Population demographics influence genetic responses to fragmentation: A demogenetic assessment of the ‘one migrant per generation’ rule of thumb

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ABSTRACT

Fragmented landscapes reduce gene flow and impair long term population viability. Stream networks are particularly susceptible to fragmentation because dispersal is constrained to linear upstream and downstream movements. Despite these potential effects, infrequent migrations can maintain genetic diversity and as few as one migrant per generation (OMPG) is commonly suggested as sufficient gene flow to minimize losses in genetic diversity. However, demography varies by taxa, space and time, making such a generalized rule of thumb unlikely to be applicable across a diverse array of fragmentation scenarios and species. We utilized a demogenetic model to evaluate the OMPG rule and simulate the influence of population demographics on the rate of genetic changes following fragmentation in a headwater meta-population of brook trout (Salvelinus fontinalis). A single migrant per generation increased allelic diversity by an average of 15% and decreased genetic differentiation by 31% following 40 years of simulations compared to complete isolation, however OMPG was not sufficient to prevent significant changes in within- or between-population genetic metrics in all but the largest population scenario ($N = 500$). Less than 10 individuals were typically required to achieve no changes in both genetic metrics, yet this pattern was dependent on the source populations and will be context-specific given the population sub-structuring in a given stream network. Sensitivity analyses indicated the parameter controlling the proportion of mature females spawning annually was the most influential on population genetic responses in isolated populations, suggesting that when fewer females contribute to each generation the population is more likely to experience rapid changes in allelic frequency through genetic drift. This finding supports the use of metrics such as effective population size and the number of effective breeders in predicting population stability and viability following fragmentation. Variability in population dynamic processes and associated responses to fragmentation suggest that generalized rule of thumbs for management should be used with caution. Particularly when violations of the underlying theoretical assumptions exist, consideration of demographic processes (i.e. vital rates, species specific life history strategies and dispersal) and genetic structuring will allow for more appropriate conservation recommendations.

1. Introduction

Fragmented landscapes reduce local genetic diversity by preventing gene flow among isolated populations and increasing rates of genetic drift (Allendorf, 1983; Slatkin, 1981, 1980). Maintaining even low levels of functional connectivity, however, can have beneficial effects on genetic populations and as few as one migrant per generation (OMPG) has been suggested as sufficient gene flow to minimize losses in genetic diversity (Mills and Allendorf, 1996; Spieht, 1974; Wright, 1931). Preserving genetic diversity increases a population’s evolutionary potential and ability to adapt to environmental changes, indicating its application as a metric for measuring future viability (Frankel, 1974; Lande and Shannon, 1996; Vida, 1994). Preventing losses in genetic diversity, therefore, is a conservation priority; particularly in human-dominated landscapes where changes in land use and habitat alterations often act as barriers to gene flow. While the OMPG rule of thumb is referenced in the scientific literature for purposes of maintaining genetic connectivity for species conservation and management applications (Edmands and Timmerman, 2003; Newman and Tallmon, 2001; Palumbi, 2003; Weeks et al., 2011), it has also drawn skepticism for its...
general population size, $N$, is often questioned (Fernandez et al., 2008; Mills and Allendorf, 1996; Sanchez-Molano et al., 2013; Wang, 2004).

The OMPG rule of thumb is based on the theoretical underpinnings of population genetics and simplified assumptions of an idealized population (Spith, 1974; Wright, 1931). Although one effective (i.e. reproductively successful) migrant per generation is assumed to counteract genetic drift and deleterious effects of inbreeding, it has been described as merely a guideline that should be interpreted with caution (Mills and Allendorf, 1996; Spith, 1974; Varvio et al., 1986; Wang, 2004). Such caveats and complications with the rule were even revealed in Wright’s (1931) seminal paper. In particular, the assumption in ideal populations that effective population size, $N_e$, is equal to the population size, $N$, is violated frequently in natural populations, which could increase the minimum requirement for gene flow to prevent adverse effects of isolation (Vucetich and Waite, 2000). The rule is also based on the island model of migration, such that migrants are equally likely to be sourced from an infinite number of subpopulations, which is unlikely given distributions and dispersal across a heterogeneous landscape.

Incorporating demographic components into the genetic evaluation of the OMPG rule will reveal more realistic applications to natural systems. Demographic characteristics of populations are subject to both spatial and temporal variability (Gaillard et al., 2000; Garcia, 2008; Petty et al., 2005), indicating that genetic responses to fragmentation are likely subject to context-specific variability and raise the importance of better understanding how the OMPG rule functions across a diverse array of real-world fragmentation scenarios. Studying the interactions between demographic and genetic population mechanisms has been an increasingly popular theme in recent literature and has developed into an emerging field termed demogenetics (Frank et al., 2011). Despite not being explicitly labeled as such, demogenetic relationships have conceptually been a focus of theoretical biology for decades and are foundational in population dynamics and life history theories (Lande, 1988; Lowe and Allendorf, 2010; Samson et al., 1985).

Effective population size, for example, is largely driven by reproductive success and the number of contributing adults in a population (Falconer, 1989; Wright, 1931). Population size itself is a concern for fragmented populations because smaller populations are more likely to experience stochastic changes in allelic frequencies due to genetic drift and have lower effective population sizes (Allendorf et al., 2013; Ellstrand and Elam, 1993; Falconer, 1989; Wright, 1931). Further, demographic characteristics can alter the population responses to fragmentation; variation in life history strategies and population demographics can act as a buffer against local extinctions (González-Suárez and Revilla, 2013; Moore et al., 2014; Schindler et al., 2010).

Empirical support aimed to explore these relationships across a range of fragmentation scenarios would allow for better understanding of such complex interactions.

Predictive models can be useful tools in scenarios when long-term monitoring is not logistically feasible. Particularly when populated with empirical data, models can provide realistic projections under a range of simulated conditions. Genetic simulations are a common method employed to study the influence of migrants on metapopulation and subpopulation viability (e.g. Ellstrand and Elam, 1993; Falconer, 1989). However, similar to the foundations of the OMPG rule, these types of theoretical applications may not sufficiently capture the heterogeneity in population demographics of the study systems (Lowe and Allendorf, 2010). The onset of demogenetic simulation models has been an improvement in these techniques, by considering both demographic and genetic traits concurrently (Frank et al., 2011). Questions directed towards studying the effects of future climate change (Landguth et al., 2014), non-native species range expansion (Tyutyunov et al., 2013), adaptive evolution (Oddou-Muratorio and Davi, 2014), responses to fragmentation (Jager et al., 2001; Landguth et al., 2010), and influence of non-native hybridization (Frank and Baret, 2013) have been evaluated with demogenetic modeling techniques. These recent advances provide the foundation necessary to use demogenetic modeling to address the OMPG rule of thumb, anchored with empirical data from a well-studied system.

Lotic ecosystems are particularly susceptible to fragmentation due to their dendritic, linear structure (Fagan, 2002; Perkin and Gido, 2012; Zwick, 1992). Contrary to terrestrial habitats where movements can take many paths across the landscape, dispersal of obligatory aquatic organisms is constrained to upstream and downstream movements and stream segments can be fragmented by a single barrier. Although fragmentation can occur naturally via waterfalls or steep gradients, it is more commonly associated with anthropogenic barriers such as dams and road crossings (Yamamoto et al., 2004). The effects of barriers can range across multiple ecological scales from single species population dynamics to alterations in ecosystem functioning (Fagan, 2002; Forman and Alexander, 1998; Layman et al., 2007; Ward and Stanford, 1983). These characteristic features of stream ecosystems make them important model systems for studying the effects of fragmentation on genetic structuring (Fraser et al., 2014; Whiteley et al., 2013; Wofford et al., 2005). Remediation of deleterious fragmentation effects in populations can be accomplished either through habitat restoration or barrier removal, to reestablish natural connectivity (Jansson et al., 2007; Kemp and O’Hanley, 2010), or through human mediated dispersal of individuals across barriers or between isolated populations (Frankham, 2015; Whiteley et al., 2015). A better understanding of how low levels of connectivity affect genetic population stability while considering demographic population parameters would aid in the development of both types of conservation actions focused on promoting gene flow.

In this study we used a demogenetic model derived from empirical data to simulate barrier effects on the fine-scale genetic structuring of a brook trout (Salvelinus fontinalis) population in a well-studied headwater stream network in northwestern Connecticut, USA. We simulated the effect of a new barrier across multiple locations in the stream network and tested the degree of genetic changes over a 40-year time period. Our objectives were to 1) evaluate the OMPG rule of thumb as it applies to brook trout fine-scale genetic structuring, 2) determine how the size of the isolated population affects this relationship, and 3) identify demographic variables that influence the ability of an isolated population to resist genetic changes following fragmentation. We hypothesized that OMPG would not be sufficient to limit reductions in allelic diversity and increases in genetic differentiation due to the small population sizes found in headwater streams and changes in genetic populations would be exacerbated when demographic conditions violate theoretical assumptions of the rule.

2. Methods

2.1. Study area and taxa

Jefferson Hill-Spruce Brook, a 7.7 km stream network located in northwestern Connecticut, was used as the model system in a spatially explicit, individual based demogenetics simulation program, CDMetaPOP (Landguth et al., 2016). The system was comprised of two second-order streams, Jefferson-Hill Brook (JHB) and Spruce Brook (SB), which intersect at a confluence prior to emptying into a 5th-order stream with no obvious physical barriers present at the downstream end. Seasonal barriers prevent upstream movement into SB and the downstream tributary of JHB (Fig. 1). The fish community was representative of a typical headwater stream in northeastern U.S., with self-sustaining populations of brook trout, blacknose dace (Rhinichthys atratus), longnose dace (Rhinichthys cataractae), and white sucker (Catostomus commersoni).

Brook trout are typically a resident stream salmonid species with a historical native distribution throughout much of the Appalachian range (MacCrimmon and Campbell, 1969). They are commonly used as an indicator of ecosystem health and habitat quality (e.g. Steedman, 1999).
as their preferred habitat consists of cool and well oxygenated streams. They are a fall spawning species which exhibit iteroparous and often polygamous reproductive strategies with low variability in family reproductive success (Hudy et al., 2010; Kanno et al., 2011a). Sensitivity to watershed land use alterations (Kanno et al., 2015a, 2015b; Kocovsky and Carline, 2006), presence of non-native species (Fausch and White, 1981; Larson and Moore, 1985), and warming stream temperatures (Meisner, 1990) have reduced their distribution across much of their native range with extant populations commonly fragmented and isolated to small headwaters (Hudy et al., 2008). Jefferson Hill-Spruce Brook is an example of such small, isolated brook trout populations, with a catchment area of 14.56 km². Remediating and preventing effects of fragmentation are a central component of brook trout conservation (EBTJV, 2011) and improving the understanding of population responses to fragmentation would greatly assist future efforts.

2.2. Data collection

Empirical data for the model were collected from 2008 to 2010 as part of a multi-tiered research project aimed at studying brook trout reproductive systems (Kanno et al., 2011a), fine-scale genetic structure (Kanno et al., 2011b), abundance and spatial distributions (Kanno et al., 2012), stream temperature modeling (Kanno et al., 2014c), and spatial variability in adult survival (Kanno et al., 2014b). Data were used at the finest resolution possible, which included three spatial levels: patch (abundance and survival), multi-patch (temperature), and sub-population (genetics and dispersal). Brook trout were collected continuously along the study stream in 152 50-m patches in 2008 and 2009. Genetic data from a mean of 3.3 (standard deviation, s = 1.1) individuals per patch suggested the presence of fine-scale genetic structuring in the system, a result of low overall dispersal rates observed in resident stream salmonids (Kanno et al., 2011b; Wilson et al., 2004). A single genetic cluster was found upstream of the seasonal barrier in SB and JHB was comprised of four genetic clusters, one of which was upstream of another seasonal barrier (Fig. 1). Seven out of 20 pairwise dispersal rates between the five delineated sub-populations were found to be significantly different from zero based on Bayesian estimates using genetic data, ranging in rates of 6 to 11% per generation (Kanno et al., 2011a). To estimate patch abundance, capture probabilities were assessed using three-pass electrofishing in 15 patches for adults (> 80 mm) and young of the-year (YOO; ≤ 80 mm). Tem-
perature data were collected using HOBO temperature loggers spaced every three patches (150 m) throughout the stream (Model U22-001, Onset Computer Inc., Bourne, MA, USA). On average, JHB was slightly cooler than SB, with mean summer temps of 18.3 °C and 19.0 °C, respectively; however, thermal heterogeneity was observed within the system (Kanno et al., 2014c). An open N-mixture model was used to generate estimates of adult apparent survival per 50 m patch (Dail and Madsen, 2011; Kanno et al., 2014b). A more thorough description of each method used to generate model parameters can be found in the original referenced literature (Kanno et al., 2014b, 2012, 2011a, 2011b).

2.3. Model description

Cost-Distance Meta-Population (CDMetaPOP) is an individual based simulation program which expands upon previous programs, CDPOP (Landguth and Cushman, 2010) and CDFISH (Landguth et al., 2012b) by allowing spatially explicit representation of heterogeneous patterns of biotic and abiotic variables through a network of patches (Landguth et al., 2016). The program models biological processes (e.g. vital rates, dispersal, mating) by simulating a series of individual movements over a landscape of resistance surfaces. Vital rates can vary by age, size, or sex as well as temporally to mimic variations observed in representative biologic scenarios. All processes can vary by deterministic or stochastic forms. The model operates on an annual timescale where both male and female individuals are tracked through dispersal, reproduction, growth, and mortality events with pre-spawning outputs of individual morphologic and genotypic information within a spatial context. Model outputs can be further processed by a series of post-hoc analyses to measure genetic relatedness among predefined clusters. Additional descriptions of model workflow can be found in Landguth et al. (2016) and in the following sections, and example input files with the input parameters used in this study are provided as supplementary material (Tables S1–S5).

2.4. Model parameters

2.4.1. Abundance and mortality

Initial patch abundances, \( N \), were estimated from the sum of catchable (> 40 mm) brook trout per patch and were corrected by a capture probability of 0.70 for adults and 0.55 for YOY (Kanno et al., 2011a). Carrying capacity, \( K \), for each patch was set to a value of 1.5 \( N \) (Table S1) to achieve stability in model abundance throughout the simulated time frame according to initial starting conditions (\( N_{init} = 2100 \)). Additionally, a modified Ricker model, \( N_{t+1} = N_t e^{\left(1 - \frac{N_t}{K}\right)} \), was used to control density dependent mortality by simulating size specific competition of habitat and resources (Landguth et al., 2016). Mortality was applied at the patch level by size class; if the abundance of a given class within a patch exceeded the patch specific carrying capacity then individuals were randomly selected to survive. The density dependent packing value, \( D_o \) of \( = 0.6447 \) was used to retain a population size structure comparable to the observed distribution in the study system. Typical of headwater brook trout populations, the population was predominantly composed of small-bodied individuals (i.e. YOY and young adult [80-140 mm; presumably < age 2]), with few individuals reaching sizes of > 190 mm during the two years of field observations. Following pre-spawning movements, individuals were sorted by age and a density dependent mortality was applied according to patch level carrying capacity and the CDMetaPOP packing algorithm (Landguth et al., 2016). A density independent mortality was also applied at the patch level to simulate differential survival rates based on patch level habitat heterogeneity, obtained from estimates of adult (> 80 mm, > age 1) survival from Kanno et al. (2014a, 2014b, 2014c). Egg mortality (i.e. overwinter mortality) and YOY mortality estimates were not available from the study system. They were set at 0.6 and 0.7, respectively, sourced from literature estimates for resident stream populations of brook trout and were further evaluated in sensitivity analyses (Kanno et al., 2015a, 2015b; Marschall and Crowder, 1996; Table 1).

2.4.2. Genetics and dispersal

Genetics were initialized randomly to individuals in each patch based on allele frequencies of the five delineated sub-populations (Fig. 1; Table S2) at eight microsatellite loci with a mean of 11.5 alleles per locus (range 4–24; Kanno et al., 2011b). Subsequent offspring genotypes were assigned based on parental genotypes through Mendelian inheritance. Dispersal, defined here as movements from natal patches, in the model was controlled through two different parameters. First, individuals were assigned as “strayers” (local dispersal) or “migrants” (fall spawning movements) based on patch level movement probabilities. Values for these parameters were set at 0.25 and 0.50, respectively, based on mark and recapture data and the remaining individual remained in their resident patch (Kanno et al., 2011b; Table S3). Individuals assigned as strayers or migrants were then moved into neighboring patches according to an asymmetrical movement matrix, allowing for different movement probabilities in upstream and downstream directions. Within the model the distinction between strayers and migrants is both the timing of the movements (spring vs fall) and also the attempt to return back to the individual’s natal patch. While strayers are moved into new patches permanently,
migrants have the potential to move back to their original natal grounds following spawning events. These “return” movements are subject to the same movement probabilities specified in the barrier scenarios (see Simulation Scenarios). Movement probabilities between subpopulations were set according to the bi-directional pairwise dispersal estimates of Kanno et al. (2011a) based on genotype data (Table S4). Using genetic data to parameterize movement probabilities in the model provided a more appropriate measure of effective dispersal, or the movement of genes, compared to mark and recapture data which does not guarantee gene flow between groups of individuals. Using a combined approach of mark and recapture data to specify the individual probability of straying or migrating from natal patches, paired with the movement probabilities based on genetic data was determined to be the best way of representing the study system within the model. Dispersal probabilities were scaled by gender to reflect the two fold increased rate of dispersal observed of males compared to females (Hutchings and Gerber, 2002).

2.4.5. Growth and reproduction

Mean and standard deviations of size classes were specified according to observed length-frequencies of Kanno et al. (2012); Table S5). Individual growth was determined using a modified Von Bertalanffy (1938) growth equation, $L = L_{\infty}(1 - e^{-k(t + 1 - t_0)})$, where the new size ($L$) is a function of the maximum size ($L_{\infty}$), growth rate ($k$), size class ($l$), and initial size class ($l_0$). The equation was modified to have spatially explicit temperature based incremental growth rates with a maximum growth rate 13°C, a temperature at which brook trout physiological processes are optimized (McCormick et al., 1972). Parameter estimates were sourced from studies of brook trout growth in headwater stream systems found in neighboring states; $L_{\infty}$ was set at 350 mm, $k$ at 0.45, and $t_0$ at $-0.09$ (Omland and Parrish, 2007; Xu et al., 2010; Table 1). The largest observed brook trout in the study system was 294 mm, indicating the chosen value of $L_{\infty}$ (350 mm) was appropriate for the asymptotic length parameter.

Males and females were assumed to become sexually mature by 100 mm, at which size both sexes were found to be sexually mature in the study system (Kanno et al., 2011a). Fecundity was described by a size-based relationship for brook trout in western Massachusetts (approximately 84 km from our system), $y = 0.00187x^{2.190}$, where $x$ was the female length in mm and $y$ was the number of eggs (Letcher et al., 2007; Table 1). The percent of spawning females, or the likelihood that a mature female lays eggs in a given year, could not be estimated with the empirical dataset, but was likely a fraction of the total mature adult population (Kanno et al., 2011a). Pedigree reconstructions suggest a varying proportion of the mature brook trout population contributes to annual YOY cohorts (Coombs, 2010; Hudy et al., 2010; Kanno et al., 2011a). The value was set to 0.75 and was included in the sensitivity analyses to evaluate the relative importance of the parameter uncertainty to model outputs (Table 1). A sex ratio of 0.50 was assigned to the model simulation runs in accordance with previous genetic analyses (Kanno et al., 2011a).

2.5. Simulation scenarios

Barriers were simulated one at a time at six different locations throughout the stream network to observe the variation in the resulting genetic change in the isolated populations (Fig. 1). The locations of simulated barriers were chosen based on empirically derived genetic clusters to provide three comparable above-barrier abundances ($N = 150, 300,$ and 500) between the two headwater streams to evaluate the influence of population size on responses to fragmentation. The sizes chosen are representative of the lower range of those observed in studies of small, isolated brook trout populations (Whiteley et al., 2013; Wood, 2014). Concurrently, the variation in genetic structuring between the two streams provides a contrast to evaluate the influence of preexisting conditions on fragmentation responses. A single genetic cluster was found in SB whereas JHB consisted of four distinct genetic clusters (Kanno et al., 2011b).

Four independent scenarios with average annual migrants ($N_m$) ranging from zero (complete barriers) to three (partial barriers) were simulated for each of the six barrier locations, for a total of 24 combinations of $N$ and $N_m$ between both headwaters. Each scenario was initiated with a ten-year burn-in period and ten years of baseline conditions followed by 40 years with the simulated barrier. Barrier effects on genetic populations can be detected in as few as a single generation depending on the genetic metric used (Landguth et al., 2010). Brook Trout generation times can range from 0.83–1.91 (Letcher et al., 2007), indicating within 40 years genetic metrics should be approximately 50% of the equilibrium value following the addition of a new barrier (Landguth et al., 2010). The focus of our simulations was to observe relative differences between scenarios as opposed to an absolute magnitude of genetic change that would be reached at equilibrium. Simulations were therefore limited to 40 years post-barrier implementation for logistical reasons surrounding the extensive computational requirements. We performed 100 independent Monte Carlo replicates for each of the 24 scenarios, a replication standard performed in other demogenetic simulation studies (Landguth et al., 2014; Piou and Préost, 2012). In all cases migrants were sourced from the genetic subpopulation of closest downstream proximity (Fig. 1).

Pairwise movement matrices were used to implement barriers into the model (Table S4). Cross-barrier movement probabilities were set to zero in complete barrier scenarios and were incrementally adjusted upwards from zero to allow the desired number of migrants to cross the barrier in $N_m = 1, 2$ and 3 scenarios. Due to movement being controlled by individual probabilities, we were unable to control the exact number of migrants crossing the barrier. Thus, the scenarios of one, two, and three migrants represents average migrant counts confirmed post-simulation based on the source and destination patch between years for each individual included in the model output. The movements across the barrier are the combined result of both straying and migration movements of individuals that moved from below the barrier into the upstream population. These simulations more likely represent natural dispersal over a barrier, such as a waterfall or steep gradient, of which passability may fluctuate over time depending on flow conditions. Simulating human mediated dispersal, which would likely be a more precise number and given season each year, would provide a contrast to this study to assess the importance of variance in migration rates and timing of migration events into isolated populations. Average above barrier allelic diversity, $A_g$ (Allendorf, 1986), and an unbiased estimator of population differentiation, $G_{st}$, (Crow and Aoki, 1984; Nei and Chesser, 1983; Varvio et al., 1986), were calculated every five years using the post-simulation processing extension of CDMetaPOP 1.0 to evaluate genetic change over the simulation time period (Landguth et al., 2016). In all cases significance was determined based on non-overlapping 95% confidence intervals with simulations under baseline (i.e. no-barrier) conditions from Monte Carlo replications of genetic metric estimates. Finally, we evaluated the number of migrants required to achieve no changes by increasing the number of migrants crossing the barrier until no significant changes were observed in either genetic metric. Comparisons were made between headwater streams by only simulating a single barrier in each scenario, while allowing the alternative stream to remain unaltered.

2.6. Sensitivity analyses

Two sensitivity analyses were used to evaluate the relative influence of demographic parameters on model outputs. We included 15 parameters in the analyses that influence mortality, growth, dispersal, or reproduction in the simulated populations (Table 1). Parameters were selected based on either 1) not having estimates for our study system, as in the case of egg mortality, fecundity and female spawning frequency, or 2) have been previously identified as influencing population
responses to fragmentation, such as maturation and juvenile survival (Letcher et al., 2007). Standard Regression Coefficients (SRC) were estimated with assumed linear relationships between model inputs and outputs to evaluate the magnitude and directionality of the coefficient for each parameter (Saltelli et al., 2004, 2000). Simulations were conducted as described previously, but limited to the low population size (N = 150), zero migrant (N_m = 0) barrier scenario to represent the scenario with the greatest potential degree of genetic changes. To evaluate the differences between the two headwater streams, replicates of the analysis were conducted for both JHB and SB. For each stream 500 simulation runs were parameterized with values selected from the uniform distribution of each of the parameters in Table 1. All other parameters were held constant as described previously. Following 40 years of simulations the genetic metrics, A_q and G_q were calculated and used to estimate regression coefficients for each input parameter. The src function of the sensitivity package in R (v3.1.2; R Core Team, 2015) was used with 1000 bootstrap replicates to estimate all coefficients with their associated 95% confidence intervals (Pujol et al., 2015). Comparisons between the metrics were made with absolute values of SRC outputs to account for decreases in allelic diversity and increases in genetic differentiation.

Second, we conducted a variance-based sensitivity analysis using the Extended Fourier Amplitude Sensitive Test (extended-FAST) method to estimate first order and total sensitivity indices for all 15 parameters (Saltelli and Tarantola, 1999). While first order indices represent direct relationships between model parameters and model outputs, total indices reflect the interactive effects of the suite of model parameters. These indices can further identify indirect relationships among the suite of parameters and their influence on genetic changes. The advantage of this method is the ability to interpret quantitative effects on model outputs for each input parameter independently (first order) and the interactive effects (total) without the assumption of a linear relationship (Saltelli and Tarantola, 1999). The fast99 function of the sensitivity package in R (v3.1.2; R Core Team, 2015) was used to generate inputs for the 15 parameters, p, with 100 replicates, n, for a total sample size, n*p, of 1500 combinations distributed uniformly across the ranges detailed in Table 1. The 1500 combinations were then independently assigned to the simulation runs in CDMetaPOP, again using the low population size (N = 150), zero migrant (N_m = 0) barrier scenario in JHB. Only a single population was included due to the low population size (N = 150). For instance, allelic diversity in JHB decreased from 0.73 to 0.63, 0.70, and 0.71 in the small, intermediate, and large populations, respectively, in the isolation scenario (i.e. zero migrants).

A greater number of migrants per year reduced the extent of fragmentation-induced genetic changes (Figs. 2 and 3). Although a single migrant per year did not provide sufficient gene flow to prevent significant changes in the majority of scenarios over the 40 year timeframe, the greatest reduction in such changes was found with a single migrant. Increasing the number of migrants from one to three produced increases in allelic diversity and decreases in differentiation, however these changes were much lower in magnitude compared to the first individual and often did not result in significant differences (Fig. 3). The number of migrants required to provide no changes in genetic metrics varied between streams and across the range of population sizes. No number of individuals moved from only the subpopulation of downstream proximity was sufficient to prevent all changes in JHB. Migrant individuals must have been sourced from multiple subpopulations, corresponding to the natural dispersal throughout the stream in the absence of the barrier. When migrants were selected in such a manner the number required was inversely related to isolated population size; nine, four, and two individuals were sufficient to prevent changes in the small, intermediate and large population, respectively. This relationship was less pronounced in SB as six, ten, and six individuals had to be moved across the barrier to prevent changes in allelic diversity in the small, intermediate and large population, respectively. Alternatively, eight, 20, and six were needed to prevent changes in genetic differentiation. It should be noted that these results were based on producing no statistically significant differences in genetic metrics, which may not necessarily correspond with biologically relevant changes in genetic populations. In the intermediate SB population, for example, seven migrants produced a 2.42% decrease in allelic diversity, but 20 were required to produce statistically insignificant changes.

Comparisons between the two headwaters yielded contrasting results according to the two genetic metrics calculated, with genetic differentiation being more affected by fragmentation compared to allelic diversity (Fig. 2 and 3). Significant changes in genetic differentiation were observed in 23 of the 24 (95.86%) scenarios, however only 18 of 24 (75.00%) had significant changes in allelic diversity. At low population sizes (N = 150) JHB tended to have greater proportional changes (final-initial/initail) in genetic differentiation (range 167.21–429.33%) compared than SB (range 0.08–273.28%; Figs. 2 and 3).

3.2. Sensitivity analysis

The SRC sensitivity analysis suggested that, among the 15 parameters analyzed, the variable controlling the proportion of mature females contributing to the offspring cohort had the greatest influence on the two output metrics across both streams (μ_{abs} = mean |SRC| = 0.43), followed by straying rate (0.27) and sex ratio, defined in the model as percent females (0.09; Fig. 4). Based on 95% confidence intervals there were no significant differences in the absolute values of the SRC values for the 15 parameters between streams or output metrics. A notable distinction between the two headwaters was the frequency of isolated population extinction prior to completion of the simulation. While 7 of the 500 simulations (1.4%) in SB went extinct, none of the 500 (0.0%) JHB simulations was extinct before year 50. To evaluate what parameters were likely influencing the rate of isolated population extinction in SB, we conducted Student’s t-tests for each parameter, comparing the mean parameter value between the simulations that went extinct with those that did not. Percent of spawning females was the only significant parameter with a Bonferroni corrected p value of 0.0033.

First order indices ranged from 0.02 to 0.50 and total sensitivity indices ranged from 0.25 to 0.92 across the two output metrics (Fig. 5). Similar to the SRC analysis, percent of spawning females had the highest first order index for both allelic diversity (0.50) and genetic differentiation (0.40) as well as total indices (0.93 and 0.89) among the
parameters included in the analysis. The percent of annual strayers had first order indices of 0.15 and 0.14 and total indices of 0.64 and 0.76 for allelic diversity and genetic differentiation, respectively. Unlike the SRC analysis the percent of females (i.e. sex ratio) was not among the most influential parameters.

4. Discussion

Our demogenetic evaluation of the OMPG rule of thumb found such a rate of gene flow insufficient to prevent changes in the genetics of most isolated populations and highlighted the role of both demographic and genetic constituents in the population responses to fragmentation. These results supported our predictions and also the skepticism surrounding the applicability of the rule of thumb to biological systems for conservation purposes of maintaining allele frequencies between populations (Fernandez et al., 2008; Lowe and Allendorf, 2010; Mills and Allendorf, 1996; Varvio et al., 1986). However, our demogenetic simulation results tended to align with the one to ten migrants per generation proposed by Mills and Allendorf (1996). Perhaps more importantly, we have further supported the importance of maintaining and promoting even scarce levels of connectivity at local scales to slow down reductions in genetic diversity in isolated population fragments. We have also demonstrated that demographic parameters shape population responses to fragmentation, suggesting that even at local scales the effect of demographic processes on genetic vulnerability should be considered when prescribing potential conservation actions and particularly those that aim to promote connectivity between populations.

Comparisons between our barrier scenarios indicated that populations respond differently to fragmentation dependent on pre-existing demographic and genetic conditions. As expected due to the relationship between population size and rate of genetic drift (Allendorf et al., 2013), the largest populations (N = 500) were subject to a lesser degree of genetic change. While the range of sizes in this analysis were small compared to intact natural populations, they were realistic for isolated brook trout populations (Bassar et al., 2016; Wood, 2014). Between the two headwater streams, SB had greater observed changes in allelic diversity whereas JHB had much greater changes in genetic differentiation. This contrast was explained by the pre-existing genetic structuring. Of the four genetic clusters in JHB, three contribute migrants to the headwaters on an annual basis (Kanno et al., 2011b). In our simulations migrants were sourced from the closest downstream genetic cluster, to simulate the most likely selection for source migrants during natural dispersal or management based translocation. By only allowing individuals from the closest downstream genetic cluster across the barrier, our simulations did not fully capture the expected natural dispersal from more distant clusters in the network into the isolated population in JHB which led to changes in the genetic population upstream of the barrier. However, selecting individuals from multiple clusters which corresponded to natural dispersal only required two to eight individuals, depending on the scenario. The isolated population in SB was more likely to become extirpated during the sensitivity analyses, despite having equal population sizes, due to the contrasting densities in the two systems. Lower densities in SB (x̄ = 13.00, s = 6.37) compared to JHB (x̄ = 24.14, s = 6.84) increased the probability of local extinction, suggesting the presence of fine scale metapopulation dynamics where extirpation at the patch (i.e. 50 m stream reach) level lead to increased localized extinction at the population level (Hanski, 1998). The results of these simulations suggest, despite being in close geographic proximity and part of a cohesive headwater network, the effect of fragmentation can vary considerably from stream to stream.

The parameter controlling the percent of mature females successfully reproducing in a given year was the most influential in the output of allelic diversity and genetic differentiation in isolated populations. While many studies have aimed at studying brook trout reproductive strategies through genetic pedigree reconstructions (Hudy et al., 2010;
Kanno et al., 2011a), considerably less is known about the percentage of mature adults that annually contribute to a given offspring cohort. Population metrics such as effective population size, $N_e$, and number of breeders, $N_b$, often aim to assess this relationship, and in particular these values are described as a ratio to adult population abundance (Hare et al., 2011; Waples, 2005; Wright, 1931). Both metrics draw upon the conceptual basis that a proportion of the total adult spawning pool contributes to the offspring cohort in a given year, and increasing the diversity among them can improve a population’s ability to persist in a fragmented landscape (Palstra and Ruzzante, 2011; Whiteley et al., 2013, 2012). Having baseline knowledge of these metrics would help better predict changes in populations following fragmentation.

Contrary to the findings of our sensitivity analyses focused on genetic effects, other studies have found juvenile survival and growth as the most important parameters in both resident trout population models (Harvey and Railsback, 2012; Letcher et al., 2007; Marschall and Crowder, 1996) and demogenetic models for salmonid species (Frank and Baret, 2013; Piou and Prévost, 2012). While such parameters were ranked lower in our sensitivity analyses, the relatively high YOY total index suggests the parameter had interactive effects in our model. Mortality among young year classes may have a similar effect on the genetic composition by allowing a higher genetic diversity to persist to the next age class, increasing the likelihood of future adaptive potential (Letcher et al., 2007). For a short-lived species such as brook trout which commonly reach maturity by their second spawning season (i.e. age 1+), the annual reproductive potential and success can increase the likelihood of annual variability in genetic composition.

Reproductive success among brook trout is often skewed towards small family sizes (< 3) in headwater populations of brook trout (Hudy et al., 2010; Kanno et al., 2014a, 2011a) and low variability in reproductive success with a large percentage of adult contribution has been suggested as a mechanism for maintaining genetic variation (Hudy et al., 2010; Kanno et al., 2011a; but see Kanno et al., 2014a). Maintaining these reproductive contributions, therefore, is linked to future genetic diversity and the likelihood of persistence.

Lotic systems are particularly susceptible to fragmentation and at risk of metapopulation extinction due to their dendritic orientation (Fagan, 2002), and the resulting disruption of ecological processes has been emphasized for decades (Ward and Stanford, 1983). Removal of man-made barriers, in particular dams and impassable road culverts, is a common focus for re-establishing connectivity in stream systems. In human-dominated highly-fragmented landscapes, deciding where to focus such restoration actions can become a complicated task which requires a weighting of multiple ecological, social and logistical considerations. The restoration of fragmented stream populations to date has been, in practice, prioritized and evaluated by a “miles upstream” approach based on suitable habitat and mitigation cost (Kemp and O’Hanley, 2010). In this approach restoration actions are prioritized based on maximizing the miles of reconnected habitat following the removal of a barrier or restoration of habitat. Although the strategy has an inherent appeal due to its simplicity and its prioritization of maximum habitat gains, it may fail to recognize the presence of spatial heterogeneity in ecological processes such as dispersal and gene flow. Our demogenetic simulations highlighted the importance of a broader perspective in which stream barrier restoration actions could instead be based on the amount of genetic connectivity a given restoration action would facilitate. This perspective is consistent with calls for aquatic conservationists to develop a riverscape ecological perspective in parallel to the landscape ecology insights that inform terrestrial conservation and management (Fausch et al., 2002; Fig. 3. Changes in allelic diversity (top) and population differentiation (bottom) following fifty years of simulated barrier conditions in two headwater streams. Labels on the x-axis indicate stream (JHB: Jefferson-Hill and SB:Spruce) and population size (150, 300, 500). Error bars represent 95% confidence intervals based on 100 independent Monte Carlo replicates, which were used to determine significant differences between simulation scenarios.
In scenarios where restoring connectivity is not feasible due to logistical or monetary restraints, translocation of individuals for purposes of increasing genetic diversity or fitness (i.e. genetic restoration and genetic rescue, respectively) is another potential management tool to minimize the effects of fragmentation (Frankham, 2015; Weeks et al., 2011). More commonly conceptualized at larger scales, such as the seminal example of the Florida panther *Puma concolor coryi* (Hedrick, 1995; Pimm et al., 2006), the same principles can be applied to finer scale fragmentation concerns. At regional watershed scales genetic rescue has been effective in brook trout experimental trials, indicating its potential to reduce the risk of inbreeding and increase long-term viability of isolated populations (Robinson, 2015). Deciding how many individuals (Mills and Allendorf, 1996) to move and from what source populations (Whiteley et al., 2015) are important considerations prior to using translocation as a management tool. In our model migrants were sourced from directly below the simulated barrier. This strategy, however, failed to capture the natural dispersal patterns in JHB, which lead to increased genetic differentiation compared to SB. The previously studied differences between the two headwater streams stress the need for documenting the underlying dynamics of dispersal and connectivity between groups of individuals prior to implementing translocations. When individuals were sourced from multiple sub-populations, based on genetic connections supported by analyses on the empirical data, < 10 individuals were typically required to prevent genetic changes. Interestingly, these results align well with the one-to-ten migrants per generation posited by Mills and Allendorf (1996). Understanding the genetic population dynamics of a system, in particular how individuals from genetic clusters disperse and interact (Mills and Allendorf, 1996), is thus vital to designing future genetic rescue strategies with a goal of preserving genetic diversity and maximizing the resilience of fragmented populations.

Additional life history characteristics not considered in our model of both the migrant individuals and receiving population may also contribute to fragmentation responses. An implicit assumption of the OMPG rule is that migrants are reproductively successful in the receiving population, and thus the rule is more accurately described as one effective migrant per generation (Wang, 2004). In our model we...
assumed that migrant individuals would have the same likelihood of reproductive success, which is probable due to the smaller spatial scale and similarities between up and down stream habitats in our system. The effect of migrants on the recipient population, however, could vary depending on the age and sex of migrants and also be dependent on species specific mating systems (Allendorf et al., 2013). Further, family or selection based survival could also contribute to rapid changes in the genetics of populations. Although selective neutrality is an assumption of the OMPG rule (Mills and Allendorf, 1996), individuals with certain phenotypic characteristics may be at a selective advantage to the newly established conditions following isolation and could alter the projection of the genetic population (Fraser et al., 2014; Letcher et al., 2007). Our model was populated with neutral microsatellite genotypes and mortality was based on a density-dependent function of patch scale carrying capacity with no selection specified, however other applications have targeted such questions in a demogenetic framework (Landguth et al., 2012a). Future demogenetic models could further explore the importance of both individual and family based reproductive success to determine how such parameters influence the role of migrants in maintaining genetic diversity following fragmentation.

The benefits of maintaining or facilitating migrations between subpopulations has been well documented across many taxa with theoretical (Wang, 2004; Wright, 1931), experimental (Newman and Tallmon, 2001; Spielman and Frankham, 1992) and simulated (Lindemayer and Lacy, 1995) support. Maintaining levels of genetic diversity through connectivity increases the likelihood for populations to adapt and persist under changing environmental conditions (Lande and Shanno, 1996). Although the collective body of literature justifies the importance of maintaining rare dispersal events, evaluations of the OMPG rule, including the demogenetic assessment described in this study, highlight that it is a rule of thumb that is unlikely to be applicable to many wild populations (Mills and Allendorf, 1996; Spieth, 1974; Varvio et al., 1986; Wang, 2004). Particularly when violations of the underlying theoretical assumptions exist, the optimal number of migrant individuals will vary; often up to ten individuals (or more) may be required to prevent losses in genetic diversity, as suggested by our simulations and Mills and Allendorf (1996). Understanding how genetic and demographic mechanisms interact in response to a changing environmental can provide a more holistic view of underlying population dynamics, can be used to prioritize future conservation actions, and hopefully help maintain more resilient populations connected by rare dispersal events. This line of thinking is necessarily context specific, and is yet another example of how well intentioned conservation rules of thumb, like OMPG, are in need of transition towards integrating usage of more sophisticated decision support tools that capitalize on more realistic simulations like those presented here.

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Appendix A. Supplementary Materials

Example input files for CDMetaPOP with parameters used in this study can be found in the online version, at http://dx.doi.org/10.1016/j.biocon.2017.02.043.

References

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Wofford, J.E.B., Gresswell, R.E., Banks, M.A., 2005. Influence of barriers to movement of


