

Persistent ecological effects of a salmon-derived nutrient pulse on stream invertebrate communities

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Abstract. Pulsed resource subsidies can have ecological effects that persist over time. These subsidies can be particularly important in aquatic ecosystems, which are often resource-limited. Anadromous salmon (*Oncorhynchus* spp.) deliver annual nutrient pulses to many freshwater ecosystems around the North Pacific. 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 density, 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 salmon density and with higher stream temperatures. Invertebrate diversity was more closely related to stream habitat characteristics than to salmon density. These results suggest that salmon nutrients have a greater impact on stream invertebrate population sizes than on the variety of taxa that inhabit these streams. The three most common invertebrate families—grazing mayflies (Heptageniidae), predatory stoneflies (Chloroperlidae), and chironomid midges (Chironomidae)—all increased in abundance with salmon density. Stream habitat variables (temperature, pH, and substrate size) also explained significant variation in the abundances of the three groups. These results suggest that salmon nutrients retained in the watershed from previous years help support 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.

Key words: aquatic conservation; ecosystem-based management; fisheries; food web; Fraser River; marine-derived nutrients; nutrient pulse; *Oncorhynchus nerka*; productivity; resource subsidy.

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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 ecolog-

ical 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, 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, which 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 die, often in high densities (Groot and Margolis 1991). This provides a nutrient subsidy that can both directly influence organisms that consume salmon eggs or carcasses (e.g., Bilby et al. 1998, Minakawa et al. 2002) and indirectly alter ecosystem processes when organisms switch their diets to salmon (Zhang et al. 2003). Decomposing carcasses can also 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).

The impacts of the nutrient subsidy provided by spawning salmon are potentially tempered in the short-term by the 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 through mechanisms such as the overwinter freezing of carcasses, slow decomposition of skeletal remains, adsorption of nutrients onto substrate biofilms, hyporheic storage, and tight internal cycling of salmon nutrients stored within organisms (Gende et al. 2002, Naiman et al. 2002). Streambed disturbance by spawning salmon may also assist nutrient retention through the re-suspension of fine sediment, which can aggregate with salmon matter into larger particles (Rex and Petticrew 2008). 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 as to the extent that salmon nutrients persist in and have ecological effects on 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-derived nutrients (Merritt et al. 2008). In coastal southeast 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. 2003, Lessard and Merritt 2006). 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). The possible ecological effects of salmon nutrients on stream invertebrates in inland streams, which generally do not experience the high fall and winter discharge events that are typical of many rainfall-driven coastal streams and thus may retain more salmon nutrients, has not been investigated.

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), it will become

increasingly useful to understand the links between salmon caught in fisheries and changes to stream ecosystems (e.g., DFO 2005, Piccolo et al. 2009). 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 a large 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 density and environmental variables to explain 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 density, which may occur if salmon nutrients retained in the watersheds increase nutrient-limited resources.

METHODS

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. 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 (Appendix A). The watersheds are forested and common riparian species include hybrid white spruce (*Picea glauca* × *P. engelmannii*), black cottonwood (*Populus balsamifera*), Sitka alder (*Alnus viridis*) and devil’s club (*Oplopanax horridus*). Water flows are highest in the spring as a result of snowmelt and lowest from late July to mid September, when these sockeye populations spawn, and also from November to February, when most precipitation falls as snow. Total annual precipitation in the region is around 500 mm of which on average 200 mm is snowfall. Macdonald et al. (1992) provide a detailed description of the region and four of the streams.

Salmon abundance

The 21 study streams represented a gradient of salmon density at relatively low population sizes during the study period (2006 salmon density = 0–0.32 fish m⁻²; Appendix A). 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.

We measured salmon abundance as the density of adult sockeye salmon (fish m⁻²) that were in the 500 m study reach in which we sampled invertebrates and habitat data. Salmon density (D) was calculated as:

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

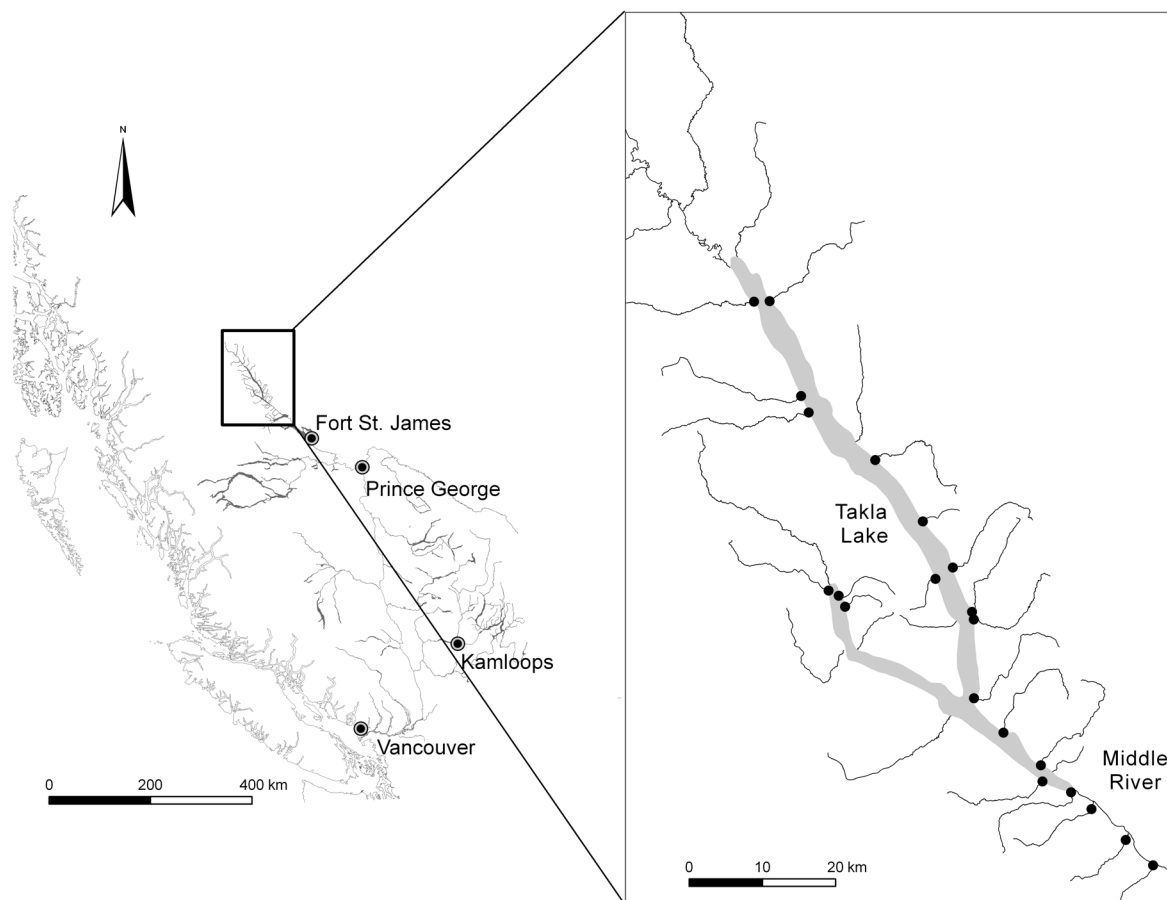


Fig. 1. Location of the 21 study streams in the Stuart River drainage of the Fraser River, British Columbia, Canada.

where F is the DFO estimate of the spawning population size in the 500 m section, w is the section-specific wetted width (m) and l is the length of the section (m). Initially, we considered salmon density both during the year prior to sampling (2006), in order to emphasize 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. Density 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 (Verspoor et al. 2010). 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 multi-year metrics

were highly correlated with each other ($r > 0.99$ in all cases) and with 2006 salmon density ($r > 0.82$). Since results did not differ among metrics, we present results for only 2006 salmon density. This study therefore 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.

Invertebrate collection and identification

Benthic invertebrates were collected over a period of one month immediately prior to salmon spawning (July 1–August 2, 2007; Appendix A). 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 identified independently 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 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).

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 Appendix B. We also expected that the sampling date 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 5 2007–Aug 5 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 were 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, 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 haphazardly selected and 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 5× 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

Table 1. The three dominant invertebrate families identified (i.e., comprising greater than 20% of total invertebrate abundance) and their mean absolute abundance, their mean percentage of total invertebrate abundance (of a cumulative abundance of 78%), their primary functional feeding group, and their mean percentage of that functional feeding group, across the 21 study streams.

Order	Family	Absolute Abundance (number m ⁻²)	Percent of Total Abundance	Primary Feeding Group	Percent of Feeding Group
Ephemeroptera	Heptageniidae	871	35	Scraper	91
Plecoptera	Chloroperlidae	525	21	Predator	80
Diptera	Chironomidae	544	22	Collector (Predator)	56

without flooding, was averaged across 16 measurements within the study reach taken to the nearest 10 cm.

Data analysis

First, we conducted an analysis that ranked the relative importance of the environmental variables in describing invertebrate abundance and diversity. Then we assessed the relative importance of salmon density, two environmental variables selected from the first 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, co-linearity 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 correlations 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 co-linearity was not of substantial concern. While we used the literature to choose our environmental variables, we had no prior reason to expect any variable to be 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 density 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 models with different combinations of variables based on the principal of parsimony, balancing optimal fit with the number of parameters used (Anderson 2008). The environmental variables were then ranked according to the sum of their model weights (Appendix C). The top two variables were selected, to avoid over-fitting models given the sample size of streams ($n = 21$).

In the second step of the analyses, we considered the two selected environmental variables, plus salmon density and sampling date, as our four final explanatory variables of invertebrate abundance and diversity. No variable had a VIF above two, which suggested co-linearity 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. Salmon density was square-root transformed in all models to improve model assumptions. No interaction terms were included as none were hypothesized a priori. As in the first step of the analyses, 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_{topmodel}/w_i and can be interpreted as the likelihood that the top ranked model is better than model i . For all analyses we present only models with a $\Delta\text{AICc} < 2$. Results for all models can be found in Appendix D. When the top model was multivariate and contained salmon density as an explanatory variable, we present both observed versus fitted plots for the top model and bivariate plots of individual explanatory variables for comparison (Fig.2). 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).

RESULTS

Total abundance and family level diversity

Total invertebrate abundance increased with both salmon density and stream temperature ($\text{total invertebrate abundance} = 3326\sqrt{\text{salmon density}} + 587\text{temperature} - 4522$, $R^2 = 0.48$, Fig. 2a). This was the best of three models with a $\Delta\text{AICc} < 2$ (Table 2a). Across all models, temperature explained differences in total invertebrate abundance better than salmon density, while both variables explained invertebrate abundance better than pH or sampling date (Table 3).

Family level invertebrate diversity was greater in higher gradient streams and streams with smaller substrate ($\text{Family Level Diversity} = 0.20\text{gradient} - 0.12\text{substrate} + 4.08$, $R^2 = 0.45$). This model had more than twice the support of the next best model, which contained gradient only (Table 2b). All models with a $\Delta\text{AICc} < 2$ contained a positive relationship between stream gradient and invertebrate diversity. Salmon density showed a weak negative relationship to diversity ($\text{Family Level Diversity} = 4.01 - 1.29\sqrt{\text{salmon density}}$, $R^2 = 0.18$, $p = 0.06$, Appendix D). However, across all models salmon density did not explain differences in invertebrate diversity as well as stream gradient or

substrate size (Table 3).

Dominant family abundance

The abundance of heptageniid mayflies increased with salmon density, stream temperature, and substrate size ($\text{Heptageniidae abundance} = 989\sqrt{\text{salmon density}} + 149\text{temperature} + 117\text{substrate size} - 1632$, $R^2 = 0.52$, Fig.2b). This was the best of five models with a $\Delta\text{AICc} < 2$. Of these five models for heptageniid abundance, four showed a positive relationship with substrate size, three had a positive relationship with salmon density, and three showed a positive relationship with stream temperature. Across all 15 models, substrate size better explained variation in heptageniid abundance than either salmon density or stream temperature, which explained similar amounts of variation (Table 3). Sampling date explained little variation in heptageniid abundance (Table 3).

Chloroperlid stoneflies followed a similar pattern to heptageniid mayflies, with higher numbers in streams that had more salmon and warmer water ($\text{Chloroperlidae abundance} = 814\sqrt{\text{salmon density}} + 82\text{temperature} - 563$, $R^2 = 0.50$, Fig.2c). This was the only model with a $\Delta\text{AICc} < 2$ (Table 2d). Across all models, salmon density explained the most variation in chloroperlid abundance of all the explanatory variables considered, while stream temperature explained considerably more variation than either substrate size or sampling date (Table 3).

Chironomids were also most abundant in warmer streams with more salmon ($\text{Chironomidae abundance} = 1153\sqrt{\text{salmon density}} + 205\text{temperature} - 1899$, $R^2 = 0.47$, Fig. 2d). This was the best of three models with a $\Delta\text{AICc} < 2$. Of the three models, all showed that abundance of chironomids increased with stream temperature, two showed a positive relationship with salmon density, and two showed a negative relationship with stream pH (Table 2e). Across all models, stream temperature better explained variation in chironomid abundance than either salmon density or stream pH, which explained similar amounts of variation (Table 3). Sampling date explained little variation in chironomid abundance (Table 3).

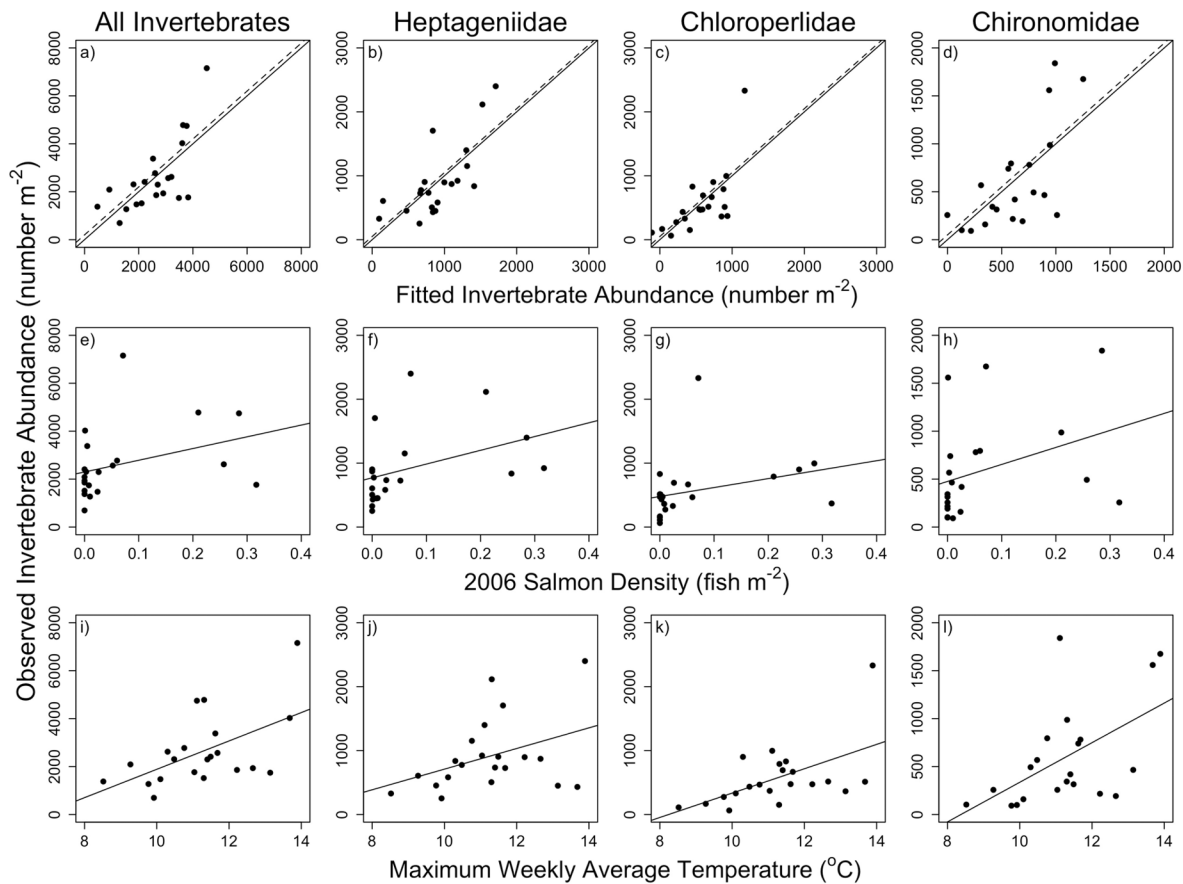


Fig. 2. Row 1: Bivariate plots of observed versus fitted values for the top model of a) total invertebrate abundance (number m^{-2}), b) Heptageniidae abundance (number m^{-2}), c) Chloroperlidae abundance (number m^{-2}), d) Chironomidae abundance (number m^{-2}) fitted with regression (dashed) and 1:1 (solid) lines. The top model of each response variable contained 2006 salmon density (square-root transformed, fish m^{-2}) and maximum weekly average temperature (MWAT, $^{\circ}C$) as explanatory variables, while the model of Heptageniidae abundance additionally contained substrate size (geometric mean of substrate intermediate axis diameter, cm). Row 2: Bivariate plots of 2006 salmon density versus e) total invertebrate abundance, f) Heptageniidae abundance, g) Chloroperlidae abundance, h) Chironomidae abundance. Row 3: Bivariate plots of MWAT versus i) total invertebrate abundance, j) Heptageniidae abundance, k) Chloroperlidae abundance, l) Chironomidae abundance.

DISCUSSION

We found that total invertebrate abundance, including the abundance of grazing heptageniid mayflies, predatory chloroperlid stoneflies, and chironomid midges, was positively related to salmon density and to stream habitat variables, particularly temperature, across 21 streams. In contrast, family level invertebrate diversity (Orders: Ephemeroptera, Plecoptera, Trichoptera, Diptera) was best described by stream habitat

variables alone. These correlations suggest that invertebrate community diversity in the summer is most strongly influenced by local stream habitat but that the previous years' fall salmon nutrient pulse may increase total invertebrate abundance. Thus, streams with larger salmon populations and higher temperatures may also be more productive.

Grazing heptageniid mayflies were the most abundant family and comprised greater than 90% of a feeding group that primarily eats

Table 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).

Model	K	R ²	ΔAICc	w _i	ER	Model Parameters	Estimate	SE
a) Total Invertebrate Abundance								
1	4	0.48	0.00	0.37	1.00	Intercept	-4522.9	2086.4
						Temperature	586.6	183.8
						Salmon Density	3326.2	1305.7
2	4	0.45	1.24	0.20	1.86	Intercept	16342.0	9282.7
						Temperature	538.0	190.8
						pH	-2578.5	1143.1
3	5	0.52	1.79	0.15	2.45	Intercept	7721.4	10407.8
						Temperature	556.1	183.4
						Salmon Density	2403.1	1501.9
						pH	-1532.3	1276.7
b) Family Level Diversity								
1	4	0.45	0.00	0.28	1.00	Intercept	4.08	0.42
						Gradient	0.20	0.08
						Substrate Size	-0.12	0.06
2	3	0.31	1.57	0.13	2.19	Intercept	3.30	0.20
						Gradient	0.24	0.08
3	4	0.39	1.97	0.11	2.68	Intercept	6.47	2.03
						Gradient	0.24	0.08
						Sampling Date	-0.02	0.01
c) Heptageniidae Abundance								
1	5	0.52	0.00	0.23	1.00	Intercept	-1631.6	818.0
						Substrate Size	116.5	52.9
						Temperature	149.4	69.2
						Salmon Density	989.4	525.9
2	4	0.42	0.47	0.18	1.27	Intercept	-1664.8	873.6
						Substrate Size	152.5	52.7
						Temperature	147.7	73.9
3	4	0.39	1.59	0.10	2.22	Intercept	3.0	340.8
						Substrate Size	123.9	57.9
						Salmon Density	974.4	576.9
4	3	0.29	1.59	0.10	2.22	Intercept	-48.2	355.7
						Substrate Size	159.3	56.6
5	4	0.39	1.77	0.09	2.42	Intercept	-1113.3	863.2
						Temperature	159.3	76.1
						Salmon density	1408.0	540.2
d) Chloroperlidae Abundance								
1	4	0.50	0.00	0.51	1.00	Intercept	-562.7	406.7
						Salmon Density	814.3	231.9
						Temperature	82.2	36.1
e) Chironomidae Abundance								
1	4	0.47	0	0.29	1.00	Intercept	-1899.3	739.9
						Temperature	204.7	65.2
						Salmon Density	1153.4	463.0
2	4	0.47	0.16	0.27	1.08	Intercept	5931.0	3208.5
						Temperature	186.3	66.0
						pH	-969.4	395.1
3	5	0.53	1.14	0.16	1.77	Intercept	3162.2	3634.2
						Temperature	192.1	64.0
						Salmon Density	771.8	524.4
						pH	-633.4	445.8

Notes: Only models with a ΔAICc < 2 are presented here. Full results are in Appendix D. k = number of model parameters, R² = model regression coefficient, AICc = Akaike Information Criterion for small sample sizes, ΔAICc = change in AICc score from top model, w_i = AICc model weight, ER = top model weight divided by model *i* weight, Temperature = maximum weekly average temperature (MWAT). Salmon density was square-root transformed in all models.

periphyton. Higher heptageniid abundances may be supported by enhanced growth or a higher nutritional quality of periphyton. All three variables that best explained heptageniid abundance could positively influence the growth,

nutritional quality, or availability of stream periphyton in our region. First, higher temperatures can increase periphyton growth by raising metabolic rates (DeNicola 1996). Second, substrate size has been shown to mediate the

Table 3. The final four explanatory variables ranked by the sum of AICc model weights ($\sum w_i$) across the 15 linear regression models evaluated for each response variable (listed in Appendix D).

Response Variable	Explanatory Variable	$\sum w_i$
Total Invertebrate Abundance	Temperature	0.94
	Salmon Density	0.65
	pH	0.37
Family Level Diversity	Sampling Date	0.16
	Gradient	0.86
	Substrate Size	0.57
	Salmon Density	0.33
Heptageniidae Abundance	Sampling Date	0.31
	Substrate Size	0.75
	Temperature	0.64
	Salmon Density	0.62
Chloroperlidae Abundance	Sampling Date	0.23
	Salmon Density	0.97
	Temperature	0.72
	Substrate Size	0.17
Chironomidae Abundance	Sampling Date	0.16
	Temperature	0.94
	pH	0.57
	Salmon Density	0.56
	Sampling Date	0.17

scouring effect of disturbance events, particularly the disturbance caused by spawning salmon (Tiegs et al. 2008). As a result, streams with larger substrate may experience less scouring, thus facilitating increased periphyton abundance as well as protecting the mayflies themselves from the negative effects of disturbance by spawning salmon. Finally, the growth and nutritional quality of periphyton can be increased by nutrient availability, which could be influenced by the retention of salmon nutrients in the watershed.

While a previous study of periphyton across 24 streams in the region did not find a higher standing stock of periphyton in streams with more salmon, this study was conducted in the fall, 6 weeks after spawning, when effects of salmon scouring the substrate may have been important (Verspoor et al. 2010). Circumstantial support for the hypothesis of a positive link from salmon to periphyton to grazing heptageniid mayflies comes from three lines of evidence. First, periphyton abundance in the fall was positively related to dissolved phosphorus levels, suggesting growth in these streams can be nutrient limited (Verspoor et al. 2010). 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 (Verspoor et al. 2010). Finally, there is a moderate correlation between 2006 salmon density and 2007 summer soluble reactive phosphorus levels in the study streams ($r = 0.48$, $p = 0.033$, $n = 20$), which could be influenced by salmon nutrients retained in the watersheds.

Salmon nutrients also appear to support higher chironomid abundances at this time of year. This result is similar to other studies that 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), presumably utilizing them directly as a food source, which may benefit growth and survival throughout the year. It has also been suggested that they might suffer less from substrate disturbance during spawning than larger bodied taxa, allowing the positive influence of salmon nutrients to be more obviously reflected in their abundances (Lessard et al. 2009).

A higher abundance of prey as a result of increased salmon nutrient retention in the watersheds might in turn support a larger population of predatory chloroperlid stoneflies. Unfortunately, not enough is known about the feeding biology of chloroperlids to confidently state that either heptageniid mayflies or chironomid midges are an important prey item (Stewart and Oswood 2006), although their abundances relative to other groups suggest that such an inference is reasonable. Alternatively, chloroperlids have also been known to scavenge from dead salmon eggs and alevins, which could explain their higher abundances (Ellis 1970). That they have been seen colonizing salmon carcasses in the study region supports this hypothesis (Johnston et al. 2004).

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 contrasts 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

grazer abundances decreased while 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). High discharge events following spawning are rare in our streams, 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). Salmon nutrient retention may therefore 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 density or by stream habitat variables alone. Although salmon density was correlated with family level invertebrate diversity, stream habitat variables better explained variation in the response variable. The explicit incorporation of habitat variables that affect invertebrate community dynamics can reduce the risk of overestimating the ecological role of salmon in comparative studies. Further, if there is still a signal from salmon density, inference about their ecological role across large spatial and temporal scales holds greater weight.

Although this study cannot yet be generalized across regions and salmon species, the results are based on a large spatial comparison that suggests that increasing the abundance of spawning salmon can correspond with increased invertebrate abundance, including heptageniid mayflies, chironomid midges 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 can have persistent ecological consequences, likely as a result of nutrient retention within the ecosystem. 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). Further, as emerging adult aquatic insects can provide an important nutrient pulse to riparian ecosystems (Richardson et al. 2010; but see Francis et al. 2006), our findings highlight how one resource subsidy can influence another. 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).

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APPENDIX A

Table A1. Watershed characteristics, sampling date, and 2006 salmon density for the 21 study streams.

Stream	Order	Magnitude	Length (km)	Bankfull Width (m)	Sampling Date (2007)	2006 Salmon Density (fish m ⁻²)
10 Mile	2	2	5.91	4.19	20-Jul	0
15 Mile	3	14	18.5	11.64	23-Jul	0.024
25 Mile	2	6	17.59	9.04	25-Jul	0
Ankwill	4	44	27.37	30.53	1-Aug	0.060
Bivouac	3	10	17.52	8.07	9-Jul	0.026
Crow	2	4	10.43	9.04	3-Jul	0.010
Die Hard	2	4	7.79	12.01	22-Jul	0
Forfar	3	13	15.35	7.31	28-Jul	0.285
Forsythe	4	36	25.72	13.15	31-Jul	0.005
French	3	25	23.54	9.81	2-Aug	0
Frypan	4	59	26.86	18.14	31-Jul	0.001
Gluskie	3	13	18.54	11.35	10-Jul	0.257
Hooker	2	2	6.61	3.67	1-Jul	0
Kynock	4	27	11.88	13.23	29-Jul	0.210
Leo	3	14	20.83	9.23	4-Jul	0.001
Maclaing	3	10	22.34	8.18	26-Jul	0.008
Narrows	2	6	19.71	15.51	14-Jul	0.071
Sandpoint	3	12	20.11	9.85	18-Jul	0
Shale	3	7	17.11	9.85	24-Jul	0.052
Sinta	2	20	19.52	11.06	3-Jul	0.003
Van Decar	3	14	10.61	8.28	12-Jul	0.317

Note: Magnitude is the number of first order tributaries in the watershed.

APPENDIX B

Table B1. Study site habitat characteristics across the 21 streams.

Habitat Characteristic	Mean	Range
Gradient (%)	2.1	0.6–5.8
Water Depth (m)	0.13	0.08–0.22
Temperature - Maximum Weekly Average Temperature (°C)	11.2	8.5–13.9
Light: Canopy Cover (%)	44	5–80
Substrate Size: Geometric Mean of Substrate Intermediate Axis Diameter (cm)	6.0	2.8–9.4
pH	7.7	7.2–8.2
Conductivity (µS/cm)	89	28–194

APPENDIX C

Table C1. Environmental variables ranked by the sum of AICc model weights ($\sum w_i$) across linear regression models of all variable combinations for each response variable (listed in Table 2).

Response Variable	Explanatory Variable	$\sum w_i$
Total Invertebrate Abundance	Temperature	0.88
	pH	0.62
	Light	0.48
	Substrate Size	0.35
	Watershed Size	0.23
	Gradient	0.18
	Depth	0.14
Family Level Diversity	Gradient	0.79
	Substrate Size	0.62
	Watershed Size	0.24
	Temperature	0.22
	Depth	0.17
	Light	0.17
	pH	0.16
Heptageniidae Abundance	Substrate Size	0.83
	Temperature	0.48
	pH	0.39
	Gradient	0.30
	Light	0.24
	Watershed Size	0.18
	Depth	0.16
Chloroperlidae Abundance	Temperature	0.87
	Substrate Size	0.60
	Watershed Size	0.31
	pH	0.30
	Light	0.23
	Gradient	0.22
	Depth	0.18
Chironomidae Abundance	Temperature	0.86
	pH	0.75
	Light	0.30
	Gradient	0.19
	Watershed Size	0.18
	Depth	0.16
	Substrate Size	0.15

Note: The top two variables were included in the main analyses.

APPENDIX D

Table D1. Full results of model selection using AICc for 15 linear regression models that describe i) total invertebrate abundance (number m⁻²), ii) family level diversity (Simpson's Reciprocal Index), iii) Heptageniidae abundance, (number m⁻²), iv) Chloroperlidae abundance (number m⁻²), and v) Chironomidae abundance (number m⁻²). Table headings are as described in Table 2. Salmon density was square-root transformed in all models.

Model	K	R ²	ΔAICc	w _i	ER
i) Total Invertebrate Abundance (number m ⁻²)					
Temperature + Salmon Density	4	0.48	0.00	0.37	1.00
Temperature + pH	4	0.45	1.24	0.20	1.86
Temperature + Salmon Density + pH	5	0.52	1.79	0.15	2.45
Temperature + Salmon Density + Sampling Date	5	0.49	3.27	0.07	5.12
Temperature	3	0.30	3.38	0.07	5.41
Temperature + pH + Sampling Date	5	0.46	4.47	0.04	9.35
Temperature + Salmon Density + pH + Sampling Date	6	0.53	5.47	0.02	15.41
pH	3	0.21	5.83	0.02	18.47
Salmon Density	3	0.19	6.33	0.02	23.66
Temperature + Sampling Date	4	0.30	6.36	0.02	24.02
Salmon Density + pH	4	0.27	7.37	0.01	39.87
pH + Sampling Date	4	0.21	8.87	0.00	84.43
Salmon Density + Sampling Date	4	0.20	9.30	0.00	104.62
Sampling Date	3	0.01	10.64	0.00	204.85
Salmon Density + pH + Sampling Date	5	0.27	10.81	0.00	223.00
ii) Family Level Diversity (Simpson's Reciprocal Index)					
Gradient + Substrate Size	4	0.45	0.00	0.28	1.00
Gradient	3	0.31	1.57	0.13	2.19
Gradient + Sampling Date	4	0.39	1.97	0.11	2.68
Gradient + Salmon Density	4	0.38	2.31	0.09	3.18
Gradient + Substrate Size + Salmon Density	5	0.47	2.47	0.08	3.44
Gradient + Substrate Size + Sampling Date	5	0.47	2.52	0.08	3.53
Gradient + Sampling Date + Salmon Density	5	0.46	3.03	0.06	4.55
Substrate Size	3	0.25	3.38	0.05	5.43
Substrate Size + Salmon Density	4	0.31	4.48	0.03	9.42
Salmon Density	3	0.18	5.17	0.02	13.30
Gradient + Substrate Size + Sampling Date + Salmon Density	6	0.50	5.24	0.02	13.72
Substrate Size + Sampling Date	4	0.26	6.13	0.01	21.47
Sampling Date + Salmon Density	4	0.25	6.33	0.01	23.69
Substrate Size + Sampling Date + Salmon Density	5	0.33	7.38	0.01	40.10
Date	3	0.08	7.53	0.01	43.14
iii) Heptageniidae Abundance (number m ⁻²)					
Substrate Size + Temperature + Salmon Density	5	0.52	0.00	0.23	1.00
Substrate Size + Temperature	4	0.42	0.47	0.18	1.27
Substrate Size + Salmon Density	4	0.39	1.59	0.10	2.22
Substrate Size	3	0.29	1.59	0.10	2.22
Temperature + Salmon Density	4	0.39	1.77	0.09	2.42
Salmon Density	3	0.24	3.27	0.04	5.12
Salmon Density + Sampling Date	4	0.34	3.36	0.04	5.35
Temperature + Salmon Density + Sampling Date	5	0.44	3.44	0.04	5.58
Substrate Size + Temperature + Salmon Density + Sampling Date	6	0.53	3.61	0.04	6.07
Substrate Size + Temperature + Sampling Date	5	0.43	3.85	0.03	6.84
Substrate Size + Salmon Density + Sampling Date	5	0.42	3.91	0.03	7.06
Substrate Size + Sampling Date	4	0.32	4.03	0.03	7.48
Temperature	3	0.15	5.41	0.02	14.94
Sampling Date	3	0.11	6.39	0.01	24.38
Temperature + Sampling Date	4	0.21	6.96	0.01	32.54
iv) Chloroperlidae Abundance (number m ⁻²)					
Salmon Density + Temperature	4	0.50	0.00	0.51	1.00
Salmon Density	3	0.34	2.15	0.18	2.93
Salmon Density + Temperature + Substrate Size	5	0.50	3.37	0.10	5.39
Salmon Density + Temperature + Sampling Date	5	0.50	3.62	0.08	6.10
Salmon Density + Sampling Date	4	0.36	4.80	0.05	11.01
Salmon Density + Substrate Size	4	0.35	5.24	0.04	13.71
Salmon Density + Temperature + Substrate Size + Sampling Date	6	0.51	7.44	0.01	41.18
Temperature	3	0.13	7.74	0.01	47.94
Salmon Density + Substrate Size + Sampling Date	5	0.36	8.42	0.01	67.22
Temperature + Substrate Size	4	0.21	9.00	0.01	90.16
Substrate Size	3	0.06	9.29	0.00	104.04

Table D1. Continued.

Model	K	R ²	ΔAICc	w _i	ER
Sampling Date	3	0.03	10.06	0.00	152.89
Temperature + Sampling Date	4	0.13	10.87	0.00	229.85
Temperature + Substrate Size + Sampling Date	5	0.22	12.30	0.00	468.25
Substrate Size + Sampling Date	4	0.07	12.38	0.00	488.27
v) Chironomidae Abundance (number m ⁻²)					
Temperature + Salmon Density	4	0.47	0	0.29	1.00
Temperature + pH	4	0.47	0.16	0.27	1.08
Temperature + Salmon Density + pH	5	0.53	1.14	0.16	1.77
Temperature	3	0.29	3.13	0.06	4.79
Temperature + Salmon Density + Sampling Date	5	0.48	3.15	0.06	4.84
Temperature + pH + Sampling Date	5	0.48	3.24	0.06	5.06
Temperature + Salmon Density + pH + Sampling Date	6	0.54	4.65	0.03	10.24
pH	3	0.24	4.78	0.03	10.91
Temperature + Sampling Date	4	0.3	6.04	0.01	20.50
Salmon Density	3	0.19	6.09	0.01	20.99
Salmon Density + pH	4	0.28	6.57	0.01	26.66
pH + Sampling Date	4	0.24	7.85	0.01	50.76
Salmon Density + Sampling Date	4	0.19	9.11	0	95.33
Salmon Density + pH + Sampling Date	5	0.28	10.05	0	152.13
Sampling Date	3	0	10.33	0	174.98