Quantitative links between Pacific salmon and stream periphyton

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Abstract

Species' impacts on primary production can have strong ecological consequences. Pacific salmon (*Oncorhynchus* spp.) in particular may influence stream periphyton in several ways, ranging from substrate disturbance during spawning to nutrient subsidies from senescent adults. However, the shape of relationships between the abundance of spawning salmon and stream periphyton, as well as interactions with environmental variables, are poorly understood. We examined these relationships across 24 sockeye salmon (*Oncorhynchus nerka*) spawning streams in north-central British Columbia, Canada. The influence of salmon abundance and environmental variables (temperature, light, dissolved nutrients, water velocity, watershed size and invertebrate grazer abundance) on periphyton abundance and nitrogen stable isotope signatures after spawning was evaluated using model selection and Akaike Information Criterion (AICc). The nitrogen stable isotope signature ($\partial^{15}N$) of periphyton in each stream was best predicted by a positive linear relationship with mean salmon abundance over the previous four years. This suggests the potential importance of a nutrient legacy from previous years. In contrast, periphyton abundance ($\mu g.cm^{-2}$) in each stream was negatively related to salmon density, which may result from substrate disturbance during spawning, and positively related to dissolved soluble reactive phosphorus prior to spawning. These results suggest that increased enrichment in nitrogen stable isotopes do not translate into elevated periphyton abundance. This underscores the need to evaluate ecological processes, in addition to tracing salmon derived nutrients with stable isotopes, to understand impacts of salmon on stream ecosystems.

Keywords: aquatic conservation, food web, fisheries, fish, ecosystem engineer, resource subsidy, marine-derived nutrients

Introduction

Individual species affect ecosystem structure and function through many mechanisms. The ecological consequences of impacts on primary production can be particularly far reaching. In stream ecosystems, periphyton is often the dominant form of in-stream primary production and provides an important food resource for aquatic primary consumers (Vannote et al., 1980; Lamberti, 1996). Changes in periphyton growth and abundance have been shown to regulate populations of both invertebrate primary consumers and their predators, including fish (Lamberti, 1996). Across the north Pacific, spawning anadromous salmon (*Oncorhynchus* spp.) potentially influence periphyton growth and abundance, with possible ramifications for ecosystem structure and function.

Pacific salmon can influence stream periphyton through several mechanisms. First, with more than 95% of body mass accumulated in the ocean, a semelparous life history (dying after spawning) can deliver a large annual pulse of nitrogen and phosphorus to freshwater ecosystems, which could enhance periphyton growth when nutrients are limiting (Gende et al., 2002; Naiman et al., 2002; Schindler et al., 2003). Stable isotope techniques have been used to detect the contribution of salmon-derived nitrogen to stream periphyton, an approach that is possible because the ratio of the heavy nitrogen isotope (^{15}N) to the light nitrogen isotope (^{14}N) is higher in salmon than in terrestrial nitrogen sources (Kline et al., 1990; Bilby et al., 1996; Chaloner et al., 2002). Furthermore, there are mechanisms by which salmon-derived nitrogen and phosphorus may be retained in the watershed after the spawning period, potentially having an effect on primary production in future years (Naiman et al., 2002). A second way in which salmon may affect periphyton is through physical disturbance of substrates by nest-digging and spawning activities. This can export nutrients, transport substrate and reduce periphyton abundance through scour (Moore et al., 2004; Moore et al., 2007; Hassan et al., 2008). Thus, salmon have the potential to either increase or decrease the abundance of stream periphyton, depending on the strength of the nutrient uptake pathway compared with the physical disturbance effect. Further, there are less direct routes through which salmon may affect periphyton. For example, enhanced periphyton growth could be obscured by resulting increases in invertebrate grazer populations. The outcome of these potential mechanisms by which Pacific salmon influence stream periphyton abundance is still poorly understood.

Given the variety of mechanisms that have been identified, it is perhaps not surprising that previous studies have found inconsistent relationships between salmon and periphyton. Comparisons between sites with and without salmon have shown both decreases in periphyton abundance, likely from nest digging (Minakawa and Gara, 1999; Peterson and Foote, 2000), and increases, likely through the nutrient subsidy (Schuldt and Hershey, 1995; Wipfli et al., 1998; Peterson and Foote, 2000; Chaloner et al., 2004). A comparison of three streams over three years found that salmon abundance was positively related to periphyton abundance, above a threshold value (Johnston et al., 2004). Experiments in which salmon were excluded showed increased periphyton abundance when nest-digging was prevented (Moore et al., 2004), while experimental carcass additions elevated both dissolved nutrient levels and periphyton abundance (Schuldt and Hershey, 1995; Wipfli et al., 1999; Kohler et al., 2008).

Impacts of salmon on periphyton may be mediated by environmental variables such as discharge, light, disturbance, and temperature (Mitchell and Lamberti, 2005; Chaloner et al., 2007). For example, periphyton may not respond to direct salmon nutrient subsidies if it is limited by light (Rand et al., 1992; Ambrose et al., 2004). These findings are consistent with what is known about the limiting influences on periphyton, including temperature, nitrogen, phosphorus, and light (Biggs, 1996; Borchardt, 1996; DeNicola, 1996; Hill, 1996). Periphyton abundance has also been positively related to watershed size, a landscape-level metric that can capture variation in limiting variables such as temperature and light (Lamberti and Steinman, 1997). Further, invertebrate grazers may also regulate abundance through periphyton consumption (Steinman, 1996). There is therefore a need to consider the potential interaction of these environmental variables with the influence of salmon on periphyton (Janetski et al., 2009).

Pacific salmon have declined substantially in parts of their range (Nehlsen et al., 1991; Baker et al., 1996; Slaney et al., 1996). For example, in Oregon, Washington, Idaho, and California, salmon populations are at less than 90% of historic levels and have been extirpated from 40% of their range (Gresh et al., 2000). These declines are likely to have reduced the ecosystem influence of spawning salmon. As management strategies begin to incorporate the ecological roles of salmon when setting target population sizes (e.g. DFO, 2005), predicting how changes in salmon abundance affect ecosystem processes such as primary production will become increasingly relevant (Moore et al., 2008). Consequently, there is a need to better understand the shape of relationships between salmon abundance and stream periphyton.

The shape of relationships between salmon abundance and stream periphyton may depend on the method used to measure salmon abundance and how well it describes the influence of spawning salmon on stream periphyton. For example, the total number of salmon spawning in a watershed may be the strongest correlate of direct nutrient subsidies, while salmon density (number.m^{-2}) within a stream reach may better represent the extent of substrate disturbance. Furthermore, in populations where salmon abundance is highly variable or cyclical from year to year, such as some sockeye salmon (*Oncorhynchus nerka*) populations (Levy and Wood, 1992), the direct nutrient subsidies delivered in high abundance years may carry an influence into low abundance years if there is high nutrient retention in the watershed. The importance of nutrient subsidies delivered during spawning compared to nutrients retained in the watershed from previous years could be examined by measuring salmon abundance both in the spawning year and averaging across several previous years.

The overall objective of our study was to understand the role of spawning salmon in the ecology of stream periphyton. Specifically, our study has the following novel facets aimed at filling key gaps in knowledge: (1) we studied a large number of streams (24) to quantify the shape of relationships between salmon abundance and periphyton abundance after spawning, (2) we compared these results to the relationship we described between salmon abundance and periphyton nitrogen stable isotope signatures, (3) we considered the potential for legacy effects of salmon-derived nutrients from previous years, and (4) we incorporated the potential role of environmental variables shown by previous studies to influence both periphyton abundance or nitrogen isotope signatures. Our study encompassed 24 sockeye salmon spawning streams in the Stuart River drainage of the Fraser River, British Columbia, Canada. We built linear regression models containing salmon abundance metrics and environmental variables that predicted the nitrogen stable isotope signatures ($\partial^{15}N$), chlorophyll *a* ($\mu g.cm^{-2}$), and ash-free dry mass ($\mu g.cm^{-2}$) of stream periphyton. We evaluated the relative importance of competing models with an information-theoretic framework and Akaike Information Criterion (AICc).

Methods

Study Sites

We surveyed 24 sockeye salmon spawning streams in the Stuart River drainage, the most northerly salmon spawning region of the Fraser River watershed (Fig. 1). For a detailed description of the region see Macdonald et al. (1992). Briefly, it lies at the northern end of the Sub-boreal Spruce Biogeoclimatic Zone, with higher elevations falling in the Engelmann Spruce-Subalpine Fir Zone. Common riparian species include hybrid white spruce (*Picea glauca x P. engelmannii*), black cottonwood (*Populus balsamifera*), sitka alder (*Alnus viridis*) and devils club (*Oplopanax horridus*). Sockeye salmon are the only anadromous fish in the streams. These populations are part of the “Early Stuart” complex, entering freshwater in June and migrating over 1100 km to spawn from late July to mid August in tributaries to Middle River and Takla Lake. Resident fish include bull trout

(*Salvelinus confluentus*), rainbow trout (*Oncorhynchus mykiss*), kokanee (resident *O. nerka*), prickly sculpin (*Cottus asper*), mountain whitefish (*Prosopium williamsoni*), northern pikeminnow (*Ptychocheilus oregonensis*) and burbot (*Lota lota*).

Adult Salmon Abundance

We calculated three adult salmon abundance metrics that characterize the potential ecosystem influence: a) the spawning salmon population size upstream of our study sites (2007 salmon abundance), representing the total nutrient input to the watershed b) the spawning salmon density (fish.m^{-2}) in the study reach (2007 salmon density), representing both local carcass input and substrate disturbance, and c) the mean spawning salmon population size upstream our study sites across the previous four years (four-year mean salmon abundance), which is one sockeye population cycle, representing the potential legacy of salmon-derived nutrients retained in the watershed over several years. We considered this metric to better represent the nutrient subsidy to an entire watershed than four-year mean salmon density. The Stock Assessment branch of Fisheries and Oceans Canada enumerated the number of spawning sockeye salmon in each 500 m stream reach every four days during spawning. We calculated salmon density (D) as:

$$(1)\ D = \frac{F}{wl}$$

where, F is the total number of salmon in each reach, w is the reach-specific wetted width (m) and l is the length of the reach (m). The streams represented a gradient of salmon abundance at low population sizes (2007 salmon density range = 0.0 – 0.1 fish/m^2, four-year mean salmon abundance range = 0 - 2368), although extremely low abundances in 2007 resulted in several streams having no spawning sockeye return (Appendix 1). Due to a positive correlation between 2007 salmon abundance and 2007 salmon density ($r = 0.99$, $p < 0.001$), only results using 2007 salmon density are reported, which better represented the influence of fish in the study reach. Four-year mean salmon abundance correlated highly with 2005 salmon abundance (the dominant year in the four-year population cycle), when abundance was ten times higher than the other years, and both eight-year and twelve-year mean salmon abundance ($r > 0.95$ for all), suggesting it generally represents the potential legacy effect. We did not consider four-year mean salmon abundance in models of periphyton abundance because any nutrient legacy should be captured within the measurements of pre-spawning dissolved nutrient concentrations, which are considered as covariates.

Periphyton collection and processing

Unglazed ceramic tiles were anchored in each stream at the bottom of the spawning reach, given access restrictions, to permit maximum exposure to upstream salmon-derived nutrients. Tiles were introduced in July of 2007, 2-4 weeks prior to sockeye spawning and collected 4-6 weeks after spawning had concluded in late September. Tile deployment was intended to coincide with the salmon nutrient pulse released during spawning and senescence. Tile collection occurred when periphyton abundance has been shown to stabilize (Johnston et al., 2004). Samples for ash-free dry mass (AFDM) and chlorophyll *a* (chl *a*) analyses were scraped from an area of tile (3.14 cm^2 or 1.57 cm^2), filtered onto glass fibre filters (Whatman, 25mm, 0.7μm pore size) and stored in the dark at -20˚C. Samples for stable isotope analysis were scraped from the remainder of the tile area and stored similarly, until being dried in the lab at 55°C for > 24 hours and manually ground into a fine powder. Samples (0.9-2.5 mg dry weight) were assayed for nitrogen stable isotopes using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the University of California Davis Stable Isotope Facility (http://stableisotopefacility.ucdavis.edu/). Stable isotope signatures are expressed in delta notation (δ) as ratios relative to the standard of atmospheric N^2 (nitrogen). This is expressed in 'parts per mil' (‰) according to:

$$\partial^{15}N(‰) = (\frac{R_{sample}}{R_{s\tan dard}} - 1) \times 1000 \quad (2)$$

where *R* is the ratio of heavy isotope (^{15}N) to light isotope (^{14}N) in the sample and standard. Chl *a* was extracted in methanol at 2-4°C for 24 h, measured fluorometrically (Turner TD-700 Fluorometer), corrected for pheophytin using acidification (Holm-Hansen and Riemann, 1978), and then divided by the area sampled (cm^2). The sum of pheophytin and chl *a* correlated highly with chl *a* ($r = 0.99$), demonstrating the nominal contribution of degradation products to total chlorophyll. AFDM was measured according to Steinman et al. (2006). Finally, $\partial^{15}N$, chl *a*, and AFDM were averaged across all tiles in a stream. There were originally eight or twelve tiles in each stream but losses resulted in a lesser number for some streams (range = 1-12, Appendix 1).

Environmental variables

A literature search showed water temperature, dissolved nitrogen and phosphorus concentrations, light availability, grazer abundance, and watershed size to potentially influence periphyton abundance (Table 1b). Water temperature, light availability and water velocity were shown to potentially influence periphyton nitrogen stable isotope signature (Table 1a). We also considered the number of days the tiles were in the stream (soak time) as a predictor of periphyton abundance (range = 53 – 76 days).

We characterized water temperature as the mean maximum daily temperature calculated across the spawning period (August 5th – 21st), which was measured using ibutton (DS1922L) temperature data loggers programmed to record temperatures at two hour intervals, waterproofed, and attached to an iron rod in the streambed. As equipment failure led to missing temperature data for two streams, we first performed our analyses with this reduced dataset (n=22). When temperature proved not to be a significant predictor of ∂^{15}N, chl a, or AFDM, we excluded it and repeated the analyses across all 24 streams, findgin no difference in results. Dissolved phosphorus, characterized as soluble reactive phosphorus (SRP), and dissolved inorganic nitrogen, calculated as the sum of total ammonia (NH_4-N) and nitrite plus nitrate nitrogen (NO_3-N), were sampled two or three times at one location in each stream over two-months prior to spawning. Samples were analyzed at Fisheries and Oceans Canada's Cultus Lake Laboratory according to American Public Health Association methods (APHA, 1989). Briefly, SRP was determined by the automated ascorbic acid method, NO_3-N by the automated cadmium reduction method, and NH_4-N by the automated phenate method. Light availability was characterized by percent open canopy, which was measured using a spherical densiometer at each tile at both placement and collection, and averaged. Grazer abundance was assessed by collecting benthic macroinvertebrates from riffles using a surber sampler (frame area = 0.093 m^2, 500 μm mesh), agitating the substrate within to a depth of 10 cm for 2 min. We sampled four riffles per stream in early summer (prior to spawning), pooling three surber samples within each riffle and preserving them in 95% ethanol. Insects of the orders Ephemeroptera, Plecoptera, Trichoptera, and Diptera were identified to family, with all other individuals identified to order (Merritt et al., 2008). Functional groups were assigned (Merritt et al., 2008) and the abundance of all individuals classified as grazers summed to estimate grazer density (#/m^2). Watershed size was characterized by the first axis of a principal components analysis of stream magnitude, length, and bankfull width, which explained 79% of the variation in the three variables with all variable loadings > 0.55. Stream magnitude and length were obtained from the BC Ministry of Environment's Habitat Wizard (http://www.env.gov.bc.ca/habwiz/). Bankfull width, the maximum stream width possible without flooding, was averaged across 16 measurements taken to the nearest 0.01m. Water velocity was characterized by stream gradient, which was measured across the length of stream in which the tiles were situated using a 5x Abney hand level.

Data analysis

Our statistical analyses consisted of two steps. First, we reduced in size the set of environmental variables predicted to influence periphyton nitrogen stable isotope signature and abundance (Table 1). Second, we combined the selected environmental variables with the salmon abundance metrics and tile soak time, creating linear regression models that were evaluated with an information-theoretic framework and Akaike Information Criterion (AICc).

To reduce the variables predicted to influence periphyton nitrogen stable isotope signature and abundance (Table 1) to a subset that was biologically relevant to the study system, we first examined co-linearity among them and then removed non-significant predictors, according to methods suggested by Zuur et al. (2010). Co-linearity among variables was assessed using Variance Inflation Factors. No variable exceeded a value of two, suggesting co-linearity among variables was not of concern. We then conducted a backward stepwise linear regression using all variables and sequentially dropped non-significant predictors ($p > 0.05$). A less stringent criterion of $p > 0.1$ and a manual alteration of the order in which variables were removed had little impact on the final results. As no *a priori* hypotheses for interactions were generated, none were included in the model. Gradient came through the regression procedure as a predictor of $\partial^{15}N$, soluble reactive phosphorus (SRP) as a predictor of AFDM and both SRP and canopy cover as predictors of chl *a*. As the relationship between canopy cover and chl *a* was inverse to that predicted it was dropped from further consideration.

We then combined the selected environmental variables (gradient, SRP) with the salmon abundance metrics (2007 salmon density, four-year mean salmon abundance), and tile soak time. No variable had a Variation Inflation Factor above two, which suggests co-linearity among them was not of concern, and scatterplots did not reveal any obvious non-linearity between any predictor and response variable. We created linear regression models of each response variable ($\partial^{15}N$, chl *a*, and AFDM) for all single predictors and combinations of predictors, with the caveat that two salmon abundance metrics could not be in the same model. No interaction terms were included as none were hypothesized *a* *priori*. We square-root transformed both salmon abundance metrics and $\log_{10}$ transformed gradient, SRP, AFDM and chl *a* to improve model diagnostics. We used Akaike Information Criterion corrected for small sample sizes (AICc) to evaluate the support for each model in predicting δ^{15}N, AFDM, and chl *a*. AICc evaluates the relative descriptive power of various *a priori* models with different combinations of variables based on the principal of parsimony, balancing optimal fit with the number of parameters used (Anderson, 2008). Delta AICc values, model weights (w_i), and evidence ratios (ER) were calculated to aid interpretation of the model ranking (Anderson, 2008). The ΔAICc value is the change in AICc between model*i* and the top ranked model, w_i is the probability that model*i* is the best of the set considered, and ER is the ratio of $w_{topmodel}/ w_i$ and can be interpreted as the likelihood that the top ranked model is better than model*i* (Anderson, 2008). All statistical analyses were conducted in R (R Development Core Team, 2009).

Results

Nitrogen Stable Isotope Signature

The nitrogen stable isotope signature (∂^{15}N) of stream periphyton was best predicted by four-year mean salmon abundance (Table 2a). This metric appeared in the top two models suggesting it is a better predictor than either 2007 salmon density or gradient. As a single predictor, four-year mean salmon abundance positively described ∂^{15}N ($R^2 = 0.29$, $p = 0.007$, Fig. 2), was the only model with a $\Delta AICc < 2$, had the highest model weight ($w = 0.72$), and was greater than four times more likely to be a better model than the second ranked model ($ER_2 = 4.18$). The second best model contained four-year mean salmon abundance and gradient, both predicting ∂^{15}N in the expected direction.

However, the similarity in R^2 between these models suggests that gradient explained little additional variation in $\partial^{15}N$. Support for the other three models was poor ($\Delta AICc > 2$).

One study site (Leo Creek) stood out as an outlier in the regression diagnostics of the top two models (standardised residual > 3). This stream had an upstream lake area that was almost three times greater than any other stream, heavy beaver activity (*Castor canadensis*) just upstream of our study reach (not seen in other streams), and the highest pre-spawning dissolved nutrient concentrations of all streams. We re-ran the model selection analyses excluding Leo Creek. Four-year mean salmon abundance as a single predictor remained ranked as the top model and both support for the model and model performance improved ($w = 0.80$, $ER_2 = 4.37$, $R^2 = 0.48$, $p = 0.0002$, Fig. 2).

Periphyton Abundance

Ash-free dry mass (AFDM) was best predicted by 2007 salmon density and soluble reactive phosphorus (SRP) together. This model had the highest weight ($w = 0.66$) and was more than twice as likely to be better than the second ranked model ($ER_2 = 2.17$), which also contained tile soak time (Table 3). The slightly greater R^2 of model two suggests that tile soak time explained some additional variation in AFDM. In the top model, SRP was positively related to AFDM and negatively related to 2007 salmon density ($\log_{10}(\text{AFDM}) = 0.9398 \text{x} \log_{10}(\text{SRP}) - 1.0457 \text{x} \sqrt{}(\text{2007 salmon density}) - 0.6711$, $R^2 = 0.49$). We present observed versus predicted plots for the top model (Fig. 3a) and untransformed bivariate plots of the individual predictors versus AFDM (Fig. 3c, e) for comparison. Support for the other five models was poor ($\Delta AICc > 2$).

Chlorophyll *a* (chl *a*) was also best predicted by 2007 salmon density and soluble reactive phosphorus (SRP) together. This model had the highest model weight (w = 0.52) and was more than twice as likely to be better than the second ranked model ($ER_2 = 2.43$), which contained SRP as a single predictor (Table 4). In the top model, SRP was positively related to chl *a* and negatively related to 2007 salmon density ($\log_{10}$(chl *a*) = $1.4941\mathrm{x}\log_{10}(\mathrm{SRP}) - 1.0871\mathrm{x}\sqrt{}(2007\ \mathrm{salmon\ density}) - 0.5773$, $R^2 = 0.33$). We present observed versus predicted plots for the top model (Fig. 3b) and untransformed bivariate plots of the individual predictors versus chl *a* (Fig. 3d, f) for comparison. Support for the other five models was poor (ΔAICc > 2).

Discussion

Nitrogen Stable Isotope Signature

We found a linear relationship between four-year mean salmon abundance and the nitrogen stable isotope signature ($\partial^{15}N$) of stream periphyton across 24 streams in north-central British Columbia. Each additional 1000 spawning sockeye salmon increased periphyton $\partial^{15}N$ by 2.1‰. This is the first time the shape of this relationship has been shown for periphyton. Linear or asymptotic relationships with salmon abundance have been described for nitrogen stable isotopes in juvenile coho salmon (Bilby et al., 2001) and riparian soil, vegetation, and invertebrates (Reimchen et al., 2003; Bartz and Naiman, 2005; Hocking and Reimchen, 2009). A post-hoc analysis of our data showed no improvement over the linear model when we included a quadratic function, offering no evidence for an asymptote in our study. This could be because the sockeye populations in the region are low enough that the nutrient subsidy provided does not saturate the ecosystem. Whereas the four-year mean salmon abundance across our 24 streams was typically > 70,000 fish in the early 1990s, it was just 20,000 fish from 2004-2007.

We measured three environmental variables (temperature, light, water velocity) that could potentially affect periphyton $\partial^{15}N$ (Table 1a). Of these, our data suggest that only water velocity significantly affected periphyton $\partial^{15}N$. Water velocity may control the rate at which dissolved nitrogen available to periphyton is replenished, thus affecting the rate of uptake of the different isotopes (Trudeau and Rasmussen, 2003). Stream gradient is an imperfect metric to characterize water velocity at each site where tiles were situated, but it provided an indication of relative differences among streams. However, gradient was a poor predictor of periphyton $\partial^{15}N$ compared to four-year mean salmon abundance, particularly after removing Leo Creek. This suggests that salmon abundance exerted a stronger influence on periphyton $\partial^{15}N$ than water velocity across the ranges of each variable studied here. This is the first study to explicitly consider the influence of both the salmon nutrient subsidy and environmental variables on periphyton $\partial^{15}N$. Despite the strong importance of salmon abundance, greater than 50% of variation in periphyton $\partial^{15}N$ remained unexplained. The contribution of terrestrial nitrogen sources is a likely source of this variation.

We tested two salmon abundance metrics; one chosen to represent reach-specific nutrient input during the spawning period (2007 salmon density) and the other to capture the potential legacy of salmon-derived nutrients from previous years (four-year mean salmon abundance). Our results suggest that the legacy effect of salmon-derived nutrients from previous years did influence periphyton $\partial^{15}N$. This result could be due to two properties of the system. First, 2007 was a year of very low salmon returns. Only 4,500 sockeye returned across all 24 streams compared to the four-year average of 20,000. Second, the dominant year of the four-year population cycle exhibited in these sockeye populations was in 2005 when 51,000 salmon returned, delivering a much larger nutrient subsidy. The performance of the salmon abundance metrics might not differ in a year of higher abundance. Studies could examine the nutrient legacy through stable isotopes of dissolved inorganic nitrogen prior to spawning.

Periphyton Abundance

Periphyton abundance in our study was best predicted by a combination of salmon abundance and environmental variables. Ash-free dry mass (AFDM) and chlorophyll *a* (chl *a*) were both negatively related to salmon density and positively related to pre-spawning soluble reactive phosphorus concentrations, although the model fit was better for AFDM. The small amount of variation in AFDM or chl *a* explained by tile soak time confirms that the tiles were collected when periphyton abundance had stabilized.

We measured six environmental variables (water temperature, light availability, dissolved phosphorus and nitrogen, grazer abundance, and watershed size) that could affect periphyton abundance through either growth rate or rate of loss (Table 1b). Of these, we found pre-spawning soluble reactive phosphorus to be the most important predictor, suggesting that phosphorus limited periphyton growth in the streams. Dissolved nutrient concentrations prior to spawning could be influenced by salmon-derived nutrients retained in the watershed from previous years. For example, phosphorus contained in the salmon skeleton, which degrades slowly, may be released into the streams over several years. Salmon-derived phosphorus cannot be detected in dissolved nutrient concentrations using stable isotope analyses as it has just one stable isotope.

We found a negative relationship among streams between spawning-year salmon density and periphyton abundance. This suggests that spawning salmon may have exerted a greater influence on periphyton abundance by removing it through substrate disturbance than by the immediate nutrient subsidy they provided. However, a positive relationship, above a threshold value of 300kg of carcass (dry weight) per unit discharge, has previously been described between salmon biomass per unit discharge and chl *a* across multiple sites and years within three of the same streams (Johnston et al., 2004). The highest salmon density in 2007 was an order of magnitude lower than the highest density recorded in their study (1996-1998).

It is important to note that periphyton abundance at a single point in time does not measure primary productivity directly. Periphyton growth rates could be high when abundance is low if periphyton removal is elevated by grazing or streambed scour. Indeed, if the salmon-derived nutrient subsidy from previous years increased overall ecosystem productivity, resulting in a greater abundance of grazing invertebrates, periphyton abundance could be reduced. Our finding that salmon abundance from previous years best predicts periphyton ∂^{15}N supports the notion of a nutrient legacy effect. Furthermore, we found a significant positive relationship between salmon abundance and grazer abundance prior to spawning (Verspoor, unpublished data). Although we predicted that grazers could regulate periphyton abundance, this variable did not explain significant variation in periphyton abundance. Nonetheless, as it is correlated with salmon abundance, it could contribute mechanistically, alongside scour by substrate disturbance, to the negative relationship between salmon density and periphyton abundance.

In conclusion, we have found that although salmon abundance was positively related to periphyton nitrogen stable isotope signature it was negatively related to periphyton abundance. Thus, uptake of salmon-derived nitrogen does not translate into increased periphyton abundance. This may be because the physical disturbance of spawning salmon outweighs the influence of their nutrients, with an additional possible effect of invertebrate grazers. Our finding that dissolved phosphorus levels prior to spawning also predict periphyton abundance confirms the importance of considering such environmental variables alongside of effects of salmon. Finally, our evidence for a nutrient legacy from previous years in periphyton nitrogen isotope signatures of periphyton suggests the potential for long-term ecological impacts of salmon-derived nutrients in freshwater ecosytems. These findings suggest that attempts to incorporate the wider ecological role of salmon into conservation management (e.g. DFO, 2005) should exercise caution in the use of stable isotopes as a proxy for direct evidence of salmon impacts on freshwater ecosystems and consider the potential for a nutrient legacy effect.

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Figure Legends

Figure 1. Locations of the 24 study streams in the Stuart River drainage of the Fraser River watershed in north-central British Columbia, Canada.

Figure 2. Plot of four-year mean salmon abundance versus periphyton nitrogen stable isotope signature (∂^{15}N), with the outlying Leo Creek labeled. Although four-year mean salmon abundance was square-root transformed in the analyses, data are presented untransformed here. The fitted linear relationship is for untransformed data and excludes Leo Creek ($y = 0.0007x+1.1404$, $R^2 = 0.43$, $p = 0.0007$).

Figure 3. Bivariate plots of observed versus predicted values for the top model of a) ash-free dry mass (AFDM) and b) chlorophyll *a* (chl *a*), fitted with a 1:1 line. Bivariate plots of c) AFDM versus SRP, d) chl *a* versus SRP, e) AFDM versus 2007 salmon density, and d) chl *a* versus 2007 salmon density. Although SRP, AFDM, and chl *a* were $\log_{10}$-transformed and 2007 salmon density was square-root transformed in the analyses, the data are presented untransformed.

Figure 1.

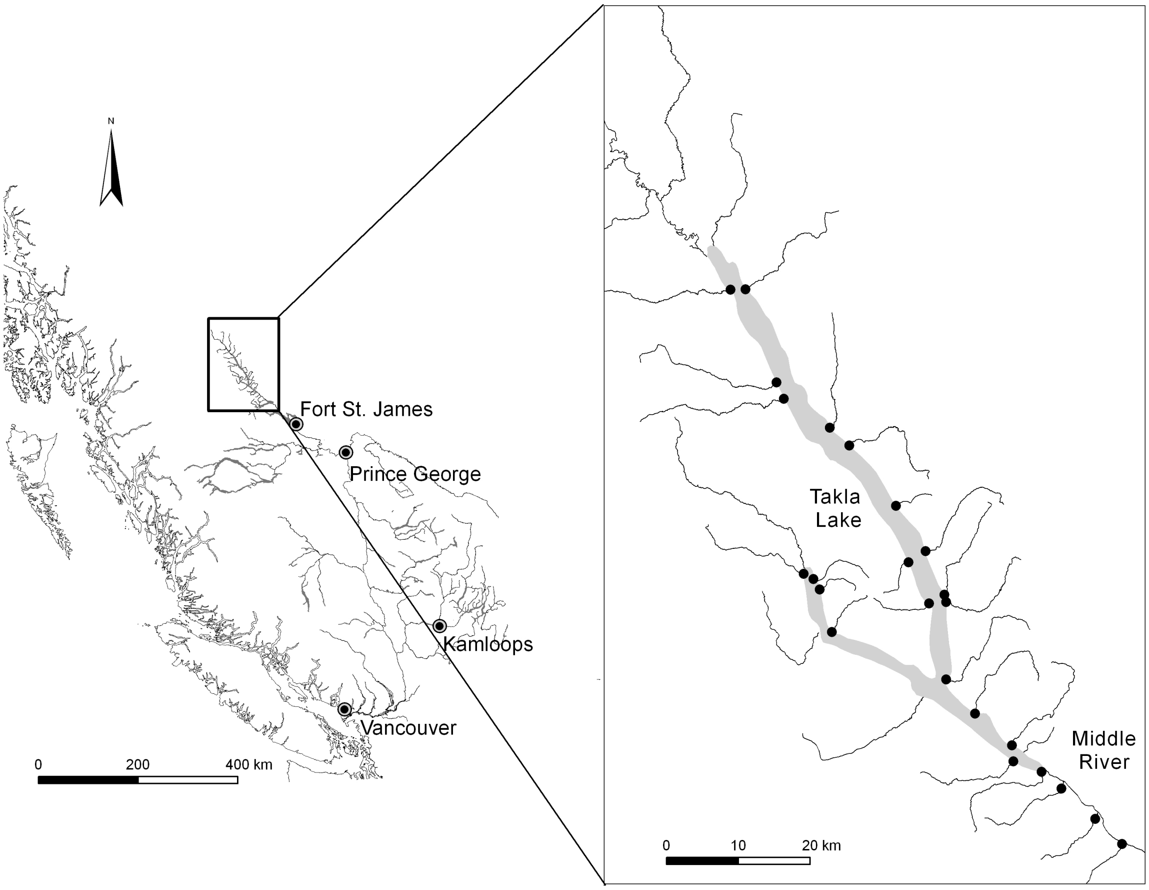
N
Fort St. James
Prince George
Kamloops
Vancouver
0
200
400 km
Takla
Lake
Middle
River
0
10
20 km

Figure 2.

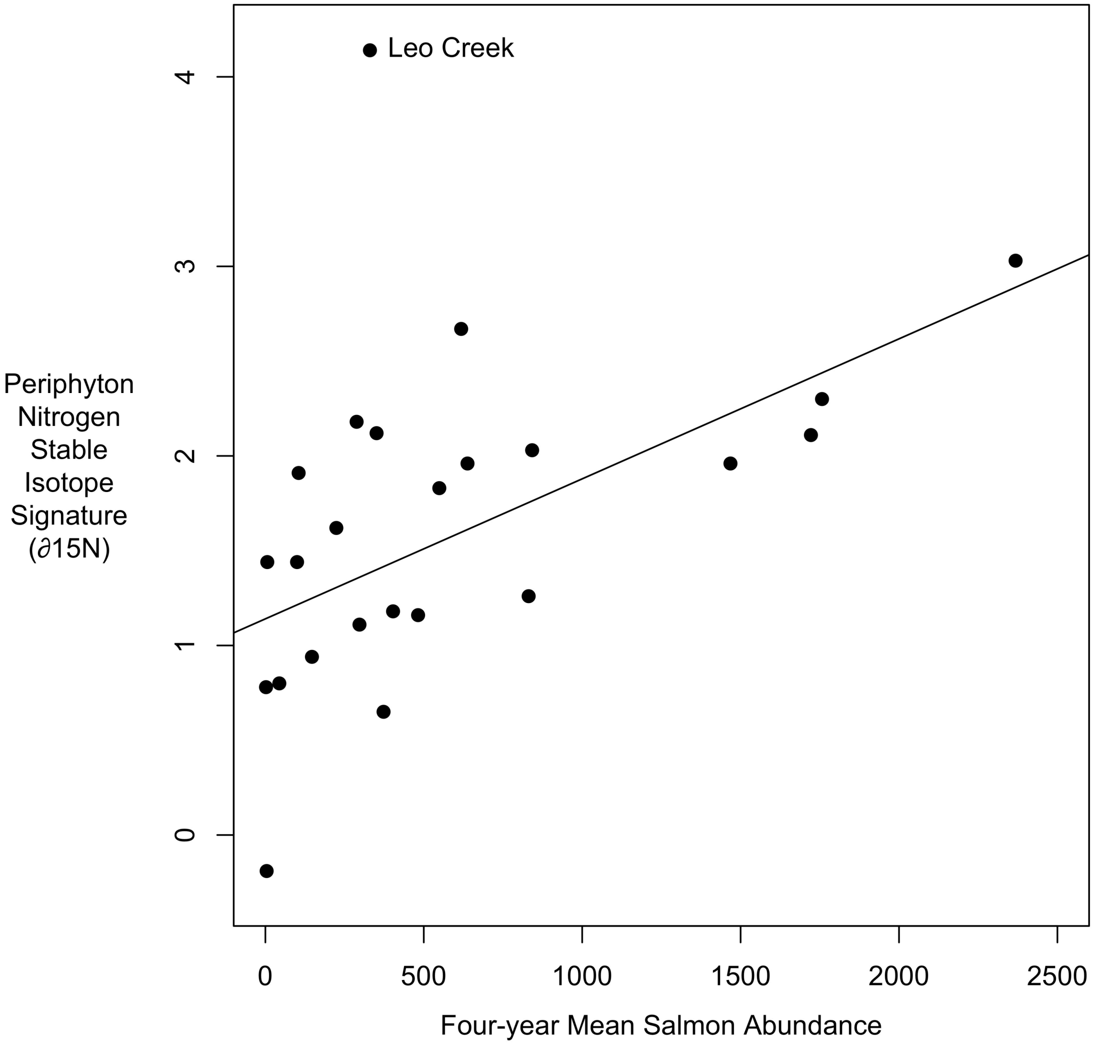
Leo Creek
Periphyton Nitrogen Stable Isotope Signature (∂15N)
0
1
2
3
4
0
500
1000
1500
2000
2500
Four-year Mean Salmon Abundance

Figure 3.

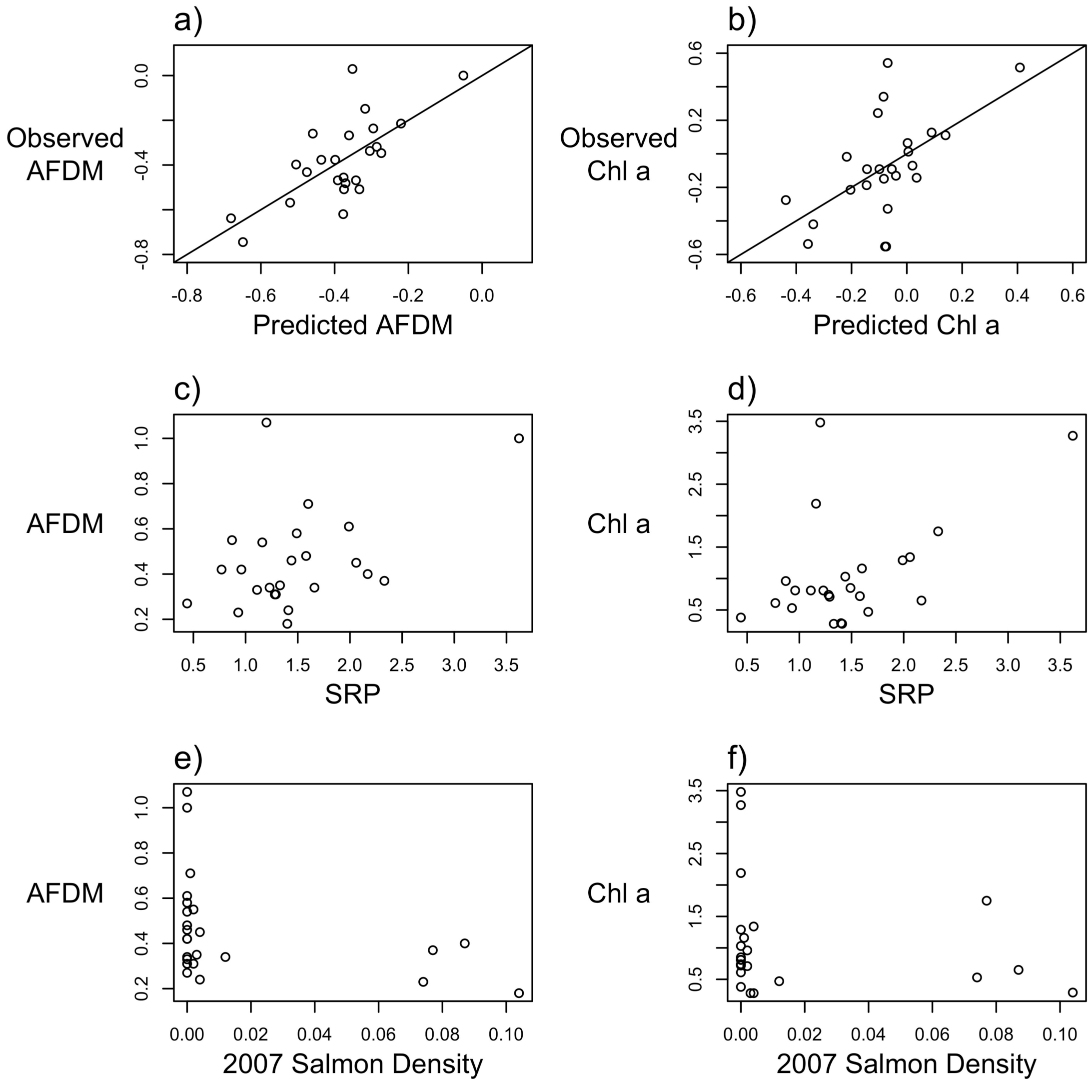
a)
Observed AFDM
0.0
-0.4
-0.8
-0.8
-0.6
-0.4
-0.2
0.0
Predicted AFDM
b)
Observed Chl a
0.6
0.2
-0.2
-0.6
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
Predicted Chl a
c)
AFDM
1.0
0.8
0.6
0.4
0.2
0.5
1.0
1.5
2.0
2.5
3.0
3.5
SRP
d)
Chl a
3.5
2.5
1.5
0.5
0.5
1.0
1.5
2.0
2.5
3.0
3.5
SRP
e)
AFDM
1.0
0.8
0.6
0.4
0.2
0.00
0.02
0.04
0.06
0.08
0.10
2007 Salmon Density
f)
Chl a
3.5
2.5
1.5
0.5
0.00
0.02
0.04
0.06
0.08
0.10
2007 Salmon Density

Table Legends

Table 1. *A priori* predictions for the potential influence of environmental variables on: a) the nitrogen stable isotope signature ($\partial^{15}N$) of stream periphyton and b) periphyton abundance (chlorophyll *a* and ash-free dry mass). The mechanism, direction of influence and metric used to characterize each environmental variable is described.

Table 2. Results of model selection using Akaike Information Criterion (AICc) for five linear regression models that predict the nitrogen stable isotope signature ($\partial^{15}N$) of periphyton. Results are presented: a) including Leo Creek (n=24) and b) excluding Leo Creek (n=23). Gradient was $\log_{10}$-transformed and both salmon abundance metrics were square-root transformed. k = number of model parameters, R^2 = model regression coefficient, p = model significance, AICc = Akaike information criterion for small sample sizes, ΔAICc = change in AICc score from top model, w_i = AICc model weight, ER = top model weight/model*i* weight.

Table 3. Results of model selection using Akaike Information Criterion (AICc) for seven linear regression models that predict periphyton ash-free dry mass (AFDM). SRP = soluble reactive phosphorus, Soak Time = Number of days the tiles were in the stream. SRP and AFDM were $\log_{10}$-transformed and 2007 salmon density was square-root transformed. Table headings are as described in Table 2.

Table 4. Results of model selection using Akaike Information Criterion (AICc) for seven linear regression models that predict periphyton chlorophyll *a*. SRP = soluble reactive phosphorus, Soak Time = Number of days the tiles were in the stream. SRP and chl *a* were $\log_{10}$-transformed and 2007 salmon density was square-root transformed. Table headings are as described in Table 2.

Table 1.

a)

Variable	Mechanism	Direction	Metric	References
Temperature	Water temperature can increase metabolic activity and thus increase nitrogen stable isotope signatures.	Positive	Mean Maximum Daily Temperature (˚C)	(Friberg et al., 2009) (MacLeod and Barton, 1998)
Light	Light availability can increase metabolic activity and thus increase nitrogen stable isotope signatures.	Positive	% Canopy Open	(MacLeod and Barton, 1998)
Velocity	Greater flow can reduce the boundary layers around periphyton and thus decrease nitrogen stable isotope signatures.	Negative	Gradient (%)	(Trudeau and Rasmussen, 2003) (MacLeod and Barton, 1998)

b)

Variable	Mechanism	Direction	Metric	References
Temperature	Water temperature can limit metabolic activity and thus periphyton growth.	Positive	Mean Maximum Daily Temperature (˚C)	(Lamberti and Steinman, 1997) (Biggs, 1996) (DeNicola, 1996)
Dissolved Phosphorus	Phosphorus has been shown to limit periphyton growth in some areas.	Positive	Soluble Reactive Phosphorus (μg/L)	(Lamberti and Steinman, 1997) (Biggs, 1996) (Borchardt, 1996)
Dissolved Nitrogen	Nitrogen has been shown to be limit periphyton growth in some areas.	Positive	Dissolved Inorganic Nitrogen (μg/L)	(Lamberti and Steinman, 1997) (Biggs, 1996) (Borchardt, 1996)
Light	Light availability can limit photosynthetic activity and thus periphyton growth.	Positive	% Canopy Open	(Lamberti and Steinman, 1997) (Biggs, 1996) (Hill, 1996)
Grazers	Invertebrate grazers feed on and reduce periphyton abundance.	Negative	Grazer Density (individuals/m^2)	(Biggs, 1996) (Steinman, 1996)
Watershed Size	Has a demonstrated relationship with primary productivity.	Positive	PCA of stream length, width, and magnitude	(Lamberti and Steinman, 1997) (Biggs, 1996)

Table 2.

a)

Model (including Leo Creek)	k	R^2	p	ΔAICc	w_i	ER
1. Four-year Mean Salmon Abundance	3	0.29	0.007	0.00	0.72	1.00
2. Four-year Mean Salmon Abundance + Gradient	4	0.29	0.03	2.86	0.17	4.18
3. Gradient	3	0.11	0.11	5.35	0.05	14.50
4. 2007 Salmon Density	3	0.10	0.13	5.55	0.04	16.03
5. Gradient + 2007 Salmon Density	4	0.15	0.18	7.19	0.02	36.50

b)

Model (excluding Leo Creek)	k	R^2	p	ΔAICc	w_i	ER
1. Four-year Mean Salmon Abundance	3	0.48	0.0002	0.00	0.80	1.00
2. Four-year Mean Salmon Abundance + Gradient	4	0.48	0.001	2.95	0.18	4.37
3. 2007 Salmon Density	3	0.25	0.02	8.69	0.01	77.05
4. Gradient + 2007 Salmon Density	4	0.28	0.04	10.64	0.00	204.05
5. Gradient	3	0.15	0.07	11.55	0.00	322.63

Table 3.

Model	**k**	**R^2**	**p**	**ΔAICc**	**w_i**	**ER**
1. 2007 Salmon Density + SRP	4	0.49	< 0.001	0.00	0.66	1.00
2. 2007 Salmon Density + SRP + Soak Time	5	0.52	0.002	1.55	0.30	2.17
3. 2007 Salmon Density	3	0.24	0.02	6.66	0.02	27.88
4. 2007 Salmon Density + Soak Time	4	0.24	0.05	9.25	0.01	102.10
5. SRP	3	0.15	0.06	9.28	0.01	103.54
6. SRP + Soak Time	4	0.18	0.12	11.20	0.00	269.94
7. Soak Time	3	0.00	0.84	13.04	0.00	679.35

Table 4.

Model	**K**	**R^2**	**p**	**ΔAICc**	**w_i**	**ER**
1. 2007 Salmon Density + SRP	4	0.33	0.02	0.00	0.52	1.00
2. SRP	3	0.18	0.04	1.78	0.21	2.43
3. 2007 Salmon Density + SRP + Soak Time	5	0.33	0.04	3.23	0.10	5.02
4. SRP + Soak Time	4	0.18	0.12	4.68	0.05	10.41
5. 2007 Salmon Density	3	0.08	0.19	4.70	0.05	10.51
6. Soak Time	3	0.05	0.30	5.41	0.03	14.98
7. 2007 Salmon Density + Soak Time	4	0.14	0.20	5.85	0.03	18.61

Appendix 1: Watershed characteristics, the number of tiles collected and soak time, 2007 salmon density and four-year mean salmon abundance for the 24 study streams.

Stream	Order	Magnitude	Length (km)	Bankfull Width (m)	# Tiles Collected	Tile Soak Time (Days)	2007 Salmon Density	Four-year Mean Salmon Abundance
10 Mile	2	2	5.91	4.19	7	64	0	6
15 Mile	3	14	18.5	11.64	7	61	0	147
25 Mile	2	6	17.59	9.04	8	61	0	2
Ankwill	4	44	27.37	30.53	7	53	0.002	831
Bivouac	3	10	17.52	8.07	7	72	0.012	482
Blanchette	2	5	10.61	8.65	6	63	0	44
Crow	2	4	10.43	9.04	5	75	0.004	373
Die Hard	2	4	7.79	12.01	8	62	0	4
Forfar	3	13	15.35	7.31	6	62	0.074	842
Forsythe	4	36	25.72	13.15	8	54	0	297
French	3	25	23.54	9.81	8	52	0	105
Frypan	4	59	26.86	18.14	8	55	0.001	638
Gluskie	3	13	18.54	11.35	12	72	0.087	1722
Hooker	2	2	6.61	3.67	7	76	0	100
Hudson	3	11	18.4	9.05	8	61	0	224
Kynock	4	27	11.88	13.23	6	61	0.104	2368
Leo	3	14	20.83	9.23	8	76	0	330
Maclaing	3	10	22.34	8.18	8	60	0	403
Narrows	2	6	19.71	15.51	12	70	0.004	1757
Point	2	5	9.68	7.75	8	76	0	288
Sandpoint	3	12	20.11	9.85	6	65	0.003	618
Shale	3	7	17.11	9.85	4	62	0.002	351
Sinta	2	20	19.52	11.06	3	76	0	549
Van Decar	3	14	10.61	8.28	1	70	0.077	1468