QUANTITATIVE LINKS BETWEEN PACIFIC SALMON AND FRESHWATER ECOSYSTEM STRUCTURE

by

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Abstract

Spawning Pacific salmon affect freshwater ecosystems through substrate disturbance and the marine-derived nutrient pulse they deliver. I examined relations between a) salmon abundance and stream periphyton after spawning, and b) salmon abundance and invertebrate communities in the spring. I used 24 sockeye salmon (Oncorhynchus nerka) spawning streams in central British Columbia, Canada. After spawning, periphyton was enriched in salmon nitrogen but abundance was negatively related to salmon abundance, likely from substrate disturbance during spawning. Thus nutrient enrichment does not always translate into increased abundance. In the spring, the abundance of grazing mayflies and predatory stoneflies was positively related to salmon abundance, probably from increased algal growth caused by salmon nutrients delivered in previous years. Thus the salmon nutrient pulse can have ecological effects that extend long after spawning. The influence of spawning salmon on freshwater ecosystems differs through the year, across ecosystem components, and in relation to salmon abundance.

Keywords: aquatic conservation; ecosystem engineer; ecosystem-based management; fisheries; food web; marine-derived nutrients; nutrient pulse; Oncorhynchus; resource subsidy; salmon ecology
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Introduction

Interactions among species and between organisms and their habitat are integral to the structure and function of all ecosystems (Krebs 2001). These range from biotic interactions such as predation or competition to the delivery of nutrient subsidies and physical modifications of habitats. Some organisms exert a particularly strong influence on ecosystem structure and function (Mills et al. 1993, Power et al. 1996). Understanding how changes in the abundance of such species affect ecosystems is important to the study of ecology (Power et al. 1996) and the conservation of natural systems (Soule et al. 2003, 2005).

Species that deliver nutrient and energy subsidies can have a strong influence on consumer life histories and population dynamics (Polis et al. 1997, Ostfeld and Keesing 2000). They also perform an important function by connecting ecosystems through the transfer of nutrients and energy (Lundberg and Moberg 2003). Species can also influence the availability of nutrients and energy to other organisms by physically altering both biotic and abiotic habitat, an interaction referred to as ecosystem engineering (Jones et al. 1994). Both nutrient subsidies and ecosystem engineering play an important role in stream ecosystems (Moore 2006, Richardson et al. 2010).

Across the north Pacific, spawning anadromous salmon (*Oncorhynchus* spp.) interact with stream ecosystems by delivering a nutrient pulse and modifying habitats through their spawning activities. With more than 95% of their body mass accumulated in the ocean and a semelparous life history (dying after spawning), Pacific salmon deliver a large annual nutrient pulse to potentially nutrient-limited freshwater streams (Groot and Margolis 1991). Salmon tissue and eggs are a food source for many species, from fish to aquatic invertebrates, while primary producers can take up dissolved nutrients released from decomposing carcasses (reviewed by Willson and Halupka 1995, Cederholm et al. 1999, Gende et al. 2002, Naiman et al. 2002, Schindler et al. 2003). Stable isotope techniques have been widely used to detect the presence of salmon-derived nitrogen in
stream organisms, 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 (e.g. Kline et al. 1990, Bilby et al. 1996, Chaloner et al. 2002, Claeson et al. 2006). Spawning salmon also cause significant substrate disturbance through their mating behaviour and nest-digging, which can scour and transport substrate, mobilise and export organic matter, dislodge invertebrates and salmon eggs, and potentially drive the evolution of stream organism life histories (e.g. Moore et al. 2007, Moore and Schindler 2008, Moore et al. 2008, Moore and Schindler 2010). Pacific salmon may therefore have a strong effect on some stream ecosystems, particularly as they can spawn in large numbers and at high densities.

The magnitude of the ecosystem influence of spawning salmon is likely to depend on salmon abundance, which is relevant as Pacific salmon populations have declined substantially across parts of their range (Nehlsen et al. 1991, Baker et al. 1996, Slaney et al. 1996, Gresh et al. 2000). The many commercial, recreational, and aboriginal fisheries that target salmon along their return migration to freshwater can have strong impacts on salmon populations. As management strategies begin to incorporate the ecological roles of salmon when setting escapement goals (i.e. the number of fish that managers wish to let “escape” the fishery and return to the streams to spawn), connecting the salmon caught in fisheries to stream ecosystems will become increasingly useful (e.g. DFO 2005). Thus, there is a need to understand relationships between salmon abundance and their effects on stream ecosystems.

Studies have shown conflicting evidence on the direction and strength of salmon impacts on stream ecosystems. For example, comparisons between sites with and without salmon have shown spawning salmon to either increase periphyton abundance, likely through the nutrient subsidy (e.g. Schuldt and Hershey 1995, Wipfli et al. 1998, Chaloner et al. 2004), or decrease periphyton abundance, likely through substrate disturbance (Minakawa and Gara 1999, Peterson and Foote 2000). Most studies have shown that total invertebrate abundance decreases during the spawning period likely because of substrate disturbance (e.g. Minakawa and Gara 2003, Lessard and Merritt 2006, Moore and Schindler 2008, Honea and Gara 2009), although some taxa, such as chironomid midges,
have shown increased abundance (Chaloner et al. 2004, Lessard and Merritt 2006). However, the response of different invertebrate taxa following spawning has varied considerably. Some studies have shown persistent reductions in abundance while others have either recovered their pre-spawning abundances rapidly or even shown increased abundances shortly after spawning (Minakawa and Gara 2003, Lessard and Merritt 2006, Honea and Gara 2009, Lessard et al. 2009). These differing results have been attributed to the influence of both the nutrient subsidy and substrate disturbance. Further, the substrate disturbance caused by spawning salmon may also drive the evolution of stream invertebrate life histories (Moore and Schindler 2010). The few studies that have researched the impact of spawning salmon on resident fish suggest that they have a positive impact on growth and condition, primarily through increased food availability in the form of salmon eggs, tissue, and invertebrates dislodged by substrate disturbance (Foote and Brown 1998, Scheuerell et al. 2007, Moore et al. 2008). While experiments such as carcass additions and salmon exclusions have isolated the impacts of either the nutrient subsidy or substrate disturbance and shown more predictable outcomes, they are less representative of natural spawning events. It has been shown experimentally that the salmon nutrient subsidy increases the growth rate of some stream invertebrates and resident fish (Bilby et al. 1998, Chaloner and Wipfli 2002, Ito 2003, Wipfli et al. 2003, Wipfli et al. 2004). The impacts of naturally spawning salmon on stream ecosystems thus remain difficult to anticipate.

Variation in the abiotic environment across the range of habitats in which Pacific salmon spawn is likely to be partially responsible for the differing relationships observed. Pacific salmon spawn on both sides of the ocean, across a wide range in latitude (from the arctic to California or South Korea), and from just above estuaries to over 1,000 km inland (Augerot 2005). There are landscape-level differences in climate and watershed geomorphology that likely influence the impact that spawning salmon have on stream ecosystems. Salmon nutrient retention in the watershed and thus the potential for ecological impacts via this mechanism will depend on stream hydrology, among other things (Gende et al. 2002). For example, nutrient retention might be lower in streams that experience high discharge events during or soon after spawning, as is common in rainfall-driven coastal watersheds (e.g. Minakawa and Gara 2005), compared to inland streams...
with a predominantly snowmelt-driven hydrology (e.g. Gottesfeld et al. 2004). While the majority of research has been conducted in coastal watersheds of the eastern Pacific, we still know little about the ecosystem influence of spawning salmon across other parts of their spawning range (Janetski et al. 2009).

At a smaller scale, variation in local habitat will also mediate the ecological impact of spawning salmon on stream ecosystems. The abundance and composition of stream periphyton, invertebrates, and fish communities are all strongly influenced by stream habitat. For example, the abundance of stream periphyton is affected by stream discharge, light, temperature, and water chemistry (Biggs 1996, Borchardt 1996, DeNicola 1996, Hill 1996). In streams where periphyton growth is limited by light or temperature, the nutrients delivered by spawning salmon will likely have less of an impact on periphyton abundance (e.g. Rand et al. 1992, Ambrose et al. 2004). Habitat characteristics vary both across streams (spatially) and between years (temporally) and likely contribute to the variation observed in the ecosystem impacts of spawning salmon (Mitchell and Lamberti 2005, Chaloner et al. 2007). Further, the ecological impact of spawning salmon can also be affected by human land-use activities through changes to stream habitats (Tiegs et al. 2008). Consequently, there is a need to consider the effect of these habitat variables on relationships between spawning salmon and stream ecosystems, and few studies have done this explicitly (Janetski et al. 2009).

The relative importance of the mechanisms by which spawning salmon can influence stream ecosystems also varies temporally, in relation to both the annual timing of the spawning period and time elapsed since spawning. First, depending on the species, run-timing group, and location, salmon can spawn any time between mid-summer and mid-winter (Quinn 2005). The ecological impact of the nutrient subsidy may be limited if delivered at time of year when primary productivity is limited by temperature or light (Naiman et al. 2002). Second, the substrate disturbance associated with spawning is a short-term impact confined to the duration of the spawning period, whereas the nutrient subsidy may have impacts throughout the year or even in subsequent years. While, the availability of salmon tissue and eggs as a food source is confined to spawning and the subsequent period of carcass decomposition, which can be extended by overwinter freezing of carcasses, the availability of salmon nutrients to primary producers may
extend throughout the year (Gende et al. 2002). This will depend on the extent of nutrient retention in watersheds via slow decomposition of skeletal remains, adsorption of nutrients onto substrate biofilms and organic matter, and nutrient storage within organisms (Gende et al. 2002, Naiman et al. 2002). Thus, studies at different times of year can yield important insights into the influence of the different mechanisms by which salmon affect stream ecosystems.

The overall objective of this thesis is to understand the influence of spawning Pacific salmon on stream ecosystems and how this relates to salmon abundance. To do this, I examined relationships between the abundance of spawning salmon and two major components of the stream ecosystem - periphyton and invertebrates. I used a natural comparison of 24 streams in central British Columbia, Canada, that were used by sockeye salmon (*Oncorhynchus nerka*) for spawning. This is the largest spatial comparison to examine the ecological role of spawning salmon in streams. To date there has also been relatively little research on the ecosystem impacts of spawning salmon in inland streams (Janetski et al. 2009). Furthermore, I explicitly considered the potential influence of stream habitat characteristics on stream periphyton and invertebrates, which could mediate the impacts of spawning salmon. This is the first time that the relative importance of both spawning salmon and stream habitat features to stream ecosystems has been examined.

In Chapter 1, I consider the influence of spawning salmon on stream periphyton in late September, four to six weeks after spawning has concluded. The hypothesised influence of the salmon nutrient subsidy on periphyton is opposite to the expected impact of substrate disturbance caused by spawning activities. I examined the outcome of these opposing mechanisms through relationships between periphyton abundance and the abundance of spawning salmon. Alongside, I compared the influence of spawning salmon to the influence of stream habitat characteristics that are known to influence periphyton abundance. In a separate analysis, I examined the uptake of salmon nitrogen by stream periphyton using stable isotopes and simultaneously considered the influence of stream habitat on periphyton nitrogen stable isotope signature. I used salmon abundance over multiple years to test for the contribution of salmon nutrients from previous years to
periphyton nitrogen stable isotope signatures, which would indicate long-term salmon nutrient storage in the ecosystem.

In Chapter 2, I studied the influence of spawning salmon on stream invertebrate communities in July, over ten months since the last spawning period. At this time of year, I predicted the influence of spawning salmon to be through nutrients retained in the watershed from previous years, which could support greater ecosystem productivity. Specifically, I examined the relative influence of spawning salmon and stream habitat characteristics on stream invertebrates by evaluating models of invertebrate abundance and diversity that contained both salmon abundance and habitat features. By comparing relationships between salmon abundance and invertebrate abundance among common invertebrate taxa from different feeding guilds, I investigated the pathways by which salmon nutrients influence stream invertebrates at this time of year.

In the Conclusion, I briefly summarise the key findings of the two data chapters and discuss their contribution to the understanding of how spawning salmon effect stream ecosystems. I also identify uncertainties and remaining knowledge gaps and propose avenues by which future research could build upon the findings of this thesis.

References


1: Quantitative Links Between Pacific Salmon And Stream Periphyton

In press with *Ecosystems*.

Jan J. Verspoor, Douglas C. Braun, John D. Reynolds

JJV and JDR designed the study, JJV and DCB performed the research, JJV analysed the data, DCB contributed to the statistical methods and JJV and JDR wrote the paper.

1.1 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.

1.2 Introduction

Individual species affect primary productivity through many mechanisms. Herbivory can increase primary productivity by maintaining plants in a state of rapid growth (e.g. McNaughton, 1985) and alter plant community composition (e.g. Howe et al., 2006). Species that deliver nutrient subsidies can stimulate primary production when nutrients are limiting (Polis et al., 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 et al., 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 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, which contain marine-derived nitrogen, than in natural freshwater or terrestrial nitrogen sources (e.g. Kline et al., 1990; Bilby et al., 1996; Chaloner et al., 2002; Claeson et al., 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 et al., 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 (e.g. Moore et al., 2004; Moore et al., 2007; Hassan et al., 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 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 (Johnston et al., 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 et al., 2004; Tiegs et al., 2009), while experimental carcass additions elevated both dissolved nutrient levels and periphyton abundance (e.g. Schuldt and Hershey, 1995; Wipfli et al., 1999; Kohler et al., 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 is also 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 et al., 2007). For example, periphyton may only respond to direct salmon nutrient subsidies when not limited by light (Rand et al., 1992; Ambrose et al., 2004). Further, human land-use activities can change environmental variables (e.g. substrate
size) that affect the link between salmon and periphyton (Tiegs et al., 2008). There is a need to consider the effect of these environmental variables on relationships between salmon and periphyton (Janetski et al., 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 et al., 1991; Baker et al., 1996; Slaney et al., 1996; Gresh et al., 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 (i.e. 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 (e.g. DFO, 2005; Moore and Schindler, 2008; Moore et al., 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 $a$ content and ash-free dry mass) 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.

1.3 Methods

1.3.1 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 (Fig. 1.1) 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 in late June 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 four-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 (Table 1.5). 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 Table 1.6. The watersheds are forested and 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*). Water flows are highest in the spring as a result of snowmelt and lowest from late 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 et al. (1992).

### 1.3.2 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 four 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. 2007 salmon density ($D$) was calculated as:

\[
D = \frac{F}{wl}
\]

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$^{-2}$, Table 1.5).

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. Both upstream salmon abundance and local salmon density were summed over four 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:

\[
X = \sum X_i \times e^{(-\lambda \times t)}
\]

where \( X_i \) is upstream salmon abundance or salmon density in year \( i \), \( \lambda \) describes the rate of nutrient loss from the system, and \( t \) is the number of years since 2007. Metrics were calculated for values of \( \lambda \) that correspond to a salmon nutrient half-life in the watershed of six months, one, two, and four years. The multi-year metrics of upstream salmon abundance were highly correlated \((r > 0.98 \text{ in all cases})\), as were the multi-year metrics of salmon density \((r > 0.97 \text{ in all cases})\), 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 six month salmon nutrient half-life in models of periphyton nitrogen stable isotope signatures. All three reported salmon abundance metrics were positively correlated \((2007 \text{ upstream salmon abundance versus } 2004-2007 \text{ upstream salmon abundance, } r = 0.89; 2007 \text{ upstream salmon abundance versus } 2004-2007 \text{ salmon density, } r = 0.74; 2004-2007 \text{ upstream salmon abundance versus } 2004-2007 \text{ salmon density, } r = 0.79)\). 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.

1.3.3 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, two to four weeks prior to sockeye spawning. Periphyton was sampled from the tiles four to six
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, Table 1.5).

We measured two proxies for periphyton abundance: chlorophyll \( a \) (chl \( a \), \( \mu g \text{ cm}^{-2} \)) and ash-free dry mass (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 fibre filters (Whatman, 25 mm, 0.7 \( \mu m \) pore size) and stored in the dark at -20°C. 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\(^2\)). Linear regression showed chl \( a \) to be strongly related to total chlorophyll (total chlorophyll = 1.10 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 et al. (2006). Mean chl \( a \) and AFDM was 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 > 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 (\( \delta \)) as ratios relative to the standard of atmospheric \( \text{N}_2 \) (nitrogen). This is expressed in ‘parts per thousand’ (‰) according to:

\[
\delta^{15}N(\text{‰}) = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000
\]

where \( R \) is the ratio of heavy isotope (\( ^{15}\text{N} \)) to light isotope (\( ^{14}\text{N} \)) in the sample and standard. Finally, \( \delta^{15}N \) was averaged across all tiles in a stream.
1.3.4 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 1.1b). Water temperature, light availability and water velocity have been shown to influence periphyton nitrogen stable isotope signatures (Table 1.1a). 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, Table 1.5).

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 two hours 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 δ¹⁵N, 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 (NH₄-N) and nitrite plus nitrate nitrogen (NO₃-N), were sampled two or three times at one location in each stream over two 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, NO₃-N by the automated cadmium reduction method, and NH₄-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 5x Abney hand level. Percent open canopy was measured at each tile location using a spherical densiometer and the mean value from tile placement and collection used 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 et al. (2008). Ten percent of samples were independently identified to verify accuracy as greater than 95%. Functional feeding group designations were made using Merritt et al. (2008) and the abundance of all individuals classified as grazers was summed to estimate grazer abundance (number per m²).

1.3.5 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, chlorophyll \(a\) content, and ash-free dry mass. 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 et al. (2010). First, we examined co-linearity among all explanatory environmental variables using Variance Inflation Factors (VIF) (Table 1.1). 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 co-linearity 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 > 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 $\delta^{15}$N, soluble reactive phosphorus (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 ($\delta^{15}$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 log$_{10}$ 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 $\delta^{15}$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 $\Delta$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 $w_{top\ model}/w_i$ 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 (e.g. Naiman et al., 2002; Schindler et al., 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:

$$X = \frac{\partial^{15}N_{\text{periphyton}} - \partial^{15}N_b}{\partial^{15}N_{\text{sockeye}} - \partial^{15}N_b}$$

where $\partial^{15}N_{\text{periphyton}}$ was the mean nitrogen stable isotope signature of periphyton, $\partial^{15}N_{\text{sockeye}}$ was the nitrogen stable isotope signature of sockeye salmon, and $\partial^{15}N_b$ was the nitrogen stable isotope signature of the combined pool of other nitrogen sources. We used a value of 11.29 ‰ for $\partial^{15}N_{\text{sockeye}}$ (Johnson and Schindler, 2009). We used the mean value of periphyton $\partial^{15}N$ across nine “control” sites; three streams that had a 2004-2007 upstream salmon abundance of fewer than ten fish (Table 1.5) and six streams where we sampled periphyton above the extent of salmon spawning (J. Verspoor, unpublished data) to approximate $\partial^{15}N_b$. 
1.4 Results

1.4.1 Periphyton Nitrogen Stable Isotope Signature

In the top model, 2004-2007 upstream salmon abundance had a positive relationship to the nitrogen stable isotope signature ($\delta^{15}$N) of stream periphyton ($R^2 = 0.28$, Fig. 1.2). This model had four times more support than the second ranked model, which contained both 2004-2007 upstream salmon abundance and gradient (Table 1.2a). The similarity in $R^2$ between the top two models shows that gradient explained little additional variation in $\delta^{15}$N. All other models had a $\Delta$AICc > 3.

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 (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 1.2b). 2004-2007 upstream salmon abundance remained as the top model and model fit improved ($R^2 = 0.47$, Fig. 1.2).

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 $\delta^{15}$N used for all non-salmon sources was 0.66 ‰ but ranged from -0.19 ‰ to 2.32 ‰ across periphyton collected from “control” sites.

1.4.2 Periphyton Abundance

In the top model, salmon density in 2007 had a negative relationship to the ash-free dry mass (AFDM) of stream periphyton, while pre-spawning soluble reactive phosphorus (SRP) had a positive relationship to AFDM ($\log_{10} AFDM = 0.94\log_{10} SRP – 1.05\sqrt{2007 salmon density} – 0.67$, $R^2 = 0.49$). This model had twice as much support as the second ranked model, which contained 2007 salmon density, SRP and tile soak time (Table 1.3). 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 ($\Delta$AICc > 3).
present observed versus fitted plots for the top model and untransformed bivariate plots of the individual explanatory variables versus AFDM for comparison (Fig. 1.3).

In the top model, 2007 salmon density had a negative relationship to the chlorophyll $a$ (chl $a$) content of stream periphyton, while pre-spawning soluble reactive phosphorus (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 1.4). 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 chl $a$ for comparison (Fig. 1.3).

1.5 Discussion

1.5.1 Periphyton Nitrogen Stable Isotope Signature

We found a positive log-linear relationship between 2004-2007 upstream salmon abundance and the nitrogen stable isotope signature ($\delta^{15}N$) of stream periphyton across 24 streams in north-central British Columbia. This is the first time that periphyton $\delta^{15}N$ has been described across a gradient in salmon abundance. Relationships between $\delta^{15}N$ and salmon abundance have previously been shown for juvenile coho salmon, terrestrial invertebrates, and riparian soil and vegetation (Bilby et al., 2001; Reimchen et al., 2003; Bartz and Naiman, 2005; Hocking and Reimchen, 2009).

Although we fit a log-linear model, the relationship between salmon abundance and periphyton $\delta^{15}N$ should actually be a positive function that saturates as the contribution of salmon nitrogen to periphyton $\delta^{15}N$ nears 100%. However, the periphyton $\delta^{15}N$ values in this study were low relative to the $\delta^{15}N$ 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 $\delta^{15}N$ chosen for all non-salmon sources of nitrogen, which varied widely among the “control” sites used to estimate it. Therefore, while the contribution of salmon nitrogen to periphyton $\delta^{15}N$ 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 $^{15}N$ 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 $>70,000$ fish, whereas it was just 20,000 fish from 2004-2007.

We expected three environmental variables (temperature, light, and water velocity) to affect periphyton $^{15}N$ (Table 1.1a). Of the three variables, periphyton $^{15}N$ 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 $^{15}N$ compared to salmon abundance, particularly after removing the outlier, Leo Creek. This suggests that salmon abundance had a stronger influence on periphyton $^{15}N$ 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 $^{15}N$. While 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 $^{15}N$ 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, while 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 $^{15}N$. 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 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 across all streams and delivered a much larger nutrient subsidy. While 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.

1.5.2 Periphyton Abundance

Periphyton abundance was best described by a combination of salmon density and environmental variables. Both ash-free dry mass (AFDM) and chlorophyll $a$ (chl $a$) were negatively related to 2007 salmon density and positively related to pre-spawning soluble reactive phosphorus 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 1.1b). Of these, pre-spawning soluble reactive phosphorus 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 soluble reactive phosphorus after removing the outlying Leo Creek ($r = 0.42$, $p = 0.044$).

As pre-spawning soluble reactive phosphorus 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 six 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. This general finding 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 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 et al., 2004). In their study from 1996-1998, 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 (e.g. Chaloner et al., 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 et al. 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 et al., 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.
1.6 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 (e.g. DFO, 2005) should exercise caution in the use of 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.

1.7 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. 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 chlorophyll $a$ and ash-free dry mass 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.
1.8 References


enrichment caused by Pacific salmon in stream ecosystems. Freshwater Biology 54: 1864-1875.


1.9 Figures

Figure 1.1: Location of the 24 study streams in the Stuart River drainage of the Fraser River, British Columbia, Canada.
Figure 1.2: Plot of log_{10}-transformed 2004-2007 upstream salmon abundance (total number of fish) versus periphyton nitrogen stable isotope signature ($\delta^{15}N$), with the outlying Leo Creek labeled. The fitted linear relationship excludes Leo Creek ($\delta^{15}N = 0.599 \log_{10} 2004-2007$ upstream salmon abundance + 0.379, $R^2 = 0.47$).
Figure 1.3: 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 $a$, $\mu$g cm$^{-2}$), which both contain $\sqrt{2007}$ salmon density (fish m$^{-2}$) and log$_{10}$ soluble reactive phosphorus (SRP, $\mu$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 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 bivariate plots are presented untransformed.
Table 1.1  *A priori* predictions for the potential influence of environmental variables on: a) periphyton nitrogen stable isotope signatures ($\delta^{15}$N) 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.

### a)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mechanism</th>
<th>Direction</th>
<th>Metric</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>Water temperature can increase metabolic activity and thus increase nitrogen stable isotope signatures.</td>
<td>Positive</td>
<td>Mean Maximum Daily Temperature ($^\circ$C)</td>
<td>(Friberg et al., 2009) (MacLeod and Barton, 1998)</td>
</tr>
<tr>
<td>Light</td>
<td>Light availability can increase metabolic activity and thus increase nitrogen stable isotope signatures.</td>
<td>Positive</td>
<td>% Canopy Open</td>
<td>(MacLeod and Barton, 1998)</td>
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<tr>
<td>Velocity</td>
<td>Greater flow can reduce the boundary layers around periphyton and thus decrease nitrogen stable isotope signatures.</td>
<td>Negative</td>
<td>Gradient (%)</td>
<td>(Trudeau and Rasmussen, 2003) (MacLeod and Barton, 1998)</td>
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</table>

### b)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mechanism</th>
<th>Direction</th>
<th>Metric</th>
<th>References</th>
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</thead>
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<tr>
<td>Temperature</td>
<td>Water temperature can limit metabolic activity and thus periphyton growth.</td>
<td>Positive</td>
<td>Mean Maximum Daily Temperature ($^\circ$C)</td>
<td>(Lamberti and Steinman, 1997) (Biggs, 1996) (DeNicola, 1996)</td>
</tr>
<tr>
<td>Dissolved Phosphorus</td>
<td>Phosphorus has been shown to limit periphyton growth in some areas.</td>
<td>Positive</td>
<td>Soluble Reactive Phosphorus ($\mu$g/L)</td>
<td>(Lamberti and Steinman, 1997) (Biggs, 1996) (Borchardt, 1996)</td>
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<tr>
<td>Dissolved Nitrogen</td>
<td>Nitrogen has been shown to be limit periphyton growth in some areas.</td>
<td>Positive</td>
<td>Dissolved Inorganic Nitrogen ($\mu$g/L)</td>
<td>(Lamberti and Steinman, 1997) (Biggs, 1996) (Borchardt, 1996)</td>
</tr>
<tr>
<td>Grazers</td>
<td>Invertebrate grazers feed on and reduce periphyton abundance.</td>
<td>Negative</td>
<td>Grazer Density (individuals/m²)</td>
<td>(Biggs, 1996) (Steinman, 1996)</td>
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<tr>
<td>Watershed Size</td>
<td>Has a demonstrated relationship with primary productivity.</td>
<td>Positive</td>
<td>PCA of stream length, width, and magnitude</td>
<td>(Lamberti and Steinman, 1997) (Biggs, 1996)</td>
</tr>
</tbody>
</table>
Table 1.2  Results of model selection using AICc for seven linear regression models that describe periphyton nitrogen stable isotope signatures ($\delta^{15}$N). 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 log10-transformed and 2004-2007 salmon density was square-root transformed. k = number of model parameters, R$^2$ = model regression coefficient, p = model significance, $\Delta$AICc = change in AICc score from top model, $w_i$ = AICc model weight, ER = top model weight divided by model $i$ weight.

### a)

<table>
<thead>
<tr>
<th>Model (including Leo Creek)</th>
<th>k</th>
<th>R$^2$</th>
<th>p</th>
<th>$\Delta$AICc</th>
<th>$w_i$</th>
<th>ER</th>
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<tbody>
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<td>0.008</td>
<td>0.00</td>
<td>0.63</td>
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<tr>
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<td>0.15</td>
<td>4.15</td>
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<tr>
<td>4. 2007 Upstream Salmon Abundance</td>
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<tr>
<td>5. Gradient</td>
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<td>0.11</td>
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<tr>
<td>6. 2004-2007 Salmon Density + Gradient</td>
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<tr>
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### b)

<table>
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<th>Model (excluding Leo Creek)</th>
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<th>p</th>
<th>$\Delta$AICc</th>
<th>$w_i$</th>
<th>ER</th>
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<td>0.00</td>
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<td>0.17</td>
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<td>5. 2007 Upstream Salmon Abundance + Gradient</td>
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Table 1.3  Results of model selection using AICc for seven linear regression models that describe 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 1.2.

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>R$^2$</th>
<th>p</th>
<th>∆AICc</th>
<th>$w_i$</th>
<th>ER</th>
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<td>1. 2007 Salmon Density + SRP</td>
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<td>0.49</td>
<td>&lt;0.001</td>
<td>0.00</td>
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<td>1.00</td>
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<td>2. 2007 Salmon Density + SRP + Soak Time</td>
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<td>0.01</td>
<td>102.10</td>
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<td>0.01</td>
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<td>0.00</td>
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<td>0.84</td>
<td>13.04</td>
<td>0.00</td>
<td>679.35</td>
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Table 1.4  Results of model selection using AICc for seven linear regression models that describe periphyton chlorophyll $a$ (chl $a$). 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 1.2.

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>$R^2$</th>
<th>$p$</th>
<th>$\Delta$AICc</th>
<th>$w_i$</th>
<th>ER</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. 2007 Salmon Density + SRP</td>
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<td>0.33</td>
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<td>2. SRP</td>
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<td>3.23</td>
<td>0.10</td>
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</tr>
<tr>
<td>4. SRP + Soak Time</td>
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<td>6. Soak Time</td>
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<td>0.05</td>
<td>0.30</td>
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<td>0.14</td>
<td>0.20</td>
<td>5.85</td>
<td>0.03</td>
<td>18.61</td>
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Table 1.5  Watershed characteristics, number of tiles collected (i.e. sample size), tile soak time, and salmon abundance metrics for the 24 study streams.

<table>
<thead>
<tr>
<th>Stream</th>
<th>Stream Order</th>
<th>Stream Magnitude</th>
<th>Main Channel Length (km)</th>
<th>Stream Bankfull Width (m)</th>
<th>Number of Tiles Collected</th>
<th>Tile Soak Time (days)</th>
<th>2007 Salmon Density (fish m(^{-2}))</th>
<th>2004-2007 Mean Upstream Salmon Abundance (number of fish)</th>
</tr>
</thead>
<tbody>
<tr>
<td>10 Mile</td>
<td>2</td>
<td>2</td>
<td>5.91</td>
<td>4.19</td>
<td>7</td>
<td>64</td>
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<tr>
<td>15 Mile</td>
<td>3</td>
<td>14</td>
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<td>11.64</td>
<td>7</td>
<td>61</td>
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<td>25 Mile</td>
<td>2</td>
<td>6</td>
<td>17.59</td>
<td>9.04</td>
<td>8</td>
<td>61</td>
<td>0</td>
<td>2</td>
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<td>Ankwill</td>
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<td>44</td>
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<td>30.53</td>
<td>7</td>
<td>53</td>
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<td>Bivouac</td>
<td>3</td>
<td>10</td>
<td>17.52</td>
<td>8.07</td>
<td>7</td>
<td>72</td>
<td>0.012</td>
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<td>8.65</td>
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<td>63</td>
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Table 1.6  Study site habitat characteristics across the 24 streams.

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<th>Habitat Characteristic</th>
<th>Mean</th>
<th>Range</th>
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<tbody>
<tr>
<td>Gradient (%)</td>
<td>2.1</td>
<td>0.6 – 5.8</td>
</tr>
<tr>
<td>Water Depth (m)</td>
<td>0.26</td>
<td>0.17 – 0.34</td>
</tr>
<tr>
<td>Maximum Weekly Average Temperature (°C)</td>
<td>11.3</td>
<td>8.5 – 13.9</td>
</tr>
<tr>
<td>Canopy Cover (%)</td>
<td>63</td>
<td>42 - 96</td>
</tr>
<tr>
<td>Geometric Mean of Substrate Intermediate Axis Diameter (cm)</td>
<td>40</td>
<td>6 - 117</td>
</tr>
<tr>
<td>Pre-spawning Soluble Reactive Phosphorus (µg/L)</td>
<td>1.47</td>
<td>0.44 – 3.62</td>
</tr>
<tr>
<td>Pre-spawning Dissolved Inorganic Nitrogen (µg/L)</td>
<td>8.71</td>
<td>3.45 – 21.77</td>
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</tbody>
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2: Persistent Ecological Effects Of A Salmon-Derived Nutrient Pulse On Stream Invertebrate Communities

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JJV and JDR designed the study, JJV and DCB did the fieldwork, MMS identified the invertebrates, JJV analysed the data, DCB contributed to the statistical methods and JJV and JDR wrote the paper.

2.1 Abstract

Pulsed resource subsidies can have ecological effects that persist over time. Resource subsidies can be particularly important in aquatic ecosystems, since they are often resource-limited. Migratory salmon (Oncorhynchus spp.) deliver annual nutrient pulses to many freshwater ecosystems of the Pacific Northwest. The persistent ecological consequences of this nutrient subsidy are poorly understood across the range of Pacific salmon and likely depend on stream habitat, background nutrient dynamics, and the abundance of spawning salmon. Using a model selection approach, we examined relationships among spawning salmon abundance, stream habitats, and the abundance and diversity of stream invertebrates ten months after salmon spawning, across 21 streams in central British Columbia, Canada. Total invertebrate abundance increased with increasing salmon abundance and stream temperature. Invertebrate diversity was more closely related to stream habitat characteristics than to salmon abundance. These results indicate that salmon nutrients have a greater impact on stream invertebrate population sizes than on the range of taxa that inhabit these streams. Of the three most common invertebrate families, the abundance of both grazing mayflies (Heptageniidae) and predatory stoneflies ( Chloroperlidae) increased with increasing salmon abundance and stream temperature. The abundance of chironomid midges (Chironomidae) was more closely related to stream temperature and pH than to salmon abundance. These results suggest that salmon nutrients retained in the watershed from previous years increase stream productivity the following year, which in turn supports greater abundances of some
invertebrate taxa. Thus the pulsed nutrient subsidy provided by spawning salmon may have ecological effects that persist many months, or even years, after it is delivered.

### 2.2 Introduction

Flows of nutrients across ecosystem boundaries can exert an important influence on the structure and function of recipient ecosystems (Polis et al., 1997). Resource subsidies that arrive as pulses can drive consumer life histories and population dynamics and have wide ecosystem consequences (Ostfeld and Keesing, 2000; Holt, 2008; Schmidt and Ostfeld, 2008). These ecological effects can persist long after the pulse itself has diminished (Yang et al., 2008). Resource subsidies play a particularly important role in stream ecosystems due to their large interface with the terrestrial environment relative to stream size (Richardson et al., 2010). For example, leaf litter input to streams can influence the population dynamics of direct consumers and their predators (e.g. Wallace et al., 1999). Therefore, streams provide an ideal system for studying pulsed resource subsidies and their ecological effects (Richardson et al., 2010), which may occur across diverse ecosystems through common mechanisms (Yang et al., 2008).

Across the north Pacific, millions of anadromous salmon (*Oncorhynchus* spp.) deliver an annual nutrient subsidy to freshwater ecosystems that can have important ecological consequences (reviewed by Gende et al., 2002; Naiman et al., 2002; Schindler et al., 2003; Janetski et al., 2009). Pacific salmon accumulate more than 95% of their body mass in the ocean before migrating to freshwater where they spawn and then die, often in high densities (Groot and Margolis, 1991), providing a nutrient subsidy that can influence organisms that consume salmon eggs or carcasses directly (e.g. Bilby et al., 1998; Minakawa et al., 2002). Additionally, decomposing salmon carcasses can elevate dissolved nutrient levels, which may increase primary productivity and improve the nutritional quality of biofilm if nutrients are limited (e.g. Johnston et al., 2004; Peterson and Matthews, 2009). Furthermore, this nutrient subsidy may indirectly alter ecosystem processes, such as slowing leaf litter decomposition by detritivores switching their diet to salmon carcasses (Zhang et al., 2003).
The impacts of the nutrient subsidy provided by spawning salmon are potentially tempered in the short-term by the simultaneous substrate disturbance caused by spawning salmon, which can scour algae and dislodge invertebrates, exporting them downstream (Moore and Schindler, 2004, 2008). Further, as salmon populations spawn anywhere from mid-summer to mid-winter and the benefits of nutrient addition to stream productivity may vary with time of year, the seasonal environment when salmon spawn may limit the impacts of the nutrient pulse (Naiman et al., 2002). However, salmon nutrients may be retained in watersheds for months, or years, after spawning and thus have ecological effects long after they are delivered.

Salmon nutrients may be retained in streams through mechanisms such as overwinter freezing of carcasses, slow decomposition of skeletal remains, and adsorption of nutrients onto substrate biofilms, including within the hyporheic zone (Gende et al., 2002). Paradoxically, streambed disturbance by spawning salmon may also assist salmon nutrient retention through the re-suspension of fine sediment, which can aggregate with salmon matter into larger particles (Rex and Petticrew, 2008). Finally, tight internal cycling of salmon nutrients accumulated in the ecosystem over multiple salmon runs and stored within organisms, including within the riparian zone, may also increase nutrient availability throughout the year (Naiman et al., 2002). Salmon nitrogen has been detected in multiple trophic levels year-round using stable isotope techniques, thus demonstrating the persistence of salmon nutrients within freshwater ecosystems (e.g. Bilby et al., 1996; Hicks et al., 2005; Honea and Gara, 2009). However, it remains an open question whether the ecological impacts of salmon nutrients persist in and affect the ecology of streams throughout the year.

Retention of salmon nutrients in streams long after spawning and its associated physical disturbance could result in bottom-up ecological effects. In particular, stream invertebrate communities are often resource-limited (Richardson et al., 2010) and feed across a spectrum of basal food sources that could be enhanced by salmon nutrients (Merritt et al., 2008). In coastal southeastern Alaska, chironomid midges had higher abundances over ten months after spawning in two stream reaches that received a salmon nutrient pulse, while several mayfly genera showed the opposite relationship (Lessard et al., 2009). Many other taxa showed no difference in abundance or growth (Lessard et al.,
In coastal Washington, six months after spawning there was no difference in stream invertebrate community composition and abundance between one stream reach with and one without spawning salmon (Minakawa and Gara, 2003; Honea and Gara, 2009). It is probable that the retention of salmon nutrients in streams, and thus their influence on stream invertebrate populations, varies with latitude, climate, and watershed geomorphology across the range of Pacific salmon (Gende et al., 2002). If streams experience high discharge events during or soon after spawning, as is common in rainfall-driven coastal watersheds (e.g. Minakawa and Gara, 2005), much of the salmon nutrient pulse may not be retained. The possible ecological effects of salmon nutrients on stream invertebrates in inland watersheds, which typically do not experience high discharge events that coincide with spawning (e.g. Gottesfeld et al., 2004) and thus may retain more salmon nutrients, has not been investigated. Any persistent effect of salmon nutrients on stream invertebrate communities could have wide ecological consequences as invertebrates are an important food for fish, including stream-rearing juvenile salmon, and terrestrial predators (e.g. Marczak and Richardson, 2007; Scheuerell et al., 2007).

The magnitude of any persistent ecological effect of salmon nutrients will likely vary in relation to salmon abundance, which is important as Pacific salmon populations have declined across many parts of their range (e.g. Gresh et al., 2000). Further, as management strategies begin to incorporate the ecological importance of salmon when setting escapement goals (i.e. the number of fish that managers wish to let “escape” the fishery and return to the streams), understanding the links between salmon caught in fisheries and changes to stream ecosystems will become increasingly useful (e.g. DFO, 2005). To date, the persistent ecological influence of salmon nutrients on stream invertebrates has not been compared across a number of streams that represent a gradient in salmon abundance.

The objective of this study was to test for persistent ecological effects of a fall salmon nutrient pulse on summer stream invertebrate communities in inland stream ecosystems. We conducted the largest spatial comparison to examine relations between salmon abundance and invertebrate community composition and abundance. This is also the first study to simultaneously consider the role of stream habitat characteristics predicted to potentially influence invertebrate abundance and diversity. Specifically, we
evaluated the relative ability of salmon abundance and environmental variables to
describe differences in total invertebrate abundance and diversity, and the abundance of
common invertebrate families. This enabled us to test whether stream invertebrate
abundance increased with increasing salmon abundance, which may occur if nutrient-
limited resources are increased by salmon nutrients retained in the watersheds.

2.3 Methods

2.3.1 Study Sites

We surveyed 21 sockeye salmon (*Oncorhynchus nerka*) spawning streams in the
Stuart River drainage at the most northern extent of the Fraser River, British Columbia,
Canada (Fig. 2.1). Sockeye salmon are the only anadromous fish in the streams. These
populations are part of the “Early Stuart” complex, entering freshwater in July and
migrating over 1100 km to spawn from early to mid August in the low reaches of
tributaries to Middle River and Takla Lake. These populations show four-year cyclical
abundance like many Fraser River sockeye (Levy and Wood, 1992), with highest
abundances in 2005, 2001, 1997, and every four years prior. 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 (Table 2.4). The watersheds are
forested and common riparian species include hybrid white spruce (*Picea glauca x P.
engelmannii*), black cottonwood (*Populus balsamifera*), Sitka alder (*Alnus viridis*) and
devils club (*Oplowanax horridus*). Water flows are highest in the spring as a result of
snowmelt and lowest from late July to mid September, when these sockeye populations
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 et al. (1992).
2.3.2 Salmon Abundance

The 21 study streams represented a gradient of salmon abundance at relatively low population sizes during the study period (2006 spawning population range = 0 – 4816 fish; Table 2.4). The spawning population size was estimated by Fisheries and Oceans Canada (DFO) personnel, who conducted foot surveys every four days during the spawning period to count the number of live and dead sockeye across all spawning grounds. Finer scale counts were also recorded for 500 m stream sections. The spawning population in each stream was calculated by multiplying the “peak” abundance of adult salmon by an expansion factor. The “peak” abundance was determined as the highest number obtained by adding the live count of adult salmon from a 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.

In this study, we measured salmon abundance as the number of adult sockeye salmon that were upstream of the study reach in which we collected invertebrates and habitat data. We consider this metric as a proxy for total upstream salmon nutrient input to the watershed and chose it instead of salmon density in the study reach (fish m\(^{-2}\)) as it better represents the total nutrient subsidy delivered to an entire watershed. This metric was obtained by correcting the spawning population in the entire stream, as estimated by DFO, by the proportion of fish in and upstream of the study reach, which we determined using the 500 m section counts from DFO. Initially, we considered salmon abundance both the year prior to sampling (2006), in order to consider the contribution of salmon nutrients from the most recent spawning event, and over four years prior (2003-2006), in order to consider the additional contribution of salmon nutrients from earlier years. Abundance was summed from 2003 to 2006 with the contribution of earlier years down-weighted by a negative exponential function that described a rate of salmon nutrient loss from the watershed, as described in Chapter 1. This was done for rates of loss that corresponded to salmon nutrient half-lives in the watershed of one, two, and four years. These three metrics were highly correlated with each other (\(r > 0.99\) in all cases) and with 2006 salmon abundance (\(r > 0.80\)). Because results were unlikely to differ among
metrics, we tested and present results for only 2006 salmon abundance. As such, we consider that this study tested for the legacy of salmon nutrients that entered the watersheds at least 10 months prior to when invertebrates were sampled, but cannot rule out a contribution of nutrients from earlier years.

2.3.3 Invertebrate Collection and Identification

Benthic invertebrates were collected over a period of one month immediately prior to salmon spawning (July 1st – August 2nd, 2007; Table 2.4). We visited each stream once and surveyed a single study reach, defined as 30 times mean bankfull width and split into four study sections of equal length, at the furthest downstream extent of salmon spawning that was accessible given transportation and time limitations. Three Surber samples (frame area = 0.09 m², 500 µm mesh) were collected, by agitating the substrate within the frame to a depth of 10 cm for 2 min, from riffle habitat in each section, resulting in four combined samples per stream. The combined samples were washed into plastic bottles, preserved in 95% ethanol, and transported back to the laboratory.

These samples were sub-sampled using a Folsom Plankton Splitter and picked under magnification until a total count of at least 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 et al. (2008). Ten percent of samples were independently identified to verify accuracy as greater than 95%. Abundances were adjusted by the proportion of the sample that was picked and then averaged across the four samples to obtain abundances for each stream (number m⁻²). Finally, dominant taxa were identified as those that on average comprised more than 20% of total invertebrate density across all streams. Three dominant families were identified: Heptageniidae (Order: Ephemeroptera), Chloroperlidae (Order: Plecoptera) and Chironomidae (Order: Diptera; Table 2.1). Functional feeding group designations were assigned using Merritt et al. (2008). Family level diversity of the orders Ephemeroptera, Plecoptera, Trichoptera, and Diptera (EPTD) was measured using Simpson’s Reciprocal Index (Magurran, 2004). The orders EPTD comprised ~ 97% of all invertebrates across the 21 streams (range 86-99%). Simpson’s
Reciprocal Index is more sensitive to changes in the abundance of common families than the addition of rare families. There was little difference in the number of families found across the 21 streams (range = 13 – 20).

2.3.4 Environmental Variables

The distribution and abundance of stream invertebrates are also influenced by a wide range of stream habitat characteristics (Hynes, 1970; Vinson and Hawkins, 1998). Substrate, temperature, flow, and water chemistry seem to be consistently important (Allan and Castillo, 2007). We characterized water temperature, light availability, substrate size, water depth, stream gradient, watershed size, pH, and conductivity across our study streams and present values for the mean and range in Table 2.5. We also expected that the date we sampled a stream might be important as community composition could have changed over the one-month sampling period, especially as the emergence timing of stream invertebrates may be adapted to avoid the substrate disturbance associated with salmon spawning (Moore and Schindler, 2010).

We characterized water temperature as the maximum weekly average temperature (MWAT) over the proceeding year (Aug 5th 2007 – Aug 5th 2008), as temperatures were not recorded prior to this period. MWAT in 2007-2008 was highly correlated with MWAT in 2008-2009 (r = 0.97), which suggests that relative temperature differences among streams are likely conserved during the study period. Stream temperature was measured using waterproofed ibutton (DS1922L) data loggers that we programmed to record temperature every two hours and attached to iron rods imbedded in the stream.

Light availability was characterized by percent canopy cover, which was measured using a spherical densiometer at the location of each Surber sample and averaged across a stream. Substrate size was quantified as the mean intermediate axis (to the nearest 1 mm) across ten stones measured in each riffle sampled. Conductivity and pH were measured three to five times at a single location in each stream and averaged. Water depth was measured to the nearest 1 cm at the location of each individual Surber sample and averaged across a stream. Percent stream gradient was measured across the study reach using a 5x Abney hand level.
We used the first axis of a principal components analysis of stream magnitude, length, and bankfull width as a metric of 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 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 within the study reach taken to the nearest 10 cm.

2.3.5 Data Analysis

First, we conducted an exploratory analysis that ranked the relative importance of the environmental variables in describing invertebrate abundance and diversity. Then we assessed the relative importance of salmon abundance, two environmental variables selected from the exploratory step (explained below), and sampling date as explanatory variables of invertebrate abundance and diversity. In both steps, linear regression models for all combinations of explanatory variables were evaluated with an information-theoretic framework and Akaike Information Criterion adjusted for small sample sizes (AICc). Model averaging was used to assess the importance of individual explanatory variables (Anderson, 2008).

Initially, collinearity among environmental variables was assessed using Variance Inflation Factors (VIF), according to Zuur et al. (2010). 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. We found conductivity and pH to be highly co-linear (r = 0.85). As pH contributes to conductivity, and has a direct relationship to a variety of important physiological processes, we retained pH and dropped conductivity from further consideration. All remaining environmental variables had a VIF below three, which demonstrated that collinearity was not of substantial concern. While we used the literature to choose our environmental variables, we had no a priori hypotheses for any one being more important than any other. However, given the number of streams we surveyed it was appropriate to reduce the number of environmental variables that we
considered alongside salmon abundance and sampling date in our final models. We assessed the relative importance of each environmental variable according to methods suggested by Anderson (2008). To do this, we created linear regression models of each response variable for all combinations of environmental variables. We had no a priori hypotheses for interactions between environmental variables, so included none in the models. We used AICc to evaluate the support for each model in describing the response variable. 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. The environmental variables were then ranked according to the sum of their model weights (Table 2.6). The top two variables were selected, which was appropriate to avoid over-fitting models given the sample size of streams (n = 21). For comparison, we conducted a backward stepwise linear regression using all environmental variables and sequentially dropped non-significant explanatory variables (p > 0.05). In all cases the variables selected by the stepwise regression also had the highest summed AICc model weights.

In the main analyses, we considered the two selected environmental variables, plus four-year mean salmon abundance, and the sampling date, as our four final explanatory variables of invertebrate abundance and diversity. No variable had a VIF above two, which suggested collinearity among them was not of concern. Scatterplots did not reveal any obvious non-linearity between an explanatory and response variable. We then created linear regression models of each response variable for all combinations of the four explanatory variables. No interaction terms were included as none were hypothesized a priori. As in the exploratory step, we used AICc to evaluate the support for each model in describing the response variable. Delta AICc values (ΔAICc), model weights (w_i), and evidence ratios (ER) were calculated to aid interpretation of the model ranking (Anderson 2008). The ΔAICc value is the difference 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). For all analyses we present only models with a ΔAICc < 2 in Table 2.2. Results for all models can be found in Table 2.7. When the top model was multivariate and contained salmon abundance as an
explanatory variable, we present both observed versus fitted plots for the top model and bivariate plots of the individual explanatory variables for comparison. We also assessed the relative importance of each variable across all models by ranking them according to summed model weights. All statistical analyses were conducted in R (R Development Core Team, 2009).

2.4 Results

2.4.1 Total Abundance and Family Level Diversity

In the best model, total invertebrate abundance increased as both salmon abundance and temperature increased (total invertebrate abundance = 0.89salmon abundance + 499.39temperature – 3546.06, \( R^2 = 0.57 \), Fig. 2.2). This was the only model with \( \Delta \text{AICc} < 2 \) (Table 2.2a). Both salmon abundance and temperature explained differences in total invertebrate abundance similarly well across all models (Table 2.3).

In the best model, family level invertebrate diversity was greater in higher gradient streams and streams with smaller substrate (Family Level Diversity = 0.20gradient – 0.12substrate + 4.08, \( R^2 = 0.45 \)). This model had more than twice the support of the next best model, which contained gradient only (Table 2.2b). All models with a \( \Delta \text{AICc} < 2 \) contained gradient. Salmon abundance alone showed a weak negative relationship to diversity (Family Level Diversity = 3.99 – 0.0003salmon abundance, \( R^2 = 0.22 \), \( p = 0.03 \), Table 2.7). However, across all models salmon abundance did not explain differences in invertebrate diversity as well as stream gradient or substrate size (Table 2.3).

2.4.2 Dominant Family Abundance

In the best model, Heptageniidae abundance increased as both salmon abundance and temperature increased (Heptageniidae abundance = 0.42salmon abundance + 118.18temperature – 677.55, \( R^2 = 0.57 \), Fig. 2.3). This model had slightly greater support than the second ranked model, which contained salmon abundance only (Table 2.2c). All models with a \( \Delta \text{AICc} < 2 \) contained salmon abundance. Across all models, salmon
abundance better explained variation in Heptageniidae abundance than stream temperature, substrate size, or sampling date (Table 2.3).

In the best model, Chloroperlidae abundance increased as both salmon abundance and temperature increased \((\text{Chloroperlidae abundance} = 0.17\text{salmon abundance} + 77.65\text{temperature} – 475.40, R^2 = 0.42, \text{Fig. 2.4})\). This model had almost twice the support of the second ranked model, which contained salmon abundance only (Table 2.2d). All models with a \(\Delta AICc < 2\) contained salmon abundance. Across all models, salmon abundance better explained variation in Chloroperlidae abundance than stream temperature, substrate size, or sampling date (Table 2.3).

In the best model, Chironomidae abundance was higher in warmer streams and streams that had lower pH \((\text{Chironomidae abundance} = 186.30\text{temperature} – 969.44\text{pH} + 5930.99, R^2 = 0.47)\). This model had more than twice the support of the next best model, which contained salmon abundance and temperature (Table 2.2e). All models with a \(\Delta AICc < 2\) contained temperature. Salmon abundance alone showed a positive relationship to Chironomidae abundance \((\text{Chironomidae abundance} = 0.26\text{salmon abundance} + 427.1, R^2 = 0.19, p = 0.047, \text{Table 2.7})\). However, across all models salmon abundance did not explain differences in Chironomidae abundance as well as temperature or pH (Table 2.3).

### 2.5 Discussion

This is the first study of the ecological effects of a fall salmon nutrient pulse on summer invertebrate communities in inland salmon-spawning streams. We found that total invertebrate abundance was positively related to salmon abundance and stream temperature across 21 streams. In contrast, family level invertebrate diversity (Orders: Ephemeroptera, Plecoptera, Trichoptera, Diptera) was best described by stream habitat variables alone. These findings imply that invertebrate community diversity at this time of year is related to the local stream habitat but that the fall salmon nutrient pulse may increase total abundance. This suggests that productivity in the summer is higher in streams with larger salmon populations.
Variation in the influence of salmon abundance across different taxa and feeding groups may indicate pathways by which salmon nutrients could enhance ecosystem productivity and invertebrate abundance so long after salmon spawning. We examined relationships between salmon abundance and the abundance of the three most common invertebrate families, which comprised ~ 78% of all invertebrates collected. Salmon abundance was positively related to the abundance of grazing heptageniid mayflies and predatory chloroperlid stoneflies but did not describe chironomid abundance as well as habitat variables alone.

Grazing heptageniid mayflies were the most abundant family and comprised greater than 90% of a feeding group that primarily eats periphyton. Higher abundances may be supported by enhanced growth or nutritional quality of periphyton, as a result of salmon nutrients retained in the watershed. This hypothesis is supported by results from Chapter 1. First, periphyton abundance in the fall was positively related to dissolved phosphorus levels, suggesting growth in these streams can be nutrient limited. Second, stable isotope analyses of periphyton in the fall showed the incorporation of salmon nitrogen that was delivered in previous years, indicating that long-term salmon nutrient retention does occur in these streams. Additionally, there is a moderate correlation between 2006 salmon abundance and soluble reactive phosphorus levels in the 21 streams (Verspoor, unpubl. data), which could be a result of salmon nutrient contributions.

It seems possible that a greater abundance of heptageniid mayflies might in turn support a larger population of predatory chloroperlid stoneflies. Unfortunately, not enough is known about the feeding biology of chloroperlid stoneflies to confidently state that these mayflies are an important prey item (Stewart and Oswood, 2006). Nonetheless, it seems reasonable that higher numbers of food-limited primary consumers and their predators might be supported by either enhanced in-stream primary productivity or more nutritionally valuable biofilms, as a result of salmon nutrients retained in the watershed from at least ten months earlier.

While salmon nutrients appear to support higher grazer abundances, we found no evidence that they increase chironomid abundances at this time of year. This result differs from other studies, which have found spring and summer chironomid abundances to be
positively related to salmon nutrient pulses the previous year (Lessard and Merritt, 2006; Lessard et al., 2009). Chironomids have been shown to colonize salmon carcasses (e.g. Chaloner et al., 2002) and the direct benefit they receive from salmon at this time could increase fecundity or over-winter survival, leading to greater abundances the following year (Lessard and Merritt, 2006). Our results suggest that any direct benefit from salmon carcasses is not manifested in chironomid abundance the following year. Chironomids may also be less negatively affected by substrate disturbance during spawning than larger bodied taxa, such as heptageniid mayflies (Lessard et al., 2009). As a consequence, they could benefit from competitive release through a reduction in the abundance of other taxa (Lessard et al., 2009). This would appear unlikely in our streams as we find increased abundances of the other two most common taxa. Alternatively, chironomid production may have increased in response to salmon nutrients but not be seen in our measurements of abundance due to higher predation rates. If chironomids are preyed upon by chloroperlid stoneflies, the higher abundances of chloroperlid stoneflies that we observed may be evidence for this effect.

This is the first study to present evidence of a positive response to salmon nutrients in grazing invertebrate populations so many months after salmon spawning, likely through an algal-mediated pathway. This finding is in contrast to studies that did not detect any persistent influence of spawning salmon on grazer abundance so many months after spawning (Minakawa and Gara, 2003; Honea and Gara, 2009) and studies where the abundance of grazing mayflies decreased and chironomid abundances increased (Lessard and Merritt, 2006; Lessard et al., 2009). These differences show that the delayed ecological influence of salmon nutrients varies greatly among regions. The immediate ecological influence of salmon nutrients, which is tempered by the concurrent streambed disturbance associated with spawning activities, also differs across the geographic range of Pacific salmon (Janetski et al., 2009). As such, it appears that both the short- and long-term ecological effects of spawning salmon and the nutrient pulses they deliver are region specific.

The range of Pacific salmon spans substantial variation in latitude, climate, geomorphology, and ecology (Augerot, 2005). The extent of salmon nutrient retention in a watershed will be influenced by variation in seasonal high discharge events and winter
freezing in relation to the spawning period, as well as stream variables such as large wood and pools, which facilitate carcass retention (Cederholm and Peterson, 1985; Cederholm et al., 1989; Minakawa and Gara, 2005). The coincidence of salmon spawning and seasonal leaf-litter input, which may vary across regions, could facilitate salmon nutrient retention (Peterson and Matthews, 2009). Previous studies of the persistent ecological effects of salmon nutrients on stream invertebrates have occurred in streams with rainfall driven hydrology characterized by high fall discharge events and that may not freeze predictably over winter (Minakawa and Gara, 2003; Lessard and Merritt, 2006; Honea and Gara, 2009; Lessard et al., 2009). Across our study streams, high discharge events following spawning are rare, winter freezing usually occurs within two months of spawning, large wood and pools play an important role in carcass retention, and a large deposition of leaf litter coincides with initial carcass decomposition (Gottesfeld et al., 2004; Johnston et al., 2004). Consequently, salmon nutrient retention may be higher and lead to stronger ecological effects the following year.

In addition to influencing salmon nutrient retention in the watershed, stream habitat variables can also interact with the ecological effects of salmon nutrients (e.g. Tiegs et al., 2008; Moore and Schindler, 2010). We found that the abundance and diversity of summer stream invertebrate communities was best explained by a combination of stream habitat variables and salmon abundance or by stream habitat variables alone. Although salmon abundance was correlated with both family level diversity and chironomid abundance (Table 2.7), stream habitat variables better explained variation in the response variable. The explicit incorporation of habitat variables that reasonably describe invertebrate community dynamics can reduce the risk of overestimating the ecological role of salmon in comparative studies. Further, if salmon abundance or presence remains in the best models, inference about their ecological role across large spatial and temporal scales holds greater weight.

This study is the largest spatial comparison of stream invertebrate communities across a gradient in salmon abundance. Although the study is comparative and cannot yet be generalized across regions and salmon species, the results suggest increasing the abundance of spawning salmon in these watersheds will correspond to increased invertebrate abundance, primarily of heptageniid mayflies and chloroperlid stoneflies.
Studies that describe how the ecological role of salmon in streams changes with salmon abundance across space and time (e.g. Chaloner et al., 2007; Moore and Schindler, 2008; Moore et al., 2008) both enhance our understanding of stream ecology and assist in ecosystem-based management of salmon populations.

Our findings suggest that the annual resource pulse delivered by spawning Pacific salmon has persistent ecological consequences, likely as a result of nutrient retention within the ecosystem. The effects appear to be proportional to the magnitude of the nutrient pulse, although we did not test for non-linear relationships. Salmon nutrients are one of many resource pulses, including terrestrial leaf litter and invertebrate inputs, which play an important role in stream ecology (Richardson et al., 2010). Although responses to resource pulses may differ among ecosystems (Nowlin et al., 2008), studying the ecological effects of different resource pulses contributes to the general understanding of a widespread phenomenon in nature (Yang et al., 2008).

2.6 Conclusion

Total stream invertebrate abundance was positively related to salmon abundance whereas invertebrate diversity was best described by local stream habitat. More specifically, the abundance of grazing heptageniid mayflies and predatory chloroperlid stoneflies was positively described by salmon abundance but the abundance of chironomid midges was best described by local stream habitat. Thus, salmon nutrients retained in the watershed appear to support higher abundances of grazing invertebrates over ten months after the spawning run. This is likely to be achieved through increased growth or nutritional quality of stream periphyton, the primary food source of grazing mayflies. Stream habitat variables also play an important role in determining stream invertebrate abundance and diversity. This confirms the need to consider the abiotic environment in studies of relationships between salmon and their ecosystems, particularly over larger spatial and temporal scales. Our results contrast with studies of invertebrate communities in coastal salmon spawning streams. However, salmon nutrient retention, and thus the persistent ecological influence of salmon nutrients, is likely to differ across the range of Pacific salmon although the mechanisms of retention are still poorly understood for salmon nutrients in streams. We suggest the use of caution in general
inference about the ecological effects of salmon nutrients across regions that differ in climate and stream geomorphology, particularly when incorporating the ecological role of salmon into conservation management. That the consequences of a resource pulse are dependent on the abiotic context in which it is delivered is of wide ecological relevance.

2.7 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. We appreciate help from DFO staff, including Keri Benner, Tracy Cone, Herb Herunter, Dennis Klassen, Erland MacIsaac, and David Patterson for logistical support and valuable advice on the field sites. We appreciate field support from Rudi Verspoor and Mike Sawyer and lab support from Jenny Bain, Heather McDermott, Sue Salter, and Tereza Zagar. We thank Marianne Fish, Morgan Hocking, Phil Molloy, Wendy Palen, and John Richardson for help with the manuscript.

2.8 References


Bilby RE, Fransen BR, Bisson PA, Walter JK. 1998. Response of juvenile coho salmon (Oncorhynchus kisutch) and steelhead (Oncorhynchus mykiss) to the addition of
salmon carcasses to two streams in southwestern Washington, USA. Canadian Journal of Fisheries and Aquatic Sciences 55: 1909-1918.


interaction project: study description and design. Canadian Technical Report of Fisheries
and Aquatic Sciences No. 1899.


Marczak LB, Richardson JS. 2007. Spiders and subsidies: results from the

Merritt R, Cummins K, Berg M, 2008. An introduction to the aquatic insects of

Minakawa N, Gara RI. 2003. Effects of chum salmon redd excavation on benthic
communities in a stream in the Pacific Northwest. Transactions of the American Fisheries

Minakawa N, Gara RI. 2005. Spatial and temporal distribution of coho salmon
carcasses in a stream in the Pacific Northwest, USA. Hydrobiologia 539: 163-166.

Minakawa N, Gara RI, Honea JM. 2002. Increased individual growth rate and
community biomass of stream insects associated with salmon carcasses. Journal of the

anadromous sockeye salmon (Oncorhynchus nerka). Canadian Journal of Fisheries and
Aquatic Sciences 61: 1582-1589.


Moore JW, Schindler DE. 2010. Spawning salmon and the phenology of
emergence in stream insects. Proceedings of the Royal Society B doi:

Moore JW, Schindler DE, Ruff CP. 2008. Habitat saturation drives thresholds in


2.9 Figures

Figure 2.1: Location of the 21 study streams in the Stuart River drainage of the Fraser River, British Columbia, Canada.
Figure 2.2: Bivariate plots of a) observed versus fitted values for the top model of total invertebrate abundance (number m$^{-2}$), which contains 2006 salmon abundance and maximum weekly average temperature (MWAT, °C) as explanatory variables, fitted with regression (dashed) and 1:1 (solid) lines, b) MWAT versus total invertebrate abundance, fitted with a regression line, and c) 2006 salmon abundance versus total invertebrate abundance, fitted with a regression line.
Figure 2.3: Bivariate plots of a) observed versus fitted values for the top model of Heptageniidae abundance (number m$^{-2}$), which contains 2006 salmon abundance and maximum weekly average temperature (MWAT, °C) as explanatory variables, fitted with regression (dashed) and 1:1 (solid) lines, b) MWAT versus Heptageniidae abundance, fitted with a regression line, and c) 2006 salmon abundance versus Heptageniidae abundance, fitted with a regression line.
Figure 2.4: Bivariate plots of a) observed versus fitted values for the top model of Chloroperlidae abundance (number m$^{-2}$), which contains 2006 salmon abundance and maximum weekly average temperature (MWAT, °C) as explanatory variables, fitted with regression (dashed) and 1:1 (solid) lines), b) MWAT versus Chloroperlidae abundance, fitted with a regression line, and c) 2006 salmon abundance versus Chloroperlidae abundance, fitted with a regression line.
2.10 Tables

Table 2.1  The three dominant invertebrate families identified (i.e. comprising greater than 20% of total invertebrate abundance) and their mean abundance, their mean percentage of total invertebrate abundance, their primary functional feeding group, and their mean percentage of that functional feeding group, across the 21 study streams.

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>Abundance (number m$^{-2}$)</th>
<th>% Total Abundance</th>
<th>Primary Feeding Group</th>
<th>% Feeding group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ephemeroptera</td>
<td>Heptageniidae</td>
<td>871</td>
<td>35</td>
<td>Scraper</td>
<td>91</td>
</tr>
<tr>
<td>Plecoptera</td>
<td>Chloroperlidae</td>
<td>525</td>
<td>21</td>
<td>Predator</td>
<td>80</td>
</tr>
<tr>
<td>Diptera</td>
<td>Chironomidae</td>
<td>544</td>
<td>22</td>
<td>Collector (Predator)</td>
<td>56</td>
</tr>
</tbody>
</table>

**Sum = 78%**
Table 2.2  Results of model selection using AICc for 15 linear regression models that describe a) total invertebrate abundance (number m$^{-2}$), b) family level diversity (Simpson’s Reciprocal Index), c) Heptageniidae abundance, (number m$^{-2}$) d) Chloroperlidae abundance (number m$^{-2}$), and e) Chironomidae abundance (number m$^{-2}$). Only models with a $\Delta$AICc < 2 are presented here. Full results are presented in Appendix 3. k = number of model parameters, $R^2 = $ model regression coefficient, AICc = Akaike Information Criterion for small sample sizes, $\Delta$AICc = change in AICc score from top model, $w_i = $ AICc model weight, ER = top model weight divided by model $i$ weight, Temperature = Maximum Weekly Average Temperature (MWAT).

\[
\begin{array}{|l|c|c|c|c|}
\hline
Model & K & R^2 & \Delta\text{AICc} & w_i & \text{ER} \\
\hline
\text{Salmon Abundance + Temperature} & 4 & 0.57 & 0.00 & 0.50 & 1.00 \\
\hline
\text{Gradient + Substrate Size} & 4 & 0.45 & 0.00 & 0.29 & 1.00 \\
\text{Gradient} & 3 & 0.31 & 1.57 & 0.13 & 2.19 \\
\text{Gradient + Salmon Abundance} & 4 & 0.39 & 1.87 & 0.11 & 2.54 \\
\text{Gradient + Date} & 4 & 0.39 & 1.97 & 0.11 & 2.68 \\
\hline
\text{Salmon Abundance + Temperature} & 4 & 0.57 & 0.00 & 0.30 & 1.00 \\
\text{Salmon Abundance} & 3 & 0.49 & 0.47 & 0.24 & 1.27 \\
\text{Salmon Abundance + Date} & 4 & 0.54 & 1.43 & 0.15 & 2.05 \\
\end{array}
\]
<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>R²</th>
<th>ΔAICc</th>
<th>w_i</th>
<th>ER</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature + pH</td>
<td>4</td>
<td>0.47</td>
<td>0.00</td>
<td>0.38</td>
<td>1.00</td>
</tr>
<tr>
<td>Temperature + Salmon Abundance</td>
<td>4</td>
<td>0.42</td>
<td>1.93</td>
<td>0.15</td>
<td>2.63</td>
</tr>
</tbody>
</table>
Table 2.3  The final four variables ranked by the sum of AICc model weights ($\Sigma w_i$) across the 15 linear regression models evaluated for each response variable (as listed in Table 2).

<table>
<thead>
<tr>
<th>Total Invertebrate Abundance</th>
<th>Family Level Diversity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variable</td>
<td>$\Sigma w_i$</td>
</tr>
<tr>
<td>Salmon Abundance</td>
<td>0.92</td>
</tr>
<tr>
<td>Temperature</td>
<td>0.91</td>
</tr>
<tr>
<td>pH</td>
<td>0.29</td>
</tr>
<tr>
<td>Sampling Date</td>
<td>0.19</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Heptageniidae Abundance</th>
<th>Chloroperlidae Abundance</th>
<th>Chironomidae Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variable</td>
<td>$\Sigma w_i$</td>
<td>Variable</td>
</tr>
<tr>
<td>Salmon Abundance</td>
<td>0.96</td>
<td>Salmon Abundance</td>
</tr>
<tr>
<td>Temperature</td>
<td>0.50</td>
<td>Temperature</td>
</tr>
<tr>
<td>Sampling Date</td>
<td>0.29</td>
<td>Substrate Size</td>
</tr>
<tr>
<td>Substrate Size</td>
<td>0.20</td>
<td>Sampling Date</td>
</tr>
</tbody>
</table>
Table 2.4  Watershed characteristics, sampling date, and 2006 spawning population sizes for the 21 study streams. Magnitude is the number of first order tributaries in the watershed.

<table>
<thead>
<tr>
<th>Stream</th>
<th>Order</th>
<th>Magnitude</th>
<th>Length (km)</th>
<th>Bankfull Width (m)</th>
<th>Sampling Date (2007)</th>
<th>2006 Spawning Population (No. of Fish)</th>
</tr>
</thead>
<tbody>
<tr>
<td>10 Mile</td>
<td>2</td>
<td>2</td>
<td>5.91</td>
<td>4.19</td>
<td>20-Jul</td>
<td>0</td>
</tr>
<tr>
<td>15 Mile</td>
<td>3</td>
<td>14</td>
<td>18.5</td>
<td>11.64</td>
<td>23-Jul</td>
<td>138</td>
</tr>
<tr>
<td>25 Mile</td>
<td>2</td>
<td>6</td>
<td>17.59</td>
<td>9.04</td>
<td>25-Jul</td>
<td>0</td>
</tr>
<tr>
<td>Ankwill</td>
<td>4</td>
<td>44</td>
<td>27.37</td>
<td>30.53</td>
<td>1-Aug</td>
<td>1673</td>
</tr>
<tr>
<td>Bivouac</td>
<td>3</td>
<td>10</td>
<td>17.52</td>
<td>8.07</td>
<td>9-Jul</td>
<td>104</td>
</tr>
<tr>
<td>Crow</td>
<td>2</td>
<td>4</td>
<td>10.43</td>
<td>9.04</td>
<td>3-Jul</td>
<td>44</td>
</tr>
<tr>
<td>Die Hard</td>
<td>2</td>
<td>4</td>
<td>7.79</td>
<td>12.01</td>
<td>22-Jul</td>
<td>0</td>
</tr>
<tr>
<td>Forfar</td>
<td>3</td>
<td>13</td>
<td>15.35</td>
<td>7.31</td>
<td>28-Jul</td>
<td>4117</td>
</tr>
<tr>
<td>Forsythe</td>
<td>4</td>
<td>36</td>
<td>25.72</td>
<td>13.15</td>
<td>31-Jul</td>
<td>32</td>
</tr>
<tr>
<td>French</td>
<td>3</td>
<td>25</td>
<td>23.54</td>
<td>9.81</td>
<td>2-Aug</td>
<td>0</td>
</tr>
<tr>
<td>Frypan</td>
<td>4</td>
<td>59</td>
<td>26.86</td>
<td>18.14</td>
<td>31-Jul</td>
<td>1321</td>
</tr>
<tr>
<td>Gluskie</td>
<td>3</td>
<td>13</td>
<td>18.54</td>
<td>11.35</td>
<td>10-Jul</td>
<td>2749</td>
</tr>
<tr>
<td>Hooker</td>
<td>2</td>
<td>2</td>
<td>6.61</td>
<td>3.67</td>
<td>1-Jul</td>
<td>0</td>
</tr>
<tr>
<td>Kynock</td>
<td>4</td>
<td>27</td>
<td>11.88</td>
<td>13.23</td>
<td>29-Jul</td>
<td>4816</td>
</tr>
<tr>
<td>Leo</td>
<td>3</td>
<td>14</td>
<td>20.83</td>
<td>9.23</td>
<td>4-Jul</td>
<td>10</td>
</tr>
<tr>
<td>Maclaing</td>
<td>3</td>
<td>10</td>
<td>22.34</td>
<td>8.18</td>
<td>26-Jul</td>
<td>78</td>
</tr>
<tr>
<td>Narrows</td>
<td>2</td>
<td>6</td>
<td>19.71</td>
<td>15.51</td>
<td>14-Jul</td>
<td>2227</td>
</tr>
<tr>
<td>Sandpoint</td>
<td>3</td>
<td>12</td>
<td>20.11</td>
<td>9.85</td>
<td>18-Jul</td>
<td>0</td>
</tr>
<tr>
<td>Shale</td>
<td>3</td>
<td>7</td>
<td>17.11</td>
<td>9.85</td>
<td>24-Jul</td>
<td>257</td>
</tr>
<tr>
<td>Sinta</td>
<td>2</td>
<td>20</td>
<td>19.52</td>
<td>11.06</td>
<td>3-Jul</td>
<td>14</td>
</tr>
<tr>
<td>Van Decar</td>
<td>3</td>
<td>14</td>
<td>10.61</td>
<td>8.28</td>
<td>12-Jul</td>
<td>2487</td>
</tr>
</tbody>
</table>
Table 2.5  Study site habitat characteristics across the 21 streams.

<table>
<thead>
<tr>
<th>Habitat Characteristic</th>
<th>Mean</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gradient (%)</td>
<td>2.1</td>
<td>0.6 – 5.8</td>
</tr>
<tr>
<td>Water Depth (m)</td>
<td>0.13</td>
<td>0.08 – 0.22</td>
</tr>
<tr>
<td>Temperature - Maximum Weekly Average Temperature (°C)</td>
<td>11.2</td>
<td>8.5 – 13.9</td>
</tr>
<tr>
<td>Light - Canopy Cover (%)</td>
<td>44</td>
<td>5 - 80</td>
</tr>
<tr>
<td>Substrate Size - Geometric Mean of Substrate Intermediate Axis Diameter (cm)</td>
<td>6.0</td>
<td>2.8 – 9.4</td>
</tr>
<tr>
<td>pH</td>
<td>7.7</td>
<td>7.2 – 8.2</td>
</tr>
<tr>
<td>Conductivity (µS/cm)</td>
<td>89</td>
<td>28 – 194</td>
</tr>
</tbody>
</table>
Table 2.6  Environmental variables ranked by the sum of AICc model weights ($\Sigma w_i$) across linear regression models of all variable combinations for each response variable (as listed for Table 2). The top two variables were included in the main analyses.

<table>
<thead>
<tr>
<th>Variable</th>
<th>$\Sigma w_i$</th>
<th>Variable</th>
<th>$\Sigma w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Invertebrate Abundance</td>
<td></td>
<td>Family Level Diversity</td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>0.88</td>
<td>Gradient</td>
<td>0.79</td>
</tr>
<tr>
<td>pH</td>
<td>0.62</td>
<td>Substrate Size</td>
<td>0.62</td>
</tr>
<tr>
<td>Light</td>
<td>0.48</td>
<td>Watershed Size</td>
<td>0.24</td>
</tr>
<tr>
<td>Substrate Size</td>
<td>0.35</td>
<td>Temperature</td>
<td>0.22</td>
</tr>
<tr>
<td>Watershed Size</td>
<td>0.23</td>
<td>Depth</td>
<td>0.17</td>
</tr>
<tr>
<td>Gradient</td>
<td>0.18</td>
<td>Light</td>
<td>0.17</td>
</tr>
<tr>
<td>Depth</td>
<td>0.14</td>
<td>pH</td>
<td>0.16</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Variable</th>
<th>$\Sigma w_i$</th>
<th>Variable</th>
<th>$\Sigma w_i$</th>
<th>Variable</th>
<th>$\Sigma w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heptageniidae Abundance</td>
<td></td>
<td>Chloroperlidae Abundance</td>
<td></td>
<td>Chironomidae Abundance</td>
<td></td>
</tr>
<tr>
<td>Substrate Size</td>
<td>0.83</td>
<td>Temperature</td>
<td>0.87</td>
<td>Temperature</td>
<td>0.86</td>
</tr>
<tr>
<td>Temperature</td>
<td>0.48</td>
<td>Substrate Size</td>
<td>0.60</td>
<td>pH</td>
<td>0.75</td>
</tr>
<tr>
<td>pH</td>
<td>0.39</td>
<td>Watershed Size</td>
<td>0.31</td>
<td>Light</td>
<td>0.30</td>
</tr>
<tr>
<td>Gradient</td>
<td>0.30</td>
<td>pH</td>
<td>0.30</td>
<td>Gradient</td>
<td>0.19</td>
</tr>
<tr>
<td>Light</td>
<td>0.24</td>
<td>Light</td>
<td>0.23</td>
<td>Watershed Size</td>
<td>0.18</td>
</tr>
<tr>
<td>Watershed Size</td>
<td>0.18</td>
<td>Gradient</td>
<td>0.22</td>
<td>Depth</td>
<td>0.16</td>
</tr>
<tr>
<td>Depth</td>
<td>0.16</td>
<td>Depth</td>
<td>0.18</td>
<td>Substrate Size</td>
<td>0.15</td>
</tr>
</tbody>
</table>
Table 2.7 Full results of model selection using AICc for 15 linear regression models that describe a) total invertebrate abundance (number m$^{-2}$), b) family level diversity (Simpson’s Reciprocal Index), c) Heptageniidae abundance, (number m$^{-2}$) d) Chloroperlidae abundance (number m$^{-2}$), and e) Chironomidae abundance (number m$^{-2}$). Table headings are as described in Table 2.

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>$R^2$</th>
<th>$\Delta$AICc</th>
<th>$w_i$</th>
<th>ER</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salmon Abundance + Temperature</td>
<td>4</td>
<td>0.57</td>
<td>0.00</td>
<td>0.50</td>
<td>1.00</td>
</tr>
<tr>
<td>Salmon Abundance + Temperature + pH</td>
<td>5</td>
<td>0.60</td>
<td>2.01</td>
<td>0.18</td>
<td>2.74</td>
</tr>
<tr>
<td>Salmon Abundance + Temperature + Date</td>
<td>5</td>
<td>0.58</td>
<td>2.66</td>
<td>0.13</td>
<td>3.78</td>
</tr>
<tr>
<td>Temperature + pH</td>
<td>4</td>
<td>0.45</td>
<td>4.93</td>
<td>0.04</td>
<td>11.75</td>
</tr>
<tr>
<td>Salmon Abundance</td>
<td>3</td>
<td>0.36</td>
<td>5.09</td>
<td>0.04</td>
<td>12.73</td>
</tr>
<tr>
<td>Salmon Abundance + Temperature + pH + Date</td>
<td>6</td>
<td>0.61</td>
<td>5.12</td>
<td>0.04</td>
<td>12.95</td>
</tr>
<tr>
<td>Salmon Abundance + pH</td>
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<td>0.40</td>
<td>6.86</td>
<td>0.02</td>
<td>30.93</td>
</tr>
<tr>
<td>Temperature</td>
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<td>0.30</td>
<td>7.07</td>
<td>0.01</td>
<td>34.24</td>
</tr>
<tr>
<td>Temperature + pH + Date</td>
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<td>0.46</td>
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<td>0.01</td>
<td>59.17</td>
</tr>
<tr>
<td>Salmon Abundance + Date</td>
<td>4</td>
<td>0.36</td>
<td>8.17</td>
<td>0.01</td>
<td>59.31</td>
</tr>
<tr>
<td>pH</td>
<td>3</td>
<td>0.21</td>
<td>9.52</td>
<td>0.00</td>
<td>116.83</td>
</tr>
<tr>
<td>Temperature + Date</td>
<td>4</td>
<td>0.30</td>
<td>10.05</td>
<td>0.00</td>
<td>151.97</td>
</tr>
<tr>
<td>Salmon Abundance + pH + Date</td>
<td>5</td>
<td>0.40</td>
<td>10.35</td>
<td>0.00</td>
<td>176.68</td>
</tr>
<tr>
<td>pH + Date</td>
<td>4</td>
<td>0.21</td>
<td>12.56</td>
<td>0.00</td>
<td>534.19</td>
</tr>
<tr>
<td>Date</td>
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<td>0.01</td>
<td>14.33</td>
<td>0.00</td>
<td>1296.04</td>
</tr>
</tbody>
</table>
### Table

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>$R^2$</th>
<th>$\Delta$AICc</th>
<th>$w_i$</th>
<th>ER</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gradient + Substrate Size</td>
<td>4</td>
<td>0.45</td>
<td>0.00</td>
<td>0.29</td>
<td>1.00</td>
</tr>
<tr>
<td>Gradient</td>
<td>3</td>
<td>0.31</td>
<td>1.57</td>
<td>0.13</td>
<td>2.19</td>
</tr>
<tr>
<td>Gradient + Salmon Abundance</td>
<td>4</td>
<td>0.39</td>
<td>1.87</td>
<td>0.11</td>
<td>2.54</td>
</tr>
<tr>
<td>Gradient + Date</td>
<td>4</td>
<td>0.39</td>
<td>1.97</td>
<td>0.11</td>
<td>2.68</td>
</tr>
<tr>
<td>Gradient + Substrate Size + Date</td>
<td>5</td>
<td>0.47</td>
<td>2.52</td>
<td>0.08</td>
<td>3.53</td>
</tr>
<tr>
<td>Gradient + Salmon Abundance + Date</td>
<td>5</td>
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Conclusion

In Chapter 1, I provide evidence that higher abundance of spawning salmon leads to higher nitrogen stable isotope signatures of stream periphyton but reduces periphyton abundance. This suggests that enrichment from salmon nitrogen does not always translate into increased periphyton abundance, likely because substrate disturbance was the more influential mechanism by which spawning salmon affected periphyton in the study. While evidence for the importance of substrate disturbance to stream ecosystems has been found in previous studies (e.g. Moore and Schindler 2008, Moore et al. 2008, Moore and Schindler 2010), rarely have both stable isotope analyses and measures of ecosystem impacts been presented together. These findings suggest that there is need for caution when inferring ecological effects from stable isotope evidence for the incorporation of salmon nutrients into food webs, for which there is a significant body of research.

I also showed that the nitrogen stable isotope signature of periphyton was best described by a measure of salmon abundance that spanned multiple years. This finding suggests that some salmon nutrients are retained in these watersheds for longer than a year after they are delivered and is the first direct test for a “nutrient legacy” using metrics of salmon abundance to differently characterize the ecosystem influence of spawning salmon. The results support the notion that salmon nutrients could have ecological effects that persist for months, or even years, after they are delivered. Future research could use salmon abundance metrics that characterize this “nutrient legacy” in different ways to test the timeframe over which salmon nutrients exert an ecosystem influence.

In Chapter 2, I provided evidence that summer stream invertebrate abundance was positively influenced by the abundance of spawning salmon and stream habitat characteristics together, whereas invertebrate diversity was principally influenced by stream habitat alone. Furthermore, of the three most common invertebrate families, the abundance of both grazing mayflies and predatory stoneflies was positively influenced by salmon abundance. This is the first evidence that salmon nutrients that are retained in
watersheds over ten months after spawning can have an ecological effect on invertebrates, probably through an algal-mediated bottom-up pathway. Thus salmon nutrients may positively influence periphyton growth prior to spawning. While Chapter 1 suggests that substrate disturbance is the primary mechanism by which Pacific salmon influence periphtyon during and immediately after spawning, this chapter indicates that the nutrient subsidy has a stronger influence later in the year. As such, it is important that the ecological influence of spawning salmon is studied throughout the year.

Recent studies have called for the spatial and temporal scope of research on the impacts of spawning salmon to be expanded, so as to consider how the impacts vary across regions and in relation to both habitat characteristics and the abundance of spawning salmon (Mitchell and Lamberti 2005, Chaloner et al. 2007, Janetski et al. 2009). To that effect, this thesis represents the largest spatial comparison of spawning salmon impacts on stream ecosystems to date. It is also the first time that the effects of both habitat characteristics and spawning salmon abundance on stream ecosystems have been tested simultaneously. Furthermore, this research was conducted in inland salmon streams, where little work on the ecosystem influence of spawning salmon has previously taken place. These three facets of this thesis represent both a novel contribution and an important step forward in the understanding of how spawning Pacific salmon interact with freshwater ecosystems.

The number of streams that surveyed is a major strength of this study. However, the resulting field logistics and laboratory processing time inherently imposed constraints on the temporal replication that could be achieved. Fieldwork spanned just a single year and within that, the samples collected represent a snapshot in time. Although not feasible for this thesis, future studies should expand their temporal scope to consider how the ecosystem influence of spawning salmon changes both through the year (e.g. Honea and Gara 2009) and across years (e.g. Chaloner et al. 2007) and ideally combine this with good spatial replication (e.g. Moore and Schindler 2008, Moore et al. 2008).

The simultaneous consideration of the influence that habitat and salmon abundance have on stream ecosystems is an essential step forward in understanding how spawning salmon influence streams. The incorporation of habitat variables that are
known to be important to either periphyton or invertebrates reduces the risk of overestimating the ecological role of salmon in a comparative study such as this. Furthermore, in analyses where the abundance of spawning salmon shows a greater or similar influence to stream habitat, inference about their ecological role across large spatial and temporal scales holds greater weight. The scale of replication (in this case the number of streams surveyed) limited the number of habitat variables that could be considered in a single model as well as the capacity to test for interactions between salmon abundance and stream habitat. Expanding the spatial and temporal scope of studies will always face feasibility issues. Incorporating within-site replication into statistical analyses, using hierarchical structuring to increase power, might enhance future research into how habitat mediates the ecological impacts of spawning salmon.

It has long been appreciated that spawning salmon are important to freshwater and adjacent terrestrial ecosystems (e.g. Shuman 1950, Mossman 1958, Nicola 1968). A flurry of research over the last two decades has confirmed this, although their influence appears to vary considerably across space and time (reviewed by Gende et al. 2002, Naiman et al. 2002, Schindler et al. 2003, Janetski et al. 2009). Their ecosystem impacts depend on their abundance, which is influenced, among other things, by the myriad of fisheries that target salmon. In order to conserve and protect the integrity of the ecosystems in which Pacific salmon spawn and in turn depend on for their own persistence, it is essential to understand how salmon caught in fisheries are linked to changes in freshwater ecosystems. This requires knowledge of relationships between spawning salmon abundance and their ecosystem impacts (e.g. DFO 2005). This thesis contributes towards the knowledge required to incorporate the importance of spawning salmon to freshwater ecosystems into the future management of Pacific salmon populations.

References


