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Long-Term Effects of Salmon Subsidies on Terrestrial and Freshwater Invertebrate Communities

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Abstract

Pacific salmon (*Oncorhynchus* spp.) provide a flux of nutrients into terrestrial and freshwater food webs during the spawning season, which has been shown to positively increase the abundance and biomass of terrestrial and freshwater invertebrates. Previous research has shown that, in the immediate post-spawning period, salmon-derived subsidies (ie., resources produced outside the principal ecosystem) in the form of salmon carcasses provide a surplus of nutrients that can cause two-fold increases in the abundance and biomass of terrestrial invertebrates. Here, we quantify terrestrial and freshwater invertebrate abundance, biomass, and composition to determine if the salmon subsidy has a lasting effect on invertebrates into the pre-spawning period the following year. We hypothesize that if a lasting effect is present, the abundance and biomass of invertebrates collected at the salmon-bearing reaches will be greater when compared to those collected in the salmon-absent reaches. Terrestrial and freshwater invertebrates were collected and identified from above and below a salmon barrier in the pre-spawning season at two streams: Sugsaw Creek and Sarita Falls on the West Coast of Vancouver Island, BC. Abundance and biomass displayed a significant negative correlation for both terrestrial and freshwater invertebrates, demonstrating a bottom-up trophic level community. We collected a greater invertebrate abundance and biomass below the falls with the exception of terrestrial invertebrates at Sugsaw Creek. Outliers were noted for orders such as Diptera and Coleoptera. There was little difference in invertebrate diversity across any of the locations. Our results indicate that there is no yearly legacy effect of salmon subsidies on terrestrial and freshwater invertebrates into the pre-spawning season. The importance that nutrient transfer across ecosystem boundaries have on structuring community food webs has long since been demonstrated, and through our findings, we hope to contribute to the notion that salmon play key roles in structuring not only freshwater but terrestrial communities as well.

Keywords — Invertebrates, Trophic Levels, Community Ecology, Salmon Subsidy, Size Spectra

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1. Introduction

Anadromous salmon (*Oncorhynchus* spp.) return annually to freshwater streams and rivers for the spawning season in late summer, and transfer marine-derived nutrients to terrestrial and freshwater systems [1]. A considerable influx of salmon biomass can enter freshwater sources from the ocean [1] and provide a nutrient pulse to otherwise nutrient-limited areas, such as the temperate rainforests located along the coastline of the Pacific Northwest [2]. Salmon derived nutrients are transferred to the surrounding ecosystems through a variety of mechanisms. As salmon carcasses begin to accumulate in terrestrial and freshwater habitats, they effectively transport nutrients such as nitrogen and phosphorus to the surrounding riparian vegetation and soil communities [2, 3]. Deceased salmon are then colonized by carcass-specialist terrestrial invertebrates that are in turn consumed by organisms higher up in the food chain, effectively transferring energy between trophic levels [4, 5].

Marine subsidies represent a key nutrient source for terrestrial and freshwater ecosystems, and in both cases, contribute extensively towards structuring the community composition and food webs [2]. Communities where the main nutrient and energy source is smaller organisms found at the base of the food chain typically occur as a bottom-heavy trophic level pyramid [6, 7]. Species abundance within this type of community is thus limited by the amount of nutrients and energy that is available [2]. Nutrient limitation is determined by a multitude of factors including: primary production, temperature, ecological interactions, and the metabolic rate and body size of the organism. The invertebrate abundance-body size relationship within a community can be used to determine energy flow and productivity of the ecosystem [6]. The slope of the abundance-body size relationship represents the rate at which abundance changes with increasing body size [7]. The slope can be interpreted as the efficiency of energy transfer between trophic levels, or the rate at which energy is being lost as it is transferred from one trophic level to another. The y-intercept, on the other hand, represents the baseline productivity within the ecological system and is thus related to the abundance of smaller-bodied organisms found in lower trophic levels [7]. Both the slope and intercept can shift in response to local changes in nutrient availability occurring in the ecosystem [2]. An increase in the intercept would indicate an overall increase in the abundance and body mass for that particular community, implying that an increase in productivity occurred over the entire system as a result of the marine subsidy. A steeper or shallower slope would indicate that a specific trophic level (lower or higher respectively) - determined by body mass - is receiving more resources and is more highly subsidized relative to the other levels.

Salmon-derived nutrients that are transferred to terrestrial and freshwater ecosystems have been shown to influence the structure of invertebrate communities [2]. Salmon derived nutrients can alter terrestrial primary production (3) which, in turn, can alter the diversity and composition of riparian invertebrate communities [5]. Evidence for this is demonstrated by an increase in the abundance-body size intercept and thus the productivity of terrestrial invertebrate communities immediately following a salmon spawning event [8]. Alternatively, salmon redds disturb sediments and therefore may alter benthic freshwater invertebrate abundance and productivity [9]. While the long-term effects of salmon subsidies on invertebrate communities have been well-documented in terrestrial ecosystems [2, 3], to our knowledge, these effects on invertebrate abundance and biomass have yet to be thoroughly studied in freshwater ecosystems. Thus, our study aims to add to the existing knowledge of the long-term effects of salmon subsidies in terrestrial invertebrate communities, as well as further explore these effects in freshwater invertebrate communities. Specifically, we test if there is a long-term change in either the slope or intercept of the abundance-body size relationship for invertebrates above and below salmon barriers indicating a legacy effect of marine subsidies. We examined the effects of marine subsidies on terrestrial and freshwater invertebrate communities by measuring: (i) biomass, (ii) abundance, (iii) slope and intercept of the abundance-body size relationship, and (iv) species diversity in the pre-spawning period, almost one year after the previous salmon return.

We aim to determine if the effects on invertebrate size and abundance from salmon-derived nutrients last into the pre-spawning period the following year, or if these effects occur strictly in the short term when salmon carcasses are present. Specifically, we ask: (a) if the terrestrial and freshwater invertebrate communities are size-structured, (b) if there is an observable difference in abundance or biomass between the control and salmon-bearing communities, (c) if there is a difference for terrestrial or freshwater communities in the slope or intercept between the control and salmon-bearing communities, and (d) if there is any difference between terrestrial or freshwater invertebrate diversity between the control and salmon-bearing locations. If a legacy effect of the salmon subsidy from the previous year is present on the invertebrate community, we expect an increase in the intercept and a shallower slope, indicating a net increase in productivity over the entire ecosystem as a result of the salmon nutrient subsidies. We would also expect that the size and abundance of both the terrestrial and freshwater invertebrates would be greater below the falls than above, since that is where salmon spawning occurs.

2. Materials and Methods

2.1. Site Descriptions

We sampled terrestrial and freshwater communities from two streams: Sugsaw Creek (48°50′15.80"N, -125°06′22.30"W) and Sarita Falls (48°54′10.4"N, -124°55′15.7"W), both located on the western coast of Vancouver Island, near Bamfield, British Columbia (Fig. 1). These salmon-bearing streams were chosen due to the presence of a waterfall at each location; serving as a physical barrier to the upstream migration of salmon (hereafter referred to as our control reaches). Sites below the waterfall represent areas that salmon are able to access (hereafter referred to as our salmon-bearing reaches). At Sugsaw Creek, the control site above the falls was relatively flat on either side. For the salmon-bearing site below the waterfall however, the riparian profile became very steep on both sides of the stream. The canopy cover over the stream at both sites was fairly dense. There was an increasingly steep slope on either side of the stream for both sites above and below the falls. For both sites, there was almost no canopy cover. For each location, we further measured several forest and stream characteristics above and below the waterfalls including: bankfull width, wetted width, canopy cover, thalweg depth, stream bank slope, and substrate sizes (Tab. 1).

Cutthroat trout (*Oncorhynchus clarkii*), as well as Chum (*O. keta*), Coho (*O. kisutch*), and Pink (*O. gorbuscha*) salmon have been found in Sugsaw Creek in late August [10], which were limited to the lower sections of the stream before the waterfall barrier. The species observed in Sarita River include Chum (*O. keta*), Chinook (*O. tshawytscha*), and Coho (*O. kisutch*) salmon [11, 12]. We chose these streams based on their close proximity, though considering that they contain different species, we are unable to assume that they experience similar amounts of salmon biomass during the spawning season. For both streams, we expect to observe similar effects on the abundance and biomass of terrestrial and freshwater invertebrates.

2.2. Sampling Methods

To determine size spectra relationships and assess the terrestrial invertebrate community found in the riparian forest surrounding these salmon barriers, we set up 18 pitfall traps [13] both above and below the falls at both streams. Pitfall traps were set up at Sugsaw Creek and Sarita Falls on July 12, 2018. At Sugsaw Creek we set the traps in a 3×3 grid with each trap approximately 1.5 m apart. We plotted the grids on either side of the stream both above and below the falls in locations with similar canopy cover and vegetation density. At Sarita Falls we set up 9×9 grids in a similar manner on one side of the stream both above and below the falls due to the steep and rocky terrain of the forest making it difficult to set traps on the other side. All traps were set within 20m of the stream on either side. We collected the traps after 48 hours and stored invertebrates in 15% ethanol.

We collected freshwater invertebrates along two transects both above and below the falls at both locations. Freshwater samples were collected at Sugsaw Creek on July 12, 2018, and at Sarita Falls on July 14, 2018. Each transect was within 100 metres from the falls and ran perpendicular to the stream's flow. We agitated stream sediment for two minutes in front of a Surber net sampler (30×30 cm quadrat, 1 m net length) that was placed facing upstream. At Sugsaw Creek we placed the Surber net at three different locations along each transect, while at Sarita Falls we placed the Surber net at four different locations due to the larger wetted width of this stream (Tab. 1). We stored collected invertebrates in 15% ethanol and also measured substrate sizes at each location where we took a Surber net sample (Tab. 1).

We classified all caught invertebrates to order using identification guides and literature [14, 15]. We counted the abundance of each order for each ecosystem environment (above or below the falls) and location (Sarita Falls or Sugsaw Creek). We then measured the overall dry mass for each invertebrate order and calculated a mean body mass in milligrams per individual as well as total biomass.

2.3. Data Analysis

Size spectra and abundance versus - body mass data were binned by invertebrate order and plotted to assess the fit of individual slopes and compare the above and below locations for both streams. To determine slope, intercept, and the net size spectra at each location, we fit linear regression models to each subset of the data (Sarita Terrestrial, Sarita Freshwater, Sugsaw Terrestrial, Sugsaw Freshwater; Tab. 2). To further assess each dataset, we performed an analysis of covariance (ANCOVA) to examine the relationship between the slopes and intercepts of the individual location data above and below the falls (Tab. 3). Shannon-Wiener indices were calculated to assess diversity at each location. All statistical analyses were performed in R v3.5.1 [16].

3. Results

We caught and classified to order a total of 1,211 terrestrial and freshwater invertebrates above and below for Sugsaw Creek and Sarita Falls. This included a total of 14 terrestrial and 16 freshwater invertebrate orders. The most abundant terrestrial and freshwater order was Collembola and Diptera respectively.

Our terrestrial pitfall traps caught a total abundance of 87 invertebrates in the Sarita Terrestrial control reach, while a total abundance of 100 invertebrates was caught in pitfall traps in the salmon-bearing reach (Fig. 2A). This equated to 9442.2 mg in invertebrate biomass caught in the control reach, and 10203.7 mg in invertebrate biomass caught in the salmon-bearing reach (Fig. 2B). In the Sugsaw Terrestrial control reach, our pitfall traps caught a total invertebrate abundance of 78, and 35359.5 mg in invertebrate biomass, while we caught a total invertebrate abundance of 136 and 12209.0 mg in biomass in the salmon-bearing reach (Figure 2A and 2B).

During our freshwater Surber net sampling, we caught a total abundance of 275 invertebrates in the control reach compared to 294 in the salmon-bearing reach at Sarita Falls (Fig. 2C). This equated to 13631.7 mg and 17687.1 mg in invertebrate biomass collected in the Sarita Freshwater control and salmon-bearing reaches respectively (Fig. 2D). In the Sugsaw Freshwater control reach we caught a total invertebrate abundance of 49 and 15011.0 mg in biomass, while we caught a total invertebrate abundance of 192 and 16630.1 mg in biomass in the salmon-bearing reach (Fig. 2C and 2D).

We found negative relationships between abundance and body mass for both terrestrial and freshwater invertebrates at Sugsaw Creek and Sarita Falls (Fig. 3). Sarita Terrestrial (Fig. 4A), had a significant ($p < 0.05$) relationship between abundance and body mass ($R^2 = 0.90$ and 0.94 at the control and salmon-bearing sites), with slope values of -0.85 for control and -1.05 for salmon-bearing reaches (Tab. 2). However, the difference in slope was not significant ($p = 0.28$). Sarita Freshwater (Fig. 3B) had a non-significant relationship due to two outliers identified as Diptera larvae escaping the size spectrum ($p > 0.05$, $R^2 = 0.17$, and 0.02 for control and salmon-bearing sites respectively). The slopes were determined to be -0.36, and -0.18 for control and salmon-bearing respectively, but were not significantly different ($p = 0.73$) (Tab.2).

Sugsaw Terrestrial had significant slopes ($p < 0.001$, $R^2 = 0.57$; $p < 0.001$, $R^2 = 0.92$ for Sugsaw control and salmon-bearing sites, respectively). Slope values for the Sugsaw control and salmon-bearing sites were calculated to be -0.72 and -0.88 respectively (Fig. 3C). Sugsaw Freshwater slopes were also found to be significant ($p < 0.001$, $R^2 = 0.72$; $p < 0.001$, $R^2 = 1.00$ for the control and salmon-bearing sites respectively). Slope values for control and salmon-bearing sites were -0.92, and -1.02 respectively. The outlier at approximately 2.75 mg is noteworthy, which was determined to be Dipteran larvae (Fig 3D).

There was no statistical difference between the slopes or intercepts of the abundance body mass relationships in control reaches verses salmon-bearing reaches for either terrestrial (Fig. 3A and 3C) or freshwater (Fig. 3B and 3D) invertebrate communities at both Sarita and Sugsaw locations (Tab. 3).

There were minimal differences in the calculated Shannon-Weiner diversity index values between both terrestrial and freshwater invertebrate communities in control and salmon-bearing sites at both locations (Fig. 4). Salmon-spawning reaches generally had lower invertebrate diversity than control reaches. The largest difference was seen for Sarita Terrestrial (0.34), while the smallest difference was seen for Sugsaw Terrestrial (0.16). The location with the highest and lowest diversity of terrestrial invertebrates was the salmon-bearing sites at Sugsaw Creek (1.82) and Sarita Falls (1.17) respectively. The location with the highest and lowest diversity of freshwater invertebrates was the control site at Sarita Falls (1.92) and salmon-bearing site at Sugsaw Creek (1.66) respectively. The only invertebrate community which saw a higher diversity in the salmon-bearing sites was in the terrestrial invertebrates we collected at Sugsaw Creek.

4. Discussion

Our study has shown that during the pre-salmon spawning season, terrestrial and freshwater invertebrate communities below a salmon barrier are not differentially structured compared to invertebrate communities above a salmon barrier (Fig. 3). This implies that the salmon subsidization to invertebrate communities that occurs during the spawning season [2] is immediate and does not last into the pre-spawning season of the next year. However, there are a few orders of invertebrates which did not follow this trend. For instance, freshwater Diptera at both locations showed higher abundances than expected both above and below the fall barriers (Fig. 3B & 3D). This observation would be expected during the salmon-spawning season because fly larvae are carcass-specialists [2]. As this study was conducted during the pre-spawning period, before the carcasses are available, escape of the size spectra cannot be explained by salmon subsidies, especially as the control region does not receive salmon subsidies. The peak in Dipteran larvae may possibly be explained by their life cycle. These larvae emerge in the summer and the latter portion of the spring [2]. We may have captured this emergence event during the time of our sampling which may account for the large quantity of these larvae in our samples.

We obtained a greater abundance and biomass for all of the salmon-bearing sites with the exception of Sugsaw Terrestrial. The high biomass obtained for Sugsaw Terrestrial relative to the salmon-bearing site was contrary to what we initially predicted. A likely explanation may be due to the fact that the pitfall traps for Sugsaw control were the sole traps that were set in a flat area near the stream. For the other three locations (Sugsaw salmon-bearing and Sarita control and salmon-bearing), pitfall traps were set directly into a steep slope overlooking the stream to ensure that they were within 20 m of it in order to guarantee that the collected invertebrates were representative of the riparian community.

The steepness of the terrain has a significant effect in determining the composition, biomass, and density of the nearby riparian vegetation [17, 18], which in turn will affect biological stream components such as nutrient flow, exchange of organic and inorganic matter, and the movement of organisms [19]. These factors may affect the species composition, biomass, and abundance of terrestrial invertebrates that are found in the area. The Sugsaw control site may have provided a more favourable habitat for terrestrial invertebrates due to the flatness of the slope and dense riparian vegetation in this area. The other locations experienced substantially lower values for biomass, which may be because the traps were set along a steeper gradient and in more open areas.

Alternatively, another aspect of the environment that may have been a factor includes canopy cover. The abundance of terrestrial invertebrates and specifically the input of such invertebrates into stream systems is highest in closed-canopy areas [19]. The greater degree of canopy cover found at Sugsaw Creek may account for the high biomass found at the control site.

An additional observation to make note of is that the control site for Sugsaw Terrestrial was the only site where a slug (Stylommatophora) was found in addition to a substantial number of beetles (Coleoptera). Beetles can be found in areas where there is lots of vegetative foliage [20], which may explain the spike in beetle abundance for the control location at Sugsaw Creek.

Abundance-body mass relationships serve to demonstrate the effects of salmon subsidies on the ecosystem. Although our findings found no statistically significant differences in slope or intercept, we do see observable changes in slope amongst the abundance-body mass plots. We observe a steepening of the slope below the falls (compared to the control group above the falls), at Sarita Terrestrial, Sugsaw Terrestrial, and Sarita Freshwater (Fig. 3). This suggests that smaller and more abundant individuals are being preferentially selected over the larger ones, and thus smaller and more abundant individuals comprise a larger portion of the trophic pyramid than expected. Our results indicate that there are no observable overall increases in the intercept. This suggests that the effects of salmon nutrient subsidies are transient, occurring during and immediately after the salmon run when carcasses are available, and slowly diminishing until the effects are no longer observable in the invertebrate population. For the freshwater invertebrates, additional reasoning may be that they have either already been consumed by the salmon directly or lost through the subsequent bioturbation as the salmon construct their spawning redds [21].

The difference in slope and intercept between freshwater and terrestrial communities at our sample sites were negligible. Observed differences in orders such as Coleoptera and Diptera that escaped the size spectrum serve as the only distinguishing factor. We predicted that there would be a difference between both habitats because of the various impacts that salmon have, depending on the ecosystem. As the spawning season approaches, salmon entering freshwater streams subject invertebrates to bioturbation (the disturbance of sediments) and therefore disrupt their natural habitats [22, 23, 24]. They also consume these organisms directly, which is another factor that is not experienced by terrestrial communities. Since both ecosystems are impacted by salmon in unique ways, differences between them were expected. However, both communities seem to have been equally unenriched by salmon subsidies in the pre-spawning season, suggesting that there is no long term effect on either habitat from the previous spawning season.

Freshwater invertebrate diversity was similar between control and salmon-bearing reaches during the pre-spawning season. This is expected as salmon density has been shown to have weak effects on freshwater invertebrate diversity, which is instead predominantly impacted by stream characteristics, such as streambed substrate size [25]. Both streams had significantly similar substrate sizes (Sarita: $p = 0.19$; Sugsaw: $p = 0.64$) between control and salmon-bearing sites at both locations (Tab. 1), which could also explain why there was little difference in freshwater invertebrate diversity. We also showed that terrestrial and freshwater invertebrate diversity was minimally higher for the control site at every location, the only exception being for Sugsaw Terrestrial, where a greater invertebrate diversity was seen in the salmon-bearing site.

Forests surrounding both Sugsaw Creek and Sarita Falls have experienced logging activities in the past, which would have contributed to alterations in freshwater and terrestrial habitats, further impacting the organisms that live within these areas. In Sarita specifically, extensive logging activities have occurred in the 1950s and 1960s [11], and even more recently within the past year. This expansive logging could potentially impact invertebrate communities in both terrestrial and freshwater ecosystems and may explain the results obtained for invertebrate diversity. For instance, reduction of riparian forest due to logging can result in reduced canopy cover, nutrient inputs, habitat complexity and input of woody debris into the stream [11]. This can result in degraded freshwater habitats and potentially alter freshwater invertebrate diversity. The extent of the logging below the falls seemed to extend closer to the stream at both locations, thus making the aforementioned effects more prominent below the falls which may explain why the lower diversity was observed in the freshwater invertebrates at Sugsaw Creek and Sarita Falls.

Investigating the relationship between abundance and body size in terrestrial and freshwater invertebrates can provide insight into community structure and energy flow between trophic levels in different ecosystems [2]. The mechanisms through which marine subsidies may impact the size spectrum relationship of freshwater and terrestrial communities has not been extensively researched. Through this study, however, insight can be gained into the possible long-term effects that salmon subsidies from the previous spawning season may have on invertebrate communities. Shifts in local species abundance or body mass due to a nutrient subsidy may lead to changes in local community structure and trophic cascades. This may also have implications for organisms located higher up in the food chain such as predaceous invertebrates or vertebrate consumers [8].

5. Conclusion

Through abundance-size spectra analysis, we confirmed the presence of a size-structured ecosystem with a bottom-heavy trophic pyramid. We did not observe significant intercept increases during the pre-spawning season, indicating that salmon subsidy effects last only during and shortly after the spawning season. Even though our results show that there is no legacy effect, a multi-year study period conducted periodically throughout the year would further our understanding. This way, direct comparisons could be made between pre-spawning and spawning events. By examining how salmon abundance may vary on a year to year basis, greater understanding could be obtained regarding how exactly salmon subsidies affect invertebrate abundance and biomass. Additionally, the short-term effects that these nutrient pulses have on community structure in different habitats (terrestrial and freshwater) would be studied. Since freshwater ecosystems are impacted differently by salmon through factors like predation and bioturbation the instant they enter the streams to spawn, we may expect to observe delayed effects for the terrestrial system. It would be interesting to note when exactly such effects start to fade and how long after until the observable differences in the scaling relationship (abundance and body size) for invertebrates between above and below the falls shifts back. Further research could focus on the specific effects that the added nutrient subsidy in the form of salmon carcasses would have on the surrounding riparian vegetation, and how this could further influence the scaling relationship for invertebrates.

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7. Tables and Figures

Table 1: *Stream characteristics for locations above and below the waterfall barriers at Sugsaw Creek and Sarita Falls.*

Site	Location	Coordinates	Distance Between Sites (m)	Bankfull Width (m)	Wetted Width (m)	% Canopy Cover	Thalweg Depth (m)	Slope Left Side	Slope Right Side	Number of Traps	Average Intermediate Substrate Size (cm)
Sugsaw Creek	Above	48°50′15.80"N, -125°06′22.30"W	156.6	5.6	3.3	35	0.23	10	10	18	3.25
	Below	48°50′23.69"N, -125°06′8.51"W		13.4	8.7	0	0.11	32	28	18	3.6
Sarita Falls	Above	48°54′9.09"N, -124°55′12.17"W	189.2	31	29	0	0.76	15	22	18	5.54
	Below	48°54′9.78"N, -124°55′20.51"W		49	37	0	0.51	28	30	18	4.36

Table 2: *Summary table of linear regression models performed for each regression line plotted in Figure 3.*

Method	Location	Ecosystem	Slope	R^2	P-Value
Simple Linear Regression	Sarita Above	Terrestrial	-0.85	0.90	1.12e-3
	Sarita Below	Terrestrial	-1.05	0.94	3.17e-4
	Sarita Above	Freshwater	-0.36	0.17	0.27
	Sarita Below	Freshwater	-0.18	0.02	0.67
	Sugsaw Above	Terrestrial	-0.72	0.57	6.99e-3
	Sugsaw Below	Terrestrial	-0.88	0.92	1.112e-5
	Sugsaw Above	Freshwater	-0.92	0.72	4.08e-3
	Sugsaw Below	Freshwater	-1.02	1	1.132e-15

Table 3: *Summary table of ANCOVA results from each location sampled including interaction parameters. Note: If body mass*above.below is significant, the slopes are significantly different, and if above.below is significant, the intercepts are significantly different.*

Method	Ecosystem	Parameter	Test of	P-Value
ANCOVA	Terrestrial	body mass	Slope	4.89e-8
		above.below	Intercept	0.27
		body mass*above.below	Slope	0.18
	Freshwater	body mass	Slope	5.14e-4
		above.below	Intercept	0.58
		body mass*above.below	Slope	0.49

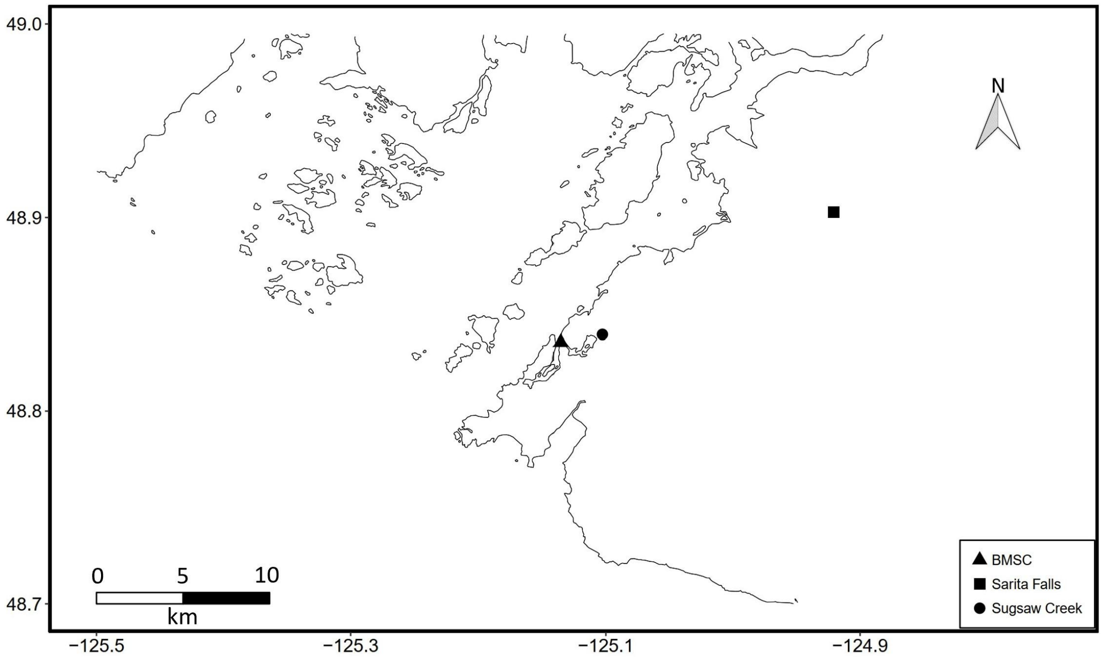

Figure 1: *Site map of Barkley Sound, Vancouver Island, BC. Depicted are the sites that were sampled above and below waterfalls barriers at Sugsaw Creek and Sarita Falls. Also depicted is Bamfield Marine Sciences Centre (BMSC) for reference. Map was generated using R v3.5.1.*

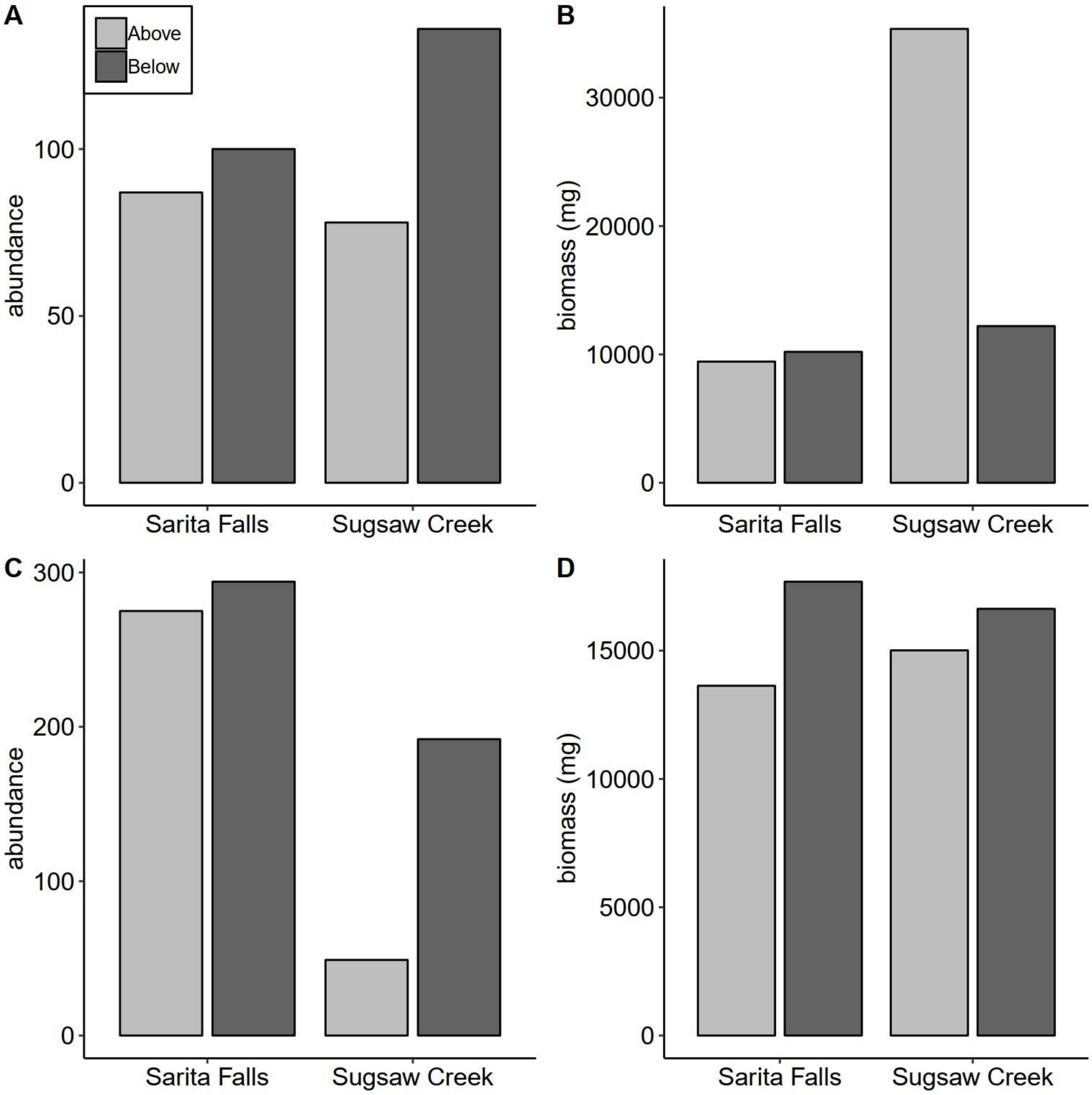

Figure 2: *Total abundance and biomass values from invertebrates captured in Surber net and pitfall traps plotted against location. (A, B) Terrestrial, (C, D) Freshwater. Dark bars indicate below the falls (salmon-bearing) and light bars indicate above the falls (control).*

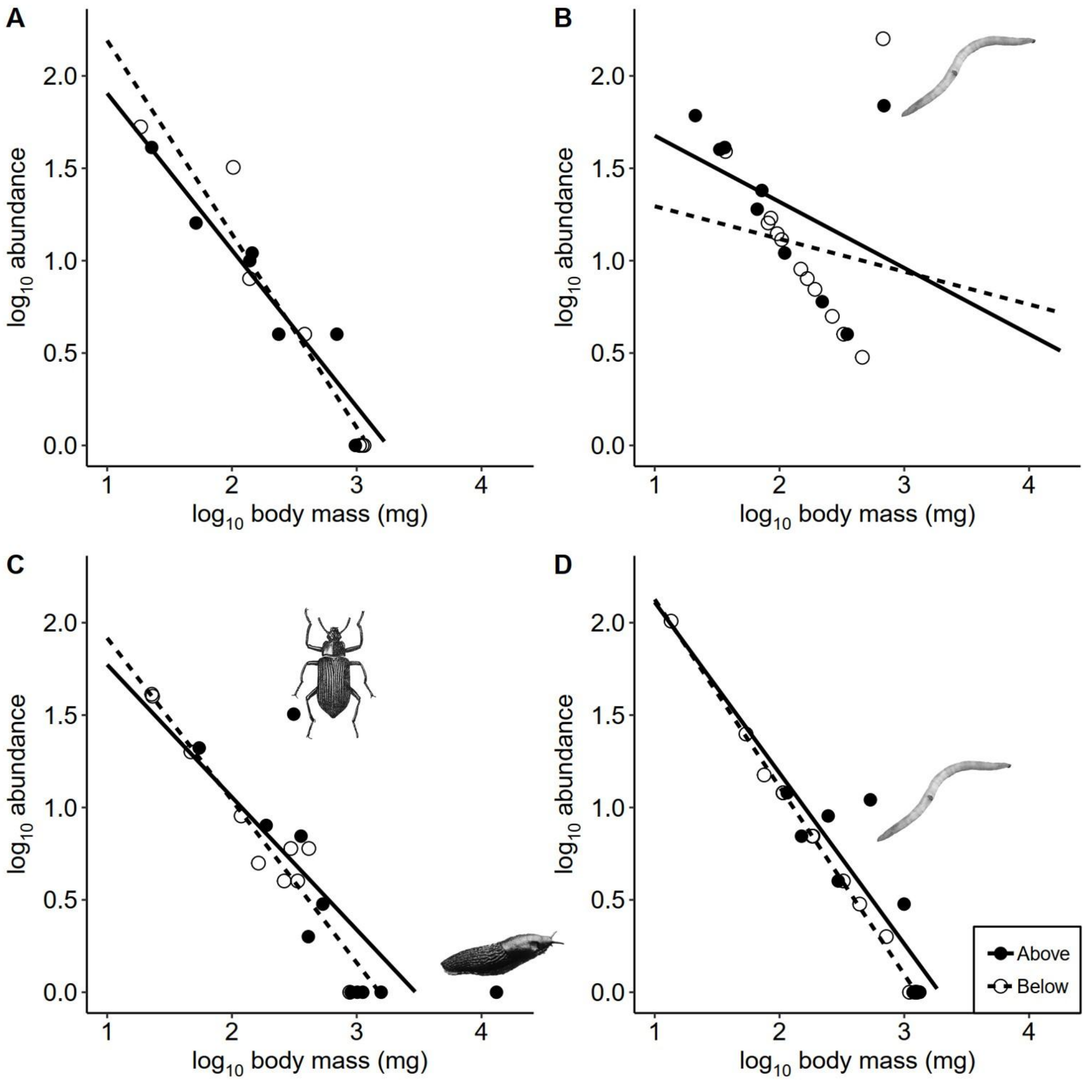

Figure 3: *Log_{10} abundance plotted against log_{10} body mass of freshwater and terrestrial invertebrate species. (A) Sarita Terrestrial, (B) Sarita Freshwater, (C) Sugsaw Terrestrial, (D) Sugsaw Freshwater. Locations above the falls are denoted by solid lines/filled circles, locations below the falls are denoted by dashed lines/empty circles. Images of invertebrates emphasize outlier Orders. Clockwise: Diptera larvae, Stylommatophora, and Coleoptera.*

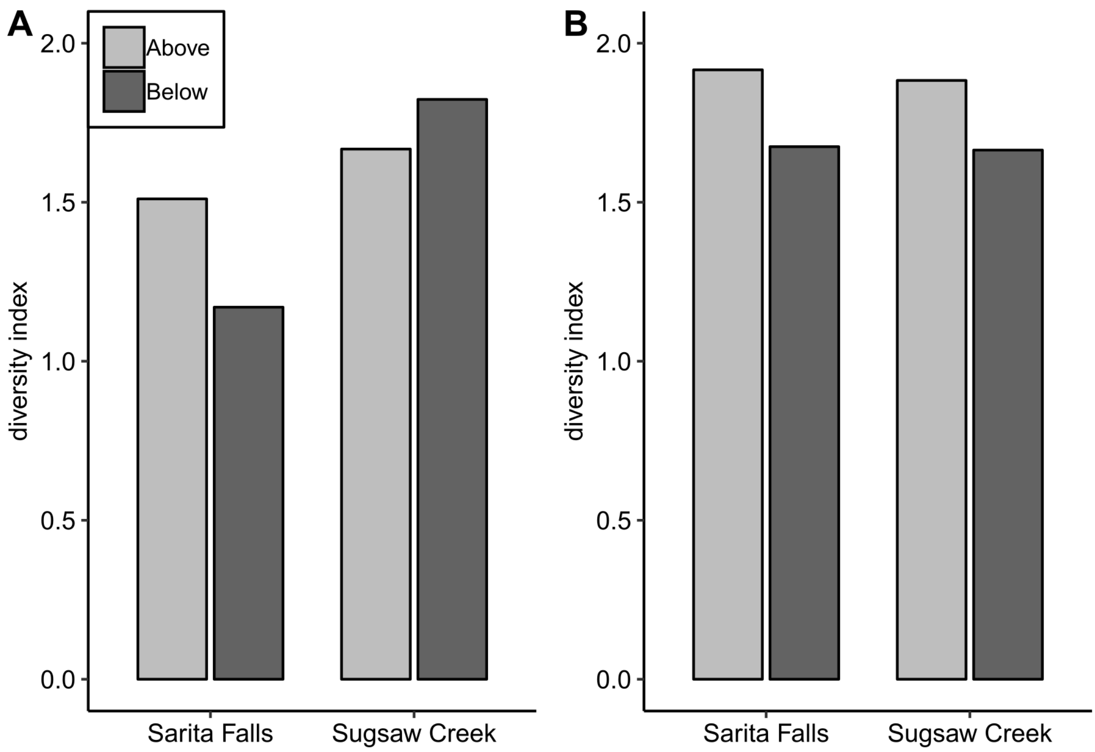

Figure 4: *Shannon-Weiner Diversity Index values of (A) terrestrial and (B) freshwater invertebrate communities above (light grey) and below (dark grey) salmon barriers at both Sugsaw Creek and Sarita Falls.*