Predicting cutthroat trout (*Oncorhynchus clarkii*) abundance in high-elevation streams: revisiting a model of translocation success

Michael K. Young, Paula M. Guenther-Gloss, and Ashley D. Ficke

Abstract: Assessing viability of stream populations of cutthroat trout (*Oncorhynchus clarkii*) and identifying streams suitable for establishing populations are priorities in the western United States, and a model was recently developed to predict translocation success (as defined by an index of population size) of two subspecies based on mean July water temperature, pool bankfull width, and deep pools counts. To determine whether the translocation model applied to streams elsewhere with more precise abundance estimates, we examined the relation between electrofishing-based estimates of cutthroat trout abundance and these habitat variables plus occupied stream length. The preferred model was (population size)$^{1/2}$ = 0.00508(stream length (m)) + 5.148 (N = 31). In contrast, a model based on data from the original translocation model included stream temperature and deep pool counts as variables. Differences in models appear to largely have a methodological rather than biological basis. Additional habitat coupled with increased habitat complexity may account for the form of the abundance – stream length relation in the electrofishing-based model. Model-derived estimates imply that many cutthroat trout populations are below thresholds associated with reduced risk of extinction. We believe that this model can reduce uncertainty about projected population sizes when selecting streams for reintroductions or evaluating unsampled streams.

Résumé : La détermination de la viabilité des populations de truites fardées (*Oncorhynchus clarkii*) des cours d'eau et l'identification des milieux d'eau courante adéquats pour l'établissement des populations constituent des priorités dans l'ouest des États-Unis; un modèle mis au point récemment permet de prédire le succès des transferts (défini par un indice de taille de population) de deux sous-espèces à partir de la température de l'eau en juillet, de la largeur des fosses à plein bord et du nombre de fosses profondes. Afin de déterminer si le modèle de transfert s'applique à des cours d'eau situés ailleurs avec de meilleures estimations de densité, nous avons examiné la relation entre les estimations d'abondance des truites fardées basées sur la pêche électrique et les variables de l'habitat ci-haut, plus la longueur du cours d'eau occupé. Le meilleur modèle est (taille de la population)$^{1/2}$ = 0,00508 (longueur du cours d'eau, en m) + 5,148 (N = 31). En revanche, un modèle basé sur les données utilisées dans le modèle original de transfert comprend comme variables la température de l'eau et le nombre de fosses profondes. Les différences entre les modèles semblent avoir une base plus méthodologique que biologique. Un nombre plus important d'habitats et une complexité plus grande des habitats peuvent peut-être expliquer la forme de la relation entre l'abondance et la longueur du cours d'eau dans le modèle basé sur la pêche électrique. Les estimations fournies par les modèles laissent croire que plusieurs des populations de truites fardées se trouvent à une densité inférieure au seuil associé à un risque réduit d'extinction. Nous croyons que ce modèle peut réduire l'incertitude reliée aux projections de tailles de populations lors du choix de cours d'eau pour fins de réintroduction ou pour l'évaluation de cours d'eau non inventoriés.

[Traduit par la Rédaction]

Introduction

Inland subspecies of cutthroat trout (*Oncorhynchus clarkii*) have substantially declined throughout most of their historical range over the last 150 years (Behnke 1992; Duff 1996). Consequently, biologists have made extensive efforts to found new populations, reestablish extirpated populations, and assess the size and probability of persistence of both (Hepworth et al. 1997; US Fish and Wildlife Service 1998; Kruse et al. 2001). Some of this work has

Received 30 July 2004. Accepted 29 June 2005. Published on the NRC Research Press Web site at http://cjm.nrc.ca on 24 September 2005.
J18240

M.K. Young.[1] US Forest Service, Rocky Mountain Research Station, 800 East Beckwith Avenue, Missoula, MT 59801, USA.
P.M. Guenther-Gloss.[2] US Forest Service, Medicine Bow-Routt National Forests, Brush Creek – Hayden Ranger District, P.O. Box 249, Saratoga, WY 82331, USA.
A.D. Ficke. Department of Wildlife and Fishery Biology, Colorado State University, Fort Collins, CO 80526, USA.

[1]Corresponding author (e-mail: mkyoung@fs.fed.us).
[2]Present address: The Nature Conservancy, P.O. Box 1176, Saratoga, WY 82331, USA.

 doi: 10.1139/F05-149

been directed at developing models that relate cutthroat trout presence or abundance to habitat characteristics (Bozek and Rahel 1992; Kruse et al. 1997; Dunham et al. 1999). In one such model, Harig and Fausch (2002) established that the potential for small streams to harbor self-sustaining populations of greenback cutthroat trout (*Oncorhynchus clarkii stomias*) and Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*) in Colorado and New Mexico was a function of summer water temperature, number of deep pools, and pool bankfull width. They concluded that this model could also be used to assess risk of extinction of existing populations of these and closely related subspecies in comparable environments.

The Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*) is among the suite of cutthroat trout subspecies in the Rocky Mountains and occupies cold, high-elevation streams in much of its remaining range (Young et al. 1996). Marked declines in its distribution relative to its historical range have led to special designation by government agencies (CRCT Task Force 2001) and to a petition for listing under the US Endangered Species Act (US Fish and Wildlife Service 2004). There have been simulations of population viability under a variety of habitat structure and reintroduction scenarios (Hilderbrand 2002, 2003) and thorough inventories of sites for introductions (CRCT Task Force 2001). For these reasons, the Harig and Fausch (2002) model (hereafter the translocation model) merits consideration by biologists working with this subspecies. In preliminary evaluations, Harig et al. (2000) used it to assess the likely success of a reintroduced population of Colorado River cutthroat trout, and Young and Guenther-Gloss (2004) demonstrated that model output was related to electrofishing-derived abundance estimates of greenback cutthroat trout populations in northern Colorado.

Initially, we assembled data on Colorado River cutthroat trout populations in Colorado and Wyoming to perform similar analyses, but these data had two crucial distinctions from those used to develop the original model. First, most of the populations that we sampled had persisted indefinitely, whereas some streams in which populations failed to become established were used to develop the translocation model. Second, trout abundance was treated as a categorical variable (i.e., levels of translocation success) in the model, whereas we chose to examine the relation of habitat to abundance analyzed as a continuous variable. This also permitted us to include similarly obtained data on greenback cutthroat trout from northern Colorado (Young and Guenther-Gloss 2004). Consequently, we broadened our goals to include examining relations between stream characteristics and cutthroat trout abundance, devising a method to estimate the abundance of cutthroat trout in unsampled streams, and providing guidance for selecting streams likely to produce populations exceeding standards for viability. Our objectives were to (*i*) develop a model relating the same habitat variables in the translocation model, plus occupied stream length, to the abundance of age-1 and older Colorado River cutthroat trout and greenback cutthroat trout sampled by electrofishing, (*ii*) attempt to validate the model by conducting a similar analysis of the data of Harig and Fausch (2002) for greenback cutthroat trout and Rio Grande cutthroat trout but limited to those streams in which translocations were at least partially successful, and (*iii*) use the preferred model for electrofishing-based estimates to predict amounts and kinds of habitat necessary to sustain populations thought to meet conservation thresholds.

Methods

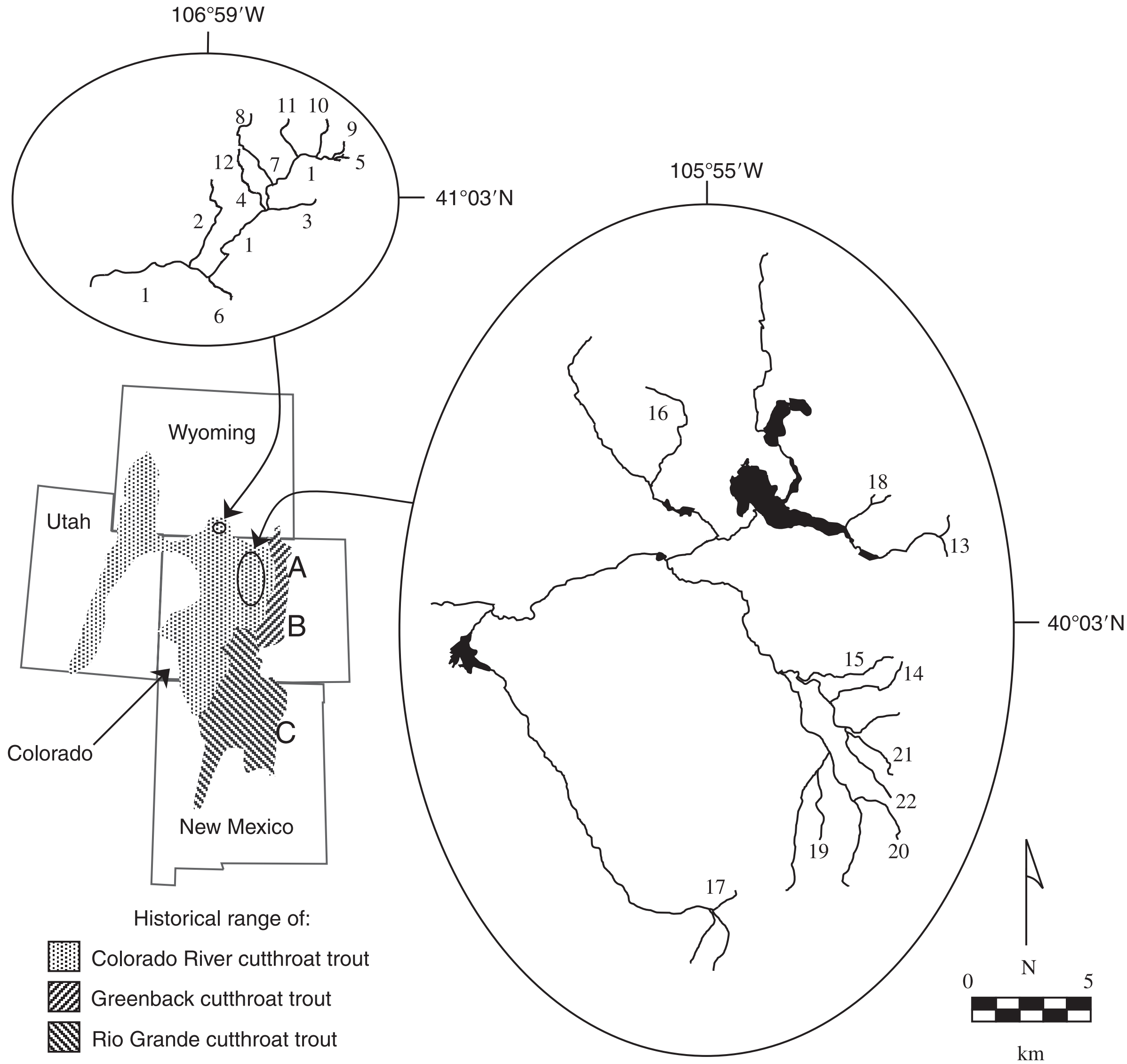
Field sites

To address the first objective, we used three sets of data: electrofishing-based abundance estimates of greenback cutthroat trout in the South Platte River basin in Colorado (N = 9 streams) (Young and Guenther-Gloss 2004) and of Colorado River cutthroat trout in headwater streams in the Little Snake River basin in Wyoming (N = 12) and the upper Colorado River basin in Colorado (N = 10) (Fig. 1). To fulfill the second objective, we used the ocular counts of abundance of 21 populations of greenback cutthroat trout in the South Platte and Arkansas River basins in Colorado and of Rio Grande cutthroat trout in the Rio Grande basin in Colorado and New Mexico (Harig and Fausch 2002). All populations of Colorado River cutthroat trout in Wyoming were believed to be indigenous, whereas those in Colorado were either indigenous or had persisted for decades after stocking (Young et al. 1996). All Rio Grande cutthroat trout and most greenback cutthroat trout populations were relatively recent introductions (Harig and Fausch 2002; Young et al. 2002). Stocks represented a mixed heritage; some were believed to be genetically pure and others were introgressed with nonindigenous cutthroat trout or rainbow trout (*Oncorhynchus mykiss*).

Segments of named streams (from US Geological Survey 1 : 24 000 maps) with allopatric populations of cutthroat trout were typically treated as the sampling units. Barriers to migration (desiccated reaches, artificial barriers, or waterfalls) isolated most populations from upstream invasions of nonnative fishes. In Wyoming, two-way fish migration was possible between all tributaries and the mainstem North Fork Little Snake River (the lower boundary of which was blocked from upstream fish migration by a weir) except the upper portions of Deadman, Harrison, Ted, and Third creeks and the main stem itself, in which water diversions isolated additional populations upstream. Downstream and upstream segments in Deadman and Harrison creeks and the main stem were treated as different sampling units, whereas the short downstream segments of Ted and Third creeks (<450 m) were pooled with the main stem. In the upper North Fork Little Snake main stem and in some Colorado streams, small (<2.5 m bankfull width), short (generally <1000 m) named tributaries to the primary sampling streams were also sampled and pooled with the primary streams for our analyses.

There was broad overlap in the ranges of the physical characteristics of these streams (Table 1) and in climate, hydrology, and trout population characteristics. Most were high-elevation, perennial streams with snowmelt-dominated flows and gravel–cobble–rubble channels. Riparian overstory vegetation usually consisted of coniferous forests of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*) interspersed with sites dominated by quaking aspen (*Populus tremuloides*), deciduous shrubs, and meadows. Because most streams contained barriers, cutthroat trout probably exhibited resident life histo-

Fig. 1. Map of the US central Rocky Mountains showing 22 streams sampled to estimate cutthroat trout (*Oncorhynchus clarkii*) abundance, general locations of previous sampling, and historical ranges of Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*), greenback cutthroat trout (*Oncorhynchus clarkii stomias*), and Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*). Circled areas denote locations of streams sampled in this study (refer to Table 1 for stream names associated with numbers). A, streams with greenback cutthroat trout sampled by Young and Guenther-Gloss (2004) and Harig and Fausch (2002) in the South Platte River basin; B, streams with greenback cutthroat trout sampled by Harig and Fausch (2002) in the Arkansas River basin; C, streams with Rio Grande cutthroat trout sampled by Harig and Fausch (2002).



ries with movements limited to a few kilometres (Young 1996). Cutthroat trout spawned after peak flows from late May to early July and fry typically emerged from August to September. Stream temperatures generally declined markedly by late September, with ice and snow cover often beginning to form in October. The short growing season produced slow-growing fish that rarely exceeded 250 mm total length.

Study design

Methods for estimating fish abundance followed Young and Guenther-Gloss (2004). We measured thalweg length of each stream with a drag tape, flagged 100-m intervals and electrofishing sites, and noted whether fish were present. We surveyed at least 500 m upstream of the last observation of fish or until a stream became largely uninhabitable or unlikely to support many fish (i.e., it was <0.5 m wetted width, above a waterfall, or originated from a spring). All sampling was conducted during late-summer low flows.

We used double sampling (Cochran 1977) to estimate abundance of cutthroat trout ≥75 mm total length (age 1 and older). Crews, usually consisting of one person electrofishing and two people netting, first made a single electrofishing pass without block nets in 25-m reaches at systematic intervals. Intervals between electrofishing reaches varied from 50 to 400 m to ensure an adequate number of samples in the shortest streams and resulted in sampling 5%–45% of each stream (Table 1). For second-stage samples, about every fourth sample reach was electrofished two or three times to produce a multiple-pass removal estimate of trout abundance. This sampling frequency ensured that at least four or

Table 1. Characteristics of cutthroat trout (*Oncorhynchus clarkii*) streams in Wyoming and Colorado used in the models.

Stream	% of stream sampled	Trout abundance (≥75 mm)	Elevation (m)	Occupied stream length (m)	Pools ≥30 cm residual depth	Mean pool bankfull width (m)	Mean July water temperature (°C)
Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*), Little Snake River Basin, Wyoming							
1. NFLSR (lower)	10	4776	2252	14 545	385	7.5	9.7
2. Solomon	10	1705	2327	5 700	62	3.4	10.0
3. Green Timber	25	684	2523	3 150	83	3.3	9.3
4. Harrison (lower)	17	574	2518	2 557	66	2.8	9.7
5. NFLSR (upper)	17	378	2727	2 417	129	2.7	9.2
6. Rose	17	343	2365	1 670	33	3.5	10.1
7. Deadman (lower)	25	308	2584	1 322	45	4.4	9.6
8. Deadman (upper)	19	244	2740	3 175	116	3.4	8.0
9. Rhodine	23	177	2762	1 318	53	2.4	8.7
10. Ted (upper)	25	158	2724	1 940	53	2.7	8.5
11. Third (upper)	23	102	2720	1 315	45	3.0	10.3
12. Harrison (upper)	45	76	2760	553	12	2.0	8.5
Colorado River cutthroat trout), upper Colorado River Basin, Colorado							
13. Buchanan	15	2531	2774	5 725	63	6.5	10.8
14. Cabin	10	1354	2914	6 054	212	5.0	9.7
15. Hamilton	23	798	2865	3 225	46	2.1	8.5
16. Trail	10	594	2780	6 185	131	3.2	9.8
17. McQueary	21	379	3182	2 671	52	5.0	7.7
18. Roaring Fork	23	278	2731	4 164	160	4.9	9.0
19. Little Vasquez	18	115	2920	2 675	130	2.9	7.6
20. Jim	16	102	2853	2 225	10	3.9	7.2
21. Middle Fork Ranch	20	54	2896	2 395	28	4.8	7.7
22. South Fork Ranch	17	30	2939	2 880	26	3.0	8.2
Greenback cutthroat trout (*Oncorhynchus clarkii stomias*), South Platte River Basin, Colorado							
	5–21	170–7347	2323–2926	1 640–13 201	26–172	2.3–4.1	6.1–14.2
Greenback cutthroat trout and Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*), Colorado and New Mexico							
	100	16–1278	2400–3293	1 000–20 500	12–361	2.3–5.4	6.0–14.6

Note: Numbers associated with stream names refer to the numbers in Fig. 1. Ranges for data on greenback cutthroat trout and Rio Grande cutthroat trout are from Harig and Fausch (2002) and Young and Guenther-Gloss (2004). NFLSR, North Fork Little Snake River. Percentage of stream sampled refers to the proportion of occupied stream length sampled for fish by electrofishing or visual methods.

five reaches would be sampled with multiple electrofishing passes in each stream in case calculating stream-specific catchability was required. In wider streams, two electrofishing crews worked side by side. To estimate population size of greenback cutthroat trout in Colorado and in tributaries containing Colorado River cutthroat trout in Wyoming, we multiplied the inverse of overall catchability for each set of streams by mean abundance of fish in single-pass catches in the sample reaches of a particular stream, extrapolated to the length of that stream (Bohlin et al. 1989). We deemed overall catchability appropriate because many of the same individuals (and the same crew leaders) formed these crews annually and they used the same equipment to sample these waters, and within each river basin, geology, habitat type, and riparian vegetation were comparable. Furthermore, we considered the stream-specific estimates based on fewer samples to be less likely to produce accurate estimates of population size in the set of comparable streams than would an estimate of overall catchability. In contrast, the abundance estimates for Colorado River cutthroat trout in Colorado were not collected in the same year and stream-to-stream variation in catchability was higher (M.K. Young, unpublished data); consequently, we used stream-specific catchability estimates to calculate abundance. We also used a separate estimator of catchability to calculate abundance of Colorado River cutthroat trout in the North Fork Little Snake River main stem in Wyoming because it was much larger and catchability was lower than for other streams in this area. All estimates for greenback cutthroat trout streams were based on samples collected in 1999, whereas those for Colorado River cutthroat trout represented the mean of four annual estimates from 1996 to 1999 (Wyoming) or one-time sampling between 1998 and 2002 (Colorado). We regard these population estimates as conservative because depletion electrofishing tends to underestimate abundance (Bohlin 1982; Peterson et al. 2004), although cutthroat trout in small streams typically yield high catchabilities (Dunham et al. 1999; Young and Guenther-Gloss 2004).

Habitat inventories varied by state. For Colorado streams, crews measured habitat in accordance with the methods of Harig and Fausch (2002). They recorded bankfull width, maximum depth, and tail crest depth for pools where pool length was at least half of bankfull width and censused the number of pools with residual depths of at least 30 cm. For streams in Wyoming, habitat components were only measured in electrofishing reaches (10%–45% of each stream); the means for reaches in a stream were extrapolated to the rest of that stream. We regarded such sampling as adequate because it greatly exceeded reach lengths (20–40 wetted or bankfull widths) generally used to describe geomorphic variables (Kaufmann et al. 1999). Also, only wetted width was measured, so we estimated pool bankfull width for Wyoming streams by multiplying pool wetted width by 1.5, the ratio between bankfull and baseflow wetted width based on measurements previously taken in two of the study streams (P.M. Guenther-Gloss, unpublished data).

Water temperatures were measured with thermographs (recording interval ≤2 h) set in relatively deep, well-mixed pools in Wyoming streams in 1997, 1998, and 2000 and in Colorado streams in 2001 and 2002. We used within- and among-stream and climatic comparisons from this 5-year period to develop a standardized mean July water temperature for each stream. Full-month mean July water temperatures were estimated for some Wyoming streams from the ratio of partial- to full-month means for nearby streams with complete July data. In Steelman Creek (Colorado), mean July stream temperature was estimated for 2001 by subtracting the mean difference for all other sampled Colorado streams (1.1 °C) from the 2002 temperature for Steelman Creek. We addressed the potential effect of climatic variation between years by examining annual deviation from the 92-year mean July air temperature at Steamboat Springs, Colorado (located in similar montane topography approximately equidistant between Colorado and Wyoming field sites; Western Regional Climate Center 2003). July air temperature in 1997 did not differ from the 92-year mean; all following years were warmer than average, with 2002 the warmest of all (3.3 °C above the mean). Unadjusted mean July stream temperatures also followed that pattern: all 10 Colorado streams were warmer in 2002 than in 2001, and 9 of 10 comparable Wyoming streams were warmer in 2000 than in 1997 or 1998. Thus, stream temperatures from 1998 to 2002 were adjusted downward using the ratio of study year to 92-year mean July air temperature to minimize effects of annual climatic variation on water temperatures used in the model. Finally, temperatures from multiple recording locations and multiple sampling years were averaged (in part to address other variables influencing water temperature, such as discharge) to provide a single temperature value for each stream.

Analyses

We treated fish abundance as a continuous dependent variable and assessed its relation to occupied stream length (m) and the three variables in the translocation model: mean July water temperature (°C), pool bankfull width (m), and number of pools with residual depths ≥30 cm. We included the latter because it was the simplest estimator of habitat availability and a necessary adjunct to the estimates of population size. Before developing models, we created a correlation matrix to assess collinearity among the physical variables and avoided simultaneous inclusion of those variables with significant correlations >0.60. We then used multiple linear regression to create models of all remaining possible subsets of the four explanatory variables (N = 11 possible models; see below). We examined residuals to detect outliers and heteroscedasticity and to evaluate overall model fit. Consequently, we applied a square root transformation to electrofishing-derived abundance estimates to correct for heteroscedasticity; visual counts required no such transformation. We selected a preferred model for each data set based on three criteria: weights (w) of Akaike's Information Criterion adjusted for small sample sizes (Burnham and Anderson 2002), all regression coefficients significantly different from zero, and ease of measurement of model variables. We considered all models with values of w within 10% of the best approximating model to have reasonable levels of support. To correct for multiple estimates of the significance of regression coefficients, we used a Bonferroni-corrected value of $P \leq 0.0125$ (=0.05/4, where 4 is the number of variables for which we generated estimates). Variables in order of their ease of measurement were water temperature = stream length → pool count = pool bankfull width. We deemed water temperature as one of the two easiest variables to measure because it could be obtained from only two site visits, to set and retrieve thermographs, although measurements needed to be collected in different years to estimate mean values. Occupied stream length was considered comparably easy to obtain because although the entire occupied stream channel needed to be traversed (to measure channel length), detailed surveys were not necessary and a single visit would be adequate to estimate occupied habitat barring dramatic environmental changes. In contrast, counts of pools ≥30 cm residual depth and pool bankfull width could be derived only from whole-stream inventories or extrapolated estimates of measured habitat types. Because streams with electrofishing-based abundance estimates originated from three distinct locations (the South Platte, Colorado, and Little Snake River basins), we included location as a categorical variable in the final regression model to determine whether there was a significant location-level effect (Dunham and Vinyard 1997). We conducted additional validation of the electrofishing-based model by using a jackknife approach, i.e., excluding one observation, reconstructing the model with the 30 remaining observations, predicting the response of the excluded observation, and examining the correlation between predicted and observed abundances (Olden and Jackson 2000).

Finally, we calculated means and 95% inverse prediction intervals (Zar 1984) of stream length predicted to support various population sizes of age-1 and older cutthroat trout based on the preferred model for electrofishing data. This enabled direct comparisons with previous work linking trout abundance to stream size (Hilderbrand and Kershner 2000). We did not consider predictions appropriate for the preferred model for visual counts because such counts may produce unreliable estimates of fish abundance (Bozek and Rahel 1991; Young and Guenther-Gloss 2004). Unless otherwise stated, results of statistical tests were considered significant if $P \leq 0.05$.

Results

Because occupied stream length and number of deep pools were highly correlated (r = 0.82, P < 0.001 for electrofishing estimates; r = 0.80, P < 0.001 for visual counts), we did not include both variables in any model. Of the 11 remaining models for streams with electrofishing estimates, three models including combinations of stream length, water temperature, and pool bankfull width had the highest model

Table 2. Model selection statistics associated with the four highest ranking models relating mean July water temperature, pool bankfull width, counts of pools ≥30 cm residual depth, and occupied stream length to estimates of fish abundance.

Variable(s)	ln(*L*)	*K*	AIC_c	Δ	*w*
Electrofishing counts, Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*) and greenback cutthroat trout (*Oncorhynchus clarkii stomias*)					
Temperature, stream length	–60.926	4	131.390	0.000	0.612
Stream length	–63.499	3	133.887	2.497	0.175
Temperature, pool width, stream length	–60.882	5	134.165	2.775	0.153
Visual counts, greenback cutthroat trout and Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*)					
Temperature, pool count	–103.150	4	216.800	0.000	0.794
Temperature, pool width, pool count	–103.002	5	220.003	3.203	0.160

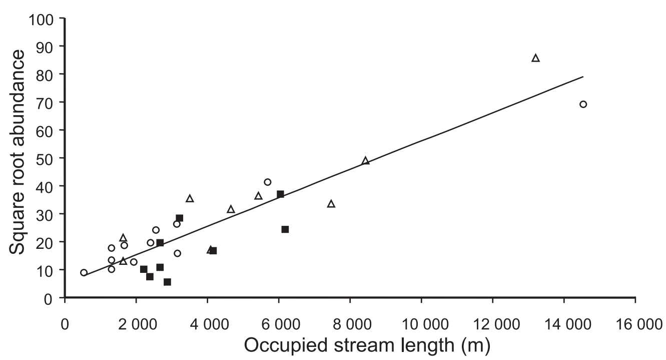
Note: Models are ordered by *w*. ln(*L*), maximized log-likelihood; K, number of parameters; AIC_c, Akaike's Information Criterion adjusted for small sample size; Δ, change in AIC_c; *w*, Akaike weight.

Table 3. Coefficients of variables of the highest ranking models relating mean July water temperature, pool bankfull width, sum of pools ≥30 cm residual depth, and occupied stream length to estimates of fish abundance.

Constant	Mean July water temperature (°C)	Mean pool bankfull width (m)	Pools ≥30 cm residual depth	Occupied stream length (m)
Electrofishing counts, Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*) and greenback cutthroat trout (*Oncorhynchus clarkii stomias*)				
–13.58	2.26*			0.00464*
5.15*				0.00508*
–12.03	2.20*	–0.37		0.00472*
Visual counts, greenback cutthroat trout and Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*)				
–820.69*	91.39*		2.32*	
–903.97*	92.54*	20.74	2.30*	

Note: Models are ordered as in Table 2. An asterisk denotes that a coefficient is statistically different from zero at $P \leq 0.0125$.

Fig. 2. Relation of abundances of Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*) in Colorado (squares) and Wyoming (circles) and greenback cutthroat trout (*Oncorhynchus clarkii stomias*) in Colorado (triangles) to occupied stream length. The line represents the regression model (population size)$^{1/2}$ = 0.00508(occupied stream length (m)) + 5.148.



weights (Table 2). Pool bankfull width was not significantly different from zero (Table 3), so the model containing this variable was not considered further. The model including temperature and stream length had the highest model weight but required more intensive data collection from several years. Despite that it did not have the highest model weight, we regarded the model with stream length alone (Fig. 2) as the preferred model because it was the most parsimonious, required the least effort for data collection, and accounted for a large proportion of the variation in trout abundance (r^2 = 0.81). Also, differences in predicted abundances between the preferred model and best approximating model were small (median = 81 fish, range = 3–789 fish). For streams with visual counts, the best approximating model included stream temperature and number of deep pools as variables. The only other model with a reasonable level of support included those two variables and pool bankfull width. Because the latter variable was again not significantly different from zero, we regarded the best approximating model as the preferred model for visual counts.

Dummy regression with stream location and occupied stream length in a model using electrofishing estimates indicated that stream location did not substantially affect the model (i.e., neither the location coefficient (P = 0.43) nor location × length coefficient (P = 0.95) was significantly different from zero); thus, pooling locations in the preferred model was acceptable (Fig. 2). Jackknife validation suggested that the preferred model for electrofishing-based data was very precise (r = 0.88) but biased (slope coefficient = 0.80, 95% confidence interval = 0.63–0.97).

Table 4. Means and 95% inverse prediction intervals of stream length predicted to support particular population sizes of age-1 and older cutthroat trout (*Oncorhynchus clarkii*) and stream length predictions from Hilderbrand and Kershner (2000) assuming a density of 200 fish·km^{-1}.

		95% prediction interval		
Population size	Predicted stream length (m)	Lower bound	Upper bound	Predicted stream length (m) (200 fish·km^{-1})
500	3 387	2 923	3 800	2 500
1000	5 209	4 783	5 710	5 000
2000	7 787	7 107	8 718	10 000
2500	8 825	8 008	9 965	12 500
5000	12 901	11 497	14 907	25 000

Projections of stream length needed to produce populations of 500–5000 age-1 and older cutthroat trout reflected the form of the relation between abundance and occupied stream length (Table 4). Assuming a uniform density of 200 fish·km^{-1} (as in Hilderbrand and Kershner 2000) slightly underestimated necessary stream lengths for small populations but greatly overestimated habitat needed to produce the largest populations.

Discussion

In the streams that we evaluated, occupied stream length was the single best predictor of cutthroat trout abundance. Bradford et al. (1997) reported a similar pattern for coho salmon (*Oncorhynchus kisutch*) smolts in western North America. Other studies have demonstrated that basin area, arguably a surrogate of stream length, is highly correlated with the presence or size of salmonid populations (Kruse 1998; Dunham and Rieman 1999; Dunham et al. 2002). Harig and Fausch (2002) noted that basin area was the only landscape-scale variable correlated with translocation success of cutthroat trout but offered little predictive power. Occupied stream length, however, is a more accurate measure of habitat availability than basin area (Dunham et al. 2002) because it accounts for the presence of natural barriers that constrain distributions of fish populations. Such barriers commonly limited the upstream and downstream extent of the allopatric populations that we sampled and defined habitat patches supporting discrete populations. Not addressed by our models were possible barriers within the occupied patches. Whether these were current obstructions to upstream migration could not be ascertained because allopatric populations of cutthroat trout occupied the areas upstream and downstream. Within-patch barriers would create subpopulations in a stream, with the upstreammost segment isolated from patches downstream and at greater risk of extinction from extreme disturbance (Dunham et al. 1999; Kruse et al. 1997). Data on emigration and immigration rates in a more advanced model would enable these streams to be evaluated as a series of partially isolated segments rather than as the cumulative total of occupied habitat.

We attribute the contrast in the response of fish abundance in the different models, as a function of the square of occupied stream length in the electrofishing-based model and as a linear function of water temperature and deep pool counts in the model for visual counts, to four factors. First, we suspect that colder streams probably diminished trout activity and detectability by observers (Thurow 1994). Second, efficiency of visual sampling probably declined as stream size and depth increased (Heggenes et al. 1990), and Young and Guenther-Gloss (2004) noted that visual counts ranged from 1% to 24% of electrofishing estimates and were only weakly correlated with them. Third, the absence of deep pool counts from the preferred model for electrofishing data implied that deep pools accounted for habitat availability less well than a more generic measure of available habitat or that rules for defining deep pools (i.e., that they be at least half as long as the bankfull width and at least 30 cm residual depth) excluded much suitable habitat. Alternatively, this variable may have been important in the original translocation model because trout are more easily observed in deep pools rather than in more turbulent or shallower sites, a bias much less evident in electrofishing data (Heggenes et al. 1990). Fourth, Bradford et al. (1997) noted that streams must be fully seeded for the habitat size – fish abundance relation to hold. Most streams that we sampled had supported cutthroat trout populations for decades and had little angling mortality; thus, populations may have approached the carrying capacity of the habitat, whereas Harig and Fausch (2002) examined populations of more recent origin in which this relation would be less certain. Also, streams with marginally successful translocations could be markedly influenced by small differences in pool numbers, width, or temperature, and some unsuitable patches may contain populations whose long-term persistence is unlikely (Morita and Yamamoto 2002). Consequently, we cannot regard the model based on visual counts as validating the model based on electrofishing estimates but believe that this discrepancy arose primarily from differences in the sampling methodologies used and streams chosen rather than shortcomings of the electrofishing-based model.

The failure of pool bankfull width to be included in either preferred model or to be significantly related to fish abundance when considered alone, despite that longer and presumably wider streams contained greater densities of fish, may have resulted from where bankfull width was measured. Pool bankfull width is a function not only of stream size but also of pool type, and because plunge, dammed, lateral scour, and trench pools have unique morphologies, variation attributable to pool type could overwhelm trends in width associated with stream size. Traditionally, measurements of bankfull width have been obtained in riffles or other channel units of fairly homogeneous width (Rosgen 1996), and we suspect that more consistent measures of overall stream width that enabled estimates of stream area may have been included in a preferred model and improved its performance.

Alternatively, because abundance increased in proportion to the square of occupied stream length in the electrofishing-based model, this relation may reflect increases in both habitat availability and diversity. Not only is supplemental habitat present in longer streams, but they are more likely to contain a complete suite of complementary habitats (e.g., temperature refugia, off-channel ponds, overwintering pools, summer rearing sites, or spawning areas suitable at varying flows) (Rieman and McIntyre 1995; Schlosser and Angermeier 1995). The lack of upstream–downstream trends in cutthroat trout density in these and other Rocky Mountain streams (Young and Guenther-Gloss 2004; M.K. Young, unpublished data) implies that habitat complexity contributes to the functional response between abundance and stream length. Also, temporal variation in habitat availability and the magnitude of disturbance are more pronounced in smaller streams and may influence this pattern.

The square root transformation of electrofishing estimates of fish abundance was necessary because the variance about the estimates increased with increasing stream size, producing a wedge-shaped distribution of points (Terrell et al. 1996). Theoretically, quantile regression on the uppermost distribution of points might suggest maximum carrying capacities that could be produced by streams of a given length (Dunham et al. 2002). Yet because none of the other habitat variables that we examined were included in the final regression model, we can offer little guidance on what habitat elements might be suppressing fish abundance in streams below such a regression line. This variation may also have arisen in part from the collection of abundance data in different years. Regardless, it seems more reasonable for rare subspecies of cutthroat trout to estimate average, rather than maximum, fish abundances when evaluating streams for introductions or the viability of existing populations.

To address issues of model precision and generality (Fausch et al. 1988), we tried to ensure that streams from different basins shared similar environmental characteristics and that sample sizes were adequate. Although cross-validation of the electrofishing-based model demonstrates that it is fairly accurate, the inherent bias (probably introduced by the square root transformation of abundance) limits its generality. Therefore, applications of the preferred model for electrofishing estimates should be restricted to systems comparable to those that we evaluated: small, high-elevation streams warm enough to permit recruitment. This model does not apply where high water temperatures (>22 °C) limit survival and growth (Dunham et al. 2003; Schrank et al. 2003). The streams used to develop the preferred model also were relatively free of human-associated disturbance, other than summer water withdrawals in some systems. Land management has often been associated with the decline in or absence of salmonid populations (Poff and Huryn 1998; Dunham and Rieman 1999; Pess et al. 2002); thus, populations in altered systems may not conform to model predictions. In addition, we urge care in applying the model to streams subsidized by lake populations or interrupted by large numbers of beaver ponds. Although we included one such stream, McQueary Creek, in our sampling, a headwater lake possibly inflated the abundance and certainly the size of cutthroat trout; four of the eight largest trout that we sampled overall were in the vicinity of the lake. Finally, we suggest caution in applying the model to other subspecies. For example, whereas occupied stream length was significantly positively correlated ($r^2 = 0.71$, $P < 0.001$, $N = 19$) with the square root of abundance of allopatric Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) in streams in the Bighorn River basin in Wyoming (Kruse et al. 2001, p. 6), the slope coefficient ($b = 0.00259$) was about half that ($b = 0.00508$) in the equation for streams in the central Rocky Mountains. That abundance still increased as the square of occupied stream length suggests that this functional relation may have some generality and merits testing with other subspecies in small, cold streams.

A variety of sources have hypothesized that persistence of trout populations, particularly with respect to long-term evolutionary potential, is related to abundances of 500–5000 fish (McIntyre and Rieman 1995; Allendorf et al. 1997; Hilderbrand and Kershner 2000). Our estimates of mean stream lengths necessary to produce populations of these sizes differed from those of Hilderbrand and Kershner (2000) because they assumed constant cutthroat trout densities of 100–300 fish·km^{-1}, whereas we found that trout density was positively correlated with occupied stream length and ranged from 10 to 557 fish·km^{-1}. Nevertheless, both analyses imply that many streams containing cutthroat trout support populations well below thresholds thought to afford resilience to environmental perturbation and loss of genetic variation (Allendorf et al. 1997; McElhany et al. 2000). For example, mean length of all recovery streams for greenback cutthroat trout was 4790 m (Young et al. 2002), for which we would predict a population size of 870 fish ≥75 mm (95% confidence interval = 701–1057 fish). Similarly, 40% of streams constituting the core conservation populations for Colorado River cutthroat trout in Colorado, Utah, and Wyoming are no more than 3000 m long (US Fish and Wildlife Service 2004); on average streams of this length would be predicted to contain 416 or fewer fish (95% confidence interval = 298–554 fish). Encouragingly, the preferred model demonstrated that relatively minor increases in habitat length led to disproportionately greater increases in abundance, implying that extending available habitat, particularly the downstream end, might be a key strategy for enhancing population viability.

Selecting streams for reintroductions and evaluating viability of existing populations of rare subspecies of cutthroat trout are politically controversial, biologically critical, and fraught with uncertainty (Young and Harig 2001). We believe that use of the preferred model for electrofishing data can reduce the ambiguity associated with predicting potential average size of reintroduced populations or mean size of unsampled populations, with two additional caveats. First, although map-derived estimates of potential occupied stream length may be a useful first approximation, the importance of barriers in structuring populations mandates that lengths be verified by field surveys. Second, there is substantial support that mean July water temperature was positively related to fish abundance in models based on electrofishing estimates and visual counts, probably reflecting increases in productivity at warmer temperatures. More importantly, because low water temperatures (mean summer water temperature <7.5 °C) can inhibit cutthroat trout recruitment (Harig and Fausch 2002; Peterson 2002; M. Coleman and K.D. Fausch, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, USA, unpublished data), prudent management dictates that decisions on conservation priorities and habitat protection must also consider whether summer water temperatures surpass the threshold necessary for successful recruitment. A single year of data collection might be sufficient to demonstrate whether temperatures are likely to be sufficiently warm. Finally, in the event that estimates of mean July water temperature and stream length are available, use of the model containing both variables will provide slightly more accurate estimates of population size.

Acknowledgements

We thank many individuals for help in the field and G. Horstman, K. Rogers, and B. Atkinson (Colorado Division of Wildlife) and A. Harig (Trout Unlimited) for sharing data. We also thank J. Dunham, A. Harig, D. Schmetterling, K. Rogers, and an anonymous reviewer for their comments on earlier drafts of the manuscript and R. King for a thorough biometrical review. The US Forest Service through the Arapaho-Roosevelt National Forests, Medicine Bow-Routt National Forests, Rocky Mountain Research Station, Region 2 Fish Habitat Relationships Program, and the interregional Inland Cutthroat Trout Initiative provided funding for this work.

References

Allendorf, F.W., Bayles, D., Bottom, D.L., Currens, K.P., Frissell, C.A., Hankin, D., Lichatowich, J.A., Nehlsen, W., Trotter, P.C., and Williams, T.H. 1997. Prioritizing Pacific salmon stocks for conservation. Conserv. Biol. **11**: 140–152.

Behnke, R.J. 1992. Native trout of western North America. Am. Fish. Soc. Monogr. No. 6.

Bohlin, T. 1982. The validity of removal method for small populations — consequences for electrofishing practice. Inst. Freshw. Res. Drottningholm Rep. **60**: 15–18.

Bohlin, T., Hamrin, S., Heggberget, T.G., Rasmussen, G., and Saltveit, S.J. 1989. Electrofishing — theory and practice with special emphasis on salmonids. Hydrobiologia, **173**: 9–43.

Bozek, M.A., and Rahel, F.J. 1991. Comparison of streamside visual counts to electrofishing estimates of Colorado River cutthroat trout fry and adults. N. Am. J. Fish. Manag. **11**: 38–42.

Bozek, M.A., and Rahel, F.J. 1992. Generality of microhabitat suitability models for young Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) across sites and among years in Wyoming streams. Can. J. Fish. Aquat. Sci. **49**: 552–564.

Bradford, M.J., Taylor, G.C., and Allan, J.A. 1997. Empirical review of coho salmon smolt abundance and the prediction of smolt production at the regional level. Trans. Am. Fish. Soc. **126**: 49–64.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer, New York.

Cochran, W.G. 1977. Sampling techniques. 3rd ed. John Wiley & Sons, New York.

CRCT Task Force. 2001. Conservation agreement and strategy for Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in the states of Colorado, Utah, and Wyoming. Colorado Division of Wildlife, Fort Collins, Co.

Duff, D. (*Editor*). 1996. Conservation assessment for inland cutthroat trout: distribution, status and habitat management implications. US For. Serv. Northern, Rocky Mountain, Intermountain, and Southwestern Regions, Logan, Utah.

Dunham, J.B., and Rieman, B.E. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. Ecol. Appl. **9**: 642–655.

Dunham, J.B., and Vinyard, G.L. 1997. Incorporating stream level variability into analyses of site level fish habitat relationships: some cautionary examples. Trans. Am. Fish. Soc. **126**: 323–329.

Dunham, J.B., Peacock, M.M., Rieman, B.E., Schroeter, R.E., and Vinyard, G.L. 1999. Local and geographic variability in the distribution of stream-living Lahontan cutthroat trout. Trans. Am. Fish. Soc. **128**: 875–889.

Dunham, J.B., Cade, B.S., and Terrell, J.W. 2002. Influences of spatial and temporal variation on fish–habitat relationships defined by regression quantiles. Trans. Am. Fish. Soc. **131**: 86–98.

Dunham, J.B., Schroeter, R., and Rieman, B. 2003. Influence of maximum water temperature on occurrence of Lahontan cutthroat trout within streams. N. Am. J. Fish. Manag. **23**: 1042–1049.

Fausch, K.D., Hawkes, C.L., and Parsons, M.G. 1988. Models that predict standing crop of stream fish from habitat variables: 1950–1985. US For. Serv. Gen. Tech. Rep. PNW-GTR-213.

Harig, A.L., and Fausch, K.D. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. Ecol. Appl. **12**: 535–551.

Harig, A.L., Fausch, K.D., and Guenther-Gloss, P.M. 2000. Application of a model to predict success of cutthroat trout translocations in central and southern Rocky Mountain streams. *In* Wild trout VII. *Edited by* D. Schill, S. Moore, P. Byorth, and B. Hamre. Trout Unlimited, Bethesda, Md. pp. 141–148.

Heggenes, J., Brabrand, Å., and Saltveit, S.J. 1990. Comparison of three methods for studies of stream habitat use by young brown trout and Atlantic salmon. Trans. Am. Fish. Soc. **119**: 101–111.

Hepworth, D.K., Ottenbacher, M.J., and Berg, L.N. 1997. Distribution and abundance of native Bonneville cutthroat trout (*Oncorhynchus clarki utah*) in southwestern Utah. Great Basin Nat. **57**: 11–20.

Hilderbrand, R.H. 2002. Simulating supplementation strategies for restoring and maintaining stream resident cutthroat trout populations. N. Am. J. Fish. Manag. **22**: 879–887.

Hilderbrand, R.H. 2003. The roles of carrying capacity, immigration, and population synchrony on persistence of stream-resident cutthroat trout. Biol. Conserv. **110**: 257–266.

Hilderbrand, R.H., and Kershner, J.L. 2000. Conserving inland cutthroat trout in small streams: how much stream is enough? N. Am. J. Fish. Manag. **20**: 513–520.

Kaufmann, P.R., Levine, P., Robison, E.G., Seeliger, C., and Peck, D.V. 1999. Quantifying physical habitat in wadeable streams. EPA/620/R-99/003. US Environmental Protection Agency, Washington, D.C.

Kruse, C.G. 1998. Influence of non-native trout and geomorphology on the distributions of indigenous trout in the Yellowstone River drainage of Wyoming. Ph.D. dissertation, University of Wyoming, Laramie, Wy.

Kruse, C.G., Hubert, W.A., and Rahel, F.J. 1997. Geomorphic influences on the distribution of Yellowstone cutthroat trout in the Absaroka Mountains, Wyoming. Trans. Am. Fish. Soc. **126**: 418–427.

Kruse, C.G., Hubert, W.A., and Rahel, F.J. 2001. As assessment of headwater isolation as a conservation strategy for cutthroat trout in the Absaroka Mountains of Wyoming. Northwest Sci. **75**: 1–11.

McElhany, P., Ruckelshaus, M.H., Ford, M.J., Wainwright, T.C., and Bjorkstedt, E.P. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. NOAA Tech. Memo. NMFS-NWFSC-42.

McIntyre, J.D., and Rieman, B.E. 1995. Westslope cutthroat trout. *In* Conservation assessment for inland cutthroat trout. *Edited by* M.K. Young. US For. Serv. Gen. Tech. Rep. RM-GTR-256. pp. 1–15.

Morita, K., and Yamamoto, S. 2002. Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. Conserv. Biol. **16**: 1318–1323.

Olden, J.D., and Jackson, D.A. 2000. Torturing data for the sake of generality: how valid are our regression models? Ecoscience, **7**: 501–510.

Pess, G.R., Montgomery, D.R., Steel, E.A., Bilby, R.E., Feist, B.E., and Greenberg, H.M. 2002. Landscape characteristics, land use, and coho salmon (*Oncorhynchus kisutch*) abundance, Snohomish River, Wash., U.S.A. Can. J. Fish. Aquat. Sci. **59**: 613–623.

Peterson, D.P. 2002. Population ecology of an invasion: demography, dispersal, and effects of nonnative brook trout on native cutthroat trout. Ph.D. dissertation, Colorado State University, Fort Collins, Co.

Peterson, J.T., Thurow, R.F., and Guzevich, J.W. 2004. An evaluation of multipass electrofishing for estimating the abundance of stream-dwelling salmonids. Trans. Am. Fish. Soc. **133**: 462–475.

Poff, N.L., and Huryn, A.D. 1998. Multi-scale determinants of secondary production in Atlantic salmon (*Salmo salar*) streams. Can. J. Fish. Aquat. Sci. **55**(Suppl.): 201–217.

Rieman, B.E., and McIntyre, J.D. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Trans. Am. Fish. Soc. **124**: 285–296.

Rosgen, D. 1996. Applied river morphology. Wildland Hydrology, Pagosa Springs, Co.

Schlosser, I.J., and Angermeier, P.L. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. Am. Fish. Soc. Symp. **17**: 392–401.

Schrank, A.J., Rahel, F.J., and Johnstone, H.C. 2003. Evaluating laboratory-derived thermal criteria in the field: an example involving Bonneville cutthroat trout. Trans. Am. Fish. Soc. **132**: 100–109.

Terrell, J.W., Cade, B.S., Carpenter, J., and Thompson, J.M. 1996. Modeling stream fish habitat limitations from wedge-shaped patterns of variation in standing stock. Trans. Am. Fish. Soc. **125**: 104–117.

Thurow, R.F. 1994. Underwater methods for study of salmonids in the Intermountain West. US For. Serv. Gen. Tech. Rep. INT-GTR-307.

US Fish and Wildlife Service. 1998. Greenback cutthroat trout recovery plan. US Fish and Wildlife Service, Denver, Co.

US Fish and Wildlife Service. 2004. Endangered and threatened wildlife and plants; 90-day finding on a petition to list the Colorado River cutthroat trout. Fed. Regist. **69**: 21151–21158.

Western Regional Climate Center. 2003. Monthly average air temperature at Steamboat Springs, Colorado (Site 057936) for the period 1910–2003. Desert Research Institute. Available from http://www.wrcc.dri.edu [accessed 10 December 2003].

Young, M.K. 1996. Summer movements and habitat use by Colorado River cutthroat trout in small, montane streams. Can. J. Fish. Aquat. Sci. **53**: 1403–1408.

Young, M.K., and Guenther-Gloss, P.M. 2004. Population characteristics of greenback cutthroat trout in streams: their relation to model predictions and recovery criteria. N. Am. J. Fish. Manag. **24**: 184–197.

Young, M.K., and Harig, A.L. 2001. A critique of the recovery of greenback cutthroat trout. Conserv. Biol. **15**: 1575–1584.

Young, M.K., Schmal, R.N., Kohley, T.W., and Leonard, V.G. 1996. Conservation status of Colorado River cutthroat trout. US For. Serv. Gen. Tech. Rep. RM-GTR-282.

Young, M.K., Harig, A.L., Rosenlund, B., and Kennedy, C. 2002. Recovery history of greenback cutthroat trout: population characteristics, hatchery involvement, and bibliography. Version 1.0. US For. Serv. Gen. Tech. Rep. RMRS-GTR-88WWW. Available from http://www.fs.fed.us/rm/pubs/rmrs_gtr88.

Zar, J.H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, N.J.