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Genetic effects of local extinction

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GENETIC EFFECTS OF LOCAL EXTINCTION

By

DAVID TALLMON

Presented in partial fulfillment of the requirements

for the degree of

Master of Science

UNIVERSITY OF MONTANA

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The metapopulation concept has become popular as conservation biologists attempt to understand the effects of increased fragmentation and isolation of natural populations. I used two versions of a simulation model to examine the genetic patterns produced by a metapopulation structure. One version was used to examine the effects of local extinction on nuclear and mitochondrial genetic variation under two extreme patterns of migration: island and one-dimensional stepping stone. The results suggest nuclear genome based genetic measures are unlikely to discern clearly a stable population structure from a metapopulation structure with frequent local extinction and recolonization. However, a comparison of nuclear and organellar allelic diversity may be useful in determining the historical role of local extinctions in population structure under very restrictive conditions. I compare modeling results to empirical data from two salmonids, bull trout (Salvelinus confluentus) and sockeye salmon (Oncorhynchus nerka), and conclude that frequent historical extinctions in the populations studied are unlikely. I used the second version of the model to project the effects of different management approaches on the effective population size ($N_e$) of a collection of subpopulations linked by a generalized stream structure. These results suggest connectivity, or gene flow, alone may not maintain a large $N_e$ if local extinctions occur.
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# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABSTRACT</td>
<td>ii</td>
</tr>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>iii</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>v</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>v</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>METHODS</td>
<td>6</td>
</tr>
<tr>
<td>Retrospective Model</td>
<td>7</td>
</tr>
<tr>
<td>Prospective Model</td>
<td>9</td>
</tr>
<tr>
<td>RESULTS AND DISCUSSION</td>
<td>13</td>
</tr>
<tr>
<td>Retrospective</td>
<td>13</td>
</tr>
<tr>
<td>Prospective</td>
<td>23</td>
</tr>
<tr>
<td>SUMMARY</td>
<td>28</td>
</tr>
<tr>
<td>APPENDIX</td>
<td>45</td>
</tr>
<tr>
<td>LITERATURE CITED</td>
<td>53</td>
</tr>
</tbody>
</table>
# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Migration and extinction rates examined using retrospective model</td>
<td>33</td>
</tr>
<tr>
<td>2 Migration and extinction rates examined using prospective model</td>
<td>34</td>
</tr>
<tr>
<td>3 Effects of local extinction on heterozygosity and divergence</td>
<td>35</td>
</tr>
<tr>
<td>4 Pairwise comparisons of alternative management approaches on $N_e$</td>
<td>37</td>
</tr>
</tbody>
</table>

# LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Flow diagram of basic model structure</td>
<td>38</td>
</tr>
<tr>
<td>2 Stream pattern of migration used in prospective model</td>
<td>39</td>
</tr>
<tr>
<td>4 Effects of local extinction on average within subpopulation heterozygosity ($H_s$) and total heterozygosity ($H_t$)</td>
<td>40</td>
</tr>
<tr>
<td>3 Effects of local extinction on divergence ($F_{st}$)</td>
<td>41</td>
</tr>
<tr>
<td>5 Effects of local extinction on nuclear and mitochondrial allelic diversity</td>
<td>42</td>
</tr>
<tr>
<td>6 Genetic patterns expected under alternative metapopulation structures</td>
<td>43</td>
</tr>
<tr>
<td>7 Genetic effects of alternative management patterns on effective population size</td>
<td>44</td>
</tr>
</tbody>
</table>

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INTRODUCTION

Humans are harming many species, primarily by reducing and fragmenting natural habitat. Although the consequent reduction and fragmentation of existing populations into smaller subpopulations is well documented, the effects are just beginning to be understood (Bierregaard et al. 1992, Mills 1995, Hanski et al. 1995a,b). As a result, metapopulation theory, which has its origins in the exploration of how subpopulation extinction and recolonization affect regional persistence, has become an active area of research in conservation biology.

The attractiveness of metapopulation structure to conservation biologists and managers stems in part from the concept of connectivity. It makes intuitive sense that a large number of independently fluctuating subpopulations linked by dispersal will be more stable than would unlinked subpopulations (Levins 1969, Brown and Kodric-Brown 1977). In addition, it is appealing from a management perspective to have several interconnected subpopulations located near enough to each other that extinct subpopulations can be re-established by dispersers from neighboring subpopulations.
The development of metapopulation concept has been thoroughly reviewed by Hanski and Gilpin (1991) and Hastings and Harrison (1994). As formally defined by Levins (1969, 1970), a metapopulation consists of a collection of subpopulations that persist on a regional level because migration among subpopulations balances local extinctions. The change in the proportion of occupied patches \( p \) through time is described by

\[
\frac{dp}{dt} = mp(1-p) - ep,
\]

where \( m \) = migration rate and \( e \) = extinction rate. This model can be solved to determine the equilibrium proportion of extant subpopulations in a metapopulation:

\[
\hat{p} = 1 - \frac{e}{m}.
\]

A comparison of Levins' metapopulation definition to currently used definitions illustrates how the metapopulation concept has broadened in scope. Whereas Levins' definition applied to a collection of linked, equivalent subpopulations in which extinction and recolonization are important, Hanski and Gilpin (1991) broadened this definition to include "systems of ... local populations connected by dispersing individuals".
Metapopulation structure has been ascribed to the population structure of many species and metapopulation theory has become a new paradigm in conservation biology (Doak and Mills 1994). However, it appears in some cases that little attention has been paid to the fit of empirical data to theoretical predictions.

Critical reviews of existing empirical data by Harrison (1991) and Hastings and Harrison (1994) illustrate the difficulty in collecting sufficient empirical demographic data to determine the applicability of metapopulation theory to the population structure of many taxa, although there are some exceptions (Hanski and Thomas 1994, Hanski et al. 1995b). Clearly, logistic and financial constraints will make it difficult to record reasonable estimates of local extinction and recolonization frequency for most long-lived species. In addition, the current population structure and distribution of a species may be unrepresentative of its evolutionary past.

An understanding of historical population structure is critical to effective conservation because this understanding can guide short-term management so as to avoid potential consequences of altering population structure, such as inbreeding or outbreeding depression, and suggest a
long-term goal for restoration. Genetic data may be our best hope for discerning historical population structure (Grant and Leslie 1993, Milligan et al. 1994, Slatkin 1987) because the distribution of genetic information is shaped by historical population structure, and there exists a base of predictions from theoretical genetic models helpful in the interpretation of empirical data (Appendix).

Unfortunately, most genetic theory useful for interpreting historical population structure is based on an assumption of equilibrium levels of subpopulation divergence. It has been shown previously that genetic divergence equilibrium may be an invalid assumption if local extinctions occur (Wade and McCauley 1988, Whitlock and McCauley 1990), and may take many generations to reach even in the absence of local extinction (Allendorf and Phelps 1981, Varvio et al. 1986). Since local extinction must be included in any metapopulation model, discerning metapopulation structure using genetic information may be difficult.

Some researchers have shown frequent local extinction and recolonization may produce genetic patterns different from those expected from a stable population structure. For example, Sjogren (1991) used knowledge of regional population demography along with genetic data to
provide evidence of low heterozygosity in a pool frog metapopulation relative to a collection of stable subpopulations. Grant and Leslie (1993) used a simulation model to demonstrate the possibility of detecting historical metapopulation structure using a comparison of mitochondrial and nuclear genetic variation. Specifically, Grant and Leslie (1993) developed a simulation model which suggested reduced mitochondrial variation relative to nuclear variation may be an indicator of frequent local extinction in natural populations. Unfortunately, this model did not include any influx of variation, such as mutation or immigration, that may serve to obscure otherwise clear genetic patterns.

I used two variants of a simulation model to examine genetic patterns produced by several metapopulation structures. I incorporated mutation into what is referred to hereafter as a retrospective model, in which a collection of subpopulations were subjected to varying rates of local extinction and migration. Then, I determined whether or not the resulting metapopulation genetic patterns are clearly distinguishable from alternative population structures. I compared these results to empirical genetic data from two salmonids, bull trout (*Salvelinus confluentus*) and sockeye salmon (*Oncorhynchus nerka*), in order to determine if these
species have historically conformed to a metapopulation structure. Salmonids may serve as useful test cases for metapopulation models because their subdivided population structure may naturally lend itself to a metapopulation structure and because there exists a great deal of genetic information available for this taxon. I used another version of this simulation model, hereafter referred to as the prospective model, to project the effects of different metapopulation structures on the effective population size \( (N_e) \) of a collection of subpopulations linked by a generalized stream structure. I used empirical data from bull trout populations to help assign values to the variables in the model and to frame the results in a management context.

METHODS

I used two variants of an individual-based simulation model to examine metapopulation structure (Figure 1). The basic structure of the model is as follows. To begin each simulation, 100 individuals are assigned to each of 20 subpopulations. Individuals are assigned a sex, two alleles at two nuclear loci and a maternally inherited mitochondrial allele. Each generation, local extinction \( (e) \) occurs followed by migration.
(m) and reproduction. This model differs from previous analytical metapopulation models (Slatkin 1977, Wade and McCauley 1988, Whitlock and McCauley 1990, Whitlock 1992) in that an extinct subpopulation can remain so for many generations and can be recolonized only if at least one male and one female immigrate to that subpopulation in the same generation. Fifty pairs of females and males are randomly chosen among immigrant and resident individuals in each subpopulation to produce the next generation of 100 individuals. The demography of the model was simplified, though the essential features of a metapopulation were incorporated, in order to focus on the genetic effects of metapopulation structure. Demographic simplifications are discrete generations, immediate subpopulation rebound to carrying capacity following successful recolonization, no sex-biased dispersal, and constant rates of extinction and migration.

**Retrospective Model**

Genetic patterns were generated under a wide range of population structures. Each retrospective simulation was stopped at the 1000th generation and summary data produced. One important difference
between this version of the model and previous modeling efforts is that all first generation individuals are homozygous for the same nuclear and mitochondrial alleles and mutation adds genetic variation to the collection of subpopulations at the average rate of one new allele per locus per 2000 individuals.

Two possible extremes of migration pattern were used; one based upon Wright’s (1931) island model and another based upon Kimura and Weiss’s (1964) one-dimensional stepping stone. Under the finite island model of migration, migrants are equally likely to disperse to any subpopulation, whereas stepping stone model migrants are limited to one of two neighboring subpopulations. These two migration patterns effectively bound what might occur in the natural world. I investigated several rates of migration and extinction with both migration patterns (Table 1).

Since each replicate simulation (N=60) was stopped at the 1000th generation and summary data produced, the resulting view of population structure is similar to the "snapshot" view revealed by empirical data sampled from natural populations. I base the allelic diversity estimates on alleles with frequencies greater than 0.05 in any one subpopulation.
because less common alleles may not be observed in samples from natural populations.

**Prospective Model**

The prospective version of the model projects the influences of different patterns of migration and stochastic and deterministic extinction on $N_e$. The primary differences between this version and the retrospective version are that subpopulations are now organized into a generalized stream structure, four migration patterns are used, and individuals are assigned unique alleles to begin each iteration. Each replicate simulation (N=50) was run for 100 generations and mutation ignored, so only the decay of genetic variation was observed. I used the rate of decay of heterozygosity estimate the metapopulation $N_e$.

Under the stream structure, subpopulations are positioned as mainstem or tributary subpopulations (Figure 2). I simulated the effects of four different migration patterns: island, stream/island, stream, and homing, because one of the greatest unknowns about salmonid population structure is how individuals move between subpopulations. These migration patterns can be dichotomized: island and stream/island allow for
long distance dispersal while stream and homing limit migration to nearest neighbor subpopulations. Migrants disperse randomly among subpopulations under the island migration pattern. With the stream/island pattern, migrants have a probability of 0.5 of dispersing to either an adjacent subpopulation or the remaining subpopulations. Mainstem subpopulations serve as connecting units in neighbor-mediated gene flow between tributary subpopulations. In the stream pattern of migration, migrants have an equal probability of moving to any adjacent subpopulation. The homing pattern limits migrants to adjacent subpopulations and further reduces to 0.1 the likelihood individuals will move between mainstem and tributary subpopulations.

I examined the effects of several combinations of migration rate and deterministic and stochastic extinction with each migration pattern (Table 2). The simulations were run for 50 generations before any deterministic extinction was imposed upon the subpopulations in order to allow the migration pattern to have an effect on the distribution of genetic variation.

My goal was to examine the trade-off between maximizing connectivity among subpopulations while causing the deterministic
extinction of more subpopulations versus eliminating mainstem subpopulations while conserving, but further isolating clusters of tributary subpopulations. In the former case (Trib), one tributary at a time goes extinct for a 10 generation interval, starting at the 51st generation. Trib is designed to mimic the effects of a resource management plan which causes the extinction of all subpopulations in a tributary, but eliminates only one tributary at a time. In a given generation, those subpopulations not in the deterministically extinct tributary remain linked to one another, yet are still subject to stochastic extinction.

In the latter case (Main), mainstem subpopulations are eliminated deterministically but none of the tributary subpopulations are subject to deterministic extinction (though still subject to stochastic extinction). Under Main, gene flow among tributaries occurs only via long distance dispersal, because intermediate subpopulations are extinct. Essentially, Main and Trib offer a comparison between management plans that would eliminate more subpopulations but allow for greater connectivity and those that would cause the deterministic extinction of fewer subpopulations but fragment them into small clusters, respectively.
Heterozygosity \((H)\) is lost from a finite population at a rate inversely proportional to \(N_e\) following the equation

\[
-\Delta H = \frac{1}{2N_e}.
\]

Therefore, a goal of conservation efforts has been to maximize \(N_e\) and, thereby, slow the loss of genetic variation (e.g. Ryman et al. 1995).

Although model results were produced in the form of heterozygosity and statistical tests performed on square-root, arcsine-transformed data, I discuss our results in terms of \(N_e\) since it is perhaps a more tangible concept for management. \(N_e\) was estimated using

\[
N_e = \frac{1}{2(1-(\frac{H_o}{H_i})^t)}
\]

where \(H_o = \) observed heterozygosity, \(H_i = \) initial heterozygosity, \(t = \) time in generations.
RESULTS AND DISCUSSION

Retrospective

I examined the effects of local extinction on genetic patterns under a wide range of migration rates (Table 3). The effects of local extinction on heterozygosity can be seen in Figure 3. Any local extinction decreases total heterozygosity ($H_t$) and average within subpopulation heterozygosity ($H_s$) under the stepping stone model, but low rates of extinction relative to migration ($e \approx 0.1m$) have little detectable effect on heterozygosity under the island model of migration (Figure 3). However, high rates of local extinction ($e \approx 0.1m$) decrease $H_s$ and $H_t$ under both migration patterns.

If subpopulations are stable $H_t$ and genetic divergence ($F_{st}$) are larger under the stepping stone model than under the island model (Figure 3). As shown by Kimura and Weiss (1964), this occurs because migration is limited to adjacent subpopulations under the stepping stone model and genetic differences accumulate between subpopulations. Accordingly, because a large proportion of the total genetic variation under the stepping stone model results from differences among subpopulations, a slight increase in the extinction rate above zero decreases $H_t$ under the stepping
stone model more than under the island model. The general trend of increased extinction leading to decreased heterozygosity is robust to changes in migration pattern and migration rate.

Although it is clear metapopulation structure decreases heterozygosity, these data indicate low heterozygosity levels alone will not be very useful in discerning the historical role of local extinction in natural populations. Although Sjogren (1991) provides an important empirical example of how local extinction may decrease heterozygosity, it is a rare case in which the regional demographic history of a species is documented. In most cases regional population history is unknown and low heterozygosity could be ascribed to a recent species-wide bottleneck, phylogenetic constraints, or local population turnover (e.g. see Merola 1994). Furthermore, heterozygosity is a metric estimated by collapsing data from many loci and so may obscure information available at the level of the individual locus. Therefore, in most cases it may be difficult to conclude much about historical population structure from heterozygosity estimates alone.

The effects of increasing local extinction on another common population genetics measure, $F_{st}$, appear somewhat dependent upon
migration pattern (Figure 4). $F_{st}$ generally increases slightly as the local extinction rate approaches the migration rate under the island model. Under the stepping stone model, the increase in $F_{st}$ with an increase in extinction rate is more dramatic, and $F_{st}$ is prone to larger fluctuations and has a larger standard error. With either migration model, there does not appear to be a clear threshold effect of local extinction on $F_{st}$.

The main problem with using $F_{st}$ as an indicator of a frequent local extinctions is that a given $F_{st}$ estimate derived from genetic data can be ascribed to a wide number of possible population structures. Furthermore, the increase in the standard error of $F_{st}$ as the extinction rate approaches and surpasses the migration rate suggests empirical genetic results taken from a set of populations with frequent population extinction could yield a wide range of $F_{st}$ estimates, especially if the number of polymorphic loci is small. This may explain previous empirical results which suggested $F_{st}$ estimated from a single allozyme locus, decreased as a result of local extinctions (Dybdahl 1994).

These results suggest gene flow estimates derived from $F_{st}$ may underestimate gene flow in a metapopulation with high rates of extinction and migration. For example, a comparison of island model gene flow
estimates with a high rate of migration \((m = 0.15)\) and \(e = 0.0\) in one case, and \(e = 0.15\) in the other case, yields mean \(F_{st}\) estimates of 0.038 and 0.071, respectively. The corresponding estimates of gene flow are \(Nm = 6.33\) for the former, and \(Nm = 3.27\) for the latter. Thus, in cases where populations may have been subject to periods of frequent local extinction and migration, gene flow will likely be underestimated. This result is interesting because it contrasts with Whitlock (1992), who found a moderate migration rate \((m > 0.05)\) would erase the effects of local extinction on \(F_{st}\) and suggests \(F_{st}\) may be misleading under a wider range of demographic rates than previously thought.

Most modeling research to date suggests \(F_{st}\) may be of limited use in discerning population structure (Wade and McCauley 1988, Whitlock and McCauley 1990). Even comparisons of organellar and nuclear \(F_{st}\) are unlikely to be useful in cases where the frequencies of extinction and recolonization are unknown, because the two genomes approach mutation-drift equilibrium at different rates (McCauley 1995). As a result, gene flow estimates based on \(F_{st}\) may not be very trustworthy as a basis for conservation planning in cases where local extinction and recolonization may have been historically frequent.
As the local extinction rate approached and exceeded the migration rate, average mitochondrial and nuclear allelic diversity decreased. Average mitochondrial allelic diversity was always lower than average nuclear allelic diversity (Figure 5). This is due to the difference in effective population size between the two genomes (Grant and Leslie 1993). At high rates of extinction relative to the migration rate, mitochondrial variation is more likely to be purged while nuclear variation persists. However, in some individual iterations at high rates of extinction and migration, there was greater mitochondrial than nuclear allelic diversity. Consequently, local extinction does not appear to affect the two genomes differently enough for a comparison of nuclear and mitochondrial allelic diversity to be consistently useful in discerning a stable population structure from one with high rates of migration and extinction.

Only at high rates of migration \((m = 0.15, m = 0.20)\) and even higher rates of local extinction \((e > m)\) was mitochondrial variation frequently purged while nuclear allelic diversity remained (Figure 5). This suggests a comparison of mitochondrial and nuclear diversity that revealed no mitochondrial variation and some nuclear variation would
suggest the possibility of historical metapopulation structure. However, because this pattern was not consistent in all iterations at high migration and extinction rates, a lack of this pattern in the two genomes does not mean a historical metapopulation structure can be definitively eliminated.

**Interpretation of Empirical Data**

One goal of conservation biologists is to effectively manage and restore threatened species. If genetic data can help clarify the historical population structure of a species, then management goals will be better defined. These results indicate it is unlikely any single genetic measure will clearly and consistently differentiate between alternative population structures. However, it may be possible to use a comparison of genomic diversity along with the other population genetic measures discussed above to determine whether or not high rates of local extinction and migration are likely to have played an important role in the evolution of a collection of populations. These simulations suggest several useful patterns may emerge from genetic data. For most species, mtDNA restriction site and nuclear allozyme data will be available, so I base this discussion on the assumption these two markers will be used (Figure 6).
For species with historically stable populations and high rates of migration relative to extinction, there are several genetic expectations (Figure 6). Primarily, there should be a large amount of mitochondrial and nuclear variability. A comparison of these two markers should reveal more mitochondrial than allozyme allelic diversity because mtDNA has a much higher mutation rate. If the migration rate is high, nuclear $F_{st}$ should be low and mitochondrial divergence higher, due to $N_e$ differences between the two genomes. In addition, most alleles should be widely distributed and both $H_s$ and $H_f$ should be high. If the migration rate is low, nuclear $F_{st}$ should be high and the mitochondrial estimate higher still. Also, there may be private alleles and large $H_p$ but smaller $H_s$.

For species with high rates of local extinction relative to the migration rate, there are also several genetic expectations. Indicators should include low nuclear and mitochondrial $H_s$ and $H_p$, and large variability among loci in $F_{st}$ estimates. At very high rates of local extinction and migration our results suggest very little mitochondrial variability and possibly only a single mitochondrial allele may remain.
Application to Salmonids

I compare the model results to genetic data sampled from populations of bull trout in the upper Flathead River drainage in Montana and sockeye salmon from Cook Inlet, Alaska. I use allozyme and mitochondrial data to determine if bull trout populations of the upper Flathead River Basin have historically been subjected to frequent local extinction and recolonization. Only 5 of 43 allozyme loci were polymorphic (N = 868), with only two alleles present at each polymorphic locus (Kanda et al. in press). Expected heterozygosity ranges from zero to 0.022 within subpopulations and total heterozygosity is low (H_t = 0.0145). Divergence is high (F_st = 0.395), with most differentiation due to differences among drainages. Enzyme restriction of mtDNA (N = 256) yielded 8 haplotypes, high within population haplotype diversity (H_s = 0.323), and significant divergence among subpopulations (G_st = 0.386). However, there is very little nucleotide diversity within subpopulations (p = 0.002226) and little sequence divergence among subpopulations (p = 0.000860).

A comparison of this empirical data to the model results presents an interesting test case. It is clear that there is little allozyme variation. This
can be explained either by very frequent extinction and recolonization or a historical bottleneck. However, the relatively large amount of mtDNA variation and the number of mitochondrial alleles present appears too high, relative to the allozyme diversity, to suggest frequent subpopulation turnover or a recent severe bottleneck, so a true metapopulation structure as defined by Levins' (1969) is unlikely. There is little nuclear variability and not much mtDNA sequence divergence, so a plausible explanation is a historical bottleneck event and subsequently stable subpopulations. Since the mitochondrial mutation rate is much higher than the mutation rate of allozyme allelomorphs, mtDNA variation has increased more rapidly since the bottleneck and produced the present pattern of genetic variation (Wade et al. 1994).

Allozyme and mtDNA restriction site data from four Cook Inlet sockeye salmon populations were also examined (Allendorf et al. in prep). A survey of 21 allozyme loci revealed an average of 2.1 alleles per locus, high heterozygosity within subpopulations ($H_s = 0.131$) and divergence among subpopulations ($F_{st} = 0.176$). Analysis of 5 microsatellite and RAPD loci from these same populations yielded greater genetic variation ($H_s = 0.641$ and $H_s = 0.298$, respectively), but much less divergence.
among subpopulations ($F_{st} = 0.084$ and $F_{st} = 0.059$, respectively) than revealed by alcozymes. Analysis of mtDNA restriction site data revealed 6 haplotypes, high haplotype diversity within subpopulations ($H_s = 0.262$) and some genetic divergence ($F_{st} = 0.244$).

The sockeye salmon populations do not fit a metapopulation structure with frequent local extinction, as revealed by a comparison of empirical data to model results. Rather, the high nuclear and mitochondrial polymorphism, high within subpopulation heterozygosity, and a lack of private alleles suggest historically stable subpopulations exchanging an average of at least a few individuals among subpopulations each generation.

The bull trout and sockeye salmon populations examined have quite different population structures. Bull trout populations share fewer migrants each generation and may have suffered a bottleneck or frequent local extinction and recolonization long ago. In contrast, the sockeye salmon populations maintain a large amount of genetic variation at all markers examined and appear to share at least a few migrants per generation. A comparison of empirical data from these two species to the
model results suggests neither has recently conformed to a metapopulation structure with frequent local extinction.

These analyses suggest the retrospective model is useful for understanding the historical role of local extinction in a set of populations. Further, these analyses suggest managers may be able to use genetic data to determine if frequent local extinction may have played an important role in determining population structure and allow them to make conservation decisions based on their findings.

Prospective

The comparison of retrospective model results to empirical data suggests bull trout from the upper Flathead River drainage have not, in recent history, been subject to a metapopulation structure with frequent local extinction. This has two implications. First, traditional theoretical models used to estimate gene flow may yield reasonable approximations, and second, the current fragmentation and decline of existing subpopulations is unlikely to be reflective of their historic population structure.
Bull trout appear to be especially sensitive to impacts from resource extraction because of their strict habitat requirements (reviewed by Fraley and Shepard 1989). Bull trout typically spawn in cold mountain streams, where incubating eggs require temperatures of less than 4°C. Maturing juvenile bull trout may actually reside under and between cobbles in stream beds. Individuals then either remain in natal streams (resident form) or migrate to a higher order stream or lake to mature (migratory form) before returning as adults to spawn at natal sites. Bull trout appear to be sensitive to human impacts such as dams and diversions, which may eliminate the migratory form. Logging may also be a threat since it can increase stream sedimentation and water temperatures, known threats to bull trout egg and juvenile survivorship.

I use empirical bull trout data to help bound the range of parameter values used in the prospective model. Assuming equilibrium levels of divergence among subpopulations, I estimate gene flow among subpopulations based on an $F_{st}$ estimate derived from empirical data. Specifically, gene flow can be estimated using the following equations for
the island and stepping stone models, respectively:

\[
Nm = \left(1 - \frac{1}{F_{st}}\right) \left(1 - \frac{1}{F_{st}}\right)
\]

Since bull trout gene flow patterns are unlikely to fall exactly under either migration model, I use them to bound the likely rate of gene flow. Mutation rate (\(\mu\)) can be ignored in the island model, but may have a large impact on gene flow estimates in the stepping stone model (Keenan 1995). If I use the empirical estimate of \(F_{st} = 0.395\), assume \(\mu = 1 \times 10^{-6}\) as estimated from electrophoretic studies (Nei 1987 pp 31-32) and a generous historical population size of \(1 \times 10^8\), I can estimate upper bounds for the migration rate under the stepping stone model.

The estimated number of migrants each generation under the island and stepping stone models are \(Nm < 1\) and \(Nm = 7.3\), respectively. (Note: If the historical \(N_e\) was much smaller than the estimated \(1 \times 10^8\) used in the stepping stone equation, then both models would suggest \(Nm < 1\).) A historically large \(N\) would necessarily mean \(m\) was extremely small since their product is not very large. However, in order to project the effects of
a range of possible current extinction rates, I use migration rates ranging from \( m = 0.02 \) to \( m = 0.10 \). I assume extinction rates less than or equal to the migration rates, since extinction rates greater than the migration rates would lead to metapopulation extinction and render \( N_e \) concerns trivial.

The prospective model results agree with previous investigations which showed metapopulation structure can grossly decrease \( N_e \) relative to census population size (Maruyama and Kimura 1980, Gilpin 1991). This is apparent even in those runs (Stoch) which include only stochastic extinction and no deterministic extinction (Figure 7). Further it is apparent that the migration pattern has a large impact on \( N_e \). Generally, less restricted gene flow patterns increase \( N_e \) for a given set of demographic input. This result makes intuitive sense based on the findings of decreased heterozygosity under the more restrictive stepping stone model used in the retrospective simulations. When deterministic extinction is added to stochastic extinction, this effect is magnified.

For example, in Trib simulations \( N_e \) was one-third to one-fifth that under the homing pattern compared to the island pattern of migration. The relevance of this result for conservation planning is that underlying
assumptions about the way individuals move among subpopulations may greatly impact the way a proposed management plan will affect the retention of genetic variation.

Examination of the two migration patterns (stream and homing) most likely to be accurate for bull trout, based on existing genetic data and the degree of fragmentation that has already occurred, yields a consistent pattern. In all pairwise t-tests of Main and Trib management alternatives, Main retains more genetic variation (Table 4). These results are statistically significant and in some cases quite dramatic. Accordingly, eliminating subpopulations while maximizing connectivity, and hence, the possibility for gene flow and recolonization, is not necessarily the best management approach from a genetic perspective.

This result is unlikely to be surprising to those who have thought about the effects of extinction on genetic diversity. An increased number of deterministically extinct subpopulations will reduce genetic variation. What may not be as obvious is that maximizing connectivity among subpopulations alone will not necessarily effectively maintain genetic diversity. This is especially true if the migration rate is low and the migration pattern restrictive. Consequently, for species with these
characteristics of migration, long-term persistence may be better secured by maintaining existing clusters of subpopulations with restricted gene flow among clusters rather than by concentrating on maximizing connectivity.

SUMMARY

The genetic effects of metapopulation structure include a reduction of mitochondrial and nuclear genetic variation. This has been shown previously in models that focused on metapopulation $N_e$ (Maruyama and Kimura 1980, Gilpin 1991). Local extinction decreases heterozygosity and allelic diversity, while generally increasing divergence relative to the case with stable subpopulations. The retrospective model results suggest metapopulation structure is likely to be differentiable from a stable population structure using a comparison of nuclear and mitochondrial allelic diversity, as well as other genetic measures, only at high rates of extinction and migration. However, even at the high rates of extinction and migration examined, this pattern is not always evident. At low rates of local extinction, there does not appear to be any clear genetic pattern
that can be used to differentiate this population structure from a collection of stable subpopulations.

The rates of local extinction likely to be detectable using a comparison of nuclear and organellar genetic variation seem unreasonably large for most vertebrates. Indeed, a comparison of variation in these two genomes will be useful only when genetic drift and extinction have purged mitochondrial variation faster than it is introduced by mutation and immigration. In addition, the extinction rate must not be large enough to also purge nuclear variation or cause regional metapopulation extinction. It is not surprising comparisons of model results to empirical data from bull trout and sockeye salmon populations do not suggest either has historically conformed to a metapopulation structure with frequent local extinction. The bull trout populations examined here have too much mitochondrial variation relative to nuclear variation to suggest frequent extinction and recolonization. The sockeye populations examined have large amounts of both nuclear and mitochondrial genetic variation, suggesting historically high rates of migration relative to local extinction.

Historical population structure may be less of an important consideration than current fragmentation and subdivision for some species.
The prospective version of the model showed decreased effective population size as a result of adding deterministic extinctions to stochastic extinctions. It is clear from the retrospective model that increased extinction and recolonization will decrease genetic variation. However, the projections of alternative bull trout metapopulation management schemes suggest conserving existing small clusters of subpopulations might be a better alternative to focusing on maximizing gene flow among subpopulations if the later means the subpopulations also suffer increased deterministic extinction.

The demography of this simulation model was simplified in order to concentrate on the genetic effects of local extinction and migration. The effects of immediate subpopulation rebound to carrying capacity following recolonization served to minimize the effects of drift after recolonization and to increase the number of individuals available to accumulate mutations and to recolonize other subpopulations. Relaxing this assumption would decrease the demographic stability of the metapopulation and decrease the amount of genetic variability, especially at high rates of extinction. Thus, the pattern of low mitochondrial variation relative to nuclear variation at high rates of extinction may be
clearer for organisms with low reproductive rates. However, this model may be quite reasonable for highly fecund taxa such as salmonids. In addition, I assumed generations were non-overlapping. Overlapping generations would cause divergence between cohorts within subpopulations and create a Wahlund effect between generations (Waples 1990).

Some other demographic simplifications may have made the predictive value of the genetic measures overly optimistic. I assumed a true metapopulation structure in which all subpopulations share the same demographic properties, such as carrying capacity, migration and extinction rate. It is clear that most species do not conform to this population structure (Harrison 1991). If one or more subpopulations is essentially permanent then the genetic expectations should change, as this subpopulation could serve as a long-term reservoir of genetic variation. However, while it is clear that some subpopulations will be more stable than others, it is unclear over how many generations a stable subpopulation must persist in order to alter genetic patterns produced here.

It should be noted that the probabilities of local extinction and migration remained constant throughout each simulation. Harrison (1991)
has suggested that such a true metapopulation structure is unlikely. It may be more likely that periods of metapopulation structure are interspersed with periods of relative stability. If this is true, then the number of generations since the most recent metapopulation event will affect how easily this structure can be detected.

Finally, although this paper focuses on computer generated genetic data I do not wish to neglect the importance of ecological data and other genetic measures. Genetic patterns such as linkage disequilibrium and Nei’s $D$ may prove useful supplementary measures for detecting frequent extinction and recolonization events. From these simulations, it seems there will be no single genetic measure that will provide clear evidence of historical extinction and colonization. Most likely, a thorough understanding of metapopulation structure will require both genetic and ecological evidence and understanding.
Table 1: Migration and local extinction rates examined with retrospective model using both the stepping stone and island models of migration.

<table>
<thead>
<tr>
<th>Migration Rate</th>
<th>Extinction Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.02</td>
<td>0.0, 0.0025, 0.008, 0.01, 0.02, 0.025</td>
</tr>
<tr>
<td>0.10</td>
<td>0.0, 0.01, 0.02, 0.05, 0.08, 0.10, 0.15, 0.20</td>
</tr>
<tr>
<td>0.15</td>
<td>0.0, 0.01, 0.08, 0.10, 0.25, 0.30</td>
</tr>
<tr>
<td>0.20</td>
<td>0.0, 0.05, 0.10, 0.15, 0.20, 0.25, 0.30, 0.35</td>
</tr>
</tbody>
</table>
Table 2: Migration and local extinction rates examined with prospective model.

<table>
<thead>
<tr>
<th>Migration Rate</th>
<th>Extinction Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.02</td>
<td>0.0, 0.02</td>
</tr>
<tr>
<td>0.04</td>
<td>0.0, 0.02</td>
</tr>
<tr>
<td>0.05</td>
<td>0.0, 0.05</td>
</tr>
<tr>
<td>0.10</td>
<td>0.0, 0.05</td>
</tr>
</tbody>
</table>
Table 3: Migration and extinction rate effects on mean heterozygosities, $(H_t)$ and $(H_s)$, and mean divergence $(F_{st})$ under the island and stepping stone models of migration.

<table>
<thead>
<tr>
<th>Mig. Rate</th>
<th>Ext. Rate</th>
<th>Island</th>
<th>Stepping Stone</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$H_s$</td>
<td>$H_t$</td>
</tr>
<tr>
<td>0.02</td>
<td>0.0</td>
<td>0.460</td>
<td>0.553</td>
</tr>
<tr>
<td></td>
<td>0.0025</td>
<td>0.456</td>
<td>0.554</td>
</tr>
<tr>
<td></td>
<td>0.008</td>
<td>0.431</td>
<td>0.532</td>
</tr>
<tr>
<td></td>
<td>0.01</td>
<td>0.416</td>
<td>0.516</td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>0.391</td>
<td>0.493</td>
</tr>
<tr>
<td></td>
<td>0.025</td>
<td>0.355</td>
<td>0.452</td>
</tr>
<tr>
<td>0.10</td>
<td>0.0</td>
<td>0.534</td>
<td>0.552</td>
</tr>
<tr>
<td></td>
<td>0.01</td>
<td>0.548</td>
<td>0.572</td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>0.504</td>
<td>0.525</td>
</tr>
<tr>
<td></td>
<td>0.05</td>
<td>0.379</td>
<td>0.401</td>
</tr>
<tr>
<td></td>
<td>0.08</td>
<td>0.329</td>
<td>0.347</td>
</tr>
<tr>
<td></td>
<td>0.10</td>
<td>0.323</td>
<td>0.343</td>
</tr>
<tr>
<td></td>
<td>0.15</td>
<td>0.249</td>
<td>0.266</td>
</tr>
<tr>
<td></td>
<td>0.20</td>
<td>0.202</td>
<td>0.218</td>
</tr>
<tr>
<td>0.15</td>
<td>0.0</td>
<td>0.526</td>
<td>0.540</td>
</tr>
<tr>
<td></td>
<td>0.01</td>
<td>0.536</td>
<td>0.550</td>
</tr>
<tr>
<td></td>
<td>0.08</td>
<td>0.421</td>
<td>0.436</td>
</tr>
<tr>
<td></td>
<td>0.10</td>
<td>0.421</td>
<td>0.433</td>
</tr>
<tr>
<td></td>
<td>0.15</td>
<td>0.325</td>
<td>0.341</td>
</tr>
<tr>
<td></td>
<td>0.25</td>
<td>0.267</td>
<td>0.279</td>
</tr>
<tr>
<td></td>
<td>0.30</td>
<td>0.174</td>
<td>0.181</td>
</tr>
</tbody>
</table>

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<table>
<thead>
<tr>
<th>Mig Rate</th>
<th>Ext Rate</th>
<th>Island</th>
<th>Stepping Stone</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Hs</td>
<td>Ht</td>
</tr>
<tr>
<td>0.20</td>
<td>0.0</td>
<td>0.585</td>
<td>0.593</td>
</tr>
<tr>
<td>0.05</td>
<td>0.517</td>
<td>0.528</td>
<td>0.034</td>
</tr>
<tr>
<td>0.10</td>
<td>0.422</td>
<td>0.432</td>
<td>0.043</td>
</tr>
<tr>
<td>0.15</td>
<td>0.367</td>
<td>0.378</td>
<td>0.047</td>
</tr>
<tr>
<td>0.20</td>
<td>0.285</td>
<td>0.290</td>
<td>0.045</td>
</tr>
<tr>
<td>0.25</td>
<td>0.256</td>
<td>0.263</td>
<td>0.056</td>
</tr>
<tr>
<td>0.30</td>
<td>0.204</td>
<td>0.210</td>
<td>0.050</td>
</tr>
<tr>
<td>0.35</td>
<td>0.235</td>
<td>0.242</td>
<td>0.057</td>
</tr>
</tbody>
</table>
Table 4: Mean and standard error effective population size ($N_e$) under Main and Trib management using stream and homing migration patterns.

<table>
<thead>
<tr>
<th>Mig. Rate</th>
<th>Ext. Rate</th>
<th>Mig. Pattern</th>
<th>Main</th>
<th>Trib</th>
</tr>
</thead>
<tbody>
<tr>
<td>m=0.02</td>
<td>e=0.02</td>
<td>stream</td>
<td>276 (33.6)</td>
<td>116 (18.7)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>homing</td>
<td>289 (27.4)</td>
<td>102 (16.8)</td>
</tr>
<tr>
<td>m=0.04</td>
<td>e=0.02</td>
<td>stream</td>
<td>490 (37.6)</td>
<td>205 (34.7)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>homing</td>
<td>406 (31.0)</td>
<td>136 (23.6)</td>
</tr>
<tr>
<td>m=0.05</td>
<td>e=0.05</td>
<td>stream</td>
<td>229 (37.4)</td>
<td>120 (18.0)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>homing</td>
<td>151 (27.8)</td>
<td>76 (13.8)</td>
</tr>
<tr>
<td>m=0.10</td>
<td>e=0.05</td>
<td>stream</td>
<td>384 (29.6)</td>
<td>215 (25.2)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>homing</td>
<td>274 (16.6)</td>
<td>76 (11.0)</td>
</tr>
</tbody>
</table>
Figure 1. Flow chart illustrating the basic structure of the simulation model.
Figure 2. Generalized stream structure used in prospective model simulations.
Figure 3: The effects of local extinction on total heterozygosity (Ht) and within subpopulation heterozygosity (Hs) under the stepping stone and island models of migration.
Figure 4: The effects of local extinction on \( F_{st} \) under island and stepping stone (step) models of migration.

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Stepping Stone Model

Island Model

Extinction Rate

Figure 5: The effects of local extinction on nuclear (nuc) and mitochondrial (mt) allelic diversity under the island and stepping stone models of migration.
Figure 6: The genetic expectations for metapopulations with different demographic properties (abbrev. as in text).
Figure 7: An example of effective population size (Ne) under a single combination of extinction and migration rates, four migration patterns, and three types of extinction.
Population Genetics Theory and Local Extinction:

**Early Theory**

The first models to address population subdivision ignored local extinction and focused on how different patterns and rates of gene flow affected the distribution of genetic variation. Wright (1931) used his well known island model, which ignores spatial structuring of subpopulations, to develop the "one migrant" rule. He showed the divergence of permanent subpopulations to be dependent only upon the product of the population size \(N\) and migration rate \(m\), and that one migrant per generation \((Nmm = 1)\) is sufficient to keep all subpopulations segregating for the same alleles.

Over three decades later, Kimura and Weiss (1964) successfully incorporated geographic structuring of subpopulations into an analytical model. They suggested distant subpopulations arranged in a one-dimensional stepping stone pattern could become genetically divergent, even at high rates of gene flow, if dispersal is limited to immediately adjacent subpopulations. Kimura and Maruyama (1971) later showed one migrant per generation is sufficient to prevent significant divergence of a
finite number of subpopulations arranged in a two-dimensional stepping stone pattern.

Even today, methods based on Wright’s island model are among the most commonly used to derive gene flow estimates. Divergence estimates \( (F_{st}) \) based on nuclear allele frequency data can be used in the following equation to estimate the number of migrants exchanged by subpopulations each generation:

\[
Nm = \frac{\frac{1}{F_{st}} - 1}{4}.
\]

Similarly, Takahata and Palumbi (1985) showed divergence estimates \( (G_{st}) \) from mitochondrial restriction site data can be plugged into the equation

\[
Nm = \frac{1}{G_{st}} - 1
\]

to estimate gene flow (uniparental inheritance, equal sex ratio and equal dispersal between the sexes must be assumed).

The popularity of the island model as a gene flow estimator stems in part from its simplicity and robustness to violations of underlying assumptions. However, the island model can be misleading in some cases. For example, Larson et al. (1984) derived low estimates of gene flow with
the island model for several collections of salamander subpopulations known to be isolated from one another. In another case, Keenan (1995) showed gene flow can be underestimated by two orders of magnitude when an island model is used in cases where the one-dimensional stepping stone model is more appropriate. Further, the island model, like other models used for gene flow estimation from allele frequency data, assumes equilibrium levels of divergence for the collection of subpopulations in question. It has been shown that it may take many generations to reach this equilibrium at low rates of migration (Allendorf and Phelps 1981, Varvio et al. 1986).

Divergence

Although Wright (1940) speculated about the possible genetic effects of subpopulation extinction, only in the last twenty years has local extinction been incorporated into analytical models. The long delay is understandable, as local extinction greatly complicates matters. For example, as pointed out by Whitlock (1992), in cases where local extinctions occur the migration rate becomes critical to demographic
stability and so is important independent of its role in determining the number of migrants each generation ($Nm$).

Since Slatkin (1977) first investigated quantitatively the effects of subpopulation extinction, a number of analytical models have been used to make several generalizations useful for understanding the genetic effects of local extinction (Wade and McCauley 1988, Whitlock and McCauley 1990, Lande 1991, Whitlock 1992, Olivieri 1995). These models have been used primarily to examine conditions that might favor or disfavor group selection. Perhaps the most important result for conservation biologists to come from recent modelling efforts is that $F_{st}$, or subpopulation divergence, based on nuclear markers may not be very useful for discerning historical population structure if local extinction is frequent.

Wade and McCauley (1988) showed that extinction and recolonization will increase divergence among subpopulations unless recolonizers and migrants are drawn randomly from all extant subpopulations and the number of recolonizers is twice the number of individuals in migrant groups. These results suggest similar amounts of divergence could be reached for a collection of stable, but fairly isolated
subpopulations and a collection of subpopulations with rapid turnover and recolonizers drawn non-randomly from extant subpopulations.

**Heterozygosity**

Unfortunately, few results from analytical models that incorporate local extinction have been applied to empirical data. One exception is Maruyama and Kimura (1980), who used both analytical and simulation models to show that local extinctions can greatly decrease the amount of genetic variation expected for a population with a given census size and a mutation rate predicted by neutral theory. Their model results were supported by empirical estimates of genetic variation in *E. coli*, but they overestimated the genetic variation found in *D. willistoni* populations. Gilpin (1991) used a simulation model to show the effective population size of a metapopulation can be two orders of magnitude smaller than the census population size.

Perhaps the best empirical example of local extinction comes from Sjogren (1991). He demonstrated heterozygosity was reduced within and among pool frog populations known to be ephemeral relative to that in pool frog populations known to be more stable. Consequently, he
suggested the low heterozygosity in ephemeral pool populations may have been caused by frequent subpopulation turnover and recolonization by a small number of individuals.

**Organellar and Nuclear Genomes**

The analytical and simulation models discussed to this point have considered only nuclear data. In the past fifteen years, the attributes and limitations of mitochondrial data have been explored (Avise 1986, 1994). More recently, the usefulness of comparisons of nuclear and organellar genetic patterns for determining population structure has been investigated (Avise 1995, Paabo 1995, Wade et al. 1994, Whitlock 1995).

Grant and Leslie (1993) showed it may be possible to detect frequent subpopulation extinction with mitochondrial and nuclear data. These authors created a simulation model of a collection of linked subpopulations and observed the decay of mitochondrial and nuclear variability under several rates of extinction, migration, and recolonization. Nuclear variability decayed much more slowly than mitochondrial variability. These results fit empirical genetic data from several African vertebrate species with little or no mitochondrial variability, but normal to

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high amounts of allozyme variation. Grant and Leslie (1993) suggested these species may have evolved under a population structure approximating the metapopulation defined by Levins, in which local extinctions have been fairly common and balanced by dispersal.

These results are understandable in light of the differences in the inheritance of nuclear and mitochondrial genomes. The nuclear genome of most plants and animals is diploid, so individuals receive one allele from each parent. In contrast, the mitochondrial genome is haploid and uniparentally inherited in many species. For these species, the effective population size of the mitochondrial genome is one-fourth that of the nuclear genome. In an extreme case of subpopulation recolonization by two individuals, there can be a maximum of four nuclear alleles and one mitochondrial allele in the newly recolonized subpopulation.

As shown in previous analytical models, disequilibrium conditions produced by a metapopulation may limit the usefulness of $F_{st}$. A comparison of organellar and nuclear genomic diversity may be useful for discerning if local extinction has been frequent and, consequently, if disequilibrium conditions likely exist. If disequilibrium conditions are present, traditional models may misdirect management. Under a
metapopulation structure in which local extinction is fairly frequent and the number of founders is small, mitochondrial variability should be purged much more rapidly than nuclear variability. This contrasts with a stable population structure, in which a genetic equilibrium can be reached and the high mutation rate of mtDNA will lead to a large amount of mitochondrial allelic diversity and genetic variation.

This reasoning suggests comparisons of organellar and nuclear genetic variation may be a useful tool for determining the historical importance of local extinction in subdivided populations. It is important to point out, however, that Grant and Leslie (1993) used a coalescence model to obtain their results. With this model structure, the decay of genetic variability is observed and possible sources of new genetic variation are ignored. In reality, a metapopulation will accrue variability through mutation and immigration. Therefore, a more realistic approach to modeling metapopulation structure should include a source of genetic variation.
LITERATURE CITED


