Effects of spawning salmon on the size spectra of stream insect communities

by

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Abstract

Spawning Pacific salmon disturb stream ecosystems through their spawning behaviour and subsidize them via nutrients from carcasses. To further understand the net effects of spawning salmon in streams, I examined size distributions (size-spectra) of stream insect communities across a salmon density gradient. This size-based method offers a novel, ecologically meaningful way to understand the net effects of salmon in stream ecosystems. I used a Before-(during)-After, Control-Impact observational approach in 15 streams along the central coast of British Columbia to determine how slopes and intercepts of stream insect biomass size-spectra change before, during, and after a fall salmon run. I found no effect of salmon density on size spectra intercepts in any season and steeper size-spectra slopes (attributed to greater numbers of smaller insects and fewer larger insects) with increasing salmon density in the fall. These data may indicate differential effects of disturbance and subsidization on stream insect size classes.

Keywords: size-spectrum; biomass; aquatic insects; *Oncorhynchus*; disturbance; subsidy

I dedicate this thesis to my wonderful parents, Laura Waldo and Glenn Walquist

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sense of humor with me. Lastly, thank you to Emily Walquist for accompanying and supporting me during this endeavor.

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1.1. Introduction

Organismal body size is an important determinant of energy flow within communities (Peters 1983, Brown et al. 2004). Metabolism varies significantly with body size, and given the many effects of body size on numerous ecological traits, questions surrounding the structure and function of communities can benefit from considering species body size alongside taxonomic affiliation (Shin et al. 2005, Woodward et al. 2005, White et al. 2007). Body size is an important characteristic in aquatic ecosystems, where indeterminate growth predominates and trophic position generally increases more with ontogenetic changes in size than among species (Jennings et al. 2001, Trebilco et al. 2013).

Community size-spectra, or the ataxonomic representation of the total abundance or biomass of predetermined size classes within a community, are a useful and visually-intuitive tool within ecology (Boudreau and Dickie 1992, Kerr and Dickie 2001, Sprules and Barth 2016). The scaling of body size with abundance and biomass is often predictable, with well-described patterns that have been consistently observed within aquatic ecosystems (Sheldon et al. 1972, Trebilco et al. 2013). Two characteristics of size-spectra that reflect ecological processes within a community are the size spectrum slope, which is driven by relative abundances of smaller and larger organisms, and the intercept. The slope represents both the trophic efficiency and the relative abundances of predators and prey, or the predator-prey mass ratio, within the community and can be used to diagnose energy subsidies. For example, steep negative slopes indicate inefficient transfer of energy across trophic levels (Trebilco et al. 2013). Strongly positive slopes in a biomass size spectrum, where greater mass is observed in larger size classes, can indicate the presence of an energy subsidy when considering the constraints trophic transfer efficiency imposes on size spectra in a closed system (Hocking et al. 2013, Trebilco et al. 2016). The intercept is a measure of the productivity of a community, with higher intercepts observed in more productive ecosystems (Bianchi et al. 2000, Blanchard et al. 2005). The sensitivity of the slope and intercept of size spectra to environmental conditions make them a valuable tool for assessing how

various forms of disturbance or energy subsidies affect communities (Hocking et al. 2013, Guiet et al. 2016, Martinez et al. 2016, Trebilco et al. 2016).

The negative scaling of body size and abundance (typically a slope of -0.75 to -1), and slight positive scaling of body size and biomass (typically a slope of 0 to +0.25) are characteristic of energetically-isolated ecosystems. However, slopes deviating from these ranges can be used to diagnose and measure the magnitude and form of subsidies (Trebilco et al. 2016). Studies of aquatic and terrestrial communities have reported inverted size spectra where both abundance and biomass scale positively with body size, such as kelp forest fish communities that are subsidized by zooplankton from the wider ocean ecosystem (DelGiorgio and Gasol 1995, Trebilco et al. 2016). Transboundary subsidies could explain these cases that appear to break the rules governing body size-biomass relationships. Additionally, if the subsidy is seasonally available, as is often the case with migratory animals, the recipient community's response to the subsidy may also be predictable and measurable.

Organisms that traverse ecosystem boundaries *en masse* represent a significant source of energy that can enter the recipient ecosystem's food web at multiple trophic levels (Walsh et al. 2020). Pacific salmon are iconic migratory fishes that represent one of the greatest transfers of animal biomass from oceans and coastal waters into freshwater streams (Flecker et al. 2010, Walsh et al. 2020). After acquiring more than 95% of their adult body mass in the marine environment, salmon return in a seasonally predictable manner to coastal watersheds where they spawn and die (Watkinson 2000). This semelparous lifestyle provides nutrient-limited watersheds with a supply of marine-derived nutrients shown to subsidize all trophic levels, from stream periphyton and riparian plants to apex predators such as wolves and bears (Wipli et al. 2003, Moore et al. 2008, Hocking and Reynolds 2011, Rüegg et al. 2011, Reimchen and Fox 2013, Walsh et al. 2020). Investigations of various plants and animals in coastal watersheds have shown marine-derived nitrogen signatures or other response signals, indicating that these subsidies are incorporated into stream and riparian ecosystems (Hocking and Reynolds 2011, Holtgrieve and Schindler 2011, Rinella et al. 2013, Tonra et al. 2015). Further, elevated isotopic signatures in subsidized watersheds are known to persist through the following year (Reisinger et al. 2013). In addition to being a seasonal source of limiting nutrients, salmon cause physical disturbance to stream communities as a result of their nest digging behaviour. This scouring of the stream substrate often

depresses benthic populations and biofilm biomass, a basal resource in stream food webs, in spawning reaches (Moore and Schindler 2008, Harding and Reynolds 2014, Rüegg et al. 2020). The subsidization and disturbance caused by salmon is seasonal, with the effects of both diminishing over time as organisms, such as stream-dwelling benthic invertebrates, recolonize disturbed substrate and assimilate and disperse the energy subsidy provided.

It remains a key question as to what the relative effects of the nutrient subsidy and disturbance are on aquatic invertebrate communities and the timing of their decay. Aquatic invertebrates are abundant in the streams in which salmon spawn and have shown various behavioural, phenological, and biomass responses to spawning salmon (Lessard and Merritt 2006, Merritt et al. 2008, Moore and Schindler 2008, Harding and Reynolds 2014). Salmon density has both positive and negative effects on the abundance and biomass of aquatic invertebrates (Verspoor et al. 2011, Campbell et al. 2012, Harding and Reynolds 2014). Specifically, a study along the central coast of British Columbia revealed significant depression of invertebrate biomass in high salmon density streams in both the spring and fall seasons compared to nearby streams with no spawning salmon (Harding and Reynolds 2014). This suggests that the disturbance caused by salmon may offset any subsidy effects such as the direct fueling of specific trophic levels (Harding and Reynolds 2014). Invertebrate biomass has been shown to not return to pre-disturbance levels until the summer following the fall salmon spawning, or to not fully recover to pre-disturbance levels compared to streams with no spawning salmon (Moore et al. 2004, Moore and Schindler 2008, Harding and Reynolds 2014). Marine-derived nitrogen signatures of stream-dwelling invertebrate tissues are elevated in higher salmon density streams, implying an enrichment effect by salmon (Harding and Reynolds 2014). This enrichment effect has also been observed in the spring, when salmon are not present, even though invertebrate biomass remains depressed in higher salmon density streams, suggesting that a short or long-term enrichment effect from salmon subsidies may not offset the disturbance caused to the stream substrates and invertebrate communities during the fall spawning season. These studies suggest that both physical disturbance from spawning behaviour and energy subsidies provided by spawning salmon via carcass deposition are important mechanisms to consider in stream ecosystems. A size-based perspective of stream insect communities will augment our understanding of the cumulative role of Pacific salmon in watersheds by

identifying community-wide and seasonal biomass patterns that may go undetected when using traditional summary metrics such as total community biomass. One useful approach to understand the net effects of subsidies and disturbance on stream community structure is to consider changes to the distribution of biomass across stream insect body size classes using size spectra, while accounting for key habitat variables that are known to influence stream insect biomass (Harding and Reynolds 2014).

I provide a novel assessment to test hypotheses for how stream insects respond to spawning pink and chum salmon in 15 streams along British Columbia's central coast by examining the slopes and intercepts of the normalized biomass size spectra of these stream insect communities. I conducted two observational comparative studies using a Before-(during)-After and Control-Impact approach to evaluate the effect of salmon on aquatic insect size spectra. First, I compare stream insect size spectra in seven streams in the spring before the 2016 salmon run, in 15 streams (including the previous seven) in the fall of 2016 during the peak salmon run, and after in these same 15 streams in the spring of 2017. It is worth noting that these streams receive salmon runs annually, so the spring 2016 "before" period is following the fall 2015 salmon run. However, for the purposes of our observational approach to assessing the effects of a single salmon run, we consider spring 2016 our "before salmon" period. Second, in addition to the 15 streams that I sampled from 2016-2017, I also compared stream insect size spectra above a waterfall or logjam of sufficient height to block the passage of migrating salmon (control) and below (impact) using samples collected by Harding and Reynolds (2014) in five streams in this same region in 2008.

I expect stream insect communities along the central coast of British Columbia to be characterized by negative biomass size spectra, as this pattern has been consistently observed in stream invertebrate communities across studies from various regions (Morin et al. 1995, Martinez et al. 2016, McGarvey and Kirk 2018). In the fall, spawning salmon are expected to reduce insect community biomass, as measured by the size spectrum intercept, and the depressed intercepts would likely persist through the following spring. Disturbance caused by salmon is expected to disproportionately and negatively affect larger insects due to their weaker ability to access interstitial spaces in stream substrates to avoid disturbance, relative to smaller insects, and to their longer life cycles which affects recolonization rates. This will likely result in steeper negative slopes with increasing salmon density in the fall. However, a longer-term fertilization effect from

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salmon carcass deposition may either enhance recruitment or survival (or both) the following spring in streams with greater salmon density. Enhanced recruitment might be detected as higher abundance of smaller size classes resulting in a steepening of the size spectra slope. Enhanced survival might result in higher abundance of larger individuals, resulting in a shallower negative slope. Finally, it is possible that salmon carcass opportunists (e.g., Nemouridae and Chironomidae) may drive changes in size spectra slope and intercept in the fall through increased abundance and in the spring as a result of longer-term subsidization of these specific taxa (Chaloner et al. 2002, Verspoor et al. 2011).

1.2. Methods

1.2.1. Study Sites

This study was conducted on 15 streams (second to fourth order) within 50 km of Bella Bella, BC, Canada within the traditional territory of the Heiltsuk First Nation during the spring (June) of 2016, the fall (September/October) of 2016 and the spring (April/May) of 2017 (Fig. 1). Additionally, five streams in this region were sampled in the spring (May/June) and fall (September/October) of 2008 (Fig. 1). These five streams contain a waterfall or logjam of sufficient height to block the passage of migrating salmon. In the 2008 period, invertebrate samples were taken upstream and downstream of these salmon barriers, providing within-stream comparisons of the effects of salmon which allows us to control for stream-specific variables. While Harding and Reynolds (2014) analyzed total invertebrate biomass upstream and downstream of these barriers in this study, I revisited these invertebrate samples and measured all invertebrates individually to investigate differences in invertebrate size spectrum slope and intercept within-stream and across a salmon density gradient. The spawning length of each stream in both studies is outlined in Table 1. In both studies, I selected streams to cover a sufficient range of spawning salmon densities (0 to 2.3 kg/m^2). The anadromous salmonids that return to these streams each fall primarily consist of Pink (*O. gorbuscha*) and Chum salmon (*O. keta*), with relatively low numbers of Coho (*O. kisutch*) and Sockeye salmon (*O. nerka*). The central coast of BC within the Great Bear Rainforest is characterized by heavy rainfall, coniferous forests, nutrient-poor watersheds, and is minimally impacted by contemporary anthropogenic disturbance.
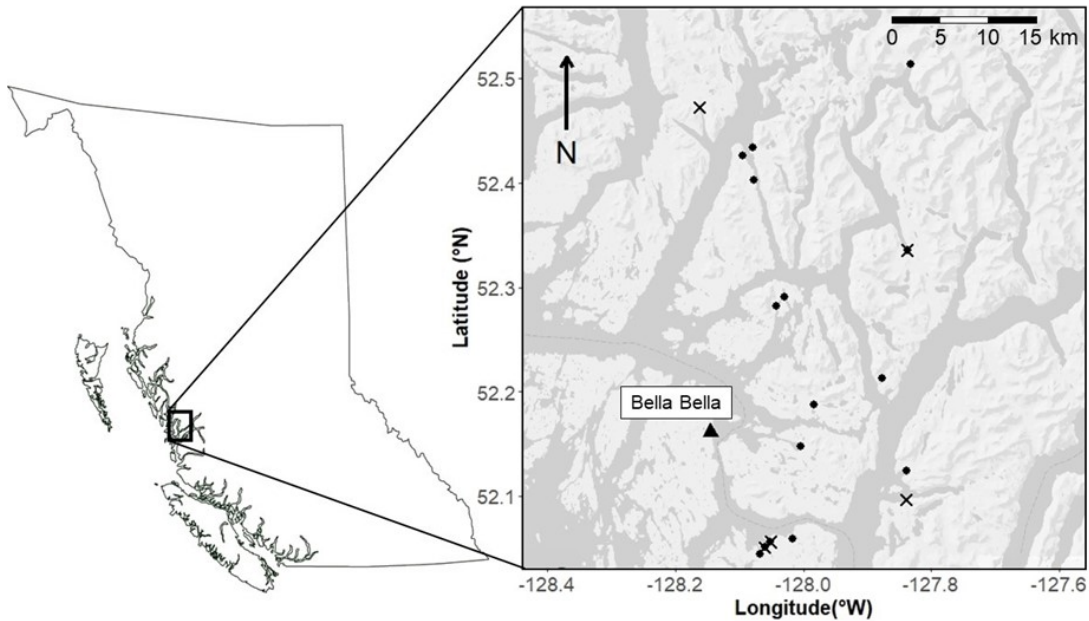
Figure 1.1. **Locations of 15 streams sampled in fall 2016 and spring 2017 (circles) and five streams sampled in spring and fall 2008 (crosses). The location of Bella Bella, BC is shown with the triangle.**

Table 1.1. **Stream-specific data for study sites. Stream location refers to the position of the site relative to any natural salmon barrier (log jam or waterfall) within that site.**

Site	Year sampled	Stream location	Catchment area (km²)	Bankfull width (m)	Spawning length(m)	Salmon density (kg/m²)
Ada	2016-2017	Downstream	9.8	11.1	435	0.97
Ada	2008	Downstream	9.8	11.1	435	0.52
Ada	2008	Upstream	9.7	10.7	0	0
Beales Left	2016-2017	Downstream	6.5	10.9	300	0.50
Bullock Main	2016-2017	Downstream	3.3	10.9	622	0.76
Clatse	2016-2017	Downstream	24.3	22.8	900	1.79
Clatse	2016-2017	Upstream	23.9	17.8	0	0
Clatse	2008	Downstream	24.3	22.8	900	0.51
Clatse	2008	Upstream	23.9	17.8	0	0
Fancy Right	2016-2017	Downstream	9.9	4.8	298	1.13
Fannie Left	2016-2017	Downstream	16.4	12.8	1500	1.04
Fell Creek	2016-2017	Downstream	7	10.9	22	2.30
Goatbushu	2016-2017	Downstream	1.7	7.5	550	0.32
Hooknose	2016-2017	Downstream	14.8	16.9	1800	0.19
Jane	2016-2017	Downstream	1.3	4.6	500	0
Jane	2008	Downstream	1.3	4.6	500	0.01

Site	Year sampled	Stream location	Catchment area (km²)	Bankfull width (m)	Spawning length(m)	Salmon density (kg/m²)
Jane	2008	Upstream	1.3	2.7	0	0
Kill	2016-2017	Downstream	0.5	3.5	453	0.39
Kunsoot Main	2016-2017	Downstream	4.9	13.1	1280	0.92
Lee	2016-2017	Downstream	11.2	12.4	700	1.04
Neekas	2008	Downstream	16.0	17.7	2100	1.60
Neekas	2008	Upstream	10.8	12.8	0	0
Sagar	2008	Downstream	36.6	15.5	180	0.45
Sagar	2008	Upstream	36.6	13.6	0	0
Troup North	2016-2017	Downstream	1.6	4.4	332	0.01
Troup South	2016-2017	Downstream	1.8	4.1	489	0.04

1.2.2. Salmon density estimates

Both migrating and dead salmon were counted during stream surveys at each site by Fisheries and Oceans Canada (DFO), the Heiltsuk First Nation, and Simon Fraser University in the fall 2016 and fall 2006-2008 seasons. Pink and chum salmon represented >90% of the observed salmon in all sampling periods. Abundance estimates represent the best available estimate of the total number of salmon returning that year. I used fall surveys of the total number of dead and live salmon observed in each stream during the peak of the salmon run by SFU personnel and DFO, along with stream-specific data and regional weight estimates of each species, to estimate salmon density for each stream (Table 1). Peak counts by SFU and DFO represent the estimated escapement for each stream, and have been shown to be very similar to estimates using an area under the curve method (Hocking and Reynolds 2011). Salmon density was calculated as:

$$D = \sum \frac{M}{L * W}$$

where D is salmon mass per unit area (kg/m²), M is total pink, chum, coho, and sockeye salmon escapement mass, L is stream spawning length, and W is stream bankfull width. For the 2016-2017 study, fall 2016 salmon escapement alone was used to estimate salmon density. Fall 2016 salmon density provided better coverage than the 3-year

average and serves as a measure of the more direct effects of disturbance and subsidization by the 2016 salmon run on invertebrate communities. We reran analyses with 3-year average salmon density and found no change in results. In the 2008 study, salmon density estimates represent a 3-year average from 2006-2008, as used by Harding and Reynolds (2014).

1.2.3. Invertebrate collection and body size determination

For the 2016-2017 period, I collected benthic invertebrates from seven streams in the spring prior to the arrival of salmon (June 3 to June 11, 2016), and from 15 streams (including the previous seven) just after peak salmon spawning (September 19 to October 18, 2016) and again in the follow spring (April 28 to June 5, 2017). I sampled invertebrates using a 500 μm mesh Surber sampler with a sampling area of 0.09 m^2. I haphazardly selected approximately three transects per stream per season (mean = 3.2, range = 1 to 6) within riffle habitats with an effort to sample evenly across the spawning length of each stream. For each season, these same transects were revisited and sampled. Within each transect, I sampled three points by disturbing the substrate to a depth of 7 cm for 2 minutes, in addition to scrubbing larger rocks present in the sampling area. I combined material collected from the three points to yield one sample per transect in all seasons: spring 2016 (n = 26), fall 2016 (n = 45), and spring 2017 (n = 48). In the 2008 study, three transects were sampled below and three transects immediately upstream of the salmon barriers in each of the five streams in both the spring (n = 30) and fall (n = 30). Transects in the 2008 study were selected randomly in each season based on mean stream width. Invertebrate collection methods at each transect and sample processing were identical in both studies. I preserved samples in 95% ethanol, before they were transported back to the lab for storage at -20°C until further processing. I used a Folsom plankton splitter to subsample a total of at least 300 individuals per sample. I used the value for the proportion of the sample picked to adjust total biomass during the size spectra calculations. I randomly selected 10% of all samples for resorting and re-identification purposes to ensure sufficient picking and identification accuracy. I identified invertebrates to the family level using Merritt et al. (2008), with the exception of Amphipoda and Collembola which were relatively uncommon.

To produce size spectra of invertebrate communities, I calculated the body mass of all individuals using length-weight conversions from 2016 to 2017 (n = 28,431), and from 2008 (n = 9,800). Body size was measured after sorting and identification. I first photographed individuals using a camera-mounted dissecting microscope and then measured body lengths digitally using ImageJ 1.51. I re-measured individuals from a small subset of samples to ensure body length estimates were consistent across the different body shapes of various taxa and found high consistency in length measurements (r^2 = 0.998). I used regional, family-level length-weight regressions and published family-level length-weight regressions from Benke et al. (1999) to convert body length to dry mass for all individuals. A total of 29 taxa were observed, comprised of 26 insect families (representing six orders), plus two orders Amphipoda and Lepidoptera, and one class Collembola. The most common families by count were Chironomidae (Order Diptera), Baetidae (Order Ephemeroptera), and Simuliidae (Order Diptera), representing 36%, 11%, and 6% of all invertebrates, respectively. By total biomass, the most common families were Hydropsychidae (Order Trichoptera, 22%), Chloroperlidae (Order Plecoptera, 11%), and Rhyacophilidae (Order Trichoptera, 9%). A summary of body size ranges and means for each family is presented in Figure 1.2.
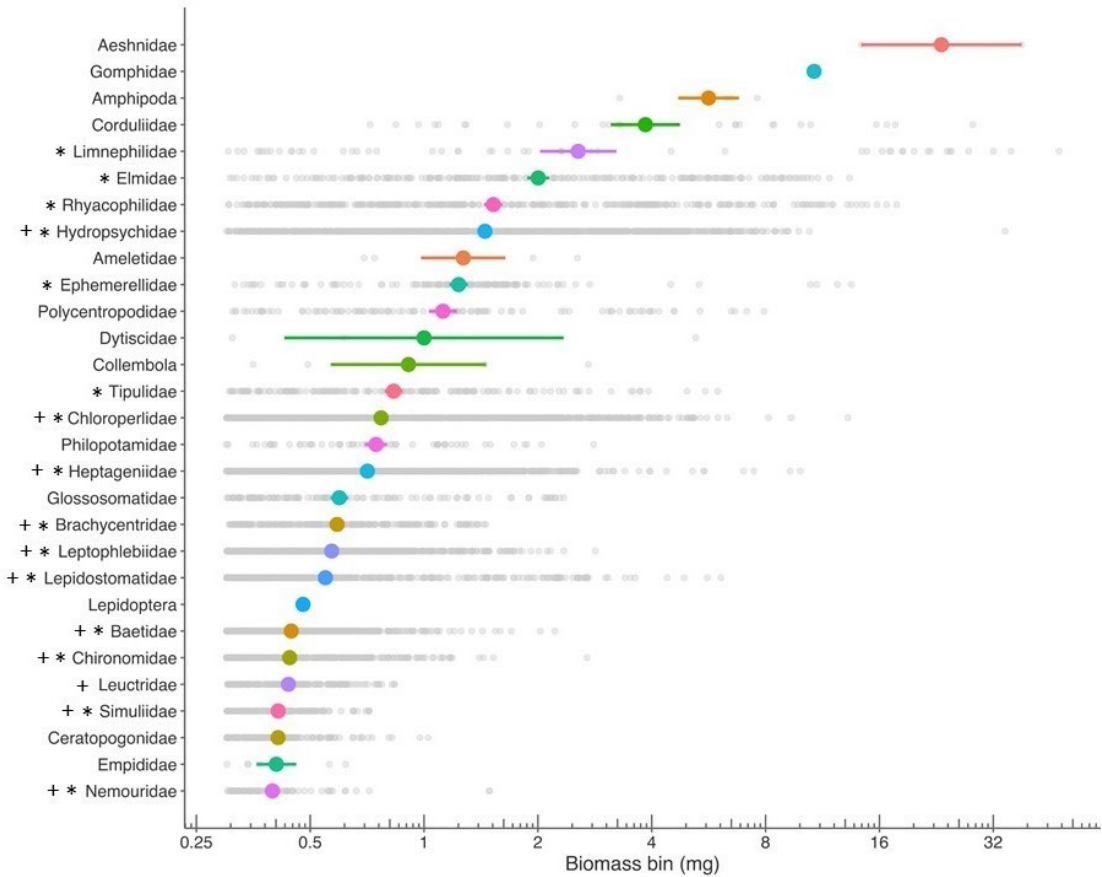
Figure 1.2.   Body size ranges and means (with bars denoting the 95% confidence interval) of all families observed. Symbols by family name indicate families that collectively represented >90% of total abundance (+) and biomass (*).

1.2.4. Habitat variables

I measured three habitat variables: stream temperature, substrate size, and biofilm biomass (measured as ash-free dry mass, AFDM). I recorded stream temperature using waterproof data loggers anchored in each stream and set to record temperature every 2 hours from the fall 2016 season sampling date to the spring 2017 season sampling date (HOBO Pendant UA-002-08). I subsequently calculated average stream temperature for each stream by averaging temperatures recorded from October 19, 2016 to April 29, 2017 (mean = 4.7°C, range = 3.8 to 5.4°C). In the spring 2017 season I estimated substrate size using methods described by Wolman (1954) at each transect where invertebrates were sampled by haphazardly selecting and measuring the intermediate axis of 30 rocks to the nearest 1 mm and calculating an average substrate size for each transect (mean = 7.3 cm, range = 3.5 to 12.5 cm). Although substrate size

was not measured in the spring 2016 or fall 2016 seasons, I did not observe any noticeable differences in substrate structure at any transect across seasons. Similarly, I sampled stream biofilm only during the spring 2017 survey and used ash-free dry mass (AFDM) as an estimate of total biofilm biomass (mean = 0.86 mg/cm^2, range = 0.3 to 2.41 mg/cm^2). At each transect, I took three biofilm samples by randomly selecting nine cobble-sized rocks (secondary axis <256mm) within the riffle. Invertebrates were removed prior to scrubbing a 1 cm^2 section from each of the nine rocks for the AFDM measurements. I rinsed and combined three of the 1-cm^2 sections to form one replicate, leaving three replicates per transect. Samples were frozen unfiltered in the dark at -20°C until I later processed them. I estimated biofilm biomass following protocols summarized in Hauer and Lamberti (2018).

1.2.5. Generating the biomass size spectra

I calculated a biomass size spectrum for each stream (and location within stream for sites with salmon barriers) for spring 2016 (n = 9), fall 2016 (n = 17) and spring 2017 (n = 18), resulting in 44 stream x time period combinations (Fig. 1.3; Appendix A). Due to the sampling constraints of our gear, individuals smaller than the 500 μm mesh size of our Surber sampler likely escaped capture and are therefore underrepresented in our data. To account for this, I removed all individuals to the left (< 0.3 mg) of the bell-shaped peak (Trebilco et al. 2016). I also removed a single dragonfly larva (family Aeshnidae) because it was more than three orders of magnitude larger than the second largest individual (155 mg compared to 47.8 mg). The inclusion of this individual would have created empty size bins, unduly influencing the size spectrum slope.

I calculated the size spectra based on the LBNbiom method from Edwards et al. (2017) as it was empirically one of the most widely used and accurate methods for calculating size spectra slopes. Normalized biomass size spectra are a useful tool among the various types of size spectra, as this method corrects for unequal bin widths on a logarithmic scale and this standardization will allow for easy comparison across studies (Sprules and Barth 2016, Edwards et al. 2017). I first binned all individuals into 9 biomass intervals of equal width on a log$_2$mass scale starting at the following sizes in the across-stream analysis (0.25, 0.5, 1.0, 2.0, 4.0, 8.0, 16.0, 32.0, 64.0) and 15 log$_2$mass intervals for the within-stream analysis (3.9 x10^{-3}, 7.8 x10^{-3}, 1.6 x10^{-2}, 0.03, 0.06, 0.13, 0.25, 0.5, 1.0, 2.0, 4.0, 8.0, 16.0, 32.0, 64.0). For each size bin, I then summed the total

biomass, while correcting for the proportion of the sample sorted and the number of transects sampled per site for each sampling period. I normalized the total biomass in each bin by dividing it by the width of its respective size bin. Finally, I calculated the size spectrum by fitting the linear regression of $\log_{10}$(normalized biomass within a size interval) against centered $\log_{10}$(mid-point of the size bin). I then used linear models to extract the slope and intercept coefficients from each size spectrum.

1.2.6. Analyses

Data from the 2016-2017 study (across-stream comparison) and the 2008 study (within-stream comparison) were analyzed separately. For the 2016-2017 study, I ran two separate Bayesian linear mixed-effect models to assess the effects of salmon density and three habitat variables on the slope and intercept of invertebrate size spectra <u>across</u> sites. For both models, I used biofilm ash-free dry mass (AFDM), substrate size, and temperature as fixed effects. I included an interaction between salmon density and sampling period (as fixed effects) to test the effect of salmon density on size spectra shape within each season, and used site as a grouping factor by specifying random intercepts. For all analyses, all continuous variables were scaled and centered by subtracting the mean and dividing by the standard deviation prior to analysis to compare relative effect sizes. I compared relative effect sizes by illustrating the posterior distributions of each estimate coefficient, a point for the mean point, and a bar to denote the 95% credible interval (CI). I inferred large effects as those whereby the 95% CI did not cross zero. I conducted the analyses using the `brms` package (Bürkner, 2016) in R v.3.5.2 (R Core Team, 2017). Each model used 2000 iterations with an initial burn-in phase of 1000 iterations. We used weakly-informative normal priors with a mean of zero and a standard deviation of 10 and achieved chain convergence on all four chains for all modelled coefficients (rhat = 1.00).

1.3. Results

1.3.1. Before-(during)-After across-stream comparison of size-spectra

The biomass size-spectra slopes were not affected by any of the three habitat variables considered. As predicted, the slopes of normalized biomass size spectra were negative at all sites in all sampling periods in the 2016-2017 study (overall mean [95%

confidence interval]: -1.11 [-1.13 to -1.09]). On average, the sampling period had a large effect on the slope, whereby the slope was strongly negative during the spring 2016 sampling period (-1.01 [-1.21 to -0.79]), slightly more negative in fall 2016 (-1.11 [-1.25 to -0.93]), and slightly less negative in spring 2017 (-0.98 [-1.14 to -0.82]; Fig. 1.4A).

Salmon density interacted strongly with sampling period to impact size spectra slope. Before salmon spawning, in spring 2016, there was a weak positive effect of salmon density on the slope (0.12 [-0.07 to 0.31]; Fig. 1.4A). Generally, the size spectra were less steep in spring (light and dark blue lines; before and after salmon spawning) than when salmon where present during the fall (red lines). With increasing salmon density, the size spectra slope was positive before salmon spawning in spring 2016 (salmon were not present in the stream at this time), became strongly negative during salmon spawning in fall 2016 (-0.25 [-0.41 to -0.07]), and weakly less negative after spawning in spring 2017 (-0.14 [-0.31 to 0.03]; Fig. 1.4AB).
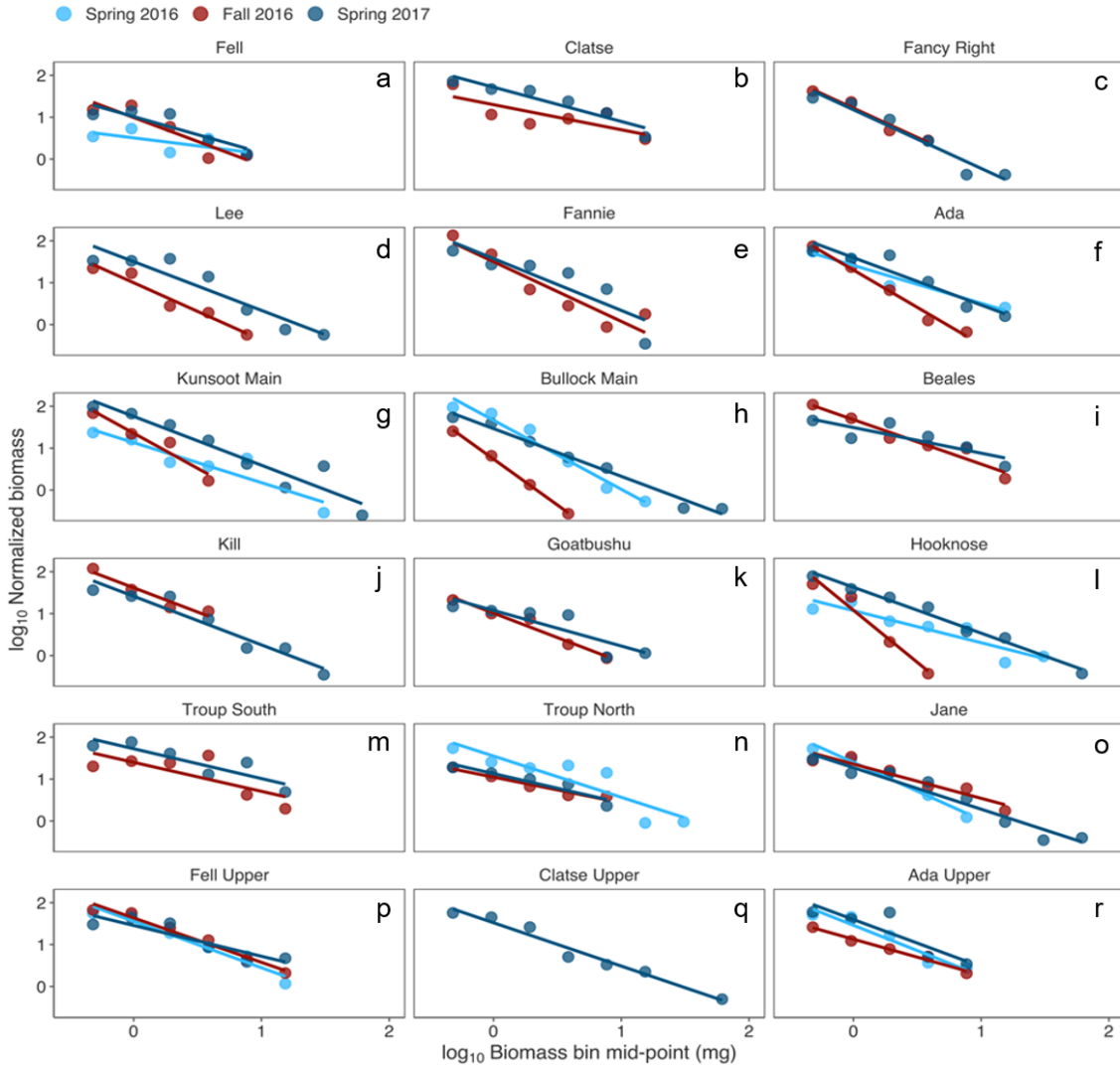
Figure 1.3. Size spectra for all three sampling periods across all sites for the 2016-2017 study (2008 study not included). Spring 2016 is shown in light blue, fall 2016 is shown in red, and spring 2017 is shown in dark blue. Three sites displayed (Ada Upper, Clatse Upper, and Fell Upper) refer to portions of the river upstream of barriers to spawning salmon, from the 2016-2017 study. Sites are ordered from left-to-right and top-to-bottom in order of the highest salmon density (top-left) to lowest (bottom-right), with the exception of the bottom row in which no salmon were present.
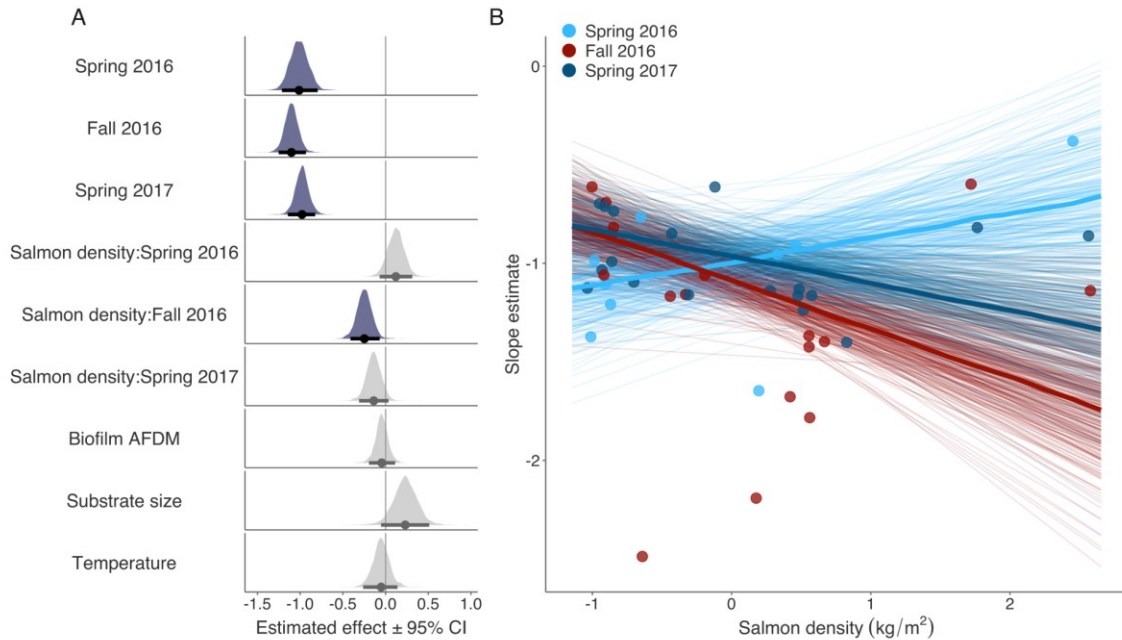
Figure 1.4. **Effects of habitat variables and salmon density on the size spectra slope coefficients. (A) Estimated effects with 95% credible intervals (CI). Variables with large effects are shown in purple whereas small/no effects are shown in grey. (B) The relationship between salmon density and sampling period, whereby spring 2016 is shown in light blue, fall 2016 is shown in red, and spring 2017 is shown in dark blue. The thin lines show draws from the posterior distribution and the thick line shows the mean posterior estimate. Points denote the raw data.**

The biomass size-spectra intercepts were not affected by any of the three habitat variables considered. On average, sampling period had a small effect on the size spectra intercept. Relative to the spring 2016 sampling period, the size spectra intercept marginally decreased during the salmon spawning in fall 2016 (1.24 [1.07 to 1.41]) and marginally increased (was greatest) after spawning in spring 2017 (1.35 [1.18 to 1.52]; Fig. 1.5A). Therefore, streams had higher insect community biomass (a greater intercept) before and after salmon spawning and the lowest community biomass (a lower intercept) in the fall 2016 season during the salmon run. Salmon density and sampling period interacted strongly: in spring 2016, salmon density had a large negative effect on the intercept, whereby increasing salmon density resulted in a lower size spectra intercept value (-0.19 [-0.41 to 0.01]; Fig. 1.5A). This pattern disappeared in fall 2016 (-0.03 [-0.21 to 0.16]) and in spring 2017 (-0.02 [-0.21 to 0.17]; Fig. 1.5AB).
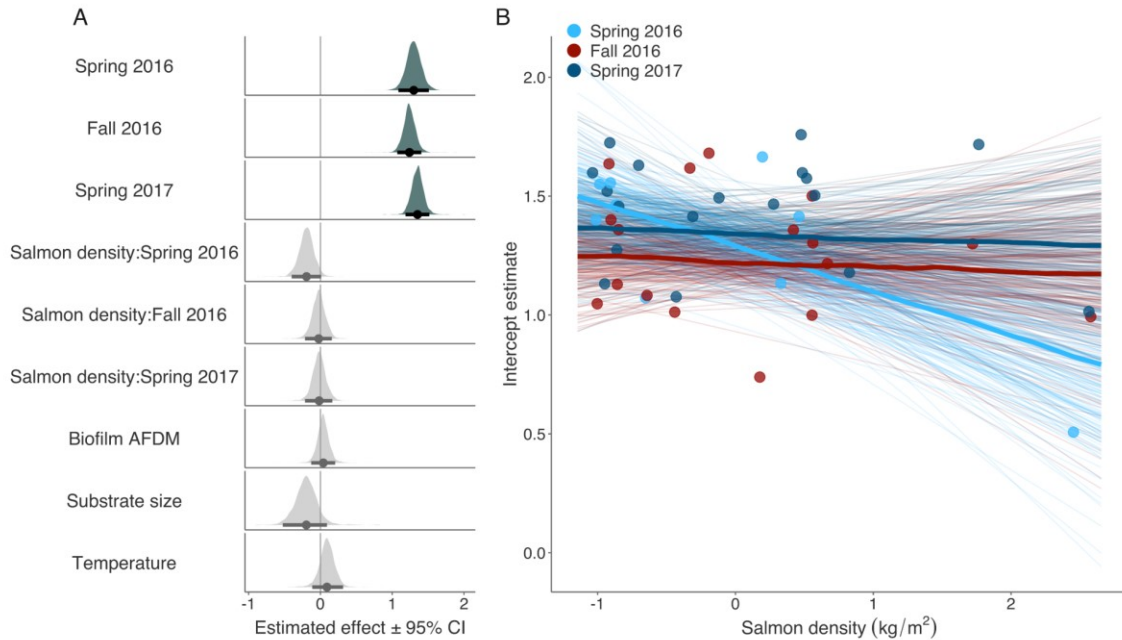
Figure 1.5. Effects of habitat variables and salmon density on the intercept of the size spectra. (A) Estimated effects with 95% credible intervals (CI). Estimates with large effects that do not overlap zero are shown in dark green whereas small/no effects are shown in grey. (B) The relationship between salmon density and height (intercept) of the size spectra and sampling period, whereby spring 2016 is shown in light blue, fall 2016 is shown in red, and spring 2017 is shown in dark blue. The thin lines show draws from the posterior distribution and the thick line shows the mean posterior estimate. Points denote the raw values.

1.3.2. Control-Impact within-stream comparison of size-spectra

The five streams that contained barriers to spawning salmon, which were sampled in the spring and fall of 2008, allowed us to control for watershed characteristics and to isolate the effects of salmon within each stream. I found no effect of season or sampling location on the size spectra slope within streams. The slope of the size spectra was, on average, marginally more negative without salmon (in stream reaches upstream of the salmon barrier) (-0.48 [-0.67 to -0.24]) compared to downstream locations with salmon (-0.43 [-0.66 to -0.21]). This pattern was consistent at four of the five streams with the exception of Sagar (Fig. 1.6). The upstream and downstream reaches of Jane Creek, the stream with almost no salmon present in the fall, showed the greatest difference in size spectra slope (Fig. 1.6).

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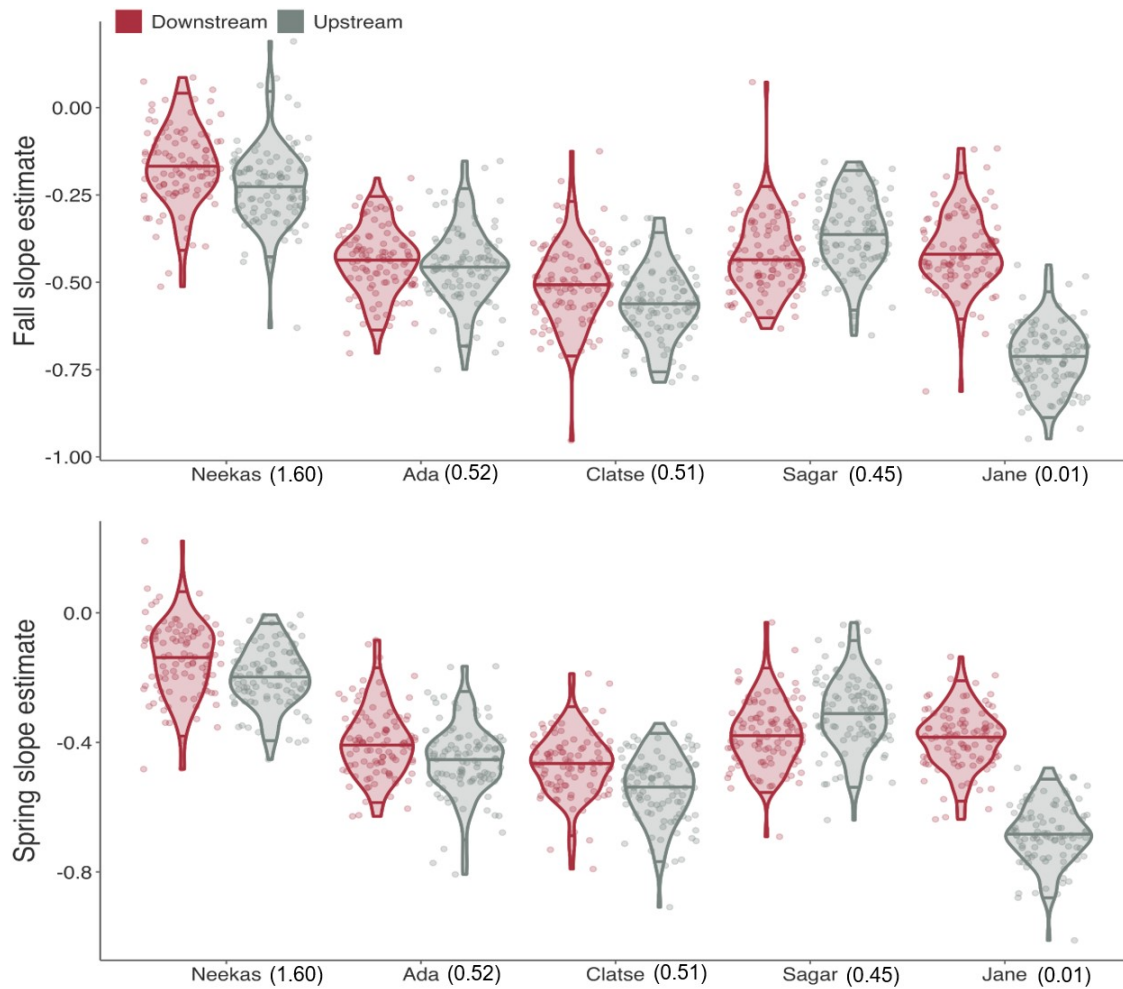
Figure 1.6. Within-stream comparison of the slopes of size-spectra (2008). (A) Model coefficient estimates with 95% credible intervals. (B) Violin plot representing the upstream (green) - downstream (red) sampling locations. Sites are ordered from highest salmon density (left) to lowest salmon density (right) with the salmon density in kg/m^2 in parentheses next to the stream name.

We also found no effect of season or sampling location on the size spectra intercept. The size spectra intercept was marginally higher in the spring (1.71 [1.32 to 2.11]) than in the fall (1.56 [1.16 to 1.95]). The intercept of the size spectra was, on average, marginally higher when sampled upstream (1.72 [1.29 to 2.11]) compared to downstream locations (1.56 [1.16 to 1.95]). This pattern was apparent at three of the five sites, with the exception of Clatse and Jane creeks.
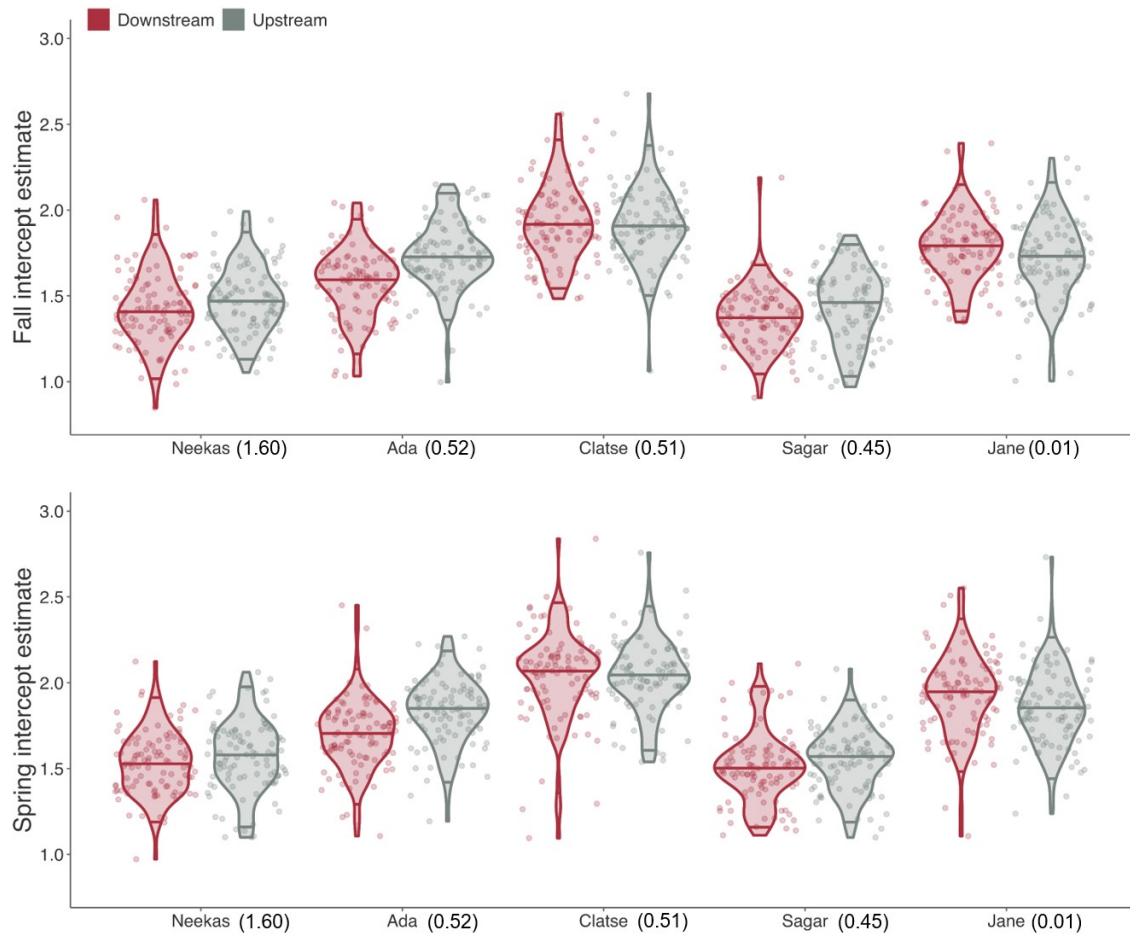
Figure 1.7. **Within-stream comparison of the intercepts of size-spectra (2008). (A) Model coefficient estimates with 95% credible intervals. (B) Violin plot representing the upstream (green) - downstream (red) sampling locations. Sites are ordered from highest salmon density (left) to lowest salmon density (right) with the salmon density in kg/m² in parentheses next to the stream name.**

1.4. Discussion

The normalized biomass size-spectra in our streams are consistent with very bottom-heavy trophic pyramids, with an average slope of -1.11. The negative slopes observed here are roughly consistent with other investigations of stream community size spectra, which also show negative scaling of body size with biomass or density even when incorporating microfauna and fishes (Cattaneo 1993, McGarvey and Kirk 2018). A quick conversion to normalized density size-spectra slopes (biomass slope – 1), an alternative to abundance and biomass size-spectra, demonstrates consistency in aquatic invertebrate slopes across regions (-2.11 in our streams, compared to values ranging

from -1.59 to -2 as reported by McGarvey and Kirk 2018). As recommended by other authors (Sprules and Barth 2016), I include raw biomass data to allow for standardized analysis and comparison across studies, as the effort to define large-scale patterns in invertebrate size-spectra continues. Although consistency in size spectra shape has been noted in aquatic invertebrate communities, considerable variation exists, including unimodal, bimodal, trimodal, and flat distributions (Hanson et al. 1989, Bourassa and Morin 1995, Solimini et al. 2001). The wide variety in sampling gear, strategy, and effort may explain much of this variation, so caution must be exercised during comparisons. Next, I consider (1) seasonality of stream insect size spectra, (2) habitat variables measured in this study, and (3) net effects of salmon on stream insect community size-spectra.

The normalized biomass size spectrum intercept provides a measure of total community biomass, or productivity, and an alternative way to estimate how stream insect biomass responds to spawning salmon (Sprules and Barth 2016). The average intercept across streams decreased marginally from spring 2016 to fall 2016 and then marginally increased the following spring (Fig. 1.5; where x=0). The lack of an interaction between salmon density and season observed here, with respect to the intercept, does not match previous findings by Harding and Reynolds (2014) that found lower invertebrate biomass with increasing salmon density, indicative of a strong disturbance effect. The strong interaction between salmon density and spring 2016 intercepts could indicate a failure of stream insects to recolonize substrates in streams that typically harbour higher salmon densities, if there was a more prominent disturbance effect in previous years. An alternative explanation is Fell Creek, the highest salmon density stream, was unique in that only one transect could be sampled below the salmon barrier due to the limited spawning length (Table 1.1). This transect was located in a very narrow section of the stream where salmon likely play a larger disturbance role. Given the weight this site holds on the high end of the salmon density distribution and the weaker community representation resulting from a single insect sample, caution should be exercised when interpreting this relationship, as this single site appears to be driving the negative relationship observed in spring 2016 for the intercept.

The seasonal patterns in average intercepts across streams could be explained by the phenology of stream insects. Stream insect taxa in temperate regions are often univoltine (i.e., one generation/year) and are typically more abundant in the summer

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when stream temperatures reach optimal growing conditions and feeding rates peak (Hershey et al. 2010). With a few exceptions, most late-instar (i.e., older) aquatic insects reach maturity and begin to emerge as reproductive adults throughout the summer, representing a net loss of total insect biomass, especially from larger size classes (Merritt et al. 2008, Moore and Schindler 2010). In the following spring when stream temperatures reach optimal growing conditions again, growth and recruitment of stream insects is high, likely resulting in an increase in size spectrum intercept. These life history traits may explain the average seasonal changes I observed in size-spectra intercept, where insect biomass is lost from the system due to emergence throughout the summer, and when warming spring temperatures produce greater invertebrate biomass following the winter season. The emergence explanation is supported by the fact that, in ten of the streams, one to two of the largest size classes that are present in spring 2017 (after salmon spawning) were entirely absent in fall 2016 (Fig. 1.3, panels a, c, d, f, g, h, j, k, l, and o).

Seasonally, averages across streams show a steepening of the size-spectrum slope from spring 2016 (before salmon spawning) to fall 2016 (during salmon spawning), followed by a moderate shallowing of the slope after salmon spawning, relative to both previous seasons, in spring 2017 (Fig. 1.4; where x=0). Changes in size spectrum slope can result from the relative gain or loss of smaller or larger individuals, or both simultaneously. The strong presence of salmon may explain the steeper slopes revealed in our streams. A combination of more pronounced emergence periods in high salmon density streams as noted by Moore and Schindler 2010, potential small-bodied salmon carcass opportunists (Chaloner et al. 2002), and physical disturbance to invertebrate communities by salmon from which smaller-bodied insects are better able to recover and/or persist through (Townsend et al 1997, Lessard and Merritt 2006) may contribute to the patterns observed in this study. While general consistency in size spectra slope is apparent across most streams, the fall 2016 season produced substantially more negative slopes in Ada Creek, Bullock Main Creek, and Hooknose Creek (Fig. 1.3, panels f, h, and l). In these three streams, the largest insect size classes disappear in fall 2016 (light blue to red, Fig. 1.3), and then they reappear in the following spring 2017 season in most streams. The general loss of biomass across most size classes (with the exception of the smallest size class in Ada and Hooknose) and disappearance of the largest size classes from spring 2016 to fall 2016 (light blue to red) appear to explain the

steepening of the slopes in these streams. The reappearance of the largest size classes and rebound of biomass across the range of body sizes in spring 2017 results in a shallowing of the average slope across streams. However, it is worth noting that the streams representing the middle of the salmon density distribution show steeper slopes than the low salmon density streams in spring 2017, which seems to be driving the weakly negative interaction between salmon density and slope in this season (Fig. 1.4). Among the five salmon-bearing streams that were sampled in spring 2016 prior to the arrival of salmon (Fig 1.3, panels a, f, g, h, and l), four of them show an increase in the biomass of the smallest size class, with the slope steepening from spring 2016 to fall 2016. Where samples were taken upstream of salmon barriers in two streams (Fell Upper and Ada Upper), the size spectra appear relatively unchanged compared to their salmon-bearing reaches downstream of the salmon barriers.

    None of the three variables thought to influence invertebrate biomass (mean stream temperature, biofilm AFDM, and substrate size) had any effect on the slope or intercept. Because I recorded average stream temperature from fall 2016 to spring 2017, and therefore included a significant period of winter temperatures that are not conducive to insect growth, it is likely that I did not capture the appropriate temperature window that would better explain variation in size-spectra slope and intercept (e.g., average summer stream temperatures). Average temperatures recorded from fall 2016 to early 2017 were significantly less (range = 3.8 to 5.4°C) than the lower threshold for invertebrate growth, which is thought to be ~10°C (Lawrence et al. 2010). Although size-spectra shape was not explained by water temperature in this study, a recent study in West Virginia streams notes water temperature as a key variable predicting seasonal changes in stream community size spectra (McGarvey and Kirk 2018).

    Substrate size varied significantly by transect and the riffles that I sampled primarily consisted of substrates ranging from pebbles to cobbles (mean = 7.3 cm, range = 3.5 to 12.5 cm). The substrate size range observed may not be wide enough to encompass the minimum size at which high flow events and spawning salmon runs no longer impact the substrate. However, a marginal effect of substrate size on both the slope and the intercept was observed, even though confidence intervals crossed zero, where the slope became shallower (i.e., less negative) and the intercept decreased with increasing substrate size. This may be explained by higher abundances of larger individuals inhabiting larger substrates and larger substrates' ability to withstand physical

disturbance and retain greater amounts of biofilm resources and larger insects. However, the marginally negative effect of substrate size on size spectra intercept contradicts the idea that larger, more stable substrates can better retain stream insect biomass. It is possible that stream insects prefer the smaller to moderate-sized substrates in the size range sampled over the larger substrates with lower interstitial complexity, and are therefore more common in the smaller substrates.

Biofilm AFDM did not explain size spectra parameters. This measure includes all organic biomass within biofilm (including algae, bacteria, fungi, detritus, etc.) which are all represented to some degree in stream insect diets. Another common measure of basal production in streams is the chlorophyll-a content of biofilms, which represents total algal content which is thought to mediate invertebrate growth. While we measured chlorophyll-a in our streams, we did not include this in our analysis. Biofilm samples were only taken in the spring 2017 season. Potential differences in year-to-year biofilm production within each stream could explain the lack of an effect on size spectra parameters.

Neither flat nor positive biomass spectra slopes, consistent with inverted biomass pyramids, occurred in any stream in any season. The lack of inverted biomass pyramids and lack of an effect of salmon density on the fall 2016 or spring 2017 size spectra intercept value suggests that a strong community-wide subsidy effect was not observed in any of these streams, regardless of spawning salmon density. However, of the five salmon-bearing streams that were sampled in all three seasons, four show an increase in biomass in the smallest size class in fall 2016 (Fig. 1.4, panels a, f, g, and I). This is consistent with studies that have found an increase in the abundance of small-bodied invertebrates known to colonize salmon carcasses (e.g., Chironomidae; see Chaloner et al. 2002). However, this pattern may also be explained by the phenology of many aquatic insects, where newly-hatched, smaller insects become more abundant from later summer through early spring following the emergence and reproduction of adults in the summer (Hershey et al. 2010). In addition to the possibility that smaller-sized invertebrates disproportionately benefit in the short term, larger invertebrates may be more negatively affected by the scouring effect of salmon, as larger insects typically have longer lifecycles than smaller insects and therefore take longer to recolonize disturbed habitat, and larger insects may be less able to access smaller interstitial spaces in stream substrates to avoid disturbance events.

Interestingly, the within-stream Control-Impact comparison from the 2008 study revealed no differences in size-spectra slope or intercept between upstream and downstream sites within each stream, regardless of the presence of salmon. However, in three of the four salmon-bearing streams, size-spectra intercepts were marginally higher in upstream vs downstream sites (Fig. 1.7; see Neekas, Ada, and Sagar Creeks), regardless of season, which is roughly consistent with observations by Harding and Reynolds (2014). These similarities suggest that the biomass estimation methods which differed between studies (batch weights by family to calculate total biomass and length-dry weight conversions followed by size-spectrum intercept estimation) may be compatible.

This study provides a novel approach to assess the net effects of salmon in stream ecosystems by examining seasonal variation in stream insect size spectra across a salmon density gradient. I found steeper negative size spectra slopes with increasing salmon density when salmon were present in streams in the fall season. A steeper negative size spectrum slope may be caused by either an increase in abundance of smaller insects, a decrease in abundance of larger insects, or both. Both likely explain the patterns observed across streams. Within the salmon-bearing streams that were sampled in all three seasons, the majority of them show an increase in biomass of the smallest size class and a decrease in, or absence of, medium to larger size classes. While comparisons of size spectra intercepts across the salmon density gradient show little seasonal effect, suggesting a minimal effect of disturbance on the insect community as a whole, site-specific patterns suggest that this disturbance may differentially affect smaller and larger size classes, whereby smaller insects are less affected, and larger insects are more affected by disturbance (Fig. 1.3). Further, the increase in biomass in the smallest size class may indicate a subsidization effect on smaller insects. For example, the colonization of and direct feeding upon salmon carcasses by small insects such as Chironomidae, or their much more rapid life cycle and post-disturbance colonization rates compared to longer-lived insects, could explain this observation. Alternatively, depending on the life histories of insect taxa observed in these streams, the increase in biomass of small insects in the fall may represent the annual recruitment of insects following the spring and summer emergence and reproduction of adult insects. Subsequently, the hatching of early instar insect larvae by late summer and early fall may result in greater biomass of small-bodied insects (Merritt et al. 2008).

The watersheds in our study region are generally characterized by nutrient-poor soils surrounding relatively short, high-gradient streams. Although stream insect size spectra slopes have been shown to be roughly comparable across regions, the ways in which these size-spectra respond to disturbance or subsidies likely vary across regions and even within streams large enough to exhibit longitudinal changes in channel morphology and community composition from headwaters to river mouths, as defined by the River Continuum Concept (Vannote et al. 1980). Future research could investigate how stream insect size spectra respond to different forms of subsidies and disturbance in larger streams with greater habitat complexity that host a variety of salmonid species outside of the predominately pink and chum salmon populations observed in this study. Functional feeding groups are a common way to classify stream insects based on how they feed in an ecosystem (Merritt et al. 2008). It is important to consider taxonomic identity which can then be tied to functional feeding role, which could help explain changes in a community's size spectrum based on the size and nature of an energy subsidy. Stable isotope analysis of stream insect size classes, especially in watersheds with marine-derived subsidy influence, would allow for direct identification of subsidized taxa or size classes, the ability to calculate predator-prey mass ratios for stream insect communities, and ultimately would provide a more robust understanding of stream insect trophic ecology. Ultimately, studies aiming to understand stream insect community structure and function would benefit from including information on individual body size, species identity, and functional feeding group assignment, as each approach reveals information that will supplement our overall understanding of these communities.

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Appendix

Table A1.   Size-spectra slope and intercept estimates by site and season with standard error in parentheses.

Site	Season	Slope estimate	Intercept estimate
Ada	Spring 2016	**-0.91** (0.18)	**1.41** (0.11)
Ada	Fall 2016	**-1.78** (0.12)	**1.30** (0.06)
Ada	Spring 2017	**-1.13** (0.19)	**1.60** (0.13)
Ada Upper	Spring 2016	**-1.21** (0.19)	**1.46** (0.10)
Ada Upper	Fall 2016	**-0.86** (0.07)	**1.13** (0.04)
Ada Upper	Spring 2017	**-1.13** (0.35)	**1.60** (0.18)
Beales	Fall 2016	**-1.06** (0.13)	**1.68** (0.09)
Beales	Spring 2017	**-0.61** (0.19)	**1.49** (0.13)
Bullock Main	Spring 2016	**-1.65** (0.15)	**1.66** (0.10)
Bullock Main	Fall 2016	**-2.19** (0.06)	**0.74** (0.02)
Bullock Main	Spring 2017	**-1.14** (0.07)	**1.47** (0.07)
Clatse	Fall 2016	**-0.60** (0.24)	**1.30** (0.16)
Clatse	Spring 2017	**-0.82** (0.14)	**1.72** (0.09)
Clatse Upper	Spring 2017	**-1.03** (0.08)	**1.52** (0.08)
Fancy Right	Fall 2016	**-1.40** (0.20)	**1.22** (0.07)
Fancy Right	Spring 2017	**-1.40** (0.17)	**1.18** (0.11)
Fannie	Fall 2016	**-1.42** (0.27)	**1.50** (0.18)
Fannie	Spring 2017	**-1.24** (0.33)	**1.58** (0.22)
Fell	Spring 2016	**-0.38** (0.24)	**0.51** (0.12)
Fell	Fall 2016	**-1.14** (0.28)	**0.99** (0.15)
Fell	Spring 2017	**-0.86** (0.26)	**1.01** (0.13)
Fell Upper	Spring 2016	**-1.11** (0.12)	**1.56** (0.08)
Fell Upper	Fall 2016	**-1.06** (0.09)	**1.64** (0.06)
Fell Upper	Spring 2017	**-0.74** (0.18)	**1.46** (0.12)
Goatbushu	Fall 2016	**-1.17** (0.13)	**1.01** (0.07)
Goatbushu	Spring 2017	**-0.85** (0.23)	**1.08** (0.16)
Hooknose	Spring 2016	**-0.77** (0.15)	**1.07** (0.12)
Hooknose	Fall 2016	**-2.49** (0.35)	**1.08** (0.13)
Hooknose	Spring 2017	**-1.10** (0.07)	**1.63** (0.06)
Jane	Spring 2016	**-1.37** (0.12)	**1.40** (0.06)
Jane	Fall 2016	**-0.82** (0.13)	**1.36** (0.09)
Jane	Spring 2017	**-0.99** (0.10)	**1.27** (0.10)
Kill	Fall 2016	**-1.16** (0.22)	**1.62** (0.08)
Kill	Spring 2017	**-1.16** (0.14)	**1.41** (0.12)
Kunsoot Main	Spring 2016	**-0.96** (0.20)	**1.13** (0.15)
Kunsoot Main	Fall 2016	**-1.68** (0.32)	**1.36** (0.12)

Kunsoot Main	Spring 2017	**-1.17** (0.15)	**1.76** (0.15)
Lee	Fall 2016	**-1.37** (0.18)	**1.00** (0.09)
Lee	Spring 2017	**-1.16** (0.19)	**1.50** (0.16)
Troup North	Spring 2016	**-0.98** (0.21)	**1.55** (0.18)
Troup North	Fall 2016	**-0.61** (0.08)	**1.05** (0.04)
Troup North	Spring 2017	**-0.70** (0.15)	**1.13** (0.07)
Troup South	Fall 2016	**-0.69** (0.30)	**1.40** (0.20)
Troup South	Spring 2017	**-0.71** (0.19)	**1.72** (0.12)