

Assessing connectivity in salmonid fishes with DNA microsatellite markers

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INTRODUCTION

Connectivity is a key consideration for the management and conservation of any species, but empirical characterizations of connectivity can be extremely challenging. Assessments of connectivity require biologically realistic classifications of landscape structure (Kotliar and Wiens 1990), and an understanding of how landscape structure affects migration, dispersal, and population dynamics (Dunning *et al.* 1992; Rosenberg *et al.* 1997; Hanski 1999; Taylor *et al.* Chapter 2). Empirical assessments of connectivity may be accomplished by studying spatial patterns of habitat occupancy through time (Sjögren-Gulve and Ray 1996; Hanski 1999; Moilanen and Hanski Chapter 3), spatially correlated changes in population demography (Bjornstad *et al.* 1999; Isaak *et al.* 2003; Carroll Chapter 15), and individual movements (Millspaugh and Marzluff 2001; Tracey Chapter 14). These approaches have provided important insights for many species, but they can be difficult to implement for species with slow population dynamics or turnover (extinction and recolonization), complex life histories, and long-distance migrations. For species with these characteristics, molecular genetic markers represent a valuable tool for understanding processes that influence connectivity (Avice 1994; Frankham *et al.* 2004; Frankham Chapter 4). In this chapter, we review applications of molecular genetic markers to assess connectivity in salmonid fishes, a group of relatively well-studied species with

characteristics that complicate non-genetic approaches to understanding connectivity. Lessons learned from salmonids may apply generally to other species that have received far less attention.

SALMONID ECOLOGY AND CONNECTIVITY

Salmonid fishes are among the most well-studied vertebrates, and for many species, much is known about habitat requirements, life-history diversity, and movement patterns. Most species of salmonids exhibit migratory behaviors. It is generally believed that salmonids have evolved such behaviors to exploit the diverse array of habitats available within the landscape or “riverscape” (Northcote 1992; Fausch *et al.* 2002) (Fig. 13.1). Salmonid fishes often rear in smaller streams and headwater lakes, with some individuals remaining in these natal habitats throughout

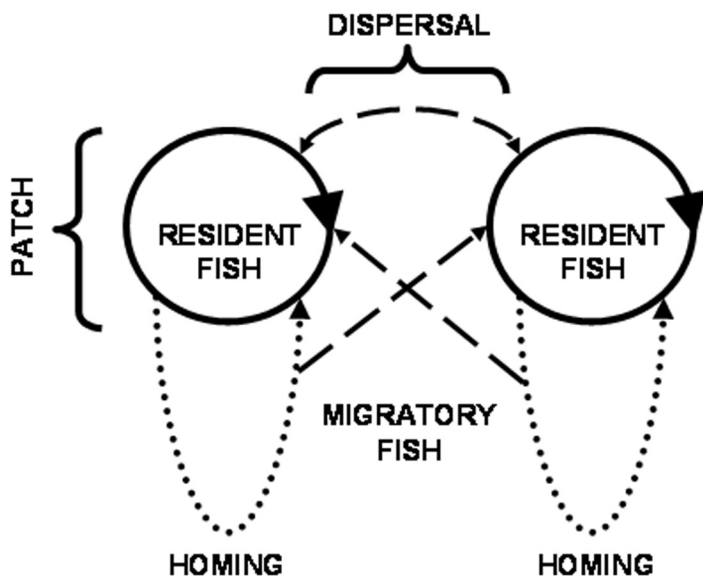


Fig. 13.1. Generalized life history of salmonid fishes, depicting spatial structuring, migratory life histories, and dispersal pathways (from Dunham *et al.* 2002). In this example, non-migratory or resident fish live within natal habitat patches with migratory individuals moving outside of patches and homing to reproduce in their natal habitats (indicated by dotted lines) or dispersing to new patches (indicated by dashed lines). Dispersal by resident fish among patches is also possible.

life. In addition to these non-migratory or “resident” individuals, some individuals may migrate beyond natal habitats to use feeding or refuge habitats, returning to their natal sites to breed (Northcote 1992). Many species or populations exhibit partial migration, with a mixture of individuals with migratory and resident life histories (Jonsson and Jonsson 1993). There are also some with largely “obligate” migratory life histories (e.g., most Pacific salmon: Groot and Margolis 1991), and others with largely resident life histories (Rieman and Dunham 2000). Spatial variation in occurrence of these life histories may have important implications for both connectivity and genetic structure among populations; because migratory fish move away from their natal habitat, they are more likely than resident fish to contribute to connectivity and genetic mixing through dispersal among populations (Hansen and Mensberg 1998; Knutsen *et al.* 2001). Understanding the ecological and evolutionary factors affecting the balance of migration and residency in salmonid fishes is a major area of active research (Hendry *et al.* 2004; Waples 2004).

As a group, salmonid fishes are habitat specialists, with specific requirements for water quality (especially cool temperatures: Elliott 1981), flow regimes (Latterell *et al.* 1998), and a variety of smaller-scale habitat features (Bjornn and Reiser 1991). Due to their specific habitat requirements, salmonids are often distributed discontinuously within or across watersheds (Dunham *et al.* 2002). The resulting landscape geometry of these habitats (e.g., habitat or patch size, degree of isolation) appears to be critical to long-term population persistence (Hanski 1999). As for many species, the general pattern observed for salmonids studied thus far is one of a greater probability of occurrence or persistence in larger and less isolated habitats. Thus, in addition to site-specific habitat features, landscape context (e.g., patch geometry) strongly influences population persistence and connectivity (Rieman and Dunham 2000; Fausch *et al.* 2002; Wiens 2002).

The general influences of landscape geometry on the persistence and occurrence of salmonids are consistent with predictions from meta-population theory (Hanski 1999), but the specific processes that contribute to these patterns are poorly understood (Dunham and Rieman 1999; Rieman and Dunham 2000; Koizumi and Maekawa 2004). Much of this uncertainty stems from a limited understanding of connectivity. Connectivity can operate in several ways to influence salmonid population persistence (Fig. 13.2). First, connectivity can support or facilitate development of migratory life histories. If a migratory life history is present within

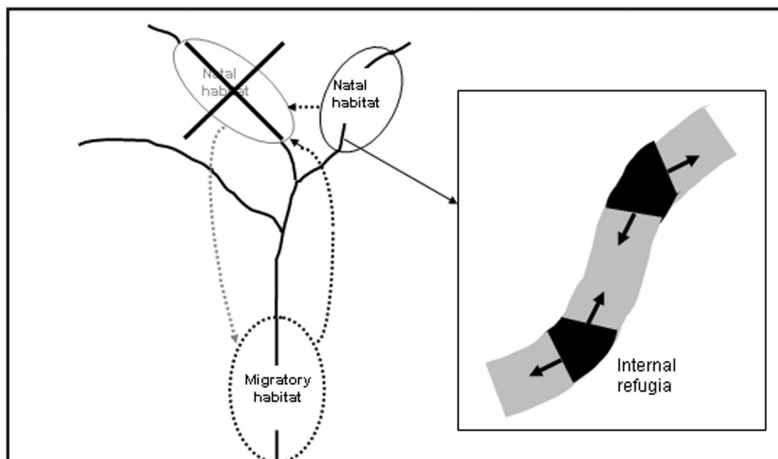


Fig. 13.2. Alternative pathways for repopulation of habitats following extirpation (Rieman *et al.* 1997; Dunham *et al.* 2003). Where individuals use both natal and migratory habitats, repopulation is possible if extirpations are not simultaneous in each habitat. On a smaller scale, repopulation may occur within streams or habitats via internal refugia. This may occur if the scale of a disturbance leading to extirpation is smaller than the size of a habitat.

a population, local extinctions within natal habitats (e.g., headwater streams) may not affect the entire population. For example, if an event causing local extinctions is short-lived, migratory fish outside of the system at the time of disturbance can repopulate natal habitats. This mechanism has been invoked to explain repopulation of habitats following local extirpations caused by wildfires, droughts, and pollution (Dunham *et al.* 1997; Rieman *et al.* 1997; Knutsen *et al.* 2001). If disturbances causing local extirpations are smaller than the natal patch size, smaller-scale or “within-patch” connectivity can be important for repopulation and persistence (Armstrong *et al.* 1994; Rieman *et al.* 1997; Dunham *et al.* 2003). Dispersal among natal patches is yet another mechanism providing gene flow and demographic support that may contribute to population persistence. This form of support is most often invoked in metapopulation theory (Hanski 1999). In summary, an understanding of connectivity in salmonid fishes requires an understanding of landscape structure including patch geometry (Dunham *et al.* 2002), migratory life histories (Northcote 1992), and dispersal processes (Quinn 1993; Rieman and Dunham 2000).

Before moving to discuss molecular markers, it is necessary to clarify how we define two key terms related to connectivity: migration and dispersal. In population genetics, migration is often used to describe gene flow – the transfer of genetic material among populations. In the salmonid literature, and with most other ecological fields, migration is defined as the movement of individuals from natal habitats across landscapes or regions to utilize complementary habitats (Dunning *et al.* 1992) in completing their life cycle. We use this definition of migration whenever possible. The term “dispersal” is also used confusingly across disciplines. In most of the ecological literature, the movement of individuals into non-natal habitats for breeding is often referred to as dispersal. In the salmonid literature this is referred to as “straying,” but to avoid confusion we use the term dispersal (Rieman and Dunham 2000). Generally, some dispersing individuals will breed successfully, whereas others may not. Genetic data generally characterize the degree of “effective” dispersal, or dispersal that contributes to gene flow (Slatkin 1987; Peacock and Ray 2001), although new techniques can characterize movement that may or may not lead to gene flow (see below).

MICROSATELLITE MARKERS AND INFERENCES ABOUT CONNECTIVITY

The literature on molecular genetics of salmonid fishes is extensive, and many studies have focused on important systematic and large-scale biogeographic questions (Ryman and Utter 1987; Nielsen and Powers 1995; Hendry and Stearns 2004). Beginning in the late 1980s, the availability of molecular markers to uncover ecological and evolutionary processes operating on smaller spatiotemporal scales has produced a generation of research attempting to quantify connectivity among local populations within and among river basins. Here, we focus on applications of a single class of these higher resolution markers, DNA microsatellites (O’Connell and Wright 1997; Goldstein and Schlotterer 1999; Sunnucks 2000). Microsatellites are specifically targeted regions of neutral DNA, which are co-dominantly inherited. Their fast mutation rate relative to other markers (Hancock 1999) confers high levels of variability and therefore high resolution for distinguishing populations and even individuals. For this reason, these markers are often used to address connectivity among populations for salmonid fishes and other species (Sunnucks 2000; Jehle and Arntzen 2002; Hendry *et al.* 2004).

High-resolution genetic markers such as microsatellites offer many opportunities for understanding connectivity, but careful analysis and interpretation of the data are required to avoid misleading conclusions (Whitlock and McCauley 1999) or confusion of biological and statistical significance (Waples 1998; Hedrick 1999, 2001). A comprehensive overview of methods for statistical analyses of genetic data is well beyond the scope of this chapter (but see Neigel 1997; Balloux and Lugon-Moulin 2001; Rousset 2001 for excellent reviews). We focus instead on selected applications of genetic techniques to assess connectivity in salmonids. We recognize two major classes of analyses for inferring connectivity from patterns of genetic variability revealed by microsatellites: methods based on predefined populations, and methods based on individuals.

Many genetic analyses used to assess connectivity require predefined populations. Populations are most often defined by the researcher as groups of individuals from relatively discrete sampling locations, which are delineated by landscape characteristics thought to restrict gene flow (e.g., rivers and mountain ranges for terrestrial species, waterfalls and dams for aquatic species, or distance for any species). Once populations are defined, population-based analyses involve summarizing information on genetic variability within populations and determining the degree of genetic differentiation among them, which is assumedly influenced by gene flow and levels of connectivity. Common examples include: Wright's F_{ST} (Wright 1951), G_{ST} (Nei 1973), R_{ST} (Slatkin 1995), rare alleles (Slatkin 1985b), and analysis of molecular variance (AMOVA: Weir and Cockerham 1984). Distance measures, such as the chord distance (D_{CE} : Cavalli-Sforza and Edwards 1967) or Nei *et al.*'s D_A distance (1983), also determine the degree of genetic similarity among populations and are commonly used to build phenograms ("trees") to visualize population relationships. While these measures alone simply characterize the degree of genetic similarity among populations, F_{ST} frequently is used to estimate rates of gene flow empirically from mathematical equations relating F_{ST} to the number of migrants per generation (see Frankham Chapter 4). However, doing so assumes that populations fit the simplistic dynamics of Wright's island model (Wright 1931, 1940). For example, populations are assumed to be in equilibrium between random genetic drift, which causes the loss of alleles over time due to the sampling of individuals each generation, and dispersal, which brings in new alleles. It is also assumed that dispersal rates among populations are symmetrical and that all populations are equal in size (Whitlock and McCauley 1999), defined by the

effective population size (N_e). In simple terms, N_e characterizes the rate at which a population loses genetic variability based on the number of individuals actually breeding each generation (see Waples 2002, 2004 for more detail). In addition to these traditional statistical approaches, more complex population-based simulation methods that make fewer assumptions about population dynamics are beginning to be applied (Shrimpton and Heath 2003; Fraser *et al.* 2004; Wilson *et al.* 2004; Neville *et al.* in press). For instance, coalescent-based methods can estimate asymmetrical migration among populations with different N_e s, thus characterizing more realistic natural scenarios (Beerli and Felsenstein 1999, 2001; Beerli 2004). Regardless of the method of estimation, population-based measures of genetic variability and differentiation may be tested for correlations with environmental variables, such as geographic distance between populations (i.e., isolation by distance based on Mantel tests) or habitat size and quality, to infer evolutionary processes (Slatkin 1993; Hutchison and Templeton 1999). A major limitation of population-based approaches is the reliance on a priori definitions of population units, which can be highly subjective (Manel *et al.* 2003).

Individual-based analyses do not rely on a priori identification of populations for inferences on gene flow and population genetic structure. These analyses identify the scale at which gene flow among individuals is restricted, which defines the breadth of “genetic neighborhoods” and leads to inferences about dispersal. A variety of spatial statistics (e.g., autocorrelation statistics, Mantel tests, kinship analyses, semivariograms) can examine the degree of structuring of genotypes and connectivity among individuals at different spatial scales (Epperson 2003; Manel *et al.* 2003; Peakall *et al.* 2003). In addition, a recently developed Bayesian clustering approach (STRUCTURE: Pritchard *et al.* 2000) defines population units by iteratively sorting individual genotypes into groups to maximize the fit of the data to theoretical expectations derived from Hardy–Weinberg and linkage equilibrium. When combined with assignment tests (see below), rates of dispersal can be estimated by identifying migrant individuals among the populations it so defined (Pritchard *et al.* 2000). Though the results may be a bit less intuitive for practical use, individual-based methods discern the existence of population structuring in a manner that is less subjective than traditional approaches.

Assignment tests are an important tool for estimating dispersal that can be based either on populations defined a priori (Paetkau *et al.* 1995; Cornuet *et al.* 1999; Banks and Eichert 2000) or by the individual-based

clustering method described above (Pritchard *et al.* 2000). Assignment tests compute the probability that an individual's multi-locus genotype belongs to each of a set of reference populations. Individuals with a higher probability of originating in a population other than that in which they were sampled are assumed to be dispersers. A major strength of assignment tests is that they circumvent the drift–migration equilibrium assumption of more traditional analyses (Davies *et al.* 1999) and can be a powerful alternative tool for estimating general dispersal patterns (Rannala and Mountain 1997; Hansen *et al.* 2001). Even when based on predefined populations, their focus on the individual as the sampling unit greatly improves their statistical power to uncover dispersal patterns (e.g., Castric and Bernatchez 2004).

The different analytical approaches outlined above (i.e., individual versus population-based approaches) also yield distinct insights about

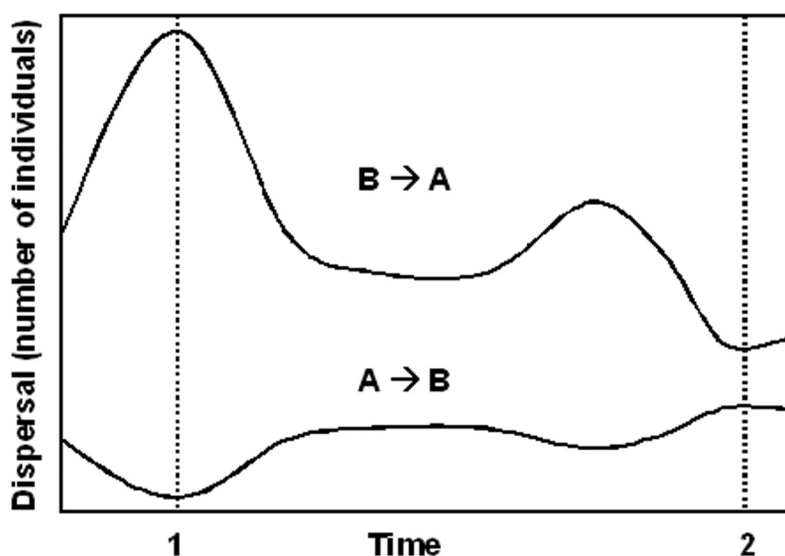


Fig. 13.3. Dispersal patterns and relationship to different measures of dispersal indicated by studies of molecular genetic markers. Arrows ($B \rightarrow A$ and $A \rightarrow B$) represent asymmetrical dispersal, which may be estimated using coalescent approaches. Dashed vertical lines (at times 1 and 2) represent two slices in time where contemporary patterns of movement might be inferred from “instantaneous” methods like the assignment test. Indirect approaches (e.g., F_{ST} , coalescent analyses) estimate long-term rates of effective dispersal (gene flow) averaged across time.

connectivity based on the temporal scale characteristic of each class of analysis (Fig. 13.3). Many methods of estimating dispersal, such as Wright's F_{ST} and coalescent-based methods, estimate long-term, multi-generational average rates of dispersal among populations "indirectly" because they require the use of mathematical equations that relate the observed degree of genetic differentiation to the migration rate (see Slatkin 1985a; Frankham Chapter 4). They also quantify only "effective dispersal," or dispersal that leads to gene flow when an individual reproduces in their new location. Because of their deeper timescale, these methods are influenced by important historical events – such as rare long-distance dispersal – not occurring at the time of study (Peacock 1997). Individual assignment tests, in contrast, quantify connectivity in terms of the number of individuals present in a given population at the time of sampling that likely originated from a different population (Waser and Strobeck 1998). When population differentiation is strong enough to give the test sufficient power (see Cornuet *et al.* 1999; Hansen *et al.* 2001), these "foreign assignments" identify potentially dispersing individuals and thus provide a "direct" measure of current movement patterns (somewhat akin to mark–recapture methods), regardless of whether individuals that moved actually contribute to gene flow (Fig. 13.3). One important caveat regarding the assignment test deserves mentioning: in cases where the test's ability to distinguish potential populations of origin is limited by low levels of differentiation, assignment tests can falsely label individuals as dispersers and more likely characterize historical levels of effective dispersal rather than current movements (Hansen *et al.* 2001; Castric and Bernatchez 2004). Still, where feasible to apply, assignment tests allow us to infer contemporary movement based on the sampling locations of genotypes without actually tracking individual movement. The combination of traditional population-based and individual-based analyses can provide both historical and contemporary perspectives on population dynamics with the same genetic data (Davies *et al.* 1999; Hansen *et al.* 2001).

ASSESSING CONNECTIVITY WITH MICROSATELLITES: CASE STUDIES

A host of recent work on salmonid fishes illustrates the utility of microsatellites and various genetic analyses for understanding the many factors that influence connectivity. Here, we focus on a selected group of species exhibiting partial migration, including charrs of the genus *Salvelinus*

and trout of the genera *Oncorhynchus* and *Salmo*. With these species, microsatellites have been used to reveal patterns of connectivity in relation to influences of river branching patterns, natural and human constructed barriers, life-history variation, historical colonization patterns, and meta-population dynamics.

Influences of stream network structure

One of the most obvious landscape influences on connectivity in aquatic ecosystems is the network structure of stream systems. Transitions in habitat conditions that occur as streams flow together within stream networks (Frissell *et al.* 1986) have been used to identify population boundaries for stream fishes (Angermeier *et al.* 2002; Dunham *et al.* 2002). Accordingly, many studies of trout and charr have found that genetic population structure can be defined in terms of drainage (e.g., Angers *et al.* 1999; Heath *et al.* 2001; Knudsen *et al.* 2002; Spruell *et al.* 2003; Narum *et al.* 2004) and stream branching patterns (e.g., Spruell *et al.* 1999; Heath *et al.* 2001; Wenburg and Bentzen 2001; Young *et al.* 2004; Neville *et al.* in press). The degree of genetic isolation among populations is also commonly related to stream distance between them, indicated by significant isolation by distance (e.g., Heath *et al.* 2001; Knutson *et al.* 2001; Taylor *et al.* 2003). However, concordance between habitat structure and genetic structure is not always observed. For instance, F_{ST} estimates in bull charr (*Salvelinus confluentus*) demonstrated significant population differentiation, but genetic relationships among populations did not correspond to their spatial proximity (Spruell *et al.* 1999). This pattern has also been observed in coastal cutthroat trout (*Oncorhynchus clarkii clarkii*; Waples *et al.* 2001). In brook charr (*Salvelinus fontinalis*), Hebert *et al.* (2000) found that the size and hydrographic characteristics (i.e., the complexity of stream branching patterns) of a region were not consistent predictors of the degree of differentiation among populations as indicated by AMOVA and chord distance phenograms. Analysis of molecular variance of brook charr in a different system found low genetic differentiation among drainages, but differentiation among populations within drainages was relatively high (Castric *et al.* 2001). This pattern was contrary to expectations based on the larger spatial scale of among-drainage comparisons. In addition, Mantel tests showed a slight correlation between geographic and genetic distances among populations in one drainage – suggesting that observed genetic patterns are shaped at least in part by dispersal – whereas populations in a nearby drainage showed no such relationship (Castric *et al.* 2001). In a different study of brook

charr in tributaries to a large lake, an individual-based clustering method (Pritchard *et al.* 2000) clustered individuals into two major groups combined across streams, contrary to expectations based on stream structure alone of four populations (Fraser *et al.* 2004). Finally, studies of brook charr and Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*) have found significant differentiation over short distances even without any obvious landscape attributes to influence dispersal (Hebert *et al.* 2000; Neville *et al.* in press).

Various factors may be invoked to explain a lack of correspondence between population genetic structure and patterns of connectivity assumed from stream networks. In several cases where genetic structure was observed within continuous habitats (e.g., within continuous reaches of streams), strong fidelity to natal sites or precise homing behavior was proposed to have created structure on a highly localized scale (Hebert *et al.* 2000; Neville *et al.* in press). A common explanation for lack of isolation by distance in both isolated and/or extremely small populations is that random genetic drift may overwhelm any genetic patterns created by dispersal related to distance or habitat structure (e.g., Spruell *et al.* 1999; Waples *et al.* 2001; Neville *et al.* in press). Alternatively, some populations may not have had sufficient time for drift–migration processes to equilibrate since the historical colonization of habitats (e.g., Castric *et al.* 2001) or due to ongoing metapopulation dynamics, discussed below.

Influences of natural and human-constructed movement barriers

Connectivity in stream networks can be interrupted partially or completely by natural barriers (e.g., waterfalls, desiccated stream segments, thermal barriers) and those constructed by humans (e.g., large dams, water diversions, weirs, and culverts). Barriers to movement have important implications for stream-living salmonids, both by reducing the effective size of populations upstream of the barrier and providing little to no opportunity for upstream dispersal by downstream populations. In this case, genetic drift due to reduced effective size (Waples 2004) should lead to detectable differences in allele frequencies between above- and below-barrier populations. In theory, both the size of the founding population and the time since isolation should be important determinants of differentiation and loss of variation via drift (Nei *et al.* 1975). Isolation of populations upstream of barriers may also lead to selection for resident life histories and loss of migratory behavior (Northcote and

Hartman 1988; Näslund 1993), but in some cases fish continue to disperse downstream over barriers (e.g., Hendricks 2002). If population sizes upstream of barriers are large enough such that genetic drift is reduced, or gene flow from the upstream population to the downstream population is large, then loss of connectivity due to movement barriers may not be evident in genetic data. Prior patterns of genetic differentiation may also be an issue. In cases where differentiation existed prior to formation of a barrier, inferences about post-barrier patterns of differentiation are confounded.

Evidence from selected studies of salmonids indicates both natural and human-caused barriers to upstream fish movement are typically associated with significant impacts on genetic diversity as assessed through a variety of analytical methods (Table 13.1). Common genetic responses to isolation by barriers include increased differentiation from other populations, loss of genetic diversity, a lack of isolation by distance, evidence of genetic bottlenecks, reduced effective population sizes, and asymmetrical patterns of gene flow. However, several studies have not revealed anticipated patterns. Populations of coastal cutthroat trout isolated upstream of impassable waterfalls in two southeast Alaska streams showed no evidence of increased differentiation or loss of diversity. Possible explanations for this pattern included insufficient power of genetic markers to detect true differences, a lack of time for differences to emerge upstream of barriers, or greater than expected dispersal over the presumed barriers (Griswold 2002). Another study (Neville *et al.* in press) employed coalescent methods, assignment tests, and tests for bottlenecks to uncover contrasting dispersal patterns and impacts on genetic diversity in Lahontan cutthroat trout above two barriers. As expected, downstream dispersal was greater than upstream dispersal over the first barrier. Fish above this barrier however, showed no evidence of genetic bottlenecks, possibly due to the large and relatively stable habitat in which these fish lived. At the second barrier, coalescent methods estimated slightly greater (but not significantly so) dispersal rates upstream than downstream, a pattern consistent with the colonization of the previously extirpated above-barrier habitat during a recent period of high flow. Assignment tests indicated no current movement into the above-barrier sample site and tests for bottlenecks demonstrated an extremely strong founder effect at this site (Neville *et al.* in press).

We are not aware of studies designed explicitly to distinguish the relative influences of natural versus human-caused barriers, which may

Table 13.1. Summary of selected studies on salmonid fishes examining the effects of barriers on patterns of genetic diversity within and divergence among populations from DNA microsatellites. Five predicted genetic responses to barriers are considered. Above-barrier populations are expected to have increased divergence and reduced genetic diversity compared to other populations. Above-barrier populations are not expected to fit a pattern of isolation by distance; divergence of populations upstream of barriers should be higher than expected based on geographic distance, due to increased drift and reduced dispersal (Hutchison and Templeton 1999). Bottleneck tests are expected frequently to identify bottlenecks upstream of barriers. Coalescent analyses are expected to reveal smaller estimated effective sizes for isolated populations and lower rates of dispersal from downstream populations

Barrier type	Species	Adherence to predicted genetic response?				References	
		Increased divergence	Decreased diversity	Impacted isolation by distance	Bottlenecks and/or reduced N_e		
Erosion dams Natural geomorphic ^a	<i>S. leucomaenis</i>	Yes	Yes	—	—	Yamamoto <i>et al.</i> (2004)	
	<i>S. confluentus</i>	Yes	Yes	Yes	—	Costello <i>et al.</i> (2003)	
	<i>O. clarkii</i>	Yes	Yes	Yes	—	Taylor <i>et al.</i> (2003)	
	<i>O. clarkii</i>	Yes	Mixed ^b	Yes	Mixed ^b	Neville Arsenault (2003)	
Culverts and natural geomorphic	<i>O. clarkii</i>	No	No	No	—	Griswold (2002)	
	<i>S. malma</i>	Yes	Yes	Yes	—	Griswold (2002)	
	<i>O. clarkii</i>	Yes	Yes	Yes	—	Wofford <i>et al.</i> , (2004)	
Water diversion Natural desiccation	<i>O. clarkii</i>	Yes	Yes	Yes	Yes	Neville Arsenault (2003)	
	<i>S. confluentus</i>	Yes	Yes	Yes	—	Bruce Rieman (pers. comm.)	

^aNatural geomorphic barriers include high waterfalls or steep, high-velocity cascades thought to restrict movement severely.

^bOne above-barrier habitat supported a large, seemingly stable population with relatively high genetic variation, while the other population was severely bottlenecked and had an extremely low N_e .

^cContrasting patterns of dispersal were found for two above-barrier populations using coalescent methods; see text.

differ based on time since isolation and influences on effective population size (e.g., Wofford *et al.* 2004; Neville *et al.* in press). However, at least one study has examined these factors in terms of population persistence (Morita and Yamamoto 2002); persistence of white-spotted charr (*Salvelinus leucomaenis*) isolated in streams above erosion barriers was a positive function of habitat size, and negatively related to time since isolation. This result implies patterns of genetic diversity should react similarly, and there is evidence to suggest this for white-spotted charr (Yamamoto *et al.* 2004). Lahontan cutthroat trout above man-made barriers displayed similar genetic impacts to those above natural barriers, suggesting that the influence of isolation on these populations was rapid (given the recent time-frame of man-made barriers) and likely compounded by poor habitat (Neville *et al.* in press).

LIFE HISTORY AND CONNECTIVITY

Dispersal in salmonid fishes can be influenced by a variety of life-history characteristics, including sex-specific dispersal and variable migratory strategies (Hendry *et al.* 2004). Fraser *et al.* (2004) used assignment tests and coalescent-based methods to demonstrate that dispersal of brook charr among streams was sex-biased, with males dispersing more among closer habitats but females being more likely to disperse among distant streams. Such a bias may reflect differences in adaptations to each environment, which dictate the fitness trade-offs of dispersal for each sex (Fraser *et al.* 2004). Assignment tests of native brown trout (*Salmo trutta*) revealed differences between resident and migratory fish in terms of their tendency to interbreed with hatchery fish: the resident component of the population had a much greater hatchery influence from interbreeding than the migratory component, likely due to increased selection against migratory hatchery fish (Hansen *et al.* 2000). In Lahontan cutthroat trout, dispersal is believed to be influenced by spatial segregation of variable life histories, with headwater sites having fish which are less migratory and lower confluence sites being more likely to contain fish with greater migration tendencies (Neville *et al.* in press). Several population-based genetic analyses (F_{ST} , coalescent analyses, assignment tests) demonstrated that fish from sites in the lower reaches of tributary streams and in downstream migratory habitats showed little or no genetic differences. In several cases fish from headwater sites were significantly differentiated from those in geographically close (< 4 km) downstream sites within the same stream even with no barriers to gene flow. These patterns suggest

behavioral differences between headwater and downstream fish in terms of their tendency to disperse (Neville *et al.* in press).

HISTORICAL FACTORS AND CONNECTIVITY

A common theme among many studies of salmonid fishes, and one that emphasizes the importance of the temporal depth afforded by molecular genetic markers, is that much of the genetic diversity observed today was shaped not by current dispersal, but by historical colonization patterns (Avice 1994). In such cases, historical demography is thought to override signals from current processes such as ongoing dispersal (Hebert *et al.* 2000; Castric *et al.* 2001). In coastal Maine, for example, AMOVA demonstrated that genetic differentiation among populations of brook charr within watersheds was much greater than differentiation among watersheds, and relationships among watersheds did not fit expectations based on geographical proximity (Castric *et al.* 2001). The authors concluded that insufficient time had elapsed since the initial colonization of this area to allow detectable differences among watersheds to accrue, but that contemporary factors modulating dispersal were important in shaping relationships among populations at smaller spatial scales, such as within watersheds. In a large-scale study of bull charr, all populations had low genetic variability, which is likely attributable to post-glacial founding events (Costello *et al.* 2003). In addition, peripheral populations, which were colonized more recently, exhibited lower levels of genetic diversity compared to those central to the species' distribution. Isolation by distance was weaker in these peripheral populations, indicating that historical colonization effects continue to mask the influence of current dispersal in these populations (Costello *et al.* 2003).

Using canonical correspondence analysis (CCA) to relate various environmental factors to genetic variability, Angers *et al.* (1999) found that altitude contributed significantly to population genetic differentiation in brook charr. Altitude is thought to have mediated historical colonization patterns, i.e., early colonizers of high-altitude areas prevented later colonizers from establishing, creating genetic differences between high- and low-altitude regions (Hamilton *et al.* 1998; Angers *et al.* 1999). Similarly, Castric *et al.* (2001) found that within-population genetic diversity declined with altitude and proposed that this may be due both to the increased isolation and magnified "founder effect" (i.e., fewer colonists reaching these habitats) characterizing high-altitude populations. An alternative explanation for these patterns could involve the influence

of contemporary physical disturbances on the likelihood of bottlenecks in headwater streams. Headwater streams are often characterized by disturbance regimes with high magnitude impacts on physical habitat (e.g., debris flows and flooding: Miller *et al.* 2003) that lead to extreme reductions in effective sizes or local extirpations (Dunham *et al.* 2003).

METAPOPULATION DYNAMICS AND CONNECTIVITY

Finally, in addition to the above large-scale changes in connectivity over historical time, it is increasingly recognized that connectivity among populations can also change due to ongoing metapopulation dynamics (Hanski 1999; Moilanen and Hanski Chapter 3). If population turnover (local extinction and recolonization) occurs in salmonids (Rieman and Dunham 2000), we would expect the genetic relationships among populations across a landscape to change on a contemporary timescale (e.g., generations, decades). Though metapopulation dynamics has been discussed extensively in the salmonid literature (Rieman and McIntyre 1995; Cooper and Mangel 1999; Dunham and Rieman 1999; Young 1999; Garant *et al.* 2000; McElhany *et al.* 2000; Rieman and Dunham 2000), relatively few studies have investigated the genetic dynamics of populations over time. Of those that have, many have found marked stability in population structure across timescales ranging from years to decades (Nielsen *et al.* 1999; Tessier and Bernatchez 1999; Hansen *et al.* 2002), suggesting that in many systems, dispersal patterns are relatively stable and extinction–colonization events may not be frequent (Hansen *et al.* 2002). However, several recent studies in systems with volatile environmental conditions, where metapopulation dynamics may be more likely, have suggested contrasting dynamics. Temporal instability in allele frequencies in steelhead (*Oncorhynchus mykiss*) and brown trout has been attributed to changes in connectivity and population structure caused by channel-blocking landslides (Heath *et al.* 2002) and extreme spatiotemporal fluctuations in stream flow and habitat conditions (Ostergaard *et al.* 2003). Extremely low effective population sizes and severe bottlenecks observed in Lahontan cutthroat trout suggest that some populations fluctuate in size and may be vulnerable to extirpation. At least one recolonization event was also well characterized by genetic data (see above, Neville *et al.* in press). These observations may not always confirm the presence of a bona fide “metapopulation” (Harrison and Taylor 1997; Hanski 1999), but they point to the importance of spatial and temporal dynamics in habitat and populations (Smedbol *et al.* 2002), and to cases

where connectivity may be especially critical for population persistence (Rieman and Dunham 2000; Dunham *et al.* 2003).

CONCLUDING THOUGHTS

Although salmonid fishes are well studied in comparison to other species, molecular markers such as DNA microsatellites continue to reveal new and important insights about connectivity. In recent years, the availability of a host of new statistical methods has greatly improved the rigor of inferences about gene flow from molecular markers, and many studies now employ multiple methods of analysis. Whether the information gained from each approach is conflicting or complementary in part depends on the nature of the assumptions behind each method, and the questions they were designed to address (e.g., historical gene flow versus contemporary movement). Often, contrasting patterns highlighted by alternative genetic approaches reveal unique insights that improve our understanding of connectivity dramatically.

Equivocal views of connectivity from analyses of molecular genetic markers can also result from incomplete consideration of the intrinsic (e.g., life-history variability) and extrinsic (e.g., stream network patterns, isolation) processes that influence genetic variability. In other words, inferences that are supported statistically with analyses of molecular markers must be also grounded in ecological reality (Hedrick 1999). In most cases, insights from molecular markers will narrow the range of possibilities for likely processes that shape connectivity, rather than pointing to a single influence (e.g., Slatkin 1993; Peacock and Ray 2001). Earlier studies of molecular genetic variation in salmonid fishes were mostly observational or exploratory in nature, and did not always provide clear implications for understanding connectivity. The challenge from this foundation is to develop more rigorous evaluations of alternative hypotheses. Within the literature on salmonid fishes, we see an encouraging trend toward studies that are designed in the context of *a priori* sets of processes hypothesized to influence connectivity and genetic variation. Insights from these attempts to integrate analyses of molecular markers with ecological processes will produce more useful assessments of connectivity.

ACKNOWLEDGEMENTS

We thank D. Isaak and J. Wenburg for helpful reviews of an earlier version of this manuscript, and L. Bernatchez, S. Jenkins, and S. Bayard de Volo

for insightful comments on another manuscript used as a foundation for this chapter.

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