Chapter 6

Synthesis of Management and Research Considerations

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The five subspecies of cutthroat trout considered in this assessment share one characteristic: the loss of populations throughout their historical ranges. Similar causes have led to these losses: the introduction of nonnative fishes, overharvest, habitat degradation, and probably habitat fragmentation. Synergism among these effects remains unstudied, and we do not understand the biology of some of these subspecies, hence our ability to reverse the loss of populations is handicapped. Ironically, such ignorance has been inappropriately interpreted as a reason to avoid management action until more research is conducted, risking the loss of these subspecies in the interim (cf. Nehlsen et al. 1991).

Nonnative Fishes and Stocks

The effects of introducing nonnative fishes depends on the species introduced. That subspecies of cutthroat trout will readily hybridize with rainbow trout or with other cutthroat trout subspecies is widely acknowledged (and is probably attributable to polyploidy in salmonids; Allendorf and Leary 1988). Yet the geographic extent of genetically pure populations (or some subspecies) is virtually unknown, because few populations from each subspecies have been examined with techniques sensitive to minor amounts of hybridization. Lack of thorough testing has led to some embarrassment; genetic analysis of a supposedly pure population of Colorado River cutthroat trout in Utah, recognized in the recovery plan as one of the few known populations in the state, revealed it to be a stocked population of Yellowstone cutthroat trout (Shiozawa et al. 1993). Some populations appear to have resisted hybridization despite the presence of nonnative congeneric fishes (Trojnar and Behnke 1974; Utter et al. 1989); this resistance may be related to reproductive isolating mechanisms, our inability to detect hybridization (such as between fine-spotted cutthroat trout and Yellowstone cutthroat trout), or chance. Understanding these mechanisms might help us protect other populations exposed to closely related nonnative fishes.

We know that certain populations of cutthroat trout contain foreign genes. Depending on the rarity of the subspecies, such hybrid populations may merit preservation as the best remaining examples of the entire subspecies (O'Brien and Mayr 1991; Dowling and Childs 1992) or of evolutionarily significant units (sensu Waples 1991) of the subspecies. For this reason, Wyoming has adopted policies protecting partially hybridized populations of Colorado River cutthroat trout, as has the Yellowstone Cutthroat Trout Working Group (1994). Alternatively, such populations are often proposed for extermination if they can be refounded with genetically pure stocks.

Brook trout or brown trout introductions have almost always led to the replacement of cutthroat trout populations. Though competition has been speculated as the cause of replacement, especially by brook trout, researchers have failed to identify the life stage or specific competitive mechanism(s) that lead to this replacement (cf. Fausch 1988,1989). Replacement of cutthroat trout by brown trout has been less studied and is also poorly understood. Again, some populations of cutthroat trout, particularly of westslope and Yellowstone cutthroat trout, have persisted despite the presence of these nonnative fishes, and understanding why might help us preserve other populations. That such persistence may be related to the evolutionary exposure of cutthroat trout subspecies to certain guilds of other fishes merits attention.

Even transfers of a subspecies within its indigenous range may be undesirable. Adjacent populations of both westslope cutthroat trout (Allendorf and Leary 1988) and Colorado River cutthroat trout (Leary et al. 1993) were found to be genetically distinct. Interbasin transfers could lead to genetic mixing and the loss of locally adapted stocks (Scudder

1989). For example, transfers of adfluvial Yellowstone cutthroat trout from Yellowstone Lake to streams containing fluvial and resident stocks in other watersheds may have contributed to the loss of unique stream-adapted genomes, but it is doubtful we will ever know because this stocking was widespread. As a final caution, if neighboring populations differ genetically, we must consider whether those differences naturally evolved or resulted from anthropogenic isolation (Fausch and Young, in press).

"Ideal" Habitat

Degraded habitat, caused by natural forces or land management, is among the most frequently identified causes of extirpated or diminished cutthroat trout populations. Actual losses of habitat, caused by water diversion, log drives, channelization, urbanization, or mining pollution, are obvious problems. But the effects of indirect activities, such as logging, livestock grazing, or recreation, have been more difficult to quantify, and their contribution to the loss of populations is equivocal.

Though we understand the basic habitat components, we know little about what constitutes "ideal" habitat for any subspecies. The presence of populations of indigenous cutthroat trout in high-elevation, low-order streams has led to suggestions that these habitats are optimal (Griffith 1988), though these streams might be viewed as among the most marginal habitats owing to their small size, short growing seasons, and environmental extremes (Lawton 1993). Because populations are largely constrained to these habitats, identifying what is preferred for occupation becomes difficult (Ruggiero et al. 1988). Nevertheless, historical accounts indicate that these fish once occupied much larger, more productive waters: Lewis and Clark captured westslope cutthroat trout in 1805 in the Missouri River near Great Falls, Montana; Bonneville cutthroat trout were abundant in Utah Lake in the late 1700's; and Colorado River cutthroat trout occupied the Green River into the 1900s. Apparently human activities, directly or indirectly, have restricted most populations to small watersheds, many of which retain pristine fish communities and habitat (Rieman and Apperson 1989). Baltz and Moyle (1993) suggested that fishes in pristine habitats are more resistant to invasion by non-native fishes, but this assertion is largely untested for many cutthroat trout subspecies, and examples to the contrary abound (papers in this volume).

There is some question on how to select the dependent variable to define what is "ideal" habitat. Almost without exception, fisheries biologists have considered the best habitat to be the one containing the greatest density or biomass of fish; virtually all models of habitat quality use density or biomass as the dependent variable (cf. Fausch et al. 1988). But Van Horne (1983) noted that animal density did not always reflect habitat quality; seasonal changes in habitat use, patchy habitats, or time lags between habitat quality and fish response could lead to a decoupling of the habitat quality-fish density relation. Similarly, Fretwell (1972) suggested that territorial defense by competitively dominant individuals could lead to greater occupation of suboptimal habitats by subdominants. Consequently, future evaluations of habitat should consider alternative indices for defining habitat quality, e.g., the population age structure, or measures of habitat characteristics that confer persistence, resilience, or stability to fish populations at the appropriate spatial and temporal scale.

I perceive, perhaps incorrectly, that many biologists regard lotic habitats as static, i.e., once the desired habitat quality and quantity is established, it will remain essentially unchanged for years. But watersheds constantly change (e.g., vegetative succession or beaver, *Castor canadensis*, invasion) and will undergo natural disturbances at unpredictable intervals (e.g., intense wildfire or 500-year floods), and fish populations must respond to the eventual changes in terrestrial, riparian, and channel characteristics. Even if we could recognize optimal habitat, maintaining it in a single stream indefinitely is fighting against natural processes, and is inconsistent with land management reform directed at maintaining plant and animal communities in perpetuity (i.e., ecosystem management; Grumbine 1994). By working with these processes, we may be able to create a mosaic of watershed ages in larger systems that will maintain optimal habitat in different portions of the basin at various times and that could provide largely suitable habitat elsewhere (cf. Pringle et al. 1988). This suitable habitat should include refugia from environmental or anthropogenic disturbance that serve as sources for recolonization (Sedell et al. 1990). The kind of refugia necessary to resist some disturbances may be obvious, e.g., deep pools during drought or groundwater upwelling during thermal extremes, but the number and complexity of refugia needed for long-term persistence is unknown.

That trout would move to and from refugia contradicts the prevailing dogma that most stream-dwelling cutthroat trout are relatively sedentary and have all of their life history needs met in small reaches, even single pools, of streams (Miller 1957; Heggenes et al. 1991; Behnke 1992). Recent research has demonstrated that many individuals move substantial distances, even within a 24-hour cycle (Young, unpubl. data). Failing to recognize the mobility of these fish could invalidate past estimates of population size and confound our ability to determine population trends (cf. Decker and Erman 1992). Consequently, we should understand when these fish move, what habitats they are moving to, and how much of a stream or how many streams they require to fulfill their life history needs.

Metapopulations

Movement may be especially critical because some populations of cutthroat trout (especially westslope and Yellowstone cutthroat trout on federally protected lands) appear to form metapopulations. Metapopulations consist of a collection of subpopulations that are linked by immigration and emigration (Hanski and Gilpin 1991). The individual subpopulations may thrive, suffer losses of genetic variation, or go extinct, but individuals from other subpopulations within the metapopulation can contribute to the growing subpopulations, restore genetic variation to small subpopulations, or found new subpopulations after extinction. The diversity of life history strategies, subpopulation dynamics, and the structure of these apparent metapopulations of cutthroat trout are unknown. Several kinds of metapopulation structures exist, depending on the interactions among subpopulation sizes, habitat area and quality, and immigration and emigration patterns, and these structures have different implications for species persistence and reserve designs (Harrison 1991).

To persist, metapopulations must consist of mobile individuals in habitats without continuous barriers to movement, and some subpopulations must escape particular environmental events that affect other subpopulations (Gilpin 1987). The linear arrangement of streams provides connectivity between subpopulations, but with two risks. First, diseases or introduced species may spread via the corridors (Simberloff 1988). Second, environmental variation can be correlated because both upstream and downstream characteristics, activities, and fish communities may influence an intermediate reach (Vannote et al. 1980; Osborne and Wiley 1992).

Whether cutthroat trout form metapopulations is controversial and speculative. Based on genetic evidence, Allendorf and Leary (1988) and Shiozawa and Evans (1994) concluded that populations of some subspecies of cutthroat trout are largely nonmigratory; the logical extension of this contention is that these subspecies did not form metapopulations in some streams. Nevertheless, whether cutthroat trout form metapopulations (and what metapopulation structure develops) has never been directly investigated.

For most populations of cutthroat trout, the question of metapopulation dynamics is moot: connectivity to other populations has been lost and will be difficult to restore without stream restoration or nonnative fish eradication. For these populations, management and research focusing on population viability, genetic drift, inbreeding depression, and extinction probabilities is paramount.

Extinction Factors

Several rules of thumb have been developed to estimate the adult population sizes needed to avoid extinction, though these rules are widely debated (Soulé 1987; Simberloff 1988; Boyce 1992). Their application is controversial because the consequences of violating these rules are primarily based on theory, not empirical evidence (Caro and Laurenson 1994; Caughley 1994). Also, the persistence of small populations of desert fishes for thousands of years (Minckley and Deacon 1991) challenges the relevance of these rules. Nevertheless, they are applied, perhaps because they offer a quantifiable target for recovery. Theoretically, demographic uncertainty, as reflected by chance individual variation in survival and reproduction, becomes less problematic once populations exceed 30 to 50 individuals (Boyce 1992). "Allee effects," which are density-dependent effects such as the difficulty in finding mates, also apply when populations are very small (Simberloff 1988). Inbreeding depression, caused by the expression of deleterious alleles, may be avoided if effective population sizes exceed 50 to 60 adult animals (Franklin 1980; Ryman and Ståhl 1980; Soulé 1987). But note that effective population sizes are almost always less than total population sizes, sometimes much less (Futuyma 1986). Alternatively, populations that survive numerical bottlenecks may avoid later inbreed-

ing depression because deleterious alleles will have been purged (Caughley 1994). To avoid the loss of genetic variation in quantitative traits (and maintain long-term adaptability to environmental change), effective populations of around 500 adults may be necessary (Franklin 1980; Lande and Barrowclough 1987).

In contrast, population extinctions from environmental changes, whether deterministic or stochastic, have been amply demonstrated. Over scales of a few years to centuries, most populations are at much greater risk from extinction from environmental stochasticity than from demographic or genetic causes (Shaffer 1987), and increasing the frequency of environmental disturbance increases the probability of extinction (Boyce 1992). Eventually, populations reduced by environmental variation also risk extinction from demographic stochasticity or the loss of genetic variation. Similarly, deterministic events, such as habitat loss, overfishing, or introductions of nonnative fish, may drive populations down and heighten their vulnerability to all stochastic risks (Gilpin and Soulé 1986; Rieman and McIntyre 1993). Generally, the smaller the population and more variable the environment, the greater the probability of extinction.

But if environmental changes are catastrophic, extinction may be probable regardless of the size of the population (Shaffer 1987; Mangel and Tier 1994). For example, Propst et al. (1992) estimated there were almost 4,000 Gila trout in Main Diamond Creek in New Mexico in the late 1980s (ironically, the size and number of populations had convinced managers to pursue downlisting of this species from endangered to threatened; P.R. Turner, New Mexico State University, pers. commun.). Immediately after a fire had burned a portion of the Main Diamond Creek watershed in 1989, a rainstorm apparently caused flooding and toxic ash flows that exterminated the Main Diamond Creek population (other than 566 fish that were rescued during the fire and sent to a hatchery). Because this stream is separated from any other perennial stream containing this species, Gila trout failed to recolonize it. An adjacent watershed, South Diamond Creek, was also burned, and the sampled population declined from over 1,000 fish to fewer than 40. Similar fates for many isolated populations of cutthroat trout might be expected.

McIntyre and Rieman (this volume) speculated that populations of cutthroat trout of fewer than 2,000 individuals face a substantially higher risk of extinction than do larger populations. Many populations of the subspecies considered here fall below that level. Allendorf (1988) suggested that cutthroat trout may be at further risk because their large phenotypic variation and low heritability of traits sensitizes them to environmental conditions and potentially to environmental variation. Also, Dennis et al. (1991) and Nunney and Campbell (1993) suggested that population variability was correlated with the probability of persistence, and populations of trout are thought to fluctuate widely (mean annual fluctuation = 138%, maximum annual fluctuation = 1,073% in 10 western streams; Platts and Nelson 1988). Therefore, if we disregard the effects of movement on population estimates, many cutthroat trout populations would seem prone to extinction. Unfortunately, most studies of extinction probabilities have focused on mammals, birds, and invertebrates (e.g., Murphy et al. 1990; Dennis et al. 1991; Harrison 1991; Stacey and Taper 1992), and their life history characteristics are very different from those of fishes (cf. Thomas 1990). To further complicate the issue, cutthroat trout may tolerate large environmental variation; for example, the number and timing of annual spawning runs depended on the variability in peak flows in a Nevada stream (Nelson et al. 1987). Moreover, cutthroat trout have survived catastrophic environmental changes; this species persisted in a stream exposed to the Mount St. Helens eruption by occupying refugia, presumably habitats created by coarse woody debris (Hawkins and Sedell 1990). Until we understand how life history characteristics, phenotypic plasticity, population structure, and disturbances affect persistence, the probability of extinction of populations is largely speculative.

Conservation Considerations

Because all five subspecies of cutthroat trout continue to decline, ideally all remaining populations, regardless of size, should be conserved to maintain the full genetic variation within each subspecies (Allendorf and Leary 1988). Yet this straightforward guidance presents myriad problems. For example, managers commonly install expensive, permanent barriers on streams containing cutthroat trout to prevent the upstream migration of introduced species. Though effective, these barriers must be regularly maintained at some cost. Furthermore, they isolate cutthroat trout populations from other populations (and possibly from critical habitats), and these populations then risk losses of heterozygosity from genetic drift and are vulnerable to extinction caused by fire,

drought, toxic spills, road failures, or debris torrents (Propst et al. 1992). Extinct populations of cutthroat trout may be reestablished by stocking (another cost), but a hatchery stock (founded and maintained at some expense) will be less well adapted to a watershed than the indigenous stock (Krueger and May 1991; Demarais et al. 1993) and may be even more susceptible to future extinction. Finally, biologists have also failed to acknowledge the consequences of barriers for other aquatic biota; the near complete lack of information should be cause for caution.

Alternatives to "blocking and stocking" merit consideration. Griffith et al. (1989) found that translocations of wild-caught animals were about twice as successful at establishing new populations as were captive-reared animals. Also, transfers of nearby, genetically pure, wild stocks to refound extinct populations avoid the artificial selection and genetic drift often associated with hatchery rearing (Waples and Teel 1990) and may be cheaper. Such transfers also maintain the genetic integrity of locally evolved populations of each subspecies (Shiozawa and Evans 1994). Barriers will probably remain essential, but should be viewed as temporary measures used to prevent invasion before movement corridors are reopened. Reconnecting watersheds should decrease the probability of extinction of all populations and may entail fewer direct costs, but mandates vigilance against the introduction of nonnative fishes or pathogens and is more difficult to establish politically. Also, we should avoid reconnecting genetically distinct endemic stocks; Scudder (1989) argues that the most isolated populations may be the most evolutionarily valuable, because they may have been subjected to the most rigorous selection. But Propst et al. (1992) argued that human-induced isolation has led to genetically unique stocks of Gila trout, and that these stocks should be recombined before being introduced elsewhere.

Given these caveats, managers still have at least three sound tactics for ensuring the persistence of these five subspecies of cutthroat trout: (1) extensively survey streams within their historical ranges to identify remaining populations and highlight unique ones (Leopold's first rule of intelligent tinkering); (2) reestablish probable metapopulations disrupted by human activities (assuming that long-isolated populations can produce migrant individuals); and (3) protect and expand these populations within their historical ranges by including well-distributed refugia, essential habitats, and movement corridors in designated aquatic habitat reserves (for details, see Frissell 1993; Rieman and McIntyre 1993; Moyle and Yoshiyama 1994).

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