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# MINIMUM HABITAT REQUIREMENTS FOR ESTABLISHING TRANSLOCATED CUTTHROAT TROUT POPULATIONS

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*Abstract.* Translocation is an important management strategy in conservation programs for endangered or threatened species, including native cutthroat trout (*Oncorhynchus clarki*) in the western United States. Most subspecies of cutthroat trout have declined to <5% of their historical range, and both historical and translocated populations now persist in small isolated fragments of habitat. Success rates for translocations of fishes are generally <50%, and habitat quality or quantity are frequently cited as the cause of failure. Therefore, we conducted field surveys of stream-scale habitat and measured basin-scale habitat using a Geographic Information System for 27 streams where two subspecies of cutthroat trout were translocated in Colorado and New Mexico, to identify specific habitat attributes that contribute to the success of translocations.

We used polytomous logistic regression to develop models that predict three categories of cutthroat trout translocation success (high, low, absent) from habitat attributes at two spatial scales. Models based on stream-scale habitat attributes indicated that cold summer water temperature, narrow stream width, and lack of deep pools limited translocations of cutthroat trout. Cold summer temperatures are known to delay spawning and prolong egg incubation, which reduces the growth of fry and likely limits their overwinter survival. Furthermore, small streams with few deep pools may lack the space necessary to permit overwinter survival of a sufficient number of individuals to sustain a population. Models based on basin-scale habitat were not as effective as stream-scale habitat models for distinguishing among translocation sites with high, low, or absent population status but indicated that a minimum watershed area of 14.7 $km^2$ was useful as a coarse filter for separating sites with high numbers of cutthroat trout from those with low or absent status. Watersheds larger than this are expected to encompass low-elevation habitat that provides warmer summer temperatures and to have relatively wide stream channels of sufficient length to provide an adequate number of deep pools. These results indicate that the appropriate scale of habitat measurement for predicting cutthroat trout translocation success in fragmented watersheds is at the patch rather than landscape scale, which is similar to results for other salmonids and vertebrate taxa in general.

*Key words: cutthroat trout; greenback cutthroat trout; habitat fragmentation; information-theoretic approach; landscape scale; patch scale; polytomous logistic regression; restoration; Rio Grande cutthroat trout; salmonid habitat; translocation.*

## INTRODUCTION

Translocation of individuals to establish, reestablish, or supplement a population is an important management strategy in the conservation of endangered or threatened animals (Griffith et al. 1989). In reviews of recovery plans for threatened or endangered species, 70% of all recovery programs (Tear et al. 1993), and over 80% of programs for fish (Williams et al. 1988), called for translocations. Some highly publicized translocation programs have successfully founded self-sustaining populations (e.g., American bison [*Bison bison*], Kleiman 1989; Peregrine Falcon [*Falco peregrinus*], Millsap et al. 1998), establishing translocation as an effective management tool. However, success rates for translocations of birds, mammals, and fish are generally <50% (Williams et al. 1988, Griffith et al. 1989, Simons et al. 1989, Hendrickson and Brooks 1991, Harig et al. 2000*a*), with habitat quality of the translocation site, number of individuals released, and the proximity of the site to the core of the species' historical distribution cited as the main factors influencing success (Griffith et al. 1989, Wolf et al. 1996, 1998). Although these general patterns are useful for identifying research needs, they do not provide specific information for selecting a translocation site with a high probability of success. Numbers of individuals needed to establish self-sustaining populations and factors defining sufficient habitat are specific to particular taxa. Unfortunately, most translocations have been inadequately studied, monitored, and reported (Minckley 1995, Hodder and Bullock 1997), so there is a need for quantitative assessment of specific ecological factors that contribute to the success or failure of translocations.

Native subspecies of cutthroat trout (*Oncorhynchus*

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*clarki*) in the western United States have been reduced to a small portion of their historical range, nearly all <5%, primarily due to habitat degradation and interactions with nonnative salmonids (Gresswell 1988, Behnke 1992, Young 1995*a*). Of the 14 subspecies recognized (Behnke 1992, three are undescribed), two are extinct, three are listed as threatened under the Endangered Species Act, and conservation plans have been developed for most others. Establishing new cutthroat trout populations through translocation of genetically pure trout into fishless waters or those treated with toxicants to remove nonnative salmonids remains one of the few management strategies available to increase their range (Stuber et al. 1988, Young 1995*b*, USFWS 1998). However, of 37 attempts to establish allopatric populations of greenback cutthroat trout (*O. c. stomias*), only 38% were successful, whereas 30% were reinvaded by nonnative salmonids, 27% apparently had unsuitable habitat, and 5% were suppressed by other factors (Harig et al. 2000*a*). Similarly, 46% of 28 Rio Grande cutthroat trout (*O. c. virginalis*) translocations established naturally reproducing populations, whereas 32% were reinvaded, and 21% had unsuitable habitat (Harig and Fausch 1996, Alves 1998; A. L. Harig and K. D. Fausch, *unpublished data*, New Mexico Department of Game and Fish [NMDGF], *unpublished data*). Reinvasion by nonnative salmonids results in translocation failure because cutthroat trout readily hybridize with spring-spawning rainbow trout (*O. mykiss*), and are apparently displaced by fall-spawning brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*, Wang and White 1994). Isolating barriers, while protecting some cutthroat trout populations from upstream migration of nonnative salmonids, restrict them to areas that may be too small or have insufficient habitat to support a viable population (Moyle and Sato 1991, Moyle and Yoshiyama 1994). Therefore, an analysis of cutthroat trout translocations to identify factors that promote establishment and persistence of populations is likely to improve the success of future translocations.

Habitat quality is considered an essential component of translocation success (IUCN 1987, 1995, Kleiman 1989, Minckley 1995) and was the factor most often cited as leading to translocation failure (Griffith et al. 1989, Wolf et al. 1996, 1998). Success requires habitat of sufficient quality to meet the life history requirements of the species (Williams et al. 1988) and of sufficient area to support a self-sustaining population despite demographic and environmental stochasticity (Moyle and Sato 1991). In effect, some conservation programs for mammals have recommended against translocations because insufficient habitat was available (Ruth et al. 1998, Struhsaker and Siex 1998). Therefore, research on the minimum habitat requirements of a species may be necessary to identify suitable translocation sites, particularly if factors contributing to translocation failure are unknown (Hodder and Bullock 1997).

There are few empirical data on minimum habitat requirements for entire salmonid populations because fish ecologists have historically focused on fine spatial scales to understand how environmental factors influence local abundance and dynamics (cf. Gowan et al. 1994, Schlosser and Angermeier 1995). High natural spatial and temporal variation among sites at fine spatial scales can mask factors that influence stream fish populations (Hicks et al. 1991, Dunham and Vinyard 1997, Lohr and Fausch 1997), resulting in habitat models that lack generality beyond the stream or watershed for which they were developed (Fausch et al. 1988, Rieman and McIntyre 1995). Moreover, many stream fishes vary their habitat use during their life cycle, requiring different temperatures, flow, substrate, and physical structure at each life history stage (Bisson et al. 1981, Schlosser 1995). These habitats may be separated (Schlosser 1991, Schlosser and Angermeier 1995), especially in disturbed watersheds (Fausch et al. 1995), so fine spatial scales may not capture the spatial heterogeneity and connectivity of habitat patches needed to maintain persistent populations (Torgersen et al. 1999, Labbe and Fausch 2000). Therefore, analyses that include coarse-scale processes are likely to be most appropriate for stream populations of salmonids like cutthroat trout.

The goal of our research was to identify macrohabitat attributes that promote establishment and persistence of translocated native cutthroat trout populations isolated in high-elevation headwater streams by fish movement barriers. Based on the literature of stream salmonid ecology, we developed a series of a priori hypotheses about stream-scale and basin-scale habitat attributes that potentially limit translocated cutthroat trout populations. At the stream scale, persistent salmonid populations require sufficient habitat to support enough adults to sustain a population, refuge from high flow during spring snowmelt runoff, sufficient clean (i.e., silt-free) gravel to construct spawning redds, optimum summer temperatures to allow spawning, incubation, and emergence prior to the onset of winter, and refuge from low temperature and low flow during winter (Bisson et al. 1981, Behnke 1992). Therefore, we predicted that cutthroat trout persistence is less likely in streams having short length, few pools, small or shallow pools, pools with little physical structure providing refuges from flow, little clean spawning gravel, or low winter or summer water temperatures.

Stream ecosystems may be viewed as hierarchically organized physical environments (Frissell et al. 1986), so theoretically the functional processes that structure basins at coarser scales (i.e., subbasin and drainage basin) also influence habitat at the stream scale (Platts 1979, Lanka et al. 1987, Poff 1997). Thus, basin-scale factors that govern vegetative patterns, drainage networks, erosive mechanisms, and fluvial processes should be useful for predicting potential habitat quality for stream salmonids (Poff and Ward 1989, Nelson et al. 1992, Rieman and McIntyre 1995). For example, streams at high elevation and latitude or with a north-facing aspect may have colder temperature regimes that cannot support overwintering trout or successful reproduction, and those with high basin relief and steep channel slope may not have sufficient refuge from high flow, especially for juveniles. Based on this theory, we predicted that cutthroat trout persistence is less likely in sites with small watershed area, short channel length, high elevation, high basin relief, high latitude, steep channel slope, or a north-facing aspect.

For study, we chose greenback and Rio Grande cutthroat trout, two subspecies with nearly identical ecological requirements. We compared habitat attributes at stream and basin scales in streams where translocations successfully established a naturally reproducing population to those where translocated populations were extirpated for reasons apparently related to habitat size or quality rather than invasion by nonnative salmonids. We developed models using habitat attributes measured at these two scales based on our hypotheses about salmonid ecology and selected the models that best predicted probability of translocation success. These models will be valuable to managers for choosing future restoration sites with a high probability of establishing a cutthroat trout population through translocation and for identifying whether populations in fragments of historical habitat are likely to persist.

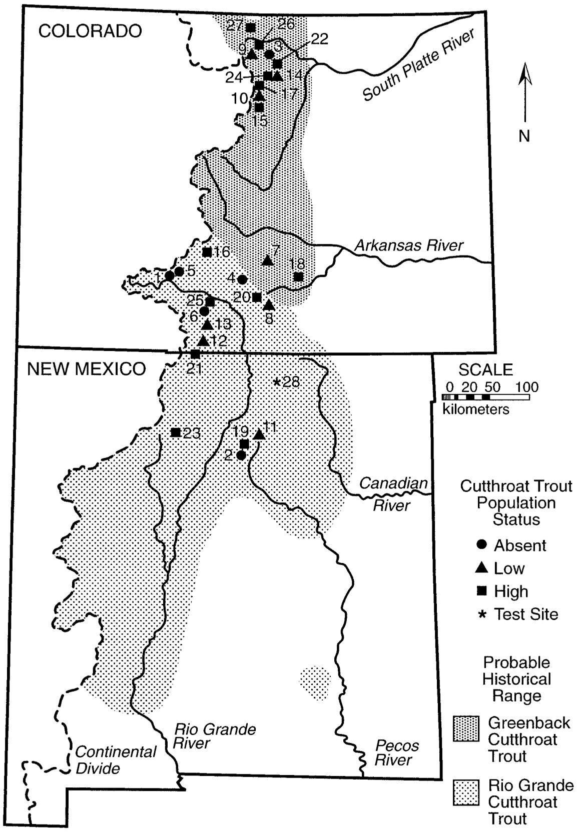


FIG. 1. Approximate historical range of greenback and Rio Grande cutthroat trout (adapted from Behnke 1992; Stumpff and Cooper 1996) and location of the 28 study streams where cutthroat trout were translocated. Stream numbers correspond to Table 1.

## METHODS

### *Study sites*

We selected 27 cutthroat trout translocation streams (12 greenback and 15 Rio Grande) in Colorado and New Mexico for study (Fig. 1, Table 1). These sites represented all but two known stream translocations not invaded by nonnative salmonids of these cutthroat trout subspecies made throughout their historical range through 1995 (Harig and Fausch 1996, Harig et al. 2000*a*; NMDGF, *unpublished data*). Streams were surveyed a median of 13 yr after initial translocation (range 3–31 yr), which we judged to be long enough for natural reproduction to occur and numbers to increase, or for the population to decline or die out. We also included one stream where a translocation was conducted in 1997 as a test site to demonstrate use of the final model. Translocations into lakes alone were excluded because lake and stream habitat are not directly comparable.

Before translocation of wild or hatchery cutthroat trout, streams were either barren of fish or chemically treated with a fish toxicant (antimycin or rotenone) to remove nonnative salmonids. Unpublished data from natural resource agencies on the frequency, number, size, and source (hatchery-reared, wild broodstock, or wild) of translocated cutthroat trout were incomplete (Harig 2000), but did not suggest that initial stocking practices influenced success of most cutthroat trout translocations. In some streams, cutthroat trout populations were established from introductions of relatively few wild fish (e.g., 182 for San Francisco Creek), whereas others failed to support high numbers of cutthroat trout despite repeated stocking of both hatchery and wild individuals (e.g., five stocking events totaling >6200 individuals in May Creek). Typically, Rio Grande cutthroat trout populations were founded from one to three translocations averaging 30 to 1000 wild fish ranging from fry to small adults (15 cm). Most greenback cutthroat trout populations were founded from two to five introductions of 400 to 5000 hatchery fry and juveniles (<8 cm), although small adults were sometimes included.

All translocation sites (Table 1) were streams above 2400 m in elevation with headwaters extending up to 3600 m. Habitat generally alternated between steep, forested reaches with conifers in riparian zones, and low-gradient, meandering reaches lined with forbs, willows (*Salix* spp.), or cottonwoods (*Populus* spp.). Mean channel gradients, measured from digital data using a Geographic Information System (GIS), ranged from 7.3% to 20.2%, but were likely higher than actual gra-

TABLE 1. Characteristics of the 28 study streams in Colorado and New Mexico where cutthroat trout were translocated.

| Stream | Stream | Subspecies | Translocation year | Number of age-1 and older trout | Stream length (km) |
|---|---|---|---|---|---|
| Absent status | | | | | |
| 1 | Benito Creek | RG | 1985 | 0 | 2.6 |
| 2 | Doctor Creek | RG | 1995 | 0 | 3.5 |
| 3 | Hourglass Creek | GB | 1965 | 0 | 2.8 |
| 4 | Little Medano Creek | RG | 1986 | 3 | 3.1 |
| 5 | Unknown Creek | RG | 1985 | 1 | 3.7 |
| 6 | West Fork San Francisco Creek | RG | 1979 | 0 | 4.6 |
| Mean (SE) | | | | | |
| Low numbers of trout | | | | | |
| 7 | Cottonwood Creek | GB | 1983 | 67 | 5.3 |
| 8 | Little Ute Creek | RG | 1978 | 16 | 2.2 |
| 9 | May Creek | GB | 1980 | 65 | 4.7 |
| 10 | Ouzel Creek† | GB | 1981 | 36 | 1.0 |
| 11 | Pecos River | RG | 1992 | 26 | 5.8 |
| 12 | Rio de los Pinos | RG | 1984 | 49 | 3.1 |
| 13 | Rough Canyon & Rhodes Gulch† | RG | 1985 | 40 | 4.9 |
| 14 | West Creek† | GB | 1979 | 82 | 5.0 |
| Mean (SE) | | | | | |
| High number of trout | | | | | |
| 15 | Cony Creek† | GB | 1989 | 129‡§ | 4.9 |
| 16 | East Middle Creek | RG | 1989 | 117§ | 3.5 |
| 17 | Fern Creek† | GB | 1982 | 61§ | 2.4 |
| 18 | Greenhorn Creek† | GB | 1988 | 173 | 3.4 |
| 19 | Jacks Creek† | RG | 1993 | 322‖ | 11.0 |
| 20 | Medano Creek† | RG | 1987 | 1278 | 20.5 |
| 21 | Nabor Creek | RG | 1982 | 719§ | 5.6 |
| 22 | North Fork Big Thompson River | GB | 1971 | 112§ | 1.8 |
| 23 | Rio Cebolla | RG | 1995 | 778‖ | 6.7 |
| 24 | Roaring River† | GB | 1984 | 124‡ | 6.9 |
| 25 | San Francisco Creek | RG | 1979 | 193‡ | 12.4 |
| 26 | Sheep Creek | GB | 1982 | 661 | 11.6 |
| 27 | Williams Gulch | GB | 1981 | 319 | 4.1 |
| Mean (SE) | | | | | |
| Test translocation site | | | | | |
| 28 | Powderhouse Creek | RG | 1997 | | 4.3 |

*Notes:* Characteristics include relative population status, subspecies of cutthroat trout (GB, greenback; RG, Rio Grande), year of initial translocation (Harig and Fausch 1996, Harig et al. 2000, NMDGF, *unpublished data*), total number of trout observed, summer stream length, elevation of the lower terminus, mean stream gradient, and four habitat variables used in the ''best'' models to predict probability of translocation success. Group means and standard errors (in parentheses) based on relative population status are shown for the four habitat variables used in the best models (RD = residual depth).

† Waterfalls or steep cascades divided these streams into multiple reaches, but cutthroat trout populations downstream potentially depended on emigration from upstream reaches.

‡ Minimum abundance of age-1 and older trout was probably underestimated due to deep, turbulent, or turbid water.

§ Minimum abundance of age-1 and older trout was probably underestimated due to a lake or large beaver pond where it was not possible to make accurate visual counts.

‖ Minimum abundance of age-1 and older trout was probably underestimated due to thick riparian or aquatic vegetation.

dients due to greater stream sinuosity (and therefore greater channel length) on the ground than can be shown on maps. Length of summer habitat for cutthroat trout ranged from 1.0 to 20.5 km and was isolated from encroachment of nonnative salmonids by fish movement barriers including waterfalls, cascades, steep gradients, dry channels, or manmade structures like rock-filled gabions (Harig 2000). Nine streams also had waterfalls or steep cascades in their middle reaches that divided them into multiple habitats (Table 1). We considered them single populations because downstream reaches potentially depended on emigration of cutthroat trout from upstream areas.

### *Field surveys of stream-scale habitat and cutthroat trout abundance*

We conducted field surveys of stream-scale habitat and cutthroat trout abundance along the entire length of each translocation stream from the downstream fish movement barrier upstream to the end of pool habitat, where the bankfull channel width was <2.0 m and wetted width usually ≤1.0 m. Surveys were conducted

TABLE 1. Extended.

| Minimum elevation (m) | Mean gradient (%) | Mean July daily temperature (°C) | Mean bankfull pool width (m) | No. deep pools (RD ≥ 30 cm) | Watershed area (km²) |
|---|---|---|---|---|---|
| 3281 | 13.3 | 4.8 | 1.8 | 12 | 5.1 |
| 2520 | 20.2 | 10.2 | 3.2 | 22 | 7.1 |
| 2861 | 12.3 | 4.2 | 3.8 | 94 | 9.5 |
| 2588 | 16.5 | 7.1 | 2.1 | 35 | 16.2 |
| 3125 | 7.3 | 6.5 | 1.0 | 2 | 8.5 |
| 2890 | 14.8 | 9.5 | 2.8 | 13 | 7.2 |
| | | 7.1 (1.0) | 2.5 (0.4) | 30 (14) | 8.9 (1.6) |
| 2470 | 10.8 | 7.1 | 2.6 | 131 | 9.2 |
| 3262 | 16.0 | 7.8 | 4.5 | 22 | 8.9 |
| 2718 | 12.2 | 8.4 | 3.3 | 144 | 12.5 |
| 3159 | 17.3 | 6.0 | 4.1 | 12 | 7.0 |
| 3178 | 8.4 | 9.2 | 2.9 | 61 | 11.3 |
| 3206 | 12.8 | 8.7 | 3.2 | 36 | 9.5 |
| 2738 | 13.4 | 8.3 | 2.7 | 29 | 10.3 |
| 2496 | 17.0 | 7.1 | 4.1 | 117 | 25.3 |
| | | 7.8 (0.4) | 3.4 (0.3) | 69 (19) | 11.7 (2.0) |
| 2904 | 10.5 | 9.0 | 5.4 | 146 | 14.5 |
| 2939 | 14.8 | 9.7 | 3.2 | 46 | 14.2 |
| 2818 | 17.0 | 7.7 | 4.5 | 56 | 6.8 |
| 3107 | 16.6 | 8.4 | 2.9 | 121 | 7.3 |
| 2531 | 11.5 | 9.8 | 3.6 | 197 | 18.4 |
| 2502 | 13.2 | 10.5 | 4.1 | 361 | 77.8 |
| 2545 | 12.7 | 14.5 | 3.8 | 74 | 11.9 |
| 3293 | 13.6 | 8.1 | 3.1 | 18 | 8.3 |
| 2495 | 8.8 | 14.6 | 3.0 | 69 | 37.1 |
| 2881 | 16.4 | 9.9 | 4.9 | 21 | 14.6 |
| 2400 | 9.1 | 8.8 | 3.9 | 88 | 42.5 |
| 2828 | 9.5 | 7.8 | 4.1 | 318 | 36.1 |
| 2758 | 7.3 | 10.8 | 2.3 | 105 | 9.0 |
| | | 10.0 (0.6) | 3.8 (0.2) | 125 (30) | 22.9 (5.7) |
| 2928 | 10.6 | 10.0 | 2.2 | 5 | 10.0 |

during June through October 1996 through 1998. During the first two years, we randomly selected streams from among 29 sites in Colorado where either cutthroat trout subspecies had been translocated and managers reported that nonnative salmonids had not invaded. However, we found that brook trout had invaded six of them, so in 1998 we randomly selected five additional translocation streams (of seven known, NMDGF, *unpublished data*) from the rest of the range of Rio Grande cutthroat trout in New Mexico. One of these later proved to have been translocated after 1995, and so is used as a test of the final model.

We counted the number of fish observed in each pool and fast-water channel unit (i.e., riffle, run, or cascade, Hawkins et al. 1993) to determine the minimum number of trout. These visual fish counts were not intended as population estimates, but as measures of minimum trout abundance for classifying relative translocation success and developing models. The number, species, and approximate size of each fish were determined using polarized glasses by carefully approaching channel units from downstream. Cutthroat trout generally hold positions in open water near the surface (Griffith 1972, Young 1996, Nakano et al. 1998), so are highly visible. Afterwards, we also used a depth staff to sweep beneath undercut banks, large woody debris, and boulders to detect any additional fish. Usually, none were found. We recorded water transparency to assess whether the fish count was hindered by turbidity, turbulence, deep water, low light levels, or thick vegetation, and thereby underestimated relative to other streams. However, most streams were small and clear with open pools that lacked complex habitat, so cutthroat trout were easily observed.

We surveyed stream-scale habitat at each pool, defined as a channel unit that was at least one-half channel width long, relatively deep (residual depth ≥18 cm) and slow flowing, with a gentle water surface slope (cf. Hawkins et al. 1993). We measured bankfull pool width, residual depth, presence of sediment-free substrate, and physical habitat structure for trout (Table 2). The number of variables we could include in a

TABLE 2. Habitat factors included in stream-scale models calculated from variables measured during basin-wide field surveys of translocation streams.

| Habitat variable | Definition |
|---|---|
| Stream length | Length (km) of stream surveyed from the fish movement barrier upstream to the end of pool habitat (<2.0 m bankfull width), measured from a 1:24,000 USGS topographic quadrangle. |
| Number of pools | Total number of pools at least one-half channel width long with residual depths ≥ 18 cm. Pools were identified according to Hawkins et al. (1993) as channel geomorphic units formed by interactions among discharge, sediment load, and channel resistance to flow. |
| Bankfull pool width | Grand mean bankfull width (m) of all pools, calculated from measures at the downstream, center, and upstream ends of each pool, at the height where the water surface is level with the floodplain (Dunne and Leopold 1978). |
| Deep pools | Number of pools with residual depth ≥30 cm, calculated from the maximum depth minus the maximum tail crest depth measured at the downstream hydraulic control that forms the pool (Lisle 1987). This depth criterion was based on the median residual depth of all pools surveyed in all streams. |
| Large woody debris | Number of pools with at least one piece of large woody debris, which was at least 15 cm in diameter for 3 m of length (adapted from Richmond and Fausch 1995) and at least partially in or suspended over the bankfull channel (including pieces forming pools). |
| Boulders | Number of pools with at least one boulder, which was >50 cm in diameter in all dimensions and within the bankfull channel, including those forming the stream bank if they protruded into the pool. |
| Undercut bank | Number of pools with at least 0.2 m of undercut bank, which was at least 10 cm undercut, no more than 15 cm above the water surface, and had a minimum water depth of 10 cm (adapted from Fausch and Northcote 1992). |
| Clean gravel | Number of pools with at least 25% area as clean gravel (6–63 mm in diameter, free from silt) in the downstream quarter of the pool, estimated visually. |

model of translocation success was limited by the modest sample of streams available, so we calculated the geometric mean of the number of pools that had large woody debris, boulders, or ≥0.2 m of undercut bank to create one variable indicating the number of pools with physical structure.

Stream temperatures were measured (±0.2°C) for each translocation stream at least every 96 min for a minimum of one year using either an Optic StowAway or TidbiT thermograph (Onset Computer Corporation, Pocasset, Massachusetts) placed in the largest pool. Thermographs were placed in each stream when first surveyed and replaced each year. Thermal regimes were measured for three years (1996–1999) in 8 streams, at least two years in 16 streams, and at least one year in all 28 streams. We analyzed four thermal characteristics; mean daily temperature for each month from June through August to encompass periods of egg incubation and emergence of cutthroat trout fry, and for the 3-mo period from December through February to measure mean overwinter temperatures. Daily temperatures were averaged for four translocation streams that contained more than one thermograph.

### *Measurement of basin-scale habitat using digital data*

A Geographic Information System and digital map data were used to measure basin-scale habitat attributes for the 28 cutthroat trout translocation streams surveyed in the field and all 70 known remnant, historical stream populations not invaded by nonnative salmonids (7 greenback and 63 Rio Grande). Digital elevation models (DEMs) corresponding to 1:24 000 scale topographic quadrangles were provided by the U.S. Forest Service (USFS) Geometronics Unit in Salt Lake City, Utah or purchased from the U.S. Geological Survey (USGS). These 7.5-min grids were in raster format with 30 × 30 m resolution.

We used the hydrological modeling tools in the GRID module of Arc/Info (ESRI 1995, specific commands are listed in uppercase letters) to quantify basin attributes (Table 3) from the DEMs using a series of functions that set up proper DEM conditions and delineated basin boundaries and stream networks. The DEMs were first converted to elevation grids (DEMLATTICE), sinks were filled using appropriate procedures in GRID (FLOWDIRECTION, SINK, WATERSHED, ZONALFILL, ZONALMIN, FILL), and adjacent quadrangles were joined (MOSAIC). Sinks, which are areas surrounded by higher elevations, are usually data errors resulting from the spatial interpolation procedure used to create the DEM and can create false stream networks. Lakes were also filled even though they are natural sinks because they were part of cutthroat trout stream habitat and not modeled as separate basins.

Stream networks were identified from the depressionless grids using the commands FLOWDIRECTION to find the steepest descent from each cell, and FLOWACCUMULATION to calculate the number of upslope cells contributing flow to each cell. Cells that accumulated flow from at least 1000 other cells (CON) were used to delineate stream channels because this value most closely matched the smallest flowing channels in field surveys. Cells with no flow accumulation were used to identify drainage basin boundaries. We set the downstream end of cutthroat trout basins at the fish movement barrier (SNAPPOUR) to delineate the wa-

TABLE 3. Basin-scale habitat factors measured for each translocation stream using a Geographic Information System and digital data derived from USGS digital elevation models. (Specific commands from the Arc/Info hydrological modeling tools (ESRI 1995) are given in uppercase letters.)

| Habitat variable | Definition |
|---|---|
| Watershed area | Total upslope area ($km^2$) contributing flow to the basin outlet, calculated as planimetric watershed area (ZONALGEOMETRY). |
| Main channel length | Surface length (km) measured along the main channel (excluding tributaries) from the basin outlet to the headwaters. The GIS defined channels in cells where flow accumulation exceeded 1000 upslope cells and incorporated changes in elevation in its calculation (SURFACELENGTH). |
| Total channel length | Surface length (km) computed by summing the length of all stream segments within the drainage basin, including tributary streams, which may also provide trout habitat. Channels were defined as for main channel length (SURFACELENGTH). |
| Drainage density | The total length of stream channels per unit basin area ($km/km^2$), calculated as total channel length divided by watershed area. |
| Latitude | The latitude of the basin outlet in Universal Transverse Mercator coordinates (m; CELLVALUE). |
| Elevation | Minimum elevation above sea level (m), measured at the basin outlet. |
| Basin relief | The difference between the highest and lowest elevations occurring within a basin (m; SLOPE). |
| Basin slope | The percentage change in elevation quantified for each basin as mean percentage rise (SLOPE). |
| Stream slope | The percentage change in elevation quantified for each stream network as mean percentage rise (SLOPE). |
| Stream aspect | The mean direction of the stream network measured as compass degrees either clockwise or counterclockwise from north (FLOWDIRECTION, SETMASK). Data were restricted to values between 0° and 180°, which correspond to a north and south aspect, respectively (RECLASS). Streams with an east- or west-facing aspect have intermediate values. |

tershed (WATERSHED). Other data layers, including elevation, stream network, flow direction, and slope (SLOPE), were then cropped to calculate watershed area, channel length, latitude, stream aspect, and topographic relief (Table 3).

### *Statistical models of translocation success*

We used the hypotheses described in the *Introduction* to develop four sets of formal a priori statistical models predicting cutthroat trout translocation success: one from summer water temperatures (number of models [$R$] = 5), a second from water temperature and stream-scale habitat attributes ($R$ = 19), a third from basin-scale habitat attributes ($R$ = 19), and a fourth from a combination of the variables in the ''best'' models of the previous model sets ($R$ = 15). Each group of models was a nested set that represented formal hypotheses about attributes that potentially limit persistence of translocated cutthroat trout populations (Burnham and Anderson 1998). Summer water temperatures were analyzed as a separate model set to determine which month was the best measure to include in models of stream-scale habitat attributes. For all analyses, the 27 streams were assumed to be a random sample of all streams where managers might attempt translocations of these cutthroat trout subspecies. Given this, the resulting models can be used to predict success of future translocations into streams having habitat attributes within the data ranges of the streams we measured.

Response variables for the models were based on ranked categories of translocation success (absent, low, high) determined from our visual estimates of cutthroat trout minimum abundance. We assumed that streams supporting relatively *high* numbers of cutthroat trout had minimally sufficient habitat to support at least short-term persistence, streams supporting relatively *low* numbers had marginal habitat, and streams *absent* cutthroat trout had insufficient habitat. Number of independent variables in each model was limited to three in all but the combination model set because too many variables can result in a statistically unstable model for small data sets (i.e., over-fitting; Burnham and Anderson 1998). Therefore, interaction and quadratic terms were excluded except for the interaction between latitude and elevation in models of basin-scale habitat. All pairwise correlations of independent variables were evaluated to assess multicollinearity.

Models were fit using ordinal polytomous logistic regression (PLR; Agresti 1996, SAS Institute 1996). Ordinal PLR directly incorporates ordering of response categories, which results in models with simpler interpretations and potentially greater power than ordinary multicategory logit models (Agresti 1996). Model diagnostics included the Score Test for Proportional Odds Assumption to determine the validity of choosing ordinal over nominal PLR, and Deviance and Pearson goodness-of-fit statistics to examine model fit (SAS Institute 1996). For specific habitat models where the difference between predicted values for two or more status categories was negligible, binary logistic regression was used for pairwise comparison of these subsets of the data.

One or more ''best approximating'' models were selected from each set of candidate models using Akaike's Information Criterion corrected for small-sample bias ($AIC_c$; Burnham and Anderson 1998). Models were ranked using $AIC_c$ weights, which is a measure of the weight of evidence in favor of a model given the data. Only models with a reasonable level of support are presented (i.e., weights ≥1/10 of that for the highest ranking model; D. R. Anderson, *personal communication*). The model with the highest weight was considered the best model. However, if no one model was clearly best, then models within two $AIC_c$ points of the highest weighted model were considered competing models. Results from averaging competing models based on $AIC_c$ weights provide a more precise, stable inference than using only one best model (Burnham and Anderson 1998). Model selection based on an information-theoretic approach such as this is superior to traditional hypothesis testing for this data set because it allowed comparison of more than two models at once, balanced precision and bias in selecting an appropriate model, and did not require that the data were collected from a formal designed experiment (Burnham and Anderson 1998). It has been successfully used in similar ecological research to define optimal habitat for Northern Spotted Owl (*Strix occidentalis caurina*) juvenile survival (Franklin et al. 2000).

## RESULTS

### *Relative population status*

The 27 study streams were classified based on their relative population status to compare habitat variables and develop models of translocation success. Population status was based on minimum number of age-1 and older cutthroat trout observed during the visual survey (Table 1). If less than four trout were observed, then it was assumed that the stream was unable to support a cutthroat trout population and assigned a rating of absent. In no streams in this category did other factors like turbidity reduce visibility of trout. Streams where less than 100 trout were observed supported relatively low numbers of cutthroat trout and were rated low. Streams with more than 100 cutthroat trout were rated high. In this category, counts less than 200 trout were likely underestimates relative to other surveys because all but one of these streams had lakes or large beaver ponds, habitats where accurate visual counts were not possible. All other streams with such complex habitats had counts greater than 200 cutthroat trout and were ranked as high, so we ranked the streams with counts between 100 and 200 trout as high also.

We assessed the accuracy of our categories by comparing our basin-wide visual counts and subsequent status rating to estimates of standing stock (kilograms per hectare) made by two-pass removal electrofishing (cf. Otis et al. 1978) in shorter reaches of 22 streams for which data were available from natural resource management agencies. Our visual estimates of minimum trout density (no. per kilometer) were positively correlated with agency standing stock estimates (kilograms per hectare, $r = 0.70$, $P = 0.003$, $n = 22$), and in 21 of 22 cases yielded similar status ratings to those designated by fisheries managers (i.e., unstable, potentially stable, stable; Alves 1998, USFWS 1998). The discrepancy in estimates by the two methods may be attributed primarily to differences in the length and habitat of reaches sampled. Our visual sample included the entire stream whereas electrofishing estimates were for shorter reaches (typically 50–200 m; cf. Harig and Fausch 1996), usually near the downstream terminus, that are often not representative of all habitat.

### *Models of translocation success based on summer water temperature*

The mean daily water temperature for June through August, which encompasses the period of spawning, egg incubation, and fry emergence for cutthroat trout, ranged from 2.0° to 12.9°C among study streams in June, 4.2° to 14.6°C in July (Table 1), and 4.9° to 13.9°C in August. Streams classified as absent had colder temperatures than streams with low numbers of cutthroat trout, and both had colder temperatures than streams with high numbers of cutthroat trout for all months and combinations of consecutive months except for June. Examination of the $AIC_c$ values and their weights ranked the model based on mean daily water temperature for July and August combined the highest ($AIC_c = 51.420$, $w = 0.289$), followed by July ($AIC_c = 51.656$, $w = 0.256$), then August ($AIC_c = 52.416$, $w = 0.175$). Other months and combinations of months had $AIC_c$ values >55.0 and weights ≤0.040. July temperatures were chosen to represent summer temperatures in all subsequent models because they predicted translocation success nearly as well as July–August temperatures, and because a thermograph malfunctioned in August in one stream where temperatures were measured for only one year. There was no significant difference in stream temperatures among years ($P = 0.15$ for year effect for 16 streams measured two years or more by two-way ANOVA), and the average difference among years was only 0.6°C (SE = 0.08), so temperatures measured the year after the habitat survey were used in models.

### *Models of translocation success based on water temperature and stream-scale habitat*

The $AIC_c$ values and their weights for 19 nested candidate models based on mean July water temperature, mean overwinter temperature, and stream-scale habitat data collected during field surveys indicated that the model including summer temperature, bankfull pool width, and number of deep pools was the ‘‘best’’ model for predicting success of cutthroat trout translocations (Tables 4 and 5):

TABLE 4. Statistical models predicting cutthroat trout translocation success from water temperature and stream-scale habitat data collected during field surveys, basin-scale habitat measured from digital data, and a combination of stream- and basin-scale attributes from the best models.

| Model | $-2$ (ln$L$) | $K$ | AIC$_c$ | $w$ |
|---|---|---|---|---|
| A) Water temperature and stream-scale habitat | | | | |
| Summer temperature, pool width, number of deep pools | 32.661 | 5 | 45.518 | 0.289 |
| Summer temperature, pool width | 36.860 | 4 | 46.678 | 0.162 |
| Summer temperature, pool width, number of all pools | 34.140 | 5 | 46.997 | 0.138 |
| Summer temperature, pool width, number of pools with structure | 34.441 | 5 | 47.298 | 0.118 |
| Summer temperature, pool width, stream length | 35.374 | 5 | 48.231 | 0.074 |
| Summer temperature, pool width, number of pools with clean gravel | 35.497 | 5 | 48.354 | 0.070 |
| Summer temperature, number of deep pools | 38.908 | 4 | 48.726 | 0.058 |
| B) Basin-scale habitat | | | | |
| Watershed area | 49.394 | 3 | 56.437 | 0.212 |
| Watershed area, basin relief | 47.211 | 4 | 57.029 | 0.158 |
| Watershed area, latitude | 48.228 | 4 | 58.046 | 0.095 |
| Watershed area, basin relief, latitude | 45.949 | 5 | 58.806 | 0.065 |
| Watershed area, stream aspect | 49.006 | 4 | 58.824 | 0.064 |
| Watershed area, elevation | 49.076 | 4 | 58.894 | 0.062 |
| Main channel length | 51.864 | 3 | 58.907 | 0.062 |
| Watershed area, main channel length | 49.268 | 4 | 59.086 | 0.056 |
| Watershed area, basin slope | 49.306 | 4 | 59.124 | 0.055 |
| Main channel length, stream aspect | 50.717 | 4 | 60.535 | 0.027 |
| Watershed area, elevation, latitude | 47.948 | 5 | 60.805 | 0.024 |
| Main channel length, elevation | 51.141 | 4 | 60.959 | 0.022 |
| C) Stream- and basin-scale habitat | | | | |
| Summer temperature, pool width, number of deep pools | 32.661 | 5 | 45.518 | 0.413 |
| Summer temperature, pool width | 36.860 | 4 | 46.678 | 0.231 |
| Summer temperature, pool width, watershed area | 35.563 | 5 | 48.420 | 0.097 |
| Summer temperature, number of deep pools | 38.908 | 4 | 48.726 | 0.083 |
| Summer temperature, pool width, number of deep pools, watershed area | 32.647 | 6 | 48.847 | 0.078 |

*Notes:* Akaike's Information Criterion corrected for small sample size (AIC$_c$), calculated from the log likelihood ($-2$[ln$L$], number of parameters ($K$), and sample size ($n$=27), and AIC weights ($w$) were used to select the "best approximating" models from each set of a priori candidate models. Only models with weights $\geq$1/10 of that for the highest ranking model are presented.

$$P(\text{``absent''}) = \frac{\exp(11.454 - 0.891t - 1.451w - 0.017d)}{1 + \exp(11.454 - 0.891t - 1.451w - 0.017d)}$$

$$P(\text{``low + absent''}) = \frac{\exp(14.077 - 0.891t - 1.451w - 0.017d)}{1 + \exp(14.077 - 0.891t - 1.451w - 0.017d)}$$

where $P$ = probability of a stream having a population status of absent, or low and absent combined, $t$ = mean daily water temperature (degrees Centigrade) for July, $w$ = mean bankfull width of pools (meters), and $d$ = total number of deep pools. Point estimates for probability of a stream being in the low and high categories were calculated as $P$(low) = $P$(low + absent) − $P$(absent) and $P$(high) = 1 − $P$(low + absent) (Fig.

TABLE 5. Maximum-likelihood estimates of intercept and slope parameters from ordinal polytomous logistic regression for the four "best approximating" models predicting cutthroat trout translocation success from water temperature and stream-scale habitat collected during field surveys.

| Model | Intercept 1 | Intercept 2 | Mean July temperature | Pool width | Number of pools† |
|---|---|---|---|---|---|
| Summer temperature, pool width, number of deep pools‡ | 11.454 (4.460) | 14.077 (4.868) | −0.891 (0.355) | −1.451 (0.713) | −0.017 (0.010) |
| Summer temperature, pool width | 10.345 (3.853) | 12.688 (4.179) | −0.889 (0.336) | −1.460 (0.646) | ··· ··· |
| Summer temperature, pool width, number of all pools | 10.369 (4.052) | 12.846 (4.398) | −0.765 (0.334) | −1.433 (0.676) | −0.008 (0.006) |
| Summer temperature, pool width, number of pools with structure§ | 10.277 (3.970) | 12.749 (4.327) | −0.816 (0.330) | −1.352 (0.668) | −0.012 (0.009) |

*Note:* Standard errors are in parentheses.
† Three models included number of pools that met specific criteria.
‡ Deep pools were all pools with a residual depth ≥30 cm.
§ Pools with structure refer to the geometric mean of the number of pools with large woody debris, the number of pools with boulders, and those with ≥0.2 m of undercut bank.

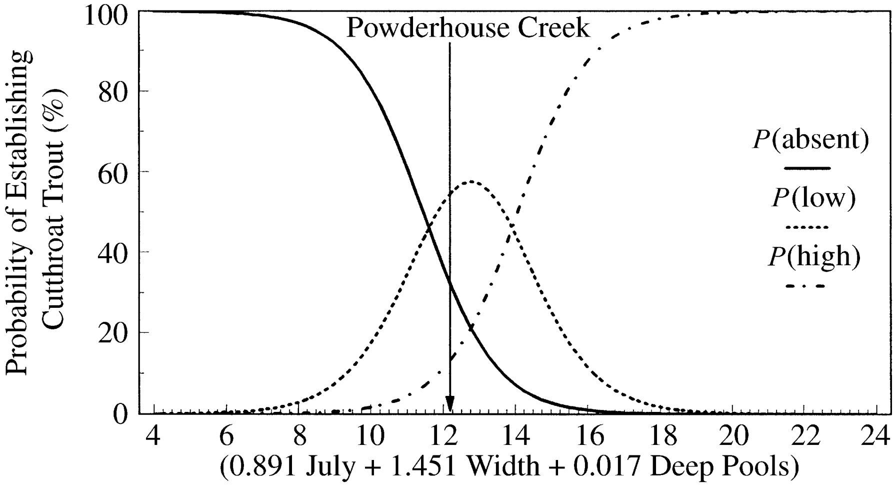


FIG. 2. The "best" model for predicting success of translocated cutthroat trout populations from stream-scale habitat attributes. Curves show the predicted probability of translocation success based on a polytomous logistic regression function (shown on the abscissa) of mean daily water temperature for July (°C), mean bankfull pool width (m), and total number of deep pools (residual depth ≥30 cm). This model predicts that the translocation to Powderhouse Creek has only a 13% probability of supporting high numbers of cutthroat trout, 54% of supporting low numbers, and 33% of supporting no cutthroat trout (shown by the arrow).

2). Translocation streams with a high or low abundance of cutthroat trout had warmer July water temperatures, greater bankfull widths, and more deep pools than streams with fewer cutthroat trout (i.e., high > low > absent, Table 1).

The $AIC_c$ weight for this model was relatively low (0.286) and only about twice as likely as the next best model (0.162), so the next three models within two $AIC_c$ points were considered competing models (Burnham and Anderson 1998). In this case, a weighted average of the responses from all four models can be used to predict cutthroat trout translocation success, providing a more precise prediction than using the best model alone (Burnham and Anderson 1998). However, all four models contained summer water temperature and bankfull pool width (Table 5), and the third variable in three of the models was a measure of the number of pools, all of which were highly correlated ($r \geq 0.95$, $P = 0.001$). Moreover, predicted values for the best model and those from a weighted average of the four competing models differed by only 3%, on average (SE = 0.4, range 0–12%). Therefore, to simplify application by managers, we recommend using only the best model to predict cutthroat trout translocation success, recognizing that the variance will be greater than estimated because of the closely weighted competing models.

### *Models of translocation success based on basin-scale habitat*

The $AIC_c$ values and their weights for the 19 nested candidate models based on basin-scale habitat measured from digital data using a GIS indicated that the model including watershed area alone was the "best" model for predicting success of cutthroat trout translocations (Table 4). Two additional models within two $AIC_c$ points were considered competing models (Table 6), so a weighted average of their responses could be used to predict cutthroat trout translocation success. However, none of the three top models detected differences between absent and low status categories ($P \geq 0.24$ for test of independence by binary logistic re-

TABLE 6. Maximum-likelihood estimates of intercept and slope parameters from ordinal polytomous logistic regression for the three "best approximating" models predicting cutthroat trout translocation success from basin-scale habitat measured from digital data.

| Model | Intercept 1 | Intercept 2 | Watershed area | Basin relief | Latitude |
|---|---|---|---|---|---|
| Watershed area | 0.251 | 1.804 | −0.123 | ··· | ··· |
| | (0.869) | (0.916) | (0.069) | ··· | ··· |
| Watershed area, basin relief | −1.177 | 0.478 | −0.176 | 0.002 | ··· |
| | (1.366) | (1.337) | (0.096) | (0.002) | ··· |
| Watershed area, latitude | 9.901 | 11.529 | −0.125 | ··· | −0.000002 |
| | (9.184) | (9.265) | (0.068) | ··· | (0.000002) |

*Note:* Standard errors are in parentheses.

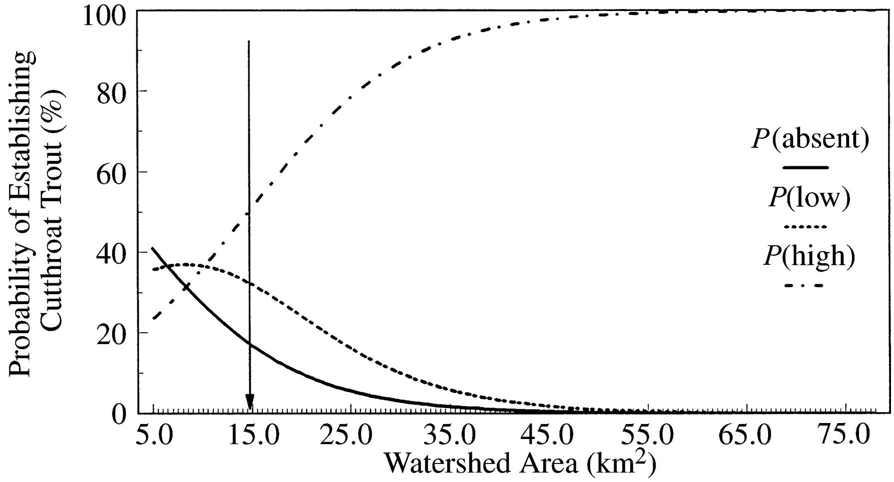


FIG. 3. The ''best'' model for predicting success of translocated cutthroat trout populations from basin-scale habitat attributes. Curves show the predicted probability of translocation success as a function of watershed area (km$^2$). Translocations have greater than a 50% chance of establishing high numbers of cutthroat trout in watersheds >14.7 km$^2$ (shown by the arrow).

gression). Nevertheless, they were able to detect differences between translocation streams in the high vs. absent or low categories.

The three top models all included watershed area as a critical habitat factor, and basin relief was correlated with watershed area ($r = 0.42$, $P = 0.03$), so watershed area alone may prove most useful as a coarse filter for predicting translocation success (Table 6):

$$P(\text{``absent''}) = \frac{\exp(0.251 - 0.123a)}{1 + \exp(0.251 - 0.123a)}$$

$$P(\text{``low + absent''}) = \frac{\exp(1.804 - 0.123a)}{1 + \exp(1.804 - 0.123a)}$$

where $P$ = probability of a stream having a cutthroat trout population status of absent, or low and absent combined, and $a$ = planimetric watershed area (square kilometers). Although this model cannot detect differences between absent and low population status, the point estimates can be used to identify a minimum watershed area that has a high probability of supporting high numbers of cutthroat trout (Fig. 3). Thus, translocations into watersheds >14.7 km$^2$ have greater than a 50% chance of establishing high numbers of cutthroat trout.

### *Models of translocation success based on stream- and basin-scale habitat*

The AIC$_c$ values and their weights for 15 nested candidate models developed from combinations of habitat variables used in the best models with stream- and basin-scale habitat (i.e., July water temperature, bankfull pool width, number of deep pools, and watershed area) indicated that the stream-scale habitat models described previously explained the data better than models also using basin-scale habitat attributes (Table 4). Models that included watershed area were not within two AIC$_c$ points of the best model so were not considered competing models.

## DISCUSSION

### *Stream habitat attributes limiting cutthroat trout*

Greenback and Rio Grande cutthroat trout were originally distributed throughout the large river systems within their historical range (Fig. 1, Behnke 1992), but the streams available for translocations have primarily been small, isolated, headwater sites that provide only marginal habitat at best. Many of these streams failed to sustain robust cutthroat trout populations despite repeated stocking of genetically pure fish. Although a true experiment would be required to establish a direct cause-and-effect relationship between habitat and translocation success, our field surveys of stream-scale habitat indicated that low summer water temperature and habitat size are critical factors limiting populations of translocated cutthroat trout.

Many greenback and Rio Grande cutthroat trout translocation sites apparently have temperatures that are too cold to support natural reproduction. Cutthroat trout spawn during the spring and are stimulated by rising water temperatures (Behnke 1992), but cold water temperatures can delay spawning into late summer and prolong egg incubation, resulting in low embryo survival or increased time to fry emergence (Hubert et al. 1994, Stonecypher et al. 1994, Hubert and Gern 1995). Late-hatching fry may be unable to acclimate to a rapid decrease in water temperature or may starve during winter, so survival may depend on their ability to grow large enough to withstand metabolic deficits (Hunt 1969, Cunjak and Power 1987, Shuter and Post 1990). Therefore, in streams that support low numbers of cutthroat trout, cold temperatures (≤7.8°C mean daily temperature for July) likely prevent successful reproduction and recruitment during most years, whereas in streams ranked as high, summer water temperatures are probably warm enough (mean = 10.0°C, SE = 0.6) to allow successful reproduction.

Our stream-scale habitat model also indicated that habitat size and abundance, as measured by mean bankfull pool width and number of deep pools, are factors limiting translocated cutthroat trout populations. Other studies have found similar positive relationships between stream width and trout presence or abundance (Nelson et al. 1992, Clarkson and Wilson 1995, Kruse et al. 1997, Dunham and Rieman 1999), and a manipulative experiment that increased the number of deep pools caused increased abundance of adult trout in six northern Colorado streams (Gowan and Fausch 1996*a*). Larger streams can support larger populations, which are less vulnerable to environmental and demographic stochasticity (Lande 1993), and are more likely to provide enough habitat heterogeneity to meet the diverse habitat needs of salmonids. For example, although juveniles may be able to overwinter in relatively shallow pools or runs in low-elevation streams (e.g., Griffith and Smith 1993), adult trout are believed to need large pools to survive the winter (Cunjak and Power 1986, Chisholm et al. 1987). Therefore, translocation streams ranked absent or low probably lacked sufficient or appropriate habitat to promote survival of enough individuals to sustain a population.

Our data also supported three other models of translocation success with similar variables, indicating that total number of pools and pools with physical structure (large woody debris, boulders, undercut banks) also limit cutthroat trout populations. Salmonids favor pools created by large woody debris, boulders, or lateral scour beneath stream banks (Bisson et al. 1981, Griffith and Smith 1993, Flebbe and Dolloff 1995) probably because they provide cover through high habitat complexity (Fausch and Northcote 1992, Richmond and Fausch 1995) and abundant food through invertebrate habitat (Angermeier and Karr 1984, Benke et al. 1985). Nelson et al. (1992) and Young (1996) also reported that abundance of all pools and those with physical structure were associated with presence of trout, corroborating our models. Although a weighted average from all four models could be used to predict translocation success with slightly greater precision (3%, on average), it is unlikely that this increase is worth the extra time, effort, and money needed to measure physical structure in large numbers of pools ($n$ = 24–571 for our streams).

### *Appropriate spatial scales for isolated trout populations*

Studying species distributions over multiple spatial scales to identify the appropriate scale for management has become prevalent in stream ecology (e.g., Allan et al. 1997, Torgersen et al. 1999, Labbe and Fausch 2000), partly due to the emergence of landscape ecology (Wiens 1995). Investigations of resident stream salmonids have also expanded in spatial scale since the discovery that many fish in these populations move substantial distances (Gowan et al. 1994, Gowan and Fausch 1996*b*, Young 1996). Traditional habitat studies at the microhabitat scale (see Fausch et al. [1988] for review) have failed to develop general principles to guide management of fishes, so a coarser scale approach has been proposed (Schlosser and Angermeier 1995).

We studied habitat for cutthroat trout at two scales, stream and basin scale, which roughly correspond to patch (i.e., local habitat characteristics) and landscape scales in the ecological literature. Stream-scale models indicated that summer water temperature, pool width, and deep pools were critical factors limiting translocated cutthroat trout populations, but models of basin-scale habitat were not as effective for distinguishing between successful and unsuccessful translocations. In a review of studies on a wide array of taxa that considered both patch and landscape scales for detecting species presence and abundance, Mazerolle and Villard (1999) found that landscape variables were significant predictors in more than half the studies (59%), but patch characteristics were significant in nearly all studies (93%). Similarly, coarse-scale geomorphic variables are often good predictors of presence or abundance of salmonids when measured at the reach level, which approximates the patch scale (e.g., Lanka et al. 1987, Fausch 1989, Clarkson and Wilson 1995). For example, channel slope was a significant predictor of trout occurrence in stream reaches of the central Rocky Mountains (Chisholm and Hubert 1986, Kruse et al. 1997), but mean slope of the entire stream was not an important predictor of cutthroat trout translocation success in our models of basin-scale habitat.

Watershed area was the one basin-scale habitat attribute found to be useful as a coarse filter for predicting translocation success. Based on model results, watersheds larger than 14.7 $km^2$ are predicted to have >50% probability of supporting high numbers of cutthroat trout. This is not surprising considering the wealth of studies, most recently on metapopulation dynamics (Thomas et al. 1992, Wenny et al. 1993, Rieman and McIntyre 1995, Dunham and Rieman 1999), that support the species–area relationship; i.e., the probability that a species will be present in a habitat patch increases with increasing area (MacArthur and Wilson 1967, Diamond 1975). Large watersheds encompass lower-elevation habitats that probably provide warm summer water temperatures for cutthroat trout, and have relatively wide stream channels of sufficient length to provide an adequate number of deep pools. Large watersheds are also likely to have sufficient input of large woody debris and boulders to create physical structure in pools. Only 1 of 6 streams where translocations failed had watersheds $>14.7\ km^2$, but 8 of 13 streams with high populations had basins $\leq 14.7\ km^2$, so estimating the probability of translocation success in watersheds $\leq 14.7\ km^2$ will require measuring stream-scale habitat throughout the basin. For example, five of the eight latter streams had lakes or large beaver ponds, which likely increase the probability of supporting high numbers of cutthroat trout. Beaver ponds are ephemeral and not usually marked on maps, so attributes measured strictly at the basin scale would not be useful for predicting persistence of cutthroat trout populations in small watersheds.

Landscape-scale habitat variables have been useful for predicting presence or abundance of some species with large spatial habitat requirements such as mammals with large home ranges (Mladenoff et al. 1999) and birds with high dispersal capabilities (Ganey et al. 1990, Bellamy et al. 1998), but the landscape scale must be carefully defined for each taxon (Mazerolle and Villard 1999). The appropriate scale for predicting habitat attributes limiting cutthroat trout translocation success is determined by interactions between ecological processes and the organism's life history (Schlosser and Angermeier 1995). Greenback and Rio Grande cutthroat trout historically occupied connected watersheds with high habitat heterogeneity that were large enough to support their movements and sustained the diverse habitat required by different life stages (Young 1995*a*). However, most populations of these subspecies are now isolated in small watersheds (5–78 $km^2$) and cannot emigrate if their habitat needs are not met. This habitat fragmentation has presumably eliminated the mobile life history component from many cutthroat trout populations and reduced their spatial habitat use. Therefore, basin-scale analyses may be too coarse to identify whether an isolated habitat can support cutthroat trout, particularly if many critical habitat attributes are locally controlled. For example, water temperatures in small, mountain streams are difficult to predict without site-specific data on factors such as stream aspect, riparian canopy, air temperature, stream discharge, and meteorology (e.g., Morse 1970, Smith and Lavis 1975, Bartholow 1993). We found weak correlations between basin-scale measures of stream aspect, elevation, and latitude vs. July water temperature measured in the field ($r$ = 0.44, −0.42, −0.41, respectively, $P \leq 0.03$), but these variables did not improve the model based on watershed area alone. Therefore, measuring accurate site-specific surrogate variables for stream temperature would require much more effort than simply measuring temperature directly using thermographs.

### *Management implications*

This research identified critical habitat attributes that allow successful translocation and at least short-term persistence of cutthroat trout populations in isolated headwater streams. Managers can use these models to evaluate potential translocation sites and identify current populations at greatest risk from extirpation (Harig et al. 2000*b*). For example, stream habitat was measured in Powderhouse Creek, a site where the translocation was too recent (1997) to assess success. The watershed is only 10 $km^2$, so our basin-scale model is not useful as a coarse filter. However, the stream-scale model for Powderhouse Creek, which has 10.0°C mean daily July water temperature, 2.2 m mean bankfull pool width, and five deep pools, predicts a 33% probability of supporting no trout, a 54% probability of supporting low numbers, and only a 13% chance of high numbers of cutthroat trout (Fig. 2). Given this, managers will need to decide whether establishing a small population of cutthroat trout by translocation is worth the time, money, and effort, considering that it may not achieve long-term persistence.

The short-term (3–31 yr) success of a translocation, judged from the minimum abundance of cutthroat trout during our surveys, does not necessarily ensure long-term population persistence (e.g., >100 yr, Rieman and McIntyre 1993). It is assumed that populations established through translocation will be long lasting, but this may not be true for streams supporting low numbers of cutthroat trout. Small populations are at greater risk from demographic and environmental stochasticity (Propst et al. 1992, Reiman and McIntyre 1993), so it is likely that the trout population will eventually be extirpated in many streams ranked as low. Furthermore, basin-scale models of cutthroat trout translocation success were unable to detect differences in streams with no trout vs. those with low numbers, which suggests that these streams are geomorphically more similar to one another than to streams with high numbers of trout. As such, we suspect that cutthroat trout populations in streams ranked as low are more likely to dwindle than increase toward the high status category.

The basin-scale model of translocation success also may be useful for identifying historical populations at the greatest risk of extirpation. Although the habitat attributes necessary to establish a translocated population may not be identical to those that have sustained historical populations, managers have limited time and budgets to devote to stream surveys so a coarse filter such as minimum watershed area could be used to prioritize streams. At last count, there were 50 streams in New Mexico with remnant historical populations of Rio Grande cutthroat trout that remained free from nonnative salmonids (NMDGF, *unpublished data*). Almost half of these (24) are in watersheds $\leq 14.7\ km^2$ and may warrant first attention (Fig. 4). Populations in many streams have not been surveyed in 10 or more years and may be at risk of extirpation, particularly if invading nonnative salmonids are reducing their available habitat. Similarly in Colorado, 4 of 13 historical populations of Rio Grande cutthroat trout and 4 of 7 historical populations of greenback cutthroat trout also persist in small watersheds $\leq 14.7\ km^2$ and may be at

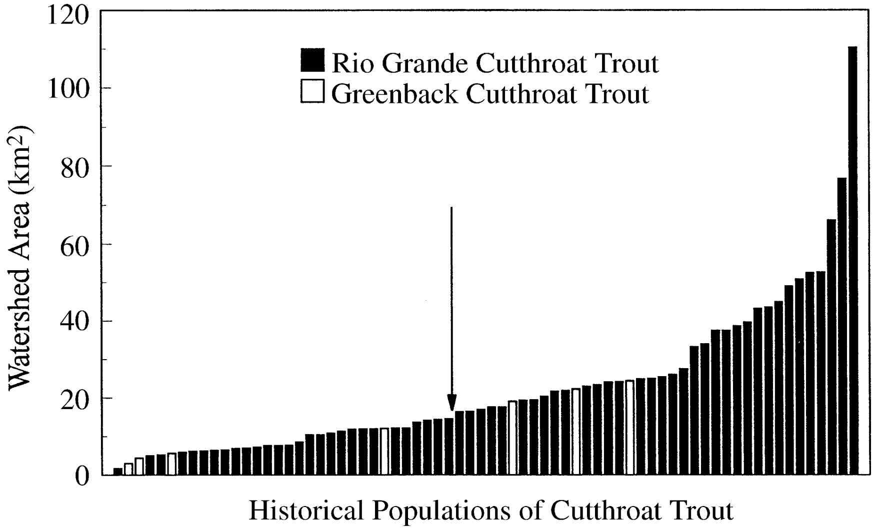


FIG. 4. The distribution of watershed area ($km^2$) for 70 historical stream populations of greenback and Rio Grande cutthroat trout. Thirty-two populations in watersheds <14.7 $km^2$ (shown by the arrow) may be at greater risk from extirpation due to insufficient habitat (see *Discussion*: *Management implications*).

risk. None of these small watersheds include lakes, which may reduce probability of extirpation, so field surveys of stream-scale habitat could identify if they have appropriate summer water temperatures, are wide enough, and have a sufficient number of deep pools to support high numbers of cutthroat trout.

Despite the low success rates for translocations of fishes (e.g., Simons et al. 1989, Harig et al. 2000*a*), our research is one of the few attempts to determine specific factors influencing their translocation success (cf. Williams et al. 1988). It demonstrates that measuring attributes of local habitat over a whole watershed scale that matches the life history of the organism can be highly useful for identifying critical habitat factors (Torgersen et al. 1999, Labbe and Fausch 2000). A multi-scale analysis such as this could also identify minimum habitat requirements for other threatened or endangered taxa, thereby improving translocation success. The models we developed from stream- and basin-scale habitat attributes will be valuable tools for fisheries managers concerned with the conservation of Rio Grande and greenback cutthroat trout (Harig et al. 2000*b*), particularly if included in an active management program that tests and refines these models with data from recent and future translocation sites. Moreover, these results may also be applicable to other closely related subspecies of cutthroat trout in central and southern Rocky Mountain streams (e.g., Colorado River cutthroat trout, *O. c. pleuriticus*) because similar habitat attributes probably limit their populations.

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## LITERATURE CITED

Agresti, A. 1996. An introduction to categorical data analysis. John Wiley and Sons, New York, New York, USA.

Allan, J. D., D. L. Erickson, and J. Fay. 1997. The influences of catchment land use on stream integrity across multiple spatial scales. Freshwater Biology **37**:149–161.

Alves, J. 1998. Status of Rio Grande cutthroat trout in Colorado. Management Report, Colorado Division of Wildlife, Denver, Colorado, USA.

Angermeier, P. L., and J. R. Karr. 1984. Relationship between woody debris and fish habitat in a small warmwater stream. Transactions of the American Fisheries Society **113**:716–726.

Bartholow, J. M. 1993. Sensitivity of the U.S. Fish and Wildlife Service's Stream Network Temperature Model. Pages 247–257 *in* H. J. Morel-Seytoux, editor. Proceedings of the Thirteenth Annual American Geophysical Union, Fort Collins, Colorado, USA.

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society Monograph 6. American Fisheries Society, Bethesda, Maryland, USA.

Bellamy, P. E., N. J. Brown, B. Enoksson, L. G. Firbank, R. J. Fuller, S. A. Hinsley, and A. G. M. Schotman. 1998.

The influences of habitat, landscape structure and climate on local distribution patterns of the nuthatch (*Sitta europaea* L.). Oecologia **115**:127–136.

Benke, A. C., R. L. Henry, D. M. Gillespie, and R. J. Hunter. 1985. Importance of snag habitat for animal production in southeastern streams. Fisheries **10**(5):8–13.

Bisson, P. A., J. L. Nielsen, R. A. Palmason, and L. E. Grove. 1981. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. Pages 62–73 *in* N. B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Bethesda, Maryland, USA.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Chisholm, I. M., and W. A. Hubert. 1986. Influence of stream gradient on standing stock of brook trout in the Snowy Range, Wyoming. Northwest Science **60**:137–139.

Chisholm, I. M., W. A. Hubert, and T. A. Wesche. 1987. Winter stream conditions and use of habitat by brook trout in high-elevation Wyoming streams. Transactions of the American Fisheries Society **116**:176–184.

Clarkson, R. W., and J. R. Wilson. 1995. Trout biomass and stream habitat relationships in the White Mountains area, east-central Arizona. Transactions of the American Fisheries Society **124**:599–612.

Cunjak, R. A., and G. Power. 1986. Winter habitat utilization by resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences **43**:1970–1981.

Cunjak, R. A., and G. Power. 1987. The feeding and energetics of stream-resident trout in winter. Journal of Fish Biology **31**:493–511.

Diamond, J. M. 1975. Assembly of species and communities. Pages 342–444 *in* M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA.

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

Dunham, J. B., and G. L. Vinyard. 1997. Incorporating stream level variability into analyses of site level fish habitat relationships: some cautionary examples. Transactions of the American Fisheries Society **126**:323–329.

Dunne, T., and L. B. Leopold. 1978. Water in environmental planning. W. H. Freeman and Company, San Francisco, California, USA.

ESRI. 1995. ARC/INFO. Version 7.0.3. Environmental Systems Research Institute, Redlands, California, USA.

Fausch, K. D. 1989. Do gradient and temperature affect distributions of, and interactions between, brook charr (*Salvelinus fontinalis*) and other resident salmonids in streams? Physiological Ecology Japan, Special Volume **1**:303–322.

Fausch, K. D., C. Gowan, A. D. Richmond, and S. C. Riley. 1995. The role of dispersal in trout population response to habitat formed by large woody debris in Colorado mountain streams. Bulletin Français de la Pêche et de la Pisciculture **337/338/339**:179–190.

Fausch, K. D., C. L. Hawkes, and M. G. Parsons. 1988. Models that predict the standing crop of stream fish from habitat variables: 1950–85. General Technical Report PNW-213. USDA Forest Service, Portland, Oregon, USA.

Fausch, K. D., and T. G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences **49**:682–693.

Flebbe, P. A., and C. A. Dolloff. 1995. Trout use of woody debris and habitat in Appalachian wilderness streams of North Carolina. North American Journal of Fisheries Management **15**:579–590.

Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs **70**:539–590.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management **10**:199–214.

Ganey, J. L., M. E. Alderson, R. P. Balda, and D. R. Patton. 1990. Developing a large-scale model for Mexican spotted owl habitat. Pages 182–190 *in* P. R. Krausman and N. S. Smith, editors. Managing wildlife in the southwest. Arizona Chapter of the Wildlife Society, Phoenix, Arizona, USA.

Gowan, C., and K. D. Fausch. 1996*a*. Long-term demographic responses of trout populations to habitat manipulation in six Colorado streams. Ecological Applications **6**:931–946.

Gowan, C., and K. D. Fausch. 1996*b*. Mobile brook trout in two high elevation Colorado streams: re-evaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences **53**:1370–1381.

Gowan, C., M. K. Young, K. D. Fausch, and S. C. Riley. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Sciences **51**:2626–2637.

Gresswell, R. E. 1988. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, Maryland, USA.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. Science **245**:477–480.

Griffith, J. S. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho. Journal of Fisheries Research Board of Canada **29**:265–273.

Griffith, J. S., and R. W. Smith. 1993. Use of winter concealment cover by juvenile cutthroat trout and brown trout in the South Fork of the Snake River, Idaho. North American Journal of Fisheries Management **13**:823–830.

Harig, A. L. 2000. Factors influencing success of cutthroat trout translocations. Dissertation. Colorado State University, Fort Collins, Colorado, USA.

Harig, A. L., and K. D. Fausch. 1996. Compilation of data on Colorado waters containing Rio Grande cutthroat trout. Technical Report No. 904-96. Colorado Division of Wildlife, Montrose, Colorado, USA.

Harig, A. L., K. D. Fausch, and P. M. Guenther-Gloss. 2000*b*. Application of a model to predict success of cutthroat trout translocations in central and southern Rocky Mountain streams. Pages 141–148 *in* D. Schill, S. Moore, P. Byorth, and B. Hamre, editors. Management in the new millennium: are we ready? Proceedings of Wild Trout VII, 1–4 October 2000, Yellowstone National Park. Montana State University, Bozeman, Montana, USA.

Harig, A. L., K. D. Fausch, and M. K. Young. 2000*a*. Factors influencing success of greenback cutthroat trout translocations. North American Journal of Fisheries Management **20**:994–1004.

Hawkins, C. P., J. L. Kershner, P. A. Bisson, M. D. Bryant, L. M. Decker, S. V. Gregory, D. A. McCullough, C. K. Overton, G. H. Reeves, R. J. Steedman, and M. K. Young. 1993. A hierarchical approach to classifying stream habitat features. Fisheries **18**(6):3–11.

Hendrickson, D. A., and J. E. Brooks. 1991. Transplanting short-lived fishes in North American deserts: review, assessment, and recommendations. Pages 283–298 *in* W. L. Minckley and J. E. Deacon, editors. Battle against extinction: native fish management in the American West. University of Arizona Press, Tucson, Arizona, USA.

Hicks, B. J., J. D. Hall, P. A. Bisson, and J. R. Sedell. 1991. Responses of salmonids to habitat changes. Pages 483–518 *in* W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication 19, Bethesda, Maryland, USA.

Hodder, K. H., and J. M. Bullock. 1997. Translocations of native species in the UK: implications for biodiversity. Journal of Applied Ecology **34**:547–565.

Hubert, W. A., and W. A. Gern. 1995. Influence of embryonic stage on survival of cutthroat trout exposed to temperature reduction. Progressive Fish-Culturist **57**:326–328.

Hubert, W. A., R. W. Stonecypher, W. A. Gern, and J. Bobbit. 1994. Response of cutthroat trout embryos to reduced incubation temperatures at different developmental stages. Progressive Fish-Culturist **56**:185–187.

Hunt, R. L. 1969. Overwinter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. Journal of Fisheries Research Board of Canada **26**:1473–1483.

IUCN. 1987. Position statement on translocations of living organisms: introductions, reintroductions, and re-stocking. International Union for Conservation of Nature and Natural Resources Council, Gland, Switzerland.

IUCN. 1995. Guidelines for re-introductions. International Union for Conservation of Nature and Natural Resources Council, Gland, Switzerland.

Kleiman, D. G. 1989. Reintroduction of captive mammals for conservation: guidelines for reintroducing endangered species into the wild. BioScience **39**:152–161.

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

Labbe, T. R., and K. D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. Ecological Applications **10**:1774–1791.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist **142**:911–927.

Lanka, R. P., W. A. Hubert, and T. A. Wesche. 1987. Relations of geomorphology to stream habitat and trout standing stock in small Rocky Mountain streams. Transactions of the American Fisheries Society **116**:21–28.

Lisle, T. E. 1987. Using ''residual depths'' to monitor pool depths independently of discharge. Research Note No. PSW-394. USDA Forest Service, Berkeley, California, USA.

Lohr, S. C., and K. D. Fausch. 1997. Multiscale analysis of natural variability in stream fish assemblages of a western Great Plains watershed. Copeia 1997:706–724.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

Mazerolle, M. J., and M. Villard. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. Ecoscience **6**:117–124.

Millsap, B. A., P. L. Kennedy, M. A. Byrd, G. Court, J. H. Enderson, and R. N. Rosenfield. 1998. Scientific review of the proposal to de-list the American peregrine falcon. Wildlife Society Bulletin **26**:522–538.

Minckley, W. L. 1995. Translocation as a tool for conserving imperiled fishes: experiences in western United States. Biological Conservation **72**:297–309.

Mladenoff, D. J., T. A. Sickley, and A. P. Wydeven. 1999. Predicting gray wolf landscape recolonization: logistic regression models vs. new field data. Ecological Applications **9**:37–44.

Morse, W. L. 1970. Stream temperature prediction model. Water Resources Research **6**:290–302.

Moyle, P. B., and G. M. Sato. 1991. On the design of preserves to protect native fishes. Pages 155–170 *in* W. L. Minckley and J. E. Deacon, editors. Battle against extinction: native fish management in the American West. University of Arizona Press, Tucson, Arizona, USA.

Moyle, P. B., and R. M. Yoshiyama. 1994. Protection of aquatic biodiversity in California: a five-tiered approach. Fisheries **19**(2):6–18.

Nakano, S., S. Kitano, K. Nakai, and K. D. Fausch. 1998. Competitive interactions for foraging microhabitat among introduced brook charr, *Salvelinus fontinalis*, and native bull charr, *S. confluentis*, and westslope cutthroat trout, *Oncorhynchus clarki lewisi*, in a Montana stream. Environmental Biology of Fishes **52**:345–355.

Nelson, R. L., W. S. Platts, D. P. Larsen, and S. E. Jensen. 1992. Trout distribution and habitat in relation to geology and geomorphology in the North Fork Humboldt River drainage, northeastern Nevada. Transactions of the American Fisheries Society **121**:405–426.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs **62**.

Platts, W. S. 1979. Relationships among stream order, fish populations, and aquatic geomorpholgy in an Idaho river drainage. Fisheries **4**(2):5–9.

Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society **16**:391–409.

Poff, N. L., and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences **46**:1805–1818.

Propst, D. L., J. A. Stefferud, and P. R. Turner. 1992. Conservation and status of Gila trout, *Oncorhynchus gilae*. Southwestern Naturalist **37**:117–125.

Richmond, A. D., and K. D. Fausch. 1995. Characteristics and function of large woody debris in subalpine Rocky Mountain streams in northern Colorado. Canadian Journal of Fisheries and Aquatic Sciences **52**:1789–1802.

Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. General Technical Report INT-302. USDA Forest Service, Ogden, Utah, USA.

Rieman, B. E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Transactions of the American Fisheries Society **124**:285–296.

Ruth, T. K., K. A. Logan, L. L. Sweanor, M. G. Hornhocker, and L. J. Templeton. 1998. Evaluating cougar translocation in New Mexico. Journal of Wildlife Management **62**:1264–1275.

SAS Institute. 1996. SAS procedures guide for personal computers. Version 6.12. SAS Institute, Cary, North Carolina, USA.

Schlosser, I. J. 1991. Stream fish ecology: a landscape perspective. BioScience **41**:704–712.

Schlosser, I. J. 1995. Critical landscape attributes that influence fish population dynamics in headwater streams. Hydrobiologia **303**:71–81.

Schlosser, I. J., and P. L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. American Fisheries Society Symposium **17**:392–401.

Shuter, B. J., and J. R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. Transactions of the American Fisheries Society **119**:314–336.

Simons, L. H., D. A. Hendrickson, and D. Papoulias. 1989.

Recovery of the Gila topminnow: a success story? Conservation Biology **3**:11–15.

Smith, K., and M. E. Lavis. 1975. Environmental influences on the temperature of a small upland stream. Oikos **26**: 228–236.

Stonecypher, R. W., W. A. Hubert, and W. A. Gern. 1994. Effect of reduced incubation temperatures on survival of trout embryos. Progressive Fish-Culturist **56**:180–184.

Struhsaker, T. T., and K. S. Siex. 1998. Translocation and introduction of the Zanzibar red colobus monkey: success and failure with an endangered island endemic. Oryx **32**: 277–284.

Stuber, R. J., B. D. Rosenlund, and J. R. Bennett. 1988. Greenback cutthroat trout recovery program: management overview. American Fisheries Society Symposium **4**:71–74.

Stumpff, W. K., and J. Cooper. 1996. Rio Grande cutthroat trout (*Oncorhynchus clarki virginalis*). Pages 74–86 *in* D. A. Duff, editor. Conservation assessment for inland cutthroat trout: distribution, status, and habitat management implications. USDA Forest Service, Ogden, Utah, USA.

Tear, T. H., J. M. Scott, P. H. Hayward, and B. Griffith. 1993. Status and prospects for success of the Endangered Species Act: a look at recovery plans. Science **262**:976–977.

Thomas, C. D., J. A. Thomas, and M. S. Warren. 1992. Distributions of occupied and vacant butterfly habitats in fragmented landscapes. Oecologia **92**:563–567.

Torgersen, C. E., D. M. Price, H. W. Li, and B. A. McIntosh. 1999. Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. Ecological Applications **9**:301–319.

USFWS. 1998. Greenback cutthroat trout recovery plan. U.S. Fish and Wildlife Service, Denver, Colorado, USA.

Wang, L., and R. J. White. 1994. Competition between wild brown trout and hatchery greenback cutthroat trout of largely wild parentage. North American Journal of Fisheries Management **14**:475–487.

Wenny, D. G., R. L. Clawson, J. Faaborg, and S. L. Sheriff. 1993. Population density, habitat selection and minimum area requirements for three forest-interior warblers in central Missouri. Condor **95**:968–979.

Wiens, J. A. 1995. Landscape mosaics and ecological theory. Pages 1–26 *in* L. Hansson, L. Fahrig, and G. Merriam, editors. Mosaic landscapes and ecological processes. Chapman and Hall, London, UK.

Williams, J. E., et al. 1988. American Fisheries Society guidelines for introductions of threatened and endangered fishes. Fisheries **13**(5):5–11.

Wolf, C. M., T. Garland, and B. Griffith. 1998. Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts. Biological Conservation **86**:243–255.

Wolf, C. M., B. Griffith, C. Reed, and S. A. Temple. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conservation Biology **10**:1142–1154.

Young, M. K., editor. 1995*a*. Conservation assessment for inland cutthroat trout. General Technical Report RM-256. USDA Forest Service, Fort Collins, Colorado, USA.

Young, M. K. 1995*b*. Synthesis of management and research considerations. Pages 55–61 *in* M. K. Young, editor. Conservation assessment for inland cutthroat trout. General Technical Report RM-256. USDA Forest Service, Fort Collins, Colorado, USA.

Young, M. K. 1996. Summer movements and habitat use by Colorado River cutthroat trout (*Oncoryhnchus clarki pleuriticus*) in small, montane streams. Canadian Journal of Fisheries and Aquatic Sciences **53**:1403–1408.