Ecology of Freshwater Fish 2014: 23: 556–571

ECOLOGY OF
FRESHWATER FISH

Patch size but not short-term isolation influences occurrence of westslope cutthroat trout above human-made barriers

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Accepted for publication September 28, 2013

Abstract – Habitat fragmentation in aquatic systems has led to widespread isolation of stream fishes. Metapopulation theory predicts that persistence is directly related to local patch size and its characteristics, but because these relationships tend to be taxon-specific, empirical data are important. We assembled 246 observations of occurrence of westslope cutthroat trout (WCT), a taxon of concern in the western U.S. and Canada, in stream networks isolated for up to 100 years (median 40 years) above human-made barriers, mostly culverts, at road crossings within U.S. National Forests. We used logistic regression to analyse how WCT occurrence varied with patch size, isolation time and stream-level covariates. Occurrence was positively related to stream length and habitat quality within the isolated stream network and negatively related to elevation and channel gradient. Unexpectedly, the probability of occurrence was not related to how long a habitat patch had been isolated. At the median elevation (1354 m) and channel gradient (14%), and where habitat quality was poor, WCT were likely to occur (probability >0.5) if an isolated stream network was at least 1.7 km. If habitat quality was high, about 0.2 km of habitat produced the same probability. Although there are important limitations, this analysis provides the first empirical estimate for how patch size and patch-level characteristics influence persistence of WCT in isolated stream networks.

Key words: Cutthroat trout; isolation; occurrence; patch size; persistence; habitat quality

Introduction

For species that exist as metapopulations, occurrence in networks of habitat (patches), should be directly related to patch characteristics, such as size and connectivity (Hanski 1994; Dunham & Rieman 1999). These relationships are important to conservation because of pervasive habitat fragmentation and population isolation (Wilcove et al. 1998). From a patch size perspective, the question is 'how small is too small?' or 'how big is big enough?' to ensure population persistence. The idea applies across ecosystems and taxa—patch size and persistence (or occurrence) of species are generally positively related (Mazerolle & Villard 1999; Prugh et al. 2008; but see Pellet et al. 2007). The concept is particularly relevant for freshwater stream fishes given life within dendritic networks (Fagan 2002), the expectation of spatial population structure and life-history expression (Rieman & Dunham 2000) and interactions with invasive species (Peterson et al. 2008).

Biologists focused on conserving stream fishes typically assume that populations in larger patches are more likely to persist in isolation than those in smaller patches. The premise is that larger stream networks will contain larger populations and a greater diversity of habitats (Hilderbrand & Kershner 2000; Young et al. 2005), including internal refugia, that

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doi: 10.1111/eff.12108

Ecology of FRESHWATER FISH

together buffer against the demographic, genetic and stochastic processes that could lead to extirpation (Lande 1988; Frankham 2005). Empirical support for this premise comes from the positive relationship between stream network size (hereafter synonymous with patch size) and occurrence of indigenous populations of white-spotted char (*Salvelinus leucomaenis*, Morita & Yamamoto 2002), bull trout (*S. confluentus*, Rieman & McIntyre 1995; Dunham & Rieman 1999; Dunham et al. 2002) and Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*, Dunham et al. 2002), and translocated populations of greenback (*O. c. stomais*) and Rio Grande cutthroat trout (*O. c. virginalis,* Harig & Fausch 2002). The relationships also vary among species (Dunham et al. 2002; Fausch et al. 2006; Perkin & Gido 2011) and are influenced by a suite of biotic and abiotic variables, such as the presence of non-native species or habitat suitability, as well as how long populations have been isolated (Rieman & McIntyre 1995; Morita & Yamamoto 2002; Fukushima et al. 2007; Tsuboi et al. 2010).

Identifying the patch characteristics related to population persistence is of particular importance to managers of cutthroat trout in western North America, because many subspecies have undergone range-wide declines (Young 1995) and relict populations are often isolated in headwater stream networks (Hilderbrand & Kershner 2000; Shepard et al. 2005; Roberts et al. 2013). For example, the westslope cutthroat trout (WCT, *O. c. lewisi*) is the most widely distributed subspecies of interior cutthroat trout, occurring in the interior Columbia, Fraser, Missouri and Saskatchewan River drainages of the western U.S. and southern Canada (Behnke 2002). The number, size and distribution of populations of WCT have declined (Shepard et al. 2005), and the fish is now a taxon of concern for federal, state, provincial and tribal authorities (e.g., http://www.dfo-mpo.gc.ca/species-especes/index-eng.htm; http://fieldguide.mt.gov/). Shepard et al. (2005) estimated that 81% of the so-called conservation populations of WCT were relatively small, isolated populations. Continuing encroachment by non-native trout species such as brook trout (*S. fontinalis*, Fausch et al. 2009) and further habitat loss associated with climate change (e.g., Wenger et al. 2011a,b) may increase the frequency of local extinctions.

To date, the relationship between patch characteristics and occurrence of isolated WCT populations has not been quantified. To fill this data gap, we fit logistic regression models to presence–absence data for WCT above human-made barriers in Montana and Idaho. Our first objective was to quantify the relationship between occurrence, patch size and isolation time. Our second objective was to determine whether biotic and abiotic factors—brook trout presence, habitat quality, temperature, elevation and channel gradient—also affected persistence following isolation. Our hope was to develop information that could be used to better assess the vulnerability of isolated populations of WCT because their conservation will require prioritisation of limited management resources.

Methods

Occurrence data

We used a combination of found and sampled data to characterise the occurrence of WCT in streams isolated by human-made barriers, primarily culverts at stream-road crossings. The data set was developed in three phases. First, we queried U.S. Forest Service (USFS) fishery biologists in ten National Forests (NF) in Montana and Idaho (USFS Region 1) for observations of fish presence and habitat conditions in streams above fish migration barriers across the region (Hendrickson et al. 2008). We limited the observations to structures rated as total barriers to upstream passage, based on a set of screening criteria and the physical characteristics of the structure and site (USFS 2003). We gave biologists a standardised questionnaire (Appendix S1) and spreadsheet to record responses. We asked them to confirm barrier location and an approximate installation date, if known. Biologists were asked to record presence or absence of WCT and other trout species upstream and downstream of the barrier, based on a minimum amount of sampling (see below). A species was considered 'present' if it had been detected by sampling within the past decade. We assumed, as have others, that WCT historically occurred in virtually any accessible stream upstream of an established population (Shepard et al. 2005; Wenger et al. 2011a,b). Cutthroat trout were considered 'absent' if they had not been detected in the last decade during any of at least three discrete sampling events — using single- or multipass electrofishing or snorkelling — in which each event sampled at least 50 m of stream. The discrete sampling events could have been in different years, and a single sampling event of 150 m length could suffice. Fish occurrence was categorised as 'unknown' in all other cases.

Second, we needed to determine whether the found data provided adequate representation of patch sizes across the subspecies' range and encompassed patch size gradients observed for similar species (e.g., Dunham et al. 2002; Morita & Yamamoto 2002). To do this, we conducted a preliminary analysis to estimate watershed area above each barrier and fit a limited number of occurrence models. We used logistic regression to model occurrence of WCT as a function

of watershed area, which was estimated in a geographic information system (GIS). The preliminary analysis indicated a positive relationship between WCT occurrence and watershed size. Estimates of the probability of WCT occurrence were high and precise in watersheds >1750 ha, but declined and were imprecise below this threshold.

Third, to augment the found data, we sampled additional streams with fish passage barriers, targeting streams in patches <1750 ha that had not been recently surveyed. There were more than 200 possible streams containing patches <1750 ha, and we did not have the resources to sample them all. For logistical reasons, we stratified sampling by NF and by patch size. Across NFs, we apportioned greater sampling effort to those with more inventoried culvert barriers. For example, out of a 12-week field season, we dedicated 4 weeks to sampling in the Lolo NF, which had 103 isolated patches. In contrast, we spent only 1 week each sampling in the Beaverhead-Deerlodge NF and Nez Perce NF, as they both had only 14 such patches. In each NF, we further stratified potential sample patches into three size categories (<250, 250–1000 and 1000–1750 ha) and generated a random list of sample sites within each category. We then sampled, in order, from that list. Additional opportunistic surveys were conducted at other sites as time permitted.

The sampling was designed to minimise the likelihood of falsely concluding WCT were absent. The standard protocol was to survey up to six discrete 30-m reaches (150–180 m total) above the barrier and focus sampling in those habitats most likely to contain WCT (Appendix S2). Generally, the initial reach was adjacent to and upstream from the barrier, and subsequent reaches were systematically distributed and separated by at least 150 m. In smaller stream networks where fish habitat was much <1 km, reach spacing was smaller. If WCT were detected in a reach, sampling ceased at the end of that reach and WCT were judged present. If WCT were not detected in any reach, they were judged absent. Sampling consisted of open- or closed-site, upstream-directed, backpack electrofishing with pulsed DC and two- or three-person crews. From an independent pilot study, we estimated capture probabilities of 0.37–0.68 depending on fish size and concluded that application of the sampling protocol would result in a false absence error rate of <0.1 per stream across a range of fish sizes and densities (Appendix S3).

Independent variables

Patch size has commonly been measured as watershed area (Rieman & McIntyre 1995; Dunham et al. 2002; Morita & Yamamoto 2002). However, area may not provide the best estimate of the habitat available to fish because of variation in drainage density caused by differences in climate, vegetation, soils, topography and lithology (Knighton 1998). Thus, we examined the effect of patch size as represented by three measures: watershed area, stream length and stream length <17% channel gradient (Table 1). Watershed area (variable name *area*) was

Table 1. Metrics and summary statistics for predictor variables used to model occurrence of westslope cutthroat trout in 246 isolated stream networks (patches).

Hypothesis	Variable name or abbreviation	Description	Units	Median (range) or frequency (N) †
Patch size	*Area*	Contributing watershed area upstream of barrier	ha	484.5 (30.8–1861.7)
Patch size	*Stream length*	Stream length upstream of barrier location, from 30-m TauDEM stream layer	m	5389 (15–220,007)
Patch size	*Stream length <17%*	Stream length <17% channel gradient upstream of barrier location, from 30-m TauDEM stream layer	m	3858 (0–205,719)
Isolation effect	*Time*	Isolation time for the stream network based on the barrier installation date (nearest decade)	year	40 (0–100)
Covariate	*Habitat quality*	Assessment of habitat quality that represents the extent of human land use impact and disturbance in the watershed	High, medium, low	High (45), medium (142), low (59)
Covariate	*Gradient*	Weighted average channel gradient for all stream segments upstream of the barrier location, from 30-m TauDEM stream layer	Elevation·distance^{-1}	14% (3–29%)
Covariate	*Elev*	Elevation at the culvert derived from 90-m DEM	m	1354 (428–2391)
Covariate	*Temp*	Mean summer air temperature based on June–August monthly averages, 1971–2000 from 2-km PRISM grid	°C	14.4 (10.3–17.9)
Covariate	*Brook*	Occurrence of brook trout	Present, absent, unknown	Present (43), absent (163) unknown (40)

TauDEM is Terrain analysis using Digital Elevation Model; DEM is Digital Elevation Model; and PRISM is Parameter-elevation Regressions on Independent Slopes Model.

†Median and range are reported for continuous variables, and frequencies (N) are tabulated for categorical variables.

calculated in a GIS as the catchment area upstream from the barrier. Total stream length upstream from the barrier (*stream length*) was calculated from a 1:24,000 TauDEM curvature-based stream model with a 25-pixel (2.25-ha) accumulation threshold of upward curved cells (Tarboton 2012). This model initiated a stream equivalent to its position on a U.S. Geological Survey 1:24,000 scale quadrangle map. The variable *stream length <17%* is the total stream length above the barrier with high-gradient reaches (>17%) excluded as potentially unsuitable habitat for WCT (e.g., Wenger et al. 2011a). If the entire stream exceeded a gradient of 17%, the site was assigned a minimum habitat length of 50 m to permit variable transformation.

We estimated time since isolation (*time*) from information provided by USFS biologists (Table 1, Appendix S1). Installation dates were not available for all barriers. Often, biologists could provide only a range of years or a specific decade, based on the known or believed date of road construction. Consequently, we standardised the installation dates to the nearest decade. Field sampling occurred during 2007–2008, so the period from 2000 to 2009 was considered the current decade. A barrier installed from 2000 to 2009 was assigned a *time* of 0 year, a barrier installed from 1990 to 1999 was assigned a *time* of 10 years, and so forth. Nineteen barriers were described as being built only before a specific date, and these were assigned to the most recent decade specified by that date.

Covariates

We considered five covariates — brook trout presence, habitat quality, temperature, elevation and channel gradient—that have been associated with the occurrence or density of cutthroat trout (Table 1). Occurrence of brook trout (*brook*) in isolated stream networks was assessed by the same minimum sampling criteria as for WCT.

We assumed that watersheds without human disruption and that did not have any other obvious limiting factor supported diverse aquatic habitats and populations that were generally resilient to natural disturbance. Land management, such as livestock grazing, timber harvest, mining and road building, can simplify and degrade stream habitats and should be associated with reduced population densities of stream-dwelling WCT (Kershner et al. 1997; Valdal & Quinn 2011). USFS biologists provided a qualitative assessment of *habitat quality* in the stream network adjacent to the barrier using a three-category rating system (high, medium or low) to reflect the extent of human disruption and random disturbance (wildfire) to watershed processes that create and maintain fish habitat (Appendix S1). A 'high' rating denoted pristine or comparatively unaltered watersheds but for the barrier, whereas 'low' reflected extensive disruption (e.g., flow alteration, siltation, lack of cover or post-wildfire debris flows) that could limit carrying capacity, survival and population size. A 'medium' rating designated habitats intermediate to those rated 'high' or 'low'.

Temperature strongly influences the growth of individual WCT (Bear et al. 2007) and ultimately constrains their distribution in accessible habitats (e.g., Paul & Post 2001; Sloat et al. 2005; Wenger et al. 2011a). Stream temperatures were not available for most barrier sites, so we used air temperatures as a surrogate (Rieman et al. 2007; Wenger et al. 2011a). Mean summer air temperature during June–August (*temp*) was calculated from PRISM (The Climate Source 2012) for the 2-km grid containing the barrier.

Stream gradient and related habitat factors can also limit fish distribution and abundance (Fausch 1989; Bozek & Hubert 1992; Wenger et al. 2011a). Channel gradient (*gradient*) was calculated as the weighted average of valley bottom slopes for all stream segments upstream from the barrier using a 30-m TauDEM stream model (Tarboton 2012).

The distribution and abundance of cutthroat trout is sometimes correlated with elevation (Bozek & Hubert 1992; Paul & Post 2001). In some cases, this may be an artefact of encroachment upon non-native trout (Paul & Post 2001; McMahon et al. 2007) or a response to other habitat factors, such as stream width, gradient and particularly temperature, that are also correlated with elevation (e.g., Kruse et al. 1997). Elevation at the barrier location (*elev*) was defined using a 90-m digitial elevation model (Digital Data Services Inc. 2004).

Final dataset – observations of occurrence

We identified 500 fish passage barriers as potential observations and augmented this list by surveying for fish occurrence at 144 reaches in 67 streams across 6 NF during 2007. Median reach length at directly sampled sites was 30.4 m (range 18–1600 m), median wetted width was 1.7 m (range 0.85 – 4.2 m) and median water temperature at time of sampling was 9.0 °C (range 1.5–18.0 °C). Westslope cutthroat trout occurred above a barrier in 38 of the 67 streams. We then excluded from the potential observation list all sites lacking barrier installation dates, information on habitat quality or sufficient sampling to determine occurrence of WCT (see Methods, Occurrence data; Appendix S1). The final dataset for analysis included 246 observations of cutthroat trout occurrence (206 of brook trout, which were present at 43 sites) from two major river drainages in the USA (Figs. 1 and 2). Westslope cutthroat trout occurred at 172 of 222

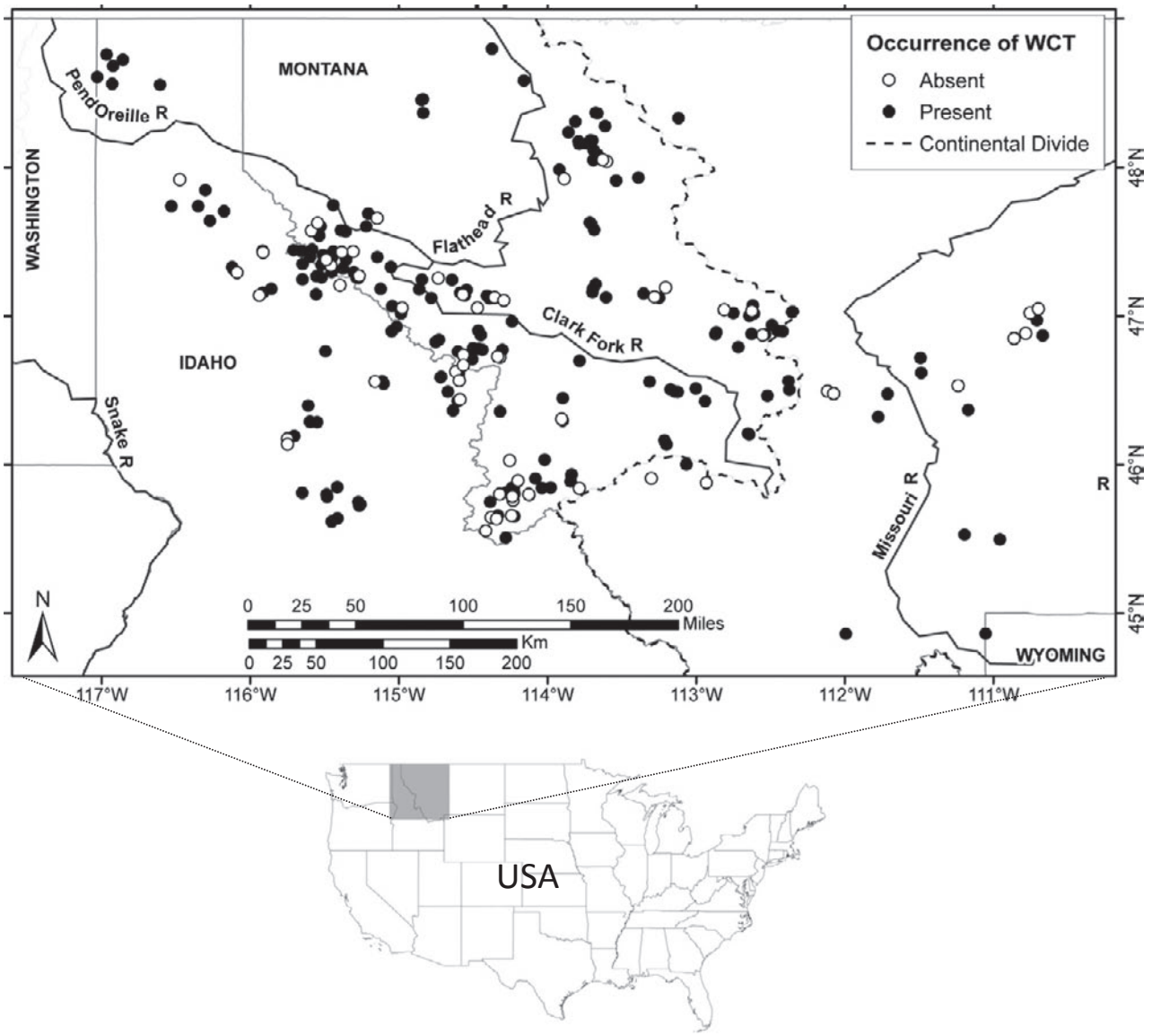

Fig. 1. Presence of westslope cutthroat trout (N = 187) (WCT) in isolated stream networks above human-made barriers (N = 246) in U.S. Forest Service Region 1.

sites in the Columbia River basin, and 15 of 24 sites in the Missouri River basin. Road culverts constituted 225 of the 246 barriers. The remainder included dams (14), water diversions (3) and road fill, mine tailings, chemicals and a hydroelectric facility (1 each).

Analyses

Our analyses were conducted in five steps. First, we identified the association among potential predictor variables using Pearson correlation analysis. We then selected the best predictor among related or correlated sets of variables by single-factor logistic regression to avoid fitting redundant models. Within each set of moderately-to-highly correlated variables ($|r| > 0.3$), we chose a single-best predictor by model selection based on Akaike's information criterion (AICc; Burnham & Anderson 2002) and Hosmer–Lemeshow goodness-of-fit statistics.

Next, we fit a set of four *a priori* candidate models to estimate the effect and relative strength of patch size, isolation time and their interaction on occurrence of WCT. The global model represented the hypothesis that the effect of isolation would be stronger in smaller patches. Alternative models reflected the hypotheses that the effect of isolation time is constant across patch size (no interaction) or that patch size and isolation time do not influence the occurrence of WCT (single-factor models). Logistic models were fit with the glm function (general linear model with binomial errors) or lrm function in the 'rms' package (Harrel 2012) using R 2.14.2 software (R Development Core Team 2012). Variables for patch size were transformed by natural logarithms to improve model fit (e.g., Rieman

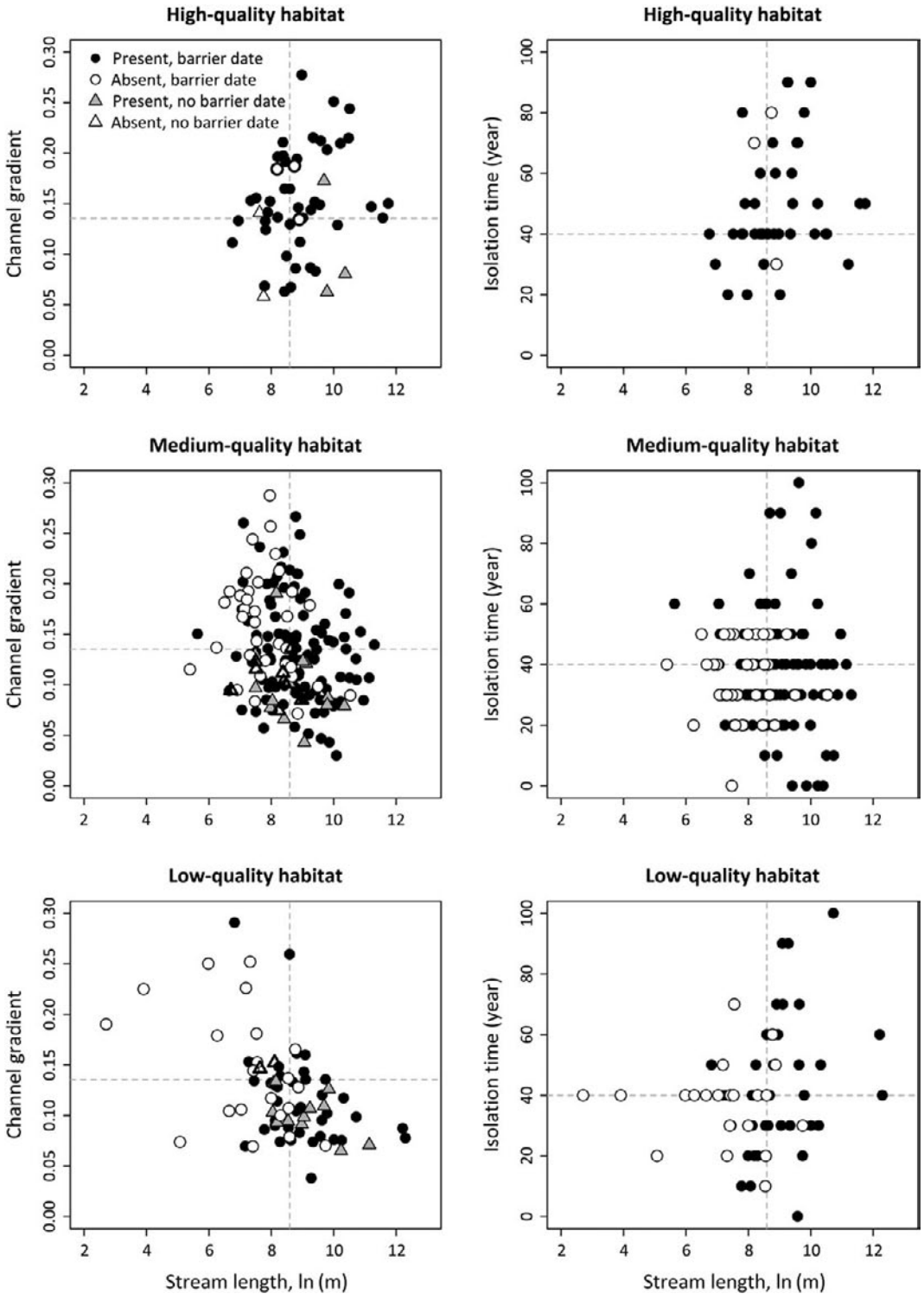

Fig. 2. Occurrence of westslope cutthroat trout (WCT) in isolated stream networks as a function of stream length, habitat quality, channel gradient and isolation time. Left-hand plots also include 41 observations (not used for model fitting) for which time since isolation was unknown. Dotted reference lines are the median values for each variable.

& McIntyre 1995). We used AICc and individual variable weights to discriminate among these hypotheses.

To account for the possibility that the response of WCT would be similar for sites that were close together (i.e., spatially autocorrelated), we also fit multilevel mixed models (Wagner et al. 2006; Wenger et al. 2011b). The mixed models had the same fixed effects as the *a priori* models, but included a random intercept term for *sub-basin* (29 different sub-basins for the 246 observations). We fit the mixed models with

lmer in the package 'lme4' (Bates et al. 2011) and also with a bootstrap approach in the package 'glmmML' (Broström & Holmberg 2011). We determined whether we needed to account for spatial autocorrelation by comparing the parameter estimates and standard errors for the fixed-effect and mixed models and testing the significance of the random effect. This approach was repeated for the covariate models (see below).

Brook trout and WCT might respond similarly to patch size and isolation time, which could confound other relationships. For that reason, we screened brook trout as a potential predictor by testing whether occurrence of both species was independent by Fisher's exact test, and whether there were correlations between the occurrence of brook trout and the continuous independent variables by using polyserial correlation with package 'polycor' (Fox 2010).

We then fit a series of models that included covariates for elevation, channel gradient and habitat quality. The global model included the most-supported *a priori* candidate variables, all uncorrelated covariates and two-way interaction terms. Reduced models included an additive effects model (global model minus interaction terms) and a set of covariate interaction models that included the primary effects (patch size and isolation) plus their interaction with each covariate, taken one at a time. Hypotheses were assessed by AICc, variable weights and parameter estimates. We compared parameter estimates and predictive accuracy with confusion matrices, the receiver operating characteristic using package 'pROC' (Robin et al. 2011), Cohen's kappa statistic (κ) and *k*-fold cross-validation with the cv.binary function in package 'DAAG' (Maindonald & Braun 2012).

Results

Screening of variables

The three patch size variables were highly correlated, as were *elev* and *temp*, and *gradient* and *stream length <17%* (Table 2). *Stream length* outperformed *area* or *stream length <17%* (ΔAIC >3.4) in predicting occurrence of WCT; *elevation* was supported more than *temperature* (ΔAIC >6). For subsequent model fitting, we used the uncorrelated variables *stream length*, *gradient* and *elev*.

Fisher's exact test indicated that occurrences of WCT and brook trout were not independent ($P = 0.005$); brook trout were more likely to be present if WCT were present. Occurrence of brook trout was highly correlated with all patch size variables ($r = 0.56$–0.73; Table 2). In addition, logistic regression indicated that both trout species had statistically equivalent responses to patch size and isolation time (Appendix S4). Thus, we excluded *brook* as a covariate in subsequent analyses because a primary objective was to determine patch size relationships for WCT.

Modelling

Candidate models

We did not detect lack-of-fit for the global *a priori* candidate model for WCT (Hosmer–Lemeshow: d.f. = 8, $\chi^2 = 3.02$, $P = 0.93$), or evidence of overdispersion (residual deviance·d.f.$^{-1} = 0.92$). *Stream length* was positively associated with occurrence of WCT, but there was no association with *time* (Table 3). Variable weights were 1.0 for *stream length,* but only 0.37 for *time*. Cutthroat trout were present in 76% of the sites in the data set for which *time* was calculated ($N = 246$), and 71% of the sites for which *time* was not available ($N = 41$). These percentages were not statistically different (two-sample test for equality of proportions: $P = 0.6$), from which we inferred that the exclusion of these 41 observations did not bias the results with respect to isolation time.

The most-supported model included only patch size and accounted for 63% of the AIC weight. Parameter estimates and standard errors were similar

Table 2. Correlation among GIS-derived predictors and occurrence of brook trout, which were used to model occurrence of westslope cutthroat trout in isolated stream networks. See Table 1 for variable abbreviations and definitions.

	Correlation coefficients among predictor variables						
	Gradient	*Time*	*Area*	*Stream length <17%*	*Stream length*	*Elev*	*Temp*
Time	0.16						
Area	−0.18	0.10					
Stream length <17%	−0.54	0.04	0.83				
Stream length	−0.21	0.11	0.96	0.84			
Elev	−0.24	−0.06	−0.24	−0.09	−0.23		
Temp	0.08	0.02	0.27	0.16	0.25	−0.68	
Brook	−0.47	−0.06	0.56	0.73	0.62	−0.07	0.08

Values are Pearson correlation coefficients ($N = 246$ for cutthroat trout) or polyserial correlations ($N = 206$ for brook trout, *brook*).
Patch size variables (*area*, *stream length* and *stream length <17%*) were transformed using natural logarithms, and GIS is geographic information system.

Table 3. Model selection results for four candidate models to predict occurrence of westslope cutthroat trout in isolated stream networks. All models include an intercept term (not shown), and primary variables are total stream length (*stream length*), and isolation time (*time*).

Model variables	Parameter estimate (SE)	No. parameters	Log likelihood	Δ AICc	AICc weight
Stream length	**0.994 (0.47)**	4	−110.78	3.72	0.10
Time	0.001 (0.095)				
Stream length × *time*	0.001 (0.011)				
Stream length	**1.020 (0.18)**	3	−110.78	1.66	0.27
Time	0.007 (0.010)				
Stream length	**1.032 (0.18)**	2	−110.98	0.00	0.63
Time	0.011 (0.008)	2	−134.60	47.24	0.00

AICc is the Akaike information criterion corrected for finite sample sizes, Δ AICc is the relative difference in AICc values between the top-ranked model (Δ AICc = 0) and all other models, and AICc weight is the normalised relative likelihood.
Parameter estimates in bold have 95% confidence intervals that do not include 0.

Table 4. Model selection results for covariate models to predict occurrence of westslope cutthroat trout in isolated stream networks. Patch size is *stream length*; see Table 1 for additional variable abbreviations.

Model no.	Model variables	Parameter estimate (SE)	No. parameters	Log likelihood	Δ AICc	AICc weight
1	*Intercept*, *stream length*, *elev*, *gradient*, *habitat quality*, all two-way interactions	—	15	−99.33	12.70	0.002
2	*Intercept*	−1.25 (2.28)	6	−102.85	0.00	0.943
	Stream length	**0.833 (0.188)**				
	Elev	**-1.36×10^{-3} (0.60×10^{-3})**				
	Gradient	**−8.17 (3.68)**				
	Habitat quality 'med'	**−1.41 (0.66)**				
	Habitat quality 'low'	**−1.97 (0.70)**				
3	*Intercept*	−4.08 (6.71)	4	−109.62	9.36	0.009
	Stream length	0.778 (0.811)				
	Elev	-2.02×10^{-3} (4.54×10^{-3})				
	Stream length × *elev*	-1.42×10^{-4} (5.53×10^{-4})				
4	*Intercept*	−0.0171 (5.20)	6	−106.23	6.77	0.032
	Stream length	0.303 (0.598)				
	Habitat quality 'med'	−7.14 (5.53)				
	Habitat quality 'low'	−9.08 (6.00)				
	Stream length × *habitat quality* 'med'	0.695 (0.642)				
	Stream length × *habitat quality* 'low'	0.881 (0.701)				
5	*Intercept*	−1.14 (4.14)	4	−109.10	8.32	0.015
	Stream length	0.343 (0.501)				
	Gradient	−42.8 (29.0)				
	Stream length × *gradient*	4.75 (3.56)				

AICc is the Akaike information criterion corrected for finite sample sizes, Δ AICc is the relative difference in AICc values between the top-ranked model (Δ AICc = 0) and all other models, and AICc weight is the normalised relative likelihood.
Parameter estimates in bold have 95% confidence intervals that do not include 0.

for the fixed-effect and mixed models. For the patch size model, the parameter estimate for *stream length* was 1.033 (SE = 0.182) in the fixed-effects model and 1.059 (SE = 0.198) for the mixed model ('glmmMR' with 10,000 bootstrap estimates). The random term (*subbasin*) was not statistically significant in any model ($P \geq 0.41$). Consequently, we concluded that the variation in occurrence of WCT among subbasins was similar and that a multilevel model was not warranted.

Covariate models

We did not detect lack-of-fit in the global covariate model that included *stream length*, the covariates *elev*, *gradient* and *habitat quality*, and their two-way interactions (Hosmer–Lemeshow: $\chi^2 = 5.37$, $P = 0.72$). The additive model was the most supported (AIC weight = 0.943), and the 95% confidence interval for slope estimates of interaction terms in the single-factor covariate models all included zero (Table 4). Overall, models with *habitat quality* accounted for 0.977 of the AIC weight. Habitat degradation reduced the probability of occurrence in the expected order (high quality > medium quality > low quality), but the difference between medium- and low-quality habitat was small (Table 4). The probability of occurrence also declined with increasing elevation and gradient, though their relative influence was less than that of *habitat quality*. Among single-factor covariate models (Table 4, model nos. 3, 4 and 5), those with *gradient* and *elev* had

Table 5. Model performance for single-factor, patch-only and most-supported covariate models to predict occurrence of westslope cutthroat trout in isolated stream networks.

	Model predictions (confusion matrix) for occurrence of WCT			
	Covariate model 2 (additive)		Single-factor, patch-only model	
Observation	Absent	Present	Absent	Present
Absent	25	34	15	44
Present	9	178	10	177
	Model performance estimate (95% confidence interval)			
AUC	0.815 (0.751–0.878)		0.776 (0.709–0.843)	
k-accuracy	0.811 (0.796–0.825)		0.777 (0.760–0.787)	
Cohen's κ	0.439 (0.287–0.592)		0.250 (0.073–0.427)	

Area under the curve (AUC) estimates for the receiver operating characteristic, mean of 1000 repetitions of fivefold cross-validation results (*k*-accuracy) and Cohen's κ statistic (with 95% confidence intervals) are listed for each model.
Models with AUC >0.7 are generally considered useful (Fielding & Bell 1997; Manel et al. 2001), and the AUC for the covariate model was significantly greater than the patch-only model at the 95% level (DeLong's test for correlated curves: $Z = -2.22$, $P = 0.026$).
The variables for each model are presented in Table 3 (single-factor, patch-only model) and Table 4 (covariate model).

AICc values that were 1.55 and 2.59 units greater than the model with habitat quality. We did not detect evidence of spatial autocorrelation when *sub-basin* was treated as a random effect ($P \geq 0.56$ for 10,000 bootstraps), and parameter estimates were the same for fixed-effect and mixed models with the same structure. Subsequent analyses focused exclusively on results from the fixed-effects models.

Model performance

The best covariate model correctly predicted more than 95% of WCT presences in the data set, and single-factor, patch-size-only model correctly predicted slightly <95% (Table 5). The models performed less well when predicting absences. The covariate model correctly predicted 42.4% of the absences, whereas the patch-only model predicted 25.4%. Results from ROC and 5-fold cross-validation indicated that the covariate model was well calibrated and outperformed the patch-size-only model. However, parameter estimates for the patch size term in each model were similar (95% confidence intervals: 0.67–1.40 for the patch-only model, 0.46–1.21 for the covariate model).

With both models, increasing patch size was associated with an increase in the probability of occurrence. When *stream length* increased from 200 m to 1000 m, the probability of occurrence was predicted to increase from 0.55 to 0.82 for high-quality sites at the median elevation (1354 m) and channel gradient (14%). The same change in the patch-only model produced an increase from 0.12 to 0.44. Habitat degradation significantly reduced the probability of occurrence for a given patch size. The probability of occurrence of WCT in a 2.2-km-long patch was 0.90 when *habitat quality* was high, 0.69 when *habitat quality* was medium and 0.55 when it was low (Fig. 3). Increasing channel gradient and elevation also reduced the probability of occurrence (Fig. 3). Regardless of the model, at the median gradient and elevation, the occurrence of WCT was predicted to be more likely than not (probability >0.5) when *stream length* was at least 1.7 km (Fig. 3).

Discussion

Patch size and correlates for persistence of WCT in isolation

A basic tenet of island biogeography is that populations in larger habitats have a greater probability of persistence than do those in smaller ones (MacArthur & Wilson 1967). As expected, the probability of persistence of WCT also increased as patch size increased, as it has for an array of riverine fish species (Dunham et al. 2002; Perkin & Gido 2011). Our data also demonstrate that WCT can persist for extended periods in relatively small habitat patches. This is consistent with previous observations of cutthroat trout that were anthropogenically or naturally isolated in stream networks consisting of a few kilometres of habitat (Young et al. 2005; Cook et al. 2010; Whiteley et al. 2010). Although cutthroat trout populations sometimes have migratory forms that have extensive seasonal migrations, for example, over 100 km (Bjornn & Mallet 1964), they also exhibit substantial flexibility in life-history traits and demographic population structure, even among small streams (Downs et al. 1997; Young & Guenther-Gloss 2004; Young 2011). This flexibility may confer a greater degree of persistence for populations of cutthroat trout and other small-stream fish species when confronted with sudden isolation (Fukushima et al. 2007; Morita et al. 2009), whatever its cause.

Watershed area has typically been used to estimate patch size for salmonids (Dunham et al. 2002; Harig & Fausch 2002; Morita & Yamamoto 2002; Endou et al. 2006), yet we found stream length outperformed area at predicting occurrence of WCT (cf. Hugueny et al. 2011). Although tempting, latitudinal and regional variation in drainage density, and thus the watershed area-stream network length relation (Knighton 1998), prevents direct comparison of our results to those elsewhere. As a consequence, it remains uncertain to what degree variation in mini-

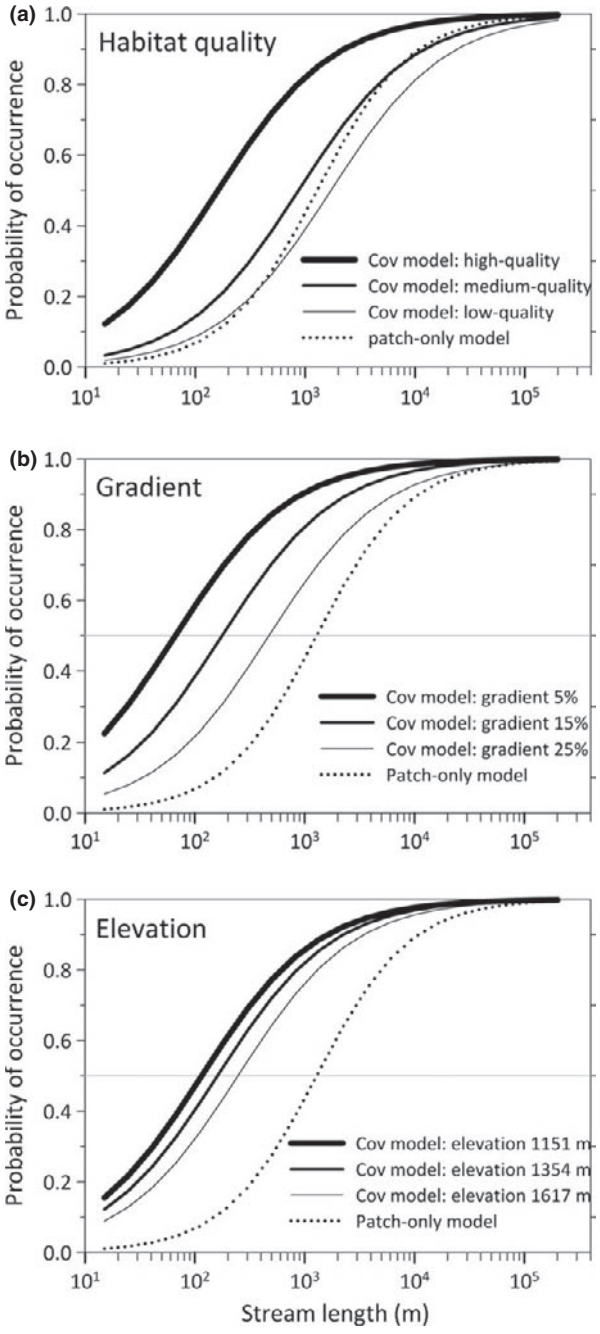

Fig. 3. Predicted occurrence of westslope cutthroat trout (WCT) in isolated stream networks as a function of patch size, habitat quality, channel gradient and elevation. Solid lines are predictions for the most-supported covariate model [cov model = (*stream length*) – (*habitat quality* 'low') – (*habitat quality* 'med') – (*gradient*) – (*elev*)] for: (a) low-, medium- and high-quality habitat with median gradient (14%) and elevation (1354 m); (b) channel gradients 5, 15 and 25% with median elevation and high-quality habitat; and (c) elevations 1151, 1354 and 1617 m (quartile values) with median gradient and high-quality habitat. The dotted line shows predictions for the patch-only model (= *stream length*). See Table 1 for additional variable abbreviations.

mum habitat sizes (measured by stream length or area) required for population persistence among salmonid fishes is attributable to taxon-specific requirements or regional hydrological patterns. Pending further research on this issue, decisions about minimum watershed sizes or stream lengths for conservation could rely on sympatric umbrella species requiring larger patches. For example, habitat networks suitable for ensuring persistence of bull trout populations appear to be several fold larger than those for WCT (cf. Rieman & McIntyre 1995; Dunham et al. 2002).

None of the covariates we considered changed the form of the underlying relationship between occurrence and patch size for WCT. In other words, the effect of statistically significant variables was additive, and covariates merely altered the location of the inflection point for the relationship. Nevertheless, habitat quality had a profound influence on the probability of occurrence in isolated stream segments. Patches necessary to sustain isolated populations of WCT in heavily managed or disturbance-prone landscapes were generally one to several kilometres longer than those in more pristine environs. Heavily managed and degraded landscapes likely have stream networks with lower habitat complexity (Horan et al. 2000), reduced carrying capacity and fewer refugia—reflected by fewer deep pools (Harig & Fausch 2002), less large wood in the stream channel or a higher proportion of fine sediment in the substrate (Weaver & Fraley 1993)—plus disrupted trophic interactions between streams and their riparian zones (Saunders & Fausch 2007) that collectively would lead to smaller fish populations at greater risk of extirpation from demographic, genetic and stochastic factors. This pattern suggests that habitat restoration may be an effective alternative in reducing the risk of population extirpation if logistical or biological concerns, such as the threat of hybridisation with or displacement of non-native species, preclude moving an isolation barrier further downstream.

The probability of occupancy by WCT decreased with increasing elevation and channel gradient, though the effects were less pronounced than for habitat quality. We assumed that elevation would be a proxy for temperature. Elevation and air temperature were indeed strongly and negatively correlated in our data set, yet elevation was a better predictor of WCT occurrence. We infer from this that temperatures at most or all sites fell below the upper thermal tolerance of WCT (e.g., Bear et al. 2007; Wenger et al. 2011a), but may have approached the lower thermal limit at higher-elevation sites. In such cases, recruitment may become sporadic because of growing season limitations for recently emerged fry (Coleman & Fausch 2007). Yet if our data set is most representative of colder, higher-elevation sites within the current range of WCT, climate warming expected during

the next few decades may not have a strong negative effect on persistence of cutthroat trout (e.g., Wenger et al. 2011b; Roberts et al. 2013). We found, as have others, that WCT are less likely to occur in very steep channels (e.g., Wenger et al. 2011a). Within the range of sites we examined, networks beginning at lower-gradient, lower-elevation sites would be preferred when managing isolated populations of WCT, but the contemporary distribution of non-native trout species tends to limit this option (e.g., Sloat et al. 2005).

Local extinction and isolation time

The probability of occurrence of WCT in isolated stream fragments was unrelated to the time since isolation. Although declines in persistence with time have been observed among some species of stream salmonids in Japanese streams isolated by erosion control dams (Morita & Yamamoto 2002; Morita et al. 2009), this pattern was not consistently evident among a suite of other sympatric species (Fukushima et al. 2007). The variation in these results may be caused by underlying differences in the data, species-specific ecological traits or the proximate cause of extirpation. For example, there might have been a lagged barrier effect at some sites in our data set. Improperly designed or installed culverts may be immediate barriers, but some structures might not act as barriers until changes in the adjacent streambed (erosion or aggradation) or displacement of the culvert (from a flood) create conditions that restrict fish movement. We explored effects for populations above 'older' (≥40 years) road crossings, but none were apparent (D. Peterson, unpublished data). Some culverts also may not function as complete barriers, which would tend to obscure both the effect of patch size and isolation time. We cannot entirely discount these issues, but the strong, consistent pattern in patch size coupled with the absence of any isolation time effect makes this less likely. In contrast, the absence of an isolation time effect for WCT, coupled with the observation that some populations have been extirpated, hints at divergent, population-specific trajectories following isolation: those populations likely to go extinct did so quickly whereas others persisted.

That many populations have resisted extirpation, however, may reflect the periodicity of disturbance that can have population-scale effects. In some streams along the eastern rim of the Pacific Ocean (Korea, Japan and Taiwan), flooding, landslides and debris flows caused by semiannual typhoons are a part of the disturbance regime (Chuang et al. 2008) to which fish communities in severely fragmented streams are vulnerable (Morita et al. 2009; Tsuboi et al. 2013). In contrast, wildfires and associated debris flows are the major natural disturbances in lotic systems in the northern Rocky Mountains, USA, and both can reduce or extirpate fish populations (Rieman & Clayton 1997; Dunham et al. 2003; Sestrich et al. 2011). Fire-related disturbances, however, typically recur at intervals of decades to centuries, and only severe fires or those that facilitate debris torrents are likely to cause declines or losses (Rieman & Clayton 1997; Sestrich et al. 2011). Thus, even relatively small basins, and their fish populations, may escape severe fire and its effects for centuries. The predicted increase in fire frequency and severity under climate change may alter this pattern (Westerling et al. 2006).

Limitations

Although the statistical relationship between occurrence and patch size was strong, there was substantial unexplained variation in these data. Several caveats and assumptions warrant discussion. First, we assumed that all barriers completely blocked upstream fish movement. The culverts were rated as total passage barriers based on objective, physical criteria (USFS 2003), but physical or simulation-based methods for rating fish passage at road culverts can overestimate the barrier effect (e.g., Burford et al. 2009). To our knowledge, fish passage has not been directly assessed at the sites in our data set. We speculate that some culverts may function as partial or intermittent barriers that restrict only some ages or sizes of fish or impede movement only under certain flows. If there were a substantial number of passable or semipassable barriers in our data set, then the models could underestimate the lower patch size threshold required for persistence of WCT.

Second, detectability of WCT was assumed to be very high for most of these sites. Based on the sampling protocol and a binomial detection estimator, even under an unlikely combination of only seven, 50-mm fish being present in 300 m^2 of habitat, the probability of detection of WCT would have exceeded 95% (Appendix S3) and detection probabilities for more typical size structures and densities of cutthroat trout would approach one. Nevertheless, failure to detect an extant population would have caused a slight overestimation of the patch size thresholds necessary for persistence that would tend to counteract the effect of semipermeable barriers. We also acknowledge that we did not measure the population sizes of WCT at our study sites and cannot say whether fish detected within a patch are part of a robust population or simply the 'swimming dead', the remaining individuals from a population that will soon pay its extinction debt (e.g., Tillman et al. 1994). Nonetheless, the lack of any temporal effect of isolation suggests this is not an important constraint that might bias the results.

Third, we recognise that total stream length, as derived from remotely sensed data, is a sometimes crude surrogate for available habitat. Natural barriers, for example, waterfalls or cascades, upstream from the human-made barriers we examined could have led us to overestimate the amount of habitat available to fish, perhaps accounting in part for the poor ability of our models to predict absences (see below). Alternatively, the upstream-most positions of fish may have gone beyond those we estimated (cf. Rosenfeld et al. 2002), in which case we would have consistently underestimated available habitat. Gauging the headwater extent of fish populations, however, remains difficult even for field studies (Fransen et al. 2006), and our use of a standardised approach to estimate stream length should have minimised the influence of this problem across basins.

Fourth, we treated absences as local extinctions, which assumes that WCT occurred historically in those waters. The subspecies remains widely distributed (Shepard et al. 2005), and other modelling efforts have made a similar assumption that appeared to be supported (Wenger et al. 2011a). Further evidence from the current study comes from the patterns of occupancy. Although WCT were judged to be absent from 59 isolated stream networks, this species was present immediately below the presumed barrier in 42 of them, implying that they once were, or could have been, upstream.

Finally, we regard model performance as uneven. The patch-only and covariate models were highly and almost equally successful at correctly predicting population presence. In contrast, the patch-only model was much less accurate than was the covariate model at accounting for population absence. This appears to indicate that patch size sets the lower threshold for whether a patch can be occupied, whereas the covariates influence whether occupancy will be realised. Although an improvement over the patch-only model, the covariate model correctly predicted fewer than 50% of the population absences, and inclusion of additional covariates might enhance the performance of this model. These might include drought-related indices that would account for cessation of stream flow or measures of the prevalence of severe fires or debris torrents, all of which could lead to immediate extirpations of fish populations in small streams (Sestrich et al. 2011; Rolls et al. 2012). Loss of genetic variation is noted as a threat for isolated populations of trout (Wofford et al. 2005; Morita et al. 2009), and measures of genetic variation, such as alleleic richness and genetic effective population size, are expected to scale with patch size (Neville et al. 2009; Whiteley et al. 2013). Genetic deterioration and inbreeding depression, however, are thought to act more slowly than other extinction processes (Lande 1988; but see Frankham 2005) and empirical evidence of inbreeding and its effects are rare in wild populations of salmonids (Wang et al. 2002; but see Morita et al. 2009).

Overall, we acknowledge that our estimates of WCT persistence with respect to patch characteristics are subject to bias, the most important of which may be the degree to which barriers actually precluded upstream fish movement. Given these uncertainties, we regard model predictions as minimum estimates of the patch sizes required to support persistent populations.

Conservation of WCT

Information from this study can be used to inform management decisions. For example, Peterson et al. (2008) developed a Bayesian network model for evaluating trade-offs between the threat of isolation for WCT versus displacement by brook trout. The patch size and persistence relationship in that model can be made more precise based on the results of this study. Adoption of the patch size-population persistence relationship that we observed would also render that model less pessimistic about the effects of isolation.

Our analyses addressed and answered some lingering questions about patch size and occurrence of WCT. Biologists can use the general relationship as a heuristic tool to assess the relative extirpation risk to isolated populations. Nonetheless, important uncertainties remain. What are the population-level thresholds or indicators for extinction? What are the proximate causes and temporal rates of extirpations? Are observations of cutthroat trout persisting in isolation for decades at very low abundance (Cook et al. 2010) simply exceptional, or do they signify something about the ability of stream salmonids to compensate ecologically or evolutionarily for the effects of long-term isolation (Vincenzi et al. 2010)? The recognition that climate change will be the major aquatic conservation challenge in coming decades has spurred interest in retrospective analyses of trout distributions to detect climate effects (Isaak et al. 2012), and assembly of large data sets to understand how climate and biotic interactions influence future distributions (Wenger et al. 2011a,b). These types of data sets might help reveal some of the temporal patterns in extirpation of inland trout, but focused long-term monitoring studies that collect more detailed data—on abundance, genetic patterns, life-history expression and demographic structure — are needed to understand the extinction process.

Re-establishing connectivity among currently fragmented habitats and isolated populations is a major focus of fishery managers in the U.S. and Japan

(Tsuboi et al. 2013). Unfortunately, further fragmentation, loss of stream habitat and changes in the distribution of non-native fishes appear inevitable under climate change (Nakano et al. 1996; Williams et al. 2009; Wenger et al. 2011b), so management by isolation will continue to be an option in a biologist's conservation toolbox. Our results should help inform decisions about the trade-offs between connectivity and isolation.

Acknowledgements

J. Gordon, S. Wenger and three anonymous reviewers provided helpful comments that improved the manuscript. D. Peterson was supported by the U.S. Forest Service (Agreement 06-IA-11221659-097) and the U.S. Fish and Wildlife Service's Abernathy Fish Technology Center. M. Enk, L. Hawdon, M. Davis, M. Jakober, B. Riggers, S. Gerdes, D. Downing, B. Roberts, J. Mickelson, J. Brammer, R. Brassfield, S. Barndt, B. Gardner, P. Van Eimeren, C. McKenna, P. Murphy, L. Walch, D. Mays, M. Fairchild, S. Dekome, R. Lindahl, C. Baconrind, E. Lider, S. Spaulding and S. Hendrickson of the U.S. Forest Service provided data on fish distributions and barrier installation dates. K. Nixon, Z. Betz, M. Novak, E. Kee, D. Schoen and D. Brewer helped with fieldwork. V. O'Byrne produced the map for Fig. 1. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service or U.S. Forest Service.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Questionnaire distributed to U.S. Forest Service biologists to collect information on occurrence of trout in isolated stream networks

Appendix S2. Sampling protocol to determine occurrence of westslope cutthroat trout in isolated stream networks

Appendix S3. Pilot study to estimate detection probability and false error rates for occurrence of westslope cutthroat trout in isolated stream networks

Appendix S4. Exploratory analysis to determine whether brook trout could be used as an independent variable to predict occurrence of westslope cutthroat trout in isolated stream networks