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Research Article

Landscape attributes and life history variability shape genetic structure of trout populations in a stream network

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Abstract

Spatial and temporal landscape patterns have long been recognized to influence biological processes, but these processes often operate at scales that are difficult to study by conventional means. Inferences from genetic markers can overcome some of these limitations. We used a landscape genetics approach to test hypotheses concerning landscape processes influencing the demography of Lahontan cutthroat trout in a complex stream network in the Great Basin desert of the western US. Predictions were tested with population- and individual-based analyses of microsatellite DNA variation, reflecting patterns of dispersal, population stability, and local effective population sizes. Complementary genetic inferences suggested samples from migratory corridors housed a mixture of fish from tributaries, as predicted based on assumed migratory life histories in those habitats. Also as predicted, populations presumed to have greater proportions of migratory fish or from physically connected, large, or high quality habitats had higher genetic variability and reduced genetic differentiation from other populations. Populations thought to contain largely non-migratory individuals generally showed the opposite pattern, suggesting behavioral isolation. Estimated effective sizes were small, and we identified significant and severe genetic bottlenecks in several populations that were isolated, recently founded, or that inhabit streams that desiccate frequently. Overall, this work suggested that Lahontan cutthroat trout populations in stream networks are affected by a combination of landscape and metapopulation processes. Results also demonstrated that genetic patterns can reveal unexpected processes, even within a system that is well studied from a conventional ecological perspective.

Introduction

Spatial and temporal landscape patterns have long been recognized as having important influences on biological processes (MacArthur and Wilson 1967; Levins 1969; Turner 1989). For example, the distribution and demographic stability of populations across landscapes has been related to the size and spatial arrangement of local habitat patches (e.g., Hanski and Simberloff 1997; Hanski 1999). Recent work has also demonstrated the contribution of factors such as the quality of local habitats, composition of habitat between patches (matrix or corridor habitats), and dispersal barriers in driving

population dynamics in a wide array of species, including insects (Fleishman et al. 2002; Hanski et al. 2002), amphibians (Funk et al. 2005), rodents (Gerlach and Musolf 2000; Walker et al. 2003) and reptiles (Berry et al. 2005). We are thus beginning to have a more complete understanding of the complex interactions between landscapes and populations. These concepts have been recognized as important in river landscapes or 'riverscapes' as well, and work in river ecosystems has recently begun to focus on the long-term dynamics of populations on landscapes (Fausch et al. 2002; Wiens 2002; Allan 2004).

Much of the work attempting to apply landscape ecology to river ecosystems has focused on salmonid fishes, especially trout, salmon, and charr (Rieman and Dunham 2000; Fausch et al. 2002). There are many reasons to suspect that landscape characteristics strongly affect the dynamics of stream-living salmonids. The hydrography of stream networks suggests clear patterns of connectivity and systematic changes in physical characteristics, such as temperature (e.g., Nakano et al. 1996) or suitable spawning substrate (e.g., Montgomery 1999), that influence salmonids. These environmental gradients often lead to structuring of populations in habitats of differing sizes that are patchy across landscapes (Dunham et al. 2002). Salmonids also display variable movement life histories, with lifetime movements ranging from only a few meters for those individuals adopting a more 'resident' life history strategy, to long distance (>50 km) annual migrations for 'migratory' individuals (Jonsson and Jonsson 1993). Riverscape structure and complexity can influence the occurrence of these dispersal strategies. For example, barriers to movement or long distances between habitats may select against migratory behavior and promote residency of individuals in upstream headwater habitats (Northcote and Hartman 1988; Näslund 1993), whereas connectivity of a stream network may favor fish with migratory life histories (Hendry et al. 2004). Variable movement by salmonids and stream fishes in general contributes to an array of spatial processes that influence population dynamics, including source–sink dynamics, habitat complementation (the use of spatially segregated habitats for the completion of life cycles), and metapopulation dynamics (Pulliam 1988; Schlosser 1995; Hanski 1999; Dunham et al. 2003).

Movements in the form of migration or dispersal therefore may strongly influence fish population dynamics in landscapes, but these phenomena are very difficult to study by conventional ecological means because of the limited scope of most ecological studies (Gowan et al. 1994; Turner et al. 2003). Whereas most ecological studies are restricted to understanding patterns occurring within localized areas and on daily to annual time scales, genetic patterns within and among populations or among individuals can be used to investigate almost any geographical scenario (see Manel et al. 2003) and can reveal the influence of processes operating on temporal scales both current and of decades or centuries or longer (Slatkin 1985; Davies et al. 1999). However, whereas a purely genetic approach can be useful, interpretations can be challenging because different population processes can lead to similar genetic patterns (Slatkin 1985; Ray 2001). Accordingly, an integrated approach that combines patterns of ecological variation with inferences from genetic markers can provide more robust insights into the organization of various demographic processes across a landscape (Neville et al. In press).

In this study, we used nuclear genetic markers (microsatellites) to infer the dynamics of stream-living trout populations within a complex riverscape. Our primary goal in this study was to use genetic inferences about population parameters to evaluate the importance of different riverscape processes affecting fish within a stream network. We hypothesized several influences of habitat size and quality, connectivity, and life history variability on local population size, stability, and dispersal. Our predictions focused on patterns of genetic diversity assumed to be related to, and 'diagnostic' of, these demographic processes. Among the three factors, we considered habitat connectivity to be the most important (Neville et al. In press). Information on habitat quality and size, and potential migratory life history behavior was then used to modify our predictions in cases where opposing or additive influences were suspected. For example, in headwater habitats where connectivity was high but resident life histories were thought to be dominant, the predicted increases in local population sizes and dispersal due to connectivity were assumed to be reduced (see below). Accordingly, we developed predictions

based on an assessment of the collective influence of these three factors on demography and, consequently, patterns of genetic structure and diversity.

First, because connectivity should increase dispersal and therefore local population stability, we predicted decreasing genetic differentiation among, and increasing diversity within, local populations as connectivity increased (Hedrick and Gilpin 1997). In addition to a general correlation between dispersal and connectivity, we predicted dispersal to be asymmetrical in reaches upstream of waterfalls, with greater gene flow from upstream to downstream populations and reduced gene flow in an upstream direction over barriers. Second, we predicted that increasing habitat quality and size should be positively related to local population size and demographic stability, due to enhanced reproduction, survival, and persistence. We thus predicted that increased quality and size would influence genetic variability in a similar fashion to increased connectivity (Hartl and Clark 1997). Third, we predicted that gene flow and genetic diversity should be higher for local populations with greater assumed proportions of migratory individuals, which are larger and potentially produce more offspring, and are more likely than resident fish to be agents of gene flow (Hansen and Mensberg 1998).

We investigated riverscape genetic patterns in a subspecies of cutthroat trout, the Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*), living in a network of stream habitats in the Lahontan Basin of the western Great Basin desert, USA. Persistence of local Lahontan cutthroat trout populations is strongly tied to landscape connectivity and local habitat (patch) size (Dunham et al. 1997, 2002), but specific processes influencing population dynamics across landscapes are poorly understood. Our specific objectives were to:

(1) Describe patterns of physical connectivity of stream habitat (e.g., presence/absence of barriers), local habitat size and quality, and potential migratory life history (resident vs. migratory) within a stream network to map a 'riverscape' upon which local population dynamics may operate.
(2) Develop *a priori* hypotheses and predictions about the influences of these factors on three key population parameters: local population size, stability, and dispersal.
(3) Test predictions by inferring population structure and demography from genetic information.

Results from this work provide new insights into the complexity of landscape processes influencing stream fishes, as well as the effectiveness of using complementary genetic methods for inferring demographic processes (Manel et al. 2003; Neville et al. In press).

Materials and methods

Species and study system

The Lahontan cutthroat trout is endemic to the Lahontan basin, a closed drainage system occupying a major portion of the western Great Basin desert in western North America (Behnke 1992). Within the eastern portion of the Lahontan basin, cutthroat trout are generally restricted to small, isolated streams, with a few exceptions where larger interconnected stream networks remain (Dunham et al. 1997, 1999, 2002). This study was conducted within one of these larger networks: the Marys River basin (Figure 1; study site encompasses 41°33′ N, 115°18′ W and above).

The upper Marys River drains an area of about 500 km^2. Streams within this network vary in stability and habitat quality, driven largely by stream flow and temperature. Summer stream flow and temperatures are consistently more suitable for Lahontan cutthroat trout at higher elevations. Stream reaches at lower elevations often dry completely. Natural waterfalls potentially restrict upstream fish movement in two streams, and a series of irrigation diversions isolate streams completely in the eastern portion of the Marys River basin (Figure 1).

Site selection and sampling

We designed our study to sample fish from a diversity of habitat types, levels of connectivity, and potential migratory life histories found throughout the system. Accordingly, we sampled 16 sites, including sites from headwater and confluence portions of most tributaries and from

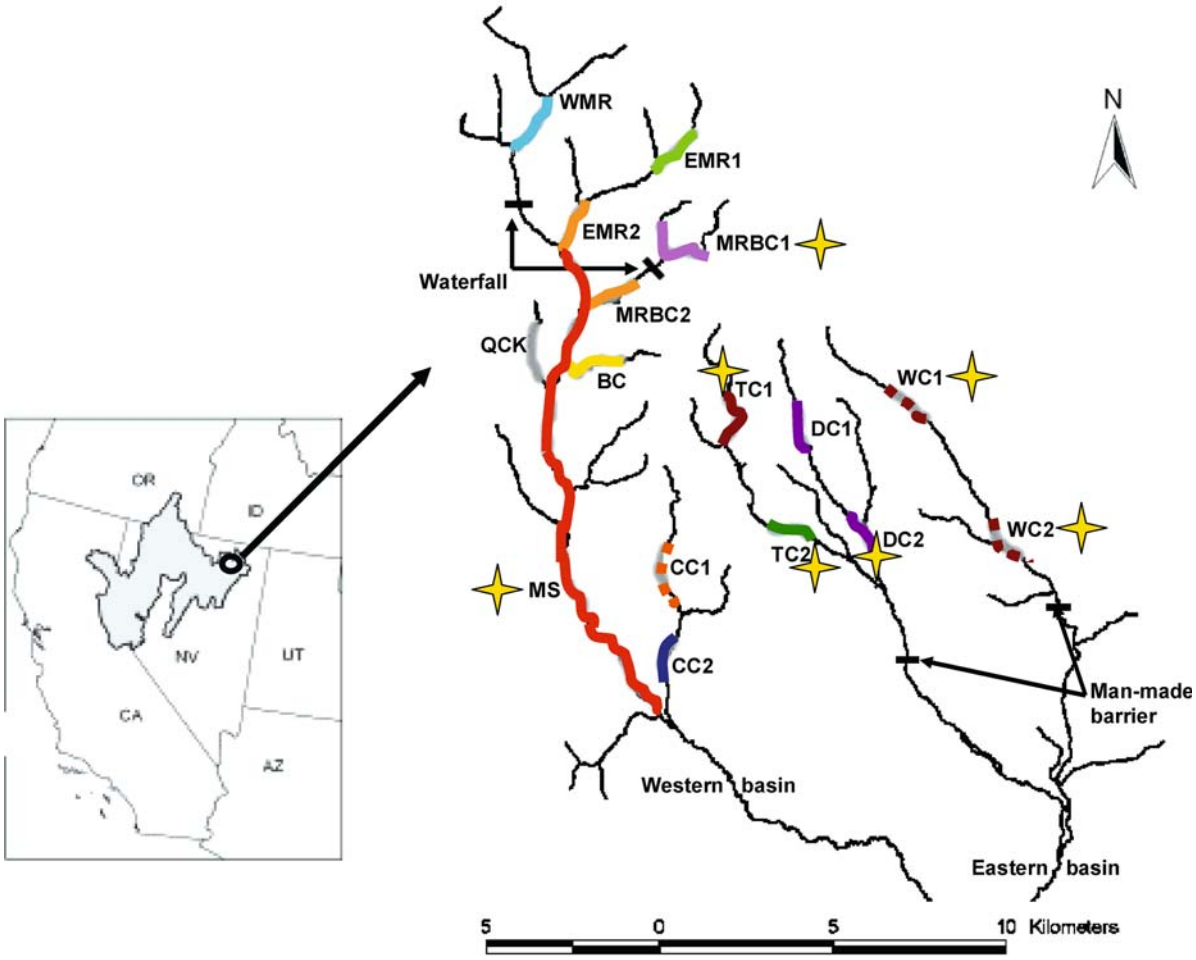

Figure 1. Map of the western United States at left with the Lahontan basin in grey and the location of the Marys River encircled. At right is the study site; sample sites are indicated by bold colored lines. Pairs of samples with similar colors had F_{ST} values that were not statistically different from each other, whereas samples with different colors were significantly differentiated from all other samples (see Table 2 for values). Stars indicate samples for which a significant bottleneck was detected using the *M* ratio. Locations of waterfalls and complete man-made barriers within the stream network are indicated.

throughout the mainstem river (Figure 1). To ensure that samples were unlikely to be biased towards sibling groups (Hansen et al. 1997), fish from three to seven segments of stream (each 25–40 m) at least 100 m apart composed the sample from each site. Segments were block-netted at both ends, and three-pass depletion sampling was used to remove age 1+fish from each segment. The mainstem river was too wide to block-net, and fish were collected by spot-sampling along most of the distribution of occupied mainstem habitat. Fin clips were collected and fish were released back into the stream segments where they were captured. Sites were sampled over 2 years (1999 and 2000).

Ranking of landscape connectivity and habitat quality

We ranked each sampled stream reach based on habitat quality and connectivity, and its most likely migratory life history (see below), and considered these factors collectively in terms of their hypothesized influences on local population size, stability, and dispersal. From these hypotheses, we developed testable predictions of expected patterns of genetic diversity within and divergence among local populations (Table 1).

Based on our long-term (> 10 year) observations and measurements of habitat characteristics and the distribution of Lahontan cutthroat trout within

the Marys River basin (Dunham et al. 1997, 1999; Neville Arsenault 2003), we ranked habitat quality on a relative scale (low, intermediate, or high; Table 1) according to known gradients of stream temperature and flow. For example, high-elevation reaches in the headwaters of large tributaries are most likely to support cold water and perennial flows. Habitat size was also considered collectively with quality (based on length of occupied stream), because larger habitats should support larger local populations. Connectivity was ranked according to the known distribution of natural and human-constructed movement barriers (Figure 1). Low connectivity was assigned to single stream reaches isolated by barriers. Intermediate connectivity was assigned to ephemeral stream reaches (e.g., reaches in Basin and Question Creeks), or reaches that are connected to nearby reaches but isolated within a portion of the Marys River basin (e.g., reaches in T and Draw Creeks; Table 1 and Figure 1). Stream reaches without barriers to fish movement were ranked as having high connectivity, regardless of distance to the mainstem Marys River or other reaches, because cutthroat trout can move long (>30 km) distances in streams (Colyer 2002; Schrank and Rahel 2004). We classified life history variation based on our own field observations and on patterns commonly found in trout, with headwater streams supporting a higher proportion of non-migratory or 'resident' fish and downstream habitats supporting a higher proportion of migratory individuals (Rieman and Dunham 2000).

Sample extraction and microsatellite analysis

A total of 1189 fish were sampled, 451 in the year 1999 and 738 in 2000. Total genomic DNA was extracted using DNeasy extraction kits (Qiagen Inc, Valencia, CA, USA). Eleven microsatellites were used for this study. Six dinucleotide loci were optimized from other salmonid species (Nielsen and Sage 2002): Omy77 (Morris et al. 1996), Ssa85 (O'Reilly et al. 1996), Sfo8 (Angers et al. 1995), Oneu8 and Oneu2 (Scribner et al. 1996), and Ssa14 (McConnell et al. 1995). Five tri- and tetranucleotide loci were identified specifically from Lahontan cutthroat trout: Och5, Och6, Och9, Och10 and Och11 (Peacock et al. 2004). Information about primers and polymerase chain reaction (PCR) protocols can be found in Nielsen and Sage (2002) and Peacock et al. (2004). PCR products were electrophoresed on either an ABI 310 or ABI 3700 automated sequencer (Applied Biosystems), including standard samples for cross-reference. Scoring was performed manually using Genescan (Applied Biosystems version 1.1.1 and 3.5.1) and Genotyper (Applied Biosystems version 2.1 and 3.5).

Statistical analysis of genetic patterns

We applied a suite of statistical methods to analyze patterns among pre-defined 'populations' (where each sample equaled a local 'population') and individuals to test our predictions about the influences of habitat attributes and life history variability on patterns of genetic variability (Table 1). The population-based analyses included Analysis of Molecular Variance (AMOVA, Weir and Cockerham 1984), F_{ST} (Goudet 2001), tests for genetic bottlenecks (Garza and Williamson 2001), and maximum likelihood coalescent-based estimates of dispersal and effective sizes (N_e, Beerli and Felsenstein 1999, 2001), while we used individual-based genotype clustering methods to evaluate genetic grouping and assignment patterns among individuals (Pritchard et al. 2000). The use of individual-based analyses can be helpful in evaluating the *a priori* population boundaries required for the use of more traditional population-based analyses (see Manel et al. 2003; Neville et al. In press). Additionally, individual-based analyses do not assume drift-migration equilibrium and they characterize current movement, which may differ from the long-term average rates of gene flow estimated by traditional population-based methods (Davies et al. 1999; Whitlock and McCauley 1999). The breadth of temporal scales and statistical assumptions encompassed by this combination of equilibrium and non-equilibrium approaches provides a more comprehensive foundation for inferring population dynamics than would either approach in isolation (Davies et al. 1999; Ingram and Gordon 2003).

In order to determine if samples from different years may be pooled, we performed an AMOVA (Weir and Cockerham 1984) as implemented in Arlequin (version 2, Schneider et al. 2000) to evaluate the amount of genetic variation parti-

Table 1. Number of individuals sampled (*n*) and predicted responses of genetic divergence and diversity for fish sampled from stream reaches in the Marys River basin.

Stream reach (sample name)	Stream reach and population characteristics				Predicted genetic pattern	
	n	Habitat quality/size	Physical connectivity	Assumed life history	Genetic divergence	Genetic diversity
West Marys River (WMR)	63	High/large	Low *	Resident	High	Low
Upper East Marys River (EMR1)	62	High/large	High	Resident	Intermediate	Intermediate
Lower East Marys River (EMR2)	53	High/large	High	Mixed	Low	High
Upper Marys River Basin Creek (MRBC1)	86	High/intermediate	Low *	Resident	High	Low
Lower Marys River Basin Creek (MRBC2)	51	High/large	High	Mixed	Low	High
Basin Creek (BC)	59	Low/small	Intermediate +	Mixed	Low	Intermediate
Question Creek (QCK)	55	Low/small	Intermediate +	Mixed	Low	Intermediate
Mainstem Marys River (MS)	204	Mixed/large	High	Migratory	Low	High
Upper Chimney Creek (CC1)	77	Intermediate/small	Intermediate +	Resident	High	Low
Lower Chimney Creek (CC2)	83	Low/small	Intermediate +	Mixed	Low	Intermediate
Upper T Creek (TC1)	85	High/large	Intermediate-low §	Resident	High	Low
Lower T Creek (TC2)	59	Low/large	Intermediate-low §	Mixed	Intermediate	Intermediate
Upper Draw Creek (DC1)	50	Intermediate/large	Intermediate-low §	Resident	High	Low
Lower Draw Creek (DC2)	58	Low/small	Intermediate-low §	Mixed	Intermediate	Intermediate
Upper Wildcat Creek (WC1)	55	Intermediate/small	Low §	Resident	High	Low
Lower Wildcat Creek (WC2)	39	Low/small	Low §	Resident	High	Low

*Above-waterfall site + Ephemerally connected.

§ Eastern basin isolated by a man-made barrier. T and Draw creek are connected to each other, but together are isolated. Wildcat is completely isolated.

tioned between years within each site, as opposed to among sites. Though significant, the temporal component of genetic structure was much smaller than the spatial component (1.8% of the overall variation was due to differences between years within sites, while 11.0% was due to differences among sites, $p < 0.001$ in both cases). Within-site samples from each year were therefore combined for all further analyses to obtain a more accurate estimate of allelic frequencies (see Waples 1990 for more detailed discussion), giving a total sample size of at least 50 individuals for all sites but one (WC2, $n = 39$, see Table 1 for sample sizes). Fourteen individuals identified by genetic fingerprints (Taberlet and Luikart 1999) as having been caught in both years were removed from the 2000 data set to avoid duplication.

Adherence of combined samples to Hardy–Weinberg equilibrium was assessed by testing for excessive or deficient F_{IS} values for each population sample at each locus using FSTAT (Goudet 2001), adjusting critical significance levels to account for simultaneous tests. F_{IS} is a measure of inbreeding among individuals relative to the subpopulation, and is used to assess whether or not samples are panmictic as assumed by population-based analyses.

Population size and stability

Genetic diversity was calculated using FSTAT and characterized for each sample as allelic richness (R_s), a quantification of the number of alleles corrected for sample size, and an unbiased measure of heterozygosity (H_E, Nei 1987). Spearman rank correlation was used to determine if observed diversity varied as predicted (Table 1). We used Garza and Williamson's (2001) M ratio to test for altered patterns in allelic size distributions indicative of bottlenecks. Statistical significance was evaluated based on a re-sampling method with 10,000 iterations, and a range (0.05–10) of 'theta' values ($4N_e\mu$, where μ is the microsatellite mutation rate and N_e represents the size of an 'ideal' population that would lose genetic variability by drift at the same rate as the population at hand). Assumed theta values influence only the statistical significance of the M ratio, not the ratio itself. For a sub-set of populations, N_e was estimated (as 'theta') using coalescent-based simulations of the genealogies among individuals within populations with MIGRATE 1.7.3 (Beerli and Felsenstein 1999, 2001). This method is useful for estimating directional migration rates and effective sizes independently, which cannot be accomplished using F_{ST} (see Beerli and Felsenstein 1999). Four separate simulations were run, with parameter estimates from each run providing starting points for the next. Results from the fourth run were used as final estimates. Due to large computer processing demands, simulations were restricted to fish collected in six sampling sites (WMR, EMR1, EMR2, MRB1, MRBC2, and MS; Figure 1) in the upper interconnected western basin, where waterfall 'barriers' and potential life history diversity were hypothesized to have particularly strong influences on genetic diversity and gene flow. Spearman rank correlation was used to determine if N_e for the six populations assessed varied as predicted (Table 1).

Population differentiation and dispersal

Genetic structure among pre-defined populations was evaluated based on F_{ST} (Weir and Cockerham 1984), calculated in FSTAT (2400 permutations, corrected for table-wide comparisons). F_{ST} characterizes the extent of genetic differentiation among populations by determining the degree of allelic variation among, vs. within, populations. We calculated average pair-wise F_{ST} values for each sample, based on all pair-wise comparisons including that sample, i.e., we averaged the non-diagonal values within each row of the full matrix of pair-wise F_{ST} values. Because these averages are not fully independent of each other (the same pair-wise F_{ST} value is used in the average for each of the two populations involved in that pair-wise comparison), we evaluated concordance between our predictions and observations of genetic differentiation graphically, as opposed to statistically. Relative rates and directionality of gene flow among a subset of populations were estimated using the coalescent approach of MIGRATE, as described above.

We also characterized population structure using an individual-based approach that does not require the *a priori* definition of populations, to evaluate concordance with inferences from population-based analyses. The Bayesian clustering

approach of STRUCTURE 2.1 (Pritchard et al. 2000) was used to determine the most likely number of genetic clusters (k) in the Marys River. STRUCTURE calculates the likelihood of different numbers of genetic clusters by iteratively sorting individual multilocus genotypes into groups to maximize the fit of the data to theoretical expectations derived from Hardy–Weinberg and linkage equilibrium. It then assigns individuals to their most likely cluster of origin. Though ideally these clusters could be used to define populations for further analyses, this is possible only in species where high differentiation confers high statistical power for individual assignments (see Cornuet et al. 1999; Parker et al. 2004). Such tangible units are unlikely to be defined in many cases for a species in interconnected habitat thought to have a migratory component. Here, we use this complementary approach as a heuristic comparison to other analyses. Based on preliminary analyses, we evaluated the likelihood of a k of 15–22, with 5 runs performed for each k, and a burn-in length of 100,000 and 30,000 MCMC replicates for each run. Ten additional runs (250,000 burn-in; 100,000 MCMC replicates) were performed using the most likely k. Because results across runs were similar, final assignments and inferences were drawn using the run from this last effort with the highest likelihood. We assumed an admixture model and correlated allele frequencies among populations (Pritchard et al. 2000).

Results

Population size and stability

None of the 176 F_{IS} values were found to be significantly different from zero in either direction when adjusted for multiple tests, suggesting that our samples were in Hardy–Weinberg equilibrium. Only a moderate degree of polymorphism was observed in this system as a whole, but samples did vary in their levels of diversity. Average allelic richness (R_s) within samples ranged from 3.38 to 6.09, while average heterozygosity (H_E) ranged from 0.42 to 0.56 for different samples. Both measures were correlated with predicted patterns, with populations with low connectivity, resident life history, or poor quality/smaller sized habitat showing lower genetic diversity (r_s = 0.77, d.f. = 15, p = 0.001, and r_s = 0.66, d.f. = 15, p = 0.006, for R_s and H_E respectively; see Figure 2).

All M ratios were below 0.80. Six samples had M ratios (M = 0.49–0.60) below the 0.68 considered diagnostic of bottlenecks (Garza and Williamson 2001), and these were statistically significant at all theta values. All of these samples were either above waterfalls or in the isolated eastern basin (Figure 1). Additionally, the M ratio for the mainstem river (0.69) was deemed significant in all simulations. Theta, as estimated by coalescent simulations, varied among populations (theta = 0.07–0.28, Figure 3), and varied in the predicted direction, but this trend was not statistically significant (r_s = 0.28, d.f. = 5, p = 0.59; Figure 2). Calculating a numerical value of N_e from theta ($4N_e\mu$) requires the input of a mutation rate (μ) for the genetic markers used. While we lack information on the mutation rate of the microsatellites used in this study, we can estimate likely N_es based on rates found in other vertebrates. N_es calculated as such ranged from 2 to 8 individuals (μ = 0.0085 in pink salmon, Steinberg et al. 2002), to 37–142 individuals (μ = 0.0005 in humans, Weber and Wong 1993).

Population differentiation and dispersal

F_{ST} values indicated significant overall differentiation, with a system-wide F_{ST} estimate of 0.12 (95% CI: 0.09–0.15). Pair-wise F_{ST} estimates varied substantially and ranged from 0.006 to 0.32 (Table 2).

Most samples were significantly differentiated from all other samples in the system (Figure 1). Two exceptions included two up- and downstream sample pairs within the same stream (Wildcat and Draw Creeks) in the isolated eastern basin. In addition, the lower sites of East Marys River (EMR2) and Marys River Basin Creek (MRBC2) were not different from each other and showed significant, but only slight differentiation from the mainstem river (Table 2). Significant within-tributary differentiation was observed between up- and downstream samples from East Marys River, Marys River Basin Creek, Chimney Creek, and T Creek, three of which have no obvious barriers to gene flow (Figure 1). Average pair-wise F_{ST} values varied as predicted with our qualitative categories

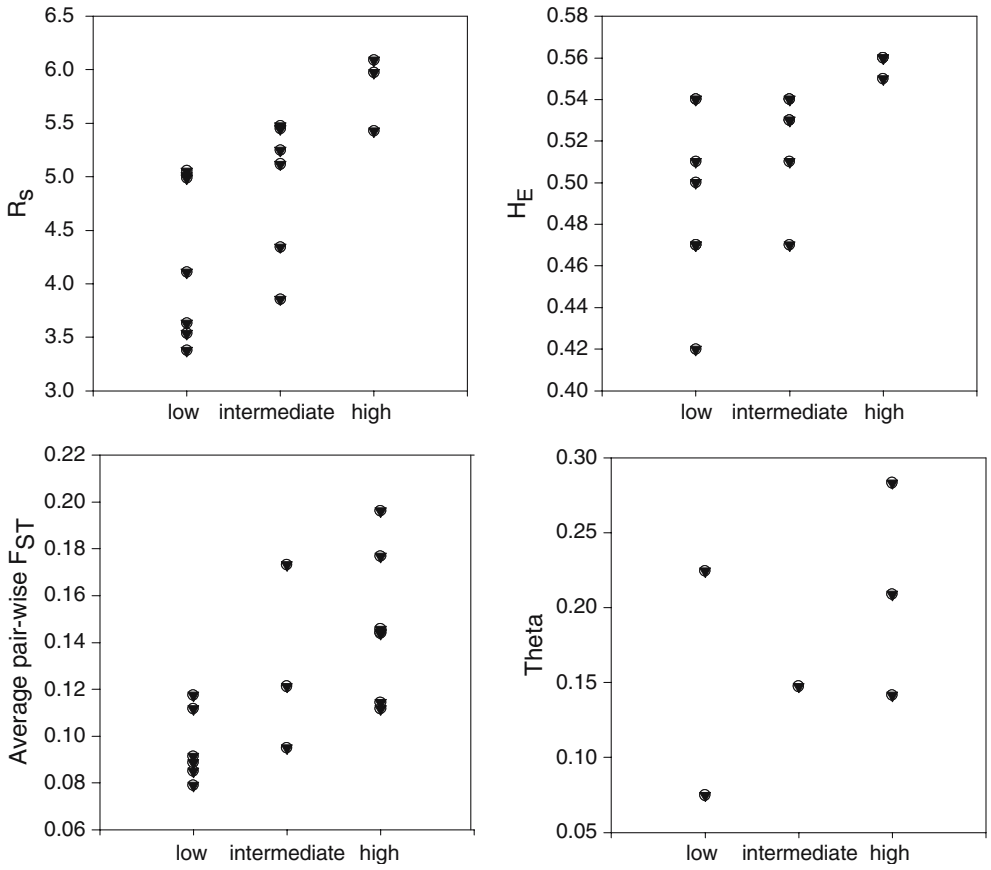

Figure 2. Observed magnitude of each genetic divergence or diversity metric versus that predicted qualitatively for Lahontan cutthroat trout populations characterized as in Table 1.

of differentiation, suggesting that populations with lower connectivity, assumed resident life histories, or poorer quality/smaller sized habitat were more differentiated from other populations (Figure 2).

Rates of gene flow as estimated by MIGRATE varied substantially among the six populations evaluated, and every pair-wise comparison demonstrated asymmetrical gene flow with non-overlapping approximate 95% confidence intervals (see Beerli and Felsenstein 2001) except that between the two headwater sites WMR and MRBC1. Total rates of gene flow into and out of two headwater sites above waterfalls (WMR and MRBC1) were low compared to those at other sites (Figure 3). Directional gene flow was significantly lower into WMR than that out of it, while total gene flow into MRBC1 was slightly higher than that out of it, but this difference was not significant. EMR1 (a headwater site with no barriers) had relatively high levels of incoming gene flow, with significantly less gene flow out to other sites and a rate similar to that out of WMR. Gene flow into and out of the lower confluence sites (EMR2, MRBC2 and MS) was comparatively high (Figure 3).

The results obtained by the model-based clustering of individuals indicated that fish from the Marys River most likely formed 20 local genetic clusters. The average Bayesian posterior probability across the five runs for $k(20)$ was 0.99, vs. 0.009 for $k(18)$, the next most likely number of clusters. In general, the clusters mirrored the results from other analyses (i.e., individuals from samples which were not significantly differentiated based on F_{ST} were grouped). Many clusters indicated at least moderate autonomy of fish from specific reaches, suggesting the organization of population structure by tributaries and occasionally within tributaries. In the western basin, almost 50% of individuals from WMR were assigned to

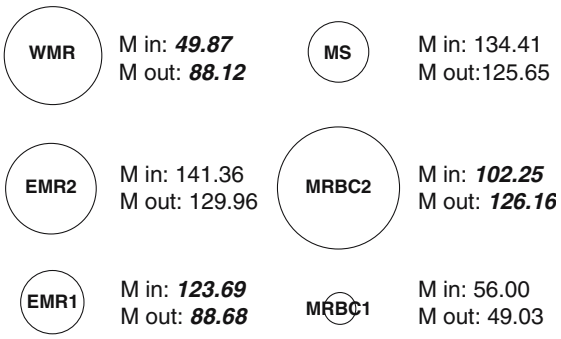

Figure 3. Estimates of gene flow into and from local samples of Lahontan cutthroat trout in the upper Marys River (Figure 1). For each sample, the size of the circle indicates the relative value of theta ($4N_e\mu$) as estimated using a coalescent-based analysis implemented in MIGRATE (Beerli and Felsenstein 1999, 2001), where N_e is the effective population size and μ is the microsatellite mutation rate. To the right of each sample is its total rate of gene flow in each direction (M in and M out, with $M = \Sigma\ M_{ij}$, $M_{ij} = m_{ij}/\mu$, and m_{ij} = migration rate per generation from i to j). Populations with significantly asymmetrical gene flow, as assessed by non overlapping 'approximate confidence bounds' (see Beerli and Felsenstein 2001) are indicated by bold, italicized M values.

Table 2. Pair-wise F_{ST} values between the populations of Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*) in the study area in Nevada. Note that non-significant F_{ST} values are given in bold.

	EMR1	EMR2	MRBC1	MRBC2	QCK	BC	MS	CC1	CC2	TC1	TC2	DC1	DC2	WC1	WC2
WMR	0.05	0.06	0.15	0.06	0.08	0.05	0.04	0.11	0.08	0.13	0.15	0.23	0.22	0.15	0.16
EMR1		0.01	0.17	0.02	0.06	0.03	0.01	0.10	0.06	0.09	0.12	0.20	0.20	0.15	0.15
EMR2			0.15	**0.01**	0.06	0.03	0.01	0.10	0.06	0.07	0.10	0.18	0.18	0.14	0.13
MRBC1				0.14	0.16	0.14	0.13	0.18	0.18	0.22	0.24	0.32	0.31	0.22	0.23
MRBC2					0.06	0.03	0.01	0.11	0.06	0.08	0.11	0.19	0.19	0.13	0.13
QCK						0.07	0.05	0.12	0.09	0.14	0.16	0.23	0.22	0.13	0.14
BC							0.02	0.10	0.06	0.09	0.10	0.18	0.17	0.15	0.15
MS								0.08	0.05	0.08	0.10	0.18	0.18	0.12	0.12
CC1									0.03	0.15	0.18	0.27	0.25	0.20	0.20
CC2										0.12	0.14	0.22	0.21	0.15	0.16
TC1											0.04	0.09	0.10	0.14	0.12
TC2												0.05	0.05	0.14	0.14
DC1													**0.01**	0.16	0.14
DC2														0.16	0.15
WC1															**0.03**

only one of the 20 clusters, and fish from QCK, CC1 and MRBC1 had substantial membership in one cluster associated with each of these sites as well (Figure 4).

Two clusters were weighted towards fish from EMRUP, though many fish from this site were also assigned to other clusters. In the eastern basin, fish from WC1 and WC2 were grouped into one highly distinctive cluster. Many fish from DC1 and DC2 were grouped into one cluster, while others assigned to a cluster including fish from neighboring TC2 and a few from TC1. Another cluster was comprised almost equally of fish from TC1 and TC2, while yet another cluster was comprised of mostly TC1 individuals (Figure 4).

One surprising result from STRUCTURE was a strongly-supported within-sample split of individuals from the above-waterfall headwater site MRBC1 into two clusters. Individuals from this sampling site were assigned exclusively and with high probabilities (mean probability of assignment = 0.82) to two separate clusters which were partitioned directly along a tributary split (Figures 1 and 4). Another interesting result was that STRUCTURE formed eight somewhat similar 'lower confluence/mainstem' clusters with little tangible geographic correspondence, though membership in each of these clusters leaned towards different regions within the mainstem river associated with various confluence reaches. For

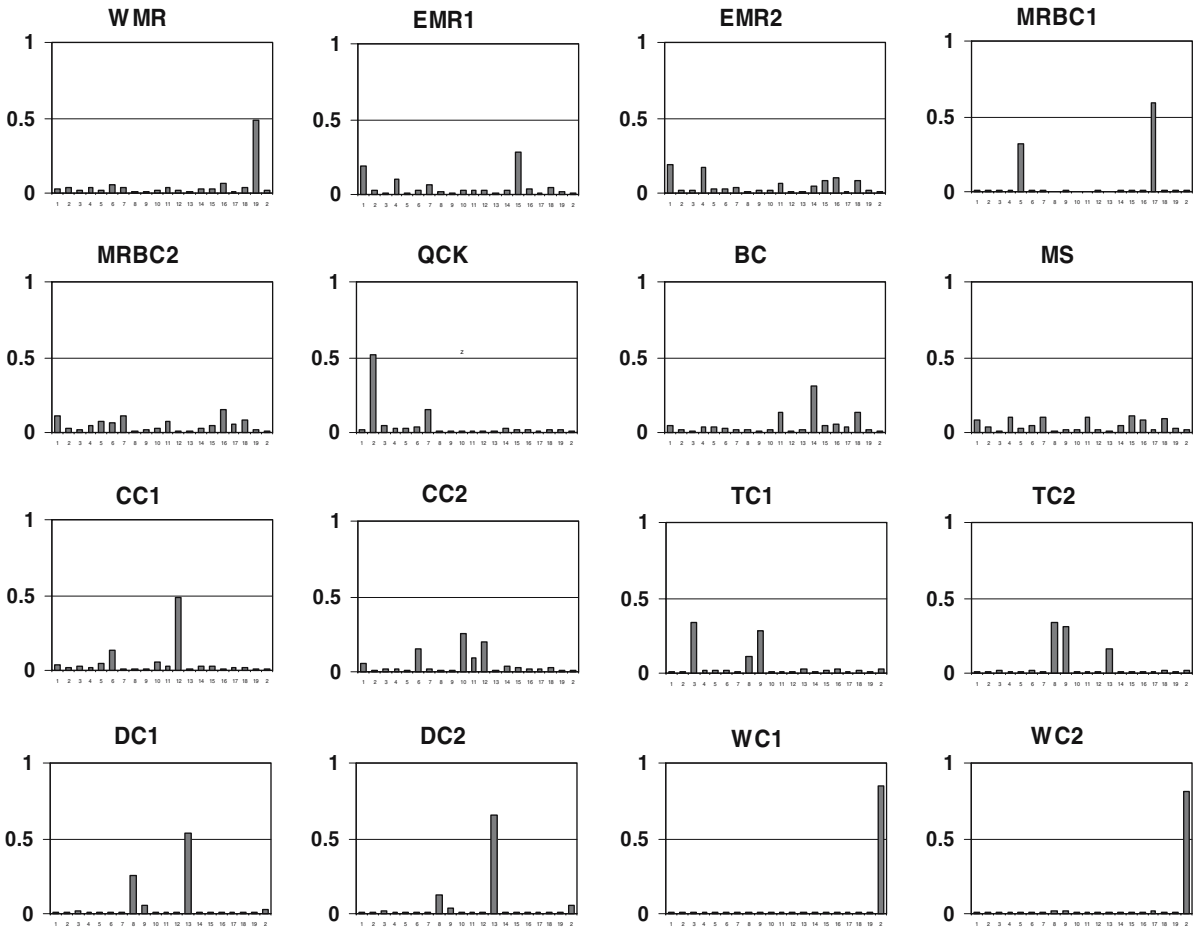

Figure 4. Proportional membership of individuals from each sample (*y* axis) in each of the 20 genetic clusters (*x* axis) defined by a Bayesian clustering algorithm implemented in STRUCTURE.

instance, one of these groups was characterized by individuals from BC, MS, CC2, MRBC2 and EMR2 (in order of contribution), another by fish from QCK, MS and MRBC2, and a third those from MRBC2, EMR2, WMR, MS and BC.

Discussion

Our study was designed to reveal the collective influences of stream connectivity, habitat quality and size, and assumed migratory life history on the size, stability, and dispersal patterns of local populations of Lahontan cutthroat trout in a complex stream network within a watershed. We were unable to disentangle the effects of each potential influence because interactions and confounding among factors are the norm in natural landscapes. Nonetheless, our approach of testing predictions from *a-priori* hypotheses about qualitative population responses of Lahontan cutthroat trout provided useful insights. Within the broader context of applying ideas from metapopulation and landscape ecology to stream fishes (Schlosser and Angermeier 1995; Rieman and Dunham 2000; Fausch et al. 2002; Wiens 2002) this landscape genetics approach (Manel et al. 2003; Neville et al. In press) revealed complex structuring of Lahontan cutthroat trout within the Marys River basin that is not easily generalized. This complexity reflects local diversity in riverscape and perhaps population characteristics. Similar complexity is also being found in a host of other species, where factors such as habitat 'patch' quality, matrix composition, life history, or population age are increasingly recognized as an important determi-

nants of observed variability in population dynamics (Hanski and Singer 2001; Fleishman et al. 2002; Walker et al. 2003; Hanski et al. 2004; Funk et al. 2005). In Lahontan cutthroat trout, such complexity is more likely to be maintained in larger basins like the Marys River. Smaller streams, watersheds or patches of suitable habitat generally represent a smaller range of conditions (e.g., Montgomery 1999) with fewer options for population persistence in the face of the dynamic conditions that typify streams (e.g., Dunham et al. 2003). As habitat fragmentation proceeds in stream networks, loss of within-patch diversity is compounded by the loss of connectivity, and eventually extinction of Lahontan cutthroat trout in smaller and more isolated patches (89% of interconnected patches in the Lahontan basin supported Lahontan cutthroat trout, while only 32% of isolated watersheds maintained trout, Dunham et al. 1997). Thus, whereas local population dynamics within patches can be complex, as observed here, it is possible to predict population persistence among patches with relatively simple patch occupancy models (Hanski 1994; Moilanen 1999; Dunham et al. 2002). Analyses at each scale have provided important clues to the general patterns of persistence of Lahontan cutthroat trout across landscapes and the specific local mechanisms that drive them within individual stream networks.

Concordance between our predictions and observed differentiation among and diversity within populations suggested the influence of connectivity on population dynamics. Genetic differentiation was highest for above-barrier populations, as has been found in other systems of trout and charr (Costello et al. 2003; Taylor et al. 2003; Wofford et al. 2005) and in other species in fragmented habitats (Gerlach and Musolf 2000; Hale et al. 2001). This effect is likely due to restricted dispersal into and out of above-barrier sites: high levels of differentiation in isolated populations in the Marys River basin were corroborated by lower levels of gene flow as estimated by coalescent methods, and more cohesive genetic clusters demonstrating reduced current movement. Additionally, the sampling effect of bottlenecks in isolated habitats may increase genetic differentiation (Hedrick 1999). In general, populations that showed the strongest evidence of genetic bottlenecks in this system were those isolated by barriers, suggesting a synergistic effect between isolation and small population sizes in influencing genetic variability, and perhaps population resiliency (see Saccheri et al. 1998; Couvet 2002).

Interestingly, there was not a marked difference in the influence of natural vs. man-made barriers on genetic patterns, despite the more recent timeframe of isolation due to man-made barriers. Contrasting patterns of dispersal and demographic stability in the various isolated streams suggest the response of populations of Lahontan cutthroat trout to barriers may be highly dependent on the habitat in which isolated populations persist. In the western basin, one population (West Marys River) housed above a waterfall in comparatively large, high-quality habitat appeared to have both restricted and asymmetrical gene flow but also to be relatively large and temporally stable (relatively large N_e, no bottleneck). The other waterfall in the western basin had been breached by trout approximately 10 years previous to our sampling, following the local extirpation of the resident population above the barrier (Dunham 1996). This newly-founded population (Upper Marys River Basin Creek) was characterized as having low gene flow and no current movement, but was strongly bottlenecked and had an extremely low effective size (N_e), consistent with the re-colonization of this smaller habitat. Almost all populations from the eastern basin, which is isolated by a relatively recent (early 20th Century) man-made barrier, displayed similar symptoms of isolation (high differentiation) and temporal instability (significant bottlenecks) despite some connectivity between two of the streams within this basin and the more recent isolation of this basin as a whole. Habitat conditions are relatively poor in much of the low-elevation eastern basin, with warmer temperatures and occasional desiccation of large reaches of stream. Seemingly, poor habitat quality can compound any effects of isolation to cause significant impacts on genetic variability, even when barriers are of relatively recent origin (see also Gerlach and Musolf 2000).

Several lines of evidence also suggest an influence of spatially-segregated life history variation on population processes and genetic patterns. The diverse patterns of differentiation throughout the watershed reveal the potential for interesting interactions among landscape structure (i.e., the degree of connectivity) and dispersal behavior in

trout. In brown trout (*Salmo trutta*), for instance, life-history variation is reflected in patterns of genetic variability that often segregate with geographic location. Freshwater resident populations, with less opportunity for dispersal, show greater divergence and lower genetic variability than migratory groups (Hansen and Mensberg 1998; Knutsen et al. 2001). In the Marys River, the potential for life history diversity was more apparent in the interconnected western sub-basin where fish have access to a greater variability of habitat types – including mainstem river habitat – than in the eastern sub-basin. As predicted, fish from the mainstem river and confluence reaches of several tributaries were found to be relatively panmictic based on population-level analyses. Individual-based clustering algorithms identified several weak clusters in the mainstem river comprised of fish from both the mainstem and various confluence reaches, suggesting this habitat houses a mix of fish from different areas. In contrast, certain headwater populations were more differentiated than their physical connectivity (i.e. with an absence of barriers) or close proximity to other sites would have indicated, alluding to a certain degree of behavioral isolation.

However, genetic patterns were not always consistent with our predictions concerning life history segregation. For instance, two of three tributaries in the isolated eastern basin did not show within-stream differentiation, which may reflect greater within-stream movement of fish from these tributaries due to the impossibility of moving among streams. Two smaller western-basin tributaries, which we had assumed were too small to house 'resident' populations, had surprisingly high levels of differentiation and genetic autonomy. Observed inconsistencies may be due to several factors: (1) our categorizations of life history variability were not entirely accurate; (2) observed genetic patterns were influenced by other, un-investigated factors; (3) life history variability does not always influence gene flow; and (4) life history interacts with habitat structure in a complex and unpredictable manner.

Overall, it is reasonable to conclude based on observed genetic patterns that the persistence of populations in the Marys River depends on connectivity and habitat complexity sufficient to maintain a metapopulation dynamic among localized populations (see Smedbol et al. 2002). Though genetic patterns are not direct evidence that turnover events have occurred in the Marys River, the extremely small effective sizes and severe bottlenecks observed here suggest that local extinctions and re-colonization events may be characteristic of these or other trout populations in volatile systems (e.g., Ostergaard et al. 2003). We have observed at least one founding event in the system (of Upper Marys River Basin Creek, see above), and it is reassuring that this event was captured by genetic data (with this population having an effective size ranging from 2 to 37 individuals depending on μ, and an extreme bottleneck, $M = 0.49$). Additionally, the splitting of this population into two genetic clusters by the individual-based clustering approach provided new insight into the possible characteristics of this population during or post colonization. Several scenarios are possible. First, despite our efforts to avoid sampling sibling groups, these two distinct clusters may represent two separate families that dominate in each tributary branch (see Hansen et al. 1997). It is also possible that this pattern emerged from a combination of high natal fidelity and little gene flow between the two stream branches, allowing fish populations from each branch to drift independently following re-colonization. Such a strong degree of differentiation is unlikely to have emerged so quickly, however, given that the site was re-colonized less than 10 years ago. A third possibility is that the site was founded two separate times: once habitat in one tributary branch was occupied, the second group of colonists was restricted to the second branch, and these initial founder effects have been maintained by reduced gene flow between the two branches. This mechanism has been proposed to explain differentiation among high- and low-altitude populations of brook trout (Angers et al. 1999).

Conclusions

The roles we inferred for multiple landscape attributes reinforce general hypotheses about the fundamental importance of migratory life history, connectivity, and habitat size and quality for stream fishes, but also the importance of specific processes within individual stream networks. Increased differentiation and lower genetic diversity

in most above-barrier sites suggest that barriers do have significant effects on population dynamics, but responses to barriers were seemingly dependent on habitat conditions where isolated populations reside. Though some patterns were difficult to predict, life history variation may also play an important role in driving genetic complexity in this system. Multiple indications that local populations of Lahontan cutthroat trout in the Marys River are small and temporally dynamic suggest that connectivity is a key factor in their probability of persistence, a point that is reinforced by ecological work across a broader array of stream networks. Finally, our results point to the importance of grounding genetic inferences in sound ecological hypotheses and predictions, but also demonstrate that genetic patterns can reveal processes that may be quite unexpected, even within a system that is well studied from a conventional ecological perspective.

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