Pulsed salmonfly emergence and its potential contribution to terrestrial detrital pools

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Abstract

Adult aquatic insects are a globally important subsidy in terrestrial food webs. However, our understanding of their importance is largely limited to studies that measure predation of live insects by terrestrial predators. Yet the flux of adult aquatic insects to terrestrial detrital pools may also be an important subsidy pathway, particularly in cases where insect production exceeds the consumption capacity of predators. We used empirical measures of giant salmonfly (Pteronarcys californica) emergence from 37 sites to model potential detrital deposition in nearshore riparian soil food webs. Typically, giant salmonflies emerge en masse for one week each year, and can be locally superabundant. Median detrital deposition by salmonflies ranged between 0.4 to 0.7 gC, 0.04 to 0.09 gN, and 0.002 to 0.005 gP/m²/yr, depending on whether 25% or 100% of available salmonflies entered detrital pools. For a small number of sites with large salmonfly populations, deposition equaled or exceeded annual secondary production of terrestrial insects, annual atmospheric N deposition, and annual atmospheric P deposition. The fact that these values rival yearly nutrient budgets is particularly striking because giant salmonfly deposition represents a subsidy from a single species emerging over a single week. The consequences of this deposition in terrestrial food webs are largely unknown, but it is likely that
salmonflies can have important effects on nearshore soil nutrient budgets similar in magnitude to those of other important ecosystem processes.

**Keywords** salmonflies; aquatic-terrestrial subsidies; *Pteronarcys*; detrital pools; insect emergence

**Graphical Abstract (add)**

Giant salmonflies (*Pteronarcys californica*) that died during emergence due to high water contribute aquatic-derived nutrients to terrestrial detrital pools (Photo Credit: Heidi Anderson).
Introduction

Ecological subsidies are fluxes of energy, materials, and nutrients that enhance populations in recipient food webs (Polis et al., 1997). They are nearly ubiquitous across ecosystems, and are particularly well-studied as fluxes across the freshwater-terrestrial boundary (Baxter et al., 2005; Richardson and Sato, 2015). In these systems, fluxes are reciprocal in the sense that the movement of terrestrial production to freshwater ecosystems, such as insect and leaf infall, is reciprocated by the movement of aquatic production to terrestrial ecosystems, such as emerging aquatic insects (Nakano and Murakami, 2001; Bartels et al., 2012; Muehlbauer et al., 2014).

The vast majority (>95%; Jackson and Fisher, 1986) of emerging aquatic insect mass does not return to the stream, but instead remains in the terrestrial ecosystem. However, the fate of that mass in terrestrial food webs is unresolved. Emerging aquatic insects can represent a large percentage of annual energy budgets for terrestrial consumer populations (Nakano and Murakami, 2001), but can also contribute substantial inputs to terrestrial detrital pools (Hoekman et al., 2011; Dreyer et al., 2015). Contributions to detrital pools may be especially important during mass emergence, in which large numbers of aquatic insects emerge over short time periods, representing a pulsed resource subsidy (Nowlin et al., 2008; Yang et al., 2010). During such pulses, consumers can become rapidly satiated, leaving the remainder of the subsidy to enter detrital pools (Yang, 2004).

One particularly striking example of a highly pulsed resource subsidy is the emergence of Pteronarcys californica (Order: Plecoptera) (Walters et al., 2018), a large stonefly commonly known as the giant salmonfly (Stark et al., 1998). Its geographic distribution in North America includes rivers draining mountain ranges found in Alaska, Arizona, British Columbia, California,
Colorado, Idaho, Montana, Mexico, New Mexico, Oregon, Utah, Washington, and Wyoming (Baumann et al., 1977; Stewart and Stark, 2002; Stewart and Oswood, 2006). This iconic insect emerges en masse from rivers in the western U.S., and is important to recreational anglers, because trout become highly active feeders during the giant salmonfly emergence. Because of their large size relative to other aquatic insects and their short emergence period (1-week), adult giant salmonflies represent a potentially large contribution of aquatic-derived energy and nutrients to nearshore terrestrial detrital pools. At productive sites, a single week of salmonfly emergence can equal or exceed the total annual emergence biomass of streams that do not have salmonflies (Walters et al., 2018). For example, salmonfly production at one site in the Colorado River was 49 gC per meter of stream bank per year (Walters et al. 2018). Using river width as a proxy of emergence production (Gratton and Vander Zanden, 2009), the predicted amount of total insect emergent production at this site should be only 18 gC/m/yr. In other words, observed giant salmonfly emergence was more than twice as large as the expected total annual emergence production.

In this study, we used direct measurements of annual giant salmonfly emergence from Walters et al. (2018) to model the amount of aquatic-derived carbon, nitrogen, and phosphorous that salmonflies could transfer to terrestrial detrital pools. Our results indicate the potential for salmonflies to contribute substantial amounts of nutrients to nearshore terrestrial detrital pools, in some cases exceeding atmospheric nitrogen deposition and terrestrial insect secondary production.

**Methods**

*Direct measurements of salmonfly emergence*
We measured giant salmonfly emergence from 37 total sites (square symbols, Figure 1) across five river basins over four years using depletion sampling of salmonfly exuviae for a total of 71 samples (Walters et al., 2018). Mean ash free dry mass (AFDM) of exuviae and adults was measured separately for males and females for all five study rivers (range of n = 12-49 for each combination of sex and river (Table S3 in Walters et al., 2018). Salmonfly C content was calculated as 0.5 × AFDM. This resulted in 71 estimates of giant salmonfly emergence in units of grams of carbon per linear meter of stream bank per year (gC/m/yr).

Analysis

To model mean salmonfly flux across our sample sites, we used an intercept-only Bayesian generalized linear mixed model. The response variable was salmonfly flux (gC/m/yr), with river, site, and year as random effects. Because the data were continuous and non-negative, we used a gamma likelihood with a log-link. To account for samples with zero emergence (n=4/71 samples), we added 0.01 to each site with zero emergence. We chose this model because it incorporated multiple sources of uncertainty in the mean amount of salmonfly emergence among rivers, sites, and years. In addition, it allowed us to use this uncertainty to make predictions of salmonfly emergence at sites other than our sample sites (see below).

We specified the model in R (version 3.4.2, R Core Team, 2017) using the brms package (Bürkner, 2017), which generates the posterior distribution using Hamiltonian Monte Carlo via rstan (Stan Development Team, 2016). A more complete description of model specifications, including choice of priors, evaluations of prior influence, and model checking, is provided in the Supplementary Material. The data and R code are freely available at https://github.com/jswesner/salmonflies.
**Estimates of deposition**

The model described above generated the posterior distribution of giant salmonfly C flux per linear meter of stream, but we needed to convert that result to units of gC per square meter of riparian land per year (gC/m\(^2\)/yr). To do this, we first separated the flux into the proportion composed of exuviae versus adults. This was necessary because the fate of exuviae and adults differs. For example, we assumed that 100% of exuviae entered detrital pools within ~1m from the stream bank, based on personal observation and on the life-history of salmonflies (Rockwell and Newell, 2009). In contrast, adults can disperse and will enter detrital pools at variable rates of mortality and distance from the stream (see below). To separate salmonfly flux into exuvia and adult proportions, we used paired exuvia and adult weights from 116 females and 186 males (Table S3 in Walters et al., 2018) to determine the average proportion of flux that was composed of exuviae. We then subtracted that proportion from each iteration of the posterior distribution of flux, resulting in a posterior distribution of exuviae and adults.

To determine the spatial distribution of adults, we used information from Muehlbauer et al. (2014), who estimated that adult stoneflies rapidly decrease in abundance with distance from the stream, such that 50% of stonefly emergence remains within 2.7 m of the stream bank (estimated from a negative power curve). Thus, to convert our measure of adult salmonfly flux (gC/m/yr) to potential riparian deposition (gC/m\(^2\)/yr), we divided each iteration of the posterior distribution of adult flux by 2 (to get 50%), and then divided that result by 2.7. This gave us an estimate of the amount of adult salmonfly deposition (g/m\(^2\)/yr) that could be expected within 2.7 m of the stream bank. This distance (2.7 m) was chosen as a simplification to allow us to estimate deposition within a fixed area. At any given site, the distance at which 50% of
salmonflies are deposited is likely to vary, so should be measured directly in future studies. However, we assume that this distance will capture an ecologically important amount of salmonfly abundance most of the time, because it is derived from a power curve (Muehlbauer et al. 2014). In other words, the remaining 50% of salmonfly abundance would be increasingly spread over larger distance, making it unlikely that deposition would be concentrated in an ecologically meaningful amount with increasing distances from the stream.

Because the proportion of salmonflies that enter detrital pools is unknown, we multiplied our estimates of adult deposition by 1, 0.75, 0.5, and 0.25, representing four different scenarios in which 100%, 75%, 50%, or 25% of available adult salmonflies (i.e. 50% of the total flux) enter detrital pools. We then added the exuvia mass to each of these scenarios to derive a posterior distribution of the total deposition of salmonflies (exuvia + adults) to the detrital pool (e.g. gC/m²/yr). These cutoffs (25-100%) were arbitrary, but represent likely ranges of deposition under variable conditions. For example, up to 7% of salmonflies died during emergence and entered the detrital pool along the Madison and Gallatin Rivers (Montana, USA) (H. Anderson, Personal communication). Assuming that a small proportion of successfully emerged adults continue to enter the detrital pool, our low estimate of 25% deposition seems reasonable. Alternatively, while it is unlikely that 100% of adult aquatic insects enter detrital pools, this value has been assumed in a previous study (Dreyer et al., 2015), thereby allowing us to compare our results to previous work and providing an upper limit on potential deposition.

In addition to fluxes of carbon (C), we also calculated fluxes of nitrogen (N) and phosphorous (P) by converting C units to N or P using published stoichiometric ratios of 6.3 for adult insect C:N and 124 for C:P (Elser et al., 2000). For the exuviae, we assumed that C and N in exuviae contained 65% of C and N in adults, based on exuvia-adult comparisons from cicadas
in Callaham et al. (2000). We also assumed that P represented the same proportion (65%),
though we are unaware of empirical measurements of this reported in the literature. It should be
noted that exuviae of beetles and cicadas contain 15-40% chitin (Liu et al. 2014), which does not
contain phosphorous. Therefore, assuming that salmonfly exuviae have similar chitin
percentages as other insects, our estimate of P might be affected by the proportion of chitin in
exuviae. However, the absolute amount of error produced by chitin is likely small, since exuviae
only represent ~13% of total emergence weight, and chitin is presumably less than half of that
(i.e. <6.5% of the total emergence weight).

Predicting deposition for new sites

The posterior distribution of the intercept from the above model (and its derived
quantities of deposition) represents uncertainty in mean salmonfly deposition across our sample
sites, which we report as the fitted estimate. However, giant salmonflies are widely distributed in
western U.S. rivers (Figure 1), and we were interested in generating a prediction of salmonfly
deposition at new, as yet unsampled, sites. To do this, we used the predict() function in the brms
package. This generated a posterior predictive distribution that simulated likely deposition values
at a new site (Hobbs and Hooten, 2015). The predictive distribution has a nearly identical median
as the fitted distribution, but has wider credible intervals because it incorporates uncertainty
using the standard deviation of the random effects terms for river, site, and year.

Results

Salmonfly deposition in riparian detrital pools
Assuming that 100% of available salmonflies enter detrital pools, modeled deposition ranged 1-3 orders of magnitude across individual sites, from 13 gC, 1.7 gN, and 0.09 gP/m²/year at one site on the Colorado River (Pumphouse) to <0.2 gC, <0.004 gN, and <0.0001 gP at another site on the Colorado River (Hwy 40 Bridge) (Figure 2).

Across all sites, the median of the posterior distribution of giant salmonfly deposition was 0.67 gC, 0.09 gN, and 0.005 gP/m²/yr (assuming 100% enters detrital pools; Table 1). If only 25% entered the detrital pool, the median deposition was 0.38 gC, 0.05 gN, and 0.005 gP/m²/yr (Table 1). The uncertainty of these estimates (95% credible intervals) ranges from nearly zero deposition for all elements up to a maximum of 1.6 gC, 0.22 gN, and 0.01 gP/m²/yr (assuming 100% deposition) (Figure 3).

Predictions for new sites

Predicted deposition at new sites revealed nearly identical median estimates of C, N, and P as for the fitted estimates above (Figure 3). However, given the wide variation in flux among sites, rivers, and years, the uncertainty in these predictions is large (Figure 3). For example, the 95% credible intervals (assuming 100% of flux enters the detrital pool) ranged up to three orders of magnitude (0.01 to 13 gC/m²/yr; 0.02 to 1.8 gN/m²/yr, and 0.0001 to 0.09 gP/m²/yr) (Table 1).

Discussion

The most important result of this study is that giant salmonflies represent a potentially substantial transfer of C, N, and P from aquatic ecosystems to nearshore terrestrial detrital pools. For example, potential salmonfly N and P deposition exceeded annual atmospheric deposition (Li et al. 2016) at some sites under all scenarios, even under the assumption that only 25% of
available salmonflies would enter detrital pools. In addition, the median carbon deposition by salmonflies of up to 0.7 gC/m²/yr was three orders of magnitude larger than the mean deposition of aquatic insects from rivers in Wisconsin (0.004 gC/m²/yr; Bartrons et al., 2013). It is worth noting that the estimate from Bartrons et al. (2013) represents deposition across a 100 meter buffer around streams, compared to our estimate that 50% of available salmonflies are deposited within 2.7 m of the stream. If we assume that the entirety of salmonflies is deposited within 100 m of the stream and ignore the changes in density with distance from the stream via decay functions (as in Bartrons et al. 2013), then our estimate would still be ~0.07 gC/m²/yr, an order of magnitude higher than the Bartrons et al. (2013) estimate. These results are particularly striking because they indicate that salmonflies could transport more than a year’s worth of nutrients in a single week, whereas nutrient transport by aquatic insects in most other temperate systems occurs over 3-4 months.

Dreyer et al. (2015) reported that chironomid midges emerging from Lake Mývatn, a hyper-productive lake, contributed between 0.4 to 10 gN/m²/yr within 50 m of the shore (assuming 100% of available midges entered the detrital pool). These values exceed our median estimate of giant salmonfly deposition (0.09 gN/m²/yr), though it is worth noting that the emergence period for midges at Lake Mývatn and surrounding lakes lasts for four months, nearly 16 times longer than the one-week emergence period for salmonflies. Moreover, nearby lakes with smaller midge populations contribute ~1% of that in Mývatn, or ~0.1 gN/m²/yr Bultman et al., 2014). For terrestrial insects, cicadas (*Magicicada cassini*) have an emergence phenology similar to salmonflies. Whiles et al., (2001) reported that 87% of cicadas emerged over 9 days at Konza Prairie Research Natural Area, representing a transfer of N from belowground to aboveground habitats that ranged from 40 to 200% of atmospheric N deposition (wet + dry).
While they did not measure the percentage of this flux that enters detrital pools as dead organic matter (as opposed to being eaten by consumers or dispersing), it was likely to be substantial due to consumer satiation in the presence of large resource pulses (Williams et al., 1993; Nowlin et al., 2008). By comparison, our model predicted that giant salmonfly deposition is likely to range from ~0 to 485% of atmospheric N deposition. This relatively large contribution of annual N deposition by cicadas and salmonflies exists even though the absolute mass of an average salmonfly pulse (~0.3 gC/m²/yr from water) is smaller than an average cicada pulse (~3 gC/m²/yr from land at Konza Prairie, estimated as 0.5 x AFDM in Whiles et al. (2001). The reason for this is that salmonflies occur in semi-arid areas of the western U.S. which have substantially lower atmospheric deposition rates than the central or eastern U.S. (Li et al., 2016), such that relatively small pulses of nutrients can have large impacts on local nutrient budgets.

We also compared giant salmonfly deposition to that of salmon carcasses, which represent another well-known transfer of freshwater or marine nutrients to riparian soils along coldwater rivers. For example, at two streams in western Washington (USA), Bilby et al. (2003) reported that between 22 and 3000 gN/m of stream bank were transferred to riparian soils. That far exceeds our median of 0.4-0.7 gN/m of stream from salmonflies. In terms of deposition, Gende et al. (2007) estimated that salmon carcasses contribute 0.7 to 6.9 gN/m²/yr in a riparian forest in Alaska. While this is an order of magnitude higher than our median of 0.09 across all sites (assuming 100% enter the detrital pools), three sites we sampled in the Colorado River had large salmonfly fluxes that would exceed 0.7 gN/m²/yr, with the highest measured site being 1.4 gN/m²/yr. Even if 25% of the total flux of salmonflies entered the detrital pool, this would still equal the low estimate of salmon carcass deposition rates.
Whether the input of salmonfly nutrients to riparian soils affects food webs structure or ecosystem function remains to be tested. However, the experimental addition of insect carcasses to terrestrial soil food webs can increase plant foliar quality (Bultman et al., 2014), increase plant growth (Yang, 2013), increase herbivore densities and rates of herbivory (Yang, 2008; Bultman et al. 2014), increase densities of detritivores, soil bacteria, and fungi (Yang, 2004; Yang and Gratton, 2014), and alter community composition of arthropods (Hoekman et al., 2011). The effects of salmonflies on these processes will depend not only on salmonfly abundance, which is highly variable, but also on local conditions such as the presence of predators, local nutrient conditions, and availability of alternative terrestrial resources. For example, atmospheric deposition in the central Rocky Mountains is ~0.4 gN/m$^2$/yr, but declines by more than half in other areas of the western U.S. (Li et al., 2016). Large salmonfly populations may therefore represent an even more important source of nutrients in some regions than in the central Rocky Mountains, where our sites were located. Finally, the availability of alternative resources, such as terrestrial secondary production, is also spatially variable and difficult to predict. However, using conversion rates based on satellite imagery of primary production in Wisconsin, Bartrons et al. (2013) estimated that secondary production of terrestrial insects was 0.02 to 0.44 gC/m$^2$/year. These are likely higher estimates than expected in the arid western areas where salmonflies occur, indicating that median salmonfly deposition rates of ~0.37 to 0.66 gC/m$^2$/yr (depending on whether 25 to 100% of available salmonflies enter detrital pools) are almost certain to exceed terrestrial secondary production. Similarly, mean atmospheric deposition of phosphorous is 0.029 gP/m$^2$/yr, but with a standard deviation of 0.039 (Tipping et al., 2014), indicating wide spatial variation that would approximate our estimates of salmonfly P deposition.
As with any modeling study, we made several assumptions that could affect estimates of giant salmonfly deposition in riparian ecosystems. For example, we assumed that 50% of salmonflies remain with 2.7 m of the stream bank. This is based on a negative power curve for stoneflies in general (Muehlbauer et al., 2014). However, the lateral distribution of salmonflies could vary widely depending on the behavior of salmonflies and the weather conditions during emergence. If weather-induced mortality is high (e.g. Rockwell and Newell, 2009), then the distribution of salmonflies is likely to be restricted to areas with ~1 m of the stream bank, which would more than double the estimates of deposition we provided here. Other sources of uncertainty, such as variation across populations, sites, and years were incorporated into our models. Thus, we feel confident that the range of values predicted here are reasonable estimates of giant salmonfly deposition across their range. In addition, our results reflect estimates derived from biomass, yet ecologists have recently recognized that fluxes of aquatic insects can have disproportionately large effects on riparian food webs relative to their biomass, because subsidy quantity is not necessarily a proxy for subsidy quality (Marcarelli et al., 2011). For example, adult aquatic insects often obtain essential fatty acids from algae that are not available to similarly sized terrestrial insects, making them important sources of fatty acids for terrestrial consumers (Gladyshev et al., 2009).

Our goal is that this modeling study spurs direct measurements of aquatic insect deposition into the terrestrial detrital pool and more investigations of the consequences of these inputs for riparian food webs. Direct measurements of these inputs and their effects are lacking for adult aquatic insects. Yet their effects may be particularly important within our study region as salmonflies are declining in some areas of the western U.S. (Stagliano and Program, 2010; Nehring et al., 2012; Walters et al., 2018; Anderson et al., Unpublished results). As is true for
many species of insects, the ecosystem-level consequences of this loss are largely unknown. Historically, insects are assumed to be of small importance to ecosystem processes due to their small relative biomass in ecosystems (Yang and Gratton, 2014). Our results appear to contradict this assumption (see Yang and Gratton, 2014 for other similar contradictions), indicating that emergence of salmonflies, and their potential mass death, can be locally superabundant at levels that rival other important ecosystem processes, such as atmospheric N deposition and secondary production of terrestrial insects.

Acknowledgments
We thank numerous technicians for help in collecting samples and raising larvae in the lab. The ideas in this manuscript benefited from discussions with L. Albertson and C. Baxter. This research was subjected to USGS review and approved for publication. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Tipping, E., Benham, S., Boyle, J.F., Crow, P., Davies, J., Fischer, U., Guyatt, H., Helliwell, R.,


Table 1. Model results for giant salmonfly deposition to terrestrial detrital pools. Values represent the expected deposition within 2.7 m of the stream bank, summarized as the median (50%) and upper and lower 95% credible intervals from the posterior distribution. Fitted values represent estimates of the deposition among sampled sites. Predicted values represent deposition expected at new sites. Percent deposition represents a range of possible deposition rates in which 25, 50, 75, or 100% of salmonflies enters the detrital pools.

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Figure 1. General distribution of *Pteronarcys californica* in the western U.S. (excluding Alaska) based on selected studies. Squares represent sites for which flux estimates (gC per meter of stream bank per year) were sampled via exuviae collections (Walters et al., 2018). Circles represent county level collection records from a study of the stoneflies of the Rocky Mountains (Baumann et al., 1979). Triangles represent collection records from sites sampled by the U.S. Geological Survey as part of the National Water-Quality Assessment Project of the National Water-Quality Program (1993-2017).
Figure 2. Potential contribution of carbon (C), nitrogen (N), and phosphorous (P) to riparian ecosystems via detrital pathways of salmonfly emergence. Values represent the amount of detrital deposition within 2.7 m of the stream bank, which is assumed to represent 50% of total emergence (Muehlbauer et al., 2014). Each dot is an estimate of deposition from 71 field samples across 37 sites from five rivers. Values are plotted for four scenarios based on the assumption that between 25-100% of total available insects enters detrital pools. For C, the horizontal reference lines indicate terrestrial secondary production in Wisconsin (Bartrons et al., 2013). For N, the thick horizontal line represents mean atmospheric deposition of dissolved inorganic N in the Rocky Mountains. The thin lines represent the range of atmospheric deposition across individual sites (Burns 2003). For P, the line indicates median total P deposition in the United States (Tipping et al., 2014).
Figure 3. Posterior distributions of the deposition of carbon (C), nitrogen (N), and phosphorous (P) within 2.7 m of the stream bank. The fitted result represents uncertainty in the mean among the sample sites. The predicted distribution represents uncertainty in the prediction of deposition at new (i.e., unsampled) sites. Results are shown across four scenarios in which 100, 75, 50, or 25% of available flux enters the detrital pool (see Table 1 for a full summary of fitted and predicted values).
Supplementary Material

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Bayesian model specifications

We used a weakly informative prior for the intercept with a normally distributed mean of 3.6 and a standard deviation of 1.5. The mean was chosen to reflect the mean emergence reported for global rivers (39 gC/m/yr, which is 3.6 after log-transforming) in Gratton and Vander Zanden (2010). The standard deviation was chosen to encompass all values reported in Gratton and Vander Zanden (2010) within at least 2 standard deviations. In other words, a value of 3.6 + two standard deviations is 3.6 + 3 = 6.6, which exponentiates to 735 gC/m/yr, encompassing the highest reported yearly emergence values from Gratton and Vander Zanden (2010) of 298 gC/m/yr. The prior for the standard deviations was a half-cauchy: Cauchy(0,1) (McElreath et al. 2016).

The model contained four chains with 5000 iterations each, discarding the first 2500 iterations as warm-up. We verified model convergence by ensuring all r-hats were <1.1 (Gelman and Rubin 1992), and we used posterior predictive checks to ensure that the model was specified correctly and could produce replicated data sets that resembled the actual data set (Hobbs and Hooten 2015). We assessed prior influence by plotting the prior versus posterior distributions (Figure S1). We also re-ran the model with different priors for the intercept, specifying either a wider standard deviation or a smaller mean (Figure S2). The results were robust to different prior specifications, indicating that most of the inference comes from the data, no the prior.
Figure S1. Comparison of the prior and posterior distributions for the intercept for the model described in the text to estimate giant salmonfly flux and subsequent deposition. The difference in the prior and posterior distribution indicates a minimal of the prior on the outcome.
Figure S2. Parameter estimates from models with three different prior specifications of the intercept. Similarity in the estimates from all parameters indicates little influence of the alternative prior specifications on the model results. Note that the results in light grey, containing a normally distributed prior with mean = 3.6 and sd = 6 (i.e. double the sd used in final model) did not converge, so the actual parameter estimates are not accurate.