater DOM observed during spawning indicates that the aromatic C content of the streamwater DOM pool decreased from $>30\%$ before spawning to as low as 18% during spawning (Weishaar et al., 2003). That these shifts in DOM quality were not matched by an increase in streamwater DOC concentrations during spawning suggests that catchment sources still dominated the bulk streamwater DOM pool and that increased metabolism of streamwater DOM probably offset some or all of the inputs of salmon-derived DOM to Peterson Creek. The increased metabolism of DOC but not necessarily DON and DOP during spawning could be driven by both enhanced microbial assimilation of organic C and inorganic N and P supplied by salmon (e.g. (Sobczak, Findlay, & Dye, 2003; Zarnetske, Haggerty, Wondzell, & Baker, 2011) and a stream metabolic priming effect associated with additions of biolabile salmon-derived organic matter to the streamwater DOM pool (e.g. (Hotchkiss et al., 2015). These pathways of salmon-driven DOM respiration would ultimately contribute to the pronounced increase in stream ecosystem respiration associated with spawning salmon (Holtgrieve & Schindler, 2011; Levi et al., 2013).

4.2 | Annual C, N, and P fluxes from salmon and catchment sources

Streamwater fluxes of dissolved N and P were greatly enhanced by spawning salmon during July–September when background catchment fluxes of inorganic N and P were relatively low due to low streamflow (July and August) and high biotic demand in terrestrial ecosystems. During the c. 8 weeks salmon were present, salmon-derived nutrients accounted for 50% and 66% of catchment fluxes of total dissolved N and P respectively, which is consistent with previous research in Fish Creek (near Juneau in southeast Alaska), where salmon nutrients made up an average of 43% of the TDN flux and 71% of the TDP flux during spawning (Mitchell & Lamberti, 2005). In the Wood River in western Alaska, (Moore et al., 2007) reported a comparable range in spawner densities ($0\text{--}0.6 \text{ fish/m}^2$) and reported a similar impact of salmon on dissolved inorganic N and P. Moore et al. (2007) also showed that salmon are an important

driver of particulate N and P fluxes due to bioturbation impacts. Thus, although we did not measure particulate nutrients, it is likely that salmon in Peterson Creek also have a strong impact on streamwater fluxes of total N and P.

In Peterson Creek, the impact of salmon on catchment nutrient fluxes may extend beyond the period when fish were visible in the stream as evidenced by the elevated concentrations of SRP and $\text{NO}_3\text{-N}$ in salmon-impacted lower Peterson during the 3-month period following spawning. This apparent legacy effect of spawning salmon on catchment nutrient fluxes could result from a number of mechanisms including: (1) the release of salmon nutrients stored in the hyporheic zone and/or epilithon (Rex & Petticrew, 2008); (2) the slow release of nutrients from salmon carcasses in the riparian zone and woody debris jams in the stream (Fellman, Hood, et al., 2008); or (3) nutrient release from salmon detritus and waste products produced by predators and scavengers that consume spawning salmon (Cederholm, Kunze, Murota, & Sibatani, 1999). We did not account for the delayed release of salmon nutrients in our salmon nutrient flux calculations and thus our estimates are conservative in this regard.

Our results indicate that salmon play an outsized role in dissolved inorganic N and P budgets of catchments where they spawn. In particular, salmon transfer abundant $\text{NH}_4\text{-N}$ and SRP, both of which tend to be retained in terrestrial ecosystems by a combination of sorption in soils and biotic demand (Olander & Vitousek, 2005; Perakis & Hedin, 2001), directly to streamwater. Salmon-derived nutrients accounted for 92% of the annual catchment flux of $\text{NH}_4\text{-N}$ and 74% of the annual flux of SRP illustrating that spawning salmon are an important driver of annual $\text{NH}_4\text{-N}$ and SRP export from small coastal catchments with healthy salmon runs. In contrast, catchment sources dominated the annual export of dissolved organic C, N, and P. This is consistent with the fact that organic soil horizons in both upland and wetland ecosystems are the dominant source of DOM to streamwater in coastal temperate rainforest catchments (D'Amore, Edwards, Herendeen, Hood, & Fellman, 2015; Oliver et al., 2017). In Peterson Creek, this was particularly true for streamwater fluxes of DOC, which are strongly correlated with discharge (Fellman, Hood, Edwards, & D'Amore, 2009), and peaked during the autumn and early winter when precipitation in southeast Alaska is greatest. Although salmon-derived organic matter was a minor contributor to catchment DOC fluxes, salmon did contribute around 15% of annual catchment fluxes of DON and DOP, which probably enhance in-stream primary productivity via remineralization to inorganic N and P (Stepanauskas, Laudon, & Jørgensen, 2000; Stepanauskas et al., 2002), and influenced the spectroscopic properties of the bulk DOM pool.

The substantial export of salmon-derived N and P during and after spawning highlights the fact that salmon are a source of N and P both to and from coastal catchments. Without a complete budget for the influx of salmon-derived nutrients into Peterson Creek, we are not able to quantify the proportion of nutrients imported by spawners that are then exported in streamwater. The total export of salmon nutrients from a catchment is also

influenced by the mass of juveniles that emigrate downstream to saltwater. Previous reports have shown that this outmigration of smolts removes an average of >10% of the N and P imported by spawners (Moore & Schindler, 2004). Despite the focus on the retention and impact of salmon derived nutrients in anadromous catchments (Bartz & Naiman, 2005), a substantial proportion of the salmon nutrients entering coastal catchments may be rapidly exported in dissolved forms to near-shore marine ecosystems. In the case of Peterson Creek, the estuary is <2 km downstream from our sampling reach meaning that salmon-derived nutrient fluxes we documented can impact primary productivity in the near-shore marine environment via the assimilation of inorganic N and P into estuarine food webs (Dafner, Mallin, Souza, Wells, & Parsons, 2007; Lui & Chen, 2011). The impact of this subsidy may extend up the food chain as evidenced by links between salmon nutrients and breeding bird density and diversity in downstream estuaries (Field & Reynolds, 2011). Ultimately, the export of salmon nutrients to estuarine ecosystems will be greatest in catchments where the travel distance to saltwater is small relative to the instream uptake lengths for inorganic N and P. Where this is the case, our findings suggest that further evaluation of the impacts of salmon nutrients on near-shore food webs is warranted.

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