The influence of biotic and environmental processes on breeding population density: insights from sockeye salmon

Douglas C. Braun, John D. Reynolds

Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby,
British Columbia, Canada V5A 1S6

Douglas C. Braun[1] Department of Biological Sciences, Simon Fraser University,
Burnaby, BC, V5A 1S6, Canada, (email: dbraun@sfu.ca).

John D. Reynolds Department of Biological Sciences, Simon Fraser University,
Burnaby, BC, V5A 1S6, Canada, (email: reynolds@sfu.ca).

[1] Corresponding author (Tel: 604 778 782 3989, Fax: 604 778 782 3496, Email: dbraun@sfu.ca).

Abstract. Species distributions and population densities are governed by interactions between biotic processes and physiological tolerances, which are mediated by the physical environment. Large-scale inter-population comparisons provide a powerful tool for testing the relative importance of each of these processes, but these have seldom been done. Here we test the role of biotic and physiological processes in governing variation in spawning densities of sockeye salmon (*Oncorhynchus nerka*) in 36 streams in the Fraser Basin of British Columbia, Canada. We used mixed-effects models to test four competing hypotheses for the importance of biotic interactions and physiological tolerances, mediated through physical characteristics of streams, acting on either adult or embryo mortality. All models that received support using Akaike's Information Criterion (ΔAICc<7) represented biotic interactions, which were predicted by hypotheses involving risk of predation on adults. The top model included a single composite predictor - cover - and was highly significant. Within this composite variable, the only significant univariate predictor was pool area, which was also involved in the adult predation hypothesis. These results suggest the importance of stream characteristics that reduce risk of predation on adults, which is mediated primarily by the amount of cover, in determining spawning sockeye salmon densities. These relationships were consistent for both a northern and southern population complex, which experience differences in abiotic conditions on the spawning grounds, as well as human impacts on the streams. Thus, identification of a small number of physical characteristics of streams provides insights into ecological processes that determine population densities, and this information can be used to guide protection and management of salmon streams.

Key words: population ecology; predation risk; Pacific salmon, conservation, fisheries, bear

INTRODUCTION

Studies that consider both biotic interactions and physiological tolerances can provide insights into species distributions and resilience to anthropogenic impacts and environmental stochasticity, which would be valuable for management and conservation of populations. Most ecological studies of relationships between abiotic habitat characteristics and populations have focused on the importance of biotic interactions such as predation risk and competition rather than physiological tolerances (Huey 1991, Parsons 2005), and studies that consider both processes are rare. These processes are especially important for populations experiencing abiotic extremes at the edge of their range. Such populations are generally thought to be limited primarily by environmental processes, whereas for central populations abundance is regulated more by biotic interactions and are more productive (Kunin et al. 2009). Understanding how both biotic interactions and physiological tolerances contribute to patterns of species distributions and densities is increasingly important given the potential impact of anthropogenic changes to environments on these two processes. For example, climate change is redistributing species according to their physiological tolerances in conjunction with changes in predators and prey (Parmesan 2006). Further, the relative importance of these two processes can influence a population’s resilience to environment stochasticity and overexploitation (Goodwin et al. 2006, Colchero et al. 2009). Many management agencies and environmental organizations are shifting towards ecosystem-based management and are also concerned with prioritizing habitats for protection or restoration. Thus, insights into the mechanisms by which physical habitat characteristics mediate population dynamics will help such agencies with habitat management.

Adult Pacific salmon returning to spawn in freshwater are ideally suited to study the interplay between biotic interactions and physiological tolerances in determining habitat-specific densities. There is evidence that survival and density of spawning salmon can be influenced by biotic interactions (Essington et al. 2000, Quinn et al. 2003). Intra-specific competition between spawning females for breeding sites can lead to superimposition of nests (i.e. nests dug earlier in the season being dug up by females that spawn later in the season). The amount of superimposition will vary with the density of adults and the availability of suitable spawning habitat (Essington 2000), determined by characteristics such as substrate size, flow characteristics, and dissolved oxygen. In addition, adult salmon can experience high rates of predation by bears (Quinn et al. 2003), a process that is influenced by the abiotic characteristics of streams such as water depth and physical complexity (Quinn et al. 2001, Gende et al. 2004).

Physiological tolerances are also important in determining densities of salmon populations. Salmon typically have strong homing to their natal streams, creating discrete populations with local adaptations (Groot and Margolis 1991, Quinn 2005). Although salmon display strong phenotypic plasticity and local adaptations (Hendry and Stearns 2004), many populations that migrate inland over long distances encounter challenging abiotic conditions during both migration and spawning. For example, in years of high temperatures, survival to and on the spawning grounds decreases due to energy depletion and increased susceptibility to disease (Gilhousen 1990, Farrell et al. 2008). Further, low pH can have substantial effects on adult salmon spawning behavior and development of embryos and juveniles (Rombough 1983, Ikuta et al. 2003). Indeed, adult salmon may avoid streams with pH lower than six (Ikuta et al. 2003).

The objective of this study is to use sockeye salmon (*Oncorhynchus nerka*) as a model for understanding relationships between abiotic habitat characteristics and animal population densities in the context of biotic interactions and physiological tolerances. We studied 36 populations distributed across two regions that experience different environmental conditions in the Fraser Basin of British Columbia, Canada (Fig 1). The Early Stuart population complex spawns in the most northern salmon-bearing watershed in the Fraser Basin, where fish can experience warm spawning temperatures and low incubating temperatures (Cope 1996). Human impacts on our study streams in this region have been minimal. The Early Summer population is further south and experiences slightly warmer spawning and incubation temperatures, with streams having been impacted by deforestation, agricultural runoff and urbanization.

We develop a series of hypotheses that incorporate biotic interactions and physiological tolerances that could affect population densities by influencing survival of adults and incubating embryos. 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 in-stream survival of adults and their young, or if adult salmon choose spawning streams based on such characteristics. For example, under the category of biotic interactions, we tested two alternative hypotheses based on either predation risk to spawning adults, or competitive interactions affecting survival of embryos in the gravel (Table 1). Each hypothesis is represented 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 Information Criterion, with analyses that 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).

METHODS

Study sites

The Stuart region (n=22 streams studied) is located in the sub-boreal spruce biogeoclimatic zone, and is home to the most northern sockeye spawning grounds in the Fraser

Basin (Fig. 1a). Sockeye destined for this region are known as the “Early Stuart” complex. They enter freshwater in June and 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=14) is located in South-Central BC in the interior cedar-hemlock biogeoclimatic zone (Fig. 1b). Sockeye in this region form part of the “Early Summer” complex. They enter freshwater 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 streams that were <26 m channel (“bankfull”) width and for which good population estimates were available. We also selected two control streams in Stuart and three in Thompson, which are accessible to sockeye but have not supported a population for more than two consecutive generations. Stream assessments were conducted during summer low flows (June-August), prior to adult sockeye entering the streams; additional measurements were taken in the fall, after spawning, of variables that were suspected to have within-year variation. A single study reach was surveyed for each stream. The length of a reach was defined as 30 times the average bankfull width (Bain and Stevenson 1999). Reaches were sampled according to a stratified random sampling method. A reach was equally divided into four sections; four transects were randomly located 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 14 abiotic variables.

Physical habitat structure consists of runs, glides, rapids, riffles, pools, large woody debris, stream wetted and bankfull width, substrate composition, percent gradient, percent cutbanks, 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. 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 (AREMP and PIBO 2004). Length and width of each pool were measured. All pieces of large woody debris (length >1.5 m and diameter >10 cm) were inventoried (Roni and Quinn 2001). Stream wetted width was a measure of the water surface perpendicular to flow and bankfull width was the maximum width that the surface water 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 ten stones were measured to the nearest 1 mm at each transect for a total of 160 counts per stream. Gradient measurements were taken for each stream section using a 5x Abney hand level. Water depth was measured (to the nearest 0.01 m) at 10-12 equidistant points across the stream channel. Cutbanks were measured as the length of the bank that was undercut divided by the total length of each bank; the average of both banks was calculated.

Spawning and incubation water temperatures were measured using ibutton (DS1922L) temperature data loggers. These were programmed to record temperatures at 2-hour 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 to end of spawning for each population complex. Incubation temperature metrics were calculated using temperatures from the peak of spawning 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 minimum and mean maximum daily temperatures were calculated. We also characterized the thermal experience of spawning adults and incubating eggs by summing the mean daily temperatures during each of these stages.

Water discharge was measured before and after the spawning period and consisted of ten depth and velocity measurements across two transects calculated according to Bain and Stevenson (1999). pH, total dissolved solids, and dissolved oxygen were measured three to five times at a single location in each stream over the course of spawning and incubation. We averaged values during spawning and incubation. Dissolved oxygen proved to be well within optimum requirements (typically >9.0mg/L and 95-100% saturation) in all streams (Bjornn and Reiser 1991), and is not considered further.

Salmon population parameters

The number of sockeye in spawning areas from 2004-2007 were enumerated by the Canadian Department of Fisheries and Oceans, and these data were used to calculate adult population metrics. We used spawner abundance to calculate population metrics, rather than egg-to-fry survival, since the former data were available for all streams and allowed us to calculate reach-specific densities. Sockeye populations in the Fraser Basin display cyclical dominance, whereby every four years abundance is particularly high (Ricker 1950, Levy and Wood 1992). These cycles may be a result of predation on juveniles in lakes and / or over-fishing, 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 sub-dominant years. To obtain a consistent comparison across populations we used population estimates from the most recent dominant year. In order to match adult population sizes to stream habitats, we calculated reach-specific spawning densities for the reaches where we measured the habitat variables. These densities were calculated as:

$$D = \frac{F}{wl} \qquad (1)$$

where D is the density of fish that have returned to a reach (fish/m^2), F is the number of fish in the last dominant year, w is the stream wetted width in meters and l is the length of the reach in meters.

Statistical analyses

We used PCA to transform the original data into orthogonal (i.e. uncorrelated) variables, thereby eliminating multicollinearity and reducing the number of variables (Graham 2003). Latent variables 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 cutbanks and percent pool area, which are highly correlated (Roni and Quinn 2001).

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 (AICc). These values represent the trade-off between model fit and model complexity, where the lowest value represents the best trade-off. All statistical analyses were conducted in R (R Development Core Team 2009). Equipment failure and adverse environmental conditions led to missing data for two of the variables, percent cutbanks (n=1), temperature (n=4) and both variables (n=1). This led to the elimination of five streams from the 38 surveyed. The analysis was initially conducted with the reduced dataset (n=33), which showed that none of the models with support (i.e. ΔAICc values < 7) included temperature variables (Anderson 2008). We therefore excluded temperature from the analyses in order to use 36 streams. There was no change in the number or order of models with ΔAICc<7, therefore we have presented the results from the analysis excluding temperature.

Due to the nested nature of our study streams within lakes and two regions, and large differences in residuals between sites grouped by lakes, we used a mixed-effects model approach. This provides two main advantages over simple linear regression by: 1) accounting for a lack of independent samples caused by correlations among variables across different scales, and 2) producing parameter estimates that can be used to predict densities in streams outside of this study (McMahon and Diez 2007, Zuur et al. 2009). Thus, this method can account for differences in overall abundance due to factors beyond the stream environment, such as differences in rearing lake productivity, ocean survival of juveniles, fishing mortality in the ocean and en route to the two regions, and migration route. 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:

$$\begin{aligned}
&Y_{ijk} = \beta_0 + \beta_m Variable_{m_{ijk}} \ldots + \gamma_k + \gamma_{j|k} + \varepsilon_{ijk} \\
&\gamma_k \sim N\left(0, \sigma^2_{\gamma_k}\right) \\
&\gamma_{j|k} \sim N\left(0, \sigma^2_{\gamma_{j|k}}\right) \\
&\varepsilon_{ijk} \sim N\left(0, \sigma^2\right)
\end{aligned} \qquad (2)$$

where Y_{ijk} is the density of salmon for observation *i* in lake *j* and region *k*. The intercept is β_0 and the term γ_k allows for intercepts to vary for each region *k* and $\gamma_{j|k}$ allows for intercepts to vary by lake *j* nested within region *k*. The coefficient for $Variable_{m_{ijk}}$ is β_m, $Variable_{m_{ijk}}$ is continuous and ε_{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 σ^2 (Zuur et al. 2009).

In order to compare the relative strength of hypotheses influencing adult densities across lakes and regions we made pair-wise comparisons of AICc values of equivalent models where we included random intercepts, constant slopes and the others had random intercepts and slopes

(Zuur et al. 2009). Mixed-effects models with varying intercepts are structured as in equation (2) and models with varying intercepts and slopes were structured as:

$$\begin{aligned} &Y_{ijk} = \beta_0 + \beta_m Variable_{m_{ijk}} ... + \gamma_k + \gamma_{j|k} + \beta_{m_{j|k}} Variable_{m_{ijk}} + \varepsilon_{ijk} \\ &\gamma_k \sim N\left(0, \sigma^2_{\gamma_k}\right) \\ &\gamma_{j|k} \sim N\left(0, \sigma^2_{\gamma_{j|k}}\right) \\ &\varepsilon_{ijk} \sim N\left(0, \sigma^2\right) \end{aligned} \tag{3}$$

where $\beta_{m_{j|k}}$ is the varying slope term and provides a coefficient estimate specific to lake *j* nested within region *k*. If a model with varying slopes across lakes and regions performs better than the random intercept model that would support the hypotheses that adult densities differed across lakes and regions. AICc values were calculated using restricted maximum likelihood (Zuur et al. 2009).

We used AICc to compete multiple alternative hypotheses (Anderson 2008) that explain sources of in-stream mortality for sockeye salmon (Table 1). We constructed 18 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). For all models we included an additional variance parameter, which assumed independent variances at the lake level, to reduce heteroscedasticity (Zuur et al. 2009). However, AICc values indicated the term was not worth the additional six-parameter estimates, so it was excluded from the final models.

RESULTS

Variables associated with biotic interactions were most important in determining densities. There were four models with ΔAICc<7, all of which described biotic interactions and not physiological tolerances (Table 3). The top four models represented the adult predation hypothesis (Table 3). Cover index is the only predictor in the top model, which represents the best trade-off between model complexity and fit, given the set of candidate models. This index (based on PCA) is composed of pool area, large wood debris and cutbanks. It was four times more likely to be selected as the top model than the next one, which contained both cover and the non-significant effect of spawning water depth (Table 4). The third and fourth models received little support. A graphical representation of the fit for the top model is in Figure 2.

There was a positive and significant relationship between cover and salmon density in the top two models (Fig. 3a, Table 4). Pool area has the highest loading for the cover index, followed by large woody debris and cutbanks (Table 2). Pool area is the only other abiotic variable that showed a statistically significant relationship with sockeye density (Table 4) in the third best model, though percent cutbanks was nearly significant (p=0.06) (Table 4). For both cover and pool area there was considerable variation among streams within lakes, as indicated by large variance around the intercepts (Fig. 3). None of the models related to the physiological tolerances (Table 1) were supported, and none of the environmental variables within those models were significant predictors of sockeye density.

To assess whether the importance of processes differs between the two regions we compared two sets of models with different random structures but with the same predictor variables. The first set of models had varying intercepts, which allows for variation among regions in variables that we could not measure, such as lake rearing environments, migration route and timing, and fishing mortality. The slopes of the relationships between the predictors and sockeye density were held constant across regions. The second allowed both the slopes and intercepts to vary. All AICc values for the constant slope, varying intercept models were lower than for the equivalent varying slope, varying intercept models. This suggests that the mechanisms important to sockeye density did not differ between regions.

DISCUSSION

We tested alternative hypotheses for potential impacts of abiotic stream characteristics on densities of spawning sockeye salmon, according to their inferred effects on mortality of spawning adults and incubating embryos. Our results revealed the importance of stream characteristics that other studies have shown to be associated with predation risk. The top model included a single predictor - a cover index, which was composed of large wood density, the percentage of pool area, and the percentage of cutbanks. This model can be used to predict the quality of spawning habitat, while providing insights into the ecological interactions that lead to the relationships with population density.

These findings suggest that during the period of our study, biological interactions played a more important role than physiological tolerances in influencing spawning sockeye densities. Few studies have explicitly compared the importance of these two processes in influencing population size across a large number of populations. High densities of large wood and strong cutbanks provide physical cover from predators. Large pools can also provide adults with a refuge from predators. For example, grizzly bears (*Ursus arctos*), an important predator (Quinn et al. 2003), are less successful in complex streams with large amounts of large woody debris and deep pools than in small, shallow streams (Gende et al. 2004). 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 most of our study streams, as are salmon carcasses with marks that are distinct indications of predation by bears (Quinn and Kinnison 1999). A few of our sites in the Thompson region are near urban centers and therefore may experience lower levels of bear predation (Crupi 2003). However, we found no evidence that lakes and regions differ in the importance of the processes influencing the variation in spawning salmon density among streams. Future studies that combine demographics of salmon consumed by bears and population parameters (e.g. density) of salmon among streams would yield further insights into how physical characteristics of streams mediate the impacts of bear predation on salmon populations.

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 to most other stream habitat studies, the temporal extent of the dataset 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). Second, it is possible that the effects of temperature on mortality in streams are trumped by downstream conditions during migrations to the spawning grounds (Macdonald 2000), which would be manifest at the level of 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 biotic interactions, specifically predation risk, they cannot rule out physical tolerances in predicting variation among streams in spawning sockeye densities.

Our results show that a very simple model that includes physical cover in streams can predict a large amount of variation in sockeye salmon population densities in 36 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 in these regions predation risk may be an important determinant of adult population densities. Therefore, it may be possible to predict the quality of spawning habitat for salmon based on a few, key abiotic stream characteristics. This information can be incorporated into prioritization of streams for conservation and restoration of salmon populations.

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TABLE 1. *A priori* hypotheses describing sources of in-stream mortality for spawning and incubating embryonic sockeye.

Process influencing habitat selection	Hypothesis	Physical variables	Mechanism	Correlation with adult density	Ref.
Biotic interactions	Adult predation	Pools	Pools provide deep water that allows adults to escape from predators	+	1
		Large woody debris	Large wood allows adults to hide and escape from predators	+	1,2,3,4
		Cutbanks	Cutbanks allow adults to hide and escape from predators	+	4
		Spawning water depth	Deep water allows adults to escape predators	+	1,5
	Incubation habitat competition	Incubation habitat	Habitats such as pools, glides, runs and riffles provide optimal incubation conditions (i.e. well oxygenated and refuge from freezing) increasing the amount of good incubation habitat available to adults	+	6,7
		Spawning discharge	Higher discharge during spawning will increase the available incubation habitat for adults	+	6,7
		Substrate composition and mean size	Appropriate substrate composition and size increases the amount of good incubation habitat available to adults	+	8,9,10
Physiological tolerances	Adult physiological conditions	Spawning temperature	High water temperatures during spawning will increase metabolic rates and can impair physiological processes, increasing pre-spawn mortality	-	6,11
		Gradient	Higher gradients increase energy expenditure required during holding and spawning events	-	12,13
		Total dissolved solids	High concentration of total dissolved solids is an indicator of poor water conditions, which may cause individuals to avoid streams	-	14
		pH	Low pH may cause individuals to avoid streams	+	14,15
	Embryo physiological conditions	Incubation temperature	Freezing water temperatures can kill eggs or impair development	+	7
		Incubation discharge	De-watering of eggs can kill eggs or impair development	+	7

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 (Bjornn and Reiser 1991), 7 (Cope 1996), 8 (Cooper 1965), 9 (Chapman 1988), 10 (Buffington et al. 2004), 11 (Farrell et al. 2008), 12 (Fukushima and Smoker 1998), 13 (Healey et al. 2003), 14 (USEPA 1986), 15 (Ikuta et al. 2003)

TABLE 2. Indices constructed using principal components analysis. 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 36 streams. Only the first principal component was used in our analysis.

Index	**Variables**	**Loadings**	**% Variance**
Cover	Percent pool area	0.66	49
	Large woody debris density	0.57	
	Percent cutbanks	0.49	
Incubation habitat	Percent suitable spawning habitat	0.53	50
	Percent fines	0.42	
	Percent spawning gravel	0.28	
	Percent cobble and boulders	-0.60	
	Geometric mean substrate size	-0.32	
Spawning water depth	Maximum water channel depth	0.54	81
	Mean water channel depth	0.49	
	Stream volume	0.50	
	Pool depth	0.48	
Spawning discharge	Maximum water channel depth	0.57	70
	Mean water channel depth	0.52	
	Stream volume	0.55	
	Spawning discharge 2008	0.33	
Incubation discharge	Maximum water channel depth	0.55	75
	Mean water channel depth	0.49	
	Stream volume	0.53	
	Incubation discharge 2007	0.42	
Water quality	pH	-0.71	95
	Total dissolved solids	-0.71	
Substrate	Percent fines	0.47	48
	Percent spawning gravel	0.34	
	Percent cobble and boulders	-0.69	
	Geometric mean substrate size	-0.43	

TABLE 3. Mixed-effects models with ΔAICc values < 7. AICc values represent the trade-off between model complexity and fit, where lower AICc values indicate better models relative to other models in the candidate set. ΔAICc is the difference in AICc values between model *i* and the best model. The Akaike weight (w_i) is the probability that model is the best of the models considered. AICc values were calculated using maximum likelihood. N is the number of streams included in the analysis and K is the number of parameters in each model.

Hypothesis	**Parameters**	**N**	**K**	**LogLik**	**AICc**	**ΔAICc**	w_i
Adult predation	Cover index	36	5	30.9	-49.83	0.00	0.67
Adult predation	Cover index + Spawning water depth index	36	6	31.05	-47.20	2.63	0.18
Adult predation	Percent pool area + Water depth index	36	6	29.74	-44.57	5.26	0.05
Adult predation	Large woody debris density + Percent cutbanks	36	6	29.02	-43.14	6.69	0.02

TABLE 4. Parameter estimates (coefficients for main effects), standard errors (SE), *t*-values and P values for mixed-effects models with ΔAICc values <7. Final models were constructed using restricted maximum likelihood.

Hypothesis	**Parameters**	**Estimate**	**SE**	***t***	***P***
Adult predation	Cover index	0.048	0.015	3.12	0.004
	Intercept	0.134	0.140	0.96	0.35
Adult predation	Cover index	0.049	0.016	3.13	0.004
	Spawning water depth index	0.006	0.012	0.50	0.59
	Intercept	0.131	0.137	0.95	0.35
Adult predation	Percent pool area	0.003	0.001	2.61	0.01
	Spawning water depth index	0.002	0.012	0.19	0.85
	Intercept	0.080	0.150	0.54	0.60
Adult predation	Large woody debris density	0.182	0.146	1.24	0.22
	Percent cutbanks	0.002	0.001	1.99	0.06
	Intercept	0.037	0.144	0.26	0.80

Figure Legends

FIG. 1. Locations of 36 study streams in two regions of the Fraser Basin: a) Stuart and b) Thompson. Study sites with sockeye salmon populations are black circles and control sites (lacking salmon) are gray circles.

FIG. 2. Observed adult spawning densities vs. fitted adult spawning densities for the top model with cover index as the only predictor.

FIG. 3. Mixed-effects regression plots with varying intercepts for: a) the cover index, and b) percent pool area as fixed effects. Numbers refer to multiple streams within lakes, 1=Takla Lake, 2=Trembleur Lake, 3=Shuswap Lake, 4=Adams Lake, 5=Momich Lake, 6=North Barrière Lake. Solid regression lines are for each stream within each lake and the dashed line shows the mean regression line.

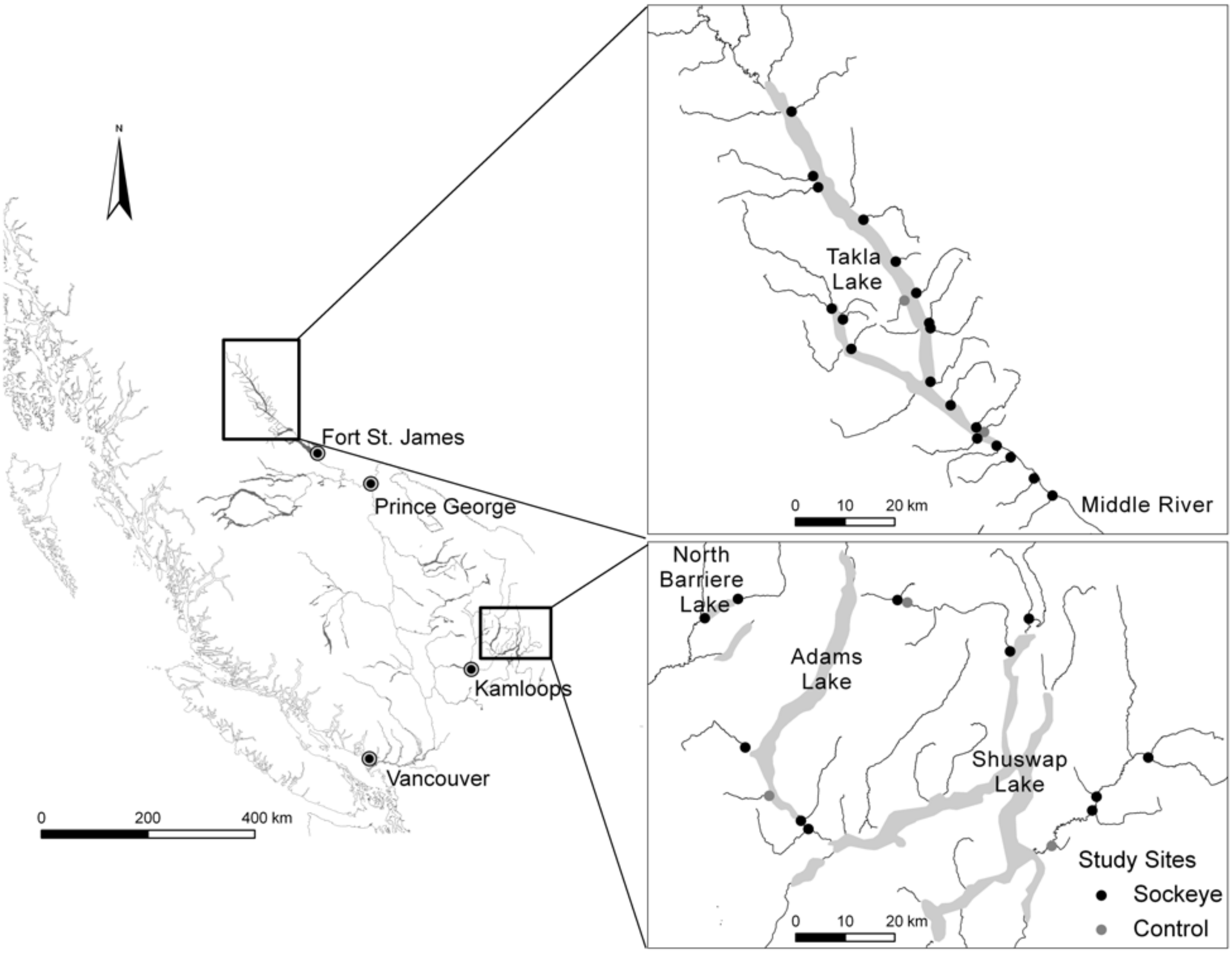
N
Fort St. James
Prince George
Kamloops
Vancouver
0
200
400 km
Takla
Lake
Middle River
0
10
20 km
North
Barriere
Lake
Adams
Lake
Shuswap
Lake
Study Sites
● Sockeye
● Control
0
10
20 km

Fig. 1.

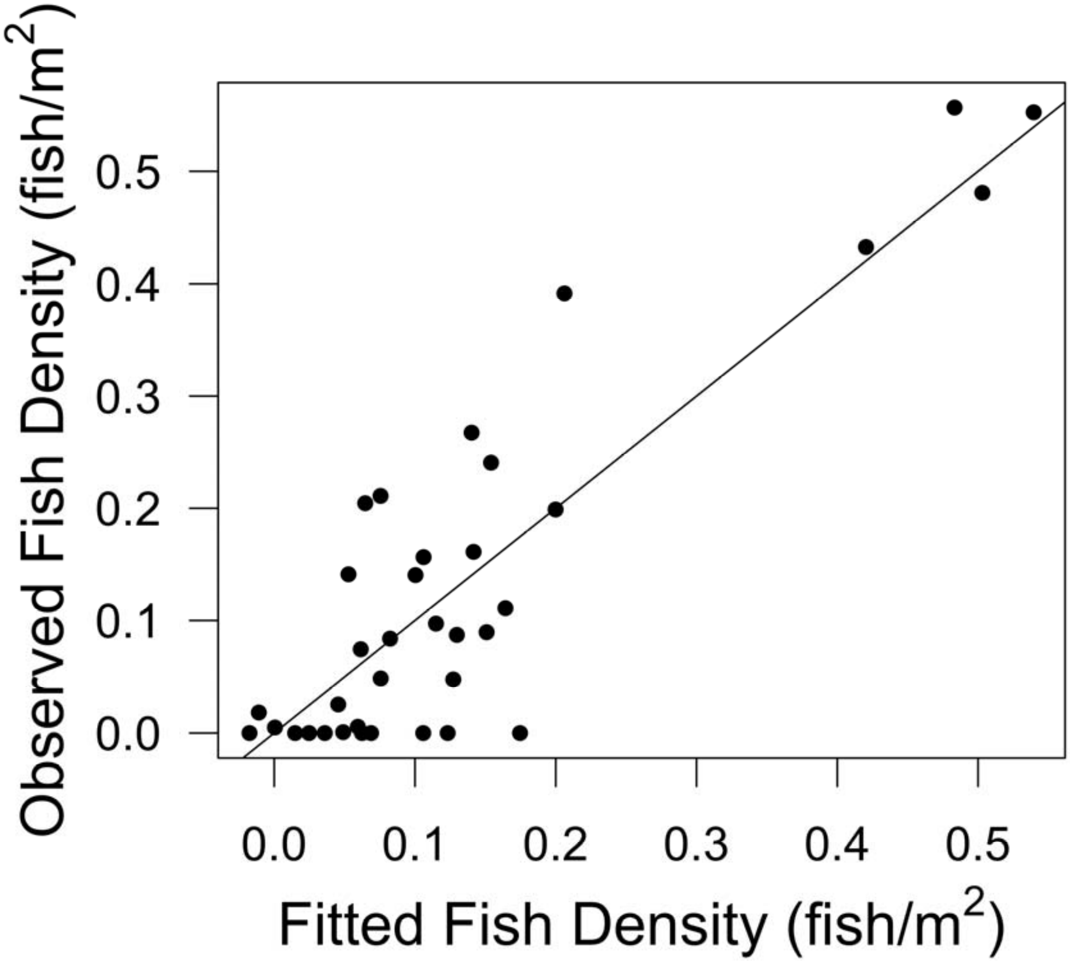
Observed Fish Density (fish/m^2)
0.0
0.1
0.2
0.3
0.4
0.5
0.0
0.1
0.2
0.3
0.4
0.5
Fitted Fish Density (fish/m^2)

FIG. 2.

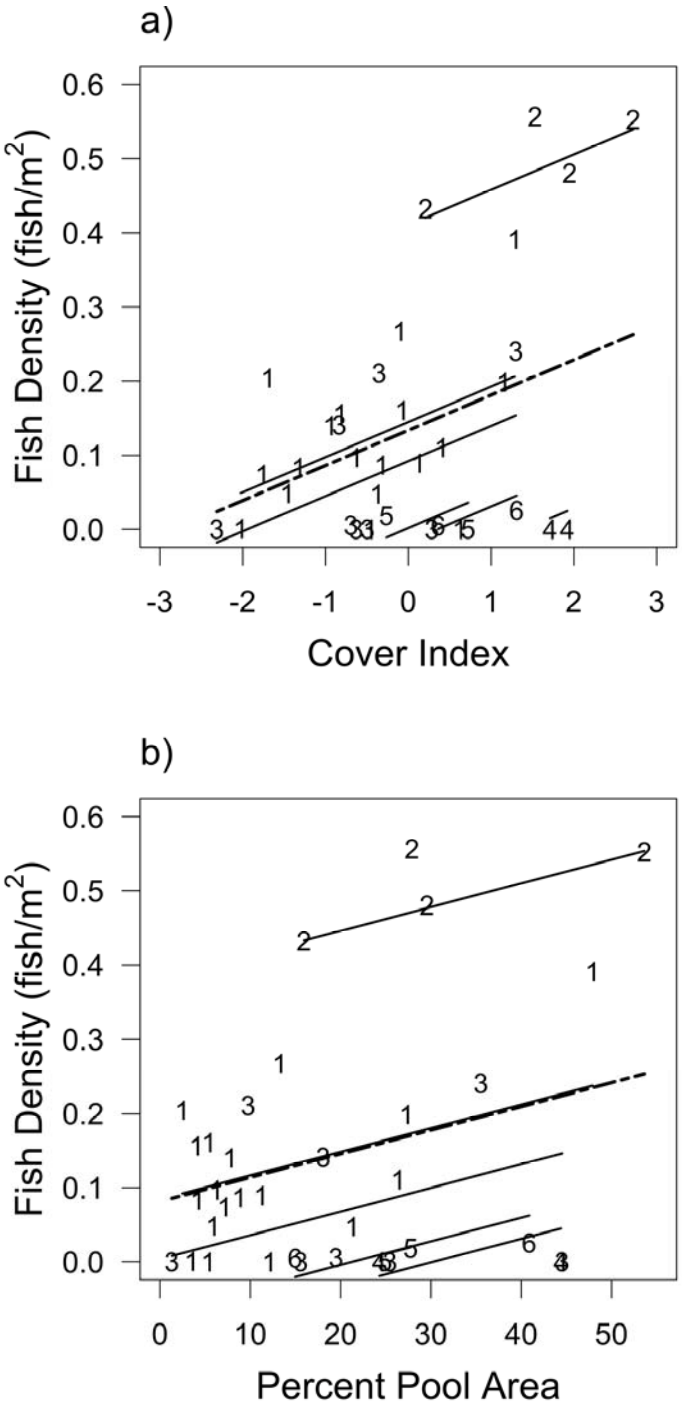
a)
Fish Density (fish/m^2)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Cover Index
-3
-2
-1
0
1
2
3
b)
Fish Density (fish/m^2)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Percent Pool Area
0
10
20
30
40
50

FIG. 3.