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ARTICLE

Estimating occupancy and detection probability of juvenile bull trout using backpack electrofishing gear in a west-central Alberta watershed

Mike C. Rodtka, Chad S. Judd, Peter K.M. Aku, and Kevin M. Fitzsimmons

Abstract: Occupancy modeling is well suited to quantitative assessment of bull trout (*Salvelinus confluentus*) distribution at multiple scales. We used models to estimate occupancy of juvenile bull trout (≤150 mm fork length) in a west-central Alberta watershed. Based on a backpack electrofishing survey of 92 sites, we assessed the relative importance of stream habitat characteristics on detection probability (p) and potential for false absences to bias occupancy estimates. Median distance to first bull trout detection was 16 m (range 0–289 m). Models including ambient water conductivity as a covariate of detection probability were most supported with an 85 $\mu S \cdot cm^{-1}$ increase resulting in over a tenfold increase in detection. Conditional detection probability using backpack electrofishing gear approached 95% in the first 200 m of effort in streams with a conductivity around 200 $\mu S \cdot cm^{-1}$. The potential for false absences in our study area was relatively low. Modeled site ($\hat{\theta}$ = 0.53; SE = 0.13) and patch-scale ($\hat{\Psi}$ = 0.47; SE = 0.12) occupancy closely corresponded to naive (i.e., assuming p = 1) estimates (0.47 and 0.43, respectively). Our results highlight the potential efficiencies of an occupancy modeling approach when assessing fish distribution, but careful consideration of model assumptions is necessary.

Résumé : La modélisation de l'occupation se prête bien à l'évaluation quantitative de la répartition des ombles à tête plate (*Salvelinus confluentus*) à différentes échelles. Nous avons utilisé des modèles pour estimer l'occupation des ombles à tête plate juvéniles (longueur à la fourche ≤150 mm) dans un bassin versant du centre-ouest de l'Alberta. À la lumière de levés par pêche électrique à l'aide d'engins dorsaux dans 92 sites, nous avons évalué l'importance relative des caractéristiques d'habitats lotiques en ce qui concerne la probabilité de détection (p) et la possibilité que de fausses absences biaisent les estimations d'occupation. La distance médiane avant la première détection d'un omble à tête plate était de 16 m (fourchette de 0 m à 289 m). Les modèles intégrant la conductivité ambiante de l'eau comme covariable de la probabilité de détection performaient le mieux, une augmentation de 85 $\mu S \cdot cm^{-1}$ se traduisant par la multiplication par plus de dix de la détection. La probabilité de détection conditionnelle à l'aide de l'engin de pêche électrique dorsal approchait les 95 % dans les premiers 200 m d'effort dans les cours d'eau présentant une conductivité de l'ordre de 200 $\mu S \cdot cm^{-1}$. Le potentiel de fausses absences dans la région à l'étude était relativement faible. L'occupation modélisée à l'échelle du site ($\hat{\theta}$ = 0,53; SE = 0,13) et de la parcelle ($\hat{\Psi}$ = 0,47; SE = 0,12) correspondait étroitement aux estimations naïves (0,47 et 0,43, respectivement, en présumant que p = 1). Nos résultats soulignent les gains d'efficacité possibles découlant d'une approche de modélisation de l'occupation pour l'évaluation de la répartition de poissons, un examen soigneux des hypothèses qui sous-tendent de tels modèles étant toutefois nécessaire. [Traduit par la Rédaction]

Introduction

Assessed as Threatened in the coterminous United States (USFWS 2008) and Alberta (Saskatchewan–Nelson rivers populations; COSEWIC 2012), bull trout (*Salvelinus confluentus*) are considered particularly sensitive to habitat change and are thought to reflect general ecosystem health (COSEWIC 2012), and their widespread decline is cause for concern. However, assessment of bull trout status has been hampered by a lack of standardized protocols for quantifying species distribution and abundance at a watershed scale (USFWS 2008; COSEWIC 2012). Current assessment protocols often focus on estimating fish abundance either directly (e.g., electrofishing, snorkel surveys) or indirectly (e.g., visual counts of redds) (USFWS 2008; COSEWIC 2012), but the patchy distribution of bull trout, variable habitat use, and demographic stochasticity make timely detection of meaningful trends in abundance difficult (Ham and Pearsons 2000; Al-Chokhachy et al. 2009). Estimates of abundance or its underlying processes (survival and reproduction) are also expensive to acquire, require extensive field surveys, and often involve the capture and marking of individuals (Al-Chokhachy et al. 2009; Noon et al. 2012). The various sampling methods used to capture and enumerate bull trout are also subject to a variety of biases, further complicating the issue (COSEWIC 2012).

The presence–absence or area occupied approach (Marsh and Trenham 2008) is an increasingly popular alternative to estimating abundance when monitoring wildlife populations. This approach involves estimation of the proportion of an area (or habitats within an area) that is occupied by a target species (MacKenzie et al. 2006). Given the difficulty of monitoring bull trout abundance, occupancy estimation appears to provide an attractive alternative for assessment of the species at the watershed scale. Indeed, assessment of the geographic distribution of bull trout is included in both the USFWS and COSEWIC status assessments (USFWS 2008; COSEWIC 2012). The detection–nondetection data

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M.C. Rodtka and C.S. Judd. Alberta Conservation Association, P.O. Box 336, Rocky Mountain House, AB T4T 1A3, Canada.
P.K.M. Aku. Alberta Conservation Association, Sherwood Park, AB T8A 6J7, Canada.
K.M. Fitzsimmons. Alberta Conservation Association, Cochrane, AB T4C 1B4, Canada.
Corresponding author: Mike C. Rodtka (e-mail: mike.rodtka@ab-conservation.com).

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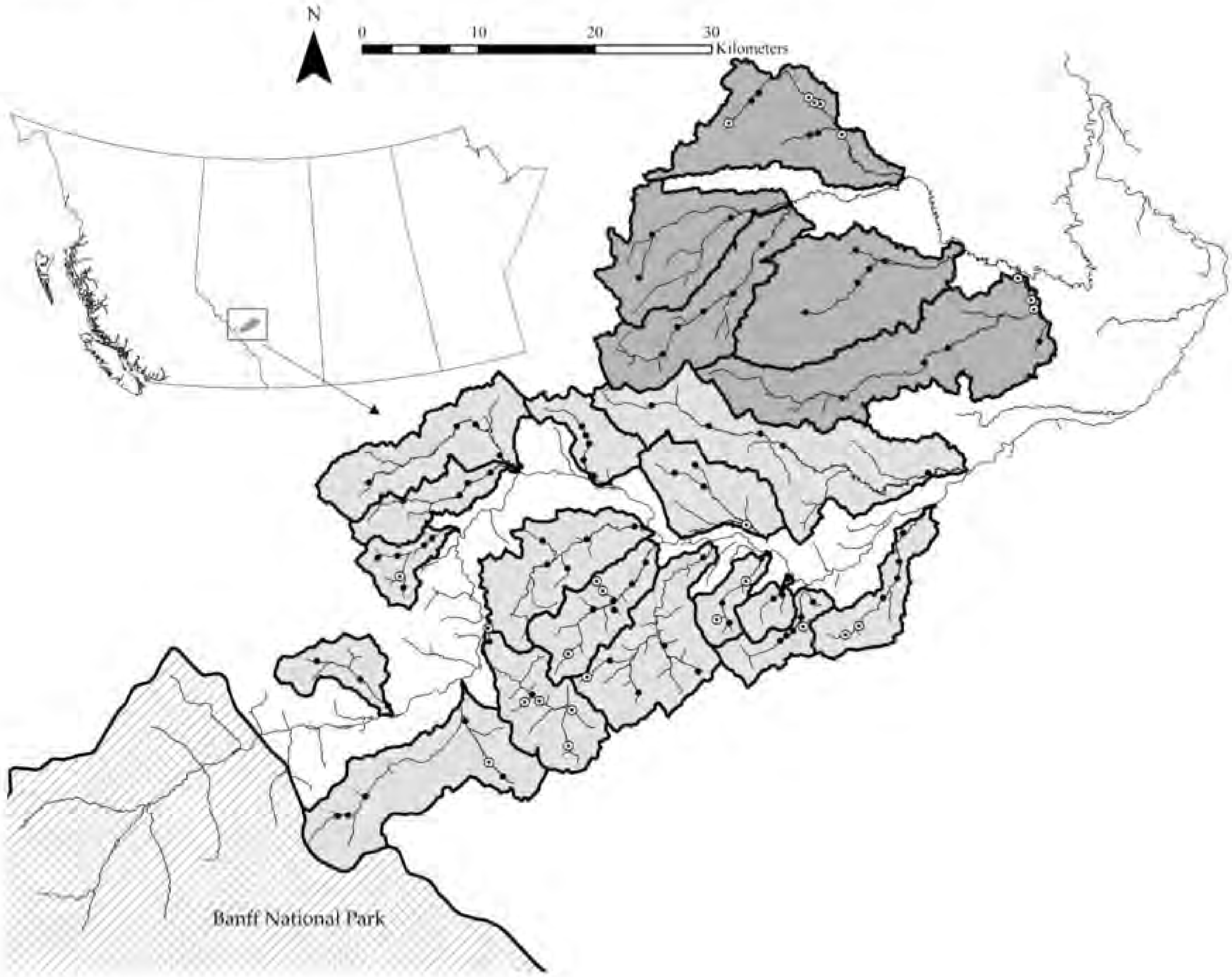
Fig. 1. Location of the 21 patches and 92 sample sites (solid circles) and 25 nonresponse sites (open circles with center dot) in the Clearwater River study area in west-central Alberta, Canada. Patches in the Prairie Creek drainage are shaded darker.



required by this approach are relatively inexpensive to acquire, may include historical survey data, and can be gathered through multiple methods (Noon et al. 2012). Of concern with this type of data are accounting for the imperfect detection of the species, the so-called false absence rate (MacKenzie et al. 2006), but survey design, statistical methods, and interpretation of distribution data based on patterns of species detection and nondetection have advanced considerably in the past decade (Marsh and Trenham 2008; Noon et al. 2012). Specifically, MacKenzie et al. (2002) describe a model and likelihood-based method for estimating site occupancy rates when detection probabilities are <1, which has subsequently been extended and adapted to a wide variety of sampling situations and ecological questions (Noon et al. 2012).

We used occupancy estimation and modeling to assess the distribution of juvenile bull trout (≤150 mm fork length; FL) within our study area and the factors affecting their detection. The potential for false absences when sampling juvenile and small stream resident bull trout may be great. Bull trout, especially juvenile fish, are cryptic and often occur at low densities in complex habitats where sampling conditions are challenging (Thurow and Schill 1996; Al-Chokhachy et al. 2009, 2010). Many early bull trout monitoring programs either failed to explicitly address false absences or assumed a (typically low) false absence rate (but see Peterson and Dunham 2003). Objectives of our study were to (*i*) assess the relative importance of readily obtained stream habitat measurements on juvenile bull trout detection using electrofishing gear and (*ii*) assess the potential for false absences to bias estimation of juvenile bull trout occupancy at the watershed scale. Recognizing the relatively limited use of these models in fisheries currently, we outline our study design and analysis in detail, allowing others to assess the utility of the approach.

Materials and methods

Study area

The Clearwater River is a sixth-order tributary to the North Saskatchewan River in west-central Alberta, Canada (Fig. 1). It occurs within the Rocky Mountain and Foothills natural regions of Alberta (Natural Regions Committee 2006), is 200 km in length, and drains an area of approximately 3200 km^2. The upper 28 km of the river occurs in Banff National Park where land-use activities are severely restricted. Land use downstream of Banff National Park includes recreational, livestock grazing, oil and gas, and forestry activities. Agricultural and residential land use increases in the lower watershed where land is principally under private ownership. Bull trout are native to the watershed and historically were the only widely distributed "trout", although brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) were introduced to the area by the 1950s and have established naturalized populations throughout much of the watershed (Rhude and Stelfox 1997). Despite protective regulations, beginning with the closure of spawning and rearing tributaries to angling in 1976 and including a harvest ban in 1995 (Rhude and Stelfox 1997), the Clearwater River bull trout population is considered High Risk of extirpation (Alberta Sustainable Resource Development and Alberta Conservation Association 2009).

Patch delineation and sample site selection

We divided our study area into sample units using a patch-based approach following Isaak et al. (2009). The narrow habitat requirements of bull trout, especially cold-water habitat for successful spawning and rearing, make patch-based assessments of bull trout distribution particularly appropriate (Dunham and Rieman 1999; Isaak et al. 2009). Our patches broadly identified suitable habitats for juvenile bull trout. Emphasis was placed on the juvenile life stage, as these fish may be more indicative of a local population than adults (Isaak et al. 2009). We considered an area occupied upon capture of at least one juvenile bull trout.

We used Strahler stream order (Strahler 1952) and stream elevation to define patches within the Clearwater River watershed. Both stream size (Rieman and McIntyre 1995; Rich et al. 2003; Ripley et al. 2005) and elevation (Paul and Post 2001; Ripley et al. 2005; McCleary and Hassan 2008) have been positively associated with bull trout occurrence. We defined bull trout patches as all third- to fifth-order streams (1:20 000 scale), any portion of which occurred above 1399 m elevation. Our elevation threshold corresponds to the approximate elevation at which maximum summer water temperature is predicted not to exceed 16 °C and defines habitats considered highly thermally suitable for bull trout (Isaak et al. 2009 and references therein). We developed linear regressions relating maximum summer water temperature to stream elevation to derive the thresholds. Regressions were based on stream temperature monitoring using data loggers distributed throughout the watershed during the summers of 2010 ($n = 13$, $r^2 = 0.58$) and 2011 ($n = 11$, $r^2 = 0.41$). A separate threshold (1149 m) was developed for Prairie Creek, a sixth-order tributary to the Clearwater River, as it exhibited a strong groundwater influence ($n = 6$ and $r^2 = 0.99$, 0.96; summers of 2010 and 2011, respectively). Patches were created using a geographical information system (GIS; ArcGIS version 10.1) and the Government of Alberta Resource Management Information Branch hydro line and flow-corrected digital elevation (25 m resolution) data layers. Of the 23 resulting patches, two were removed from the study: one occurred almost entirely within Banff National Park, where access is restricted; the other was dry at time of sampling. Mean (±SD) and minimum catchment area of the remaining patches (81.5 ± 49.2 km^2 and 17.6 km^2, respectively) were well above the minimum patch size at which bull trout occurrence may be expected (Rieman and McIntyre 1995; Dunham and Rieman 1999).

We distributed prospective sample sites at 1 km intervals in an upstream progression along the length of third- to fifth-order streams within a patch using a GIS. Sites were randomly selected without replacement from within each patch using a generalized random tessellation stratified (GRTS) design (Stevens and Olsen 2004). Sites were visited in the order in which they were drawn until a total of five sites had been sampled or nine sites visited, within each patch. Our target sample size for each patch was based on a power analysis using data collected during a pilot study in 2010, with the goal of achieving a false absence rate ≤0.2 (M.C. Rodtka, unpublished data). A subset of sample sites were inaccessible (i.e., greater than 1 km from the nearest motorized access point using truck, off-highway vehicle, or helicopter; $n = 17$) or too deep to safely wade ($n = 8$). The GRTS sampling design allowed us to dynamically adjust our sample size to accommodate these nonresponse sites while maintaining a spatially balanced sample (Stevens and Olsen 2004). Dry sites ($n = 11$) were included as response sites but removed from subsequent analyses. Stream habitat measurements at the remaining 92 sites (Table 1) were typically within the range deemed suitable for bull trout (Al-Chokhachy et al. 2010; COSEWIC 2012).

Sampling methods

We sampled sites from June to August 2011 and 2012. A handheld global positioning system (GPS) was used to locate sample sites in each patch. All site sampling commenced at the head of riffle habitat. Sample sites were 250 m long (measured with a hip chain) or 50 times the mean wetted width (Reynolds et al. 2003) rounded to the nearest 50 m, whichever was greater. We set maximum site length at 500 m (mean site length ± SD; 271 ± 56 m). Sites were sampled using a Smith-Root LR-20 or 12-B backpack electrofisher with pulsed DC (voltage 300–1000 V, frequency 30–60 Hz, and duration 2–11 ms). We adjusted electrofisher settings at each site according to water conditions and fish response. Adjustments were made to achieve a minimum input current of 4 amps as indicated by the audio output voltage indicator on the backpack unit and illicit a forced swimming response in the fish. Each site was sampled in a single pass with a two-person crew (one dipnetter and one electrofisher operator, determined randomly at the start of each site) working in an upstream direction. Fish were identified to species, enumerated, and measured (FL, mm), and electrofishing effort (seconds) was recorded at 50 m intervals within a site. We also measured the length of stream sampled to first capture of a juvenile bull trout.

Table 1. Stream habitat characteristics of the 92 sample sites surveyed June to August 2011 and 2012 for juvenile bull trout occurrence in the Clearwater River study area.

	Mean±SD	Median	Mode	Range
Temperature (°C)	8.9±3.0	—	—	3.6–21.0
Wetted width (m)	4.0±2.0	—	—	0.8–10.5
Conductivity (μS·cm^{-1})	201.5±85.5	—	—	28.0–474.0
Dominant substrate score	—	3	3	0–3
Undercut bank count	—	1	0	0–5
Stream cross-section (m^2)	1.07±0.78	—	—	0.12–3.36
Cover score	—	1	1	0–3

At all sites we measured water temperature (0.1 °C) and ambient conductivity (i.e., conductivity at ambient water temperature; 0.1 μS·cm^{-1}) prior to electrofishing. We measured stream depth (0.01 m) and wetted width (0.1 m) and visually assessed dominant substrate along transects spaced every 25 m. Water depth and dominant substrate type were assessed at three stations per transect: 1/4, 1/2, and 3/4 wetted width (1/2 only where wetted width ≤1 m). Stream cross-sectional area was calculated at each transect by multiplying mean station depth by wetted width. Substrate categories were scored based on a modified Wentworth (1922) scale and included fines (<2 mm; score 0), small gravel (2–16 mm; 1), large gravel (17–64 mm; 2), cobble (65–256 mm; 3), boulder (>256 mm; 4), and bedrock (5). Presence of an undercut was assessed at each transect for each bank and scored as yes (1) or no (0). Undercuts were defined as being at least 5 cm deep and <25 cm above the water surface. We assessed stream cover between transects qualitatively using a modification of the Environemntal Protection Agency (EPA) rapid bioassessment protocol (Barbour et al. 1999). Cover was scored as poor (<20%; 0), marginal (20%–40%; 1), suboptimal (40%–70%; 2), or optimal (>70%; 3).

Occupancy modeling

Study designs for occupancy estimation require repeated surveys of a sample unit to estimate the probability of detection (MacKenzie et al. 2006). The repeated surveys may be represented by temporal replication at discrete time occasions, replication of different observers, or spatial replication at separate locations (MacKenzie et al. 2006). For logistical reasons we used spatially replicated surveys exclusively, a common approach for large-scale studies such as ours (Pavlacky et al. 2012). However, estimating detection from spatially replicated surveys can result in biased estimates (Kendall and White 2009; Hines et al. 2010), as the models assume species detections between sites are independent (MacKenzie et al. 2006). To deal with this potential lack of independence, we used models that decompose the observation processes into detection and availability probabilities (Hines et al. 2010; Pavlacky et al. 2012). In addition to the independence of detections between sites, models assume no unmodeled heterogeneity in the probabilities of detection and occupancy, each sample site is closed to changes in occupancy over the sampling

Table 2. Stream habitat variables included in spatially dependant occupancy modeling and hypothesized relationship to juvenile bull trout electrofishing detection probability (p).

Covariate of detection probability	Description
cond	Ambient stream conductivity (μS·cm^{-1}); electrofishing efficiency generally increases with conductivity over the conductivity range observed in our study (Hense et al. 2010; Reynolds and Kolz 2012).
cs	Cross-sectional stream area (m^2); electrofishing efficiency decreases with increasing stream area (Peterson et al. 2004).
cover	Fish cover, qualitative assessment using a four-point scale; electrofishing efficiency decreases with increasing volume of rootwads (Rodgers et al. 1992).
sub	Dominant substrate size, qualitative assessment using a five-point scale; electrofishing efficiency decreases with increasing substrate size (Peterson et al. 2004).
uc	Undercut bank count; electrofishing efficiency decreases with increased incidence of undercut banks (Peterson et al. 2004).

period, and that the target species are never falsely detected (MacKenzie et al. 2006).

We used Hines et al.'s (2010) spatial-dependence model to assess habitat effects on juvenile bull trout detection at our sample sites. Detection and habitat data from 50 m segments of each sample site were used as spatial replicates for the analysis. Model parameterization allowed us to estimate the probability a site is occupied (Ψ) and the probability of detection given the site is occupied and the species is present on the segment (p). Availability parameters θ (probability the species is present on a segment given the site is occupied and the species is not present on the previous segment) and θ' (probability the species is present on a segment given the site is occupied and the species is present on the previous segment) are also included in the model (Hines et al. 2010). We identified five readily obtained, site-scale, stream habitat variables that we hypothesized may influence detection of bull trout for inclusion in our candidate set of models (Table 2).

All modeling was performed using program PRESENCE (Hines 2006). Parameters were estimated using a maximum likelihood approach; a logit link function was used to model the effect of covariates on parameters (MacKenzie et al. 2006). To distinguish the relative importance of our habitat measures on detection (p), each covariate was considered separately in our model set. We suspected that starting our sample sites at the head of a riffle may have biased p in Segment 1, so we included models where p_1 was allowed to vary from subsequent segments ($p_1 \neq p_{2...i}$); otherwise p was held constant. Occupancy (Ψ) and species availability parameters (θ, θ') were considered nuisance parameters and held constant (.) throughout. To test for spatial dependence in our dataset, we included the model [Ψ(.), $\theta = \theta'$, p(.)] (Hines et al. 2010). Thus, with five habitat measures, $p_1 \neq p_{2...i}$ and p(.) models, the test for spatial dependence, and global and null models, a total of 15 models were included in our candidate set. For all models, the option of estimating local presence before the first segment using θ and θ' was selected in the program PRESENCE.

We used Pavlacky et al.'s (2012) parameterization of Nichols et al.'s (2008) multiscale occupancy model to assess the potential for false absences to bias estimation of bull trout occupancy at the watershed scale. The multiscale model parameterization allowed us to estimate the probability of detection given the patch and sample site is occupied (p), the probability of occupancy of the sample site given the patch is occupied (θ), and the probability of patch occupancy (Ψ) (Pavlacky et al. 2012). Patches were selected based on their broad suitability as bull trout habitat, so we did not include any covariates of occupancy in our analysis. Given the sparseness of our dataset, we chose to include only those covariates of p contained in the top-ranked model(s) of the spatial-dependence analysis in our candidate set; θ was held constant throughout.

Sampling from spatially replicated surveys without replacement (as we did) can violate the closure assumption and bias occupancy estimates when the study design results in a species being unavailable for detection at a subset of survey locations (Kendall and White 2009). To address this potential bias, we treated our detection history data as though collected using a removal design when estimating multiscale occupancy (Pavlacky et al. 2012). The removal design implies surveys end after the first detection of a species within an occupied sample unit (MacKenzie et al. 2006), thereby avoiding unavailability at subsequent spatially replicated surveys. We simulated this within our dataset by treating all segments after the first at a site in which a bull trout was detected as missing data (MacKenzie et al. 2006; Pavlacky et al. 2012). Because the removal design requires a restrained parameterization where detection is held constant across survey occasions, an additional assumption of the removal design is a constant probability of detection (MacKenzie et al. 2006). To better meet this assumption, we binned our detection data into 100 m segments at each site. Binning the segments in this manner after setting all subsequent segments following the first detection to missing data resulted in an approximately monotonic decline in detection frequency, an indication of constant detection probability across segments (Pavlacky et al. 2012). The spatial-dependence model decomposes the observation process into detection and availability probabilities at the segment scale, so the removal design was not necessary for this model (Hines et al. 2010; Pavlacky et al. 2012).

All continuous covariate data were standardized to a mean of zero and standard deviation of one (MacKenzie et al. 2006) prior to analysis. We examined the fit of our global models using Pearson's χ^2 goodness-of-fit test (α = 0.05) and variance inflation factor ($\hat{c}$) (MacKenzie and Bailey 2004). Tests were nonsignificant and $\hat{c} \leq 1.0$ in all cases, so no adjustment of model selection procedures and inflation of standard errors was necessary (MacKenzie and Bailey 2004). Models were ranked using Akaike's information criterion corrected for small sample size (AIC$_c$) (Burnham and Anderson 2002). Use of AIC provides a method of ranking models; to encourage parsimony, this method applies a penalty for the number of parameters in the model (Burnham and Anderson 2002). We considered models with an AIC$_c$ score within two points (i.e., $\Delta_i \leq 2$) of the top-ranked model as receiving substantial support (Burnham and Anderson 2002). Criteria for determining effective sample size of any particular occupancy model have not been resolved (MacKenzie et al. 2006). We opted for a relatively conservative effective sample size defined as the number of sampling units included in the broadest scale analysis (i.e., n = 92 and 21 for the spatial-dependence and multiscale analyses, respectively). Following calculation of AIC$_c$, we estimated Akaike weights (w_i), which provide an approximate representation for the probability of a particular model fitting the data compared with the candidate set of models (Burnham and Anderson 2002). We used odds ratios (ORs) to examine covariate effects; OR 95% confidence limits (CLs) were calculated using the delta method (MacKenzie et al. 2006). ORs for a single unit of change were calculated as $\exp(\beta_i)$ (MacKenzie et al. 2006). An OR can range between zero and infinity;

Table 3. Model structure and summary statistics for the 15 spatial-dependence models of juvenile bull trout occupancy (Ψ) and stream habitat variables hypothesized to affect electrofishing detection probability (p).

Model	AIC_c	Δ_i	w_i	$-2\log(L)$	K
$\Psi(.)$, $\theta(.)$, $\theta'(.)$, $p_1 \neq p_{2...i}$(cond)	247.66	0.00	0.37	234.67	6
$\Psi(.)$, $\theta(.)$, $\theta'(.)$, p(cond)	248.01	0.35	0.31	237.31	5
$\Psi(.)$, $\theta(.)$, $\theta'(.)$, $p_1 \neq p_{2...i}$	251.04	3.38	0.07	240.34	5
$\Psi(.)$, $\theta(.)$, $\theta'(.)$, $p_1 \neq p_{2...i}$(uc)	251.70	4.04	0.05	238.71	6
$\Psi(.)$, $\theta(.)$, $\theta'(.)$, p(uc)	252.27	4.61	0.04	241.57	5
$\Psi(.)$, $\theta(.)$, $\theta'(.)$, $p_1 \neq p_{2...i}$(sub)	252.82	5.16	0.03	239.83	6
$\Psi(.)$, $\theta(.)$, $\theta'(.)$, $p_1 \neq p_{2...i}$(cs)	253.12	5.46	0.02	240.13	6
$\Psi(.)$, $\theta(.)$, $\theta'(.)$, $p_1 \neq p_{2...i}$(cover)	253.30	5.64	0.02	240.31	6
$\Psi(.)$, $\theta(.)$, $\theta'(.)$, $p(.)$	253.47	5.81	0.02	245.01	4
$\Psi(.)$, $\theta(.)$, $\theta'(.)$, p(cond, cover, sub, cs, uc)	254.30	6.64	0.01	234.10	9
$\Psi(.)$, $\theta(.)$, $\theta'(.)$, p(sub)	254.34	6.68	0.01	243.64	5
$\Psi(.)$, $\theta = \theta'$, $p(.)$	254.74	7.08	0.01	248.47	3
$\Psi(.)$, $\theta(.)$, $\theta'(.)$, $p_1 \neq p_{2...i}$(cond, cover, sub, cs, uc)	254.86	7.20	0.01	232.14	10
$\Psi(.)$, $\theta(.)$, $\theta'(.)$, p(cover)	254.92	7.26	0.01	244.22	5
$\Psi(.)$, $\theta(.)$, $\theta'(.)$, p(cs)	255.11	7.45	0.01	244.41	5

Note: θ = probability the species is present on a 50 m stream segment given the site is occupied and the species is not present on the previous segment; θ' = probability the species is present on a segment given the site is occupied and the species is present on the previous segment.

an OR less than one demonstrates that the response variable is less likely to occur, but if greater than one, the response variable is more likely to occur (MacKenzie et al. 2006). Unless otherwise specified, ORs from the top-ranked model within the candidate set are presented in our results. Reported cumulative detection probabilities were made conditional on species availability; cumulative probabilities were calculated using the general equation $1-(1-a)^b$, where a is the estimated parameter of interest from the top-ranked model, and b is the number of replicated units. The mean of θ and θ' was used for availability when calculating cumulative probabilities based on the spatial-dependence model.

Results

We sampled 498 segments of 92 sites in 21 patches during our study, capturing 112 juvenile bull trout. Of this effort, 313 segments (63%), 57 sites (62%) in 13 patches (62%) were sampled in 2011 resulting in the capture of 72 juvenile bull trout (64%); the remainder were sampled in 2012. Catch of juvenile bull trout ranged between 0.0 and 17.5 fish per 250 m site with a mean (±SD) catch of 0.92 (±2.75) fish per site.

Stream habitat effects on juvenile bull trout detection

We detected juvenile bull trout at 54 segments at 19 sites. Median distance to first detection of a bull trout was 16 m (range 0–289 m). Of the five habitat variables examined, water conductivity had the predominant effect on bull trout detection. Of the 15 models considered, only the top two shared a $\Delta_i \leq 2$, accounting for 68% of total model weighting (w_i) (Table 3); both models included water conductivity as a covariate of detection probability. Bull trout detection was approximately 11–14 times more likely for each SD (i.e., ≈85 $\mu S \cdot cm^{-1}$) increase in conductivity (Table 4). The relationship of remaining habitat covariates to detection probability was weak, with 95% CLs for all ORs including one. We found strong evidence for spatial dependence between 50 m segments with the $\theta = \theta'$ model receiving virtually no support. Presence of bull trout in the preceding segment approximately doubled the probability of their presence in the following segment (Table 5). Starting sampling immediately upstream of riffle habitat appears to have increased the probability of bull trout detection within the first 50 m of our sites. The top-ranked model included a variable detection probability with detection in the first 50 m (p_1) approaching 100% in occupied sites, but subsequently dropping to 72% thereafter ($p_{2...i}$) (Table 5). This variation helps explain why binning detections for the multiscale analysis improved the regularity of detection probability. Assuming a random start and

Table 4. Parameter estimates, standard errors (SE), odds ratio (OR), 95% confidence limits (CLs), and relative ranking of top-ranked models including water conductivity and four other habitat variables hypothesized to affect electrofishing detection probability (p) of juvenile bull trout.

	β			OR CLs		
Parameter	Estimate	SE	OR	Lower	Upper	Ranking
$p_1 \neq p_{2...i}$(cond)	2.42	2.13	11.20	0.17	722.68	1
p(cond)	2.64	1.28	14.06	1.15	172.49	2
$p_1 \neq p_{2...i}$(uc)	−0.30	0.22	0.74	0.48	1.14	4
$p_1 \neq p_{2...i}$(sub)	0.31	0.38	1.36	0.64	2.86	6
$p_1 \neq p_{2...i}$(cs)	−0.15	0.33	0.86	0.45	1.64	7
$p_1 \neq p_{2...i}$(cover)	0.07	0.39	1.07	0.50	2.28	8

Table 5. Comparison of back-transformed parameter estimates and standard errors (SE) of the top two ranked spatial-dependence models of electrofishing detection probability (p) of juvenile bull trout.

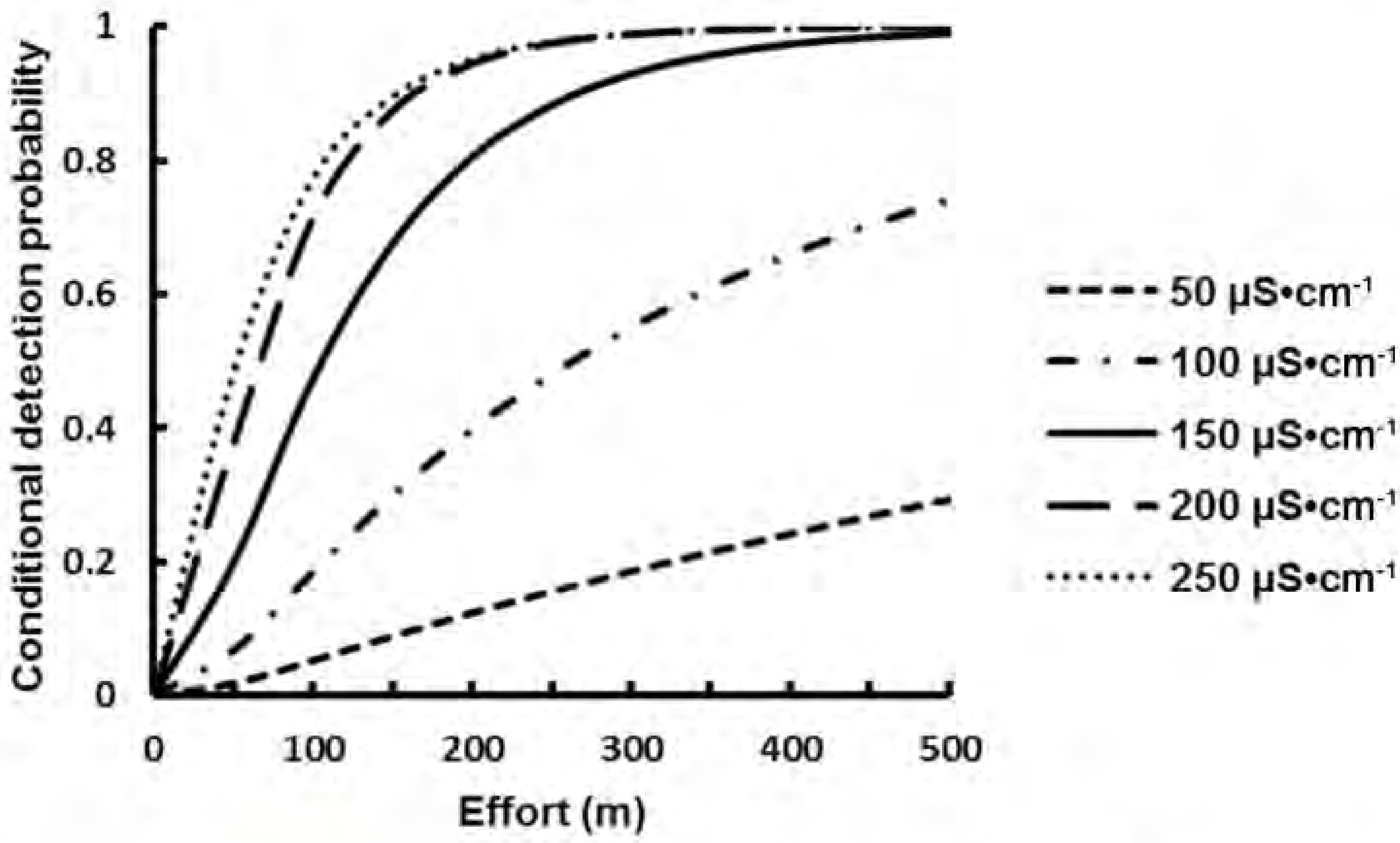
	$p_1 \neq p_{2...i}$(cond)		p(cond)	
Parameter	Estimate	SE	Estimate	SE
θ	0.34	0.15	0.38	0.11
θ'	0.72	0.21	0.68	0.14
p_1	0.96	0.15	—	—
$p_{2...i}$	0.72	0.37	0.82	0.19

mean water conductivity (i.e., ≈200 $\mu S \cdot cm^{-1}$; see Table 1), our top-ranked model predicts cumulative conditional detection probability of bull trout approached 95% within the first 200 m of effort (Fig. 2). At conductivities greater than 150 $\mu S \cdot cm^{-1}$, increasing site length beyond 200 m did relatively little to improve detection probability. Improvement in detection probability with increased effort at 50 $\mu S \cdot cm^{-1}$ was relatively modest, only approaching 30% after 500 m of sampling (Fig. 2).

Juvenile bull trout occupancy

We captured juvenile bull trout at 2.1 ± 1.1 (mean ± SD) of the sites sampled in the 9 (of 21) patches in which they were detected, corresponding to naive (i.e., assuming $p = 1$) site and patch occupancies of 47% ± 20% (mean ± SD) and 43%, respectively. The two multiscale occupancy models considered shared a $\Delta_i \leq 2$, indicat-

Fig. 2. Modeled relationship between conditional site detection probability of juvenile bull trout using backpack electrofishing gear as a function of stream distance (m) sampled at five different stream conductivities using spatial-dependence occupancy model: $\Psi(.)$, $\theta(.)$, $\theta'(.)$, $p_1 \neq p_{2...i}$(cond).



ing little support for one best model (Table 6). Although the null model was top-ranked, inclusion of water conductivity as a covariate of detection probability was essentially equally supported, receiving a model weighting of 50%. Estimated bull trout occupancies at the site and patch scales were only slightly higher than naive estimates. Bull trout occupied 53% of sites when present within a patch ($\hat{\theta}$ = 0.53; SE = 0.13) and 47% of patches ($\hat{\Psi}$ = 0.47; SE = 0.12). Estimated detection probability of the top-ranked, multiscale model was $\hat{p}$ = 0.59 (SE = 0.17), well above the threshold of 0.3 at which unbiased estimates of occupancy are expected (MacKenzie et al. 2002). Assuming 250 m sites and five sites per patch, our estimated conditional probability of detecting bull trout within a patch was nearly 88% (Fig. 3). Sampling more than three sites per patch did relatively little to improve detection probability, while detection dropped substantially when fewer than three sites were sampled (Fig. 3).

Discussion

Juvenile bull trout detection

An 85 μS·cm^{-1} increase in stream conductivity led to over an estimated tenfold increase in our probability of detection. As is typical of electrofishing surveys, we adjusted electrofisher settings according to water conditions and fish response at each site. Despite this attempt to maximize gear efficiency, stream conductivity still had a predominant effect on bull trout detection in our study. Since conductivity is considered the most important environmental measurement affecting electrofishing efficiency (Reynolds and Kolz 2012), it is surprising so few studies document its effect on salmonid detection at a watershed scale. In the only comparable study we are aware of, Hense et al. (2010) found conductivity was the most important covariate of electrofishing capture probability for eight fish species, including brook trout and brown trout. Streams with relatively low conductivities (<50 μS·cm^{-1}) occurred in both Hense et al.'s (2010) West Virginia study area and our own. Based on our results, increasing electrofishing effort (i.e., sample site length) appears to be of little value when sampling these low-conductivity streams. The probability of detecting bull trout at a conductivity of 50 μS·cm^{-1} was negligible within a 50 m site and only approached 30% after 500 m of sampling. If conditions permit, snorkeling may be a preferable sampling method to electrofishing in these situations (Bonneau et al. 1995). In contrast, sampling beyond 200 m in streams with a conductivity around 200 μS·cm^{-1} did little to improve conditional detection probability, which was already near 95%.

Table 6. Model structure and weights for two multiscale models of juvenile bull trout patch occupancy (Ψ), occupancy of the sample site given the patch is occupied (θ), and probability of detection given the patch and sample site is occupied (p).

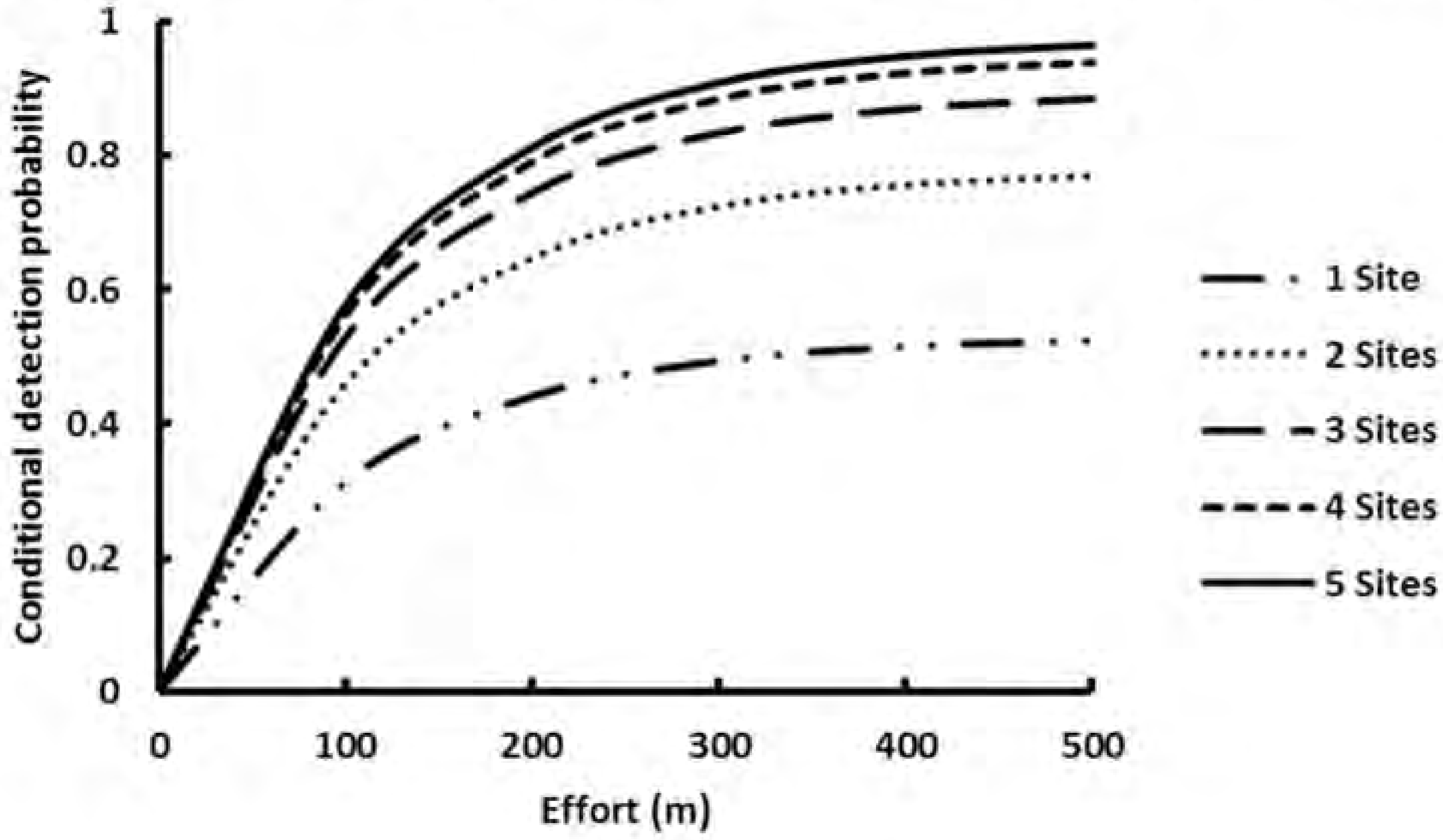
Model	AIC$_c$	Δ_i	w_i	$-2\log(L)$	K
$\Psi(.)$, $\theta(.)$, $p(.)$	113.58	0.00	0.50	106.17	3
$\Psi(.)$, $\theta(.)$, p(cond)	113.59	0.01	0.50	103.09	4

Note: Stream conductivity (cond; μS·cm^{-1}) is included as a covariate of detection probability (p).

We failed to detect any other effect of stream habitat characteristics on juvenile detection, although starting sites at the head of riffle habitat increased the probability of detection in the first 50 m to nearly 100% when bull trout were present (dropping to 72% thereafter). Several explanations for this discrepancy in detection probabilities exist, none of which are mutually exclusive. The high probability of detection we observed at the start of a site may simply reflect the increased efficiency of our electrofishing gear at capturing relatively undisturbed fish. Stream salmonids may respond to electrofishing with flight or cover-seeking behaviors (Young and Schmetterling 2012). The reaches we sampled were continuous, segments were not isolated, and our results indicated bull trout availability between segments was not independent. It is possible that gear efficiency decreased as disturbance to the site increased with progressive sampling. Related to this is the possibility that our sampling crews became less efficient at detecting bull trout as they grew fatigued over the course of sampling a site. We found indirect evidence of this possibility in our sample data. Comparing our effort in the first 50 m of a site to the average effort expended in the remainder of the site confirms that, on average, we expended 15 more seconds electrofishing effort in the first 50 m (paired t test, n = 91, p = 0.0027). To the extent that effort represents sampling diligence, we cannot discount the possibility that crew fatigue led to reduced efficiency of detecting bull trout as sampling progressed within a site.

Apart from behavioural explanations, there is the possibility of undetected habitat effects on our sampling efficiency. It is possible our habitat data were too coarse to detect effects that operated at a smaller scale (Al-Chokhachy et al. 2010) or that our models were too simplistic. Finally, for logistical reasons, we focused on

Fig. 3. Modeled relationship between conditional patch detection probability of juvenile bull trout using backpack electrofishing gear as a function of the metres of stream sampled and number of sites sampled within the patch using multiscale occupancy model: $\Psi(.)$, $\theta(.)$, $p(.)$.



rapid, qualitative assessments of some habitat conditions; a more quantitative approach may have increased our power to detect habitat effects. These limitations bear consideration but do not detract from our observation that, when present, bull trout detection approached 100% in the first 50 m of a sample site commencing at the head of a riffle under typical field conditions.

Juvenile bull trout occupancy

Our results, based on an independent assessment of juvenile bull trout detection probability at the watershed scale, indicate the bias resulting from false absences will likely be relatively small at both the site and patch scales under comparable conditions. Modeled site- and patch-scale occupancies were within 4%–6% of the naive estimates. Despite this, we caution that logistic regression models of wildlife–habitat relationships have been demonstrated to be sensitive to even low levels (5%–10%) of false absences (Gu and Swihart 2004). The magnitude and close correspondence between site- and patch-scale occupancy we observed suggests bull trout were relatively widely distributed throughout the study area. Given the bull trout's typically clumped distribution (Rieman and McIntyre 1995; Al-Chokhachy et al. 2010), we interpret this result as indication that the criteria we used to define patches were effective at broadly identifying suitable bull trout habitat in the watershed. In contrast with our results, a relatively low site-scale occupancy would indicate a locally rare species occupying a larger fraction of the landscape; a relatively high estimate of site-scale occupancy would indicate a locally common, but less widely distributed, species (Pavlacky et al. 2012).

Modeling considerations

The use of occupancy models, combined with a patch-based approach, appears well suited to quantitative bull trout presence–absence assessments such as ours, but requires careful consideration of model assumptions. Occupancy models assume no unmodeled heterogeneity in the probabilities of detection and occupancy (MacKenzie et al. 2006). We randomly determined electrofishing crew duties at each site and included covariates of electrofishing efficiency during modeling to address potential heterogeneity in detection probability. By targeting only smaller bull trout, variation in electrofishing capture efficiency attributable to fish size should also have been minimized (Peterson et al. 2004). The process of defining patches was intended to broadly identify habitats with the potential to support a local bull trout population, thereby reducing heterogeneity in occupancy attributable to habitat suitability. Targeting the juvenile life stage was also intended to reduce heterogeneity in occupancy, as juvenile bull trout are generally considered more representative of a local population than adults (Isaak et al. 2009).

The models used in our analyses assume implicitly that site-specific abundance and detectability are independent (MacKenzie et al. 2006; Dorazio 2007). This assumption is often reasonable when mean abundance within a site is either high (e.g., >10; MacKenzie et al. 2006) or very low (e.g., <1; Dorazio 2007). Essentially, detection of an individual is practically assured when mean abundance is high, while very low mean abundance is typically a result of very few individuals being available for detection; both situations diminish the scope for variable abundance to influence detectability. With an observed mean catch of 0.92 fish per 250 m site, which is typical of many Alberta bull trout populations, we believe the models used in our analysis are appropriate. Simulations indicate models that fail to account for dependence between abundance and detection, where it exists, generate negatively biased estimates of occupancy (Dorazio 2007). Models that incorporate variation in abundance into site-specific detection probabilities (not without their own suite of limiting assumptions) are an area of active research (MacKenzie et al. 2006) that we believe will be of particular relevance to future studies like ours.

Models also assume sites are closed to changes in occupancy over the sampling period (MacKenzie et al. 2006). Although our study occurred over two field seasons, patches were sampled in an irregular sequence both temporally and spatially to reduce the potential for any consistent bias in occupancy. We also sampled sites within patches intensively (4.05 ± 3.75 days (mean ± SD) between start and finish of sampling within a patch) and focused on juvenile fish, which often spend multiple years in their natal streams (Downs et al. 2006; Bowerman and Budy 2012), to further minimize the potential for changing occupancy to bias our estimates. Finally, breaking the closure assumption tends to lead to an overestimation of occupancy (Rota et al. 2009), while our modeled and naive estimates of occupancy were relatively comparable.

Models require species detections be independent (MacKenzie et al. 2006), so we chose both design- and model-based methods to account for potential nonindependence between our species detections. Our site selection process was designed to create a spatially balanced sample with a minimum of 500 m of stream between 250 m long sample sites (77% of sites ≤250 m), while both models used in our analysis included availability parameters. To minimize false detections that may bias estimators (MacKenzie et al. 2006), only captured fish were counted as detections, and all brook trout and bull trout were examined for morphological features characteristic of hybridization based on criteria in Popowich et al. (2011).

Although our objectives required comprehensive sampling, several modifications to our study design are possible that would increase the efficiency of similar studies. Our patches were defined using relatively coarse criteria; refinement of these criteria to exclude fishless areas (e.g., dry streams, sites above obvious barriers to upstream migration) should increase bull trout availability and consequently detection efficiency. We chose to continue sampling sites after first detection of a juvenile bull trout within a patch, but this is not required for the models. Stopping sampling after first detection alone, assuming no prior knowledge of bull trout distribution in the study area, would have resulted in a 27% reduction in the number of sites we sampled (67 versus 92 sites). Further efficiencies are possible, as our results indicate sampling more than three sites in a patch or over 200 m at a site resulted in marginal increases in bull trout detection probability in all but the lowest conductivity streams. Stopping sampling after first detection and reducing site length to 200 m alone would have resulted in over a 10 km reduction in the length of stream we electrofished.

In conclusion, our study design allowed us to assess occupancy and detection probability of juvenile bull trout at multiple scales. Of the five stream habitat variables we examined, stream conductivity had a predominant effect on our probability of detecting bull trout using backpack electrofishing gear. Conditional detection probability approached 95% in the first 200 m of electrofishing effort in streams with a conductivity around 200 $\mu S \cdot cm^{-1}$. These results indicate any bias in juvenile bull trout occupancy estimates resulting from the imperfect detection of the species is likely slight under comparable sampling conditions. The use of occupancy models combined with a patch-based approach appears well suited to quantitative assessment of bull trout distribution, but requires careful consideration of model assumptions.

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