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Conserving Inland Cutthroat Trout in Small Streams: How Much Stream is Enough?

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Abstract.—We examined the prognosis for long-term persistence of isolated populations of cutthroat trout *Oncorhynchus clarki* and the feasibility of using barriers to protect them from nonnative salmonids. In so doing, we estimated minimum stream lengths (MSL) required by cutthroat trout populations of varying abundances and rates of population loss to emigration and mortality. Using 2,500 individuals (>75 mm) as the target population size—corresponding to an effective population size, N_e, of 500—we estimated that more than 8 km of stream were required to maintain a population with high fish abundances (0.3 fish/m), and 25 km of stream were required to maintain a population of low abundance (0.1 fish/m). Incorporating a population loss rate of 10% increased MSL to 9.3 km for the high and 27.8 km for the low abundances. Our results suggest that many isolated populations may not persist over the long term because insufficient space exists to maintain the required N_e. Barrier construction to protect cutthroat trout from nonnative salmonids may be a necessary short-term solution, but it involves a long-term risk for maintaining viable cutthroat trout populations. We propose a watershed-based framework for cutthroat trout conservation in the central and southern Rocky Mountains that emphasizes protection of strong core populations.

Distribution and abundance of cutthroat trout *Oncorhynchus clarki* has declined throughout the western United States. Behnke (1972) estimated that 99% of the original interior cutthroat trout populations have gone extinct within the last 100 years and that only 2 of 13 subspecies of interior cutthroat trout stocks are stable or increasing in number (Behnke 1992). Historical accounts indicate cutthroat trout were once plentiful (reviewed in Trotter and Bisson 1988), but most subspecies are now restricted to small portions of their historical range, often as isolated populations with no connections to other populations. Introductions of nonnative brook trout *Salvelinus fontinalis* have typically resulted in range constriction or elimination of cutthroat trout through competition (Griffith 1988; Varley and Gresswell 1988; Fausch 1989), and rainbow trout *O. mykiss* may eliminate or isolate some cutthroat trout populations through hybridization (Allendorf and Leary 1988; Behnke 1992; Kershner et al. 1997). Dam construction on many small and large waterways has isolated many migratory populations from spawning and rearing tributaries (Thurow et al. 1988), probably resulting in loss of most fluvial populations. Logging, livestock grazing and agriculture, mining, and urban development can also fragment habitats and isolate populations by producing stream conditions unsuitable for salmonids (Meehan 1991).

The small population sizes often associated with isolation and fragmented habitats increase extinction risks through demographic and environmental variation (Fritz 1979; Smith 1980; Gilpin and Soule 1986; Hanski 1986; Sjogren 1991). Similarly, loss of connectivity and immigration among populations may substantially shorten time to extinction (Stacey and Taper 1992; Beier 1993). These processes may contribute to the decreasing probability of occurrence in salmonids as patch size decreases (Rieman and McIntyre 1995; Dunham et al. 1997). The more spatially restricted populations become, the greater the chance that a required habitat component is insufficient or missing for a life history stage (Dunning et al. 1992) or that absolute physical space necessary to maintain a given population size no longer remains. Population isolation may also reduce genetic diversity through lack of gene flow and genetic drift (Allendorf 1983; Lacy 1987; Lacy and Lindenmayer 1995) and may not provide a sufficient number of genetically diverse breeding individuals (effective population size) for a population to persist centuries into the future.

Limited physical space and population isolation

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is a problem for trout even when individuals are relatively sedentary, but this problem is exacerbated in mobile populations (e.g., Young 1994; Brown and Mackay 1995; Gowan and Fausch 1996; Young 1996). Increased movement requires greater space to accommodate individual ranges and makes connectivity within and among habitat types critical for population persistence (Dunning et al. 1992; Schlosser 1995). The presence of barriers or habitat fragmentation destroys population connectivity and may result in substantial losses of individuals from populations.

Recent management of many interior cutthroat trout populations is guided by a restrictive view that may actually endanger long-term persistence of populations and subspecies. A common management view for interior cutthroat trout populations present in streams with nonnative salmonids calls for population isolation above impassable barriers. Implemented, this approach may result in a viable short-term solution to conflicts with nonnative salmonids, but it creates additional isolated populations. Such cutthroat trout populations may still be vulnerable to invasions of nonnative salmonids through human transplantation. In addition, separation reduces the available space needed for population sizes large enough to maintain genetic diversity and reduce demographic and stochastic extinction risks, which is generally accepted to be an effective population size of at least 500 (Franklin 1980). This is problematic because recent estimates for long-term persistence of isolated populations are approximately 2,500 adults per generation (Allendorf et al. 1997) and up to 5,000 adults at any given time (Nelson and Soule 1987), as the effective population size may be a small fraction of the actual population size (Frankham 1995; Allendorf et al. 1997).

Much effort has been expended on cutthroat trout protection and restoration, as well as determinating population sizes required to maintain viability. However, no analyses have been conducted to determine what minimum stream fragment length is required to support population sizes necessary for long-term persistence. One approach is to estimate stream length requirements based on fish abundance—presumably a reflection of food and habitat quality and quantity within a stream. We use this technique to estimate the minimum stream lengths (MSL) required by cutthroat trout populations for long-term persistence under varying fish abundances and rates of population loss from emigration and mortality. Focusing on cutthroat trout populations in the Great Basin and central Rocky Mountain regions, our objectives were to provide minimum estimates of required stream lengths, evaluate the current and future status of extant population isolates, and propose a general framework for restoration and conservation based on those findings.

Methods

We constructed a simple analytic relationship to estimate MSL based on a given desired ending population size, the proportion of individuals leaving the population through emigration or mortality, and fish abundance per unit of stream length. The estimator, $\mathrm{MSL} = N(1 - s)^{-1} \cdot D^{-1}$, calculates how much stream is required to contain all of the individuals needed to arrive at a desired population size at the next spawning period (N), given a stream with D fish per unit stream length, and knowing that a proportion (s) of these fish will exit the population through the course of the year between the last and the next spawning event. It follows that more fish, and hence more stream, will be required as the proportion exiting the population (s) increases or as fish abundance per unit of stream length (D) decreases.

We hesitate calling the MSL estimator a model because it does not include parameters such as genetic diversity, catastrophic events, density dependence, fecundity, or numerous other variables used in stochastic simulation models. These parameters are important for modeling population dynamics and trajectories, but our intent was to provide an estimator of space requirements when a target population size is known. We assumed that demographic parameters affecting populations are reflected in the proportion of individuals exiting the population. For the MSL curves presented later, various levels for s can be chosen for specific populations. The MSL estimator is not a time series model but presents a static population view.

We constructed MSL curves for ending population sizes of N = 1,000, 2,500, and 5,000 individuals (>75 mm) and proportional loss varying from 0% to 50%. With s = 0%, there is no mortality, so MSL is just the space required to contain the desired population size for a given abundance level. However, when s = 50%, mortality and migration are large enough that the population must start with twice the target population size to achieve the desired target.

Cutthroat trout abundance values were gathered from four regions of varying abundance and density (Table 1): (1) Bonneville cutthroat trout *O. clarki utah* from Beaver Creek, Idaho; (2) Bon-

TABLE 1.—Mean (range) fish abundance (>75 mm) per linear meter of stream used for the minimum stream length estimator and accompanying mean (range) density for Bonneville cutthroat trout in Beaver Creek, Idaho; 4 Colorado River cutthroat trout populations in the Uinta Mountains, Utah (Horan 1996); 16 Bonneville cutthroat trout populations in southwest Utah (Hepworth et al. 1997); and 17 westslope cutthroat trout populations in western Montana (B. B. Shepard, Montana State University unpublished data). Densities were not used in the estimator and are given for comparative purposes only; NA = not applicable.

Stream or region	Mean abundance (fish/m)	Mean density (fish/m^2)
Beaver Creek, Idaho	0.35 (NA)	0.12 (NA)
Uinta Mountains, Utah	0.20 (0.12–0.3)	0.08 (0.04–0.14)
Southwest Utah	0.22 (0.12–0.55)	0.12 (0.06–0.23)
Western Montana	0.27 (0.01–1.80)	0.13 (0.01–0.97)

neville cutthroat trout populations from 16 established southwestern Utah locations (Hepworth et al. 1997); (3) Colorado River cutthroat trout *O. clarki pleuriticus* from four populations in the Uinta Mountains of Utah (Horan 1996); and (4) westslope cutthroat trout *O. clarki lewisi* from 17 stream systems in western Montana (B. B. Shepard, Montana State University, unpublished data). Abundances used in calculating MSL approximated populations from these regions; values were set at 0.3, 0.2, and 0.1 fish/m of stream length for Beaver Creek, Southwest Utah populations, and Uinta Mountains, respectively. Abundances from western Montana approximated those of Beaver Creek. We used these MSL calculations to evaluate extant populations with mapped (known) stream lengths and to discuss the potential status of other populations within the region.

Results

Estimated stream lengths varied substantially, depending on the target population size and abundance of individuals. For streams with relatively high fish abundances (0.3/m) and no population losses, we estimated that 3.3 km is required just to hold 1,000 individuals, 8.3 km for 2,500 individuals, and 16.7 km for 5,000 individuals (Figure 1). Adding a loss rate of 10% to account for population losses, such as emigration and mortality during the year, requires space for the extra individuals, increasing MSL to 3.7, 9.3, and 18.5 km for target population sizes of 1,000, 2,500, and 5,000 individuals (Figure 1).

Decreasing fish abundances to reflect streams with lower food or habitat quality resulted in marked increases in required stream lengths. For streams such as those from southwestern Utah with average fish abundances of 0.2 fish/m, baseline MSL required to hold target population sizes are 5 km for 1,000 individuals, 12.5 km for 2,500 individuals, and 25 km for 5,000 individuals (Figure 1). The space required to hold extra individuals at a 10% loss rate increases to 5.6, 13.9, and 27.8 km for 1,000, 2,500, and 5,000 individuals. Finally, baseline MSL required for streams containing populations with low abundances (0.1 fish/m) jumps to 10, 25, and 50 km for the target sizes of 1,000, 2,500, and 5,000 individuals, and accounting for a 10% loss rate further increases MSL to 11.1, 27.8, and 55.6 km for the three target populations (Figure 1).

Estimates of MSL using stream-specific abundances, habitable lengths of stream systems in Table 1, and a 10% population loss resulted in 22 of the 38 selected systems meeting MSL requirements for populations of 1,000. Only 9 of the 38 systems were adequate for populations of 2,500, and only 3 could meet MSL requirements for populations of 5,000.

Discussion

Our results indicate that if the MSL approach is valid, many populations of cutthroat trout probably lack sufficient space to maintain adequate numbers needed for long-term persistence. Even the best-case scenario of relatively high fish abundances (0.3 fish/m) equaling or exceeding most interior cutthroat trout population abundances (e.g., Herger et al. 1996; Hepworth et al. 1997; Kershner et al. 1997) require more than 8 km of stream to support 2,500 individuals, and this does not include providing for population losses in the forms of mortality and emigration (Table 2). Accounting for such losses or addressing systems with lower fish abundances requires even greater stream lengths. Using stream-specific abundance data for MSL, rather than the generic high-abundance scenario resulted in even fewer streams meeting the length requirements for 2,500 individuals. However, this may be misleading if population abundances we used for estimating MSL were lower than average at the time of sampling. Therefore, we chose not to highlight this aspect of the analysis.

Use of natural and constructed barriers to isolate cutthroat trout from potential hybridization and competition is problematic. Our calculations suggest that more space than probably exists above most barriers is required for long-term population viability. For example, the four populations of Yel-

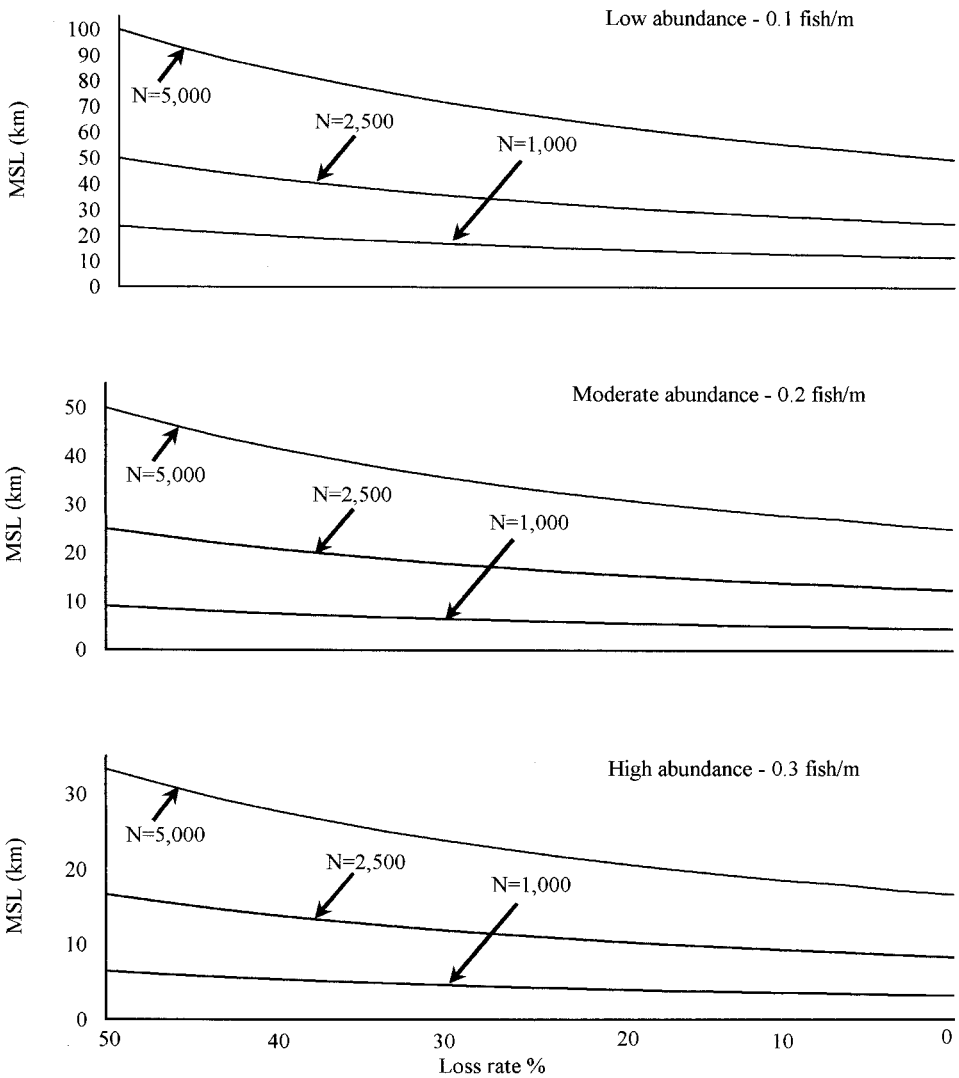

FIGURE 1.—Minimum stream length (MSL) curves for ending population sizes (N) of 1,000, 2,500, and 5,000 individuals for varying levels of population loss for low abundance Colorado River cutthroat trout populations in the Uinta Mountains (top), Utah; southwestern Utah populations of Bonneville cutthroat trout (center; data from Hepworth et al. 1997); and for Bonneville cutthroat trout in Beaver Creek, Idaho (bottom). Note different values on y-axis.

lowstone cutthroat trout *O. clarki bouvieri* introduced above fish migration barriers in the Wood and Greybull river drainages, Wyoming, occupy an average stream length of 5 km (Kruse et al. 1997). Despite the problem of insufficient stream length, failure to isolate some populations may lead to extinction from hybridization or competition. Isolation above barriers may be a necessary conservation tool when short-term, biotic extinction risks greatly exceed long-term risks, but removal of biotic threats and population restoration is critical. Thus, barrier construction must be viewed as a temporary solution for most jeopardized populations.

Although we also present MSL estimates for target population sizes of 1,000 and 5,000 for comparison, we choose to use 2,500 individuals as the benchmark. That is, a total population size of 1,000 individuals (>75 mm) is probably not enough to maintain an $N_e = 500$ because stream-resident cutthroat trout typically do not mature until 140 mm (Downs et al. 1997) and N_e is usually a fraction

TABLE 2.—Fragment lengths (including habitable tributaries) of some extant interior cutthroat trout populations. The value of 10 km was set as a classifier because it is approximately the minimum stream length required under the high fish abundance (0.3 fish/m) scenario with a 10% population loss rate. Streams within a connected system were counted as one system, and their habitable lengths were summed.

Region	Reported by	Cutthroat trout subspecies	Number of systems reported	Number of systems <10 km	System length (km)		
					Average	Median	Range
Southwest Utah	Hepworth et al. 1997	Bonneville	14	8	10.4	9.3	1.4–22.5
Uinta Mountains, Utah–Wyoming	Horan 1996	Colorado River	4	2	16.9	16.4	6.5–27.3
Western Utah–eastern Nevada	Duff[a]	Bonneville	6	3	10.1	8.8	1.7–23.0
Western Montana	Shepard[b]	Westslope	17	16	5.6	4.6	2.0–11.9

[a] D. A. Duff, U.S. Forest Service, unpublished data.
[b] B. B. Shepard, Montana State University, unpublished data.

of the actual breeding population size (Frankham 1995). In contrast, 5,000 individuals is the most preferred population size, but it probably exceeds the size necessary for population vitality, although we have no evidence to confirm this. Allendorf et al. (1997) recommend a total population size per generation of 2,500 for anadromous Pacific salmonids, approximating a per-generation $N_e = 500$. Stream-resident salmonid populations contain multiple generations that may interbreed, and individuals may reproduce yearly; so, the per-generation population size should not need to be as large as for semelparous salmonids, and 2,500 is probably sufficient.

Despite the implications of our results, insufficient space to maintain 2,500 individuals does not mean that a population will become extinct. Some isolated populations, such as those above waterfalls or in desert basins, have probably persisted for centuries and may have adapted to restricted space. However, they are probably exceptions rather than the rule, given the current status of cutthroat trout populations. To assume that all populations will behave similarly may lead to insufficient protection of many populations. Until better approaches are developed, estimating MSL can identify those stream sections that may need to be expanded, as well as candidate streams with the necessary space requirements for population reintroductions.

Space alone may not account for the ability of a population to persist. Trout in systems with high connectivity may exhibit movements on the order of tens of kilometers (Bjornn and Mallet 1964; Clapp et al. 1990; Meyers et al. 1992; Young 1994) and stream resident cutthroat trout may move several kilometers on a seasonal basis (Brown and Mackay 1995; Hilderbrand 1998). Movements of this magnitude would drastically increase the MSL required to preserve this life history trait within populations. Reducing available space could reduce or eliminate required age-specific or season-specific habitats (Dunning et al. 1992) and may further reduce population size. Similarly, limited space may increase extinction risk from local disturbances by concentrating the population into a small area and potentially reducing the amount of refugia. Therefore, MSL estimates must be considered minimum estimates of patch size requirements.

Space requirements are probably a function of food and habitat amount and quality. Chapman (1966) hypothesized that food and the degree of visual isolation regulated population density in stream-dwelling salmonids. Increasing food supply can decrease aggressiveness or the area of territory defended (Symons 1971; Slaney and Northcote 1974), whereas increased habitat complexity and cover may result in greater abundances of trout and salmon (Hunt 1969; McMahon and Hartman 1989; Riley and Fausch 1995). Food and habitat amount and quality probably exhibit an inverse relationship with space required for a population. Less food or simplified habitats should require more stream to maintain a given population size, but the degree to which food or habitat may be substituted for one another to maintain similar space requirements remains speculative. Additionally, the presence of competitor species will increase MSL either through reductions in food or habitat availability.

In its current form, the MSL estimator uses abundance of fish per unit length of stream, but fish density could also be used. Although an estimate of minimum area is not as intuitive as length, the value could be converted to length if stream widths are known. The estimator was intended for smaller streams (<7 m wide) containing

stream-resident salmonids and is not appropriate for larger, wider streams where tens of fish may exist per meter of stream. Applying MSL to such streams could result in required lengths of less than 100 m. Although this length (or area) may be sufficient to contain the desired number of individuals, more space is probably required to fulfill all life history requirements (e.g., spawning and overwintering areas) and life history strategies (fluvial, adfluvial, and stream-resident). We therefore recommend applying MSL only to smaller streams with stream-resident salmonids, preferably to isolated populations.

Proposed Conservation Framework

Population protection must occur at the watershed level because streams are catchments reflecting all up-slope impacts and processes. Degradation of a watershed will lead to degraded stream habitat. Additionally, biotic as well as physical protection must be afforded so that nonnative salmonids are controlled. Although it may appear unrealistic to limit impacts of nonnative salmonids, expecting cutthroat trout populations that are isolated above barriers to persist indefinitely is equally unrealistic. However, barriers isolating larger stream networks (>30 km) from nonnative salmonids may be important sanctuaries for cutthroat trout. We advocate, first, protecting those populations inhabiting the longest and most well-connected networks (e.g., Kershner et al. 1997). Focusing initially on the strongest populations while ignoring those more at risk appears counterintuitive, but it ensures that a population core (Rieman and McIntyre 1993) is established (i.e., adequate space for the largest populations) before expanding efforts to smaller populations.

Using the strongest populations as cores, efforts to link population fragments to cores or establish new populations in proximity to core areas could reestablish connectivity. By reestablishing connectivity, stream fragments that may not provide enough space to sustain viable populations for the long term (islands sensu Harrison 1991) can be maintained through immigration from a population core or through source-sink interactions (Pulliam 1988) with other fragments. Where no main-stem population cores exist, restoring uninhabited stream sections between populations could reestablish connectivity and immigration between populations.

Attention should be given to the spatial configuration of populations because their extinction risk may be influenced by the disturbance regime and landform characteristics. Because many population isolates are restricted to headwater reaches, they may be locally clumped, and large-scale disturbances like the Yellowstone wildfires or severe droughts could eliminate all populations in close proximity. This nearly happened to the Gila trout *O. gilae* (Propst et al. 1992). An effective conservation strategy must balance the tradeoff between maintaining the many isolated populations occupying small disjunct watersheds that will lessen catastrophic extinction risk and the risk associated with small spatially limited populations.

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