

# Relationships between habitat characteristics and breeding population densities in sockeye salmon (*Oncorhynchus nerka*)

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**Abstract:** We examine the importance of stream habitat characteristics in governing variation in spawning densities of sockeye salmon (*Oncorhynchus nerka*) across 32 streams in the Fraser River Basin, British Columbia, Canada. We used mixed-effects models to examine four competing hypotheses for the influence of abiotic stream characteristics acting on either adult salmon or embryo mortality. All models that received support using Akaike's information criterion included stream characteristics that are associated with cover. These included the percent area of pools, percentage of the banks that were undercut, and large woody debris (in that order). These results suggest the importance of stream characteristics, which reduce risk of predation on adults, in determining spawning sockeye salmon densities. Thus, identification of a small number of physical characteristics of streams provides insight into ecological processes that determine population densities. This information can be used to quantify habitat quality, which can guide habitat prioritization for conservation.

**Résumé :** Nous examinons l'importance des caractéristiques des habitats d'eau courante comme explication de la variation dans la densité de fraie des saumons rouges (*Oncorhynchus nerka*) dans 32 cours d'eau du bassin du fleuve Fraser, Colombie-Britannique, Canada. Des modèles à effets mixtes nous ont servi à examiner quatre hypothèses de rechange sur l'importance de l'action des facteurs abiotiques du cours d'eau sur la mortalité des saumons adultes ou sur celle des embryons. Tous les modèles qui ont été appuyés par le critère d'information d'Akaike incluent des caractéristiques des cours d'eau associées à la couverture. Ces caractéristiques comprennent (dans l'ordre) la surface en pourcentage des fosses, le pourcentage de rives qui sont en surplomb et les grands débris ligneux. Ces résultats laissent croire que les caractéristiques du cours d'eau qui réduisent le risque de prédation chez les adultes sont d'importance pour expliquer les densités des saumons rouges en fraie. Ainsi, l'identification d'un petit nombre de caractéristiques physiques des cours d'eau fournit un éclairage sur les processus écologiques qui déterminent la densité des populations. Ces renseignements peuvent servir à déterminer la qualité de l'habitat, ce qui peut guider la priorisation des habitats pour fins de conservation.

[Traduit par la Rédaction]

## Introduction

Impacts of habitats on animal population dynamics depend on the interplay between ecological interactions such as predation–competition and physiological requirements (Huey 1991; Parsons 2005; Parmesan 2006). Environmental conditions can mediate these ecological interactions (Pulliam and Danielson 1991). For example, climate change is redistributing species according to their physiological tolerances in conjunction with changes in predators and prey (Parmesan 2006). Insights into the mechanisms by which physical habitat characteristics mediate population dynamics can therefore benefit conservation programs and ecosystem-based management.

Adult Pacific salmon returning to spawn in fresh water are ideally suited for studies of the role of habitats in mediating survival and densities of adults. Competition between spawning females for breeding sites can lead to superimposition of nests (i.e., early nests being dug up by females that spawn later in the season), which can decrease reproductive success. The amount of superimposition varies with adult density and the availability of suitable spawning habitat (Essington et al. 2000), determined by characteristics such as substrate size, flow characteristics, and dissolved oxygen. In addition, adult salmon can experience high predation rates by bears (Quinn et al. 2003), which has been shown to depend on refugia in streams, such as deep water and physical complexity (Quinn et al. 2001; Gende et al. 2004). Empirical relationships between stream habitat and juvenile production have been explored for a number of salmonid species (Inoue and Nakano 1999; Sharma and Hilborn 2001; Bryant and Woodsmith 2009). However, few studies have developed these habitat–abundance relationships for adults. Unlike many other species of salmonids, juvenile sockeye salmon (*Oncorhynchus nerka*) do not compete in streams because they travel to lakes as soon as they emerge from the gravel.

The objective of this study is to use adult sockeye salmon as a model for understanding relationships between abiotic habitat characteristics and animal population densities in the

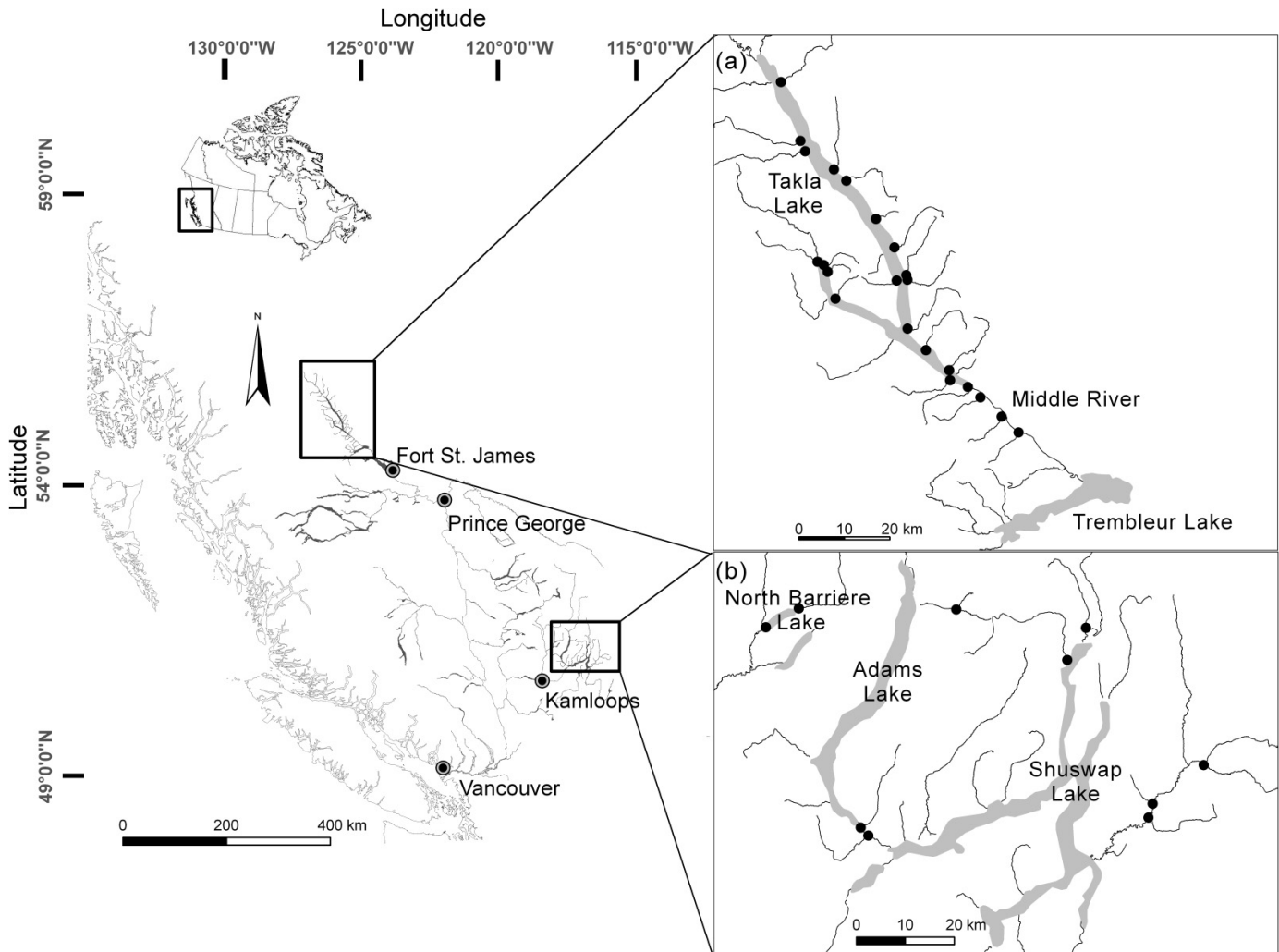
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**Fig. 1.** Locations of 32 study streams in two regions of the Fraser River Basin, British Columbia, Canada: (a) Stuart and (b) Thompson. Location in western Canada is shown in small inset.



context of ecological processes. We studied populations across 32 streams in two regions that experience very different environmental conditions in the Fraser River Basin, British Columbia, Canada (Fig. 1). The Early Stuart population complex spawns in the most northern salmon-bearing watershed in the Fraser River, where fish can experience warm spawning temperatures and low incubating temperatures (Cope 1996). Human impacts on streams in this region have been minimal. The Early Summer population complex spawns further south and experiences slightly warmer spawning and incubation temperatures, and streams have been impacted by deforestation, agricultural runoff, and urbanization.

We investigate empirical relationships between stream habitat characteristics and adult spawning sockeye salmon abundance. To do this, we develop a series of hypotheses that incorporate habitat characteristics that could affect population densities by influencing the survival of adults and incubating embryos. Details of the hypotheses are provided in Table 1. Briefly, we hypothesize that spawning salmon densities are mediated by the effects of (i) habitat cover on adult predation risk; (ii) limitations of spawning habitat for adult competi-

tion; (iii) water and temperature conditions affecting adult survival; and (iv) incubation conditions affecting embryonic survival. These hypotheses can be tested by comparisons among streams if, as is typical with salmon, there is strong homing to natal streams and thus densities reflect instream survival of adults and their young or if adult salmon choose spawning streams based on habitat characteristics that are appropriate for spawning. Each hypothesis is represented by either a single model or by multiple models, which use different combinations of abiotic variables. The relative importance of each model is assessed within an information-theoretic framework using Akaike's information criterion. Our analyses control for conditions beyond the stream environment, such as lake rearing environments, migration conditions, and fishing mortality (which occurs at sea and en route to each region).

## Materials and methods

### Study sites

We studied populations in 32 sites that are tributaries of five lakes in two regions (Supplemental Table S1, available

**Table 1.** A priori hypotheses describing sources of instream mortality for spawning and incubating embryonic sockeye salmon.

Model	Variable	Mechanism	Correlation with density	Reference
Adult predation 1	Cover index	Cover (i.e., pools, wood, and undercut banks) allows adults to hide and escape from predators	+	1, 2, 3, 4
Adult predation 2	Water quantity index	Deep water allows adults to hide and escape from predators	+	1, 2, 3, 4, 5
Adult predation 3	Cover index + water quantity index	Deep water and cover (i.e., pools, wood, and undercut banks) allow adults to hide and escape from predators	+	1, 2, 3, 4, 5
Habitat competition	Spawning habitat index	Larger amounts of habitat suitable for spawning will reduce competition among adults	+	6
Adult energetics 1	Gradient	Higher gradients increase energy expenditure required prior to and during spawning	-	6, 7
Adult energetics 2	Spawning accumulated thermal units	Fish that experience higher water temperatures during spawning will have increased metabolic rates that can lead to energy depletion and death	-	8
Adult energetics 3	Gradient + spawning accumulated thermal units	Increased energy expenditure can lead to energy depletion and death	-	6, 7, 8
Adult temperature exposure	Mean maximum temperature	High water temperatures during spawning can impair physiological processes, increasing mortality before spawning	-	9, 10
Embryo conditions 1	% fine substrate	Fine sediments can reduce oxygen uptake by embryos	-	11, 12, 13
Embryo conditions 2	Mean minimum incubation temperature	Freezing water temperatures can kill eggs or impair development	+	14

**Note:** References: 1, Gende et al. 2004; 2, Fukushima 2001; 3, Roni and Quinn 2001; 4, Deschênes and Rodríguez 2007; 5, Quinn et al. 2001; 6, Fukushima and Smoker 1998; 7, Healey et al. 2003; 8, Crossin et al. 2004; 9, Bjorn and Reiser 1991; 10, Farrell et al. 2008; 11, Cooper 1965; 12, Chapman 1988; 13, Buffington et al. 2004; 14, Cope 1996.

online<sup>1</sup>). The Stuart region ( $n = 22$  streams studied) is in the Sub-Boreal Spruce biogeoclimatic zone and is home to the most northern sockeye spawning grounds in the Fraser River Basin (Fig. 1a; Supplemental Fig. S1, available online<sup>1</sup>). Fish entering fresh water in June and destined for this region are known as the “Early Stuart” complex. They migrate over 1100 km to spawn from late July to mid-August in tributaries of Trembleur Lake, Middle River, and Takla Lake. The Thompson region ( $n = 10$ ) is located in south-central British Columbia in the Interior Cedar-Hemlock biogeoclimatic zone (Fig. 1b; Supplemental Fig. S2, available online<sup>1</sup>). Sockeye in this region form part of the “Early Summer” complex. They enter fresh water in July and migrate approximately 400 km to spawn in late August to mid-September. After embryos hatch in the gravel of streambeds, the fish migrate into “nursery lakes” where the juveniles live for 1–2 years before migrating downstream to the ocean. In this paper we use the term “population” to describe a group of fish that spawn in a single stream and “population complex” to describe a group of populations — either those in the Stuart region or those in the Thompson region.

**Data collection**

We selected sockeye salmon spawning streams in which spawning fish were counted every year. Stream habitat assessments were conducted during summer (June–August) in 2007, prior to adults entering the streams. In the Stuart region fish enter the streams during the first week of August and continue to spawn for 3 weeks; in the Thompson region fish enter the streams in the last week of August and spawn until the middle of September. In 2007 additional water quality measurements were taken after spawning (Stuart: September; Thompson: October–November) to characterize variables that might exhibit within-year variation (i.e., pH, conductivity, dissolved oxygen). We were unable to sample overwinter incubation conditions because of snow and ice. These same variables were measured again during spawning in 2008 and 2009. The locations of study reaches were selected according to accessibility. Reach length was defined as 30 times the average bankfull width, as recommended by Bain and Stevenson (1999). In each stream, a single reach was surveyed according to a stratified random sampling method. Reaches were equally divided into four sections, and four transects were located randomly within each section; thus 16 transects were surveyed per reach. Some variables were measured at transects (e.g., substrate), some at the section level (e.g., gradient), and others at the reach level (e.g., temperature). These field surveys generated data to compute metrics for 15 abiotic variables (Supplemental Table S2, available online<sup>1</sup>).

Physical habitat structure consists of runs, glides, rapids, riffles, pools, large woody debris, stream wetted and bankfull width, substrate composition, percent gradient, percent undercut banks, and water depth. Runs, glides, rapids, and riffles were identified according to Bain and Stevenson (1999). The length and width of each habitat unit was measured, and the percentage of each habitat unit was calculated. Pools were identified as habitats with an identifiable upstream crest (i.e., upward slope), a tail (i.e., outflow portion), and which had a maximum depth that was 1.5 times deeper than the tail depth

<sup>1</sup>Supplementary data are available with the article through the journal Web site (<http://www.nrcresearchpress.com/cjfas>).

(Fausti et al. 2004). The length and width of each pool was measured. All pieces of large woody debris (both >1.5 m long and >10 cm diameter) were counted following the protocol of Roni and Quinn (2001). Briefly, we included any dead pieces of wood within the stream channel; this did not include any parts of living trees. We calculated large wood density (pieces of large wood per metre of stream) by dividing the number of large wood pieces counted by the length of the survey reach. Stream wetted width was measured at the water surface perpendicular to flow, and bankfull width was measured at the maximum point that the water surface could reach without flooding (Bain and Stevenson 1999). They were measured to the nearest 0.01 m at all transects. Substrate composition was quantified using the Wolman pebble count method (Wolman 1954), whereby the intermediate axes of 10 stones were measured to the nearest 1 mm at each transect for a total of 160 counts per stream. Substrate sizes were classified as fines (0–1.2 cm), spawning gravel (1.3–10.2 cm), or cobble and boulders (>10.3 cm); the percentage of each size class was calculated. Gradient measurements were taken for each stream section using a 5× Abney hand level and mean values were used. At each transect, water depth was measured to the nearest 0.01 m at 10–12 equidistant points across the stream channel. Water depth was summarized as the mean and the mean maximum depth for each stream. Undercut banks were measured as the length of stream bank that was undercut divided by the total stream bank length; the mean of both banks was calculated.

Spawning and incubation water temperatures were measured using temperature data loggers (iButton DS1922L). These were programmed to record temperatures at 2 h intervals and were waterproofed and attached to a 1 m long iron rod inserted into the streambed. Three data loggers were installed in each stream and stratified 15–20 cm below, on, and 15 cm above the substrate. Spawning temperature metrics were based on the values from the average start (the first individuals observed on the spawning grounds) to end of spawning (the last observation of live individuals on the spawning grounds) for each population complex. Incubation temperature metrics were calculated from the temperature loggers embedded (15–20 cm) in the substrate, from the peak of spawning (defined below under “Salmon population parameters”) until estimated emergence, based on previous studies in the Stuart region (Cope 1996) and the Thompson region (Williams et al. 1989). For spawning and incubation, the mean maximum and mean minimum daily temperatures were calculated, respectively. We also characterized the thermal experience of spawning adults by summing the mean daily temperatures during the spawning period.

pH, conductivity, and dissolved oxygen were measured one to three times at a single location in each stream prior to spawning (Stuart: June–August; Thompson: late August) and twice during the early stages of incubation (Stuart: September; Thompson: October–November) during 2007. We included additional measurements during spawning for 2008 and 2009. We averaged values during spawning and incubation. All water quality variables proved to be well within optimum values (pH: min. = 6.6 and max. = 8.6 (Ikuta et al. 2003); conductivity: max. = 560  $\mu\text{S}\cdot\text{cm}^{-1}$  (US Environmental Protection Agency 1986); dissolved oxygen: typically >9.0  $\text{mg}\cdot\text{L}^{-1}$  and 95%–100% saturation (Bjornn and Reiser

1991)) in all streams and are not considered further. Discharge was also measured but because of inconsistent sampling (equipment malfunction) and the sensitivity of measurements to rainfall, discharge was excluded from the analysis. Furthermore, we included habitat variables such as gradient and water depth, which are related to discharge and are more direct measures of the potential influence of discharge on adult salmon and incubating embryos.

### Salmon population parameters

We used data collected by Fisheries and Oceans Canada (DFO) (2004–2007) to calculate the density (fish·m<sup>-2</sup>) of spawning sockeye salmon in the study reaches where we collected habitat data. Populations are estimated during spawning using visual counts every 4 days in the Stuart region and every 7 days in the Thompson region. In each stream, DFO personnel conducted foot surveys to count the number of live and dead sockeye across all spawning grounds. Finer scale counts were also recorded for stream sections that corresponded to the reaches we surveyed for habitat data. DFO personnel estimated the total abundance of spawning salmon in each stream by multiplying the “peak” surveyed abundance of spawning salmon by an expansion factor. Expansion factors are used to calibrate the observed counts, which are underestimates of the actual abundances. The peak surveyed abundance was determined as the highest value obtained by adding the live count of salmon from a single survey to the total number of dead salmon summed across all prior surveys. The live count of salmon includes both individuals spawning and migrating upstream. By the time peak abundance is observed, most fish are spawning and few are moving upstream to other reaches; therefore, our reach density metric likely reflects egg deposition. In the Stuart region, the expansion factor was calculated from data collected at counting fences on two to three streams. The expansion factor is calculated as the total number of salmon that passed through the counting fence, divided by the peak surveyed abundance. In the Thompson region, an average expansion factor of 1.8 was used in the absence of counting fences (Shubert 2007). We then calculated the abundance of spawning salmon in our study reach ( $A_R$ ) as

$$(1) \quad A_R = \frac{L_R}{L_T} \times A_T$$

where  $A_T$  is the total abundance of spawning salmon in the stream estimated by DFO,  $L_R$  is the number of live fish counted in the stream section that corresponds to our study reach, and  $L_T$  is the number of live fish counted in the entire stream. Both  $L_R$  and  $L_T$  counts are taken from the day of highest surveyed abundance. We excluded counts of dead salmon from our calculation, as it is not possible to determine where in the stream those fish had spawned. Our reach-specific densities ( $D_R$ , fish·m<sup>-2</sup>) were calculated as

$$(2) \quad D_R = \frac{A_R}{wl}$$

where  $w$  is the stream wetted width in metres, and  $l$  is the length of the reach in metres. This density metric was strongly correlated with total abundance (Pearson’s correlation:  $r = 0.79$ ,  $p < 0.0001$ ).

**Table 2.** Indices constructed using principal components analysis.

Principal component	Variable	Loading	% variance
Cover	% pool area	0.60	62
	Large wood (pieces·m <sup>-1</sup> )	0.58	
	% undercut bank	0.56	
Water quantity	Maximum water depth	0.54	79
	Mean water depth	0.50	
	Stream cross-section area	0.53	
	Pool depth	0.42	
Spawning habitat	% spawning gravel substrate	0.55	58
	% cobble and boulder substrate	-0.52	
	Geometric mean substrate size	-0.47	
	% gradient	-0.45	

**Note:** Loadings represent the influence of each variable on the principal component. Percent variance is the variance in the original variables that is explained by the principal component. All indices were constructed with 32 streams.

Some sockeye populations in the Fraser River display cyclical dominance, whereby every 4 years the population abundance is particularly high (Ricker 1950; Levy and Wood 1992). These cycles may result from predation on juveniles in lakes and (or) overfishing, but they have not been linked to stream habitat (Ricker 1950). The year and degree of dominance varies by juvenile nursery lake (Levy and Wood 1992), and many of our populations had no fish during subdominant years. To make a valid comparison across all populations, we used spawning density estimates from the most recent dominant year. While using a single year's data could mask interannual variation in abundance within streams, a strong correlation between the dominant year density and the mean density from 2004 to 2007 (Pearson's correlation:  $r = 0.88$ ,  $p < 0.001$ ) suggests this is not a problem. Finally, the dominant year adult density was  $\log_{10}$ -transformed to improve fits to model assumptions.

### Statistical analyses

We used principal component analysis (PCA) to transform some of the original data into orthogonal (i.e., uncorrelated) variables, thereby eliminating multicollinearity among variables within PCAs and reducing the number of variables used in the models (Graham 2003). Principal components were constructed using original variables that were correlated and ecologically related (Table 2). For example, a cover index was constructed using large woody debris, percent undercut banks, and percent pool area, which are highly correlated (Roni and Quinn 2001). All variables, including principal components, were assessed for collinearity using the variance inflation factor (Zuur et al. 2010). Only principal components and variables with variance inflation factor scores of less than 3 were included in our analyses (Zuur et al. 2010).

Mixed-effects models were constructed to evaluate our candidate set of a priori hypotheses and were then compared using Akaike's information criterion corrected for small sample sizes (AIC<sub>c</sub>) (Anderson 2008). All statistical analyses were conducted in R (R Development Core Team 2009). Equipment failure led to missing temperature data in three of the 32 streams. Therefore, the analysis was conducted in two steps, first with a restricted but complete data set on 29

streams and second with a larger set of streams, but without temperature. We used a mixed-effects model approach with lakes as a random effect. We compared models with and without region as a fixed factor. Mixed-effects models account for a lack of independent samples caused by correlations among variables across different scales (McMahon and Diez 2007; Zuur et al. 2009). Thus, this method can account for, although indirectly, differences in overall abundance due to factors beyond the stream environment, such as differences in rearing lake productivity. The inclusion of region as a fixed factor further accounts for differences in ocean survival of juveniles, fishing mortality in the ocean and en route to the two regions, and migration conditions. Within each of the two regions, there are multiple lakes, each with a different productivity (Shortreed et al. 2001). The size of smolts migrating to sea can influence survival (Koenings et al. 1993), and this is in part determined by lake productivity (Hyatt et al. 2004). Therefore, abundances are likely to be correlated among streams within lakes and regions. Given this nested structure and potential for sites to be correlated at different scales, we fitted the following mixed-effects model:

$$(3) \quad Y_{ijk} = \beta_0 + \beta_m \text{variable}_{mijk} \dots + \text{region}_k + \gamma_j + \varepsilon_{ijk}$$

$$\gamma_j \sim N(0, \sigma_{\gamma_j}^2)$$

$$\varepsilon_{ijk} \sim N(0, \sigma^2)$$

where  $Y_{ijk}$  is the density of salmon for observation  $i$  in lake  $j$  and region  $k$ . The intercept is  $\beta_0$  and the term  $\gamma_j$  allows for intercepts to vary for each lake. Region ( $\text{region}_k$ ) is a fixed factor with two levels: the Stuart and Thompson regions. The coefficient for  $\text{variable}_{mijk}$  is  $\beta_m$ ,  $\text{variable}_{mijk}$  is continuous, and  $\varepsilon_{ijk}$  is the residual error. Varying intercept and residual error terms are assumed to be independently and identically normally distributed ( $N$ ) with a mean of 0 and variance  $\sigma^2$  (Zuur et al. 2009).

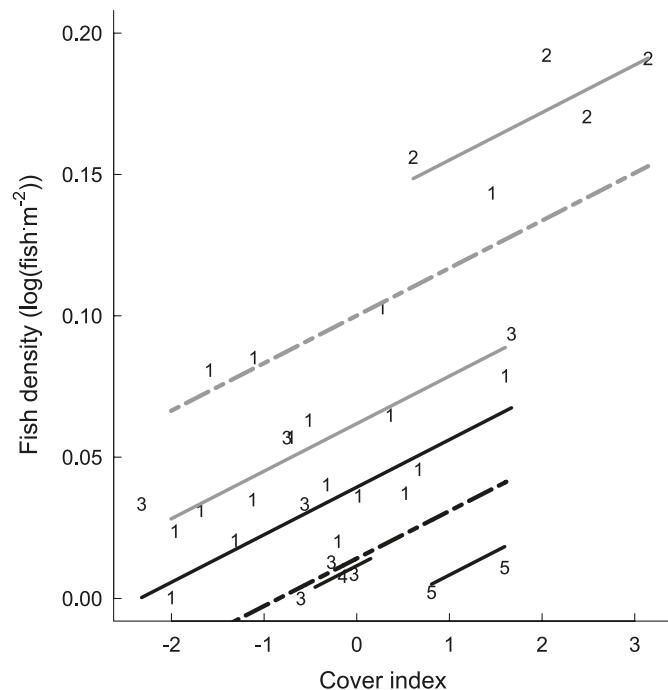
We used AIC<sub>c</sub> to compete multiple alternative hypotheses (Anderson 2008) that could explain sources of instream mortality for sockeye salmon (Table 1). We constructed 10 models to test various combinations of variables within each hypothesis. We inspected model diagnostics for heteroscedasticity, normality, and independence of residuals (Zuur et al. 2009).

**Table 3.** Initial candidate set of mixed-effects models and cover index decomposed models.

Hypothesis	Model	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$	ER
<b>Initial set of mixed-effects models</b>						
Adult predation 1	Cover index + region	5	-55.10	0.00	0.574	1.0
Adult predation 3	Cover index + water quantity index + region	6	-54.45	0.66	0.414	1.4
Embryo conditions 1	% fine substrate + region	5	-45.51	9.59	0.005	121.1
Adult predation 2	Water quantity index + region	5	-45.31	9.79	0.004	133.7
Habitat competition	Spawning habitat index + region	5	-44.17	10.93	0.002	236.0
Adult energetics 3	% stream gradient + region	5	-42.50	12.60	0.001	543.5
<b>Cover index decomposed</b>						
Post hoc	% pool area + region	5	-53.38	0.00	0.900	1.0
	% undercut bank + region	5	-48.67	4.71	0.085	10.5
	Large wood (pieces·m <sup>-1</sup> ) + region	5	-45.13	8.25	0.015	61.9

**Note:**  $AIC_c$  values represent the trade-off between model complexity and fit, where lower  $AIC_c$  values indicate better models relative to others in the candidate set.  $\Delta AIC_c$  is the difference in  $AIC_c$  values between a given model and the best model. The Akaike weight ( $w_i$ ) is the probability that model  $i$  is the best one of those considered, and the evidence ratio (ER) is the ratio of likelihood probabilities for the top model vs. model  $i$ .  $AIC_c$  values were calculated using maximum likelihood.  $K$  is the number of parameters in each model.

**Fig. 2.** Mixed-effects regression plots for the cover index with region as a fixed factor and lake as a random effect. Numbers refer to multiple streams within lakes: 1 = Takla Lake, 2 = Trembleur Lake, 3 = Shuswap Lake, 4 = Momich Lake, 5 = North Barriere Lake. Grey regression lines are for the Stuart region, and black lines are for the Thompson region; solid lines are for streams within lakes, and the dashed lines show the mean for each region.



## Results

The analysis was conducted in two steps, first with a complete data set on 29 streams and second with a restricted data set, which did not include temperature metrics, on 32 streams. The top models ( $\Delta AIC_c < 3$ ) and their ranked orders were identical for both analyses; therefore, all results are reported for the restricted data set, without temperature, to increase sample sizes. Variables associated with biotic in-

teractions provided the best fits to population densities. Two models had  $\Delta AIC_c < 3$ , both of which described biotic interactions and not physiological tolerances (Table 3). The top two models represented the adult predation hypothesis (Table 3). Cover index is the only habitat variable in the top model other than region and as predicted was positively related to adult density (Fig. 2; Table 4). This index (based on PCA) is composed of pool area, large wood debris, and undercut banks. The second best model contained both cover and water quantity (Table 3). Contrary to our prediction, water quantity was negatively related to adult density (Table 4). The addition of water quantity to cover in the second model provides little additional explanatory power given the small differences between  $AIC_c$  scores for the first and second models (Table 3). A graphical representation of the fit for the top two models is provided (Fig. 3).

All pairwise model comparisons of models that either did or did not account for regional differences showed that accounting for region was important, as indicated by lower  $AIC_c$  values. None of the models related to the physiological tolerances (Table 1) were supported, and none of the environmental variables within those models were major predictors of sockeye density.

## Post hoc analysis

To understand the finer-scale mechanisms driving the relationship between cover and salmon density, we examined each of the variables contained in the cover index principal component. The cover index was composed of three statistically and ecologically correlated variables: pool area, undercut banks, and large woody debris. Pool area has the highest loading for the cover index, followed by large woody debris and undercut banks, though the loadings for each of the variables are quite similar (Table 2). We built three new models, each containing one of these three variables and competed them using  $AIC_c$  (Table 3). The top model, which included percent pool area, had 10 times more support than the second model. All predictors had a positive relationship with adult spawning density (Fig. 4).

**Table 4.** Model parameter estimates (coefficients for main effects), standard errors (SE), *t* values, and *p* values for the initial candidate set of mixed-effects models and the cover principal component (PC) decomposed.

Hypothesis	Model parameter	Estimate	SE	df	<i>t</i>	<i>p</i>
<b>Initial set of mixed-effects models</b>						
Adult predation 1	Intercept	0.523	0.192	26	2.73	0.011
	Cover index	0.046	0.013	26	3.70	0.001
	Region	-0.245	0.116	3	-2.11	0.125
Adult predation 3	Intercept	0.536	0.200	25	2.68	0.013
	Cover index	0.043	0.012	25	3.54	0.002
	Water quantity index	-0.015	0.010	25	-1.56	0.131
	Region	-0.247	0.121	3	-2.04	0.133
Adult predation 2	Intercept	0.602	0.270	26	2.23	0.035
	Water quantity index	-0.020	0.011	26	-1.81	0.083
	Region	-0.275	0.163	3	-1.68	0.191
Habitat competition	Intercept	0.523	0.192	26	2.73	0.011
	Spawning habitat index	0.046	0.013	26	3.70	0.001
	Region	-0.245	0.116	3	-2.11	0.125
Adult energetics 3	Intercept	0.587	0.249	26	2.36	0.026
	% stream gradient	0.001	0.016	26	0.04	0.972
	Region	-0.273	0.150	3	-1.82	0.166
Embryo conditions 1	Intercept	0.556	0.251	26	2.21	0.036
	% fine substrate	0.003	0.002	26	1.77	0.089
	Region	-0.287	0.152	3	-1.89	0.155
<b>Cover index decomposed</b>						
Post hoc	Intercept	0.506	0.169	26	3.00	0.006
	% pool area	0.004	0.001	26	3.43	0.002
	Region	-0.279	0.102	3	-2.73	0.072
	Intercept	0.482	0.191	26	2.53	0.018
	Large wood (pieces·m <sup>-1</sup> )	0.283	0.178	26	1.59	0.123
	Region	-0.250	0.112	3	-2.24	0.111
	Intercept	0.448	0.188	26	2.39	0.025
	% undercut bank	0.003	0.001	26	2.48	0.020
	Region	-0.240	0.110	3	-2.17	0.119

Note: Final models were constructed using restricted maximum likelihood.

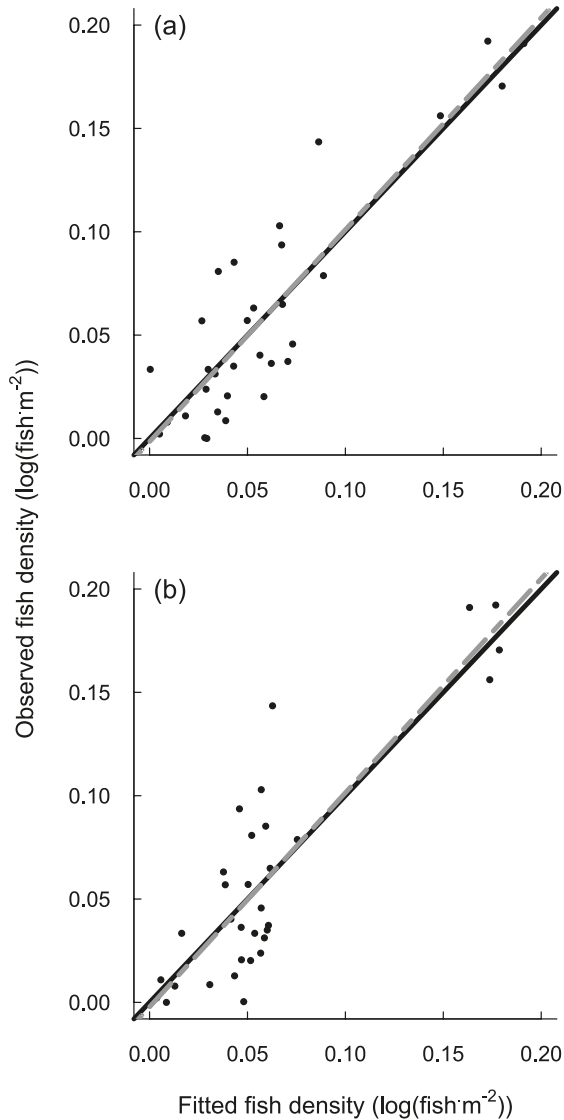
## Discussion

We compared alternative hypotheses for the potential impacts of abiotic stream characteristics on densities of spawning sockeye salmon, according to their inferred effects on mortality of either spawning adults or incubating embryos. The top model included a single habitat predictor, which was a cover index composed of the percentage of the stream that was pool habitat, the percentage of the stream bank that was undercut, and number of large wood pieces per length of stream. Of these, percent pool area had the largest explanatory power but was out-performed by the composite cover index.

Our results reveal the importance of stream characteristics, which previous studies have shown to be associated with predation risk. High densities of large wood and abundant undercut banks provide physical cover from predators. Large pools also provide adults with a refuge from predators. For example, grizzly bears (*Ursus arctos horribilis*), an important predator of spawning salmon (Quinn et al. 2003), are less successful in complex streams with deep pools and large amounts of large woody debris than in small, shallow streams (Gende et al. 2004). In complex streams, bears selected for older (stream residence 7+ days), slower sockeye

salmon, which are easier to catch, whereas in uniform streams they selected for younger (stream residence 1–3 days), quicker individuals of higher nutritional value (Gende et al. 2004). In the Alaskan streams studied by Gende et al. (2004), most female sockeye had spawned by their third day in the stream, which suggests that the impacts of bear predation on salmon populations would be greater in uniform streams than in complex ones. Furthermore, Gende et al. (2004) observed sockeye salmon using deep pools and large wood as refuge from predation by bears. Both grizzly and black bears (*Ursus americanus*) are regularly encountered on many of our study streams, as are salmon carcasses with marks that indicate bear predation (Quinn and Kinnison 1999). However, a few of our streams in the Thompson region are near urban centers and therefore may experience lower levels of bear predation (Crupi 2003). In the absence of predation, which is typical of urban streams, it is possible that the variables we have identified might not influence adult spawning densities to the same extent. Future studies that combine the demographics of salmon consumed by bears with population parameters (e.g., salmon density) among streams could yield further insights into how physical characteristics of streams mediate the impacts of bear predation on salmon populations. Furthermore, experimental approaches

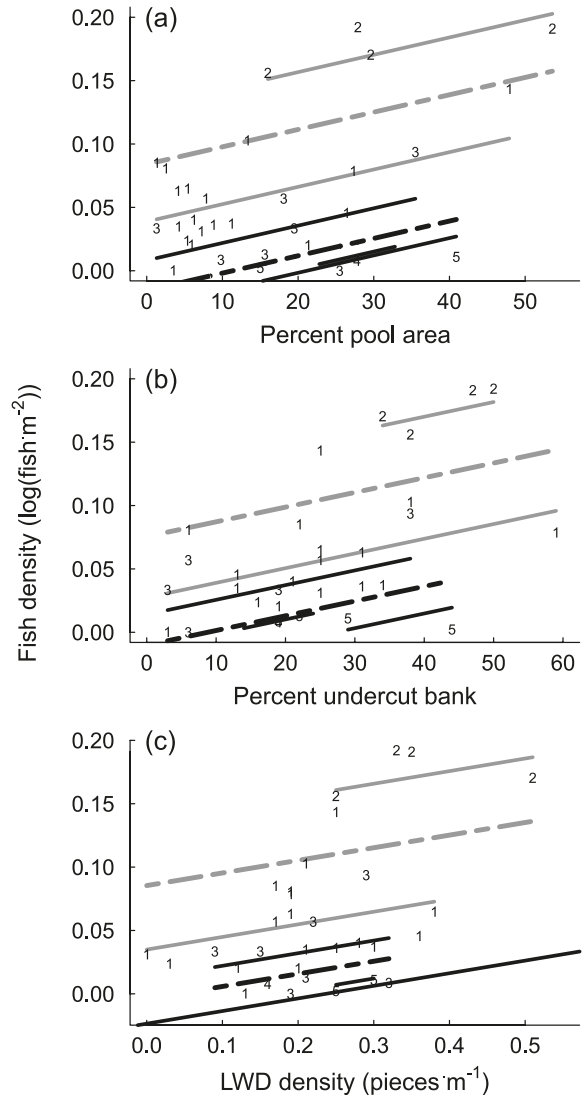
**Fig. 3.** Observed spawning densities vs. fitted spawning densities for (a) the top model with cover and (b) second ranked model with cover index and water quantity index. Both models contain region as a fixed factor and lake as a random effect. The solid black line in each figure is the 1:1 line, and the dashed grey line is the observed vs. fitted regression line.



might be possible to test directly the role of physical features in mediating predation risk.

Studies of juvenile salmonids demonstrate empirical relationships similar to the cover–density relationship observed in this study. For example, Sharma and Hilborn (2001) showed strong relationships among pool density, large wood, and juvenile coho production. Brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), and rainbow trout (*Oncorhynchus mykiss*) biomass have been shown to correlate to instream cover, the amount of overhanging vegetation (Wesche et al. 1987; Kozel and Hubert 1989), and percent undercut banks (Wesche et al. 1987). Finally, Atlantic salmon (*Salmo salar*) juveniles have been linked to instream cover (Johansen et al. 2005), and masu salmon (*Oncorhynchus masou*) to pool area (Inoue and Nakano 1999). Although the types of cover examined in these studies (including this one) vary, the importance

**Fig. 4.** Mixed-effects regression plots for (a) percent pool area, (b) percent undercut banks, and (c) large wood density. All models contain region as a fixed factor and lake as a random effect. Numbers refer to multiple streams within lakes: 1 = Takla Lake, 2 = Trembleur Lake, 3 = Shuswap Lake, 4 = Momich Lake, 5 = North Barriere Lake. Grey regression lines are for the Stuart region, and black lines are for the Thompson region; solid lines are for streams within lakes, and the dashed lines show the mean for each region. The nonsignificant regression lines for large wood are included to illustrate groupings of the data.



of cover in supporting salmonid populations in streams is consistent across a number of species and life stages.

Pools, undercut banks, and large wood could also provide low velocity habitats for fish, reducing their metabolic rates. We measured other habitat features, such as accumulated thermal units (during spawning) and stream gradient, which we believe more accurately characterize the amount of energy used by fish during spawning. Models that contained these variables were included in our candidate set of models and performed poorly relative to others.

There are a number of possible explanations for the lack of support for the physiological tolerance hypotheses. First,



while the sample size and number of variables surveyed is large in comparison with most other stream habitat studies, the temporal extent of the data set is small. Although variables such as temperature, dissolved oxygen, and pH varied among streams, values were all within ranges that are readily tolerated by this species (Bjornn and Reiser 1991; Ikuta et al. 2003; Farrell et al. 2008). However, pH, conductivity, and dissolved oxygen were sampled a limited number of times and prior to winter, and these data only represent a snapshot of the water conditions. Second, the effects of temperature on mortality in streams could be superseded by downstream conditions during migration to the spawning grounds (Macdonald 2000), which would manifest at the level of the population complex rather than at the individual population level. For some Fraser River population complexes, temperatures during adult sockeye freshwater migration have increased in recent decades (Farrell et al. 2008) and can be higher than temperatures experienced on the spawning grounds. Finally, in the northern Early Stuart population complex, alevins avoid freezing temperatures by moving down through the substrate (Cope 1996). Therefore, while our results highlight the importance of habitat characteristics that provide cover, they cannot rule out an additional role for physical tolerances in other years that may affect spawning densities.

Our results show that a very simple model that includes physical cover in streams can describe a large amount of variation in sockeye salmon population densities in 32 streams in two widely separated regions in different biogeoclimatic zones. These characteristics have been shown by other studies to reduce predation risk on adults, which suggests that predation risk may be an important determinant of adult population densities. Therefore, it may be possible to quantify the quality of spawning habitat for salmon based on a few key abiotic stream characteristics. Such quantitative assessments of habitat quality can be used to prioritize streams for conservation and restoration of salmon populations. These results can direct restoration activities in streams, such as increasing pool habitat, undercut banks, and large wood. Using a hypothesis-driven approach to relate simple habitat survey data to population densities can provide insights into the importance of ecological interactions and the underlying mechanisms that determine population densities. This approach can inform ecosystem-based management.

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