

INFLUENCE OF PHYSICAL AND BIOLOGICAL HABITAT VARIABLES  
ON JUVENILE SALMONID AND INVERTEBRATE DRIFT ABUNDANCE  
IN SOUTHWEST BRITISH COLUMBIA STREAMS

by

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## **Abstract**

Determining the physical and biological habitat variables that influence the abundance of juvenile salmonids in British Columbia streams will improve management practices. Habitat models are tools that provide insight into organisms' habitat needs and provide a more efficient mechanism for estimating population abundance than direct measurement. Models have been developed for salmonids in other jurisdictions, but very few have included invertebrate drift (a primary food source for juvenile salmonids) as a predictive variable. This is because temporal and spatial variation of drift abundance are widely assumed to be so high that drift cannot be reliably estimated without unreasonable effort. This thesis investigates the temporal and spatial variability of invertebrate drift and the impact of its inclusion in habitat models for juvenile salmonid abundance in two chapters. The first objective of the first chapter was to evaluate the temporal variability of invertebrate drift by comparing the seasonal and day-to-day variation in drift abundance to spatial variation within and between sites. The second objective was to develop predictive models for invertebrate drift abundance. Aquatic, terrestrial and total invertebrate drift abundances varied primarily between sites and very little between days or months at the same site, indicating that a single day of sampling is sufficient to assess drift abundance for comparison among sites. The abundance of invertebrate drift was related to productivity- and flow-related habitat variables. The objectives of the second chapter were to develop predictive models for juvenile salmonid abundance in southwestern BC using physical and biological habitat variables, to determine whether habitat variables differ between the Coast and Interior regions of BC, to determine the contribution of invertebrate drift to the relative predictive ability of the models, and to determine cost:benefit ratios for the predictive models and their component variables. The final models for predicting abundance of all young-of-year salmonids combined, and rainbow trout (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) individually, included variables related to stream structure and productivity, and the models for rainbow and coho showed regional differences. Invertebrate drift did not improve model fit.

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*For Scott*

## **Co-Authorship Statement**

Sandra Nicol was the primary researcher responsible for identifying and designing this research program, performing the research, analyzing the data and preparing the manuscript. However, assistance with research program identification and design, data analysis, and manuscript preparation was provided by Jordan Rosenfeld and Jonathan Shurin.



## Chapter 1: Introduction

Management and conservation of species requires accurate and efficient estimation of populations sizes. Habitat models are one way of obtaining these estimates. Models that predict population size using habitat measurements have many applications for population management and conservation. These predictive models can improve understanding of species' habitat requirements, including how these requirements interact, and they can require fewer resources to apply than direct field measurements of organism abundance. Habitat models are used to identify high quality habitat for protection, plan habitat restoration projects and monitor resource extraction activities (e.g. Binns and Eiserman 1979, Clark et al. 1993). Freshwater fish such as salmonids (Family Salmonidae) are well suited to habitat modeling due to their restricted habitat (lakes and streams, rather than patches of grassland or ocean floor) and due to the potential utility of predictive models based on simple habitat metrics relative to labour-intensive fish sampling.

Salmonid habitat is often categorized into physical features – such as the area of pools and the number of pieces of large woody debris – and biological variables that influence food abundance such as the amount of detritus. Most studies of juvenile salmonid habitat have emphasized physical variables like channel width, depth, and structure, and reach characteristics like gradient and sediment size (see Coulombe-Pontbriand and LaPointe 2004, Davies 1989, Rosenfeld et al. 2000, Sharma and Hilborn 2001) which are all related to salmonid habitat quantity or quality. The most direct measurement of food availability is invertebrate drift. Salmonids primarily feed on drifting invertebrates (Wipfli 1997) that are delivered by two mechanisms: in situ invertebrate production based on algal- or detrital-based food chains (Vannote et al. 1980), or input of terrestrial invertebrates from the riparian zone (Cada et al. 1987). Canopy cover and composition, organic sediment, temperature, and water conductivity (see Binns and Eiserman 1979, Johansen et al. 2005, Scarnecchia and Bergersen 1987) are additional variables that may influence the abundance of invertebrate prey.

Although invertebrate drift is the preferred food of many juvenile salmonids, it is

conspicuously absent from most habitat models and is rarely used to assess habitat quality (Fausch et al. 1988). Drifting invertebrates, both aquatic and terrestrial, are a primary food source for juvenile salmonids (Wipfli 1997), and elevated drift contributes to increased juvenile salmonid growth (Imre et al. 2004, Nielsen 1992, Rosenfeld et al. 2005, Slaney 1972), density (Slaney 1972) and survival (Imre et al. 2004, Nislow et al. 1998). Food supply is often estimated by proxy through measurements of canopy cover or other variables (Johansen et al. 2005). However, including a direct measurement of invertebrate drift abundance as a candidate variable in habitat models may improve the predictive ability of the models compared to indirect estimates, and may help determine the degree to which food availability limits salmonid abundance.

Invertebrate drift is perceived as difficult to quantify (Binns and Eiserman 1979, Brittain and Eikeland 1988) due to high temporal and spatial variability. This variability has led some authors to suggest that multiple samples (4-7) need to be collected on multiple days to accurately estimate invertebrate drift abundance (Allan and Russek 1985, Matthaei et al. 1998, Shearer et al. 2002). Unfortunately, such resource-intensive sampling protocols discourage investigators from using drift to assess habitat quality for juvenile salmonids. However, samples collected on a single day may be sufficient depending on the degree of temporal variation between days relative to spatial variation between sites. As one of the reasons to use habitat models is their improved efficiency, the sampling protocol for invertebrate drift will impact its inclusion in models; if drift sampling requires multiple visits to a site it will not be viewed by fisheries managers as a practical index of habitat quality.

Habitat models are often a more time-efficient way to estimate salmonid abundance than direct measurements. The predictive variables that biologists choose to include in regression analysis are usually based on expert opinion as to which variables are most effective. However, variables are rarely selected in an explicit cost-benefit framework. Assessing the cost-effectiveness of habitat models and their terms (the habitat variables) should allow fisheries scientists to choose which habitat models and component variables maximize predictive power. A cost-benefit analysis should quantify the advantages and disadvantages of various habitat variables and whole models, allowing investigators to choose to use

direct measurements of fish abundance, an existing model, or a new combination of habitat variables to estimate habitat quality.

This thesis is organized into two related studies. Chapter 2 examined the temporal and spatial variability of invertebrate drift to determine the level of sampling intensity (single visit or multiple visit) necessary to compare drift abundance between sites. If multi-day sampling is required then it is unrealistic to expect fisheries managers to use invertebrate drift as an index of habitat quality. The objectives of this study were: 1) to determine whether accurately measuring drift requires sampling on multiple days by comparing the temporal variation in drift abundance on a seasonal and day-to-day basis to spatial variation between sites, 2) to determine the range of drift between sites in Coast and Interior regions of southwestern British Columbia, 3) to develop predictive models between invertebrate drift abundance and a suite of physical and biological habitat variables, and 4) to determine the variables associated with drift abundance at a landscape scale.

Chapter 3 involved developing habitat models for young-of-the-year (YOY) rainbow trout (*Oncorhynchus mykiss*), coho salmon (*O. kisutch*), and all YOY combined using physical and biological habitat variables, including invertebrate drift. The objectives of this study were 1) to develop predictive models for juvenile salmonid abundance in southwestern BC using physical and biological habitat factors, 2) to determine whether habitat variables differ between the Coast and Interior regions, 3) to determine the contribution of invertebrate drift to the relative predictive ability of models, and 4) to determine benefit:cost ratios for predictive models and their component variables.

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## Chapter 2: Spatial and temporal variability of invertebrate drift in southwest British Columbia streams<sup>1</sup>

### Introduction

Drifting invertebrates of aquatic and terrestrial origin are a primary food source for juvenile salmonids (Wipfli 1997), and elevated drift contributes to increased juvenile salmonid growth (Imre et al. 2004, Nielsen 1992, Rosenfeld et al. 2005, Slaney 1972), density (Slaney 1972) and survival (Imre et al. 2004, Nislow et al. 1998). Invertebrates are a critical component of stream food webs, yet drift is seldom used as a measure of habitat quality in favour of aspects of habitat structure like woody debris (Fausch et al. 1988). This is largely because drift is perceived as difficult to quantify (Binns and Eiserman 1979, Brittain and Eikeland 1988), with high temporal and spatial variability. This variability has led some authors to suggest that multiple samples (4-7) need to be collected on different days to accurately estimate invertebrate drift abundance (Allan and Russek 1985, Matthaei et al. 1998, Shearer et al. 2002). Such resource-intensive sampling protocols (laboratory time required to sort and quantify a single drift sample can vary from 3 to 10 hours) have likely contributed to the limited use of drift to assess habitat quality for juvenile salmonids. However, fewer samples collected on a single day may be sufficient depending on the degree of temporal variation between days relative to spatial variation between sites. Understanding how invertebrate drift biomass varies in time and space will allow investigators to better evaluate the number of samples required to accurately characterize drift biomass, and to evaluate the potential of drift as a predictor of salmonid abundance.

The scale and magnitude of temporal variation in drift abundance will affect the sampling effort required to accurately assess prey abundance, and therefore prey availability for drift-feeding fish. Temporal variation in drift occurs at a hierarchy of scales, ranging from well-documented diel variation to variation between days and longer seasonal trends (Resh and Rosenberg 1989). Aquatic invertebrates are vulnerable to visual predators and preferentially drift at night (Flecker 1992), so that drift has relatively uniform low daytime abundance and

1 A version of this chapter will be submitted for publication:  
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peaks shortly after dark (Waters 1962), whereas terrestrial invertebrates fall into streams more frequently during the day (Rincón and Lobón-Cerviá 1997). Variation between days has also been studied but reports of the magnitude of day-to-day variation differ (Shearer et al. 2002, Williams 1980). Williams (1980) found that between-day variation in drift abundance varied up to 6 times, suggesting that investigators must sample a site on more than one day in order to estimate drift abundance. Other studies suggest that day-to-day variation is no greater than variation between replicates (Shearer et al. 2002).

Day-to-day variability in drifting aquatic invertebrates is affected by nocturnal light levels (aquatic drift is suppressed on bright nights that expose invertebrates to visual predators; Holt and Waters 1967), temporal lags that cause compensatory drifting (high night time aquatic drift after a night of suppressed drifting), life history events such as mass emergence of adults (Williams 1980) and variable discharge. Day-to-day variability of terrestrial invertebrates is generally higher than for aquatic invertebrates (Nakano et al. 1999), indicating higher variance in the factors (eg. wind) that deliver terrestrial prey from riparian zones. Total drift abundance also shows longer seasonal trends. Invertebrate drift biomass (per m<sup>3</sup>) in temperate regions tends to be higher in the summer than the winter (Brittain and Eikeland 1988, Kawaguchi and Nakano 2001, Shearer et al. 2002). Allan et al. (2003) found that drift abundance peaked in July, and others (eg. Bacon et al. 2005, Rincón and Lobón-Cerviá 1997, Slaney 1972) have observed spring peaks in drift abundance followed by summer declines. Understanding the drivers of temporal variation in drift allows improved sampling protocols for examining the mechanisms that influence prey abundance for drift-feeding fish.

Differences in average drift abundance between streams leads to spatial variation in drift at regional scales, which could be a major driver of differences in habitat capacity for juvenile salmonids. Aquatic drift abundance should be influenced by variables from one or both of two categories: those related to biotic productivity factors and those related to invertebrate entrainment in the water column. In principle, aquatic invertebrate drift should be higher in streams with greater productivity, in which case aquatic drift biomass may be associated with habitat variables that affect benthic productivity, such as temperature, stream nutrients (Richardson 1993), algae (chlorophyll-a) concentrations (Schell 1999, Shearer et al. 2003),

detritus density or quality (Chadwick and Huryn 2007), or factors such as riparian canopy cover that influence benthic primary production in light-limited streams (Wallace et al. 1997, Wipfli 1997, Wipfli and Musselwhite 2004). Flow-related physical factors that affect entrainment of benthic invertebrates into the drift, such as water velocity (Harvey et al. 2006), channel gradient, the availability of riffle habitat (Rader 1997), or flow regime (Lancaster 1999) may be associated with drift. Biomass of drifting terrestrial invertebrates is affected by the chance occurrence of an invertebrate falling into a stream; terrestrial invertebrates may be influenced by factors that affect their activity level such as temperature (Edwards and Huryn 1995), or their overall abundance in the riparian area such as canopy cover and composition. However, evidence for the importance of canopy cover composition on terrestrial invertebrate abundance is mixed (Johansen et al. 2005, Mason and MacDonald 1982, Wipfli 1997, Wipfli and Musselwhite 2004). Identifying the factors that influence drift abundance will improve understanding of how habitat influences salmonid food supply, and consequently could lead to improved management of fish habitat.

The primary objectives of this study were: 1) to determine whether accurately measuring drift requires sampling on multiple days by comparing the temporal variation in drift abundance on a seasonal and day-to-day basis to spatial variation between sites at a subset of 4 intensively sampled streams; 2) to determine the range of drift between sites in Coast and Interior regions of southwestern British Columbia, 3) to develop predictive models between invertebrate drift abundance and a suite of physical and biological habitat variables, and 4) to determine the variables associated with drift abundance at a landscape scale.

## **Methods**

### **Temporal variation: magnitude of day-to-day and seasonal variation relative to site effects**

Four sites were chosen for repeated sampling to determine the magnitude of day-to-day variation in drift biomass: one small and one large stream from the west coast of British Columbia (Coast region, Husdon and Chapman Creeks, respectively), and one small and



one large stream from the southern interior of BC (Interior region, Senn and Yard Creeks, respectively). Sites were chosen that differed in size and geographic area so that any conclusions are not limited to a specific type of stream, such as small streams in the Coast region. Sites were chosen from the pool of sties recommended by local fisheries biologists because they were representative of streams in their size classes in their regions. Each site was sampled twice per month over four months (June to September 2005), with within-month samples 1-3 days apart to minimize effects of seasonal trends on daily variation and to allow us to examine variation at two temporal scales (days and months). No sampling was conducted during or soon after precipitation to standardize the effect of weather on drift abundance. Two replicate drift samples were collected on each sampling date, yielding 16 samples per stream except for Yard Creek, where a second visit in June was cancelled due to weather.

### **Invertebrate Drift Sampling**

Invertebrate drift samples were collected at the upstream end of pools immediately below riffles to standardize habitat effects on drift and to measure the quantity of drift that a dominant fish would experience at the head of a pool. The nets were placed in separate pools, and as much as possible nets were positioned so that they did not filter the same water. At sites with no suitable pools nets were placed in riffles. Samples were collected with a 1 m long, 250  $\mu\text{m}$  mesh net with an opening 0.2 m wide, for 180-300 minutes, depending on water velocity. The depth and velocity of the water in the net opening were measured in order to calculate the volume of water sampled, and thereby the biomass of drifting invertebrates per  $\text{m}^3$ . We conducted daytime sampling rather than 24-hour sampling because daytime drift abundance is more uniform (Waters, 1962), and most juvenile salmonids are visual predators that benefit from day time drift abundance. Arguably, daytime drift samples more accurately represent prey abundance for juvenile salmonids than 24 hour drift samples where biomass is dominated by nocturnal peaks. Drift samples were collected at least two hours after sunrise and two hours before sunset to reduce daily variability in light intensity, and were not collected during or after rain events. Samples were preserved in 5% formalin and returned to the lab for sorting.

Invertebrates were sorted from detritus at 10X magnification in the laboratory and preserved in 70% ethanol for later identification and measurement using a digitizer (Roff and Hopcroft 1986). Invertebrates were identified to order with some exceptions; non-arthropods such as nematodes were identified to phylum, and common arthropods such as chironomids were identified to sub-family. Each taxon was categorized as aquatic or terrestrial in origin. Adult insects with aquatic larvae, such as Nematocera (suborder of Diptera), were counted as aquatic. The dry mass (mg) of invertebrates in each sample was calculated using published taxa-specific length-weight regressions (Benke et al. 1999, McCauley 1984, M. Wipfli unpubl., Meyer 1989, Sabo et al. 2002, Sample et al. 1993, Smock 1980).

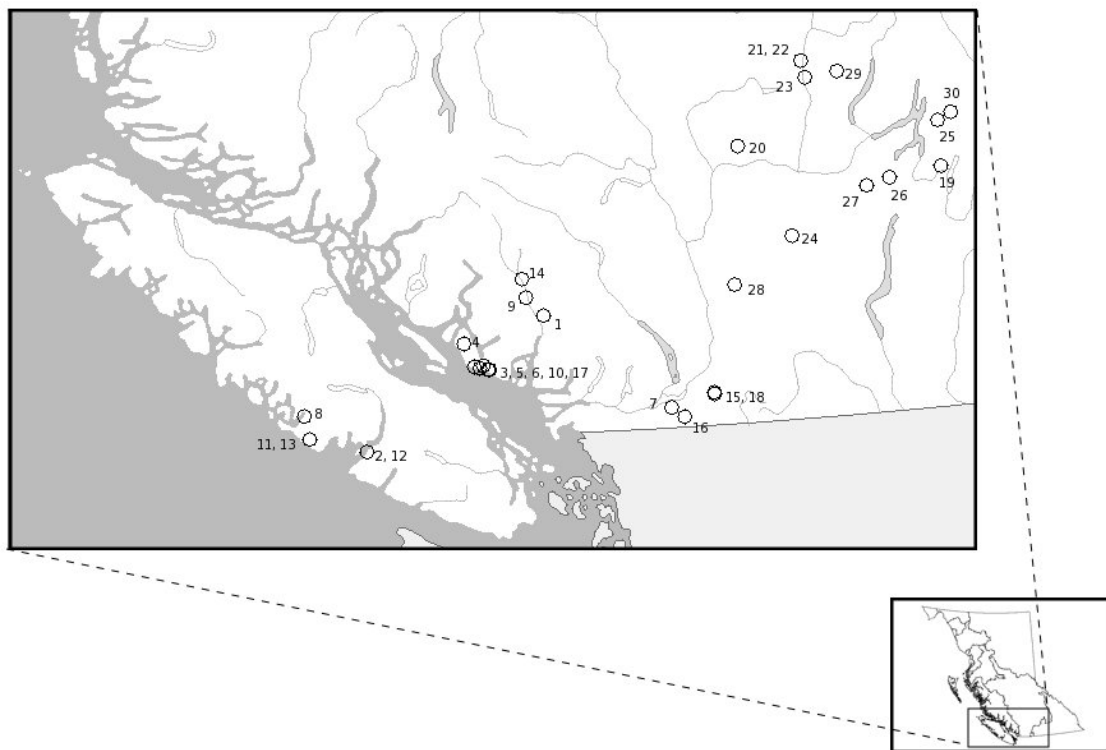
### **Temporal Variation Statistical Analysis**

The magnitude of day-to-day, monthly, and between- and within-site variance was compared with mixed model analysis of variance using the lme4 package (Bates 2007) in R 2.4.1 ([www.r-project.org](http://www.r-project.org)). The models were fit using restricted maximum likelihood (REML). Candidate models with the four combinations of fixed factors were compared to determine which best explained the variability in the drift density (mg dry mass per m<sup>3</sup> water). The full model included two fixed factors (region (Coast vs. Interior) and month (June-September)) and two random grouping factors (Julian day and site). Month was analyzed as an ordered factor to allow polynomial analyses (by default R examines the polynomial terms of an ordered factor). Site was considered to be a random factor because the four sites were chosen to be representative of the population of available sites, not for specific interest in those particular sites. The region model included region, Julian day, and site. The month model included month, Julian day and site. The random factors model included only the random factors Julian day and site. The analysis was not performed as a nested ANOVA due to complications arising from different dates; using Julian day addresses daily variation. Drift densities were log transformed so that model residuals would meet assumptions of normality. The models were compared using Akaike weights based on the Second-Order Information Criterion (AIC<sub>c</sub>, for small samples). The weights were used to calculate evidence ratios to select the best fit model (Burnham and Anderson 2002). Variance components were

calculated for the random factors to assess their relative contribution to total variance in drift abundance, with the residual variance representing variance among replicate samples collected on a single day. This analysis was applied to total invertebrate biomass, aquatic invertebrates and terrestrial invertebrates separately.

**Spatial variation: factors influencing drift abundance across multiple streams at a landscape scale**

Thirty sites (including the four sites used for the temporal study) in the Coast and Interior regions of British Columbia were sampled for drift abundance and habitat features using the protocols described above in the summer of 2005 or 2006 (Figure 2.1). At the four temporal variation sites a third sample was collected on the first August sampling date, and the three samples from that date were used for the spatial analysis. Three drift samples were taken at all other sites, and average biomasses of replicate samples were used in analysis. The 30



**Figure 2.1:** Locations of study streams in south western British Columbia, Canada. Some sites are close enough together that they share a point. Number labels refer to row labels in Appendix 1. Universal Transverse Mercator coordinates are also available in Appendix 1.

sites were chosen to cover a wide range of productivity levels and stream sizes (1.7-33.1 m channel width; Appendix 1). Measurements of habitat features were made on the same day as samples were collected when possible.

### **Habitat Measurements**

Spatial variation in drift, between and within streams, can also be considerable and is influenced by measurable habitat factors. However, the measurement of habitat effects is complicated by the impact of upstream invertebrate density, which can be detected long distances downstream (Waters 1965, Wipfli and Gregovich 2002). Habitat factors must therefore be consistent for a great enough distance that upstream invertebrate production levels do not mask their effects. That is, the impact of a short stretch of stream with no canopy cover probably cannot be detected downstream or even within that stretch due to mixing with invertebrate drift originating upstream. For this reason habitat surveys were conducted over 80-250 m and average values were calculated for the surveyed area. Invertebrate drift samples were collected within the survey area.

Habitat surveys were conducted at all 30 sites (see Moore et al. 1997) to collect information on reach-level factors that may influence invertebrate drift abundance. Average summer temperature was estimated for each site using ClimateBC V.3.2 (Wang et al. 2006) and UTM coordinates and elevation measurements for each site. Conductivity was measured once at each site. The intermediate dimension (median length of the x, y, and z axes) of the five largest water-moved particles (Hogan 1996), and the percent canopy cover and the canopy composition (percent cover of conifer, alder, and other deciduous trees) were measured at 3-5 locations spaced throughout each site. Note that the sum of the conifer, alder and other deciduous canopy cover was often greater than the total canopy cover estimate when the different types of canopies overlapped. The length and width of each channel unit (riffle, pool, glide, run, and cascade) were measured, including channel units in secondary and backwater channels. These measurements were used to calculate mean bankfull width and the percent area of each site by channel unit type. Substrate composition (fines, gravel, cobbles, boulders, bedrock, percent particulate organic matter (POM)), gradient, and depth

of each channel unit were weighted by channel unit area to calculate average values for each site.

### **Spatial Variation Statistical Analysis**

Regression models to predict total, aquatic, and terrestrial drift abundance were fit using linear models in R 2.4.1. Models were fit using ordinary least squares on transformed, centred data. In order to apply these models to new data sets the new data must be centred using the same constants as this study (see Appendix 1 to calculate variable means). Data were log transformed for normality (Appendix 1) and centred to reduce collinearity between main effects and interaction effects (Quinn and Keough 2002). After examining correlation between the measured habitat variables, explanatory variables with no correlation coefficients greater than 0.7 were selected as a starting point for model selection (if two variables were strongly correlated then the model selection process was started twice, once with each variable). These variables were average summer temperature (temp), conductivity (cond), largest particle (lp), percent alder cover, gradient, percent cover of gravel sediment (grav), and percent cover of organic sediment (org). Site elevation (elev) was related to region (region), and percent canopy cover (can) was correlated with bankful width (wb). One of elev and region (strongly related), one of can and wb, and the other seven target variables were included in four starting models for each invertebrate biomass value (total, aquatic, terrestrial). Interaction terms were added to the starting models based on improved AIC values. Terms were then removed from the starting models in a stepwise fashion until removing terms no longer improved AIC values. The models with the lowest AIC values were selected for comparison. The models were compared using Akaike weights based on the Second-Order Information Criterion (AICc for small samples). The weights were used to calculate evidence ratios to select the best fit model (Burnham and Anderson 2002). Tolerance, Cook's Distance, and normality of the residuals were checked for all selected models. Interactions included in final models were investigated using simple slopes (Quinn and Keough 2002). The simple slope of a variable is its slope when the variable that it interacts with is held constant. Generally the simple slopes are calculated at the mean of the other variable, and one standard deviation above and below the mean (low, average and high

values of the interacting variable). Simple slope calculations allow greater understanding of trade-offs and other interactions. Habitat measurements from the two regions were compared using two-sample Student's t-tests to examine differences between the regions.

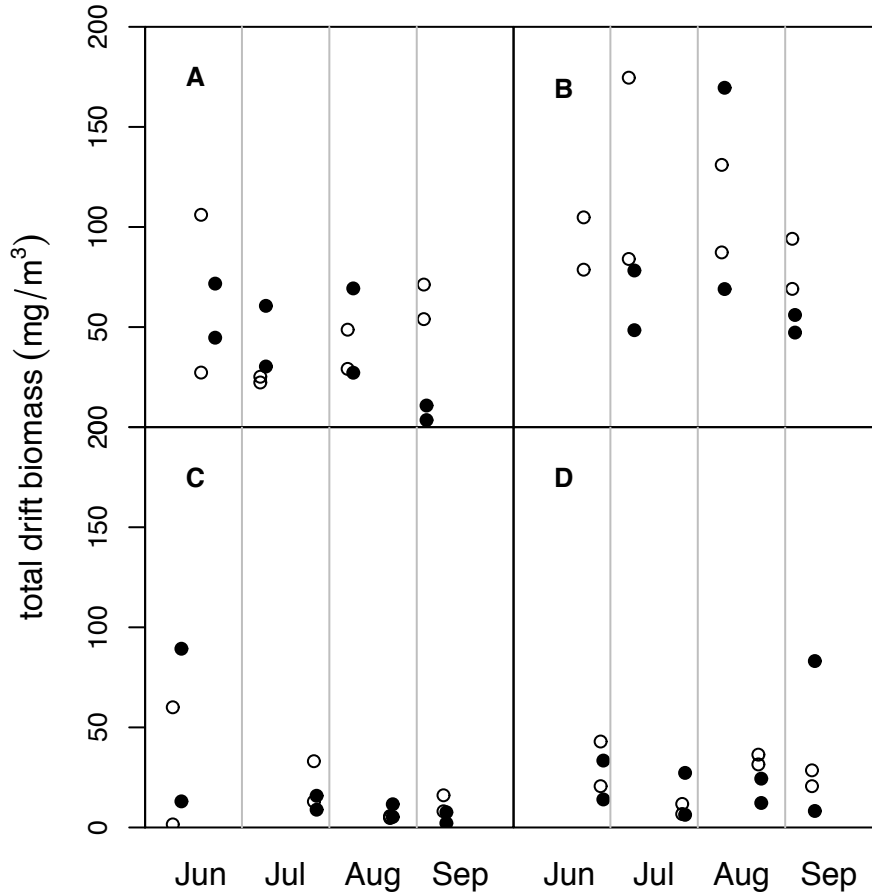
## Results

### Temporal Variation

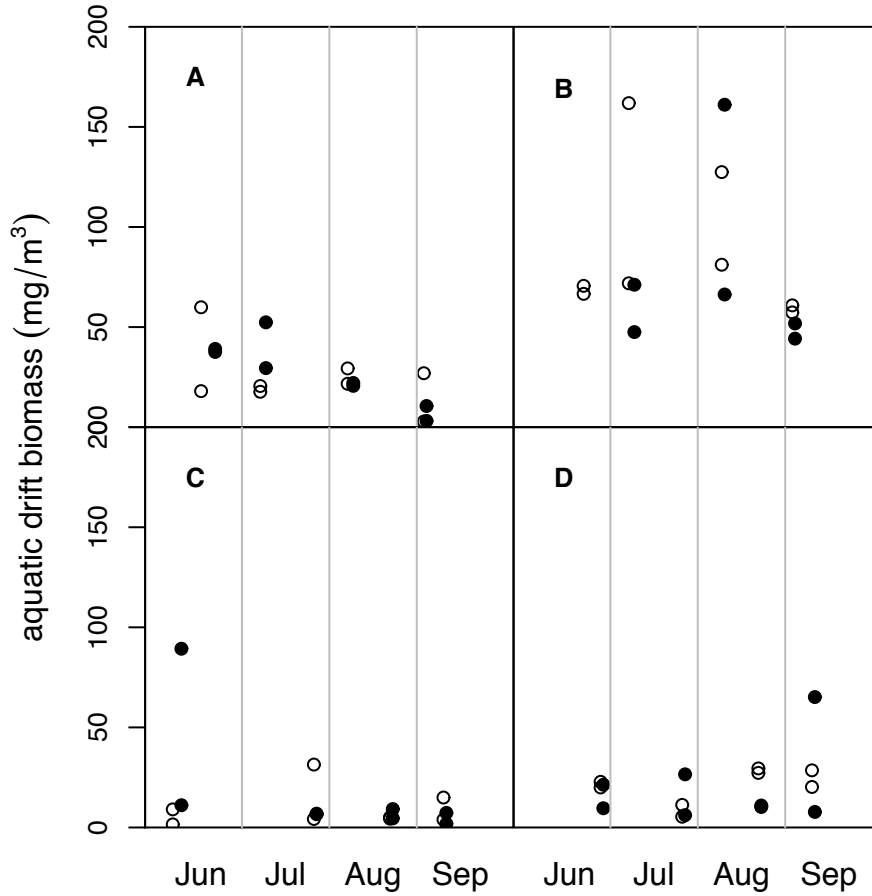
Total invertebrate drift biomass in a sample varied from 1.59 mg/m<sup>3</sup> in Husdon Creek (the small Coast stream) to 180.60 mg/m<sup>3</sup> in Yard Creek (the large Interior stream; Figure 2.2). The four sites, Chapman, Husdon, Yard and Senn had averages (over all samples) of  $26 \pm 19$  (standard deviation) mg/m<sup>3</sup>,  $19 \pm 24$  mg/m<sup>3</sup>,  $92 \pm 44$  mg/m<sup>3</sup>, and  $44 \pm 27$  mg/m<sup>3</sup>, respectively. Average drift biomass in the Interior region was three times the biomass in the Coast region ( $66 \pm 43$  vs.  $22 \pm 21$  mg/m<sup>3</sup>, respectively).

Aquatic invertebrates made up 78% of the total invertebrate biomass averaged across all samples (Figure 2.3); this proportion was consistent between sites. Terrestrial invertebrates made up the remaining 22% (Figure 2.4). Terrestrial and aquatic invertebrates also showed the same relative drift densities between sites as total invertebrates; Yard Creek had the highest drift density followed by Senn, Chapman, and Husdon. The average terrestrial and aquatic invertebrate drift densities in the Interior region greater than in the Coast region (aquatic:  $51 \pm 41$  mg/m<sup>3</sup> and  $17 \pm 18$  mg/m<sup>3</sup>, respectively; terrestrial:  $15 \pm 16$  mg/m<sup>3</sup> and  $5 \pm 10$  mg/m<sup>3</sup>, respectively).

The best fit model for total, aquatic, and terrestrial invertebrates based on AICc Akaike weights ( $\omega_i$ ) was the region model (including region<sub>fixed</sub>, site<sub>random</sub>, and Julian day<sub>random</sub>; Table 2.1). The region model had an Akaike weight 2.9 times higher than the random factors model for total invertebrate density, 1.9 times higher than the random factors model for aquatic invertebrate density, and 2.2 times higher than the full model for terrestrial invertebrate density, indicating that the region model was approximately twice as likely as the next best model for all invertebrate categories. These results suggest that there was no consistent

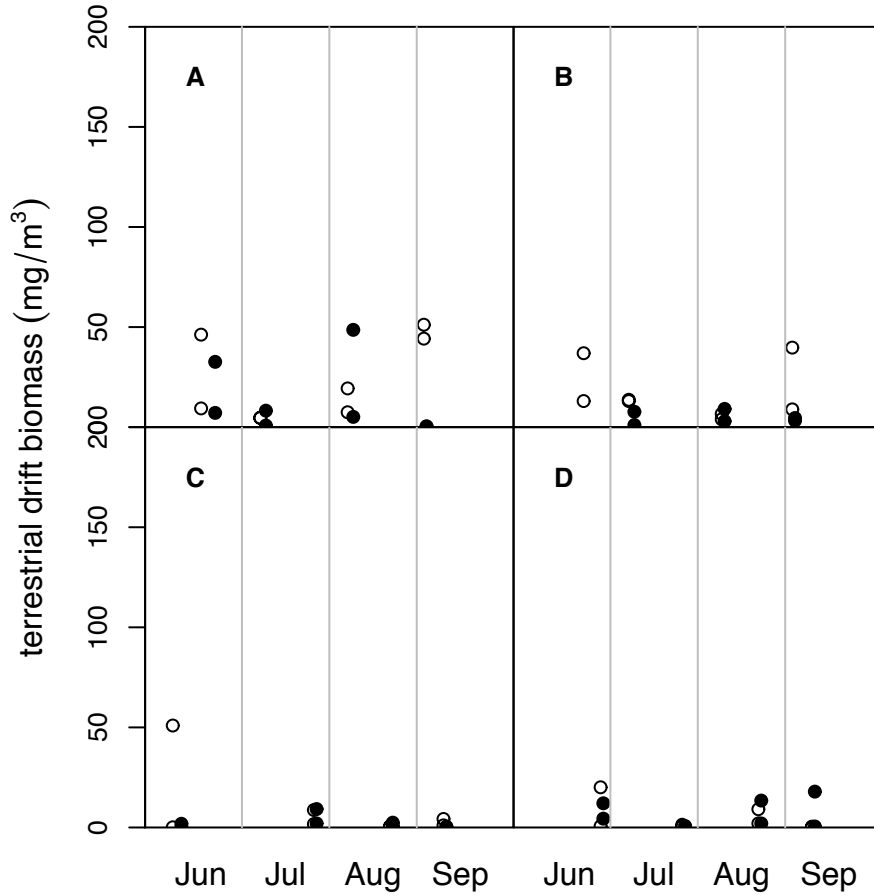


**Figure 2.2:** Total invertebrate drift biomass of samples collected at four sites (A Senn Creek, B Yard Creek, C Hudson Creek, D Chapman Creek) over four months. Open and filled circles indicate the first and second visits to the site each month. No consistent between day variation is apparent; variation between within the sites appear to be the primary sources of variation.



**Figure 2.3:** Aquatic invertebrate drift biomass of samples collected at four sites (A Senn Creek, B Yard Creek, C Husdon Creek, D Chapman Creek) over four months. Open and filled circles indicate the first and second visits to the site each month. No consistent between day variation is apparent; variation between within the sites appear to be the primary sources of variation.





**Figure 2.4:** Terrestrial invertebrate drift biomass of samples collected at four sites (A Senn Creek, B Yard Creek, C Husdon Creek, D Chapman Creek) over four months. Open and filled circles indicate the first and second visits to the site each month. No consistent between day variation is apparent; variation between within the sites appear to be the primary sources of variation.

**Table 2.1:** Likelihood ratio calculations for the temporal candidate models for total, aquatic and terrestrial drift.  $AIC_c$  is the Second-Order Information Criterion (used for small samples),  $\Delta_i$  is the difference between the  $AIC_c$  and the minimum  $AIC_c$ ,  $lik$  is the likelihood of the model given the data ( $e^{(-\frac{1}{2} * \Delta_i)}$ ),  $\omega_i$  is the likelihood of the model divided by the sum of the likelihoods for the competing models (see Burnham and Anderson 2002 ch 2). The  $\omega_{max} / \omega_i$  ratio indicates how much more likely the best model ( $\omega_{max}$ ) is compared to the candidate model ( $\omega_i$ ).

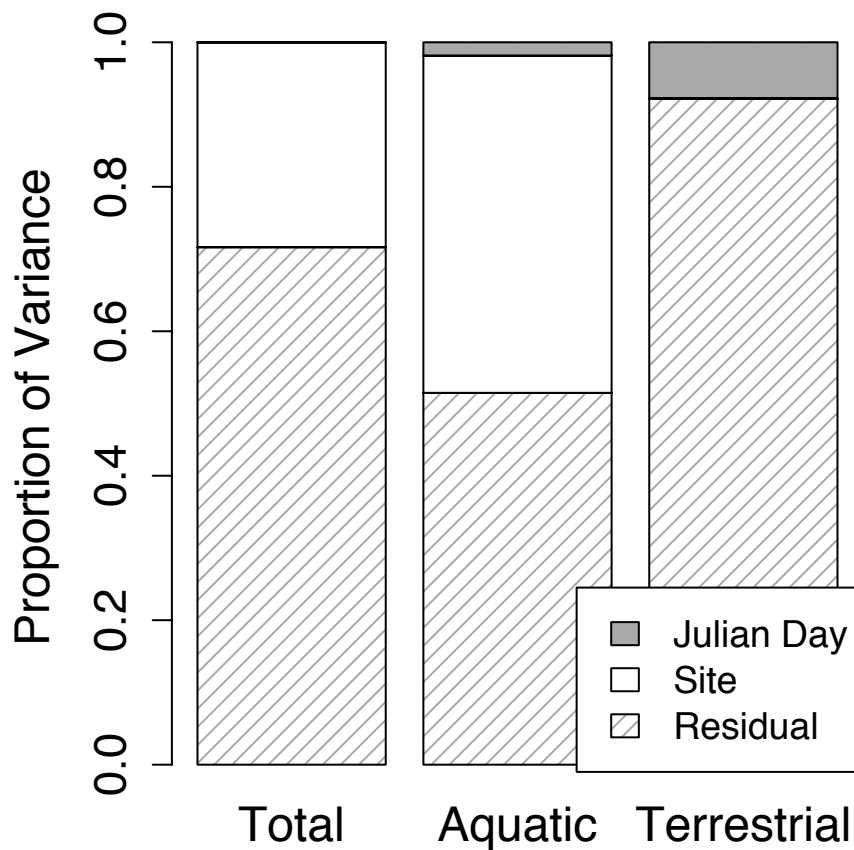
Model	$AIC_c$	$\Delta_i$	lik	$\omega_i$	$\omega_{max} / \omega_i$
Total					
region + month + Julian day + site	170.77	6.57	0.04	0.03	26.7
<b>region + Julian day + site</b>	<b>164.2</b>	<b>0</b>	<b>1</b>	<b>0.71</b>	<b>1</b>
month + Julian day + site	172.63	8.43	0.01	0.01	67.5
Julian day + site	166.31	2.11	0.34	0.25	2.9
Aquatic					
region + month + Julian day + site	168.07	6.57	0.04	0.02	26.7
<b>region + Julian day + site</b>	<b>161.5</b>	<b>0</b>	<b>1</b>	<b>0.63</b>	<b>1</b>
month + Julian day + site	169.13	7.63	0.02	0.01	45.3
Julian day + site	162.81	1.31	0.51	0.32	1.9
Terrestrial					
region + month + Julian day + site	237.11	1.6	0.45	0.29	2.2
<b>region + Julian day + site</b>	<b>235.51</b>	<b>0</b>	<b>1</b>	<b>0.65</b>	<b>1</b>
month + Julian day + site	242.66	0.03	0.02	0.02	35.5
Julian day + site	241.12	0.06	0.06	0.04	16.5

seasonal effect on any of the invertebrate groups, but that drift biomass was higher in the Interior. There was strong support for the inclusion of region in the final model; the region-only model had a likelihood weight up to 16 times higher (was 16 times more likely; Table 2.1) than the random factors model that rejected region.

The coefficients for region for total, aquatic, and terrestrial invertebrates confirm that invertebrate drift is higher in the Interior than the Coast region (Table 2.2). Variance components analysis indicated that the random variation contributed by Julian day was negligible for total and aquatic invertebrate drift and low (8%) for terrestrial invertebrates (Figure 2.5). Between-site variation is negligible for terrestrial invertebrates but contributes 28% of the random variation for total invertebrate drift and 47% for aquatic drift. Within-

**Table 2.2:** Model coefficients and standard errors for the intercept and fixed factor (region) for total, aquatic and terrestrial invertebrates temporal models.

Invertebrates	Intercept (SE)	Region (Interior) coefficient (SE)
Total	2.68 (0.39)	1.29 (0.55)
Aquatic	2.39 (0.54)	1.24 (0.76)
Terrestrial	0.46 (0.31)	1.58 (0.44)



**Figure 2.5:** Cumulative variance components of site, day, and residual (within-site) variation. The variance components show the proportion of random variation that can be attributed to site, day, and residual variation for total, aquatic and terrestrial invertebrate drift.

site variation (residual variation due to spatial replication ( $n = 2$  samples) within a site) contributed the majority of the random variation for total, aquatic and terrestrial invertebrates (72%, 51% and 92%, respectively). The high residual variation of terrestrial invertebrates indicates greater variation between replicate samples than between days, possibly due to the small number of replicates (2) collected on each day, the effects of single large terrestrial invertebrates that contribute disproportionately to biomass (e.g. a single large beetle can skew a dry weight measurement) or greater accumulations of leaves bearing terrestrial invertebrates in one drift net than another.

### **Spatial Variation**

Invertebrate biomass at the 30 sites varied over an order of magnitude from 7.9-283 mg/m<sup>3</sup>, except for one site with very high biomass (High Falls with 1062 mg/m<sup>3</sup>; Appendix 1). Average invertebrate drift biomass was  $97 \pm 191$  mg/m<sup>3</sup> for total invertebrates,  $52 \pm 46$  mg/m<sup>3</sup> for aquatic invertebrates, and  $45 \pm 169$  mg/m<sup>3</sup> for terrestrial invertebrates. Similar to seasonal samples, aquatic invertebrates made up  $76\% \pm 20\%$  of total invertebrate drift biomass; aquatic invertebrate mass was greater than terrestrial invertebrate mass at all sites except for one Coast stream (High Falls) and one in the Interior (Criss) due to the presence of several large terrestrial invertebrates (caterpillars). Total invertebrate biomass was higher in the Coast than the Interior region (100 mg/m<sup>3</sup> and 92 mg/m<sup>3</sup>), but this is largely due to a single site (High Falls) with particularly high biomass due to very large terrestrial inputs (several caterpillars fell into the stream). When this site was identified as an outlier (using a box plot) and excluded the average total invertebrate drift biomass in the Coast region fell to  $44 \pm 34$  mg/m<sup>3</sup>. Aquatic invertebrate drift biomass was  $41 \pm 38$  mg/m<sup>3</sup> in the Coast region and  $70 \pm 52$  mg/m<sup>3</sup> in the Interior, while terrestrial invertebrate drift densities in the Coast and Interior were  $8 \pm 9$  mg/m<sup>3</sup> and  $23 \pm 34$  mg/m<sup>3</sup>, respectively, with the High Falls Coast site excluded as an outlier ( $60 \pm 218$  mg/m<sup>3</sup> with High Falls site included). The High Falls site was excluded from multiple regression analysis if its Cook's Distance exceeded 1 indicating high influence (Quinn and Keough, 2002), otherwise it was included in analysis.

Total canopy cover was significantly higher in the Coast region ( $39\% \pm 29\%$  versus  $17\% \pm$

20%, Welch two-sample t-test on untransformed data:  $t = 2.48$ ,  $p = 0.02$ ). The proportion of total canopy in each category (alder, other deciduous, and canopy) did not differ between regions. Alder constituted  $52\% \pm 38\%$  of total canopy cover at Coast sites, and  $50\% \pm 34\%$  at Interior sites. Other deciduous trees were  $25\% \pm 24\%$  and  $35\% \pm 49\%$ , and coniferous trees were  $23\% \pm 27\%$  and  $28\% \pm 37\%$  in the Coast and Interior, respectively. Elevation (199 m and 517 m, Welch two-sample t-test:  $t = -6.74$ ,  $p = 1.13 \times 10^{-6}$ ) and conductivity ( $65.7 \mu\text{S} \pm 41.6 \mu\text{S}$  and  $130.0 \mu\text{S} \pm 91.2 \mu\text{S}$ , Welch two-sample t-test:  $t = -2.3$ ,  $p = 0.04$ ) were lower at Coast sites.

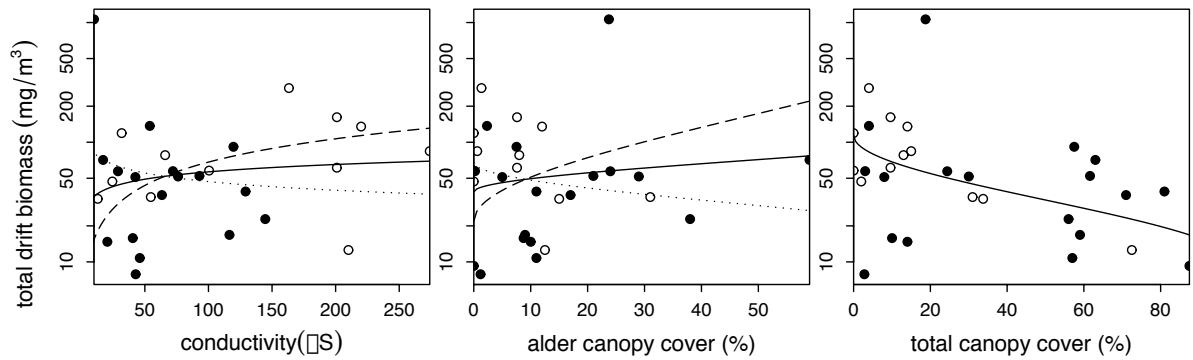
The final models predicting total, aquatic, and terrestrial invertebrate densities using habitat measurements were selected using the same evidence ratio method as for temporal variation (Table 2.3). All final models had acceptable Cook's Distance and tolerance values and normally distributed residuals. The best models for total, aquatic, and terrestrial invertebrate densities used different variables (Table 2.4). The best model for total invertebrates had an  $r^2$  of 0.28 ( $F_{4,24} = 2.38$ ,  $p = 0.08$ ), and included variables related primarily to aquatic and riparian productivity: conductivity, alder cover, canopy cover, and the interaction between conductivity and alder cover (Figure 2.6). Simple slopes analysis (Quinn and Keough 2002) of the interaction between conductivity and percent alder shows that the slope of the alder coefficient was positive (2.64) when conductivity was low (one standard deviation below the centred average of 0,  $\log(\text{conductivity}) = 0.898$ ). The alder coefficient was positive but lower (0.79) at average conductivity, and negative at high conductivity (-1.06 at one standard deviation above average conductivity). The same effect occurred for the slope of conductivity when alder was held at low, average and high values; the slope for conductivity was 0.65 at low alder cover ( $\text{SD asin}\sqrt{\text{alder}} = 0.216$ ), 0.20 at average alder cover and -0.24 at one standard deviation above average. The best model for aquatic invertebrate drift had greater predictive power ( $r^2 = 0.44$ ;  $F_{2,25} = 4.94$ ,  $p = 0.004$ ), and included region and flow-related habitat variables: gradient, bankfull width, and the interaction between region and gradient (Figure 2.7). Simple slopes analysis showed a coefficient for gradient of 0.62 in the Coast region and -0.34 in the Interior, indicating a positive effect of gradient on drift in the Coast but not in the Interior. The High Falls site did not have high influence on these two models and was included throughout the analysis. However, it had high influence for

**Table 2.3:** Likelihood ratio calculations (see Table 2.1) for the spatial candidate models for total, aquatic and terrestrial drift. Abbreviations are: grad (gradient), wb (bankfull width), cond (conductivity), ald (alder cover), reg (region), can (canopy cover), org (organic sediment), elev (elevation), lp (largest particles).

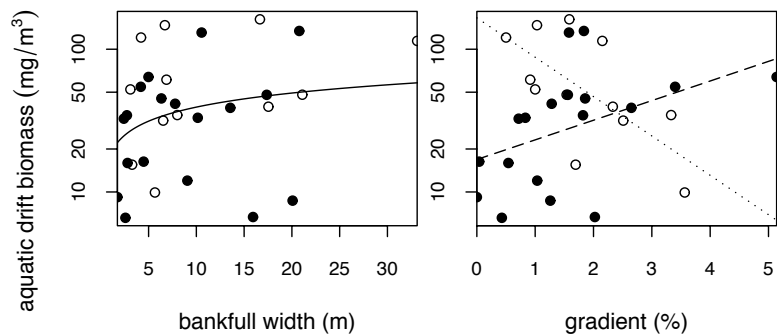
Model	AICc	$\Delta_i$	lik	$\omega_i$	$\omega_{\max} / \omega_i$
<b>Total</b>					
grad + wb + cond + ald + cond*ald	9.08	4.91	0.09	0.04	11.63
wb + cond + ald + cond*ald	7.05	2.88	0.24	0.11	4.23
cond + ald + cond*ald	6.56	2.39	0.3	0.14	3.31
reg+ reg*can + can + cond + ald + cond*ald	7.75	3.58	0.17	0.08	6
reg+ can + cond + ald + cond*ald	7.06	2.89	0.24	0.11	4.24
<b>can + cond + ald + cond*ald</b>	<b>4.17</b>	<b>0</b>	<b>1</b>	<b>0.46</b>	<b>1</b>
org + can + cond + ald + cond*ald	7.79	3.62	0.16	0.07	6.11
<b>Aquatic</b>					
cond + wb + reg + grad + reg*grad	-3.49	4.48	0.11	0.04	9.4
<b>wb + reg + grad + reg*grad</b>	<b>-7.97</b>	<b>0</b>	<b>1</b>	<b>0.34</b>	<b>1</b>
reg + grad + reg*grad	-7.7	0.27	0.87	0.3	1.15
elev + grad + elev*grad	-6.86	1.11	0.57	0.2	1.74
wb + elev + grad + elev*grad	-5.93	2.04	0.36	0.12	2.77
<b>Terrestrial</b>					
wb + grad + lp + org + ald + grav + cond + cond*ald + lp*wb	31	15.15	0	0	1949.16
org + grav + elev + cond + elev*cond	20.08	4.22	0.12	0.07	8.27
ald + grav + elev + cond + elev*cond	19.89	4.03	0.13	0.07	7.51
grav + elev + cond + elev*cond	17.03	1.18	0.56	0.31	1.8
<b>elev + cond + elev*cond</b>	<b>15.85</b>	<b>0</b>	<b>1</b>	<b>0.55</b>	<b>1</b>
elev + grad + elev*grad	-6.86	1.11	0.57	0.2	1.74
wb + elev + grad + elev*grad	-5.93	2.04	0.36	0.12	2.77

**Table 2.4:** Model coefficients and partial r<sup>2</sup> values for total, aquatic and terrestrial spatial models. Abbreviations are same as for Table 2.3.

<b>log(total drift) = 3.8 + 0.2*log(cond) – 1.6*asin(√can) + 0.8*asin(√ald) – 2.1*log(cond)*asin(√ald)</b>					
<b>r<sup>2</sup> = 0.28</b>					
	SS	df	F	p	Partial r <sup>2</sup>
conductivity	0.374	1	0.414	0.526	0.017
canopy	3.547	1	3.927	0.059	0.141
alder	1.705	1	1.888	0.182	0.073
conductivity*alder	3.891	1	4.307	0.049	0.152
residuals	21.678	24			
<b>log(aquatic drift) = 3.4 + 0.6*reg(Coast) + 0.3*grad + 0.3*wb – 1.0*reg(Coast)*grad</b>					
<b>r<sup>2</sup> = 0.44</b>					
	SS	df	F	p	Partial r <sup>2</sup>
region	1.947	1	3.365	0.08	0.118
gradient	0.102	1	0.175	0.68	0.069
bankfull width	1.765	1	3.026	0.094	0.108
region*gradient	6.660	1	11.412	0.002	0.313
residuals	14.591	25			
<b>log(terrestrial drift) = 1.9 + 0.0005*elevation + 0.2*log(cond) + 0.0022*elev*log(cond)</b>					
<b>r<sup>2</sup> = 0.31</b>					
	SS	df	F	p	Partial r <sup>2</sup>
elevation	1.699	1	1.762	0.197	0.068
conductivity	3.022	1	3.135	0.089	0.116
elevation*conductivity	4.837	1	5.017	0.035	0.173
residuals	23.139	24			

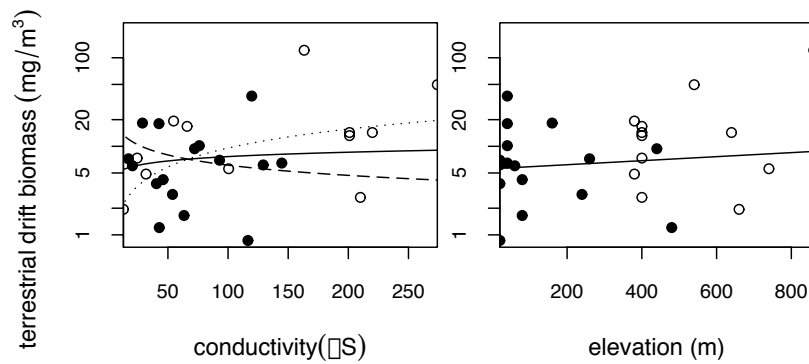


**Figure 2.6:** Scatter plots of the habitat factors included in the total drift model – conductivity, alder canopy cover and total canopy cover – against total drift. The lines indicate the model slopes, not the simple regression slopes. The solid lines indicate the model slope without any interaction effect (i.e. when all other values are held at their means). The dashed and dotted lines on the alder and conductivity graphs indicate the slope when the interacting value is low and high, respectively (i.e. the dashed line on the alder graph represents the slope of alder when conductivity is low). Analyses were performed on transformed data. Open symbols indicate Interior region sites, filled symbols indicate Coast sites.



**Figure 2.7:** Scatter plots of the habitat factors included in the aquatic drift model – bankfull width and gradient – versus total drift. The lines indicate the model slopes, not the simple regression slopes. The solid line on the bankfull width graph indicates the model slope. The dashed line on the gradient graph is the slope in the Coast region. The dotted line is the slope in the Interior. Analyses were performed on transformed data. Open symbols indicate Interior region sites, filled symbols indicate Coast sites.





**Figure 2.8:** Scatter plots of the habitat factors included in the terrestrial drift model – conductivity and elevation – against total drift. The lines indicate the model slopes, not the simple regression slopes. The solid lines indicate the model slope without any interaction effect (i.e. when all other values are held at their means). The dashed and dotted lines on the conductivity graph indicate the slopes when elevation is low and high, respectively. Analyses were performed on transformed data. Open symbols indicate Interior region sites, filled symbols indicate Coast sites. Data from High Falls, the site with high drift biomass, was excluded from the final model due to high influence and is therefore not shown on these graphs.

terrestrial invertebrates and was therefore excluded. The best model for terrestrial drift included elevation, conductivity, and the interaction between elevation and conductivity (Figure 2.8) ( $r^2$  of 0.31,  $F_{3,24} = 3.62$ ,  $p = 0.03$ ). Simple slopes analysis of the interaction between conductivity and elevation shows that conductivity has a neutral or negative effect on terrestrial drift at low elevation and a positive effect at high elevation (coefficient of -0.39 at elevation = -249, 0.16 at average elevation and 0.71 at elevation = 249). These final models all had tolerance values above 0.1, Cook's Distance values below 1, and normally distributed residuals

## Discussion

Day-to-day variation of daytime samples is much less than spatial variation between and within sites (that is, the difference in the average drift biomass between days is less than the difference between samples taken on one day), suggesting that sampling effort should be focused on collecting more samples from each site, rather than more visits to each site. This result addresses our first objective: to determine whether drift must be measured on multiple days. Shearer et al. (2002) found that day-to-day and within site variation were similar for 24 hour samples, whereas this study found greater within site variation than day-to-day variation. However, Shearer et al. (2002) came to the same conclusion that sampling effort should be concentrated on one day when the objective is to compare between sites. The daytime-only sampling used in this study probably resulted in lower variability than in Shearer et al. (2002) as only the daytime drift was captured, rather than the more variable night peaks. These results contrast with Williams (1980) and Gibson and Galbraith (Gibson and Galbraith 1975), who found high day-to-day variability, although the relative magnitudes of day-to-day, between and within site variability were not measured. Williams (1980) used 24 h samples and Gibson and Galbraith (Gibson and Galbraith 1975) used 48 h samples, capturing two successive nights of peaks, potentially increasing between sample variation. None of these studies reported controlling for rain events as we did in this study, possibly contributing to high day-to-day variation.

The majority of invertebrate drift in this study was of aquatic origin, and aquatic invertebrate drift had lower day-to-day variability than terrestrial drift (1% and 8% respectively, Figure 2.5). Other studies have found that terrestrial invertebrates constitute the majority of invertebrate drift (eg. Nakano et al. 1999), but also found greater variability in terrestrial invertebrates (Kawaguchi and Nakano 2001, Nakano et al. 1999). The greater day-to-day variability of terrestrial invertebrates may account for the higher temporal variability found in other studies compared to this study. In streams where terrestrial invertebrates contribute more to drift samples, the relatively stable levels of aquatic invertebrates may be masked by variation in terrestrial inputs. The higher temporal variability of terrestrial invertebrates may be a sampling artefact due to the lower number and larger individual biomass of terrestrial prey – a single large beetle or caterpillar is much larger than the majority of aquatic invertebrates caught in drift nets – or temporal invertebrates may be influenced by random events such as high wind. Our samples collected on windy days captured many leaves, and these leaves could have been vectors for the large numbers of Hemipterans (aphids and leaf hoppers) found in these samples.

The absence of a strong seasonal effect in this study may be caused by sampling protocol, but this result was well supported by the data. Other studies found greatest invertebrate density in midsummer (Elliott 2002, Shearer et al. 2002) and in late spring (Hansen and Closs 2007, Rincón and Lobón-Cerviá 1997). This study used small sample sizes and had large residual variation; these effects may have masked a seasonal effect. However, the Akaike weights for the model with month effect but without region effect indicate that it has low likelihood. Adding month to the random factors only model decreased the likelihood of the random factors model by 25, 32 and 2 times for the total, aquatic and terrestrial invertebrates respectively (Table 2.1), indicating strong support for dropping month from the model. The absence of a seasonal effect indicates that daytime samples collected throughout the summer months can be compared to each other, lengthening the sampling window.

Total drift biomass was most influenced by habitat factors that control food availability. Lower invertebrate densities were found in areas with more canopy cover. It is also possible that the negative influence of canopy cover was related to bankfull width; wider streams

(with less canopy cover) tended to have greater densities of drifting invertebrates, probably due to higher relative discharge. However, the models that included bankfull width instead of canopy cover were less likely according to their  $AIC_c$  values (Table 2.3), supporting the interpretation that direct shading effects are a more probable cause of the negative relationship with invertebrate densities. Alder cover has a positive influence on invertebrate drift density, indicating that detritus is a major source of food for aquatic invertebrates as found by Wipfli and Musselwhite (2004) and Rosenfeld (2000), or a direct source for terrestrial invertebrates (Mason and MacDonald 1982), or both. Conductivity also has a positive influence on total invertebrate density, suggesting that the periphyton is a major food source for aquatic invertebrates, or that conductivity and terrestrial invertebrate drift biomass are related. Shearer et al. (2003) found a density dependent relationship between chlorophyll a concentration and invertebrate drift, indicating that greater periphyton abundance can support more invertebrates and therefore higher baseline drift levels as found in this study.

The significant negative interaction between conductivity and alder density is most likely a result of the accelerating impact of conductivity on decomposition of detrital food sources (Greenwood et al. 2007). Both alder and conductivity have positive coefficients when the other is low (Table 2.4); when stream nutrient levels are low there is food available from the detritus-based food chain and when canopy levels are low there is abundant light for the periphyton-based chain. However, when alder densities are high there is less light available for periphyton. Some periphyton species, such as diatoms, are able to compensate for low light levels and produce nearly the same biomass as in full light (Rier et al. 2006), while others, such as chlorophytes, require more light (Richardson et al. 1983). Therefore when light is restricted there can be a drop in primary productivity, depending on what species of algae dominate the periphyton. In these streams the detritus-based food chain becomes more important. A large proportion of the detritus in streams is deposited in the fall, and consumed throughout the year; when nutrient levels (conductivity) are high decomposition rates increase (Greenwood et al. 2007), due to the nutrient needs of decomposers such as bacteria, and the detritus may not last through the year. Invertebrates dependent on detritus will not be able to sustain high densities if the detritus supply is too low due to decomposition. For these reasons the negative interaction between conductivity and alder density is not surprising.

Aquatic invertebrate biomass was most correlated with physical habitat variables, not the productivity variables that impacted total invertebrates. It is surprising that productivity variables were not included in the aquatic model; the physical variables may simply overwhelm the productivity variables when only aquatic invertebrates are considered. However, conductivity was included in a candidate model (Table 2.3); its exclusion may be primarily related to low sample size. Region was included in the final model as a factor variable and explained 12% of the total variation of aquatic invertebrates (Table 2.4). Invertebrate density was consistently higher in the Interior than the Coast. The inclusion of region in the final model indicates that the habitat factor(s) that caused greater density in the Interior were not measured in this study. Bankfull width had a positive but non-significant influence on aquatic invertebrate drift density, as did gradient averaged over all of the sites. Water velocity rises with gradient and bankfull width; greater water velocity results in longer invertebrate suspension distances, and greater drift densities because the time that each invertebrate spends in the drift increases (Elliott 2002). The negative interaction between region and gradient shows that the slope for gradient is significantly higher in the Coast region than in the Interior, where it is actually slightly negative (Figure 2.7). These results contrast with other examinations of invertebrate biomass that have found that food availability has the greatest impact (Richardson 1993, Rosenfeld 2000, Wipfli and Musselwhite 2004). However, flow has been shown to influence invertebrate drift biomass as well (Elliott 2002, Harvey et al. 2006). Further research into the relationship between benthic invertebrate biomass, water velocity, and drift invertebrate biomass could clarify the sources of variation of aquatic invertebrate biomass.

Surprisingly, terrestrial invertebrate drift biomass was not influenced by canopy cover or composition, but rather by elevation and conductivity. The relationship between canopy cover and terrestrial invertebrate input to streams is well studied but inconsistent (positive effect: Mason and MacDonald 1982, no effect: Wipfli, Wipfli and Musselwhite 2004). The relationship between conductivity and terrestrial invertebrate density is probably indirect. Riparian vegetation composition may influence conductivity as well as the input of terrestrial invertebrates to the stream. Alternatively, water conductivity and terrestrial

invertebrates may both be influenced by a factor that was not measured in this study such as underlying geology. Site elevation was probably included in the final model because of the significant interaction effect with conductivity. At low elevations conductivity has a negative coefficient, but at average and high elevations the coefficient is positive. The temporal variation component of this study showed that terrestrial invertebrates had more day to day variability than aquatic invertebrates; this variability makes it more difficult to determine what spatial factors influence terrestrial invertebrate density, as there is more unexplained variation than for total and aquatic invertebrates. Physical habitat features that are not usually measured for stream ecology studies such as average wind speed may influence terrestrial invertebrate drift density.

The coefficients of determination for the three final models were relatively low, but within the typical range for habitat capacity models ( $r^2$  for the total, aquatic, and terrestrial drift were 0.28, 0.44, and 0.31, respectively). Multiple regression habitat capacity models often yield similar coefficients of determination for other species (e.g. Davies 1989, Scarnecchia and Bergersen 1987). The model for total drift includes taxonomically diverse invertebrates with different habitat preferences, so the low explanatory power is not surprising. The taxa were divided into aquatic and terrestrial types, each of which is less taxonomically diverse than all taxa combined. This decreased diversity may have increased the predictive power for aquatic invertebrates but not for terrestrial. Aquatic and terrestrial biomass were affected by different habitat variables as well, and showed different levels of day-to-day variability. The terrestrial model did not have increased predictive ability like that of the aquatic model, possibly because of the greater day-to-day variability found in the temporal study. Nevertheless, these models provide some insight into the processes that affect drift biomass and suggest specific habitat factors that merit further research.

Measurable habitat factors that influence productivity and water velocity affect the abundance of juvenile salmonid prey. As prey abundance is positively correlated with growth and survival (Imre et al. 2004, Nielsen 1992, Nislow et al. 1998, Rosenfeld et al. 2005) it is an important consideration for juvenile salmonid habitat managers and fisheries scientists. Many of the habitat factors measured in this study are also used in salmonid habitat capacity

models (eg. Davies 1989, Scarnecchia and Bergersen 1987) and habitat assessment protocols (Moore et al. 1997). These habitat factors impact juvenile salmonids directly and indirectly their impact on prey abundance. As this study shows, the impact on prey abundance is complex, involving interactions between habitat factors. Because of the complexity of the relationship, the impact of habitat on invertebrate drift should be considered directly by managers and scientists. Prey habitat requirements could be incorporated into management decisions – for example, (Romero et al. 2005) discuss the practise of removing deciduous riparian vegetation in the Pacific Northwest to encourage conifers. The practise is intended to increase the supply of large woody debris, an important structural element of stream habitat, but may simultaneously decrease prey abundance. Direct measurement of invertebrate drift and a better understanding of habitat relationships could improve salmonid management practises in the future.

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## Chapter 3: Influence of physical and biological habitat factors on juvenile salmonid abundance<sup>1</sup>

### Introduction

Accurate population size estimation is fundamental to species management, from conservation of endangered species' habitat to harvest of exploited species. Models that predict abundance based on habitat characteristics serve two primary purposes in population management: they improve understanding of species' habitat requirements, and they can be a more cost-effective way to estimate abundance than direct field measurement. Habitat models are often applied to identify high quality habitat for protection, a primary objective of many conservation projects (e.g. Clark et al. 1993). They are also useful indicators of potential habitat capacity when fish abundance is depleted due to over-harvest. Designing habitat restoration projects and monitoring the effects of resource extraction on habitat quality can be addressed using predictive models as well (Binns and Eiserman 1979). Such models have been developed for a variety of taxa including mammals (Dorgelöh 2006, McAlpine et al. 2006), amphibians (Denoël and Lehmann 2006), birds (Gavashelishvili et al. 2006, Zharikov et al. 2006), and freshwater fish (see Fausch et al. 1988).

Freshwater fish such as salmonids (Family Salmonidae) are well suited to habitat modeling due to their restricted habitat in lakes and streams and the difficulty of obtaining direct population estimates. However, they are often regionally specific (Bowlby and Roff 1986) – a model developed in one location is rarely a good predictor in another – although similar variables are included in most models. Variables used in regression analysis can be divided into those that are related to the physical structure of available habitat, and those that are correlated with the abundance or productivity of prey. For example, physical habitat variables like channel width, percent pool habitat, and LWD abundance are commonly used as correlates of habitat structure. Stream gradient and sediment size (see Coulombe-Pontbriand and LaPointe 2004, Davies 1989, Rosenfeld et al. 2000, Sharma and Hilborn

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Nicol, SD, JS Rosenfeld and JB Shurin. Influence of physical and biological habitat factors on juvenile salmonid abundance.

2001) are additional variables that correlate with channel size and velocity, which can be expected to influence habitat availability for fish. Invertebrate drift is the most direct index of prey abundance for drift-feeding fishes. Invertebrate prey are delivered to fish by two primary mechanisms: in situ invertebrate production based on algal- or detrital-based food chains (Vannote et al. 1980), or input of terrestrial invertebrates from the riparian zone (Cada et al. 1987). Canopy cover and composition, organic sediment, temperature, and water conductivity (see Binns and Eiserman 1979, Johansen et al. 2005, Scarnecchia and Bergersen 1987) affect the abundance of invertebrate prey delivered from terrestrial and aquatic sources.

Invertebrate drift is conspicuously absent from the majority of juvenile salmonid habitat models (Fausch et al. 1988) even though drifting aquatic and terrestrial invertebrates are a primary food source for juvenile salmonids (Wipfli 1997), and elevated drift contributes to increased juvenile salmonid growth (Imre et al. 2004, Nielsen 1992, Rosenfeld et al. 2005, Slaney 1972), density (Slaney 1972) and survival (Imre et al. 2004, Nislow et al. 1998). Benthic chlorophyll-a, riparian canopy cover, water column nutrients (or surrogates like conductivity) are often used as expected correlates of the abundance of prey for drift-feeding fish. Benthic invertebrate abundance is sometimes used in models as a more direct measure of food availability (eg. Bowlby and Roff 1986, Jowett 1992). Invertebrate drift should be a more direct measurement of food availability, as benthic density and drift biomass are not strongly correlated (Shearer et al. 2003). Including invertebrate drift biomass as a candidate variable in habitat models may therefore improve the predictive ability of habitat capacity models and help determine the degree to which food availability limits salmonid abundance.

The predictive models or variables that biologists include in regression analysis are usually based on expert opinion and professional judgement as to which are most effective and practical to collect. However, models are rarely selected in an explicit cost-benefit framework, where the benefit is the proportion of variance in fish abundance explained by a model (or variable) and the cost is the time and effort required to collect the associated data in the field or laboratory. Assessing the cost-effectiveness of habitat models and their terms (the habitat variables) should allow fisheries scientists to choose which habitat models and component variables maximize predictive power. This improved efficiency is important for

fisheries scientists with limited resources (i.e. personnel, funding), and should allow scientists to make more informed decisions about the optimal variables to include in habitat models. For example, a variable with high predictive ability that takes more time to measure than fish abundance is clearly less efficient than a direct measurement.

The objectives of this study were 1) to develop reach-scale predictive models for juvenile salmonid abundance in southwestern BC using physical and biological habitat factors, 2) to determine whether habitat variables differ between the Coast and Interior regions, 3) to determine the contribution of invertebrate drift to the relative predictive ability of models, and 4) to do a cost-benefit analysis for predictive models and their component variables.

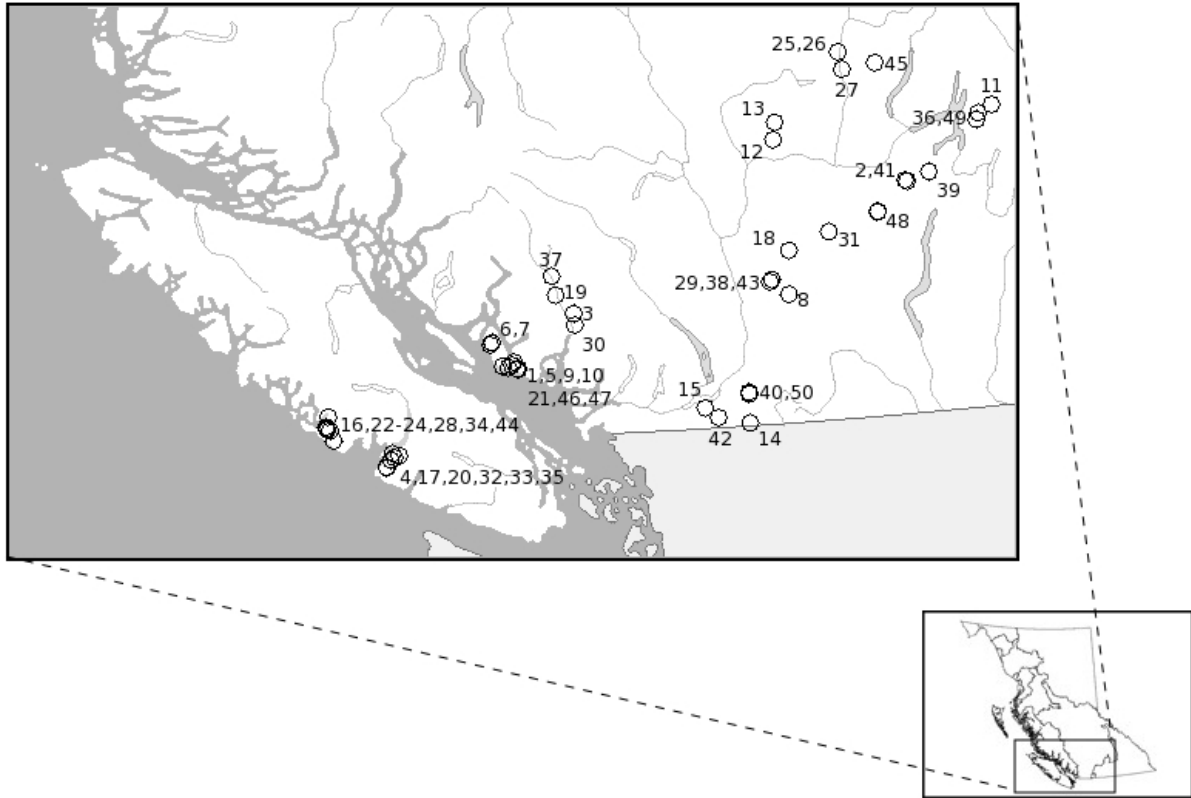
## **Methods**

### **Study Sites**

Fifty stream sites in the Coast and Interior regions of British Columbia were sampled for drift abundance and habitat features in the summers of 2005 or 2006 (Figure 3.1). Sites were chosen to span a wide range of productivities and stream sizes (1.3 – 33.1 m channel width; Appendix 2). Every effort was made to find sites with reliable accounts of spawning adults to ensure that sites would be saturated with juveniles and rearing habitat would be near carrying capacity. Sample reach lengths were 20-30 bankfull widths (80-250 m) with no major tributaries or changes in valley form, vegetation, or land use (as in Moore et al. 1997).

### **Fish density**

Data on salmonid density were either collected in the field ( $n = 19$ ) or from existing multi-pass removal data sets (Hagen 2005, Hanson 2005, Morgan 2001, Rosenfeld et al. 2000, Tschaplinski 2006). Regression analysis showed that the year fish were collected had no significant impact on fish density (fish/m<sup>2</sup>,  $F_{1,48} = 1.9$ ,  $p = 0.17$ ) or biomass (g wet mass/m<sup>2</sup>,  $F_{1,45} = 0.9$ ,  $p = 0.35$ ). For streams without existing fish abundance data, a subset of channel units were triple- or double-pass depletion electrofished in August of 2006 or 2007. Removal



**Figure 3.1:** Locations of study streams in south western British Columbia, Canada. Some sites are close enough together that they share a point. Number labels refer to row labels in Appendix 2. Universal Transverse Mercator coordinates are also available in Appendix 2.

data were used to calculate an estimate of fish abundance as described by Schnute (1983). The wetted area electrofished was measured for each site to determine the density of fish (fish per m<sup>2</sup> wetted area).

Biomass (g wet mass per m<sup>2</sup> wetted area) was calculated by multiplying the average wet mass of fish at a site by the estimated number of fish present. When only fish lengths were available biomass was estimated using the following power functions generated from the data set of fish lengths and masses collected at all sites:

$$\text{YOY: } \log(\text{mass}) = -11.73 + 3.07 \cdot \log(\text{length}) \dots \dots \dots (F_{1,3380} = 1.1 \times 10^5, p = 2.2 \times 10^{-16})$$

$$\text{rainbow: } \log(\text{mass}) = -11.54 + 3.04 \cdot \log(\text{length}) \dots \dots \dots (F_{1,1065} = 4.1 \times 10^4, p = 2.2 \times 10^{-16})$$

$$\text{coho: } \log(\text{mass}) = -12.05 + 3.14 \cdot \log(\text{length}) \dots \dots \dots (F_{1,1311} = 2.2 \times 10^4, p = 2.2 \times 10^{-16})$$

To control for seasonal effects on fish size associated with different collection dates (July 12-September 22), we tested for a relationship between calendar day and average fish biomass. There was no relationship for YOY or coho, so biomass on the day of sampling was used in regression analysis. However, there was a significant day effect for rainbow trout ( $F_{1,26} = 5.7$ ,  $p = 0.02$ ). Rainbow trout data were corrected to September 1st biomass by multiplying the number of days between the fishing date and September 1st by 0.013 (the slope of the mass-day relationship) and adding this correction to the measured mass of juvenile rainbow trout. This method maintained the existing variation in the data while correcting for the day effect.

### **Invertebrate Drift Sampling**

Invertebrate drift samples were collected at the upstream end of pools immediately below riffles to standardize habitat effects and to measure the quantity of drift that a dominant fish would experience at the head of a pool. At sites with no suitable pools, nets were placed in riffles (approximately one third of the sites). Samples were collected with a 1 m long, 250 mm mesh net with an opening 0.2 m square for a duration of 180-300 minutes. The depth and velocity of the water in the mouth of the net were measured in order to calculate the volume of water sampled, and thereby the biomass of drifting invertebrates per  $m^3$ . We sampled drift in the daytime rather than overnight because daytime drift abundance is more uniform (Waters 1962), and most juvenile salmonids are visual predators that feed during daylight. Arguably, daytime drift samples more accurately represent prey abundance for juvenile salmonids than 24 hour drift samples where biomass is dominated by nocturnal peaks (Waters 1962). Drift samples were collected at least two hours after sunrise and two hours before sunset to reduce daily variability in light intensity, and were not collected during or after rain events until flow had returned to pre-flood levels. Samples were preserved in 5% formalin and returned to the laboratory for sorting.

Invertebrates were sorted from detritus at 10X magnification in the laboratory and preserved in 70% ethanol for later identification and measurement using a digitizer (Roff and Hopcroft 1986). Invertebrates were identified to Order with some exceptions: non-arthropods such as nematodes were identified to Phylum, and common arthropods such as chironomids were



identified to sub-Family. Each taxon was categorized as aquatic or terrestrial in origin. Adult insects with aquatic larvae, such as Nematocera (Diptera), were counted as aquatic in origin. The dry mass (mg) of invertebrates in each sample was calculated using published taxa-specific length-mass regressions (Benke et al. 1999, McCauley 1984 ; M. Wipfli lab pers. comm., Meyer 1989, Sabo et al. 2002, Sample et al. 1993, Smock 1980).

### **Habitat Measurements**

Habitat surveys were conducted at all 50 sites (see Moore et al. 1997) to collect information on reach-level factors that may influence juvenile salmonid density. Average summer temperature was estimated using ClimateBC V.3.2 (Wang et al. 2006) and UTM coordinates and elevation measurements for each site. Conductivity was measured once at each site. The intermediate dimension (middle length of the x, y, and z axes) of the five largest particles likely to have been moved by the peak flow (Hogan 1996), percent canopy cover, and canopy composition (percent cover of conifer, alder [*Alnus rubra*], and other deciduous trees) were measured at 3 to 5 locations spaced throughout each site. The length and width of each channel unit (riffle, pool, glide, run, and cascade) were measured, including channel units in secondary and backwater channels. These measurements were used to calculate site mean bankfull width and the percent area of each site by channel unit type. The percent substrate composition – fines, gravel, cobbles, boulders, bedrock, and particulate organic matter (POM) – was estimated for each channel unit, as were gradient and the percent of the channel unit with protective cover. Measurements made in each channel unit were weighted by channel unit area to calculate average values for each site. All large woody debris (LWD; greater than 10cm diameter or 1m length) at each site were counted and identified as pool-forming or non-pool forming.

### **Statistical Analysis: Habitat Capacity Modeling**

Habitat capacity models were developed using ordinary least squares multiple regression with R 2.6.0. Models were fit for young of the year salmonids (all taxa combined), and for

YOY rainbow trout (*Oncorhynchus mykiss*) and YOY coho salmon (*O. kisutch*) separately. Models were fit using log-transformed density (number/m<sup>2</sup> wetted area) and log-transformed biomass (grams wet mass/m<sup>2</sup> wetted area) as response variables. All variables were centred to control for colinearity between model main effects and interaction effects (Quinn and Keough 2002). In order to apply these models to new data sets the new data must be centered using the same constants as this study (i.e. a constant must be added or subtracted to the data so that the mean equals zero; see Appendix 1 for variable means). Correlation between the habitat variables was examined to ensure that the subset selected for regression were not correlated ( $r < 0.7$ ), as strongly correlated variables make it difficult or impossible to perform the matrix inversion required to calculate regression coefficients (Zar 1999). Fourteen non-correlated

**Table 3.1:** Variables included in the starting models, with units, and abbreviations in bold. Variables marked with (\*) are correlated with each other so only one at a time was used in any starting model. The variable marked with (!), drift, was not included in the starting models for the full model selection, but was included in the starting models for the subset model selection.

Category	Variable
Productivity	organic substrate (proportion) <b>org</b>
	conductivity (µS) <b>cond</b>
	average summer temperature (°C) <b>temp</b>
	alder cover (proportion) <b>alder</b>
	canopy cover (proportion) <b>canopy</b> *
	invertebrate drift (dry mg m <sup>-3</sup> ) <b>drift</b> !
Physical Habitat	largest particle (cm) <b>lp</b>
	pool area (proportion) <b>pool</b>
	riffle (proportion) <b>riffle</b>
	gravel substrate (proportion) <b>grav</b>
	gradient (%) <b>grad</b>
	bankfull width (m) <b>wb</b> *
	percent cover for fish <b>cover</b>
	LWD pieces (m <sup>-1</sup> of stream) <b>lwd</b>
pool forming LWD pieces (m <sup>-1</sup> ) <b>lwd_pf</b>	
Regional Effects	region – Interior or Coast region
	elevation (m) <b>elev</b>

! drift was not included in the starting models

\* only one of can and wb was included in a starting model

variables were chosen to begin model selection (Table 2.1). Canopy cover and bankfull width were correlated with each other ( $r = 0.7$ ), so two starting models were used: one with the 14 variables and canopy cover, and one with the 14 variables and bankfull width for a total of 15 variables.

Two-way interaction terms were added to the starting models based on improved Akaike Information Criterion (AIC) values. Terms were then removed from the starting models in a stepwise fashion until removing terms no longer improved AIC values. The models with the lowest AIC values were selected for comparison. The models were compared using Akaike weights based on the Second-Order Information Criterion ( $AIC_c$  for small samples). Weights were used to calculate evidence ratios to select the best fit model (Burnham and Anderson 2002). Tolerance, Cook's Distance, and normality of the residuals were checked for all selected models. Interactions included in final models were investigated using simple slopes (Quinn and Keough 2002). The simple slope of a variable is its slope when the variable that it interacts with is held constant. Simple slopes were calculated at the mean of the other variable, and one standard deviation above and below the mean (low, average and high values of the interacting variable). Simple slope calculations allow greater understanding of trade-offs and other interactions by revealing changes in the sign or magnitude of the target variable coefficient, at different levels of the interacting variable.

A best model was determined for each fish species – young-of-the-year of all species combined (YOY), of rainbow only (rainbow) and of coho only (coho) – for density and biomass separately all of the available sites (the **full habitat** model); not all sites had both coho and rainbow, so the sample size was lower for these models. Because invertebrate drift was collected at only 30 of 50 sites, best models were then run using the subset of sites that also had invertebrate drift measurements (the **habitat subset** model). To determine the benefit of including invertebrate drift in the best model, invertebrate drift was then added to the subset habitat model (the **habitat + drift subset** model) and the improvement in model fit assessed using evidence ratios. Finally, models were developed using only the subset of drift sites and including drift in the starting models (the **reduced habitat + drift** model). The main function of this last analysis was to determine if the drift term was dropped during

model selection or included in the final model. If drift was dropped then the resulting habitat model was considered to be inferior to the full habitat model (based on all available data), because the reduced + drift model was based on a subset of the data. In this case only the results of the full habitat models were presented.

Region (Coast or Interior), was included in the starting models to determine if there was a region effect that was not captured by the habitat variables. Habitat measurements from the two regions were compared using two-sample Student's t-tests to assess regional differences in average habitat characteristics.

### **Statistical Analysis: Cost-Benefit Assessment**

To determine which variables explained the most variance in fish abundance for the least effort, a benefit:cost ratio was calculated for each variable included in the full habitat model, for drift from the habitat + drift subset model, and for the full habitat models themselves. Model benefit was the full or partial  $r^2$  of the model or variable, and cost was the sum of the time (in minutes) required to assess all of the variables in the model. The partial  $r^2$ , a measure of a variable's individual contribution to the predictive ability of the model, was calculated for each variable included in a final model.

Field effort measurements were made at 18 of the 50 sites. We used time (effort) as the metric of cost since labour is the primary cost for all of the variables measured. The cost for each variable was the total time at the site required to measure a variable (including any subsequent laboratory processing if needed). Field activities were timed each summer after a training period, so that all estimates of field time are based on experienced field staff. All timed field work was done with teams of two people; if the two field staff worked together to make a measurement (e.g. channel unit length) then the number of minutes for that activity were doubled. We did not include travel time to the site because it made an equal contribution to all variables, and because it would be necessary to travel to the site in order to estimate fish abundance directly. However, at more remote sites with greater travel time, the relative cost of time spent on site is lower, and therefore the benefit of reduced field time

is lower than at sites with low travel time; this trade-off was not addressed in this cost-benefit analysis.

## Results

### Study Sites

Invertebrate drift and conductivity (a correlate of nutrient levels) were higher in the Interior than the Coast whereas total canopy cover and alder cover were higher in the Coast (Table 3.2), suggesting higher prey availability at Interior sites compared to the more heavily shaded, nutrient-poor Coast. Habitat in the Coast was generally more structured with greater pool area, gravel substrate, and large woody debris. Despite the greater number of LWD pieces in the Coast region, there was no difference in the amount of pool-forming LWD between regions (0.007 pieces/m in the Coast, 0.004 pieces/m in the Interior;  $t = 1.0$ ,  $p = 0.3$ ), indicating that a higher proportion of Interior LWD pieces function in pool-formation. Interior sites also had significantly higher elevation (616 m compared to 102 m in the Coast;  $t = -10.2$ ,  $p = 5.2 \times 10^{-12}$ ).

Density of young-of-the-year (YOY) salmonids averaged  $1.0 \pm 0.93$  (standard deviation) fish per  $m^2$  of wetted habitat. Six salmonid species were collected: coho salmon, rainbow trout, cutthroat trout (*O. clarki*), chinook salmon (*O. tshawytscha*), bull trout (*Salvelinus confluentus*) and mountain whitefish (*Prosopium williamsoni*). Rainbow trout were present at 31 sites (Appendix 1) at an average density of  $0.47 \pm 0.39$  fish/ $m^2$ . Coho salmon were present at 39 sites at an average density of  $0.59 \pm 0.73$  fish/ $m^2$ . Fish biomass ( $g/m^2$ ) showed the same pattern; YOY had the greatest biomass ( $1.88 \pm 2.01$   $g/m^2$ ), followed by coho ( $1.57 \pm 2.05$   $g/m^2$ ), and rainbow ( $0.56 \pm 0.49$   $g/m^2$ ). Mean fish densities and biomasses did not differ between regions (Table 3.2).

### Habitat Capacity Models

All models included terms relating to both stream productivity and physical structure, and

**Table 3.2:** Salmonid abundance and habitat variable means (SD) in the Coast and Interior regions and the results of Welch's t-test comparing the means. Significant p-values are in bold, and show several significant differences among the habitat variables, but none for the salmonid abundances. Abbreviations are listed in Table 3.1.

	Coast mean		Interior mean		Welch's t	p
<b>Fish Abundance</b>						
YOY (fish/m <sup>3</sup> )	1.10	(0.90)	0.84	(0.97)	0.92	0.36
YOY (g/m <sup>3</sup> )	1.95	(1.38)	1.76	(2.95)	0.24	0.81
rainbow (fish/m <sup>3</sup> )	0.47	(0.42)	0.47	(0.39)	-0.05	0.96
rainbow (g/m <sup>3</sup> )	0.51	(0.48)	0.60	(0.51)	-0.5	0.62
coho (fish/m <sup>3</sup> )	0.60	(0.54)	0.57	(1.04)	0.1	0.92
coho (g/m <sup>3</sup> )	1.44	(1.01)	1.87	(3.53)	-0.4	0.7
<b>Productivity</b>						
org	0.12	(0.13)	0.07	(0.14)	1.11	0.27
cond	66.2	(37.8)	121.1	(83.7)	-2.69	0.01
temp	15.5	(0.93)	15.9	(0.95)	-1.44	0.16
alder	0.23	(0.24)	0.09	(0.12)	2.64	<b>0.01</b>
canopy	0.44	(0.26)	0.19	(0.20)	3.78	<b>&lt;0.01</b>
drift	43.7	(34.2)	92.4	(74.5)	-2.11	<b>0.05</b>
<b>Physical Structure</b>						
lp	23.9	(26.9)	37.4	(27.9)	-1.63	0.11
rifle	0.32	(0.23)	0.29	(0.26)	0.41	0.69
grav	0.34	(0.23)	0.23	(0.15)	2.02	<b>0.05</b>
grad	1.70	(1.60)	2.09	(1.04)	-1.03	0.31
wb	7.68	(5.69)	10.5	(7.54)	-1.38	0.18
pool	0.20	(0.18)	0.07	(0.11)	3.1	<b>&lt;0.01</b>
cover	0.11	(0.06)	0.09	(0.05)	1.47	0.15
lwd	0.08	(0.08)	0.02	(0.03)	3.76	<b>&lt; 0.01</b>
lwd_pf	0.01	(0.01)	0.004	(0.01)	1.04	0.3
<b>Regional Effects</b>						
elev	102		606		-9.85	<b>&lt;0.01</b>

**Table 3.3:** Model coefficients, sums of squares (SS), degrees of freedom (df), F-, p-, and partial r2 values for YOY, rainbow and coho full models. Significant p-values are in bold. Model r2 values are listed following the equations. Abbreviations are listed in Table 1. Type II ANOVA results are presented.

$\log(\text{YOY density}) = 0.3 + 0.01(\text{lp}) + 2.6(\text{pool}) + 0.4(\text{temp}) - 0.003(\text{cond}) + 0.0003(\text{elev}) - 3.1(\text{cover}) + 1.6(\text{grav}) + 2.9(\text{org}) + 0.03(\text{grad}) + 36.6(\text{lwd\_pf}) + 0.01(\text{pool})(\text{elev}) - 0.0007(\text{elev})(\text{grad}) + 54.0(\text{cover})(\text{org}) + 1.52(\text{grav})(\text{grad})$						
<b>r<sup>2</sup> = 0.75</b>						
	Coefficients	SS	df	F	P	partial r <sup>2</sup>
lp	0.01	2.02	1	6.65	<b>0.01</b>	0.17
pool	2.56	2.55	1	8.42	<b>0.01</b>	0.21
temp	0.44	3.61	1	11.9	< <b>0.01</b>	0.27
cond	-0.003	0.88	1	2.90	0.10	0.08
elev	<0.01	0.00	1	0.01	0.94	0
cover	-3.13	0.49	1	1.60	0.21	0.05
grav	1.55	0.2	1	0.67	0.42	0.02
org	2.86	3.46	1	11.42	< <b>0.01</b>	0.26
grad	0.03	1.00	1	3.30	0.08	0.09
lwd_pf	36.56	4.35	1	14.34	< <b>0.01</b>	0.31
pool:elev	0.01	2.6	1	8.59	<b>0.01</b>	0.21
elev:grad	-0.001	1.83	1	6.03	<b>0.02</b>	0.16
cover:org	53.97	4.24	1	13.97	< <b>0.01</b>	0.3
grav:grad	1.52	2.26	1	7.44	<b>0.01</b>	0.19
residuals		9.71	32			
$\log(\text{YOY biomass}) = 0.2 - 0.003(\text{lp}) + 0.3(\text{temp}) - 0.005(\text{cond}) - 0.001(\text{elev}) - 0.1(\text{grad}) - 0.02(\text{wb}) - 0.01(\text{lp})(\text{grad}) + 0.001(\text{cond})(\text{wb})$						
<b>r<sup>2</sup> = 0.65</b>						
	coefficients	SS	df	F	p	partial r <sup>2</sup>
lp	-0.003	0.34	1	0.76	0.39	0.02
temp	0.27	1.95	1	4.34	<b>0.04</b>	0.11
cond	-0.005	5.04	1	11.22	< <b>0.01</b>	0.24
elev	-0.001	3.28	1	7.31	<b>0.01</b>	0.17
grad	-0.13	0.82	1	1.82	0.19	0.05
wb	-0.02	6.31	1	14.04	< <b>0.01</b>	0.29
lp:grad	-0.01	4.00	1	8.89	<b>0.01</b>	0.2
cond:wb	0.001	2.68	1	5.96	<b>0.02</b>	0.15
residuals		15.73	35			

**Table 3.3:** continued

$$\log(\text{rainbow density}) = 0.7 + 0.03(\text{lp}) + 6.3(\text{alder}) + 0.01(\text{cond}) - 17.1(\text{cover}) + 41.2(\text{lwd}) + 0.2(\text{region}) - 5.2(\text{canopy}) - 0.04(\text{lp})(\text{region})$$

**r<sup>2</sup> = 0.83**

	Coefficients	SS	df	F	P	partial r <sup>2</sup>
lp	0.03	1.73	1	5.7	<b>0.03</b>	0.23
alder	6.3	8.11	1	26.71	< <b>0.01</b>	0.58
cond	0.01	7.16	1	23.58	< <b>0.01</b>	0.55
cover	-17.09	10.3	1	33.92	< <b>0.01</b>	0.64
lwd	41.23	13.0	1	42.93	< <b>0.01</b>	0.69
region	0.16	0.26	1	0.85	0.37	0.04
canopy	-5.22	9.17	1	30.19	< <b>0.01</b>	0.61
lp:region	-0.04	6.42	1	21.13	< <b>0.01</b>	0.53
residuals		5.77	19			

$$\log(\text{rainbow biomass}) = 0.3 + 0.03(\text{lp}) + 6.2(\text{alder}) + 0.01(\text{cond}) - 15(\text{cover}) + 33(\text{lwd}) + 0.7(\text{region I}) - 4(\text{can}) - 0.03(\text{lp})(\text{region I})$$

**r<sup>2</sup> = 0.76**

	coefficients	SS	df	F	p	partial r <sup>2</sup>
lp	0.03	2.92	1	7.41	<b>0.01</b>	0.3
alder	6.17	8.03	1	20.39	< <b>0.01</b>	0.55
cond	0.01	1.8	1	4.56	<b>0.05</b>	0.21
cover	-15.2	7.47	1	18.95	< <b>0.01</b>	0.53
lwd	32.65	7.18	1	18.23	< <b>0.01</b>	0.52
region	0.73	0.37	1	0.93	0.35	0.05
can	-3.99	5.14	1	13.04	< <b>0.01</b>	0.43
lp:region	-0.03	4.19	1	10.62	< <b>0.01</b>	0.38
residuals		6.7	17			



**Table 3.3:** continued.

$\log(\text{coho density}) = 0.3 - 0.8(\text{alder}) - 1.7(\text{pool}) - 0.9(\text{riffle}) + 0.07(\text{temp}) - 0.01(\text{cond}) + 0.001(\text{elev}) + 2.3(\text{grav}) + 1.0(\text{org}) + 0.04(\text{grad}) + 2.0(\text{lwd}) + 0.4(\text{region}) - 0.002(\text{elev})(\text{grad}) + 23.2(\text{org})(\text{region}) - 6.3(\text{tavsm})(\text{lwd})$

**$r^2 = 0.92$**

	Coefficients	SS	df	F	P	partial $r^2$
alder	-0.83	0.51	1	1.68	0.21	0.07
pool	-1.68	1.25	1	4.13	<b>0.05</b>	0.15
riffle	-0.92	1.18	1	3.89	0.06	0.14
temp	0.07	0.67	1	2.22	0.15	0.09
cond	-0.01	2.19	1	7.23	<b>0.01</b>	0.24
elev	0.001	0.21	1	0.69	0.41	0.03
grav	2.31	5.57	1	18.42	<b>&lt; 0.01</b>	0.44
org	1.04	1.52	1	5.03	<b>0.03</b>	0.18
grad	0.04	1.56	1	5.15	<b>0.03</b>	0.18
lwd	2.0	0.53	1	1.76	0.2	0.07
region	0.39	0.12	1	0.4	0.54	0.02
elev:grad	-0.002	4.33	1	14.33	<b>&lt; 0.01</b>	0.38
org:region	23.24	11.23	1	37.14	<b>&lt; 0.01</b>	0.62
tavsm:lwd	-6.33	4.57	1	15.11	<b>&lt; 0.01</b>	0.4
residuals		6.96	23			

$\log(\text{coho biomass}) = -0.1 - 1.4(\text{riffle}) - 0.003(\text{elev}) + 2.2(\text{grav}) - 0.7(\text{org}) - 0.1(\text{grad}) + 1.4(\text{region I}) - 0.002(\text{elev})(\text{grad}) + 26(\text{org})(\text{region I})$

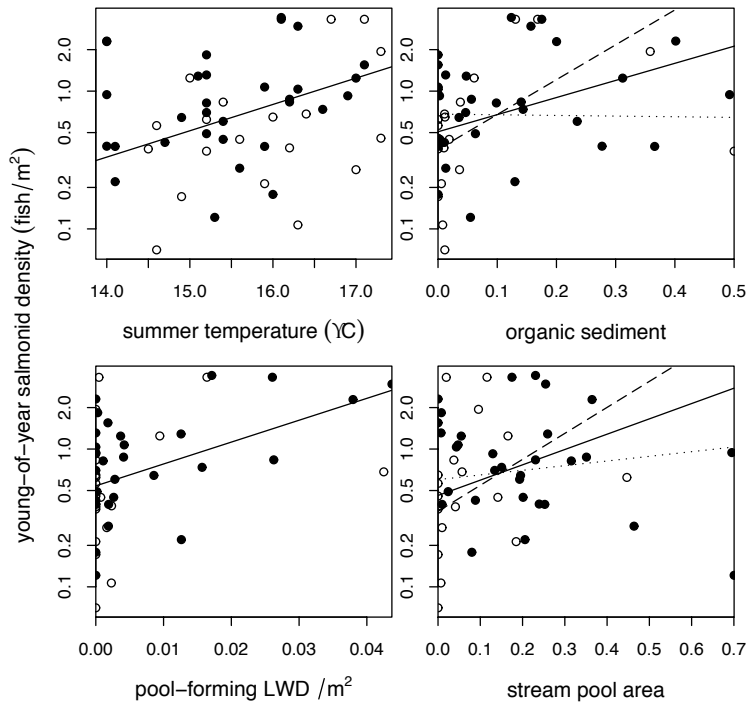
**$r^2 = 0.81$**

	coefficients	SS	df	F	p	partial $r^2$
riffle	-1.39	2.64	1	5.25	<b>0.03</b>	0.16
elev	-0.003	1.67	1	3.33	0.08	0.11
grav	2.23	5.9	1	11.74	<b>&lt; 0.01</b>	0.3
org	-0.66	0.17	1	0.33	0.57	0.01
grad	-0.1	2.02	1	4.02	0.06	0.13
region	1.38	2.15	1	4.28	<b>0.05</b>	0.14
elev:grad	-0.002	2.92	1	5.82	<b>0.02</b>	0.18
org:region	26.2	17.22	1	34.3	<b>&lt; 0.01</b>	0.56
residuals		13.56	27			

passed Cook's Distance, tolerance and normality tests. The full habitat model for YOY density explained a large proportion of the variance in fish abundance (Table 3.3;  $r^2 = 0.75$ ,  $F_{8,39} = 7.1$ ,  $p < 0.0001$ ). The biomass full habitat model had a poorer fit ( $r^2 = 0.57$ ) and is not considered in detail since it shared most terms with the density model; it is not discussed further here. The interaction terms in the density model suggested that intermediate gradients are associated with the greatest salmonid abundances (gradient and gravel for the density model). Simple slopes analysis shows that the slope of gradient was positive (0.6) when there was a lot of gravel sediment (one standard deviation above average, gravel SD = 0.2) and negative when there was very little gravel (-0.004). The model also suggested that more complex habitats are associated with greater salmonid density (coefficients for pool-forming LWD, largest particles and pool area were all positive [Figure 3.2]). Two interactions indicated regional effects: the pool-elevation interaction suggested that impact of pools was greater in the Interior (coefficient = 4.3) than the Coast (0.8), possibly because pool area was lower in the Interior (Table 3.2); the gravel-elevation interaction showed that the higher gradients (within the range of the data) were more favourable at low elevations in the Coast (elevation SD = 297) and negative at high elevations in the Interior (0.2 and -0.2, respectively).

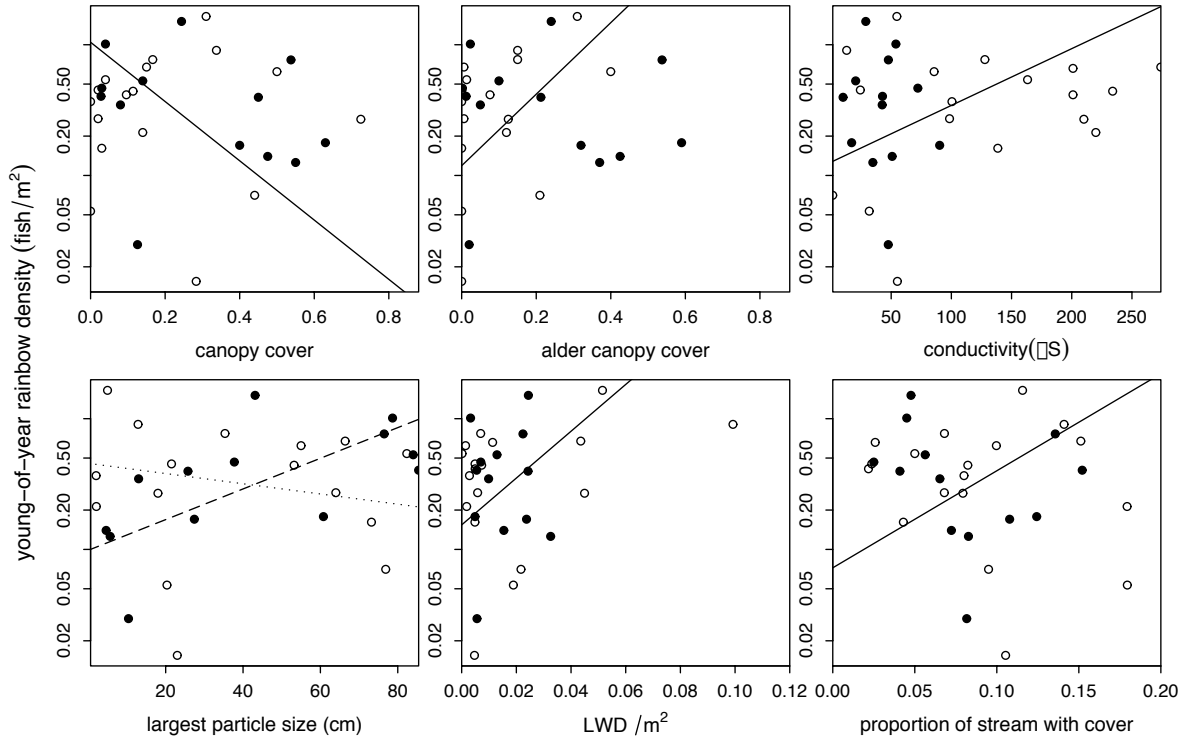
The density full habitat model for rainbow trout included productivity and physical habitat related variables and a regional effect (Table 3.3, Figure 3.3;  $r^2 = 0.83$ ,  $F_{8,19} = 11.5$ ,  $p < 0.01$ ). The biomass model had the same terms as the density model, with the same signs and similar magnitudes, so only the density model is discussed here. The rainbow trout density model included both alder and total canopy cover; while the alder coefficient was positive, the total canopy cover coefficient was negative (6.3 and -5.2). The coefficient of conductivity was also positive (0.01), in contrast with the YOY model. The model showed that rainbow abundance was greater in streams with more woody debris, but lower in streams with more cover from predators, indicating a mixed response to habitat complexity. The impact of largest particle size was slightly negative in the Interior (-0.01), but positive in the Coast (0.03).

The density full habitat model for coho salmon included more physical structure than



**Figure 3.2:** Scatter plots of the key habitat factors included in the YOY density full model (average summer temperature, organic sediment, pool-forming LWD and pool area) against YOY density. YOY density was log transformed for the analyses and is displayed on a log scale. The solid lines indicate the full model regression best fit lines, not the simple regression best fit lines. Dashed and dotted lines indicate interaction effects: in the organic sediment graph the dashed line is the slope of organic sediment when cover is high and the dotted line is the slope when cover is low. The dashed and dotted lines in the pool area graph represent the slopes at high and low elevations, respectively. Filled symbols indicate Coast region sites, the open symbols indicate Interior region sites.

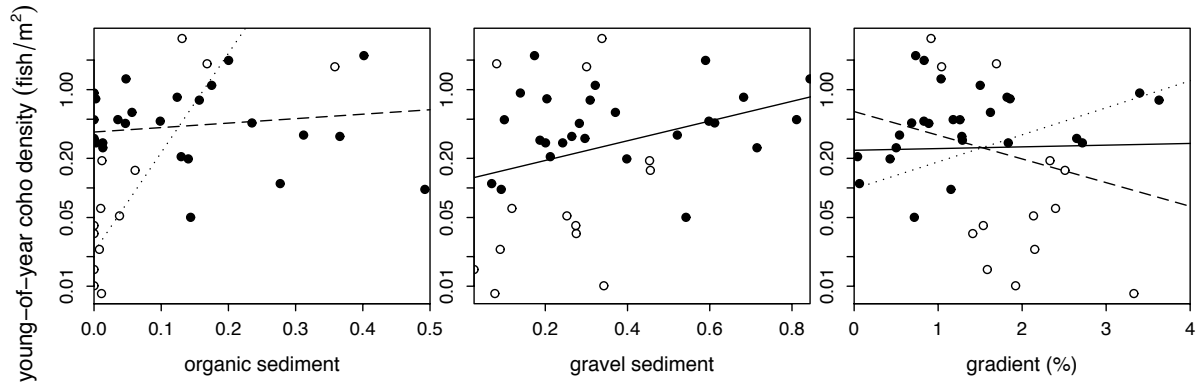
productivity variables, and both variable types showed regional differences (Table 3.3, Figure 3.4;  $r^2 = 0.91$ ,  $F_{14,23} = 18.4$ ,  $p < 0.01$ ). The biomass model only included a subset of the terms that were present in the density model so it is not discussed here. The coho models shared many similarities with the YOY models, such as the negative gradient-elevation interaction and conductivity coefficients, and the positive average summer temperature coefficient. The impact of stream structure (pool and riffle area, sediment size) on the density of coho salmon was complex and somewhat contradictory (riffle and pool both had negative coefficients but gravel had a positive coefficient). There was a regional difference in the impact of organic sediment (Figure 3.5): the coefficient of organic sediment was much larger in the Interior (24.3) than the Coast (1.0), and there was also an interaction between average summer temperature and large woody debris. The impact of an increase in temperature in areas with



**Figure 3.3:** Scatter plots of the key habitat factors included in the rainbow density full model (alder cover, canopy cover, conductivity, largest particle size, LWD, and cover) against rainbow density. Rainbow density was log transformed for the analyses and is displayed on a log scale below. The solid lines indicate the full model slopes, not the simple regression slopes. The dashed and dotted lines in the largest particles graph indicate the slopes in the Coast and Interior regions, respectively. The biomass model distributions are very similar to these and are therefore not presented. Filled symbols indicate Coast region sites, the open symbols indicate Interior region sites.

abundant woody debris (LWD SD = 0.07) was negative, but was positive in areas with low LWD (-0.38 and 0.53).

Comparisons of the habitat subset and habitat + drift subset models for the three species showed that adding drift to the full models did not significantly improve their predictive ability (Table 3.4). Evidence ratios ranged from 3.8 for the YOY biomass model to  $3.9 \times 10^{14}$  for the coho density model. That is, the full habitat model run on the subset of sites with drift data ranged from 3.8 to  $3.9 \times 10^{14}$  times more likely than the habitat + drift subset model with drift added. The  $r^2$  values of the habitat + drift subset models were not greatly improved compared to the full-subset models, despite the addition of an extra term (Table 3.4). None of the models developed using only the subset of sites that included drift data (the reduced



**Figure 3.4:** Scatter plots of the key habitat factors included in the coho density full model (organic sediment, gravel sediment, and riffle area) against coho density. On the organic sediment graph the filled symbols indicate Coast region sites, the open symbols indicate Interior region sites. Coho density was log transformed for the analyses and is displayed on a log scale below. The solid lines indicate the full model slopes, not the simple regression slopes. The dashed and dotted lines in the organic sediment graph indicate the slopes in the Coast and Interior regions, respectively. The dashed and dotted lines in the gradient graph indicate the slopes of gradient at high and low elevations. The biomass model distributions are very similar to these and are therefore not presented. Filled symbols indicate Coast region sites, the open symbols indicate Interior region sites.

habitat + drift models) included drift as a term in the final model. Therefore, drift was never retained when it was present as a starting variable. The subset models are not presented here.

The cost-benefit analysis revealed that the full habitat models are more efficient (have a higher benefit:cost ratio [ $r^2/\text{minute}$ ]) than a typical triple-pass depletion estimate of salmonid density. Typical triple pass depletion electrofishing takes approximately four person-hours (240 minutes) depending on stream size. The benefit:cost ratio for a direct measurement of fish abundance is therefore  $1/240$  minutes, or  $0.004 r^2/\text{min}$ , which is lower than the full models and many of the individual variables in this study (Table 3.5). The full habitat model ratios were all near 0.007 (Table 3.5). The total cost in person-minutes was approximately 110 minutes. Conductivity had the greatest individual term ratio at 0.64 for the rainbow density model, and drift the lowest ( $2.7 \times 10^{-5}$  for YOY density). The ratio for drift was based on partial  $r^2$  values from the habitat + drift subset models, and was low (Table 3.5) because the cost was high for both field and laboratory time. Setting and collecting three drift nets took approximately 45 person-minutes (this time does not include the time that the nets were filtering the water), and laboratory processing of a single sample could take more than

10 hours. The minimum time for laboratory processing was approximately 1 hour for one sample. The minimum cost for one site was therefore 225 minutes (3 samples), much higher than the other individual variables (1-73 minutes).

## **Discussion**

One of the more robust inferences that could be made from the model results is that juvenile salmonids are generally positively associated with habitat that is more structurally complex; LWD or pool-forming LWD had significantly positive relationships with all species. More complex habitat may support more fish because increased visual isolation reduces predation and aggression (Dolinsek et al. 2007). As the visual isolation of the fish increases, their territory size decreases (less competition for foraging space) and more fish can be supported in a habitat. Several other inferences and conclusions can be drawn from these habitat models. However, although our habitat models explained a high proportion of the variance in both density and biomass of juvenile salmonids, some of the regression coefficients and interactions were difficult to interpret in terms of underlying mechanisms.

The negative influence of conductivity in the YOY and coho models was difficult to interpret. Other studies have found positive relationships between conductivity and salmonid abundance (e.g. Coughlan et al. 2007, Scarnecchia and Bergersen 1987). Conductivity was expected to be positively related to salmonid abundance due to the positive impact of conductivity on stream productivity (e.g. Chételat et al. 1999). However, conductivity may also influence the timing of food availability by affecting decomposition rate. Greenwood et al. (2007) found that decomposition rate was positively associated with conductivity, and suggested that in streams with high conductivity detritus decompose earlier in the year, reducing the food supply for detritivorous invertebrates, resulting in lower food availability by the end of the summer growing season. The negative impact of conductivity may also have been due to unseen correlations with other variables.

Habitat variables related to stream discharge suggest that the relationships between flow and density differ between combined YOY salmonids, rainbow and coho. The YOY model

**Table 3.4:** Likelihood ratio calculations for the full-subset (best model constructed using the full data set, run on the subset of sites with invertebrate drift data) and full-subset-drift (same model with drift added) models for YOY, rainbow and coho.  $AIC_c$  is the Second-Order Information Criterion (used for small samples),  $\Delta_i$  is the difference between the  $AIC_c$  and the minimum  $AIC_c$ ,  $lik$  is the likelihood of the model given the data ( $e^{(-\frac{1}{2} * \Delta_i)}$ ),  $\omega_i$  is the likelihood of the model divided by the sum of the likelihoods for the competing models (see Burnham and Anderson 2002 ch 2). The  $\omega_{max} / \omega_i$  ratio indicates how much more likely the best model ( $\omega_{max}$ ) is compared to the candidate model ( $\omega_i$ ).

Model	$AIC_c$	$\Delta_i$	lik	$\omega_i$	$\omega_{max} / \omega_i$	$r^2$
YOY fish/m <sup>2</sup>						
full-subset	40.1	0	1	1	1	0.82
full-subset-drift	58	17.9	$1.30 \times 10^{-4}$	$1.30 \times 10^{-4}$	7692	0.82
YOY g/m <sup>2</sup>						
full-subset	6.6	0	1	0.79	1	0.69
full-subset-drift	9.29	2.69	0.26	0.21	3.76	0.74
rainbow fish/m <sup>2</sup>						
full-subset	25.4	0	1	1	1	0.85
full-subset-drift	49.3	23.9	$6.49 \times 10^{-6}$	$6.49 \times 10^{-6}$	$1.54 \times 10^5$	0.85
rainbow g/m <sup>2</sup>						
full-subset	46.15	0	1	1	1	0.77
full-subset-drift	80.2	34.04	$4.05 \times 10^{-8}$	$4.05 \times 10^{-8}$	$2.47 \times 10^7$	0.79
coho fish/m <sup>2</sup>						
full-subset	116	0	1	1	1	0.96
full-subset-drift	183	67.21	$2.54 \times 10^{-15}$	$2.54 \times 10^{-15}$	$3.94 \times 10^{14}$	0.97
coho g/m <sup>2</sup>						
full-subset	29.92	0	1	0.81	1	0.68
full-subset-drift	32.86	2.94	0.23	0.19	4.26	0.76

**Table 3.5:** Costs (person-minutes per site) and benefits (partial  $r^2$ ) values for the terms included in the full density and biomass models for YOY, rainbow and coho. Abbreviations are listed in Table 3.1. The partial  $r^2$  values for all of the variables except for drift come from the full models, whereas the partial  $r^2$  values for drift come from the full-subset-drift model run on the subset of sites with invertebrate drift data.

	YOY		YOY		rainbow		rainbow		coho		coho		
	density	benefit / cost	biomass	benefit / cost	density	benefit / cost	biomass	benefit / cost	density	benefit / cost	biomass	benefit / cost	
lp	5	0.17	0.03	0.02	0.004	0.23	0.05	0.3					
canopy	5				0.61	0.12	0.43	0.09					
alder	5				0.58	0.12	0.55	0.11	0.07	0.01			
cond	1	0.08	0.08	0.24	0.24	0.64	0.64	0.21	0.24	0.24			
temp	3	0.27	0.09						0.09	0.03			
elev	3	0	0	0.17	0.06				0.03	0.01	0.11	0.04	
grad	9 + 64	0.09	0.001	0.05	0.001				0.18	0.002	0.13	0.002	
cover	9 + 64	0.05	0.001			0.64	0.01	0.53	0.01				
org	9 + 64	0.26	0.004						0.18	0.002	0.01	0	
grav	9 + 64	0.02	0.000						0.44	0.006	0.3	0.004	
wb	64			0.29	0.005								
rifle	64								0.14	0.002	0.16	0.003	
pool	64	0.21	0.003						0.15	0.002			
lwd	29					0.69	0.23	0.52	0.02	0.02	0.07	0.002	
lwd_pf	29	0.31	0.01										
<b>full model</b>	<b>111</b>	<b>0.75</b>	<b>0.007</b>	<b>0.65</b>	<b>0.006</b>	<b>0.83</b>	<b>0.008</b>	<b>0.76</b>	<b>0.007</b>	<b>0.92</b>	<b>0.008</b>	<b>0.81</b>	<b>0.008</b>
	<b>108</b>												
	<b>106</b>												
drift	225	0.006		0.14	6.2x 10 <sup>-4</sup>	0.007	3.1x 10 <sup>-5</sup>	0.06	2.7x 10 <sup>-4</sup>	0.124	5.5x 10 <sup>-4</sup>	0.26	1.2x 10 <sup>-3</sup>
			2.7x 10 <sup>-5</sup>										



includes an interaction effect (gravel-gradient, Table 3.3) which suggests that intermediate water velocities are most beneficial for YOY abundance. The rainbow trout models include only one variable related to flow: largest particle size. The impact of largest particle size was positive in the Coast region but negative in the Interior region, probably due to differences in the habitat preferences of *Oncorhynchus mykiss* in the Coast and Interior. Steelhead trout, the anadromous variety of rainbow trout, are abundant in the Coast region, where the positive largest particle size slope indicated that rainbow (mostly juvenile steelhead) were associated with larger, more powerful streams with larger particle sizes like cobbles (as in Hill et al. 2006). The effect of discharge on coho density was unclear. Pool area had a significant negative coefficient, contrasting with other studies (e.g. Nickelson et al. 1992, Roni and Quinn 2001). The negative pool coefficient may be an anomaly specific to this data set. Most research has examined coastal coho populations; coho may respond differently to discharge in the Interior than the Coast for reasons unexamined in this study. Further research on Interior coho populations may help determine whether this result was unique to this data set, or if there are regional differences in coho abundance patterns.

The models for rainbow and coho showed regional interactions, indicating that habitat effects observed in one region cannot be generalized to others. Sites sampled in the Interior and Coast regions differed in several key attributes – notably, conductivity and drift were higher in the Interior, but alder cover, canopy cover, percent gravel substrate, percent pool, and LWD were higher in the Coast. Salmonid abundance did not differ between regions, but region was involved in significant interactions with largest particle size in the rainbow model, and organic sediment in the coho model. As discussed above, the regional interaction in the rainbow model may be related to a difference in habitat use between steelhead and rainbow juveniles. The regional interaction in the coho model was unexpected and difficult to explain. The effect may be a Type I Error, or may be related to unexplored differences in the food webs between regions (organic sediment is related to invertebrate production). The presence of regional interactions in the models confirms observations by earlier authors (e.g. Fausch et al. 1988) that regional differences affect the predictive ability of habitat models.

Invertebrate drift abundance did not significantly improve the fit of the habitat + drift

subset models using the Second-Order Information Criterion (AIC<sub>c</sub>) for small sample sizes (Burnham and Anderson 2002). However, assessing model improvement following drift inclusion using the standard Akaike Information Criterion indicated that drift significantly improved the YOY and coho biomass models. This suggests that drift may have a positive effect on salmonid biomass, but the effect was neither large nor consistent enough to be significant in our study.

Invertebrate drift positively impacts juvenile salmonid growth (Imre et al. 2004, Nielsen 1992, Rosenfeld et al. 2005, Slaney 1972), survival (Imre et al. 2004, Nislow et al. 1998) and density (Imre et al. 2004, Slaney 1972), so it seems unlikely that prey abundance has no real effect on fish abundance. The absence of invertebrate drift from the models could be an artifact of imprecise characterization of prey abundance (drift) at the different sites. We characterized prey abundance using only three replicate invertebrate drift samples, collected on a single day from each site between June and September. Other studies suggest a May peak in drift abundance (Slaney 1972), and that salmonid growth peaks in early spring (Bacon et al. 2005), before our drift sampling started, so we may not have accurately characterized differences in prey availability between sites. Within-site variability of invertebrate drift is also high; other studies suggest collecting four or more samples (e.g. Allan and Russek 1985, Shearer et al. 2002), although drift sampling (Chapter 2) suggests that two replicate samples are sufficient to detect major differences between sites. The final potential sampling issue that could have masked a relationship between drift and fish abundance was that salmonid populations may have been below carrying capacity at some sites due to low spawner abundance or high predator density. However, the models showed strong relationships with between juvenile abundance and habitat variables other than drift, suggesting that there was generally sufficient recruitment for salmonid populations to be habitat limited. Finally, drift may not be sufficiently variable among our sites to emerge as a significant factor constraining salmonid populations.

Our initial expectation of a positive relationship between drift and juvenile salmon implicitly assumes bottom-up control of fish abundance, and minimal top-down effects of fish predation. However, it is possible that fish deplete drift to varying degrees depending on site

characteristics, thereby obscuring any relationship between drift biomass and fish abundance across sites. A more realistic expectation would be a positive relationship between fish abundance and invertebrate production, rather than standing crop. Depletion of drift biomass (standing crop) through predation may cause drift concentration to poorly represent drift production. Salmonid populations have been shown to deplete stream invertebrate populations (Huryn 1998), so it is likely that some degree of top-down control occurred at some of our sites. Dependence on prey sources other than drift would also weaken the relationship with fish abundance. Although drift is the primary food source of stream salmonids, they can switch to benthic invertebrates when drift is unavailable (Nislow et al. 1998) or if forced through competition (Nielsen 1992). Finally, the range of variation in prey abundance may be small relative to other drivers of habitat quality in our data set, so that it correlates weakly with fish abundance.

The final objective of this study was to examine the cost effectiveness of different models and variables for assessing or monitoring habitat quality for juvenile salmonids. Predictive models of habitat capacity in this sense are most useful when stream habitats are not saturated (e.g. because of habitat-independent factors like over-harvesting of adults), and fish density cannot be used as a direct index of habitat quality. For streams that are heavily under-recruited, habitat-based estimates of capacity are more reliable indices of capacity than measured fish abundance (as well as potentially more cost-effective). Deviation of observed fish abundance from that predicted by habitat capacity models is also a useful way of identifying site-specific management issues (e.g. low spawner abundance from over harvest, or poor spawner access).

The cost-benefit analysis in this study showed that habitat models with strong predictive ability ( $r^2 = 0.65$  to  $0.92$ ) can be developed and the associated field data collected after less than two hours of field work, less time than typical triple-pass electrofishing. Other fish collection methods, such as single-pass electrofishing (Jones and Stockwell 1995), require less field time than triple-pass electrofishing and may therefore have higher benefit:cost ratios than the full habitat models presented here. Most of the habitat variables used in this study took small enough amounts of time to measure that they had high benefit:cost ( $r^2/\text{min}$ ) ratios.

The exception was invertebrate drift, which took more field time and much more laboratory time than any of the other variables (Table 3.5). While the benefit:cost ratios for individual variables calculated in this study are good indicators of their general predictive ability, their exact efficiency ( $r^2/\text{min}$ ) could be different when combined with other variables in regression. That is, the partial  $r^2$  values of model terms depend in part on what other terms are included in the model. Therefore, while they provide a useful starting point for evaluating the cost-effectiveness of different predictive variables, they should be considered context dependent.

This study suggests that physical habitat variables appear to be more robust predictors of fish abundance than direct measures of invertebrate drift. Future research on stream food webs, particularly on the impact of salmonid density on benthic and drifting invertebrate abundance, and on the degree to which drift accurately represents prey availability for drift feeding fish, should improve understanding of the factors that limit the abundance of stream salmonids. Further investigation of juvenile salmonid foraging behaviour (drift versus benthic feeding), especially in relation to the abundance of drift and benthic prey, could lead to more precise capacity models and improve the ability of habitat managers to consider the role of food availability during planning, monitoring, and restoration activities.

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## Conclusion

The underlying rationale for this study was to determine 1) the degree to which prey (invertebrate drift) for drift-feeding salmonids varies across time and space, and 2) whether drift abundance can be used as a significant predictor of fish abundance.

Temporal variation of invertebrate drift at the day-to-day scale is lower than spatial variation within or between sites (Figure 2.5). Therefore it is unnecessary to resample a site on successive days in order to calculate a precise estimate of invertebrate drift abundance. However, variation within sites (residual variation) was high: up to 90% of the random variation. High within site variation made estimates of drift abundance less accurate, and probably contributed to the low predictive ability of the habitat models for drift in Chapter 2. The reduced precision of these estimates may also have contributed to the rejection of drift from the salmonid habitat models in the salmonid chapter. Therefore multiple samples are necessary to estimate invertebrate drift abundance, but there appears to be no need to repeat that sampling effort on additional visits to the site. Invertebrate drift measurements could be used in habitat models for juvenile salmonids in areas with lower within site variation, or by collecting more than three samples.

Future research to characterize the variation of invertebrate drift would allow further refinement of sampling protocols, and a greater understanding of the timing of food availability for juvenile salmonids. It would be useful to determine the relationship between daytime drift samples, samples collected at dusk, and samples collected in the first hours after dark (the first night time peak, Waters 1962), in order to determine how representative daytime samples are of food availability for juvenile salmonids throughout the day and night. Examination of the environmental conditions that influence terrestrial invertebrate input (e.g. wind, rain) would also improve sampling protocols, and could explain some of the day-to-day variation of terrestrial drift (Figure 2.5).

Physical and biological habitat variables were both included in the final models predicting the abundance of young-of-the-year coho salmon, rainbow trout, and all salmonids combined,

but invertebrate drift was not included. In general, habitats with more structure were better habitat for salmonids, but there were mixed responses to all of the candidate variables. Models for individual species had higher coefficients of variation than the YOY-combined model, suggesting real differences in habitat requirements or preferences between the species. The absence of invertebrate drift from the final models may have been related to sampling problems (see Chapter 3 Discussion), but other considerations, such as complex trophic interactions, are also possible explanations.

Further research on complex trophic interactions such as the effect of habitat on foraging behaviour, prey-switching, and thresholds of food abundance that prompt changes in feeding behaviour would help explain how food availability affects salmonid abundance in a natural setting. Much of the previous research on the impacts of invertebrate drift abundance on juvenile salmonids has been conducted in artificial channels (e.g. Imre et al. 2004, Rosenfeld et al. 2005, Slaney 1972). In real stream channels, where benthic food is more abundant and other behaviour-influencing factors such as competition are present, the positive impact of invertebrate drift on salmonid growth, abundance and survival may be overwhelmed by other factors and by behaviour.

The predictive models for juvenile salmonids developed in this study are directly applicable to fisheries management projects such as habitat assessment, monitoring, and restoration. The models could be used as presented, or selected variables could be applied based on available resources; the cost:benefit analysis in Chapter 3 can provide fisheries scientists with a good starting point for management decisions related to the power of potential inventory variables. The regional differences in the rainbow and coho models indicate that there is a need for increased regional specificity in habitat assessment protocols – paradigms of fisheries management developed in the Coast region are less applicable in other regions of British Columbia than has previously been assumed. Further research on regional habitat differences and their impacts on salmonid abundance would improve the management of these species.

As do all Master of Science theses, this one had weaknesses and strengths. The scale of the

project caused weaknesses regarding sample size and data collection: it was not feasible to sort drift samples for all of the sites, or all three of the samples collected on each visit for the temporal study. Had all of the samples been sorted, invertebrate drift may have had a greater impact in the habitat models. Due to the scale of the project, data collected by other people were used extensively; the quality of the data is not being questioned, but there may have been slight differences in electrofishing method that resulted in differences between those data and my own. However, the scale of the project was also its greatest strength, and allowed this project to stand apart from many habitat modeling exercises. In an extensive review, Fausch (1988) found that the majority of habitat models were based on less than 20 sites, as were the majority of models that had coefficients of determination greater than 0.75. In contrast, the salmonid models in this study included up to 50 sites and five of the six coefficients of determination were 0.75 or more. The model with the greatest  $r^2$ , for coho density, had an  $r^2 = 0.92$  and was based on 38 sites. Fausch (1988) also found that many of the reviewed studies did not place enough emphasis on the statistical procedures used to develop models, in particular regarding poor methods for choosing the best models. In this study a great amount of emphasis was placed on researching and applying the most objective and statistically sound model selection method available, resulting in greater confidence that the most appropriate models were chosen.

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**Appendix 1:** Habitat measurements from Chapter 2 sites.

	site	code	region	Drift Invertebrate Density (mg/m <sup>3</sup> )		
				total	aquatic	terrestrial
1	Brohm	brom	C	71.2	63.9	7.2
2	Carnation	carn	C	15.8	12.0	3.8
3	Chapman	chap	C	14.7	8.7	6.0
4	Coho South	cohs	C	36.1	34.5	1.7
5	Colvin	colv	C	16.8	16.0	0.9
6	Cook	cook	C	38.8	32.6	6.2
7	Elk	elkk	C	91.5	54.6	37.0
8	Finish Early	fini	C	9.3	9.2	0.1
9	High Falls	higa	C	1062.0	130.8	931.2
10	Husdon	husd	C	10.8	6.6	4.2
11	Lost Shoe	lost	C	51.7	41.5	10.2
12	Rousseau	rous	C	51.1	33.1	18.1
13	Sandhill	sand	C	22.8	16.3	6.5
14	Shovelnose	shov	C	57.2	38.9	18.3
15	Silver Hope	silh	C	57.3	47.9	9.4
16	Slesse	sles	C	137.0	134.2	2.9
17	Wakefield	wake	C	52.2	45.2	7.0
18	Yola	yola	C	7.9	6.7	1.2
19	Crazy	craz	I	46.9	39.6	7.4
20	Criss	cris	I	84.2	34.6	49.7
21	Lemieux Main	lemm	I	61.2	48.0	13.2
22	Lemieux Side	lems	I	161.7	147.4	14.3
23	Lindquist	lind	I	77.9	61.1	16.8
24	Moore	moor	I	135.2	120.9	14.3
25	Senn	senn	I	34.8	15.5	19.3
26	Silver B	silb	I	12.6	9.9	2.6
27	Six Mile	sixm	I	57.9	52.3	5.6
28	Spius	spiu	I	283.6	161.9	121.7
29	Vermelin	verm	I	33.6	31.6	1.9
30	Yard	yard	I	119.2	114.4	4.9
	<b>average</b>			<b>97.1</b>	<b>52.3</b>	<b>44.8</b>

**Appendix 1:** continued.

		UTM coordinates				
	site	easting	northing	datum	zone	elev (m)
1	Brohm	491286	5517692	WGS84	10	260
2	Carnation	353871	5420162	WGS84	10	20
3	Chapman	447858	5478537	WGS84	10	60
4	Coho South	430330	5498771	WGS84	10	80
5	Colvin	437426	5481030	WGS84	10	20
6	Cook	444195	5481677	WGS84	10	20
7	Elk	585091	5444106	WGS84	10	40
8	Finish Early	307631	5448910	NAD27	10	40
9	High Falls	478552	5531752	WGS84	10	60
10	Husdon	448842	5478484	WGS84	10	80
11	Lost Shoe	311047	5431297	NAD27	10	40
12	Rousseau	349310	5409882	WGS84	10	40
13	Sandhill	311047	5431297	WGS84	10	40
14	Shovelnose	476144	5545906	WGS84	10	160
15	Silver Hope	617821	5454219	WGS84	10	440
16	Slesse	594561	5436690	WGS84	10	240
17	Wakefield	441671	5479843	WGS84	10	20
18	Yola	617879	5453010	WGS84	10	480
19	Crazy	384614	5650320	WGS84	11	400
20	Criss	643436	5639327	WGS84	10	540
21	Lemieux Main	693929	5701713	WGS84	10	400
22	Lemieux Side	693929	5701713	WGS84	10	400
23	Lindquist	696491	5688907	WGS84	10	400
24	Moore	681607	5569893	WGS84	10	640
25	Senn	374055	5645513	WGS84	11	380
26	Silver B	332562	5607099	WGS84	11	400
27	Six Mile	314538	5603249	WGS84	11	740
28	Spius	636528	5534836	WGS84	10	860
29	Vermelin	302950	5691650	WGS84	11	660
30	Yard	372188	5640897	WGS84	11	380
	<b>average</b>					<b>278</b>

**Appendix 1:** continued.

	site	average summer temperature (°C)	conductivity ( $\mu$ S)	largest particle (cm)	canopy cover (proportion)	alder cover (proportion)
1	Brohm	16.0	17.2	60.8	0.00	0.59
2	Carnation	15.1	40.5	5.3	0.10	0.09
3	Chapman	16.3	20.5	84.0	0.14	0.10
4	Coho South	16.1	63.4	7.4	0.71	0.17
5	Colvin	17.0	116.5	2.6	0.59	0.09
6	Cook	16.6	129.2	4.2	0.81	0.11
7	Elk	17.1	119.7	24.4	0.58	0.08
8	Finish Early	15.3	NA	NA	0.88	0.00
9	High Falls	15.9	10.0	45.0	0.19	0.24
10	Husdon	16.2	46.0	2.8	0.57	0.11
11	Lost Shoe	14.1	76.1	10.4	0.30	0.29
12	Rousseau	15.2	42.5	13.0	0.08	0.05
13	Sandhill	14.1	144.7	2.8	0.56	0.38
14	Shovelnose	15.2	28.9	43.1	0.24	0.24
15	Silver Hope	15.2	72.1	37.8	0.03	0.00
16	Slesse	15.2	53.9	78.7	0.04	0.02
17	Wakefield	16.9	92.9	36.8	0.62	0.21
18	Yola	14.7	42.8	85.4	0.03	0.01
19	Crazy	16.0	24.4	21.5	0.02	0.00
20	Criss	16.4	274.0	66.4	0.15	0.01
21	Lemieux Main	17.3	201.0	NA	0.10	0.08
22	Lemieux Side	17.3	201.0	NA	0.10	0.08
23	Lindquist	17.1	66.0	24.6	0.13	0.08
24	Moore	15.9	220.0	2.1	0.14	0.12
25	Senn	16.7	54.7	5.0	0.31	0.31
26	Silver B	17.0	210.0	18.0	0.73	0.13
27	Six Mile	15.2	100.5	2.0	0.00	0.00
28	Spius	14.6	163.3	82.3	0.04	0.01
29	Vermelin	15.0	13.0	12.9	0.34	0.15
30	Yard	16.3	31.8	20.3	0.00	0.00
	<b>average</b>	<b>15.9</b>	<b>92.3</b>	<b>29.6</b>	<b>0.28</b>	<b>0.12</b>

**Appendix 1:** continued.

	site	bankfull width (m)	pool area (proportion)	riffle area (proportion)	gravel sediment (proportion)	organic sediment (proportion)	gradient (%)
1	Brohm	5.0	0.1	0.6	0.84	0.00	5.1
2	Carnation	9.1	0.3	0.2	0.10	0.05	1.0
3	Chapman	20.1	0.0	0.3	0.68	0.00	1.3
4	Coho South	2.7	0.2	0.3	0.53	0.12	1.8
5	Colvin	2.8	0.1	0.2	0.54	0.30	0.5
6	Cook	2.4	0.2	0.5	0.14	0.14	0.7
7	Elk	4.2	0.0	0.2	0.00	0.00	3.4
8	Finish Early	1.7	0.7	0.2	0.19	0.00	0.0
9	High Falls	10.5	0.0	0.8	0.40	0.00	1.6
10	Husdon	2.6	0.2	0.1	0.26	0.14	0.4
11	Lost Shoe	7.8	0.3	0.0	0.60	0.37	1.3
12	Rousseau	10.1	0.3	0.5	0.21	0.10	0.8
13	Sandhill	4.5	0.2	0.0	0.30	0.13	0.0
14	Shovelnose	13.6	0.0	0.5	0.09	0.00	2.6
15	Silver Hope	17.4	0.0	0.4	0.20	0.06	1.6
16	Slesse	20.8	0.0	0.6	0.20	0.01	1.8
17	Wakefield	6.3	0.1	0.0	0.08	0.00	1.9
18	Yola	15.9	0.1	0.4	0.45	0.01	2.0
19	Crazy	17.5	0.0	0.3	0.08	0.01	2.3
20	Criss	8.0	0.1	0.6	0.27	0.01	3.3
21	Lemieux Main	21.1	0.0	0.5	0.30	0.00	1.5
22	Lemieux Side	6.7	0.1	0.3	0.34	0.36	1.0
23	Lindquist	6.9	0.0	0.4	0.57	0.13	0.9
24	Moore	4.2	0.2	0.0	0.08	0.01	0.5
25	Senn	3.3	0.1	0.2	0.11	0.17	1.7
26	Silver B	5.7	0.0	0.3	0.10	0.04	3.6
27	Six Mile	3.1	0.0	0.0	0.03	0.50	1.0
28	Spius	16.7	0.0	0.0	0.46	0.00	1.6
29	Vermelin	6.5	0.2	0.2	0.09	0.04	2.5
30	Yard	33.1	0.0	0.6	9.03	0.01	2.2
	<b>average</b>	<b>9.7</b>	<b>0.1</b>	<b>0.3</b>	<b>0.58</b>	<b>0.1</b>	<b>1.7</b>



**Appendix 2:** habitat measurements from Chapter 3 sites. Abbreviations follow Table 3.1.

	site	region	lp (cm)	canopy (proportion)	alder (proportion)
1	angu	C	30.5	0.60	0.07
2	bole	I	35.3	0.17	0.15
3	brom	C	60.8	0.63	0.59
4	carn	C	5.3	0.10	0.09
5	chap	C	84.0	0.14	0.10
6	cohn	C	2.5	0.83	0.05
7	cohs	C	7.4	0.71	0.17
8	cold	I	64.0	0.02	0.01
9	colv	C	2.6	0.59	0.09
10	cook	C	4.2	0.81	0.11
11	craz	I	21.5	0.02	0.00
12	cris	I	66.4	0.15	0.01
13	dead	I	53.2	0.11	0.00
14	depo	C	17.6	0.28	0.28
15	elkk	C	24.4	0.58	0.08
16	fini	C	29.0	0.88	0.88
17	fred	C	4.6	0.48	0.43
18	guic	I	23.0	0.28	0.00
19	hifa	C	25.8	0.45	0.21
20	hunt	C	27.4	0.40	0.32
21	husd	C	2.8	0.57	0.11
22	kooa	C	5.7	0.38	0.15
23	koob	C	0.6	0.49	0.00
24	kooc	C	1.0	0.38	0.00
25	lemm	I	NA	0.10	0.08
26	lems	I	NA	NA	NA
27	lind	I	24.6	0.13	0.08
28	lost	C	10.4	0.30	0.29
29	maka	I	73.2	0.03	0.00
30	mash	C	76.5	0.54	0.54
31	moor	I	2.1	0.14	0.12
32	pach	C	5.6	0.55	0.37
33	rous	C	13.0	0.08	0.05
34	sand	C	2.8	0.56	0.38
35	sari	C	10.4	0.13	0.02
36	senn	I	5.0	0.31	0.31
37	shov	C	43.1	0.24	0.24
38	silā	I	76.9	0.44	0.21
39	silb	I	18.0	0.73	0.13
40	silh	C	37.8	0.03	0.00
41	sixm	I	2.0	0.00	0.00
42	sles	C	78.7	0.04	0.02
43	spiu	I	82.3	0.04	0.01
44	stag	C	1.2	0.52	0.25
45	verm	I	12.9	0.34	0.15
46	wake	C	36.8	0.62	0.21
47	weee	C	1.8	0.88	0.88
48	weym	I	55.0	0.50	0.40
49	yard	I	20.3	0.00	0.00
50	yola	C	85.4	0.03	0.01
	<b>average</b>		<b>28.7</b>	<b>0.35</b>	<b>0.18</b>

## Appendix 2: continued

	site	pool (proportion)	rifle (proportion)	tavsm (oC)	cond (uS)
1	angu	0.35	0.65	16.2	55.4
2	bole	0.04	0.24	15.4	127.8
3	brom	0.08	0.63	16.0	17.2
4	carn	0.26	0.20	15.1	40.5
5	chap	0.04	0.26	16.3	20.5
6	cohn	0.17	0.52	16.1	53.6
7	cohs	0.23	0.28	16.1	63.4
8	cold	0.04	0.79	14.5	98.5
9	colv	0.05	0.22	17.0	116.5
10	cook	0.15	0.46	16.6	129.2
11	craz	0.00	0.30	16.0	24.4
12	cris	0.06	0.59	16.4	274.0
13	dead	0.14	0.16	15.6	234.0
14	depo	0.13	0.58	15.2	29.9
15	elkk	0.00	0.25	17.1	119.7
16	fini	0.70	0.19	15.3	NA
17	fred	0.19	0.56	15.4	50.9
18	guic	0.01	0.00	16.2	55.2
19	hifa	0.01	0.75	15.9	10.0
20	hunt	0.20	0.55	15.4	90.3
21	husd	0.23	0.13	16.2	46.0
22	kooa	0.36	0.03	14.0	141.0
23	koob	0.24	0.01	14.0	96.3
24	kooc	0.00	0.00	14.0	34.9
25	lemm	0.00	0.54	17.3	201.0
26	lems	0.10	0.26	17.3	201.0
27	lind	0.02	0.37	17.1	66.0
28	lost	0.25	0.03	14.1	76.1
29	maka	0.00	0.70	14.9	138.6
30	mash	0.05	0.00	15.9	47.7
31	moor	0.18	0.00	15.9	220.0
32	pach	0.20	0.49	14.9	34.8
33	rous	0.32	0.46	15.2	42.5
34	sand	0.21	0.00	14.1	144.7
35	sari	0.46	0.22	15.6	47.6
36	senn	0.12	0.23	16.7	54.7
37	shov	0.01	0.53	15.2	28.9
38	sil	0.00	0.00	14.6	1.5
39	silb	0.01	0.34	17.0	210.0
40	silh	0.02	0.41	15.2	72.1
41	sixm	0.00	0.00	15.2	100.5
42	sles	0.01	0.60	15.2	53.9
43	spiu	0.00	0.00	14.6	163.3
44	stag	0.70	0.17	14.0	111.9
45	verm	0.17	0.24	15.0	13.0
46	wake	0.13	0.00	16.9	92.9
47	weee	0.25	0.20	16.3	73.6
48	weym	0.45	0.06	15.2	85.7
49	yard	0.01	0.64	16.3	31.8
50	yola	0.09	0.43	14.7	42.8
	<b>average</b>	<b>0.15</b>	<b>0.31</b>	<b>15.6</b>	<b>87.5</b>

Appendix 2: continued

	site	elev (m)	wb (m)	cover (proportion)	grav (proportion)
1	angu	20	8.59	0.16	0.37
2	bole	720	9.79	0.07	0.25
3	brom	260	4.99	0.12	0.06
4	carn	20	9.06	0.06	0.84
5	chap	60	20.07	0.06	0.10
6	cohn	40	1.48	0.21	0.32
7	cohs	80	2.73	0.14	0.68
8	cold	880	16.06	0.07	0.28
9	colv	20	2.89	0.15	0.52
10	cook	20	2.41	0.10	0.54
11	craz	400	17.55	0.02	0.45
12	cris	540	8.01	0.15	0.08
13	dead	660	11.42	0.08	0.25
14	depo	640	11.85	0.08	0.28
15	elkk	40	4.18	0.03	0.14
16	fini	40	1.74	0.08	0.31
17	fred	40	9.75	0.07	0.61
18	guic	600	8.20	0.11	0.12
19	hifa	60	10.55	0.04	0.19
20	hunt	20	8.11	0.11	0.24
21	husd	80	2.57	0.21	0.40
22	kooa	20	3.52	0.20	0.59
23	koob	20	3.20	0.12	0.07
24	kooc	20	2.37	0.23	0.17
25	lemm	400	21.10	0.02	0.27
26	lems	400	6.70	0.03	0.30
27	lind	400	6.87	0.06	0.34
28	lost	40	7.79	0.09	0.26
29	maka	820	9.39	0.04	0.34
30	mash	80	8.15	0.14	0.19
31	moor	640	4.21	0.18	0.57
32	pach	40	4.68	0.08	0.81
33	rous	40	10.14	0.07	0.60
34	sand	40	4.48	0.20	0.21
35	sari	20	15.37	0.08	0.71
36	senn	380	3.27	0.12	0.08
37	shov	160	13.56	0.05	0.30
38	silā	860	6.85	0.09	0.13
39	silb	400	5.66	0.08	0.11
40	silh	440	17.37	0.03	0.09
41	sixm	740	3.10	0.08	0.10
42	sles	240	20.77	0.05	0.20
43	spiu	860	16.66	0.05	0.03
44	stag	20	2.22	0.10	0.09
45	verm	660	6.52	0.14	0.46
46	wake	20	6.34	0.10	0.20
47	weee	40	1.30	0.10	0.31
48	weym	780	4.18	0.10	0.09
49	yard	380	33.11	0.18	0.09
50	yola	480	15.93	0.15	0.08
	<b>average</b>	<b>294</b>	<b>8.74</b>	<b>0.10</b>	<b>0.30</b>

## Appendix 2: continued

	site	org (proportion)	grad (%)	lwd (pieces/m)	lwd_pf(pieces/m)
1	angu	0.06	1.6	0.03	0.00
2	bole	0.04	2.1	0.01	0.00
3	brom	0.00	5.1	0.00	0.00
4	carn	0.05	1.0	0.04	0.01
5	chap	0.00	1.3	0.01	0.00
6	cohn	0.18	1.5	0.23	0.03
7	cohs	0.12	1.8	0.14	0.02
8	cold	0.00	1.4	0.01	0.00
9	colv	0.31	0.5	0.11	0.00
10	cook	0.14	0.7	0.14	0.02
11	craz	0.01	2.3	0.00	0.00
12	cris	0.01	3.3	0.04	0.04
13	dead	0.02	1.6	0.01	0.00
14	depo	0.05	0.9	0.08	0.00
15	elkk	0.00	3.4	0.02	0.00
16	fini	0.05	8.0	0.26	0.00
17	fred	0.23	0.7	0.02	0.00
18	guic	0.01	2.4	0.00	0.00
19	hifa	0.00	1.6	0.02	0.00
20	hunt	0.00	2.7	0.02	0.00
21	husd	0.14	0.4	0.24	0.03
22	kooa	0.20	0.8	0.20	0.04
23	koob	0.28	0.1	0.09	0.00
24	kooc	0.40	0.7	0.18	0.00
25	lemm	0.00	1.5	0.00	0.00
26	lems	0.36	1.0	0.01	0.00
27	lind	0.13	0.9	0.03	0.00
28	lost	0.37	1.3	0.03	0.00
29	maka	0.00	1.9	0.00	0.00
30	mash	0.00	1.3	0.02	0.00
31	moor	0.01	0.5	0.00	0.00
32	pach	0.04	1.2	0.03	0.01
33	rous	0.10	0.8	0.01	0.00
34	sand	0.13	0.0	0.13	0.01
35	sari	0.01	0.5	0.01	0.00
36	senn	0.17	1.7	0.05	0.02
37	shov	0.00	2.7	0.02	0.00
38	silā	0.01	4.0	0.02	0.00
39	silb	0.04	3.6	0.04	0.00
40	silh	0.06	1.6	0.01	0.00
41	sixm	0.50	1.0	0.00	0.00
42	sles	0.01	1.8	0.00	0.00
43	spiu	0.00	1.6	0.00	0.00
44	stag	0.49	1.2	0.11	0.00
45	verm	0.06	2.5	0.10	0.01
46	wake	0.00	1.9	0.03	0.00
47	weee	0.16	3.6	0.19	0.04
48	weym	0.00	4.1	0.00	0.00
49	yard	0.01	2.2	0.02	0.00
50	yola	0.01	2.0	0.01	0.00
	<b>average</b>	<b>0.10</b>	<b>1.8</b>	<b>0.06</b>	<b>0.01</b>

Appendix 2: continued

	site	shock_area (m2)	YOY (#)	rainbow (#)	coho (#)
1	angu	185.4	178	NA	109
2	bole	96.1	117	74	5
3	brom	123.5	44	22	NA
4	carn	322.0	418	NA	414
5	chap	85.1	89	46	42
6	cohn	31.1	93	NA	29
7	cohs	28.8	108	NA	19
8	cold	320.3	139	87	11
9	colv	81.2	142	NA	28
10	cook	29.8	61	NA	3
11	craz	126.5	87	57	24
12	cris	118.6	90	80	1
13	dead	179.0	80	79	NA
14	depo	77.2	54	NA	35
15	elkk	74.8	123	NA	69
16	fini	35.6	20	NA	NA
17	fred	207.3	130	29	95
18	guic	129.2	50	2	8
19	hifa	110.9	45	44	NA
20	hunt	188.1	86	32	54
21	husd	84.4	71	NA	23
22	kooa	78.7	194	NA	156
23	koob	90.5	71	NA	10
24	kooc	59.9	132	NA	125
25	lemm	48.3	22	20	2
26	lems	109.2	211	72	187
27	lind	88.9	298	NA	295
28	lost	371.3	208	NA	157
29	maka	99.1	18	16	1
30	mash	78.4	93	60	24
31	moor	108.0	23	23	NA
32	pach	135.2	90	17	67
33	rous	213.3	178	74	102
34	sand	192.1	49	NA	35
35	sari	304.5	91	9	78
36	senn	37.6	142	62	69
37	shov	150.4	290	227	48
38	sil	71.0	21	5	NA
39	silb	89.2	41	24	NA
40	silh	79.4	49	37	NA
41	sixm	60.0	28	22	NA
42	sles	167.0	232	169	48
43	spiu	135.0	94	73	2
44	stag	41.8	61	NA	4
45	verm	26.5	36	24	4
46	wake	110.2	105	NA	88
47	weee	29.5	180	NA	43
48	weym	70.7	55	44	NA
49	yard	168.6	28	9	4
50	yola	188.5	123	76	NA
	<b>average</b>	<b>120.8</b>	<b>108</b>	<b>52</b>	<b>65</b>

Appendix 2: continued.

	site	YOY/m2	rainbow/m2	coho/m2	drift (dry mg/m3)
1	angu	0.96	NA	0.59	NA
2	bole	1.22	0.77	0.05	NA
3	brom	0.36	0.18	NA	71.16
4	carn	1.3	NA	1.29	15.80
5	chap	1.05	0.54	0.49	14.72
6	cohn	2.99	NA	0.93	NA
7	cohs	3.75	NA	0.66	36.14
8	cold	0.43	0.27	0.03	NA
9	colv	1.75	NA	0.34	16.83
10	cook	2.05	NA	0.1	38.80
11	craz	0.69	0.45	0.19	46.94
12	cris	0.76	0.67	0.01	84.21
13	dead	0.45	0.44	NA	NA
14	depo	0.7	NA	0.45	NA
15	elkk	1.65	NA	0.92	91.55
16	fini	0.56	NA	NA	9.26
17	fred	0.63	0.14	0.46	NA
18	guic	0.39	0.02	0.06	NA
19	hifa	0.41	0.4	NA	1062.02
20	hunt	0.46	0.17	0.29	NA
21	husd	0.84	NA	0.27	10.79
22	kooa	2.47	NA	1.98	NA
23	koob	0.78	NA	0.11	NA
24	kooc	2.2	NA	2.09	NA
25	lemm	0.46	0.41	0.04	61.24
26	lems	1.93	0.66	1.71	161.69
27	lind	3.35	NA	3.32	77.95
28	lost	0.56	NA	0.42	51.70
29	maka	0.18	0.16	0.01	NA
30	mash	1.19	0.77	0.31	NA
31	moor	0.21	0.21	NA	135.20
32	pach	0.67	0.13	0.5	NA
33	rous	0.83	0.35	0.48	51.14
34	sand	0.26	NA	0.18	22.79
35	sari	0.3	0.03	0.26	NA
36	senn	3.77	1.65	1.83	34.82
37	shov	1.93	1.51	0.32	57.16
38	sila	0.3	0.07	NA	NA
39	silb	0.46	0.27	NA	12.55
40	silh	0.62	0.47	NA	57.29
41	sixm	0.47	0.37	NA	57.88
42	sles	1.39	1.01	0.29	137.04
43	spiu	0.7	0.54	0.01	283.62
44	stag	1.46	NA	0.1	NA
45	verm	1.36	0.9	0.15	33.59
46	wake	0.95	NA	0.8	52.20
47	weee	6.1	NA	1.46	NA
48	weym	0.78	0.62	NA	NA
49	yard	0.17	0.05	0.02	119.20
50	yola	0.65	0.4	NA	7.88
	<b>average</b>	<b>1.20</b>	<b>0.47</b>	<b>0.60</b>	<b>97.11</b>

# Appendix 3: UBC Research Ethics Board Certificate of Approval

Page 1 of 1

The University of British Columbia

## Animal Care Certificate

Application Number:	A05-0357	
Investigator or Course Director:	<a href="#">Jonathan Shurin</a>	
Department:	Zoology	
Animals Approved:	<input type="text" value="Salmon 2400"/>	
Start Date:	2005-3-16	Approval Date: 2005-5-16
Funding Sources:		
<b>Funding Agency:</b>	BC Ministry of Water, Land and Air Protection	
<b>Funding Title:</b>	Development of indicators of stream condition, function and capacity for juvenile salmon	
<b>Unfunded title:</b>	Indicators of stream condition and capacity (Sandra)	

The Animal Care Committee has examined and approved the use of animals for the above experimental project.

This certificate is valid for one year from the above start or approval date (whichever is later) provided there is no change in the experimental procedures. Annual review is required by the CCAC and some granting agencies.

**A copy of this certificate must be displayed in your animal facility**

Office of Research Services and Administration  
102, 6190 Agronomy Road, Vancouver, V6T 1Z3  
Phone: 604-827-5111 Fax: 604-822-5093