

Quantitative Links Between Pacific Salmon and Stream Periphyton

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ABSTRACT

Species' impacts on primary production can have strong ecological consequences. In freshwater ecosystems, Pacific salmon (*Oncorhynchus* spp.) may influence stream periphyton through substrate disturbance during spawning and nutrient subsidies from senescent adults. The shape of relationships between the abundance of spawning salmon and stream periphyton, as well as interactions with environmental variables, are incompletely understood and may differ across the geographic range of salmon. 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 post-spawning periphyton abundance and nitrogen stable isotope signatures, which can indicate the uptake of salmon nitrogen, was evaluated using linear regression models and Akaike Information Criterion. Periphyton nitrogen stable isotope signatures were

best described by a positive log-linear relationship with an upstream salmon abundance metric that includes salmon from earlier years. This suggests the presence of a nutrient legacy. In contrast, periphyton abundance was negatively related to the spawning-year salmon density, which likely results from substrate disturbance during spawning, and positively related to dissolved soluble reactive phosphorus prior to spawning, which may indicate phosphorus limitation in the streams. These results suggest that enrichment from salmon nutrients does not always translate into elevated periphyton abundance. This underscores the need to directly assess the outcome of salmon impacts on streams rather than extrapolating from stable isotope evidence for the incorporation of salmon nutrients into food webs.

Key words: aquatic conservation; food web; ecosystem-based management; ecosystem engineer; resource subsidy; marine-derived nutrients; nutrient pulse.

Received 8 April 2010; accepted 16 July 2010;
published online 17 September 2010

Electronic supplementary material: The online version of this article (doi:10.1007/s10021-010-9371-0) contains supplementary material, which is available to authorized users.

Author contributions: JJV and JDR designed the study, JJV and DCB performed the research, JJV analyzed the data, DCB contributed to the statistical methods and JJV and JDR wrote the paper.

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INTRODUCTION

Individual species affect primary productivity through many mechanisms. Herbivory can increase primary productivity by maintaining plants in a state of rapid growth (for example, McNaughton 1985) and alter plant community composition (for example, Howe and others 2006). Species that deliver nutrient subsidies can stimulate primary production when nutrients are limiting (Polis and others 1997). The physical modification of habitat can also have positive or negative consequences for

primary production (Wright and Jones 2004). Such changes to basal food sources can have ecological consequences at higher trophic levels. In streams, internal primary production provides an important resource for aquatic primary consumers (Minshall 1978; Lamberti 1996) and changes in primary productivity can affect populations of both invertebrate primary consumers and their predators, including fish (Lamberti 1996). Primary production is predominantly by benthic algae found within a complex assemblage of algae, bacteria, fungi, and microzoans, called periphyton or biofilm (Steinman and others 2006).

Across the north Pacific, spawning anadromous salmon (*Oncorhynchus* spp.) may influence periphyton growth and abundance, with consequences for freshwater ecosystem structure and function. With more than 95% of the salmon's body mass accumulated in the ocean, their 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 and others 2002; Naiman and others 2002; Schindler and others 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, which contain marine-derived nitrogen, than in natural freshwater or terrestrial nitrogen sources (for example, Kline and others 1990; Bilby and others 1996; Chaloner and others 2002; Claeson and others 2006). Furthermore, salmon-derived nitrogen and phosphorus may be retained in watersheds after the spawning period, which could affect primary production in subsequent years (Naiman and others 2002; Peterson and Matthews 2009). Salmon may also affect periphyton through physical disturbance of the substrate during redd-digging and spawning, which can export nutrients, transport substrate, and scour existing periphyton (for example, Moore and others 2004; Moore and others 2007; Hassan and others 2008). Thus, salmon may increase or decrease the abundance of stream periphyton, depending on the relative effects of nutrient enrichment and physical disturbance.

Given the different ways salmon can affect periphyton, it is perhaps unsurprising that there is conflicting evidence on relationships between salmon and periphyton. Comparisons between sites with and without salmon have shown both decreases in periphyton abundance, likely from redd-digging (Minakawa and Gara 1999; Peterson and

Foote 2000), and increases, likely through the nutrient subsidy (Schuldt and Hershey 1995; Wipfli and others 1998; Peterson and Foote 2000; Chaloner and others 2004). A comparison of three streams over 3 years found that salmon abundance was positively related to periphyton abundance (Johnston and others 2004). In contrast, a comparison of 10 streams over multiple years found consistent decreases in periphyton abundance across a gradient in salmon abundance (Moore and Schindler 2008). Experiments in which salmon were excluded showed increased periphyton abundance when redd-digging was prevented (Moore and others 2004; Tiegs and others 2009), whereas experimental carcass additions elevated both dissolved nutrient levels and periphyton abundance (for example, Schuldt and Hershey 1995; Wipfli and others 1999; Kohler and others 2008).

Periphyton abundance is affected by a suite of variables other than salmon, such as stream discharge, light, temperature, and water chemistry (Biggs 1996; Borchardt 1996; DeNicola 1996; Hill 1996). Periphyton abundance can also be 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). As well, invertebrates can regulate periphyton abundance through grazing (Steinman 1996). Relationships between salmon and periphyton may be mediated by these variables (Mitchell and Lamberti 2005; Chaloner and others 2007). For example, periphyton may only respond to direct salmon nutrient subsidies when not limited by light (Rand and others 1992; Ambrose and others 2004). Further, human land-use activities can change environmental variables (for example, substrate size) that affect the link between salmon and periphyton (Tiegs and others 2008). There is a need to consider the effect of these environmental variables on relationships between salmon and periphyton (Janetski and others 2009).

Relationships between Pacific salmon and periphyton may also change with salmon abundance, which is relevant as Pacific salmon have substantially declined in abundance across parts of their range (Nehlsen and others 1991; Baker and others 1996; Slaney and others 1996; Gresh and others 2000). These declines are likely to have changed the magnitude of the ecosystem influence of spawning salmon. As management strategies begin to incorporate the ecological roles of salmon when setting escapement goals (that is, the number of fish that managers wish to let "escape" the fishery and return to the streams), predicting how changes in salmon abundance affect ecosystem

processes such as primary production will become increasingly relevant (for example, DFO 2005; Moore and Schindler 2008; Moore and others 2008). Consequently, there is a need to better understand the shape of relationships between salmon abundance and stream periphyton across the geographic range of Pacific salmon.

The overall objective of our study was to understand the role of spawning sockeye salmon (*Oncorhynchus nerka*) in the ecology of stream periphyton. Specifically, our study has the following facets aimed at filling key knowledge gaps: (1) we studied a large number of streams (24) to quantify the shape of relationships between salmon abundance and periphyton abundance (measured using chlorophyll *a* [chl *a*] content and ash-free dry mass [AFDM]) after spawning, (2) we compared these results to relationships between salmon abundance and periphyton nitrogen stable isotope signatures, which show the uptake of salmon nitrogen by periphyton and explicitly test for the contribution of salmon nutrients from previous years, and (3) we incorporated the potential role of environmental variables known to influence either periphyton abundance or nitrogen stable isotope signatures.

METHODS

Study Sites

We surveyed 24 sockeye salmon spawning streams in the Stuart River drainage at the most northern

extent of the Fraser River, British Columbia, Canada (Figure 1) from 54°55'N to 55°40'N and 125°20'W to 126°15'W. Sockeye salmon are the only anadromous fish in the streams. These populations are part of the "Early Stuart" complex, entering freshwater from early to mid July and migrating over 1100 km to spawn from early to mid August in the lower reaches of tributaries to Middle River and Takla Lake. These populations show 4-year cyclical abundance like many Fraser River sockeye (Levy and Wood 1992), with highest abundances in 2005, 2001, 1997, and so on. 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*).

The streams are second to fourth order and range in main channel length from 5.9 to 27.4 km and bankfull width from 3.7 to 30.5 m (Appendix 1 in Supplemental Materials). Values for the mean and range in gradient, water depth, water temperature, canopy cover, substrate size, and pre-spawning dissolved nutrient levels at our study sites are provided in Appendix 2 in Supplemental Materials. The watersheds are forested and common riparian species include hybrid white spruce (*Picea glauca* × *P. engelmannii*), black cottonwood (*Populus balsamifera*), Sitka alder (*Alnus viridis*), and devil's club (*Oplopanax horridus*). Water flows are highest in the spring as a result of snowmelt and lowest from late

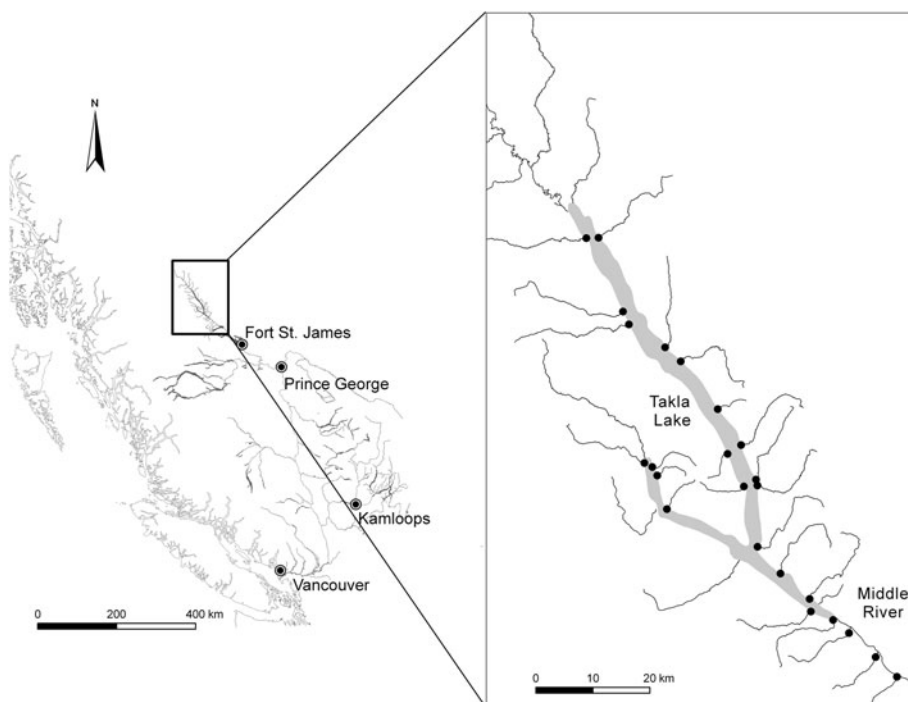


Figure 1. Location of the 24 study streams in the Stuart River drainage of the Fraser River, British Columbia, Canada.

July to mid September, when salmon spawn, and also from November to February, when most precipitation is accumulated as snow. Total annual precipitation in the region is around 500 mm of which on average 200 mm is snowfall. For a detailed description of the region and four of the streams see Macdonald and others (1992).

Salmon Abundance

All salmon abundance metrics were calculated from data provided by Fisheries and Oceans Canada (DFO). In each stream, DFO personnel conducted foot surveys every 4 days during the spawning period to count the number of live and dead sockeye across all spawning grounds. Finer scale counts were recorded for 500 m stream sections that corresponded to where we collected periphyton and habitat data. DFO personnel estimated the total number of adult salmon in each stream by multiplying the “peak” surveyed abundance of adult salmon by an expansion factor. The “peak” surveyed abundance was determined as the highest value obtained by adding the live count of adult salmon from a single survey to the total number of dead salmon summed across all prior surveys. The expansion factor was determined from data collected at counting fences on 2–3 streams as the number by which the peak surveyed abundance for the stream must be multiplied to equal the total number of salmon that passed through the counting fence.

We characterized the influence of adult salmon on periphyton abundance during the 2007 spawning period by two metrics. First, the total number of adult sockeye salmon upstream of our study sites (“2007 upstream salmon abundance”) was used as a proxy for total salmon nutrient input to the watershed. Although not all nutrients will be washed downstream this metric represents the theoretical maximum exposure. This metric was calculated by correcting the total number of adult salmon in a stream at “peak” abundance by the proportion of fish upstream of where we collected periphyton. Second, the local adult salmon density (fish m^{-2}) where periphyton was collected (“2007 salmon density”) was used as a proxy for both substrate disturbance and local nutrient input. This metric assumes no nutrient contribution from upstream. The 2007 salmon density (D) was calculated as follows:

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

where F is the total number of salmon in the section where we collected periphyton and habitat

data, w is the section-specific wetted width (m) and l is the length of the section (m). The two metrics were highly correlated ($r = 0.99$) and results did not differ between them. We report 2007 salmon density in models of periphyton abundance as it best characterizes both nutrient input and substrate disturbance. In 2007, spawning populations were small but represented a gradient of salmon abundance (2007 salmon density range = 0.0–0.1 fish m^{-2} , Appendix 1).

We characterized the potential influence of salmon abundance on periphyton nitrogen stable isotope signatures using both single-year (2007), which are described previously, and multi-year (2004–2007) metrics. Of the single-year metrics, we report 2007 salmon abundance in our models of periphyton nitrogen stable isotope signature as it best characterizes the theoretical maximum salmon nutrient exposure. The multi-year metrics represented the additional contribution of any salmon nutrients retained in the watershed from previous years. Mean upstream salmon abundance from 2004 to 2007 ranged from 2 to 2,368 fish (Appendix 1). Both upstream salmon abundance and local salmon density were summed over 4 years (2004–2007) with the contribution of earlier years weighted by a negative exponential function that described a rate of salmon nutrient loss from the watershed. These multi-year metrics (X) were calculated as follows:

$$X = \sum X_i \times e^{(-\lambda \times t)}, \quad (2)$$

where X_i is upstream salmon abundance or salmon density in year i , λ describes the rate of nutrient loss from the system, and t is the number of years prior to 2007. Metrics were calculated for values of λ that correspond to a salmon nutrient half-life in the watershed of 6 months, 1, 2, and 4 years. The multi-year metrics of upstream salmon abundance were highly correlated ($r > 0.98$ in all cases), as were the multi-year metrics of salmon density ($r > 0.97$ in all cases), and results did not differ between them. As such, we tested for the presence of a nutrient legacy but could not test its timeframe. We report 2004–2007 upstream abundance and 2004–2007 salmon density weighted by a 6 month salmon nutrient half-life in models of periphyton nitrogen stable isotope signatures. All three reported salmon abundance metrics were positively correlated (2007 upstream salmon abundance versus 2004–2007 upstream salmon abundance, $r = 0.89$; 2007 upstream salmon abundance versus 2004–2007 salmon density, $r = 0.74$; 2004–2007 upstream salmon abundance versus 2004–2007

salmon density, $r = 0.79$). We did not test a multi-year metric in models of periphyton abundance for two reasons. First, the influence of a nutrient legacy on periphyton abundance should be through pre-spawning dissolved nutrient concentrations, which we considered as covariates. Second, as single- and multi-year metrics are highly co-linear they should not be included in the same model.

Periphyton Collection and Processing

Unglazed ceramic tiles were anchored in each stream at the bottom of the spawning reach, given physical 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. Periphyton were sampled from the tiles 4–6 weeks after spawning in late September. 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).

We measured two proxies for periphyton abundance: chl *a* ($\mu\text{g cm}^{-2}$) and AFDM (mg cm^{-2}). Samples for chl *a* and AFDM analyses were scraped from an area of tile (3.14 cm^2 or 1.57 cm^2), filtered onto glass fiber filters (Whatman, 25 mm, $0.7 \mu\text{m}$ pore size), and stored in the dark at -20°C . Chl *a* was extracted in methanol at $2-4^\circ\text{C}$ 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). Linear regression showed chl *a* to be strongly related to total chlorophyll (total chlorophyll = $1.10 \text{ chl } a + 0.04$, $r^2 = 0.99$), which was calculated as the sum of pheophytin and chl *a*. This demonstrates that degradation products comprised a consistently small fraction of total chlorophyll. AFDM was measured according to Steinman and others (2006). Mean chl *a* and AFDM were calculated across all tiles in a stream.

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 more than 24 h 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 thousand” (‰) according to

$$\delta^{15}\text{N}(\text{‰}) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000, \quad (3)$$

where R is the ratio of heavy isotope (^{15}N) to light isotope (^{14}N) in the sample and standard. Finally, $\delta^{15}\text{N}$ was averaged across all tiles in a stream.

Environmental Variables

A literature search showed that periphyton abundance can be influenced by water temperature, dissolved nitrogen and phosphorus concentrations, light availability, watershed size, and grazer abundance (Table 1b). Water temperature, light availability, and water velocity have been shown to influence periphyton nitrogen stable isotope signatures (Table 1a). We also considered the number of days the tiles were in the stream (soak time) as an explanatory variable of periphyton abundance (range = 53–76 days).

We characterized water temperature as the mean maximum daily temperature across the spawning period (August 5th–21st). Stream temperature was measured using waterproofed iButton (DS1922L) temperature loggers programmed to record temperatures every 2 h and attached to iron rods imbedded in the stream. As equipment failure led to missing temperature data for two streams, we first performed our analyses with this reduced dataset of 22 streams. As temperature proved not to be a significant explanatory variable of $\delta^{15}\text{N}$, chl *a*, or AFDM, we excluded it and repeated the analyses across all 24 streams, which led to the same conclusions as with temperature included.

Dissolved phosphorus, characterized as soluble reactive phosphorus (SRP), and dissolved inorganic nitrogen, calculated as the sum of total ammonia ($\text{NH}_4\text{-N}$) and nitrite nitrogen ($\text{NO}_3\text{-N}$), were sampled two or three times at one location in each stream over 2 months prior to spawning. Samples were analyzed at DFO’s Cultus Lake Laboratory according to American Public Health Association methods (APHA 1989). Briefly, SRP was determined by the automated ascorbic acid method, $\text{NO}_3\text{-N}$ by the automated cadmium reduction method, and $\text{NH}_4\text{-N}$ by the automated phenate method.

As a proxy for water velocity, stream gradient was measured across the length of stream in which the tiles were situated using a $5\times$ Abney hand level. Percent open canopy was measured at each tile location using a spherical densitometer and the mean value from tile placement and collection used

Table 1. A Priori Predictions for the Potential Influence of Environmental Variables on (a) Periphyton Nitrogen Stable Isotope Signatures ($\delta^{15}\text{N}$) and (b) Periphyton Abundance (chl *a* and AFDM)

Variable	Mechanism	Direction	Metric	References
a)				
Temperature	Water temperature can increase metabolic activity and thus increase nitrogen stable isotope signatures	Positive	Mean maximum daily temperature ($^{\circ}\text{C}$)	Friberg and others (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)				
Temperature	Water temperature can limit metabolic activity and thus periphyton growth	Positive	Mean maximum daily temperature ($^{\circ}\text{C}$)	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 ($\mu\text{g l}^{-1}$)	Lamberti and Steinman (1997), Biggs (1996), Borchartd (1996)
Dissolved nitrogen	Nitrogen has been shown to limit periphyton growth in some areas	Positive	Dissolved inorganic nitrogen ($\mu\text{g l}^{-1}$)	Lamberti and Steinman (1997), Biggs (1996), Borchartd (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)

The mechanism, direction of influence, and metric used to characterize each environmental variable are described.

as a proxy for light availability. We used the first axis of a principal components analysis of stream magnitude, length, and bankfull width as a metric for watershed size. This axis explained 79% of the variation in the three variables and all variables loaded positively with eigenvalues greater than 0.5. Stream magnitude, which is the number of first order tributaries in the watershed, and stream 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 10 cm.

Grazer abundance was calculated from benthic invertebrate samples collected during the month immediately prior to salmon spawning (July 1st–August 2nd, 2007). Four samples were taken per stream from different riffles. Within each riffle, three separate invertebrate collections were pooled. Collections were made using a Surber sampler (frame area = 0.09 m², 500 µm mesh) by agitating the substrate within the frame to a depth of 10 cm for 2 min, washed into plastic bottles, preserved in 95% ethanol, and transported back to the laboratory. Samples were split using a Folsom Plankton Splitter and subsamples picked under magnification until a total count of over 300 individuals was reached. Ten percent of samples were independently re-picked to verify sorting efficiency as greater than 90%. Insects of the orders Ephemeroptera, Plecoptera, Trichoptera, and Diptera (EPTD) were identified to family level, with all other invertebrates identified to order, using Merritt and others (2008). Ten percent of samples were independently identified to verify accuracy as greater than 95%. Functional feeding group designations were made using Merritt and others (2008) and the abundance of all individuals classified as grazers was summed to estimate grazer abundance (number m⁻²).

Data Analysis

First, we conducted an exploratory analysis to identify the environmental variables that best described periphyton nitrogen stable isotope signatures and abundance across the 24 streams. We then evaluated the relative importance of salmon abundance, the environmental variables selected from the exploratory step (explained below), and tile soak time in describing periphyton nitrogen stable isotope signatures, chl *a* content, and AFDM. We did this by competing multiple linear regression models using Akaike Information Criterion corrected for small sample sizes (AICc).

We identified the explanatory environmental variables that best described periphyton nitrogen stable isotope signatures and abundance according to methods suggested by Zuur and others (2010). First, we examined multicollinearity among all explanatory environmental variables using variance inflation factors (VIF) (Table 1). A VIF quantifies the severity of multicollinearity in an ordinary least squares regression analysis by measuring how much the variance of an estimated regression coefficient is increased because of collinearity among explanatory variables. No variable exceeded a value of two, suggesting multicollinearity among variables was not of concern. We then conducted a backward stepwise linear regression using all variables and sequentially dropped non-significant explanatory variables ($P > 0.05$). A less stringent criterion of P greater than 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. Stream gradient came through the regression procedure as an explanatory variable of $\delta^{15}\text{N}$, SRP as an explanatory variable of AFDM and both SRP and canopy cover as explanatory variables of chl *a*. As the relationship between canopy cover and chl *a* was the inverse to that predicted, thus likely spurious, we dropped canopy cover from further consideration.

We then combined the selected environmental variables (gradient or SRP) with the relevant salmon abundance metrics (2007 upstream salmon abundance, 2007 salmon density, 2004–2007 upstream salmon abundance, or 2004–2007 salmon density), and tile soak time. No variable had a VIF above two and scatterplots did not reveal any obvious non-linearity between any explanatory and response variables. We created linear regression models of each response variable ($\delta^{15}\text{N}$, chl *a*, and AFDM) for all single explanatory variables and combinations of explanatory variables, with the restriction 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 2007 salmon density and 2004–2007 salmon density and log₁₀ transformed 2007 upstream salmon abundance, 2004–2007 upstream salmon abundance, gradient, SRP, AFDM, and chl *a* to improve fits with the model assumptions.

We used AICc to evaluate the support for each model in describing $\delta^{15}\text{N}$, AFDM, and chl *a*. AICc evaluates the relative descriptive power of various a priori models with different combinations of variables based on the principle 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 Δ AICc 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 $w_{\text{top model}}/w_i$ 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).

We used a 2-source isotope-mixing model (for example, Naiman and others 2002; Schindler and others 2005) to estimate the proportion of nitrogen in the periphyton that was derived from salmon. This model assumed that periphyton accumulated nitrogen from salmon and a combined pool of other sources in proportion to availability. It also assumed that other sources of nitrogen had a constant combined nitrogen stable isotope signature across streams and that fractionation during nitrogen uptake was independent of salmon nutrient contributions. The proportion of nitrogen in periphyton derived from salmon (X) was calculated as follows:

$$X = \frac{(\delta^{15}\text{N}_{\text{periphyton}} - \delta^{15}\text{N}_b)}{(\delta^{15}\text{N}_{\text{sockeye}} - \delta^{15}\text{N}_b)}, \quad (4)$$

where $\delta^{15}\text{N}_{\text{periphyton}}$ was the mean nitrogen stable isotope signature of periphyton, $\delta^{15}\text{N}_{\text{sockeye}}$ was the nitrogen stable isotope signature of sockeye salmon, and $\delta^{15}\text{N}_b$ was the nitrogen stable isotope signature of the combined pool of other nitrogen sources. We used a value of 11.29‰ for $\delta^{15}\text{N}_{\text{sockeye}}$ (Johnson and Schindler 2009). We used the mean value of periphyton $\delta^{15}\text{N}$ across nine “control” sites; three streams that had a 2004–2007 upstream salmon abundance of fewer than 10 fish (Appendix 1) and six streams where we sampled periphyton above the extent of salmon spawning (J. J. Verspoor, unpublished data) to approximate $\delta^{15}\text{N}_b$.

RESULTS

Periphyton Nitrogen Stable Isotope Signature

In the top model, 2004–2007 upstream salmon abundance had a positive log-linear relationship to the nitrogen stable isotope signature ($\delta^{15}\text{N}$) of stream periphyton ($R^2 = 0.28$, Figure 2). This model had four times more support than the second ranked model, which contained both

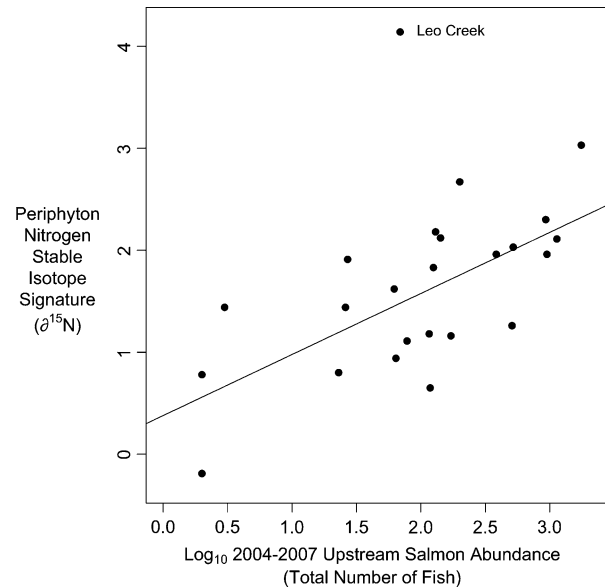


Figure 2. Plot of \log_{10} -transformed 2004–2007 upstream salmon abundance (total number of fish) versus periphyton nitrogen stable isotope signature ($\delta^{15}\text{N}$), with the outlying Leo Creek labeled. The fitted linear relationship excludes Leo Creek ($\delta^{15}\text{N} = 0.599\log_{10}$ 2004–2007 upstream salmon abundance + 0.379, $R^2 = 0.47$).

2004–2007 upstream salmon abundance and gradient (Table 2a). The similarity in R^2 between the top two models shows that gradient explained little additional variation in $\delta^{15}\text{N}$. All other models had a Δ AICc greater than 3.

One study site (Leo Creek) stood out as an outlier in the regression diagnostics of the top two models (standardized residual >3). This stream had an upstream lake area that was almost three times greater than any other stream, heavy beaver (*Castor canadensis*) activity 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 (Table 2b). The 2004–2007 upstream salmon abundance remained as the top model and model fit improved ($R^2 = 0.47$, Figure 2).

The 2-source mixing model suggested that the contribution of salmon nitrogen to periphyton across the 24 streams ranged from 0 to 22%. For reasons discussed earlier, we did not estimate a contribution of salmon nitrogen to periphyton in Leo Creek. The mean $\delta^{15}\text{N}$ used for all non-salmon sources was 0.66‰ but ranged from -0.19 ‰ to 2.32‰ across periphyton collected from “control” sites.

Table 2. Results of Model Selection using AICc for Seven Linear Regression Models that Describe Periphyton Nitrogen Stable Isotope Signatures ($\delta^{15}\text{N}$)

	<i>k</i>	<i>R</i> ²	<i>P</i>	ΔAICc	<i>w</i> _{<i>i</i>}	ER
a) Model (including Leo Creek)						
1. 2004–2007 upstream salmon abundance	3	0.28	0.008	0.00	0.63	1.00
2. 2004–2007 upstream salmon abundance + gradient	4	0.28	0.03	2.84	0.15	4.15
3. 2004–2007 salmon density	3	0.13	0.09	4.63	0.06	10.14
4. 2007 upstream salmon abundance	3	0.12	0.09	4.70	0.06	10.49
5. Gradient	3	0.11	0.11	5.03	0.05	12.38
6. 2004–2007 salmon density + gradient	4	0.17	0.13	6.18	0.03	22.01
7. 2007 upstream salmon abundance + gradient	4	0.16	0.16	6.60	0.02	27.08
b) Model (excluding Leo Creek)						
1. 2004–2007 upstream salmon abundance	3	0.47	0.0003	0.00	0.73	1.00
2. 2004–2007 upstream salmon abundance + gradient	4	0.47	0.002	2.96	0.17	4.39
3. 2007 upstream salmon abundance	3	0.33	0.005	5.49	0.05	15.58
4. 2004–2007 salmon density	3	0.29	0.008	6.55	0.03	26.46
5. 2007 upstream salmon abundance + gradient	4	0.34	0.02	7.96	0.01	53.42
6. 2004–2007 salmon density + gradient	4	0.33	0.02	8.25	0.01	61.85
7. Gradient	3	0.15	0.07	10.92	0.00	235.67

Results are presented (a) including Leo Creek (*n* = 24) and (b) excluding Leo Creek (*n* = 23). Stream gradient, 2007 upstream salmon abundance, and 2004–2007 upstream salmon abundance were \log_{10} -transformed and 2004–2007 salmon density was square-root transformed. *k* = number of model parameters, *R*² = model regression coefficient, *P* = model significance, ΔAICc = change in AICc score from top model, *w*_{*i*} = AICc model weight, ER = top model weight divided by model *i* weight.

Periphyton Abundance

In the top model, salmon density in 2007 had a negative relationship to the AFDM of stream periphyton, whereas pre-spawning SRP had a positive relationship to AFDM ($\log_{10}\text{AFDM} = 0.94\log_{10}\text{SRP} - 1.05\sqrt{2007 \text{ salmon density}} - 0.67$, $R^2 = 0.49$). This model had twice as much support as the second ranked model, which contained 2007 salmon density, SRP, and tile soak time (Table 3). The higher *R*² of the second model shows that soak time explained some additional variation in AFDM but that it was less than the penalty imposed for the additional parameter. Support for the other

five models was poor ($\Delta\text{AICc} > 3$). We present observed versus fitted plots for the top model and untransformed bivariate plots of the individual explanatory variables versus AFDM for comparison (Figure 3).

In the top model, salmon density in 2007 had a negative relationship to the chl *a* content of stream periphyton, whereas pre-spawning SRP had a positive relationship to chl *a* ($\log_{10}\text{chl } a = 1.49\log_{10}\text{SRP} - 1.09\sqrt{2007 \text{ salmon density}} - 0.58$, $R^2 = 0.33$). This model had twice as much support as the second ranked model, which contained SRP as a single explanatory variable (Table 4). Support

Table 3. Results of Model Selection using AICc for Seven Linear Regression Models that Describe Periphyton AFDM

Model	<i>k</i>	<i>R</i> ²	<i>P</i>	ΔAICc	<i>w</i> _{<i>i</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

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.

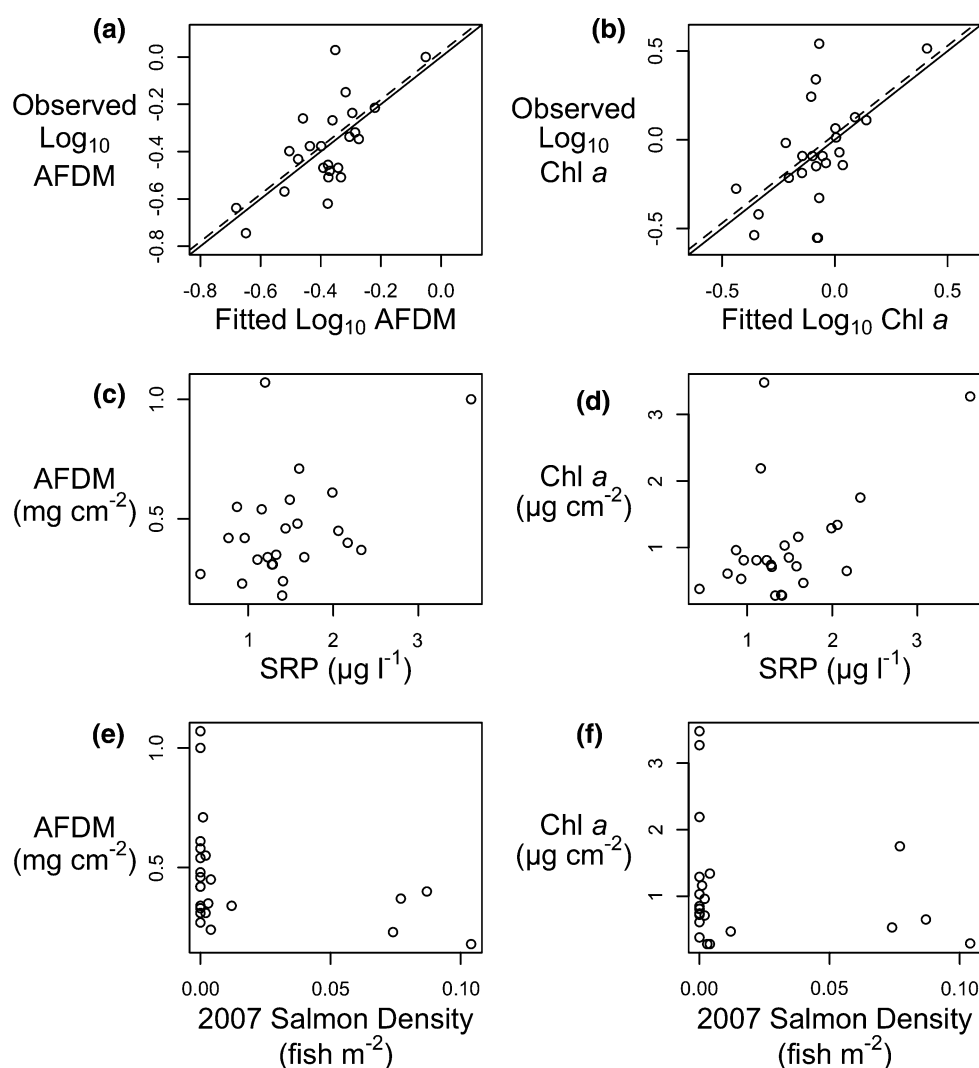


Figure 3. Bivariate plots of observed versus fitted values for the top model of **A** \log_{10} ash-free dry mass (AFDM, mg cm^{-2}) and **B** \log_{10} chlorophyll *a* (*chl a*, $\mu\text{g cm}^{-2}$), which both contain $\sqrt{2007}$ salmon density (fish m^{-2}) and \log_{10} soluble reactive phosphorus (SRP, $\mu\text{g l}^{-1}$) as explanatory variables, fitted with regression (*dashed*) and 1:1 (*solid*) lines. Bivariate plots of **C** AFDM versus SRP, **D** *chl a* versus SRP, **E** AFDM versus 2007 salmon density, and **F** *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 bivariate plots are presented untransformed.

Table 4. Results of Model Selection using AICc for Seven Linear Regression Models that Describe Periphyton *chl a*

Model	<i>k</i>	R^2	<i>P</i>	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

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.

for the other five models was poor ($\Delta\text{AICc} > 3$). We present observed versus fitted plots for the top model and untransformed bivariate plots of the individual explanatory variables versus *chl a* for comparison (Figure 3).

DISCUSSION

Nitrogen Stable Isotope Signature

We found a positive log-linear relationship between 2004–2007 upstream salmon abundance and the

nitrogen stable isotope signature ($\delta^{15}\text{N}$) of stream periphyton across 24 streams in north-central British Columbia. This study is among the first to describe periphyton $\delta^{15}\text{N}$ across a gradient in salmon abundance (also see Holtgrieve and others 2010). Relationships between $\delta^{15}\text{N}$ and salmon abundance have previously been shown for juvenile coho salmon, terrestrial invertebrates, and riparian soil and vegetation (Bilby and others 2001; Reimchen and others 2003; Bartz and Naiman 2005; Hocking and Reimchen 2009).

Although we fit a log-linear model, the relationship between salmon abundance and periphyton $\delta^{15}\text{N}$ should actually be a positive function that saturates as the contribution of salmon nitrogen to periphyton $\delta^{15}\text{N}$ nears 100%. However, the periphyton $\delta^{15}\text{N}$ values in this study were low relative to the $\delta^{15}\text{N}$ of sockeye salmon, suggesting they were far from saturated with salmon nitrogen. That periphyton derived most of their nitrogen from sources other than salmon is supported by the results of the 2-source mixing model, which estimated the highest proportion of salmon nitrogen across the 24 streams to be just 22%. This number is sensitive to the $\delta^{15}\text{N}$ chosen for all non-salmon sources of nitrogen, which varied widely among the "control" sites used to estimate it. Therefore, although the contribution of salmon nitrogen to periphyton $\delta^{15}\text{N}$ is low, the values attributed by the mixing-model are highly uncertain. It is likely that salmon nitrogen would have made a greater contribution to periphyton $\delta^{15}\text{N}$ in years when sockeye populations in the region were at higher abundances. In the early 1990s, the number of adult salmon summed across the 24 streams was typically greater than 70,000 fish, whereas it was just 20,000 fish from 2004 to 2007.

We expected three environmental variables (temperature, light, and water velocity) to affect periphyton $\delta^{15}\text{N}$ (Table 1a). Of the three variables, periphyton $\delta^{15}\text{N}$ was best described by gradient, which was used as a proxy for water velocity. Water velocity can control the rate at which the dissolved nitrogen available to periphyton is replenished, which influences the rate of uptake of the different isotopes (Trudeau and Rasmussen 2003). However, gradient poorly explained variation in periphyton $\delta^{15}\text{N}$ compared to salmon abundance, particularly after removing the outlier, Leo Creek. This suggests that salmon abundance had a stronger influence on periphyton $\delta^{15}\text{N}$ than any environmental variable we measured. This is the first study to explicitly consider the relative influence of salmon nutrients and environmental variables on periphyton $\delta^{15}\text{N}$. Although stream

gradient may have indicated relative differences among streams, it is a poor metric for water velocity at the individual tile sites. It is also positively correlated with substrate size and larger substrate could potentially reduce water velocity at the streambed through greater rugosity. Direct measurement of water velocity at the individual tile site may have described periphyton $\delta^{15}\text{N}$ better.

We tested one single-year and two multi-year salmon abundance metrics. The single-year metric represented the maximum possible exposure to salmon nutrients delivered during the 2007 spawning period, whereas the multi-year metrics captured the possible contribution of salmon nutrients from previous years. The two multi-year metrics differed in their consideration of salmon that spawned upstream of where we collected the periphyton. Our results suggest that salmon nitrogen accumulated among years in the watershed, including upstream, contributed to periphyton $\delta^{15}\text{N}$. Studies could confirm this nutrient legacy through stable isotopes of dissolved inorganic nitrogen prior to spawning. It was possible to test for this nutrient legacy for two reasons. First, 2007 salmon numbers were the lowest in decades. Only 4,500 sockeye returned across all 24 streams compared to the 4-year average of 20,000. Second, the dominant year of the 4-year population cycle exhibited in these sockeye populations was in 2005 when 51,000 salmon returned across all streams and delivered a much larger nutrient subsidy. Although we initially calculated multi-year metrics according to different rates of salmon nutrient loss from the watershed, high correlation among them prevented a test for the timeframe of the nutrient legacy.

Periphyton Abundance

Periphyton abundance was best described by a combination of salmon density and environmental variables. Both AFDM and chl *a* were negatively related to 2007 salmon density and positively related to pre-spawning SRP concentrations, although the model fit was better for AFDM. Only a small amount of variation in either AFDM or chl *a* was explained by tile soak time.

We measured six environmental variables (water temperature, light availability, dissolved phosphorus and nitrogen, grazer abundance, and watershed size) that were predicted to affect periphyton abundance (Table 1b). Of these, pre-spawning SRP best described periphyton abundance, suggesting that phosphorus may limit 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. This could explain the weak positive correlation we found between 2006 upstream salmon abundance and pre-spawning SRP after removing the outlying Leo Creek ($r = 0.42$, $P = 0.044$).

As pre-spawning SRP positively described periphyton abundance after spawning, it might be expected that the additional phosphorus delivered during spawning would further increase periphyton abundance. In contrast, we found a negative relationship among streams between 2007 salmon density and periphyton abundance. This result suggests that during the spawning period, salmon exerted a greater influence on periphyton abundance through substrate disturbance than by the nutrient subsidy they provided. Further, as periphyton samples were collected up to 6 weeks post-spawning after some recovery in abundance had probably occurred, our results likely underestimate the initial ecological effect of substrate disturbance by spawning salmon. Periphyton recovery might have been impeded by decreasing water temperatures and lower light levels, as a result of decreasing day length. The general finding that salmon exert a greater influence on periphyton abundance through substrate disturbance than the nutrient subsidy they provide is consistent with research on sockeye streams in Alaska that found decreases in periphyton abundance during spawning in streams with a salmon abundance above $0.06 \text{ salmon m}^{-2}$ (Moore and Schindler 2008).

However, a positive relationship, above a threshold value of 300 kg 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 our study streams (Johnston and others 2004). In their study from 1996 to 1998, salmon density was up to an order of magnitude greater than in this study and chl *a* was substantially higher at their high salmon abundance sites. As both the salmon nutrient contribution and degree of substrate disturbance should be greater at higher salmon abundance, the contrast in results is puzzling. The relative importance of the two mechanisms could differ as a result of temporal variation in environmental variables such as temperature or discharge (for example, Chaloner and others 2007). Another possibility is that results differ according to spatial scale (3 streams versus 24 streams) or whether

periphyton is collected from experimental substrates (our study) or natural ones (Johnston and others 2004).

Periphyton abundance at a single point in time does not measure primary productivity directly. Periphyton growth rates could in fact be high when abundances are low if periphyton removal is elevated. Indeed, spawning salmon could simultaneously have increased periphyton growth rates through the nutrient subsidy and reduced periphyton abundance through spawning activities. Larger populations of invertebrate grazers could also reduce periphyton abundance and be supported by elevated periphyton growth rates. However, invertebrate grazer abundance has generally been shown to decrease during salmon spawning through both displacement from substrate disturbance and the evolution of life history strategies whereby emergence from the streams is timed to avoid being in the stream during salmon spawning (Lessard and Merritt 2006; Moore and Schindler 2008; Honea and Gara 2009; Lessard and others 2009; Moore and Schindler 2010). As we found that pre-spawning grazer abundance did not explain significant variation in periphyton abundance, this suggests that salmon spawning was the primary driver of reduced abundance.

In conclusion, although salmon abundance was positively related to periphyton nitrogen stable isotope signatures it was negatively related to periphyton abundance. Thus, uptake of salmon-derived nitrogen does not always translate into increased periphyton abundance. This suggests that the physical disturbance of spawning salmon outweighs the immediate influence of the nutrients they deliver. This finding suggests that attempts to incorporate the wider ecological role of salmon into conservation management (for example, DFO 2005) should be viewed with caution when using stable isotopes as a proxy for direct evidence of the impacts of salmon on freshwater ecosystems. However, our use of stable isotopes to provide evidence for a nutrient legacy from previous years suggests that salmon nutrients could have ecological impacts in freshwater ecosystems beyond the year in which they were delivered. We found that dissolved phosphorus levels prior to spawning, which are correlated with past salmon abundances, also described periphyton abundance. This both confirms the need to consider the effect of environmental variables on relationships between salmon and their ecosystems and presents evidence that stream productivity may be increased as a result of long-term salmon nutrient loading.

ACKNOWLEDGEMENTS

We thank our primary funder, the Fraser Salmon and Watersheds Program, as well as the Natural Sciences and Engineering Research Council of Canada, the Watershed Watch Salmon Society, the Northern Scientific Training Program, and Fisheries and Oceans Canada (DFO). We appreciate help from DFO staff, including David Patterson, Herb Herunter, Erland MacIsaac, Tracy Cone, Dennis Klassen, Kerry Parish, and Keri Benner for logistical support, the water nutrient analyses, and valuable advice on the field sites. We acknowledge the contribution of lab space and equipment for the chl *a* and AFDM analyses by Wendy Palen and Leah Bendell, respectively. We appreciate field support from Rudi Verspoor and Mike Sawyer and lab support from Morgan Stubbs, Tereza Zagar, and Jenn Blancard. We thank Marianne Fish, Morgan Hocking, Phil Molloy, Wendy Palen, and John Richardson for help with the manuscript.

REFERENCES

- Ambrose HE, Wilzbach MA, Cummins KW. 2004. Periphyton response to increased light and salmon carcass introduction in northern California streams. *J N Am Benthol Soc* 23:701–12.
- Anderson DR. 2008. Model based inference in the life sciences—a primer on evidence. New York, USA: Springer.
- APHA (American Public Health Association). 1989. Standard methods for the examination of waste and wastewater. 17th edn. Washington (DC): American Public Health Association, American Water Works Association, and Water Pollution Control Federation.
- Baker TT, Wertheimer AC, Burkett RD, Dunlap R, Eggers DM, Fritts EI, Gharrett AJ, Holmes RA, Wilmot RL. 1996. Status of Pacific salmon and steelhead escapements in southeastern Alaska. *Fisheries* 21:6–18.
- Bartz KK, Naiman RJ. 2005. Effects of salmon-borne nutrients on riparian soils and vegetation in southwest Alaska. *Ecosystems* 8:529–45.
- Biggs BJF. 1996. Patterns in benthic algae of streams. In: Stevenson RJ, Bothwell ML, Lowe RL, Eds. *Algal ecology: freshwater benthic ecosystems*. San Diego: Academic Press, Elsevier Inc.
- Bilby RE, Fransen BR, Bisson PA. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Can J Fish Aquat Sci* 53:164–73.
- Bilby RE, Fransen BR, Walter JK, Scarlett WJ. 2001. Preliminary evaluation of the use of nitrogen stable isotope ratios to establish escapement levels for Pacific salmon. *Fisheries* 26:6–14.
- Borchardt MA. 1996. Nutrients. In: Stevenson RJ, Bothwell ML, Lowe RL, Eds. *Algal ecology: freshwater benthic ecosystems*. San Diego: Academic Press, Elsevier Inc.
- Chaloner DT, Martin KM, Wipfli MS, Ostrom PH, Lamberti GA. 2002. Marine carbon and nitrogen in southeastern Alaska stream food webs: evidence from artificial and natural streams. *Can J Fish Aquat Sci* 59:1257–65.
- Chaloner DT, Lamberti GA, Merritt RW, Mitchell NL, Ostrom PH, Wipfli MS. 2004. Variation in responses to spawning Pacific salmon among three south-eastern Alaska streams. *Freshw Biol* 49:587–99.
- Chaloner DT, Lamberti GA, Cak AD, Blair NL, Edwards RT. 2007. Inter-annual variation in responses of water chemistry and epilithon to Pacific salmon spawners in an Alaskan stream. *Freshw Biol* 52:478–90.
- Claeson SM, Li JL, Compton JE, Bisson PA. 2006. Response of nutrients, biofilm, and benthic insects to salmon carcass addition. *Can J Fish Aquat Sci* 63:1230–41.
- DeNicola DM. 1996. Periphyton responses to temperature at different ecological levels. In: Stevenson RJ, Bothwell ML, Lowe RL, Eds. *Algal ecology: freshwater benthic ecosystems*. San Diego: Academic Press, Elsevier Inc.
- DFO (Fisheries and Oceans Canada). 2005. Canada's policy for conservation of wild Pacific salmon. Vancouver, BC, Canada. <http://www.pac.dfo-mpo.gc.ca/publications/pdfs/wsp-eng.pdf>.
- Friberg N, Dybkjaer JB, Olafsson JS, Gislason GM, Larsen SE, Lauridsen TL. 2009. Relationships between structure and function in streams contrasting in temperature. *Freshw Biol* 54:2051–68.
- Gende SM, Edwards RT, Willson MF, Wipfli MS. 2002. Pacific salmon in aquatic and terrestrial ecosystems. *Bioscience* 52:917–28.
- Gresh T, Lichatowich J, Schoonmaker P. 2000. An estimation of historic and current levels of salmon production in the Northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. *Fisheries* 25:15–21.
- Hassan MA, Gottesfeld AS, Montgomery DR, Tunnicliffe JF, Clarke GKC, Wynn G, Jones-Cox H, Poirier R, MacIsaac E, Herunter H, Macdonald SJ. 2008. Salmon-driven bed load transport and bed morphology in mountain streams. *Geophys Res Lett* 35:6.
- Hill W. 1996. Effects of light. In: Stevenson RJ, Bothwell ML, Lowe RL, Eds. *Algal ecology: freshwater benthic ecosystems*. San Diego: Academic Press, Elsevier Inc.
- Hocking MD, Reimchen TE. 2009. Salmon species, density and watershed size predict magnitude of marine enrichment in riparian food webs. *Oikos* 118:1307–18.
- Holm-Hansen O, Riemann B. 1978. Chlorophyll *a* determination: improvements in methodology. *Oikos* 30:438–47.
- Holtgrieve GW, Schindler DE, Gowell CP, Ruff CP, Lisi PJ. 2010. Stream geomorphology regulates the effects of ecosystem engineering and nutrient enrichment by Pacific salmon on periphyton. *Freshw Biol*. doi:10.1111/j.1365-2427.2010.02489.x.
- Honea JM, Gara RI. 2009. Macroinvertebrate community dynamics: strong negative response to salmon redd construction and weak response to salmon-derived nutrient uptake. *J N Am Benthol Soc* 28:207–19.
- Howe HF, Zorn-Arnold B, Sullivan A, Brown JS. 2006. Massive and distinctive effects of meadow voles on grassland vegetation. *Ecology* 87:3007–13.
- Janetski DJ, Chaloner DT, Tiegs SD, Lamberti GA. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. *Oecologia* 159:583–95.
- Johnson SP, Schindler DE. 2009. Trophic ecology of Pacific salmon (*Oncorhynchus* spp.) in the ocean: a synthesis of stable isotope research. *Ecol Res* 24:855–63.

- Johnston NT, MacIsaac EA, Tschaplinski PJ, Hall KJ. 2004. Effects of the abundance of spawning sockeye salmon (*Oncorhynchus nerka*) on nutrients and algal biomass in forested streams. *Can J Fish Aquat Sci* 61:384–403.
- Kline TCJ, Goering JJ, Mathisen OA, Poe PH, Parker PL. 1990. Recycling of elements transported upstream by runs of Pacific salmon I. Delta Nitrogen-15 and Delta Carbon-13 evidence in Sashin Creek Southeastern Alaska USA. *Can J Fish Aquat Sci* 47:136–44.
- Kohler AE, Rugenski A, Taki D. 2008. Stream food web response to a salmon carcass analogue addition in two central Idaho, USA streams. *Freshw Biol* 53:446–60.
- Lamberti GA. 1996. The role of periphyton in benthic food webs. In: Stevenson RJ, Bothwell ML, Lowe RL, Eds. *Algal ecology: freshwater benthic ecosystems*. San Diego: Academic Press, Elsevier Inc.
- Lamberti GA, Steinman AD. 1997. A comparison of primary production in stream ecosystems. *J N Am Benthol Soc* 16:95–104.
- Lessard JL, Merritt RW. 2006. Influence of marine-derived nutrients from spawning salmon on aquatic insect communities in southeast Alaskan streams. *Oikos* 113:334–43.
- Lessard JL, Merritt RW, Berg MB. 2009. Investigating the effect of marine-derived nutrients from spawning salmon on macroinvertebrate secondary production in southeast Alaskan streams. *J N Am Benthol Soc* 28:683–93.
- Levy DA, Wood CC. 1992. Review of proposed mechanisms for sockeye salmon population cycles in the Fraser River. *Bull Math Biol* 54:241–61.
- Macdonald JS, Scrivener JC, Smith G. 1992. The Stuart-Takla fisheries/forestry interaction project: study description and design. Canadian Technical Report of Fisheries and Aquatic Sciences No. 1899.
- MacLeod NA, Barton DR. 1998. Effects of light intensity, water velocity, and species composition on carbon and nitrogen stable isotope ratios in periphyton. *Can J Fish Aquat Sci* 55:1919–25.
- McNaughton SJ. 1985. Ecology of a grazing ecosystem—the Serengeti. *Ecol Monogr* 55:259–94.
- Merritt R, Cummins K, Berg M. 2008. An introduction to the aquatic insects of North America. Dubuque (IA): Kendall/Hunt Publishing Company.
- Minakawa N, Gara RI. 1999. Ecological effects of a chum salmon (*Oncorhynchus keta*) spawning run in a small stream of the Pacific Northwest. *J Freshw Ecol* 14:327–35.
- Minshall GW. 1978. Autotrophy in stream ecosystems. *Bioscience* 28:767–70.
- Mitchell NL, Lamberti GA. 2005. Responses in dissolved nutrients and epilithon abundance to spawning salmon in southeast Alaska streams. *Limnol Oceanogr* 50:217–27.
- Moore JW, Schindler DE. 2008. Biotic disturbance and benthic community dynamics in salmon-bearing streams. *J Anim Ecol* 77:275–84.
- Moore JW, Schindler DE. 2010. Spawning salmon and the phenology of emergence in stream insects. *Proc R Soc B*. doi:10.1098/rspb.2009.2342.
- Moore JW, Schindler DE, Scheuerell MD. 2004. Disturbance of freshwater habitats by anadromous salmon in Alaska. *Oecologia* 139:298–308.
- Moore JW, Schindler DE, Carter JL, Fox J, Griffiths J, Holtgrieve GW. 2007. Biotic control of stream fluxes: Spawning salmon drive nutrient and matter export. *Ecology* 88:1278–91.
- Moore JW, Schindler DE, Ruff CP. 2008. Habitat saturation drives thresholds in stream subsidies. *Ecology* 89:306–12.
- Naiman RJ, Bilby RE, Schindler DE, Helfield JM. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* 5:399–417.
- Nehlsen W, Williams JE, Lichatowich JA. 1991. Pacific Salmon at the crossroads—stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16:4–21.
- Peterson DP, Foote CJ. 2000. Disturbance of small-stream habitat by spawning sockeye salmon in Alaska. *Trans Am Fish Soc* 129:924–34.
- Peterson M, Matthews R. 2009. Retention of salmon-derived N and P by bryophytes and microbiota in mesocosm streams. *J N Am Benthol Soc* 28:352–9.
- Polis GA, Anderson WB, Holt RD. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu Rev Ecol Syst* 28:289–316.
- R Development Core Team. 2009. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Rand PS, Hall CAS, McDowell WH, Ringler NH, Kennen JG. 1992. Factors limiting primary productivity in Lake-Ontario tributaries receiving salmon migrations. *Can J Fish Aquat Sci* 49:2377–85.
- Reimchen TE, Mathewson DD, Hocking MD, Moran J, Harris D. 2003. Isotopic evidence for enrichment of salmon-derived nutrients in vegetation, soil, and insects in Riparian zones in coastal British Columbia. In: Stockner JG, Ed. *Nutrients in salmonid ecosystems: sustaining production and biodiversity*. Bethesda: American Fisheries Society Symposium. pp 59–69.
- Schindler DE, Scheuerell MD, Moore JW, Gende SM, Francis TB, Palen WJ. 2003. Pacific salmon and the ecology of coastal ecosystems. *Front Ecol Environ* 1:31–7.
- Schindler DE, Leavitt PR, Brock CS, Johnson SP, Quay PD. 2005. Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska. *Ecology* 86:3225–31.
- Schuldt JA, Hershey AE. 1995. Effect of Salmon Carcass Decomposition on Lake-Superior Tributary Streams. *J N Am Benthol Soc* 14:259–68.
- Slaney TL, Hyatt KD, Northcote TG, Fielden RJ. 1996. Status of anadromous salmon and trout in British Columbia and Yukon. *Fisheries* 21:20–35.
- Steinman AD. 1996. Effects of grazers on freshwater benthic algae. In: Stevenson RJ, Bothwell ML, Lowe RL, Eds. *Algal ecology: freshwater benthic ecosystems*. San Diego: Academic Press, Elsevier Inc.
- Steinman AD, Lamberti GA, Leavitt PR. 2006. Biomass and pigments of benthic algae. In: Hauer RF, Lamberti GA, Eds. *Methods in stream ecology*. San Diego: Academic Press, Elsevier Inc.
- Tiegs SD, Chaloner DT, Levi P, Ruegg J, Tank JL, Lamberti GA. 2008. Timber harvest transforms ecological roles of salmon in southeast Alaska rain forest streams. *Ecol Appl* 18:4–11.
- Tiegs SD, Campbell EY, Levi PS, Ruegg J, Benbow ME, Chaloner DT, Merritt RW, Tank JL, Lamberti GA. 2009. Separating physical disturbance and nutrient enrichment caused by Pacific salmon in stream ecosystems. *Freshw Biol* 54:1864–75.
- Trudeau V, Rasmussen JB. 2003. The effect of water velocity on stable carbon and nitrogen isotope signatures of periphyton. *Limnol Oceanogr* 48:2194–9.

Wipfli MS, Hudson J, Caouette J. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, USA. *Can J Fish Aquat Sci* 55:1503–11.

Wipfli MS, Hudson JP, Chaloner DT, Caouette JR. 1999. Influence of salmon spawner densities on stream productivity in Southeast Alaska. *Can J Fish Aquat Sci* 56:1600–11.

Wright JP, Jones CG. 2004. Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity. *Ecology* 85:2071–81.

Zuur AF, Ieno EN, Elphick CS. 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* 1:3–14.