Bull trout (*Salvelinus confluentus*) occurrence and abundance influenced by cumulative industrial developments in a Canadian boreal forest watershed

Travis Ripley, Garry Scrimgeour, and Mark S. Boyce

Abstract: We examined relations between cumulative levels of forest harvesting and density of road networks on the occurrence and abundance of bull trout (*Salvelinus confluentus*) in the Kakwa River Basin, Alberta. Logistic regression models showed that bull trout occurrence was positively related to stream wetted width but negatively related to percent fines, percent cobbles, reach slope, and the cumulative area of the subbasin harvested and road density. Results from zero-inflated Poisson regression models typically showed that bull trout abundance was positively related to elevation and negatively related to stream width, percent fines, percent cobble, slope, and levels of forest harvesting. Using the negative relation between bull trout occurrence and percentage of subbasins harvested derived from the most parsimonious logistic regression model, we forecasted that forest harvesting over the next 20 years is projected to result in the local extirpation of bull trout from 24% to 43% of stream reaches that currently support bull trout in the Kakwa River Basin.

Résumé : Nous avons déterminé les relations entre les niveaux cumulatifs de coupe des forêts et la densité des réseaux routiers, d'une part, et la présence et l'abondance d'ombles à tête plate (*Salvelinus confluentus*), d'autre part, dans le bassin versant de la Kakwa, Alberta. Des modèles de régression logistique montrent que la présence d'ombles à tête plate est en corrélation positive avec la surface mouillée du cours d'eau et en corrélation négative avec le pourcentage de particules fines, le pourcentage de galets, la pente de la section, la surface cumulée du sous-bassin coupé et la densité des routes. Les résultats de modèles de régression de Poisson à inflation nulle montrent typiquement que l'abondance des ombles à tête plate est en relation positive avec l'altitude et en corrélation négative avec la largeur du cours d'eau, le pourcentage de particules fines, le pourcentage de galets, la pente et l'importance de la coupe des forêts. En utilisant la relation négative entre la présence d'ombles à tête plate et le pourcentage de sous-bassins versants coupés au cours des 20 prochaines années, obtenu par le modèle de régression logistique le plus parcimonieux, nous prédisons que la coupe des forêts au cours de ces 20 prochaines années devrait avoir pour conséquence l'élimination locale de l'omble à tête plate de 24–43 % des sections de cours d'eau où il habite actuellement dans le bassin versant de la Kakwa.

[Traduit par la Rédaction]

Introduction

Developing strategies that maintain biological diversity amidst increasing cumulative levels of industrial development is arguably the single largest challenge to sustainable management of boreal forest ecosystems (Schindler 1998*a*; MacDonald 2000). For stream fish assemblages, cumulative impacts of industrial activities resulting from commercial forest harvesting and oil and gas exploration can profoundly impact the quantity and quality of fish habitats. These impacts are mediated through changes in forest composition and age that increase water yield, sediment inputs, and thermal and light regimes. Additionally, the establishment of road networks can fragment streams and indirectly influence

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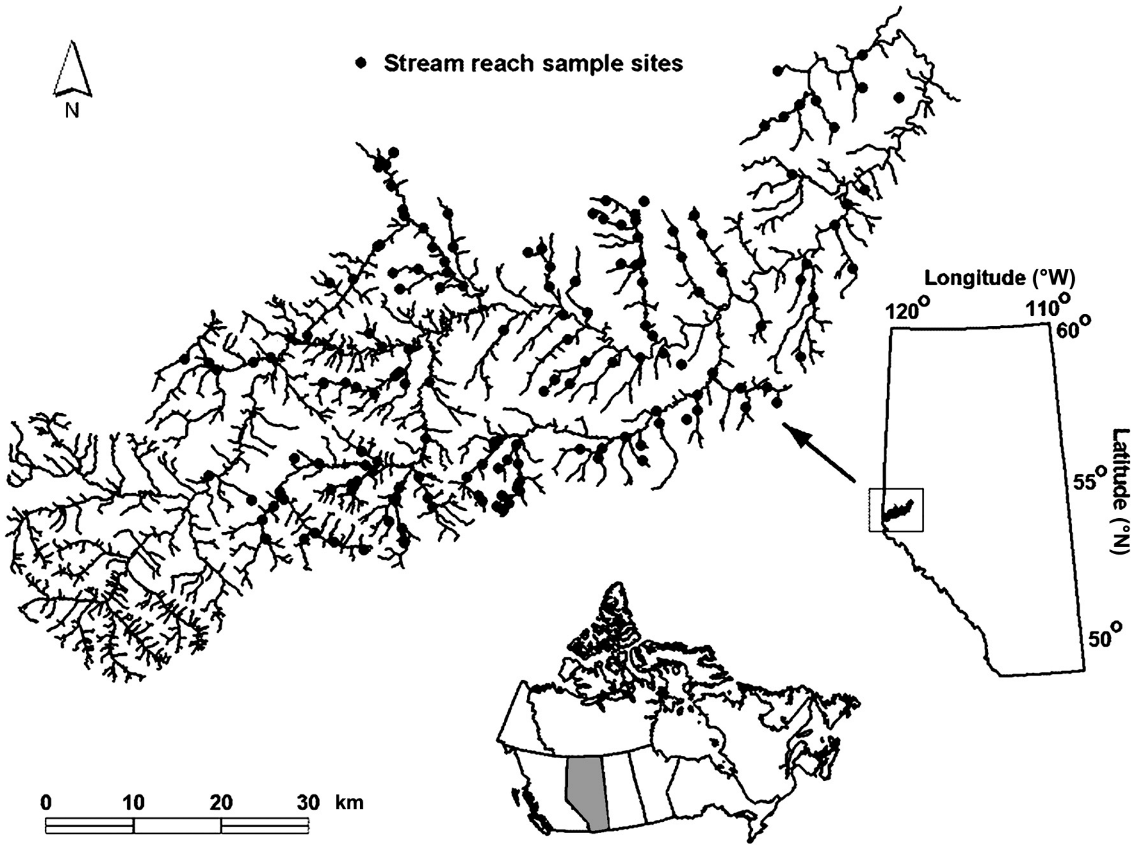
Fig. 1. Location of the 172 study sites in the Kakwa River basin in central western Alberta, Canada.



population dynamics of fish increasing angler-mediated mortality (Eaglin and Hubert 1993; Rieman and McIntyre 1995; Baxter et al. 1999). While the specific linkages between degradation of stream habitats and industrial activity are not well understood, a growing body of evidence suggests that current industrial activities often are not well aligned with the conservation of stream fish communities (Ziemer et al. 1991; Schindler 1998*b*; Baxter et al. 1999).

Declines in bull trout (*Salvelinus confluentus*) populations in North America are thought to result from impacts of industrial activity on spawning, rearing, and overwintering habitats (Rieman and McIntyre 1995; Baxter and McPhail 1999) and angler-mediated mortality (Brewin and Brewin 1997; Walty and Smith 1997; Montana Bull Trout Scientific Group 1998). In Alberta, appreciable declines in the occurrence (i.e., presence) and abundance (i.e., density and counts) of bull trout over the last decade have coincided with dramatic expansions of commercial forestry and the oil and gas sectors. This observation has raised serious concerns about the persistence of bull trout populations in the boreal forest of Alberta (Brewin and Brewin 1997; Fitch 1997; Howell and Rieman 1997).

Faced with increasing numbers of proposed industrial activities, often within the same subbasin, resource managers have adopted an approval process that includes evaluations of past, current, and forecasted levels of industrial activity and the extent that they are associated with changes in bull trout occurrence and abundance. Despite their inherent importance to watershed management, there is a paucity of empirical data defining relations between cumulative levels of industrial activity, measured in subbasins, and the occurrence and abundance of bull trout observed in individual stream reaches (but see Baxter et al. 1999). Given linkages between forest cover attributes and physicochemistry of surface waters (e.g., Carignan et al. 2000; Martin et al. 2000), it is plausible that the occurrence and abundance of bull trout at individual stream reaches may be influenced by cumulative changes in forest cover, mediated by industrial activity, in upstream areas of the subbasin (Baxter et al. 1999; Latterell et al. 2003).

Our understanding of the cumulative effects of industrial activity on the occurrence and abundance of bull trout in the Rocky Mountains of Alberta is poor. As a result, our ability to understand future impacts from industrial activities is limited. To address these issues, we considered the following two questions. First, at the subbasin level, is the occurrence and abundance of bull trout measured at the stream-reach scale related to cumulative levels of forest harvesting and overall density of road networks in the subbasin upstream? Second, are increases in industrial activity forecasted to reduce the occurrence of bull trout at the stream reach scale?

Methods

Study area

The Kakwa River watershed (3475 km^2) is located in the eastern Rocky Mountains in central western Alberta and is part of the Peace River drainage (Fig. 1). The river originates at Kakwa Lake in British Columbia and flows northeast across alpine, subalpine, and boreal cordillera ecoregions, converging with the Smoky River. The majority of the river basin is located within the subalpine and upper and lower boreal cordillera ecoregions where floodplains are dominated by alluvial materials.

Forest cover in the subalpine ecoregion is dominated by Engelmann spruce (*Picea engelmannii*) along with open-canopied dwarfed Engelmann spruce, subalpine fir (*Abies lasiocarpa*), whitebark pine (*Pinus albicaulis*), and subalpine larch (*Larix lyallii*) dominant in the uppermost portion of this zone (Strong and Leggat 1992). The upper boreal cordilleran ecoregion is dominated by closed-canopy conifer forest comprising lodgepole pine (*Pinus contorta*), whereas trembling aspen (*Populus tremuloides*), balsam fir (*Populus balsamifera*), paper birch (*Betula papyrifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), and balsam fir (*Abies balsamea*) are dominant in the lower boreal cordilleran (Strong and Leggat 1992).

Fish communities in the Kakwa watershed are numerically dominated by slimy sculpin (*Cottus cognatus*), bull trout, rainbow trout (*Oncorhynchus mykiss*), and to a lesser extent Arctic grayling (*Thymallus arcticus*) and mountain whitefish (*Prosopium williamsoni*) (Scrimgeour et al. 2003). While the Kakwa River basin supports both resident and fluvial populations, the vast majority of reaches sampled in our study likely supported fluvial populations of bull trout (P. Hvenegaard, Alberta Conservation Association, 9621-96 Avenue, Peace River, AB, T8S 1T4, Canada, unpublished data). Based on electroshocking surveys, bull trout occur in approximately 40% of stream reaches, account for 17% of the fish community, and occur at average densities of 0.3 fish·100 m^{-2} (Scrimgeour et al. 2003).

Two sets of high-gradient waterfalls located on the Kakwa and South Kakwa rivers limit upstream migration of bull trout, which have not been reported above these falls. Bull trout remain in the watershed during all life stages.

Levels of industrial activity

Current industrial activities in the Kakwa basin result predominantly from forest harvesting and exploration (e.g., seismograph exploration) and extraction of oil and gas resources. The Kakwa River basin is considered to be minimally impacted by industrial activities that have altered about 10% of the forest cover in the entire basin (Scrimgeour et al. 2003). Of this amount, the majority comprises forest harvest blocks (about 63% of all areas influenced by human activities) with roads and seismic lines accounting for the remainder of the industrial footprint (Scrimgeour et al. 2003). However, industrial activities are not uniformly distributed throughout the basin and where present have typically altered forest cover between 10% and 40% of individual subbasins (Scrimgeour et al. 2003).

While not quantified, angling pressure on bull trout is thought to be moderately low, in part because of poor access and high summer flows driven by snowmelt that create turbid water for much of the early-spring and midsummer periods. Current fishing regulations require catch-and-release for bull trout and exclusion of all angling in two of the primary bull trout spawning tributaries.

Occurrence and abundance of bull trout

We quantified the occurrence and abundance of bull trout in 172 stream reaches of first- to fifth-order streams (Strahler classification) in the Kakwa River basin between 1994 and 2001. Stream reaches were selected using a stratified random approach, with stream order and elevation as strata. Within these strata, we randomly identified 172 stream reaches located throughout the majority of the lower two-thirds of the basin where industrial activities are most predominant. This approach reduces the confounding effects of a correlation between elevation and levels of industrial activity. We also excluded stream reaches that were immediately adjacent to others (i.e., within 1 km) unless they were located in a separate subbasin. Stream reaches encompassed a wide range of wetted widths (mean ± 1, SD = 4.1 ± 2.9 m), elevations (1223.0 ± 202.2 m above sea level), and slopes (0.028 ± 0.025) and were located in subbasins ranging from 0.71 to 374.3 km^2 (38.9 ± 56.8 km^2).

Because our primary objective was to test for relations between bull trout occurrence and abundance with metrics defining cumulative level of industrial activity, we did not derive relations for specific life history stages (i.e., young of the year, juveniles, and adults). However, the vast majority (80%) of bull trout collected were young of the year and juveniles. Surveys were conducted during May–October (i.e., the summer ice-free period) after the emergence of young-of-the-year bull trout (Scrimgeour et al. 2003).

The majority of streams in the Kakwa basin are moderately inaccessible (i.e., overall mean road density <0.2 km·km^{-2}), and as a result, we accessed stream reaches from small nonpermanent roads and trails or from a helicopter. Surveys of stream reaches (mean stream reach distance = 237 m, mean electrofishing effort = 10.5 min) were completed using a single-pass approach with a Smith-Root^{TM} type 12 pulsed DC-backpack electrofisher (Smith-Root, Inc., Vancouver, Washington). Sampling was conducted when conductivity and water clarity were conducive to electrofishing success. Individual reaches were sampled by electrofishing in an upstream direction through the entire stream reach. Our sampling goal was to provide a reasonable probability of detecting bull trout while still allowing for extensive sampling of stream reaches in the Kakwa River basin. Previous surveys of bull trout in the Lynx Creek subbasin of the Kakwa River watershed indicated a catch probability of 0.57 (P. Hvenegaard, Alberta Conservation Association, 9621-96 Avenue, Peace River, AB T8S 1T4, Canada, unpublished data), and estimates of abundance on the Kakwa River were 10 bull trout·km $stream^{-1}$ (Tchir 2000). Assuming a Poisson distribution (Zar 1999), the probability of detecting bull trout was 0.74 ($p(0) = e^{-\mu}$, μ = 10 trout·1 km^{-1} × 237 m sampled × 0.57; thus, $p(\geq 1) = 0.74$).

Environmental variables

We quantified the ability of seven environmental variables to explain variance in the occurrence and abundance of bull trout in individual stream reaches (Table 1). This small suite of variables was identified from a more extensive suite of variables based on previous analyses (Scrimgeour et al. 2003) and our general understanding of the biology of bull trout in the Kakwa River basin. These variables define attributes of stream reaches where surveys of bull trout were completed and those in the subbasin above the stream reach (Table 1). Metrics defining cumulative levels of industrial activity in the subbasin represent one type of subbasin-scale attribute (Table 1). The seven predictor variables were used

Table 1. Environmental variables used to predict the occurrence and abundance of bull trout (*Salvelinus confluentus*) at 172 stream reaches in the Kakwa River basin.

Variable	Abbreviation	Units
Stream reach		
Wetted width[a]	WIDTH	m
Fine sediments[b]	FINES	%
Cobble substrate[b]	COBB	%
Elevation	ELEV	m
Stream slope[c]	SLOPE	Rise/run
Industrial disturbance		
Percentage of the subbasin harvested	HARV	%
Density of roads	ROADS	$km \cdot km^{-2}$

Note: Variables are separated into those defining stream reaches and industrial disturbance and were used to construct 27 candidate a priori models explaining variance in the occurrence and abundance of bull trout.

[a]Wetted width was measured as the width of the water surface across the stream channel.

[b]Substrate composition was determined visually by estimating the percent cover of fines (<2 mm (silt–sand)), small gravel (2–16 mm), large gravel (17–64 mm), cobble (65–256 mm), and boulder (>256 mm) in the substratum.

[c]Stream slope was calculated from rise/run based on 100 m upstream and downstream of each sample location and was derived using a digital elevation model and GIS tools.

to test 11 and 24 a priori models representing all possible combinations of variables. Environmental variables were either measured during stream surveys (i.e., stream wetted width, percent fines, and percent cobbles) or derived from queries of geographic information system (GIS) databases (i.e., elevation, slope, road density, and percentage of the subbasin harvested).

Locations of the stream reaches (i.e., the most downstream portion) were determined with a hand-held GARMIN™ model 12 global positioning unit. An individual study site (i.e., a stream reach) represented a length of stream minimally 20 times its wetted width. Stream reaches typically comprised between 100- and 300-m lengths of stream channel. We established between three and five transects perpendicular to the stream channel at equal distances from the bottom to the top of the stream reach to assist with measures of stream width and size composition of the substratum (i.e., percent fines and percent cobbles) (Table 1). The locations of representative transects were chosen after an initial visual evaluation of the stream reach and were largely based on overall variation in wetted width and the abundance of riffle, pool, and run habitats. We measured wetted width (±1 cm) along each transect and used these data to derive an overall average for the entire stream reach. In contrast, we visually estimated the size composition of riverbed materials at three to five locations along each transect and calculated an overall average for the stream reach based on the averages of individual transects within each stream reach.

The remaining four environmental variables of watershed area (i.e., elevation, slope, percent forest harvesting, and road density) were derived from queries of GIS databases that defined forest cover attributes, road, and other linear disturbances and a hydrologically corrected digital elevation model with a spatial resolution of about 3 m. Queries of all GIS data were completed using ArcView 3.1 (ESRI, Inc., Redlands California). The Alberta Vegetation Inventory was used to define levels of forest harvesting and road density. After defining the extent of individual subbasins upstream of study reaches, we used GIS tools to calculate road density and percentage of forest harvesting in each subbasin. While not quantified, field validations have shown very strong concordance between the presence of roads predicted from GIS layers and those based on field observations.

Statistical analyses and model types

Logistic and zero-inflated Poisson (ZIP) regression models were used to quantify relations between bull trout occurrence and abundance and select environmental variables (Table 2). We examined relations between bull trout occurrence and abundance and environmental variables by completing two sets of analyses. First, we derived empirical models of bull trout occurrence and abundance from subbasins that were minimally impacted by industrial activity using data from 76 of the 172 stream reaches. For these analyses, we defined minimally impacted subbasins as those where cumulative levels of forest harvesting comprised <3% of the area of individual subbasins and where road densities were $<0.02\ km \cdot km^{-2}$. Under minimal influence of anthropogenic activity, these analyses quantified the extent to which variance in bull trout occurrence and abundance could be explained from a relatively small suite of variables. Second, we used data from all 172 stream reaches to quantify the extent to which variance in bull trout occurrence and abundance could be explained by two metrics of industrial activity.

Logistic regression models

We quantified the ability of the 27 a priori models to explain the variance in the occurrence and abundance of bull trout (Table 2). These models were derived from combinations of the seven environmental variables and included between three and seven variables. Correlations among predictor variables were evaluated prior to inclusion in models to avoid colinearity, and variables were excluded when correlations were >0.7. For instance, our analyses showed that stream wetted width was strongly and positively (Pearson's correlation coefficient = 0.73) correlated to the area of individual subbasins. As a result, we retained wetted width but not subbasin area as a predictor variable. Analyses were conducted using the logistic regression option in SPSS (SPSS Inc. 2001).

Akaike's Information Criterion corrected for small sample sizes (AIC_c) was used to select the most parsimonious of the candidate logistic regression and ZIP models (Burnham and Anderson 1998; Anderson et al. 2000). Each model was evaluated by the difference in AIC_c values from the most parsimonious model (Δ_i) that was weighted against other models. Once the most parsimonious model was identified, it was validated using the receiver-operating characteristic (ROC). We chose the ROC rather than traditional classification tables because of its ability to analyse the proportion of correctly and incorrectly classified predictions over a continuous range of threshold probability cutoff levels (Fielding and Bell 1997; Boyce et al. 2002). The ROC represents the relation between sensitivity (i.e., true positive fraction)

Table 2. Summary of a priori candidate models used to evaluate relations between the occurrence and abundance of bull trout (*Salvelinus confluentus*) and environmental variables, including metrics of industrial activity, in the Kakwa River basin.

Model	Variables	*K*
1	ELEV + WIDTH + FINES	3
2	ELEV + WIDTH + COBB	3
3	ELEV + WIDTH + SLOPE	3
4	ELEV + WIDTH + FINES + COBB	4
5	ELEV + WIDTH + FINES + SLOPE	4
6	ELEV + WIDTH + FINES + COBB + SLOPE	5
7	ELEV + FINES + SLOPE	3
8	WIDTH + FINES + COBB	3
9	WIDTH + FINES + SLOPE	3
10	WIDTH + FINES + COBB + SLOPE	4
11	FINES + COBB + SLOPE	3
12	ELEV + WIDTH + FINES + COBB + SLOPE + ROADS	6
13	ELEV + WIDTH + FINES + COBB + SLOPE + HARV	6
14	WIDTH + FINES + SLOPE + ROADS	4
15	WIDTH + FINES + SLOPE + HARV	4
16	ELEV + WIDTH + FINES + COBB + SLOPE + ROADS + HARV	7
17	WIDTH + FINES + COBB + SLOPE + ROADS	5
18	WIDTH + FINES + COBB + SLOPE + HARV	5
19	WIDTH + FINES + COBB + SLOPE + ROADS + HARV	6
20	FINES + COBB + ROADS	3
21	FINES + COBB + HARV	3
22	FINES + COBB + SLOPE + ROADS	4
23	FINES + COBB + SLOPE + HARV	4
24	FINES + COBB + SLOPE + ROADS + HARV	5
25	COBB + SLOPE + ROADS	3
26	COBB + SLOPE + HARV	3
27	COBB + SLOPE + ROADS + HARV	4

Note: *K* is the number of variables. Abbreviations for variables are provided in Table 1. Models 1–11 were used to define relations between bull trout occurrence and abundance and environmental variables from stream reaches whose subbasins were minimally impacted by industrial activities. In contrast, all 27 models were used to examine global relations between bull trout occurrence and abundance and environmental variables from stream reaches whose subbasins had been influenced by varying levels of industrial activity.

against specificity (i.e., false positive fraction). The area under each curve (AUC) of the ROC plots ranges between 0.5 and 1.0. Values approaching 1.0 indicate a better predictive model and a value of 0.5 describes a model with no predictive power (Fielding and Bell 1997). General interpretations of AUC suggest that values of 0.7–0.9 indicate reasonable discrimination ability (Pearce and Ferrier 2000). The AUC from the ROC was compared with values from the best full model with that from the best model calculated when 50% of the data were withheld. Using these criteria, we identified the most parsimonious of the candidate models as well as other models that were also identified as having a moderate level of support based on the difference in AIC_c values from the most parsimonious model of <10 ΔAIC_c units (Anderson et al. 2001) combined with models where AUC ≥ 7.0.

ZIP regression models

We evaluated the ability of a generalized linear model to explain variance in the abundance of bull trout measured in individual stream reaches (i.e., number·100 m^{-2}) using a ZIP regression model (Anonymous 2001). The ZIP model is a useful means to evaluate relations between environmental variables and abundance, since it remedies the problem of overdispersion of zero-count data (i.e., stream reaches where bull trout were not detected) (Lambert 1992; Zorn 1996; Ridout et al. 1998). We tested for overdispersion of bull trout abundance data by calculating a variance to mean ratio, where ratios exceeding 1 are considered to indicate overdispersion (Zorn 1996). Lastly, we also plotted the overall distribution of density data to ensure that they approximated a negative binomial distribution.

The ZIP model was developed by including all of the positive abundance data and only sufficient zero-count data to approximate a Poisson distribution. We evaluated ZIP models using AIC_c (Burnham and Anderson 1998). Each inflated model was evaluated by the difference in AIC_c values from the most parsimonious model (Δ_i) and the Akaike weights (w_i) given to those same candidate models. To ensure that each model was a good candidate for ZIP regression, we tested each inflated portion using the Vuong statistic, which tests for overdispersion by comparing the full model with zero data against the count model, nonzero data (Vuong 1989). Analyses were conducted using the ZIP regression option in STATA (Anonymous 2001). Similar to logistic regression models, we identified the most parsimonious of the candidate zero-inflated regression models as well as other models that were also identified as having a moderate level of support (i.e., difference in AIC_c values from the most parsimonious model of <10) (Anderson et al. 2001).

Forecasting changes in bull trout

Our logistic regression models indicated that the occurrence of bull trout in individual stream reaches was negatively related to percentage of the commercial forest harvesting in subbasins upstream of the study reaches. We forecasted changes in the occurrence of bull trout at the stream reach scale using results from the most parsimonious logistic regression model predicting occurrence combined with simulated increased in forest harvesting in subbasins. To simulate the responses (i.e., occurrence) of bull trout, we used the linear predictors for each variable developed from the most parsimonious logistic regression model. We assessed the change in the probability of occurrence, based on each elevated timber harvest scenario, ranging from 5% to 35% across all subbasins in the Kakwa River watershed. This range included current overall levels of forest harvesting in the basin (i.e., 6.3%) and that is likely to be attained in 20 years (i.e., 35%).

We expected that loss (i.e., local extirpation) of bull trout populations from individual stream reaches would vary depending on the density of bull trout observed within individual stream reaches. Thus, we evaluated the effects of increases in forest harvesting on bull trout occurrence for stream reaches that supported a range of bull trout densities (i.e., very low to high). We identified four bull trout density classes from the overall density distribution from study reaches where bull trout occurred. We considered this to be a reasonable approach given that the overall distribution of bull trout densities approximated a normal distribution that could be divided into four classes based on the four density quartiles.

Results

Relations between bull trout occurrence and abundance and environmental variables from minimally impacted subbasins

Despite relatively low numbers of environmental variables, logistic and ZIP regression models accounted for moderately high amounts of variation in the occurrence and abundance of bull trout located within minimally impacted subbasins (Table 3). Logistic regression models showed that bull trout occurrence was positively related to elevation and stream width and negatively related to percent fines and stream slope (Table 3). AUCs of ROC plots ranged from 0.70 to 0.72. Similarly, ZIP regression models showed that bull trout abundance was positively related to elevation and negatively related to stream wetted width, percent cobbles, percent fines, and stream slope (Table 3).

Evaluating the cumulative effects of industrial activity on the occurrence of bull trout

We evaluated the cumulative effects of industrial activities on bull trout by testing the ability of 27 a priori models to explain variance in the occurrence and abundance of bull trout from all 172 stream reaches in the Kakwa River basin. Stream reaches were located in individual subbasins minimally impacted by industrial activity and those where up to 45% of subbasins had been commercially harvested.

Table 3. Summary of the three most parsimonious logistic and zero-inflated Poisson (ZIP) regression models predicting the occurrence and abundance of bull trout (*Salvelinus confluentus*) from stream reaches (N = 76) located in subbasins minimally impacted by industrial activity in the Kakwa River basin.

Model	Variable	Coefficient	SE	Δ_i	w_i
Logistic regression models					
1	Intercept	–1.626	1.813	0.0	0.40
	Elevation	0.003	0.002		
	Percent fines	–0.023	0.016		
	Slope	–34.110	12.594		
2	Intercept	–2.490	1.896	1.4	0.20
	Elevation	0.003	0.001		
	Width	0.095	0.102		
	Slope	–32.152	12.724		
3	Intercept	–1.990	1.989	2.0	0.14
	Elevation	0.003	0.002		
	Width	0.048	0.107		
	Percent fines	–0.020	0.017		
	Slope	–32.761	12.893		
ZIP regression models					
1	Intercept	–2.395	0.739	0.0	0.47
	Elevation	0.003	0.001		
	Width	–0.003	0.029		
	Cobble	–0.014	0.006		
2	Intercept	–2.002	0.804	0.7	0.33
	Elevation	0.003	0.001		
	Width	–0.015	0.031		
	Percent fines	–0.008	0.007		
	Cobble	–0.018	0.007		
3	Intercept	–1.936	0.858	3.0	0.11
	Elevation	0.003	0.001		
	Width	–0.017	0.031		
	Percent fines	–0.008	0.007		
	Cobble	–0.018	0.007		
	Slope	–1.252	5.715		

Note: Δ_i, ΔAIC_c; AIC_c, Akaike's Information Criterion corrected for small sample sizes; w_i, AIC_c weights. The most parsimonious logistic regression model (model 1) had an overall classification success of 65.8% and an AIC_c statistic of 97.5. The latter two models are also statistically meaningful with Δ_i < 10 (Anderson et al. 2001) and area under curve (AUC) values of ≥0.7. The zero-count portions of all of the ZIP regression models were inflated against the most parsimonious logistic regression model described from the minimally impacted sites. The most parsimonious ZIP regression model had an AIC_c statistic of 390.9.

Bull trout were present at 44% (i.e., 75 of the 172 sites) and accounted for about 21% of all fish collected. Bull trout were the most numerically dominant fish species in the majority of third- and fourth-order streams where they accounted for 74% of all captured bull trout. Logistic regression models indicated that the occurrence of bull trout was related to a relatively small suite of seven variables including elevation, stream wetted width, percent fines, percent cobble, reach slope, percent timber harvest, and density of roads.

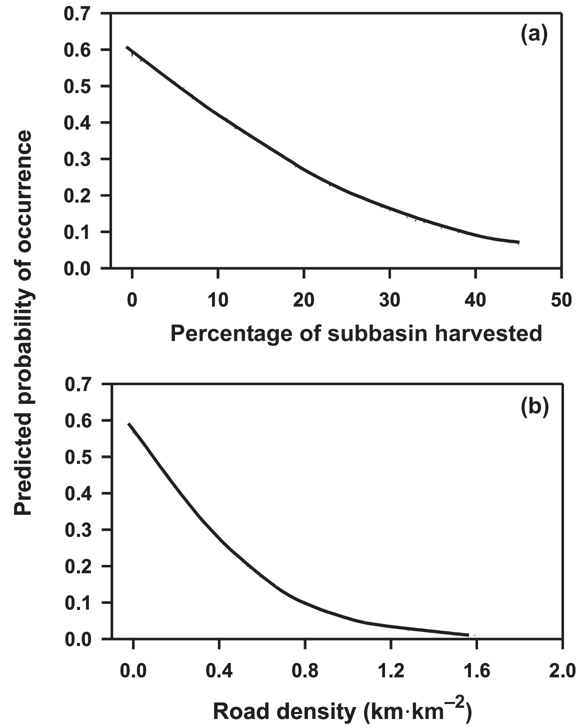
Based on AIC_c, the most parsimonious model included four environmental variables and showed that bull trout oc-

Table 4. Summary of the eight most parsimonious logistic regression models predicting the occurrence of bull trout (*Salvelinus confluentus*) in the Kakwa River basin.

Model	Variable	Coefficient	SE	Δ_i	w_i
1	Intercept	0.950	0.536	0.0	0.41
	Width	0.109	0.069		
	Percent fines	–0.033	0.012		
	Slope	–18.223	8.101		
	Percent harvested	–7.531	1.783		
2	Intercept	1.089	0.810	2.1	0.14
	Width	0.108	0.069		
	Percent fines	–0.035	0.015		
	Percent cobble	–0.003	0.015		
	Slope	–18.550	8.240		
	Percent harvested	–7.541	1.781		
3	Intercept	1.794	0.688	2.5	0.11
	Percent fines	–0.042	0.014		
	Percent cobble	–0.055	0.015		
	Slope	–22.819	7.956		
	Percent harvested	–7.460	1.750		
4	Intercept	1.927	0.697	2.7	0.11
	Percent fines	–0.037	0.014		
	Percent cobble	–0.006	0.015		
	Slope	–23.558	8.064		
	Density of roads	–1.486	1.097		
	Percent harvested	–6.387	1.848		
5	Intercept	1.265	0.826	2.7	0.10
	Wetted	0.099	0.070		
	Percent fines	–0.031	0.015		
	Percent cobble	–0.004	0.015		
	Slope	–19.532	8.371		
	Density of roads	–1.315	1.109		
	Percent harvested	–6.590	1.890		
6	Intercept	0.084	1.800	3.8	0.06
	Elevation	0.001	0.001		
	Width	0.120	0.072		
	Percent fines	–0.034	0.015		
	Percent cobble	–0.003	0.015		
	Slope	–18.736	8.284		
	Percent harvested	–6.978	1.975		
7	Intercept	0.425	1.807	4.6	0.04
	Elevation	0.001	0.001		
	Width	0.108	0.072		
	Percent fines	–0.030	0.015		
	Percent cobble	–0.004	0.015		
	Slope	–19.734	8.423		
	Density of roads	–1.258	1.107		
	Percent harvested	–6.158	2.045		
8	Intercept	0.725	0.536	9.6	0.00
	Percent cobble	0.020	0.012		
	Slope	–21.501	7.790		
	Density of roads	–2.053	0.992		
	Percent harvested	–6.493	1.759		

Note: Δ_i, ΔAIC_c; AIC_c, Akaike's Information Criterion corrected for small sample sizes; w_i, AIC_c weights. Models were derived from stream reaches (N = 172) located in subbasins impacted by the full range of industrial activity. The most parsimonious of the candidate models (model 1) had an overall classification success of 74.4% and an AIC_c statistic of 189.7.

Fig. 2. Logistic regression models of the predicted probability of bull trout (*Salvelinus confluentus*) occurrence and (*a*) percentage of the subbasin subjected to forest harvesting and (*b*) density of roads in the Kakwa River basin.



currence was positively related to stream wetted width and negatively related to percent fines, reach slope, and percent forest harvesting (Table 4). This model (AUC = 0.80) performed well even when five replicates of 50% of the data were removed (AUC = 0.85). We also quantified the predictive power of many other logistic regression models for which there was a reasonable level of support (Table 4). These models consistently indicated negative relations between the occurrence of bull trout and percent forest harvesting and road density in the subbasin (Fig. 2).

Bull trout were detected in stream reaches located at elevations ranging between 932 and 1663 m above sea level, with mean wetted widths of 5 m, and where fine materials comprised a relatively small proportion of riverbed materials (Table 5). Sites supporting bull trout were also located in subbasins containing 2.5 times fewer roads and threefold lower levels of forest harvesting compared with sites in subbasins where bull trout were not detected (Table 5).

Evaluating the cumulative effects of industrial activity on the abundance of bull trout

Bull trout were absent from many stream reaches relative to that expected from a standard Poisson distribution. Visual examination of the data combined with a variance to mean ratio test showed an overdispersion of zero-count data (variance to mean ratio = 9.67), suggesting that variance in abundance data should be analysed using a ZIP regression model.

Results from ZIP regression models indicated that bull trout abundance was positively related to elevation but negatively related to wetted width, percent fines, percent cobble, reach slope, and percent harvesting (Table 6). All models

Table 5. Characteristics of the 172 stream reaches surveyed for bull trout (*Salvelinus confluentus*) in the Kakwa River basin.

	Bull trout observed (N = 75)			Bull trout not observed (N = 97)		
Variable	Mean	SD	Range	Mean	SD	Range
Elevation (m above sea level)	1266.3	167.6	932.5–1663.7	1189.5	220.4	758.7–1855.9
Width (m)	5.0	3.1	1–15	3.6	2.6	1–12
Slope	0.03	0.02	0–0.07	0.03	0.03	0–0.13
Percent fines	8.4	11.9	0–77	24.5	27.8	0–100
Percent cobble	32.0	13.6	2–73	24.7	15.6	0–63.0
Road density ($km \cdot km^{-2}$)	0.11	0.15	0–0.60	0.27	0.32	0–1.59
Percent harvested	5.0	10.0	0–41	15.0	14.0	0–45

Note: N is the number of stream reaches where bull trout were observed and where bull trout were not observed. Slope was determined as rise/run.

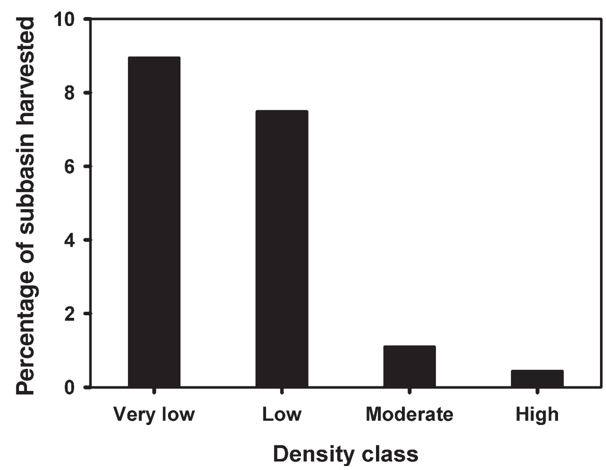
Table 6. Summary of the five most parsimonious zero-inflated Poisson (ZIP) regression models predicting the abundance of bull trout (*Salvelinus confluentus*) in the Kakwa River basin.

Model	Variable	Coefficient	SE	Δ_i	w_i
1	Intercept	–0.100	0.672		
	Elevation	0.002	0.000		
	Width	–0.041	0.025		
	Percent fines	–0.022	0.007	0.00	0.64
	Percent cobble	–0.019	0.004		
	Slope	–5.240	4.102		
	Percent harvested	–3.209	1.238		
2	Intercept	–0.115	0.674		
	Elevation	0.002	0.000		
	Width	–0.041	0.025	1.8	0.26
	Percent fines	–0.023	0.007		
	Percent cobble	–0.019	0.005		
	Slope	–5.126	4.079		
	Density of roads	0.317	0.481		
	Percent harvested	–3.510	1.332		
3	Intercept	–0.939	0.602		
	Elevation	0.004	0.001		
	Width	–0.039	0.024	5.0	0.05
	Percent fines	–0.020	0.007		
	Percent cobble	–0.019	0.004		
4	Intercept	–0.779	0.620		
	Elevation	0.003	0.001		
	Width	–0.046	0.025	6.2	0.03
	Percent fines	–0.022	0.007		
	Percent cobble	–0.020	0.005		
	Slope	–3.981	4.008		
5	Intercept	–0.713	0.636		
	Elevation	0.003	0.001		
	Width	–0.047	0.025	8.1	0.01
	Percent fines	–0.021	0.007		
	Percent cobble	–0.020	0.005		
	Slope	–4.171	4.051		
	Density of roads	–0.212	0.450		

Note: Models were selected using Akaike's Information Criterion corrected for small sample sizes (AIC_c). Δ_i, ΔAIC_c; w_i, Akaike weights. All models are statistically significant (Vuong statistic, $p < 0.05$). The zero-count portions of all the ZIP regression models were inflated against the most parsimonious logistic regression model described from all 172 sites.

showed a high significance for the Vuong statistic ($p < 0.01$) supporting use of the inflation (ZIP) model. Surprisingly, our suite of ZIP regression models identified both positive and negative relations between bull trout abundance and road density (Table 6).

Fig. 3. Comparisons of the mean percentage of forest harvesting in subbasins located upstream of reaches supporting very low to high densities of bull trout (*Salvelinus confluentus*) in the Kakwa River basin. Density classes were delineated based on the four quartiles of overall density estimates within the entire Kakwa basin. Bull trout density classes: very low, <0.08 individual·100 m^{-2}; low, 0.08–0.25 individual·100 m^{-2}; moderate, 0.26–0.75 individual·100 m^{-2}; high, >0.75 individual·100 m^{-2}.

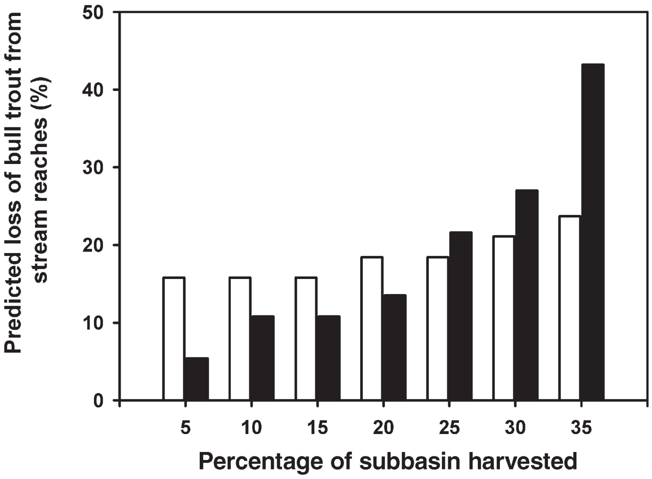


Forecasting future impacts of industrial activity

We observed marked differences in levels of forest harvesting in subbasins that supported very low to high densities of bull trout. Stream reaches that supported very low and low densities of bull trout were located in subbasins where levels of forest harvesting were at least sevenfold higher than those that supported moderate and high densities of bull trout (Fig. 3). Current levels of forest harvesting in subbasins supporting very low densities of bull trout were similar to those in subbasins supporting low densities of bull trout but markedly different from those supporting moderate and high densities of bull trout. As a result, we forecasted the impacts of increasing levels of forest harvesting on the occurrence of bull trout in stream reaches that currently support low (i.e., very low and low densities of bull trout) and high (i.e., moderate and high density classes of bull trout) densities of bull trout.

Using data from logistic regression models, forest harvesting forecasted over the next 20 years is projected to result in

Fig. 4. Predicted loss of bull trout (*Salvelinus confluentus*) from stream reaches resulting from increasing levels of forest harvesting in the Kakwa River basin. Data describe the percentage of stream reaches currently supporting very low and low (open bars) and moderate and high (solid bars) densities of bull trout that are expected to become locally extirpated under increasing levels of forest harvesting over the next 20 years. Bull trout density classes: very low and low, <0.25 individual·100 m^{-2}; moderate and high, >0.25 individual·100 m^{-2}.



the local extirpation of bull trout in 24%–43% of stream reaches depending on whether stream reaches currently support low or high densities of bull trout (Fig. 4). Increases in forest harvesting from 5% to 35% of individual subbasins are projected to result in local extirpations of bull trout from 16% to 24% of stream reaches that currently support low densities of bull trout. In contrast, local extirpations of bull trout from stream reaches that currently support high densities of fish are projected to increase dramatically from 5% under low levels of forest harvesting (i.e., 5% of subbasins harvested) to 43% of all stream reaches when 35% of individual subbasins are harvested (Fig. 4).

Discussion

General patterns in bull trout occurrence and abundance

Based on data from minimally impacted subbasins, our results indicated that bull trout occurrence was highly predictable from a relatively small set of environmental variables measured at the stream and subbasin scales. The majority of logistic regression models showed that bull trout occurrence was positively related to elevation and wetted width and negatively related to percent fines and slope. Bull trout were encountered most often at elevations of 1200–1600 m above sea level where stream reaches ranged from 2 to 8 m and that contained a paucity of fine sediments in the substratum. Results from ZIP regression models showed that bull trout abundance was positively related to elevation and negatively related to wetted width, percent cobble, percent fines, and reach slope. The negative relation between bull trout abundance and stream wetted width suggests that small streams support higher densities of bull trout than larger streams.

The majority of stream reaches supporting bull trout were located in third- and fourth-order streams located in the upper reaches of individual subbasins that provide spawning habitats in the Kakwa River basin (P. Hvenegaard, Alberta Conservation Association, 9621-96 Avenue, Peace River, AB T8S 1T4, Canada, unpublished data). These stream reaches are typically most strongly influenced by groundwater primarily in areas with topographic knickpoints (i.e., abrupt changes in the longitudinal profile of a stream valley) where elevation changes are substantial (Baxter and Hauer 2000). These stream reaches also provide continuous water flow during the prolonged winter months even at high elevations at northern latitudes of ~54° where surface ice is typically present between November and May.

Negative relations between bull trout occurrence and fine sediments and positive relations with elevation have been previously reported (Rieman and McIntyre 1995; Watson and Hillman 1997; Baxter et al. 1999). For example Watson and Hillman (1997) reported that bull trout occurred more frequently in sites with boulder and cobble substrata than in those dominated by bedrock and fine bed materials. They also reported an inverse relation between bull trout presence and fine sediments in turbulent fast-water habitats. Paul and Post (2001) observed bull trout to occur exclusively between 1500 and 1850 m above sea level in streams from the east slopes of the Canadian Rocky Mountains. Our results indicated that the vast majority of bull trout were present in reaches of third- and fourth-order streams located at elevations of 950–1600 m above sea level but were seldom (4 of 172 sites) encountered in streams, irrespective of their size, outside this elevational range.

The inverse relation between bull trout and fine sediments may arise from the negative effects of fine sediments on invertebrate abundance (e.g., Birtwell 1999; Shaw and Richardson 2001) and trophic effects on the abundance of insectivorous fish species (e.g., mountain whitefish) that are preyed upon by bull trout (P. Hvenegaard, Alberta Conservation Association, Peace River, AB T8S 1T4, Canada, unpublished data), reduced foraging and physiological performance (Waters 1995; Newcombe and Jensen 1996; Shaw and Richardson 2001), or deposition of fines that could alter exchanges at the groundwater–surface water interface (Baxter et al. 1999; Baxter and Hauer 2000). In contrast, we expect that the positive relation between bull trout occurrence and elevation is most likely related to thermal preferences and spawning requirements of bull trout (Selong et al. 2001; Dunham et al. 2003; Kishi et al. 2004).

Evaluating the cumulative effects of industrial activity

We evaluated the cumulative effects of industrial activity on bull trout by determining whether the two metrics that define cumulative levels of industrial activity of, (*i*) percentage of commercial forest harvesting in the subbasin and (*ii*) road density in the subbasin, explained variance in the occurrence and abundance of bull trout. Industrial activity occurs predominantly in the lower two-thirds of the Kakwa River watershed. As a result, we restricted our analyses of the occurrence and abundance of bull trout, measured at individual stream reaches, to those in subbasins located within a relatively narrow range of elevations.

The occurrence and abundance of bull trout from 172 stream reaches, including those influenced by appreciable levels of industrial activity, were also highly predictable from the small suite of environmental variables. In addition to other variables, the occurrence of bull trout was inversely related to (*i*) percentage of commercial forest harvesting in the subbasin and (*ii*) road density in the subbasin. Both results may appear to be somewhat surprising given the relatively low levels of forest harvesting (overall mean = 6.3% of individual watersheds) and road density (<0.2 km·km^{-2}) in the entire basin. However, when expressed at a smaller spatial scale, the percentage of individual subbasins subjected to commercial forest harvesting often exceeded 20% and road densities often exceeded 1.0 km·km^{-2}.

The majority of forest harvesting was initiated since the 1980s and has resulted in multiple forest harvest cut blocks of varying ages in the majority of the moderate-sized to larger subbasins. Our pairwise comparisons showed that mean levels of timber harvesting and road densities at sites that supported bull trout (harvesting = 5.0%, road density = 0.11 km·km^{-2}) were at least twofold lower than those where bull trout were absent (harvesting = 15.0%, road density = 0.27 km·km^{-2}). Although the percentage of forest harvesting and road density were important variables in many regression models, they were seldom the most important variables explaining variance in bull trout occurrence; similar results have been found for the majority of fish species in the Kakwa River watershed (Scrimgeour et al. 2003). We expect that the presence of percent forest harvesting and road density as statistically significant variables explaining variance in the occurrence and abundance of bull trout likely represents an early warning indicator of more profound impacts should current watershed management practices continue.

Industrial activities related to harvest blocks and the development of road networks can influence bull trout occurrence through a variety of pathways. Depending on the spatial scale, ecological region, and harvest practices, timber harvesting can increase water yields for several decades (e.g., Swanson and Hillman 1977; Hicks et al. 1991; Jones and Grant 1996). For instance, Swanson and Hillman (1977) reported annual water yield increases of 20%–30% and peak storm flow increases four to five times higher than normal after clearcut logging. Elevated water can alter the configuration of instream habitats and result in nutrient pulses (Carignan et al. 2000; Martin et al. 2000) that can alter food web structure. Harvesting practices that leave narrow (30–60 m) nonharvested riparian buffers (Alberta Environmental Protection 1994) may not fully mitigate removal of mature forest and result in elevated thermal inputs (Teti 1998), especially when the performance of nonforested buffers are compromised by wind-throw. Lastly, it is possible that forest harvesting could alter stream thermal regimes if warmer shallow surface runoff flow moderates the cooling influence of groundwater-dominated stream flow.

In contrast, road networks increase sediment inputs to streams initially during road construction and subsequently through runoff from the road surface and road approaches. Several years are required to fully establish vegetation that reduces transport of sediments from road margins into the stream channel. Perhaps more importantly, poorly designed and installed stream crossings, such as culverts, can fragment stream habitats (e.g., Warren and Pardew 1998; Tchir et al. 2004) and potentially pose substantial risk to population viability (Morita and Yokota 2002). Interestingly, both road density and percent forest harvesting were positively related to percent fines and suggest that the impacts of industrial activities on bull trout may be mediated to some extent through increased sediment inputs.

Roads networks can also increase inputs of solar radiation through removal of riparian vegetation, whereas improperly installed and maintained stream crossings can fragment stream habitats (Reid and Dunne 1984; Eaglin and Hubert 1993; Warren and Pardew 1998). Bull trout spawn in tributaries of the Kakwa River in the late fall when flow is typically low, and under these conditions, culvert outflows that are perched above the water surface (i.e., hanging culverts) can represent obstacles to their upstream movements. Interestingly, Baxter et al. (1999) reported significant declines in the abundance of bull trout spawning redds with road densities of 0.1 km·km^{-2}. While road networks provide increased access to anglers, we do not think that angling is a primary determinant of the inverse relation between road density and bull trout presence because angling effort in the Kakwa basin is generally low and angling effects are reduced by a catch-and-release provincial regulation. Lastly, studies such as ours are correlative in nature and provide only insights to the underlying mechanisms through which industrial activities influence bull trout. Additional studies that identify the causal mechanisms underlying the negative relations between forest harvesting and road networks on the occurrence and abundance of bull trout inhabiting boreal ecosystems are urgently required.

Forecasting the effects of continued forest harvesting on bull trout

Our logistic regression models revealed a negative relation between bull trout occurrence and cumulative levels of forest harvesting in individual subbasins. We used the results of the most parsimonious logistic regression model to forecast effects of increasing forest harvesting on local extirpations of bull trout from stream reaches that currently support bull trout. These analyses suggest that increases in forest harvesting are predicted to be accompanied by increasing levels of local extirpations of bull trout from stream reaches in the Kakwa River basin. Harvesting of 35% of individual subbasins is projected to result in the extirpation of bull trout from between 24% and 43% of all stream reaches that currently support bull trout and is expected to be most pronounced for reaches that support moderate and high densities of bull trout (density range > 0.25 individual·100 m^{-2}). Perhaps the most disturbing aspect of these analyses is our prediction that extirpations of bull trout from sites that currently support moderate and high densities of bull trout are projected to increase disproportionately with forest harvesting. This relation resembles a nonlinear accelerating function when forest harvesting within individual subbasins increases from the current level of ~6.3% to 35%, which may be attainable in many smaller watersheds within 20 years. The extent that projected extirpations in bull trout result from increases in forest harvesting may not be apparent for another decade. However, such effects question the long-term viability of bull trout in the Kakwa River basin, especially if such changes dramatically alter metapopulation dynamics (Dunham and Reiman 1999).

Taken together, our data suggest that the occurrence of bull trout in the Kakwa River basin is negatively related to two metrics indicative of industrial activity (i.e., percent forest harvesting and road density). If our projections are correct, increases in forest harvesting up to 35% of individual watersheds is expected to result in the local extirpations of bull trout from up to 43% of stream reaches and that these levels of extirpation may occur within 20 years. The extent to which similar levels of industrial development alter other populations of bull trout in the east slopes of the Rocky Mountains is poorly understood but is required to better understand landscape-level influences of an increasing industrial footprint (Grant et al. 1986; Ziemer et al. 1991; McGarigal et al. 2001). As advocated by Dunham et al. (2003), we urge resource managers to consider retaining large, interconnected cold-water habitats, such as that in the Kakwa River watershed, as an integral part of a conservation plan for bull trout in Alberta. This conservation plan would benefit from the development of an effective monitoring program capable of detecting changes in the distribution and abundance of bull trout and their relation to increases in industrial activities.

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