

## Effective Population Size and Genetic Conservation Criteria for Bull Trout

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**Abstract.**—Effective population size ( $N_e$ ) is an important concept in the management of threatened species like bull trout *Salvelinus confluentus*. General guidelines suggest that effective population sizes of 50 or 500 are essential to minimize inbreeding effects or maintain adaptive genetic variation, respectively. Although  $N_e$  strongly depends on census population size, it also depends on demographic and life history characteristics that complicate any estimates. This is an especially difficult problem for species like bull trout, which have overlapping generations; biologists may monitor annual population number but lack more detailed information on demographic population structure or life history. We used a generalized, age-structured simulation model to relate  $N_e$  to adult numbers under a range of life histories and other conditions characteristic of bull trout populations. Effective population size varied strongly with the effects of the demographic and environmental variation included in our simulations. Our most realistic estimates of  $N_e$  were between about 0.5 and 1.0 times the mean number of adults spawning annually. We conclude that cautious long-term management goals for bull trout populations should include an average of at least 1,000 adults spawning each year. Where local populations are too small, managers should seek to conserve a collection of interconnected populations that is at least large enough in total to meet this minimum. It will also be important to provide for the full expression of life history variation and the natural processes of dispersal and gene flow.

The concept of effective population size ( $N_e$ ) plays an important role in conservation management of fishes (Waples in press). The  $N_e$  is a measure of the rate of genetic drift and is directly related to the rate of loss of genetic diversity and the rate of increase in inbreeding within a population (Wright 1969). Conservation of populations large enough to minimize such effects has become an important goal in the management of threatened or endangered salmonids, including Pacific salmon *Oncorhynchus* sp. (McElhaney et al. 2000) and bull trout *Salvelinus confluentus* (USFWS 1998).

The ongoing fragmentation and isolation of habitat of species like bull trout have led to reductions in population size (Rieman and McIntyre 1993; Rieman et al. 1997) and presumably in  $N_e$  for many populations. A resulting loss of genetic variation can influence the dynamics and persistence of populations through at least three mechanisms: inbreeding depression, loss of phenotypic variation and plasticity, and loss of evolutionary potential (Allendorf and Ryman in press). The loss of ge-

netic variation in populations with small  $N_e$  may reduce fitness through the so-called inbreeding effect of small populations and lead to an accelerating decline toward extinction in a process termed an extinction vortex (Soulé and Mills 1998).

Because of the importance of  $N_e$ , the so called “50/500” rule has emerged as general guidance in conservation management (Franklin 1980; Soulé 1980; Nelson and Soulé 1987; see Allendorf and Ryman [in press] for a recent consideration of these criteria). The generally accepted view is that an  $N_e$  of less than about 50 is vulnerable to the immediate effects of inbreeding depression. Although populations might occasionally decline to numbers on this order without adverse effects, maintenance of adaptive genetic variation over longer periods of time (e.g., centuries) probably will require an  $N_e$  averaging more than 500 (Allendorf and Ryman in press). These numbers have been generally applied as criteria for determination of conservation status among taxa (Mace and Lande 1991) and within the salmonids in particular (e.g., Allendorf et al. 1997; Hilderbrand and Kershner 2000).

The problem in application is that  $N_e$  and the

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number of adult fish usually represented in population estimates ( $N$ ) are not equal. Estimation of  $N_e$  and even  $N$  can be complicated. Direct estimation of  $N_e$  is possible but requires either detailed information on population demographics and breeding structure (Harris and Allendorf 1989; Caballero 1994) or extensive information on genetic population structure (Waples 1991; Laikre et al. 1998; Schwartz et al. 1998). Limitations of sample size requirements, the resolution possible for all but very small populations, and time and analytical costs may restrict the utility of these methods. As a result, application of population size criteria often relies on approximations of  $N_e$  based on existing estimates of  $N$  and population simulation methods (Harris and Allendorf 1989). Even if  $N_e$  is assumed to be some fraction of  $N$  based on other work, the estimation of  $N$  can still be unclear.

The life history patterns of most salmonids are complex. Pacific salmon adults spawn and die, but except for pink salmon *Oncorhynchus gorbuscha*, there is overlap among cohorts that mature at variable ages. The adult population is replaced each year, but a single generation will encompass multiple spawning years. Trout and char, including bull trout, may spawn several times. Age at maturity varies among individuals, and once mature, not all surviving individuals will spawn in all years. Although new adults are recruited each year, the adult population as a whole is replaced gradually through time (Laikre et al. 1998).

Waples (1990) has shown for Pacific salmon, which die after spawning, that  $N_e = g \times N_b$ , where  $g$  is the average age of spawning or generation length, and  $N_b$  is the mean effective number of spawners per year. An appropriate estimate of  $N$  would be the mean number of adults observed across years times  $g$ . Hill (1972) showed that  $N_e$  in iteroparous species can be approximated by the number of first-time spawners entering the population each generation (i.e., the mean number of first time spawners times  $g$ ). For managers the interpretation of  $N$  may still remain obscure for species that spawn multiple times. Even detailed inventory and monitoring projects cannot routinely discriminate between first-time and repeat spawning individuals.

In our work with bull trout, a recent addition to the threatened species list under the Endangered Species Act of the United States (USFWS 1998), application of population conservation criteria (i.e., 50/500) was limited by these problems. Our objective was to describe the expected loss of genetic variation and to approximate  $N_e$  for a range

of population sizes and life history conditions characteristic of species like bull trout. We were primarily interested in estimating the ratio of  $N_e$  to the number of adults that might be observed in typical monitoring efforts concerned with conservation and the application of population size criteria. We use our results to show how managers can interpret annual estimates of adult abundance or spawning escapements in light of existing conservation genetic theory and general knowledge of bull trout life history.

## Methods

*Estimation of  $N_e$ .*—In an “ideal” population, the expected loss of genetic variation (represented as heterozygosity) per generation is  $\Delta H = -1/2N$ , where  $N$  is the size of the adult population (Wright 1969). For example, an ideal population of 10 adults would be expected to lose  $1/(2 \times 10)$ , or 5%, of its heterozygosity in one generation. An ideal population is one with discrete generations (all adults reproduce once and at the same age), random mating, equal sex ratio, constant population size, and an equal probability for all adults to contribute offspring to the next generation (Caballero 1994; Frankham 1995). Most populations do not fit the ideal.

To address this reality, effective population size is defined as the size of the ideal population that will result in the same amount of genetic drift as in the actual population being considered (Wright 1969). Natural populations can deviate strongly from conditions of the ideal. Family size (some adults produce more offspring than others), for example, is likely to vary substantially in salmonid fishes (e.g., Geiger et al. 1997). Strong temporal variation in population size can have a particularly important influence as well (Crow and Denniston 1988; Frankham 1995; Ray 2001). As a result  $N_e$  is expected to be smaller than the actual census number for most cases.

We used a simulation approach to track the loss of genetic variation in relation to total adult number for a series of hypothetical bull trout populations. Our results provided an estimate of the ratio of  $N_e$  to the number of adults that might actually be observed or estimated in annual population monitoring. We used a range of simulations representative of the range of life history characteristics believed to exist in bull trout populations (Pratt 1985, 1992; Fraley and Shepard 1989). We used the observed rate of loss of heterozygosity and the generation length to estimate the inbreed-

ing effective population size (Crow and Kimura 1970:345) based on the following formula:

$$H_t = H_0[1 - (1/2N_e)]^t \quad (1)$$

where  $H_t$  is the heterozygosity after  $t$  generations, and  $H_0$  is the initial heterozygosity (standardized at 1.0). In our analyses,  $t$  was the total length of the simulated period divided by the average generation time.

*The model.*—VORTEX is a stochastic, age-structured, population simulation model that tracks the genetic structure of an entire population by following the history of each individual (Miller and Lacy 1999). This flexible simulation program incorporates demographic stochasticity at each individual life history event and user-defined levels of variation in age- and sex-specific mortality, maturation schedule, and population carrying capacity. The genetic composition of a population is tracked at a single locus in each simulation. At the initiation of a simulation, each individual in the population is assigned two unique alleles. Matings are random, but the relative contribution of males and females can vary with age. Alleles are transmitted in random Mendelian fashion, and the fate of each allele is tracked through the pedigree of surviving individuals. Summary results include mean population size and growth rate (and their standard deviations [SDs]), mean number of adults, expected and observed heterozygosity as a proportion of initial condition, and a variety of statistics related to population extinctions. More detail on VORTEX is available from Lindemayer et al. (1995) and Miller and Lacy (1999).

*Parameter estimates and simulation approach.*—We did not conduct an exhaustive study of all possible population conditions or produce a precise characterization of any particular population. Rather we used the simulations to generate a range of results that would span those most likely for bull trout populations. We parameterized the model to represent the range of life histories that are reasonable, given existing knowledge (Table 1). Our rationale is explained below.

*Maturity and longevity.*—Bull trout are thought to live at least 7 or 8 years and to begin maturing between ages 4 and 7 years (Fraley and Shepard 1989; Pratt 1992; Rieman and McIntyre 1993). In our own work on Pend Oreille Lake, Idaho, we observed adults between ages 5 and 7 years (B.E.R. unpublished data), but anecdotal accounts from ongoing tagging studies suggest that some fish may live 12 years or more. Bull trout may

spawn every year or in alternate years after first maturity (Rieman and McIntyre 1993). In our analysis we used combinations of maturity and longevity that included first maturity at 4, 5, and 7 years of age, with the fish spawning only once or, alternatively, for as many as five subsequent years. In simulations with only demographic stochasticity, we assumed that 100% of females spawned each year once mature. In a second series of simulations used to characterize the variation possible in family size and adult number (see section on simulation approach), we assumed that 50% of females were expected to spawn in any year, equivalent to every-other-year spawning cycles. All males were assumed to contribute to spawning in the first series, but only 50% of males were expected to be successful in the second. Although males may actually return every year, it would not be unusual to find that not all compete successfully for mates. We assumed a sex ratio in all simulations of 1:1, with males and females maturing at the same age.

Simulation	Spawning ages	Annual adult survival	Mean generation time
S1	4–7	0.50	4.73
S2	4–7	0.50	4.73
S3	7–10	0.50	7.73
S4	5–8	0.50	5.73
S5	5–8	0.20	5.32
S6	5–12	0.50	5.97
S7	5	0.00	5.00

spawn every year or in alternate years after first maturity (Rieman and McIntyre 1993). In our analysis we used combinations of maturity and longevity that included first maturity at 4, 5, and 7 years of age, with the fish spawning only once or, alternatively, for as many as five subsequent years. In simulations with only demographic stochasticity, we assumed that 100% of females spawned each year once mature. In a second series of simulations used to characterize the variation possible in family size and adult number (see section on simulation approach), we assumed that 50% of females were expected to spawn in any year, equivalent to every-other-year spawning cycles. All males were assumed to contribute to spawning in the first series, but only 50% of males were expected to be successful in the second. Although males may actually return every year, it would not be unusual to find that not all compete successfully for mates. We assumed a sex ratio in all simulations of 1:1, with males and females maturing at the same age.

*Survival.*—Annual survival of bull trout populations has rarely been estimated, but data from Pratt (1985) suggest that survival ranges between 0.30 and 0.70 for subadult fish. We assumed that survival improved from the low to high end of this range as fish progressed from age 1 to maturity. From our own work with population estimates of spawning adults, immediate postspawning mortality appears to be about 0.50 (B.E.R. unpublished data). Because additional mortality may be associated with the year(s) of life between spawnings, we estimated adult survival rates at 0.50 and 0.25.

Survival to age 1 was used to produce a stable population (a mean instantaneous population growth rate of 0) in all simulations. We increased first-year survival with spawning age to produce equivalent numbers of adults for all scenarios because the number of adults declined with stable survival and increasing age at maturity. Our results are representative of populations that are in dynamic equilibrium (not growing or declining on average).

We are not aware of any estimates of the variation in survival attributable to the influence of environmental variation on these populations. To consider a range of possibilities, we included one series of simulations with only demographic stochasticity in mortality based on the binomial sampling error incorporated in the model. In a second series we included variation in mortality after age 1 equivalent to a standard error of about 0.10. We included greater variation in first-year survival. Because we have no empirical estimates, we chose a SD in first-year survival that produced a SD in population growth rates between about 0.30 and 0.50, values characteristic of those observed from long-term monitoring of bull trout populations in Idaho and Montana (Rieman and McIntyre 1993).

*Fecundity.*—Two attributes of VORTEX limit its utility for fish populations. One is the limited range of fecundities that can be assigned to adult females. Another is an inability to specify an age-size relationship in fecundity that correlates with growth in iteroparous fish like bull trout. To compensate for the reduced fecundities in VORTEX, we collapsed two life stages (e.g., between egg to fry and fry to age-1) as suggested in the users' manual. We varied fecundity expected for any female in direct proportion to the distribution of fecundity predicted from the bull trout growth, survival, and fecundity models reported by Rieman and McIntyre (1993) to simulate the variation in fecundity expected with females of different ages and sizes.

*Density dependence.*—Although VORTEX allows density dependence in some life history processes, we did not include it in the model. The model imposes a reflecting boundary as a carrying capacity that we did use. In essence, our populations grew or declined in size only as a function of random variation in mortality and reproduction. If a population reached carrying capacity, further reproduction was preempted, thereby representing an "all or nothing" form of density dependence. To consider the effect that a reflecting boundary might have on estimated loss of genetic variation,

we included a single simulation in which the population was initiated at carrying capacity (S2) (i.e., carrying capacity equaled the initial population size, regardless of what that size was). All other simulations used carrying capacities that were twice the initial population size, regardless of what that was.

*Simulation approach.*—As noted above, we used two series of simulations to capture the potential range of conditions possible for bull trout. In the first, we included only the demographic variation in life history processes inherent in VORTEX. We used a range of values in age at maturity, longevity, survival, and initial population size in relation to carrying capacity, to explore the influence of variation in general life history and generation time on  $N_e$  and the loss of genetic variation (S1–S7; Table 1). Being based on a stable age structure and no variation in fecundity, these simulations represent the most optimistic scenarios possible for the retention of genetic variation.

To generate a more realistic view of the potential loss of genetic variation, we included a second set of simulations that incorporated variations in parameters that might result from environmental variation and breeding structure. All of these simulations were reiterations of those in the first set (except for S2), but with additional variation in fecundity and survival, spawning frequency in females, and spawning success in males (S1<sub>v</sub>–S7<sub>v</sub>). We refer to the additional variation as "environmental variation" in the remainder of the paper. In all, we simulated 13 life history scenarios. Each scenario included five different average population sizes that ranged from about 50 to 550 adults. The initial population size was varied to produce average adult numbers distributed at five levels across this range (i.e., 50–75, 100–150, 200–250, 300–375, 450–550). The actual averages varied slightly because of the stochastic process inherent in the model. We chose the upper bound because we anticipated that loss of genetic variation would accelerate as numbers decreased to somewhere below about 500 adults. We restricted the lower bound because simulated populations much smaller than this frequently went extinct within the period of simulation as a result of demographic processes alone. Each simulation was for 200 years. Simulations for each scenario and population size were replicated 500 times.

We summarized the proportion of expected heterozygosity retained at the completion of each simulation. We estimated a mean for the replicated

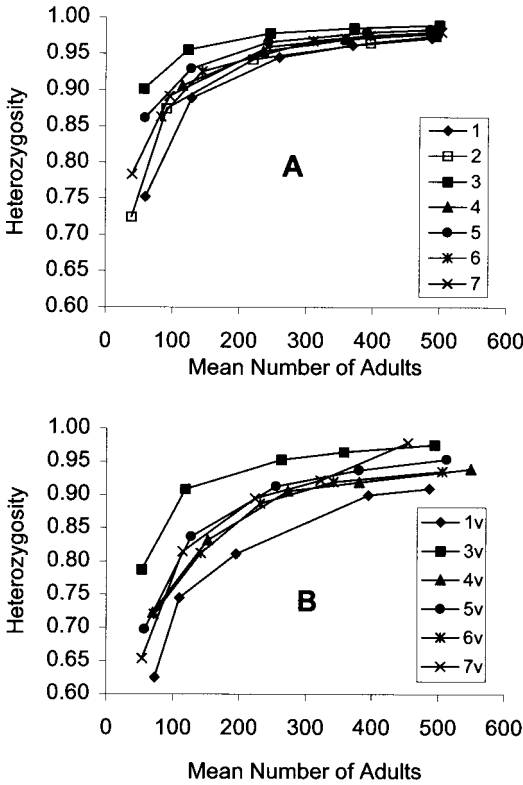


FIGURE 1.—Mean expected heterozygosity, as a proportion of the original, retained over 200 years in 500 simulations of bull trout populations with varied life history patterns and mean number of adults. Panel A includes simulations with demographic variation only, panel B simulations with both demographic and environmental variation. Simulations are as defined in the text and Table 1.

scenario–population size combinations with effective population size calculated as follows:

$$N_e = (1/2) \cdot (1 - e^{\log_e H_t/t}) \quad (2)$$

where all terms are as defined in equation (1). To contrast  $N_e$  and the  $N$  that might actually result from population inventory and monitoring, we summarized adult populations in several ways. The first measure of population was mean number of adults ( $N_{adult}$ ), defined as the mean number of individuals of spawning age in the population whether they spawn or not. The second measure was mean number of spawners ( $N_{spawn}$ ), defined as the mean number of fish that return to spawn in a given year. This number is identical to  $N_{adult}$  in simulations where spawning frequency is 1 (i.e., S1–S7; Table 1) but is approximately 0.75  $N_{adult}$  when females are expected to spawn only half of the time

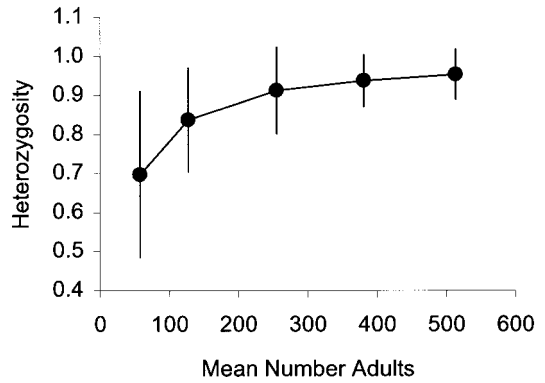


FIGURE 2.—Mean expected heterozygosity retained over 200 years in 500 simulations of bull trout populations with a single life history pattern (S5<sub>v</sub>) and varied mean number of adults. The vertical lines indicate  $\pm 1$  SD.

(i.e., S1<sub>v</sub>–S7<sub>v</sub>).  $N_{spawn}$  was used as an approximation of population size that would be consistent with typical escapement monitoring. The third measure was ideal population ( $N_{ideal}$ ), defined as the population size estimated by assuming the characteristics of an ideal population as  $N_{new} \times g$  (Hill 1972), where  $N_{new}$  is the mean number of individuals entering the adult population each year and the  $g$  is mean generation time in years; we used this estimate to compare our results with estimates of  $N_e/N$  ratios in the literature (e.g., Frankham 1995; Allendorf et al. 1997).

**Results**

In simulations that did not include environmental variation (S1–S7), the loss of heterozygosity differed among life histories and increased sharply with fewer numbers of adults (Figure 1A). Differences in heterozygosity were greatest between simulations with delayed (S3) and early (S1) maturation, but the differences were relatively minor among other life histories.

In simulations that included environmental variation (S1<sub>v</sub>–S7<sub>v</sub>), the losses of heterozygosity and differences among the extremes in life histories were more pronounced (Figure 1B). The rate of loss of genetic variation increased noticeably with simulations involving fewer than about 250–400 adults.

Although loss of heterozygosity differed among life histories, the variation within any scenario that included environmental variation was also substantial (Figure 2). The SD in the loss of genetic variation in the series of simulations for a single life history (Figure 2) was similar to or greater



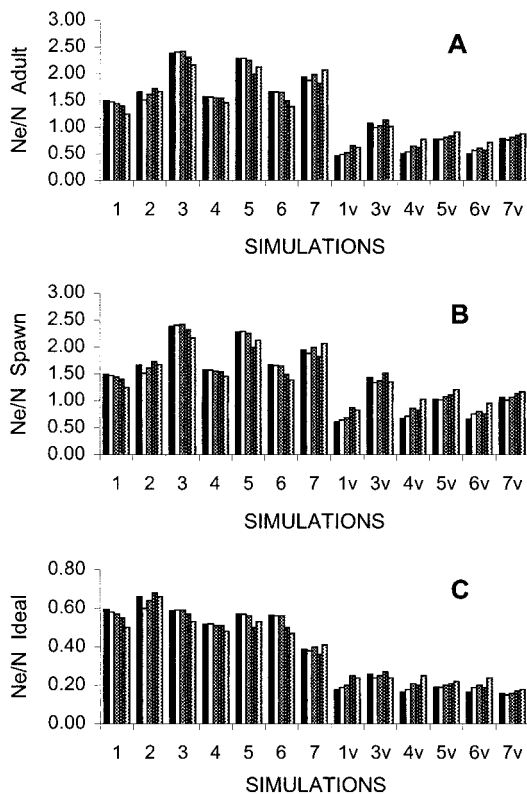


FIGURE 3.—Ratios of estimated effective population size ( $N_e$ ) to (A) the mean number of adults, (B) spawners, and (C) the ideal population in 500 simulations of bull trout populations with varied life history patterns and mean number of adults. The different bars associated with each life history scenario represent the simulations with means for the number of adults ranging from approximately 500 (leftmost bar) to 50 (rightmost bar).

than the range in the average loss of variation among all life histories (Figure 1). The SD also increased with fewer numbers of adults. Thus, not all populations will experience a loss of genetic variation, but some may lose far more than expected. The potential for substantial loss of heterozygosity also increased dramatically as population size fell.

Simulations without environmental variation produced estimates of  $N_e$  that ranged between about 1.50  $N_{adult}$  and 2.40 times  $N_{adult}$  compared with estimates between 0.5 and 1.2 when environmental variation was included (Figure 3A). Estimates of  $N_e$  relative to  $N_{spawn}$  were identical to those for total adults with no environmental variation but were slightly higher with variation included (0.6–1.5; Figure 3B). The increase resulted because the number of “spawners” was less than

the total number of adults under the assumptions associated with environmental variation. Estimates of  $N_e$  relative to the  $N_{ideal}$  ranged between about 0.38 and 0.68 without environmental variation and between about 0.15 and 0.27 with variation (Figure 3C). The ratio of  $N_e$  to the different estimates of  $N$  varied with life history scenario (e.g., S1 versus S3 or S1<sub>v</sub> versus S3<sub>v</sub>; Figure 3), but the largest differences were clearly between those simulations with and without environmental variation (e.g., S1 versus S1<sub>v</sub>). There was no apparent pattern in the ratios of  $N_e$  to the different  $N$  values associated with varied mean number of adults within each scenario; that is, the smallest or largest means were not associated consistently with the smallest or largest ratios (Figure 3).

### Discussion

Genetic variation will be lost through time in isolated populations and this loss will occur more quickly in small populations than in large ones (Allendorf and Ryman in press). Our simulations show that even populations averaging approximately 500 adults annually can lose more than 10% of original heterozygosity in 200 years; this loss is expected to accelerate dramatically as population sizes fall. A population of fewer than 100 may lose five or more times that much in the same period.

Our results also show that the variation in life history and demographic characteristics among bull trout populations will almost certainly influence the loss of genetic variation that can be expected in those populations. Some populations will face greater risks than others. In our simulations the most extreme differences in life history produced a two- to threefold range in the relative difference between  $N_e$  and the number of adults or spawners in simulations including environmental variation. The difference was between four- and fivefold if we contrast simulations with and without environmental variation. Clearly, population characteristics that we know relatively little about in many populations can strongly influence the loss of genetic variation and the relationship between  $N_e$  and the numbers we might observe in those populations.

The interaction of life history and environmental variation and their influence on  $N_e$  can be complex but, in some cases, predictable (e.g., Gaggiotti and Vetter 1999). A detailed analysis based on a better understanding of the characteristics of any real populations (e.g., Waples and Teel 1990) could produce a better understanding of the immediate

threats to a population. Without that information, managers must simply be more conservative and acknowledge a range of possible results.

Our range of estimates of  $N_e/N_{ideal}$  (0.15–0.27) for the hypothetical bull trout populations are comparable with other work. Frankham (1995) summarized estimates that averaged about 0.10 for a wide variety of wildlife species. Existing estimates for salmonids range widely (0.04–0.83) (Simon et al. 1986; Bartley et al. 1992) and may be particularly variable for hatchery populations (Bartley et al. 1992), where mating structures are highly artificial. Allendorf et al. (1997) concluded that  $N_e/N_{ideal} = 0.2$  is a reasonable approximation for wild populations of Pacific salmon. McElhane et al. (2000) suggested 0.3 as an appropriate starting point. Our results suggest that natural bull trout populations will fall in about this range.

In applying these models, it is useful to consider the ratio of  $N_e$  to the actual observations of population numbers likely to be made in the field. Based on the range of conditions we included in our analysis, estimates of  $N_e$  ranged between about 0.5 and 1.5 times the number of adults that would be observed in an annual spawning run of bull trout. Thus, a population with an average of 100 spawners per year would have an effective population size between 50 and 150. Although we did not use an exhaustive combination of parameter estimates, most of our simulations with environmental variation produced ratios close to or less than 1. In addition, our values may be overestimates because we did not account for all possible sources of variability in reproductive success (e.g., sexual selection). Therefore, in the absence of more detailed local population and demographic information, we believe the best estimate of  $N_e$  is between 0.5 and 1.0 times the mean number of adults observed annually.

### Management Recommendations

In the process of developing recovery plans, managers of threatened or endangered species must establish recovery criteria and goals for management of critical populations (W. Fredenberg, U.S. Fish and Wildlife Service, personal communication). Managers may also prioritize limited resources for habitat conservation and restoration, based on some measure of risk (e.g., Allendorf et al. 1997). If we accept the general guidance of the 50/500 criteria (Allendorf and Ryman in press), a cautious interpretation of our results would be that approximately 100 (i.e.,  $100 \times 0.5 = 50$ ) adults spawning each year would be required to minimize

the risks of inbreeding in any population. An average of 1,000 (i.e.,  $1000 \times 0.5 = 500$ ) adults spawning annually would be necessary to maintain genetic variation indefinitely. Those criteria might be relaxed if there were clear evidence that the adult population is larger than the number of fish spawning in any year (because all females do not spawn in all years), or if more precise estimates of other life history parameters and variation were available.

Few local bull trout populations are likely to support spawner numbers averaging 1,000 or more per year. The largest local spawning aggregations we are aware of contain between several hundred and several thousand adults (Rieman and McIntyre 1993; Dunham et al. 2001). Many populations may be isolated and much smaller (Rieman et al. 1997). That does not mean the latter populations should be written off as lost causes; rather, managers should recognize that those populations face greater threats associated with small population size and may require more aggressive management and more immediate attention to mitigate those threats. Improved habitat capacity and mitigation of demographic threats (e.g., excessive mortality or competition) that may compound the effects of reduced genetic variation could be important objectives.

Perhaps a more important point is that maintaining the natural connections and potential for gene flow among populations can be critical (Rieman and Dunham 2000). Dispersal and the full expression of life histories in salmonid populations require free movement of migratory fish. Metapopulation theory has been a focus of growing attention in work with fishes (Rieman and Dunham 2000) and in our own work with bull trout (Dunham and Rieman 1999; Spruell et al. 1999). At present, no simple rules guide consideration of the effective population size of a metapopulation (Hedrick and Gilpin 1997), and simulating metapopulation processes to generate estimates for bull trout would be highly speculative. Clearly, however, the natural substructuring of populations associated with metapopulations can actually enhance the maintenance of genetic diversity beyond that expected in the sum of the local populations (Ray 2001). Disruption of the natural structure could also accelerate the loss well beyond that expected from the composite of local populations (Ray 2001). At present, where local populations cannot support the minimum size necessary to maintain genetic variation, managers should seek to conserve a natural collection of populations that

is at least large enough in total to meet the minimum. For example, 10 or more interconnected populations that each support an average of at least 100 spawners would be an appropriate objective. Managers should also seek to conserve the full expression of life history and processes influencing natural dispersal and gene flow among those populations. Removal of barriers to migration, restoration of habitat conditions in migratory corridors, and the maintenance of at least some populations large enough to act as sources for dispersal could be important (Rieman and McIntyre 1993; Rieman and Dunham 2000).

Managers must often make decisions with limited information. Although population biology provides theory and sophisticated models relevant to many issues, management must often default to apparently simple rules-of-thumb, such as the 50/500 criteria for maintenance of genetic diversity. Unfortunately, that guidance is not so simple to apply; indeed, our analysis grew out of our own difficulties in interpreting  $N_e$  for species like bull trout that have overlapping generations. Our results clarify that problem and allow a more direct application of the existing guidance. We emphasize, however, that our analysis is simply an approximation, built on other approximations. Without detailed information, managers should acknowledge this uncertainty and recognize that the guidelines we have provided are conservative minimums and not goals that will assure the viability of any population.

Maintenance of genetic variation is only one issue in the challenge that faces managers charged with the conservation of species like bull trout. Mitigation of extinction threats associated with demographic processes may require larger population sizes regardless of the genetic issues (Lande 1988; Rieman and McIntyre 1993). Our work and other work with demographic and empirical models, for example, indicate that many smaller populations (e.g., less than 100 spawning adults) may be prone to extinction if they are isolated (Rieman and McIntyre 1993; Dunham and Rieman 1999). Maintenance of the full expression of life history, dispersal, and the phenotypic diversity that can be distributed among diverse habitats may be as important as maintenance of genetic variation if populations are to remain resilient and productive in the face of natural disturbances (Healey 1994; Healey and Prince 1995; Rieman and Dunham 2000). Maintenance of genetic diversity is essential, but not necessarily sufficient, for effective conservation.

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The paper by Rieman and Allendorf published in the North American Journal of Fisheries Management 21:756-764, 2001 contains an error. On page 760 the following correction is necessary:

The current equation 2 is

$$N_e = (1/2) (1 - e^{\log_e Ht/t})$$

The correct equation 2 should be

$$N_e = \frac{1}{2(1 - e^{(\log_e Ht)/t})}$$