

10. Fragmentation, connectivity and fish species persistence in freshwater ecosystems

Keith B. Gido, James E. Whitney, Joshua S. Perkin
Division of Biology
Kansas State University, Manhattan, KS 66506

Thomas F. Turner
Museum of Southwestern Biology
University of New Mexico, Albuquerque, NM 87131

10.1 Overview

Fragmentation poses one of the greatest threats to freshwater fish biodiversity (Nilsson et al., 2005; Liermann et al., 2012). Whereas damming of large rivers is perhaps the most obvious form of fragmentation (e.g., Nilsson et al., 2005), smaller, semi-permeable barriers such as road crossings (Perkin and Gido, 2012) or water withdrawals that dry sections of a river network (Falke et al., 2011) are also pose a conservation challenge. In glacial regions, lakes that are naturally connected through waterways are increasingly being isolated by summer evaporation and groundwater loss (Baki et al., 2012). Climate and land use changes also isolate populations in headwater reaches by increasing temperatures (Rahel et al., 1996) or drying of streams (Falke et al., 2011) in downstream reaches. Finally, barriers can form when the occurrence of a species, such as a large predator, inhibits the movement of prey through a dispersal corridor (Fraser et al., 1995). This severing of connectivity in aquatic habitats affects species persistence through multiple stressors (Olden chapter; Matthaei and Lange chapter) including limiting dispersal necessary to fulfil important life stages, exacerbating negative species interactions, and inhibiting recolonization following disturbance. Barriers to movement isolate small populations leading to reduced genetic diversity (Ketmaier and Bianco chapter) and potentially compromise long-term population persistence (e.g., Wooford et al., 2005).

In this chapter, we discuss how fragmentation disrupts dispersal and migration of freshwater fishes and the long-term consequences for population diversity and stability. We begin with a global overview of the problem followed by a review of theoretical and empirical methods for quantifying the effects of fragmentation on population viability. We conclude with a discussion of conservation challenges along with future research and management recommendations. The primary tenet of our review is that persistence of species in fragmented systems is dependent on the nature of barriers to dispersal and ecological traits of species, particularly their ability to complete critical life history stages within fragmented habitats (Figure 10.1). We often refer to the terms fragmentation, isolation and connectivity. Whereas there are instances where these might be used interchangeably, we consider fragmentation to represent habitats that have been partitioned into smaller habitats and by extension result in smaller populations. The terms connectivity and isolation refer to the ability or lack of ability, respectively, of fishes to disperse into or out of particular habitats.

10.2 Fragmentation of large rivers, streams and lakes

Fragmentation of large rivers is linked to declining biodiversity, but it is often difficult to separate the effects of fragmentation with concurrent alterations to river flow and other abiotic factors (e.g., temperature regimes, geomorphology). Barriers on large rivers range from reservoir dams 10s of meters high to water diversion structures less than 1m high. Damming of rivers is a relatively recent phenomenon, in that most large impoundments are less than 100 years old, with most dams constructed since the 1950s (World Commission on Dams, 2000; Olden chapter). Regardless, there have been massive declines in large river fishes that require long-distance dispersal (McIntyre chapter). Most notably are diadromous fishes (e.g., salmonids, eels, lampreys, striped bass), because barriers on large rivers inhibit movement between critical spawning, rearing, and adult foraging habitats. Potadromous fishes (e.g., sturgeon, suckers) that move considerable distances within freshwater are similarly affected by fragmentation. Mature adults of both diadromous and potadromous fishes typically move upstream to spawn while early life stages either passively (e.g., pelagic eggs and larvae) or actively (e.g., smolt) move downstream. Dams on large rivers are typically impassable to fishes at all life stages in the upstream direction unless specifically designed to allow passage. Downstream movement at

some or all life stages (i.e., drifting eggs and larvae, juveniles, adults) is more likely, albeit with increased mortality that is dependent on the outflow structure (Coutant and Whitney, 2000; Agostinho et al., 2007). Reservoirs also create barriers to dispersal that inhibit movement among tributaries entering a single reservoir (Falke and Gido, 2006; Franssen, 2012; Hudman and Gido, 2013), and there are numerous examples of species extirpations upstream of impoundments (e.g., Winston et al., 1991; Matthews and Marsh-Matthews, 2007). Another consequence of dams and other water management practices is that many large rivers have been disconnected from their floodplains, which provide vital habitats for many species of fish (e.g., Welcomme, 1979; Goulding, 1980; Lowe-McConnell, 1987; Kingsford 2000). The construction of levees, channelization of rivers for barge passage, and altered flow regimes are all culprits in reducing or eliminating lateral connectivity to off-channel habitats. Just as in-stream obstructions limit access to vital spawning habitats, reduced lateral connectivity with off-channel habitats has restricted the recruitment of many large river species (e.g., Quist and Spiegel, 2012; Winemiller et al. chapter).

Human engineered barriers in small streams are typically represented by road crossings and diversion structures. Natural barriers that impede dispersal such as waterfalls, beaver dams, dry stream reaches, and unsuitable meso-habitats are also common (Roberts and Angermeier, 2007). Like larger river barriers, obstructions in smaller systems can completely eliminate dispersal, but others are semi-permeable and allow passage (up- or downstream) under periods of high flow. Effects of semi-permeable barriers are much harder to predict (Norman et al., 2009; Anderson et al., 2012). Extinctions caused by abiotic (drying) or biotic (predation) factors should be higher in small streams than large rivers because the habitat volume is lower (Horwitz, 1978; Schlosser, 1982). Barriers in small streams will limit recolonization dynamics if populations are extirpated in these hydrological dynamic reaches above barriers (Winston et al., 1991; Luttrell et al., 1999). Although not as well quantified, food web interactions might also intensify in small isolated habitats if densities are high and prey refugia are lacking, particularly during periods of drought (Magoulick and Kobza, 2003; Creed, 2006).

Natural lakes, primarily those connected by seepage streams, are also threatened by fragmentation. Research in such lakes provides strong evidence for the role of fragmentation in

structuring fish communities (e.g., Tonn and Magnuson, 1982; Tonn et al., 1990; Hershey et al., 1999; Olden et al., 2001). Tonn and Magnuson (1982) demonstrated that piscivorous fish were only present in lakes with low winter dissolved oxygen concentrations if those lakes maintained connectivity to refugia lakes and, if present, piscivores limited the occurrence of prey species. Englund et al. (2009) found similar trade-offs between abiotic conditions and presence of predators for isolated lakes in Sweden. Olden et al. (2001) further showed that fishes in isolated seepage lakes (i.e., large distances from potential sources) were more susceptible to local extinction and recolonization rates were slower than in more connected lakes. These studies illustrate how lake isolation alters fish community structure through either abiotic (low dissolved oxygen) or biotic (predation) disturbances. Moreover, there appears to be a trade-off between the presence of refugia habitat for predators and the presence and diversity of prey fishes and other aquatic organisms. For example, Scheffer et al. (2006) reviewed the association between isolation and diversity of a variety of plants and animals and found that lake isolation limits fish diversity but increases diversity of other plants and animal taxa (e.g., amphibians and insects).

In summary, fish communities have typically evolved in a network of highly connected habitats, with the exception of headwater species in habitats isolated by natural waterfalls or ephemeral stream reaches. Stochastic environmental conditions associated with climate are more likely to structure fish communities rather than biotic interactions in lotic systems (Grossman et al., 1982). Fragmentation not only reduces habitat availability, but isolates populations that historically dispersed over much greater distances and may increase the chances and intensity of biotic interactions. Alternatively, species that evolved in lentic systems have adapted in more isolated and potentially under more intense biotic interactions than fishes in lotic systems (Jackson et al., 2001). Increasing isolation of lakes should have the greatest impact on small, shallow lakes that are connected to other lakes, but other anthropogenic activities such as non-native species or eutrophication are potentially of greater concern for resident lake species.

10.3 Conceptual framework for understanding fragmentation effects on fishes

The basic principles of Island Biogeography Theory (MacArthur and Wilson, 1967) elegantly describe how dividing populations into smaller, more-isolated habitats results in higher rates of

extinction and less opportunity for colonization. These principles can be applied to naturally isolated lakes or river basins, as evidenced by the strong relationship between freshwater fish diversity and habitat area (Eadie and Keast, 1984; Hugueny et al., 2011). However, diversity-area relationships result from both extinction and speciation events occurring over evolutionary time (Smith, 1981), while human-engineered fragmentation occurs over much shorter time scales. Thus, mechanisms for reductions in diversity might differ between natural and human-influenced fragmentation of habitats. Moreover, if barriers restrict but do not eliminate movement, reductions in diversity and abundance may not be evident due to a threshold response, or there will be lags in the response to fragmentation (Branco et al., 2012). A mechanistic understanding of declining fish abundance and diversity in fragmented habitats begins by recognizing that rates of decline are influenced by extrinsic (e.g., barrier type, disturbance regime) as well as intrinsic (e.g., life history traits of species) properties of a system (Figure 10.1). When these factors limit dispersal and recolonization, smaller populations become increasingly susceptible to extinction. This “extinction vortex” (Gilpin and Soulé, 1986) is exacerbated by an increase in genetic drift, a corresponding decrease in genetic variance and increase in genetic load (i.e., fewer individuals in the population are near optimal fitness), and concomitant reductions in population viability (Gaggiotti, 2003).

10.3.1 Intrinsic factors influencing fragmentation

Metapopulation theory (Levins, 1969) also provides a mechanistic framework for assessing the consequences of fragmentation. Most freshwater fish populations do not establish the theoretical balance between genetic drift and gene flow because they fluctuate in local abundance and periodically go extinct in response to environmental fluctuations or other factors. Nevertheless, numerous studies invoke a metapopulation framework to conceptualize the dynamics of freshwater fishes (e.g., Fagan, 2002; Falke and Fausch, 2010). In metapopulation theory, local extinction is balanced by recolonization and the genetic outcome depends on the genetic characteristics of the colonists (Whitlock and McCauley, 1990). For example, if colonists come as many propagules from a number of upstream localities to a downstream confluence (as in a dendritic model with mass effects) we would expect the newly colonized population to have higher genetic diversity, on average, than any one donor population (Morrissey and deKerchove,

2009). Conversely, if colonists come from a single, geographically adjacent locality, then we might expect lowered genetic diversity, on average, compared to remaining populations within the stream network. In general, the number of colonists and the number of distinct populations from which they originate determines overall genetic diversity under a metapopulation model with extinction and recolonization (Slatkin, 1985; Whitlock and McCauley, 1990). When the pool of colonists is restricted, theory predicts that fragmentation will lower genetic diversity for the entire metapopulation roughly proportional to the extent that barrier placement limits the geographic scope (and genetic diversity) of the colonist pool.

Because the most significant human-mediated fragmentation events occurred within the last century, genetic drift, gene flow, and natural selection should be more important forces than mutation as agents of change of genetic diversity on a recently fragmented riverscape. This is because mutation can take thousands of years to appreciably alter gene frequencies. If mutation can be safely ignored, genetic drift will reduce heterozygosity and genetic diversity at a rate that is inversely proportional to the population (census) size that has become completely isolated (i.e., closed to migration and gene flow) due to fragmentation. Thus, for a small population, detectable changes in allele frequencies will arise in a few generations, but in a very large population it may take hundreds of generations for reductions in diversity to be detectable.

Life-history and behavioral traits of species are useful in predicting their sensitivity to fragmentation. Species with complex life cycles requiring dispersal from rearing, feeding and spawning habitats, are highly sensitive to fragmentation (e.g., Rieman and Dunham, 2000; Morita and Yamamoto, 2002; Closs et al., chapter; McIntyre et al., chapter). A common phenomena of stream fish is that individuals within a populations tend to either be resident or migrant (e.g., Gowan et al., 1994; Skalski and Gilliam, 2000; Rodriguez, 2002). Salmonids provide examples of populations with dual movement strategies, and not surprisingly, fragmentation selects for resident forms at the expense of migratory forms (e.g., Morita and Yamamoto, 2002). By contrast, Humphries et al. (1999) proposed the 'low flow recruitment hypothesis' and noted that some species of large-river fishes are capable of sustaining populations in systems that have been disconnected from floodplain habitats. Body size might also be a predictor of species sensitivity to fragmentation. Blanchet et al. (2010) found that fish

with large and intermediate body size lost genetic diversity to drift more rapidly than small-bodied species following human-induced fragmentation. They acknowledged that body size, per se, may not be the only trait responsible for fragmentation sensitivity, but it may correlate with numerous other vital ecological traits such as movement behavior and feeding ecology. Other species with reproductive strategies requiring that eggs and larvae drift for an extended period of time also are sensitive to fragmentation (e.g., Dudley and Platania, 2007). Whereas many rheophilic (flowing water) specialists decline in fragmented rivers, fragmentation has less influence on eurytopic (generalist) species and limnophilic (standing water) specialists (Musil et al., 2012). It is not surprising that some species persist in fragmented habitats because most fragments are large relative to the home range of those species and can support large populations (e.g., Reid et al., 2008; Hudman and Gido, 2013).

10.3.2 Extrinsic factors influencing fragmentation

Extrinsic factors such as the disturbance regime of the system, fragment size, or barrier permeability influence population responses to fragmentation. Adverse effects on fish communities are more likely to occur in small fragments isolated with impermeable barriers in systems with frequent disturbance events. In river systems, species are likely to have different thresholds for the size of river fragments in which they can persist. For example, pelagic-broadcast spawning fishes in the Great Plains, USA appear to need > 100 river kilometres (rkm), but some species may require up to 300 rkm to persist (Perkin and Gido, 2011). This is in contrast to some benthic-dwelling fish where movement is restricted to < 5 km (e.g., Lamphere and Blum, 2012). Increasing the number of river obstacles, which also reduces fragment sizes and the probability of passage, was found to have a negative effect on young of year fishes in European rivers (Musil et al., 2012). However, when barriers allow some movement both up and downstream of the structure (i.e., through fishways), there can be limited influence on population genetic structure (e.g., Reid et al., 2008). Understanding the link between intrinsic and extrinsic properties of freshwater systems is clearly necessary to predict species responses to fragmentation.

In a fragmented system consisting of two populations of equal population size, the overall restorative effect of gene flow depends on barrier permeability, the prevailing direction of migration (e.g., whether symmetric or asymmetric), and species-specific life history features that influence vagility and migration rates between populations (e.g., body size, egg size, fecundity). In Figure 10.2, we present a conceptual model that is an extension of that presented in Figure 10.1 to develop predictions for the relative importance of genetic drift, gene flow, and natural selection, as a function of fragment size and barrier permeability. This model assumes that a hypothetical focal population is continuously and uniformly distributed in space, and then is fragmented by a barrier into two subpopulations. Additionally, we assume that all individuals complete their life histories in the fragmented subpopulations and are otherwise “idealized” as described in standard population genetic models (i.e., sex ratio equal, Poisson variance in reproductive success, random union of gametes, etc. – this means that population size (N) and N_e are equal). Thus, the model only explicitly considers extrinsic effects on genetic diversity. Under conditions of uniform distribution, fragment size relates directly to the effective population size (N_e) and predicts the response to genetic drift. Barrier permeability relates to the probability that migrants are exchanged between subpopulations, and that they breed in the recipient population. To facilitate discussion, we identified four quadrants with different general responses to fragment size and permeability. Quadrant one represents small and isolated fragments, where genetic drift is predicted to be the overriding force that changes allele frequencies each generation. At extremely small values, inbreeding effects on viability are highly likely. In quadrant 2, migration is the most important factor that impinges on allele frequencies in a small recipient subpopulation, and the overall effects depend on genetic characteristics of the subpopulation from which migrants are derived. This is analogous to a source-sink dynamic (e.g., Waits et al., 2008). Quadrant 3 represents isolated fragments that are large enough to preclude strong negative effects on diversity from genetic drift. In this case, relatively small selection coefficients may drive diversification across isolated fragments, depending on the nature of selective gradients. Finally, quadrant 4 represents a case where large fragmented subpopulations exchange many migrants through a barrier with high permeability. Subpopulations would approach panmixia at extreme values. Diversifying selection would be countered by high gene flow, but relatively small selection coefficients could drive purifying selection under these conditions. Metapopulation persistence also decreases when dispersal

opportunity in simulated riverscapes is reduced from bidirectional movement to only unidirectional movement (Jager et al., 2001; Fagan, 2002), which frequently occurs when dams limit dispersal to a downstream-only direction (Agostinho et al., 2007).

Our model is formulated to examine symmetric migration among subpopulations, but persistent unidirectional downstream movement through a barrier promotes asymmetric gene flow. If gene flow is strictly asymmetric, then the upstream population contributes and the downstream population receives migrants each generation. With respect to our model, this puts the upstream population in quadrants 1 or 3, with the effects of drift depending on fragment size alone, and the recipient population in quadrants 2 or 4. Under these conditions, we would expect diminished genetic diversity upstream versus downstream, all else being equal (Wares and Pringle, 2008). Furthermore, there is potential for strong interactions of extrinsic and intrinsic factors in shaping diversity across this simple landscape. For example, for fish species with drifting eggs or larvae, barriers may magnify advective downstream losses of propagules thereby lowering genetic diversity overall (Alò and Turner, 2005). Population models and empirical data suggest that depletion of reproductive productivity by unidirectional advection can have species-wide impacts on diversity (Wares and Pringle, 2008; Pringle et al., 2011). Lakes and ponds generally do not have persistent unidirectional flow, but physical forces such as water convection and wind can facilitate fish movement, and thereby affect gene flow rates and genetic diversity. Lakes could be modelled using the two-subpopulation case with symmetrical migration, unless physical transport forces facilitate asymmetrical movement.

10.4 Quantifying connectivity

A first step in understanding effects of fragmentation on freshwater fish communities is to quantify the relationship between connectivity and genetic, population, and community structure. Connectivity can generally be classified as structural or functional (Taylor et al., 1993). Structural connectivity refers to physical properties of aquatic habitats that facilitate or inhibit exchange among habitat units or patches. For example, structural connectivity includes characteristics of a network such as distance between habitats and permeability of barriers to movement. Functional connectivity represents the movement rates of materials or biota among

habitats that influence ecosystem processes and community structure. The classic example of functional connectivity in rivers comes from the River Continuum Concept (Vannote et al., 1980), where ecosystem processes in upstream habitats cascade to influence downstream habitats. Similarly, migration of fishes through a network of connected habitats might influence ecological interactions such as predator-prey relations (Woodford and McIntosh, 2010), transport of nutrients (Flecker et al., 2010) and population genetic structure and evolutionary potential (Morrissey and deKerchove, 2009). In this section, we review methods of quantifying structural and functional connectivity, as well as reviewing current literature illustrating the strong relationship between these aspects of connectivity.

10.4.1 Measuring structural connectivity

Efforts to quantify structural connectivity of freshwater habitats have expanded greatly in the past two decades (Fullerton et al., 2010). Wiens (2002) conceptualized how principles of landscape ecology could be integrated into stream networks, and emphasized the importance of connectivity in mediating landscape processes. He and many others (e.g., Grant et al., 2007; Erős et al., 2012) argued that streams and lakes can be dissected into a network of habitat patches with differing degrees of connectivity. This framework allowed important advances in understanding the constraints of fragmentation within aquatic systems, but there is still debate in how to quantify patches and connections among patches. A succinct definition of a patch is difficult to make because patches vary with life history traits and life stages of fishes (Schlosser and Angermeier, 1995; Fullerton et al., 2010) and with scale of analysis (Frissel et al., 1986; Fausch et al., 2002). In general, patches are defined as areas that are relatively homogeneous (in physical structure or community composition) and differ from their immediate surroundings. However, the degree to which a species (or life stage within a species) perceives heterogeneity is determined by their temporal movement patterns and resource use. For freshwater systems, patches in a riverscape have been defined from small microhabitats (e.g., grains of sand) up to entire watersheds (Winemiller et al., 2010; Erős et al., 2012). For our consideration of fragmented fish populations, relevant patch sizes range from discrete reaches (e.g., segments between tributaries) of streams to entire watersheds or lakes. Key characteristics of patches that are relevant to fragmentation include: size, distribution within the landscape, juxtaposition,

diversity, duration, and physical processes that affect patch formation (Pringle et al., 1988). Some patches are easily delimited, such as a series of lakes connected by streams. Boundaries between patches in streams can be less distinct (e.g., longitudinal gradients in physicochemical features) with some authors arguing that connections between patches, such as stream confluence zones can, in themselves, provide important habitats or patches (e.g., Grant et al., 2007). Others, for the ease of modelling, consider confluences as transition zones through which fishes simply move to get to other patches (e.g., Erős et al., 2011). Finally, structural connectivity can be naturally dynamic in some regions, including arid biomes where dewatering is a natural feature of landscapes and acts to structure stream fish communities by altering functional connectivity (Beatty et al., 2009; Jaeger and Olden, 2012; Rolls et al., 2012). Despite these complexities, most would agree that aquatic systems have discrete boundaries (shoreline, stream confluences, etc.) and can be partitioned into patches of discrete habitat. This approach has paved a way forward in quantifying structural connectivity and developing indices of fragmentation.

Quantifying structural connectivity in aquatic habitats can range from simple linear arrangement of habitat patches to complex networks of connected patches where patches and linkages vary in quality. Assessing barriers to movement along a linear arrangement of patches is useful for identifying small-scale movement patterns, such as pool-to-pool movement of stream fishes (Roberts and Angermeier, 2007). Structural connectivity might also consider lateral connectivity to floodplain or other off-channel habitats (Ward et al., 1999; Fullerton et al., 2010). More complex patch-based spatial graphs were recently recognized as a useful approach to quantifying structural connectivity among a series of connected patches including lakes and stream networks (Erős et al., 2012). This approach is derived from graph theory where patches are nodes connected by links, and graphs can be used to generate matrices that represent dispersal probability between any patch in the network (Figure 10.3). In streams, graphs and associated matrices can be refined to consider the hierarchical nature of stream networks including larger segments (heterogeneous nodes) downstream and unidirectional flow (heterogeneous links) among patches that might cause directional bias in dispersal (Grant et al., 2007; Grant, 2011; Erős et al., 2012). Incorporating fragmentation is done by increasing the resistance (i.e., decreasing transition probabilities) to dispersal among patches (Padgham and Webb, 2010; Perkin et al., 2013a). Other, related approaches include circuit theory that attempts to quantify

and visualize structural (and functional) connectivity among patches (McRae et al., 2008). This approach considers the analogous use of resistance (barriers), current (dispersal rate) and voltage (genetic difference among populations) to describe movement of individuals (and genes) among habitat patches. Other measures and approaches are reviewed in Storfer et al. (2010).

Patch-based spatial graphs and resulting matrices allow quantification of structural connectivity of patches. Complemented with indices of habitat availability, graph or network based analyses can be used to indicate the level of fragmentation within hierarchically structured aquatic systems and help prioritize systems based on structural connectivity. An example of a simple index of longitudinal connectivity in a stream network is provided by Cote et al. (2009). Their dendritic connectivity index (DCI) includes dividing the total stream network length into sections isolated by barriers and computing a weighted average of connectivity within and among all sections. The DCI can be adapted to represent life histories for diadromous fishes (requiring connectivity to the ocean) and potamodromous fishes (requiring connectivity throughout a watershed), and in both cases produces a value of 100 in the absence of fragmentation (i.e., complete natural connectivity) that declines toward zero based on the number, placement and permeability of barriers. A greater DCI value corresponds with isolation of a smaller fraction of the riverscape. Though a potential criticism of the DCI is that assignment of a static value of permeability is unrealistic because barrier permeability is generally temporally dynamic, approaches for measuring dynamic permeability have recently been developed (Bourne et al., 2011; Anderson et al., 2012) and empirical evidence suggests this is an informative measure of structural connectivity (e.g., Perkin and Gido, 2012). The DCI and related measures of longitudinal connectivity can be employed to evaluate cost-benefit approaches to assessing fragmentation and reconnecting habitats (O’Hanley and Tomberlin, 2005). In such approaches, the cost of removing or modifying a barrier to allow passage is weighed against a set budget as well as the potential gain in habitat, measured as the longitudinal length of stream reconnected following barrier removal (Kemp and O’Hanley, 2010; O’Hanley, 2011; O’Hanley et al., 2013). With such advances has come an increasing recognition of the importance of assigning ecologically relevant permeability to individual barriers because highly permeable barriers might not block fish movement (Pepino et al., 2012) and existing methods for measuring permeability might not represent interpretations by fishes (Mahlum et al., 2014).

10.4.2 Measuring functional connectivity

In most cases, quantifying structural connectivity is used to infer functional connectivity, but does not guarantee functional connectivity. Thus associating a break in structural connectivity with either direct observations of dispersal of individuals or indirect measures of connectivity that infer dispersal through analysis of spatial variation in genetic, population or community structure analysis. Arguably the best approach to directly measure functional connectivity among fish populations or communities is through the marking or tracking of individuals throughout a network of habitat patches (e.g., Warren and Pardew, 1998). Unfortunately, this can be labor intensive and tracking movement of small individuals is difficult because of tag-size limitations, increased handling stress, as well as sheer abundance and low survivorship, which requires large numbers to be tagged to assure adequate number of recaptured fishes. Coarse approximation of functional connectivity can be assessed with some indirect methods. For example, analyses of spatial autocorrelation (e.g. distance-decay relationships) of species abundance or community structure after statistically removing environmental effects can provide indirect evidence of connectivity, in that species demonstrating greater spatial autocorrelation are inferred to be more connected (Olden et al., 2001; Hitt and Angermeier, 2008; Shurin et al., 2009). A promising approach to evaluate functional connectivity, which is not constrained by the size of the study organism, is through the use of population genetics.

Population geneticists have developed a suite of indices, focused predominantly on genetic dissimilarity or Bayesian assignment tests, to infer functional connectivity across distinct localities in a network of stream or lake sampling localities. The traditional and most widely used metric is F_{ST} that is usually computed pairwise among populations to yield a symmetrical matrix of genetic distance. Wright's (1978) approximation is used to convert F_{ST} to $N_e m$, which is the product of the genetic effective population size (N_e) and the per-generation migration rate (m). More recently developed metrics, based on Approximate Bayesian Computation (ABC) procedures (e.g., BAYESASS [Wilson and Rannala, 2003], BAPS [Corander et al., 2004], GENECLASS2 [Piry et al., 2004]) allow indirect estimation of the fraction of genotypes assigned as migrants, m (where $m_{ij} \neq m_{ji}$), at each locality (where values of m_{ij} comprise the

elements of the migration matrix, \mathbf{M}). In this case, ABC approaches allow estimation of asymmetric migration (e.g., Fraser et al., 2007). Once a pairwise matrix is determined, landscape genetics approaches (Manel et al., 2003; Mullen et al., 2010) are used to evaluate the relationship of the F_{ST} or migration matrix (\mathbf{M}) and abiotic and biotic features of the stream network.

A main challenge to using genetic methods for estimation of functional connectivity is that classical population genetics theory (e.g., Wright, 1939) is based on an assumption that spatial and temporal patterns of genetic variation are shaped by the interplay of genetic drift, migration, and selection that are in equilibrium with respect to each other. In other words, classical theory assumes that all populations are stable in size, persistent in time, and connected by migration that occurs at a constant rate. This assumption is clearly violated in metapopulations that are subject to local extinction and recolonization. However, metapopulation theory that accounts for non-equilibrium dynamics has been well developed over the last 40 years and ABC approaches permit interpretation in an array of populations where extinction and recolonization are important. For populations that fluctuate in size, sampling the same localities across time steps also permits evaluation of temporal genetic stability in terms of variance in effective population size and migration rates (Wang and Whitlock, 2003). Parameters estimated via temporal approaches are based on allele frequency changes between time steps and give contemporary rather than historical insight into processes that shape allele frequencies (Waples, 1989). Historical drainage connectivity can override modern connectivity and affect estimates of F_{ST} , $N_e m$, and m based on genetic data (Poissant et al., 2005; Turner and Robison, 2006; Sterling et al., 2012). Given some of the problems with using genetic data alone to estimate connectivity and that genetic data can only measure connectivity following the successful reproduction of individuals, it is prudent to conduct simultaneous ecological and genetic studies (Lowe and Allendorf, 2010). Ecological and genetic approaches are highly complementary because they (can) use the same currency (e.g., abundance and effective population sizes, dispersal and effective migration rate, respectively) and together give insights into processes that drive distribution and abundance on the landscape that neither approach can offer alone.

10.4.3 Linking structural and functional connectivity

Not surprisingly there is strong evidence to support the link between structural connectivity and changes in functional connectivity. Dams and the associated impoundments have caused the decline of fishes including salmonids (Morita and Yamamoto, 2002), cyprinids (Winston et al., 1991), catostomids (Catalano et al., 2007), and many others. Fishes inhabiting stream segments isolated upstream of reservoirs have unique genetic structure (Hudman and Gido, 2013), including alterations to phenotypic expression, suggesting evolutionary (i.e., adaption to novel environments) consequences of fragmentation (Hass et al., 2010; Franssen, 2012; Sterling et al., 2012). Consequently, increased attention is being devoted toward understanding the ecological effects of attenuated structural connectivity (Fullerton et al., 2010). Based on recent works, it is clear that the size and isolation of stream fragments created by in-stream barriers have important consequences for stream fish community structure, but these responses can be linear or non-linear (Figure 10.4). For example, Bain and Wine (2010) found a linear relationship between stream fragment length and species richness in highly fragmented streams of New York (Figure 10.4A), and a threshold-like response in brook trout extirpation among small fragments. Similarly, Perkin and Gido (2011) documented threshold responses in extirpation of multiple cyprinids among smaller stream fragments distributed throughout the Great Plains (Figure 10.4B). In terms of fragment isolation, Pepino et al. (2012) found a linear decline in fish dispersal as road-stream culvert permeability declined (Figure 10.4C), whereas Neary (2012) reviewed the use of fish passage models such as exhaustion-threshold curves to evaluate road-stream permeability (Figure 10.4D).

Results such as those presented in Figure 10.4 suggest stream fish communities respond to the combined effects of the number, placement, and permeability of barriers distributed throughout a watershed. In general, we expect genetic structure to be the most responsive to barrier permeability, whereas population and community dynamics likely respond to both permeability and fragmentation (Figure 10.5). Thus community or population responses to fragmentation are generally strongest among watersheds characterized by many barriers with low permeability, in turn creating a large number of small stream fragments (Figure 10.5A). Under this scenario, any level of fragmentation by barriers with decreased permeability (relative to a natural stream channel) will elicit a response of the fish community, but the response will depend on the

magnitude of alteration. However, given the hierarchical organization of patches in stream networks, emergent properties such as threshold responses to fragment size or barrier permeability are common in fragmented riverscapes (discussed earlier; Grant et al., 2007; Perkin et al., 2013a). Such threshold patterns associated with fragment size (Figure 10.5B) and barrier permeability (Figure 10.5C) can result in responses of greater magnitude than expected based on the number of barriers alone. Examples of thresholds for barrier permeability might include the migration of a small number of individuals necessary to rescue genetic diversity; whereas, thresholds for fragment size might occur for species with pelagic eggs (e.g., Leslie et al., 1982) that require minimum length of stream for successful reproduction. In reality, the synergistic effects of threshold responses to both fragment size and barrier permeability contribute to community and population responses that are not predicted by the presence or number of barriers alone (Figure 10.5D). The latter scenario suggests many populations or communities will persist under low to moderate levels of fragmentation, but the nature of the response will depend on how traits of species of interest interact with the number, placement, and permeability of barriers (Branco et al., 2012; Pepino et al., 2012; Perkin et al., 2013a).

10.5 Modelling responses to fragmentation

More detailed and realistic modelling exercises are helpful in understanding metapopulation persistence, genetic structure, and gene flow, and the interactions of intrinsic and extrinsic forces that shape organism and community responses to fragmentation. Using metapopulation models, Fagan (2002) revealed that fragmentation has fundamentally different consequences for bifurcating dendritic networks compared to systems with linear geometries (e.g., only considering the mainstem of a large river), in that multiple fragmentation events in a dendritic network produced a greater number of small fragments. This result has drastic consequences for the persistence of fish metapopulations in dendritic river systems, because extinction risk increases as fragment (and presumably population) size decreases (Lande, 1993). The influence of fragment size on population persistence was further illustrated by the theoretical studies of Jager et al. (2001) and Morita and Yokota (2002) that investigated the influence of fragmentation and fragment size on white sturgeon (*Acipenser transmontanus*) and white-spotted charr (*Salvelinus leucomaenis*), respectively. These studies showed that decreasing fragment size

decreased the probability of metapopulation persistence. In addition, metapopulation persistence also decreases when dispersal opportunity in simulated riverscapes is reduced from bidirectional movement to only unidirectional movement (Jager et al., 2001; Fagan, 2002), which frequently occurs when dams limit dispersal to a downstream-only direction. Allowing bidirectional movement via the construction of fish passages, however, does not automatically increase metapopulation persistence. Jager (2006a) found that upstream movement around barriers for a white sturgeon metapopulation in a simulated riverscape was only beneficial if subsequent downstream movement was restricted for larger fish (through screening) or allowed safe passage. Similarly, the longitudinal positioning of long and short fragments interspersed among multiple barriers may also impact the influence passage construction has on the persistence of simulated metapopulations, with passageways generally being most beneficial when there is a long segment of available habitat upstream of many barriers (Jager, 2006a,b). Finally, Jager et al. (2001) found that as the number of impoundments in a simulated river network increased, genetic diversity within theoretical white sturgeon populations eroded, simulating the genetic impact impoundments may have on real-world populations. Modelling exercises such as these provide hypotheses on how fish populations and communities will respond to different levels of fragmentation.

10.6 Conservation challenges and opportunities

Different barrier types, fragment lengths, and traits of species create unique challenges for conservation. Impoundments are perhaps the greatest hurdle in that they are expensive to remove, have a large value to society (e.g., Sethi et al., 2004; Olden chapter), and might prevent the spread of non-native species (Jackson and Pringle, 2010). Nevertheless, efforts such as the Elwha Dam removal (Wunderlich et al., 1994), demonstrate that this is a feasible management option, particularly for dams with limited function or in need of repair (e.g., Gregory et al., 2002; Stanley and Doyle, 2003). Moreover, restoration efforts that reconnect isolated habitats have generally been successful at improving fish populations (Roni et al., 2012), and a number of studies show rapid colonization of former impoundment sites and upstream areas by migratory and resident fishes following dam removal (e.g., Hart et al., 2002; Catalano et al., 2007). Although dam removal is necessary for river restoration, logistical and societal challenges make

it essential to prioritize the removal of dams (Hitt et al., 2012). Fortunately, there are an increasing number of studies and options for prioritizing dam removal that conservation organizations can draw from (Fullerton et al., 2010). If dam removal is not practical, increasing connectivity through the construction of fish passage devices or mechanical movement of fishes through barriers might be alternative management solutions (e.g., Walters et al., 2014).

The removal or modification of smaller barriers such as road crossing culverts and low-head dams is much more feasible than for large dams (O’Hanley, 2011). Removing low-head dams has been successful at increasing connectivity of habitats used by anadromous (Burdick and Hightower, 2006) and potadromous (Hitt et al., 2012) species. The effects of poorly designed road crossings on freshwater fish assemblages are well documented (Gibson et al., 2005) and most prevalent in smaller, headwater streams characterized by greater slopes (Poplar-Jeffers et al., 2008). Bridges across larger streams generally span the entire channel and are less likely to cause fragmentation (see Perkin and Gido, 2012 supplemental material). The potentially large number of roads crossing small streams creates a challenge in the sheer number of barriers in need of renovation (Forman and Alexander, 1998). Similar to dam removal, a prioritization scheme will be necessary to identify those barriers that cause the greatest extent of fragmentation and therefore require renovation. To this end, metrics such as the DCI, as described above, are potential tools for prioritizations (Cote et al., 2009; Fullerton et al., 2010).

An emerging problem with efforts to mitigate fragmentation is the trade-off that increasing connectivity to reduce extinction risk of native species facilitates invasion by non-native species (Fausch et al., 2009; Jackson and Pringle, 2010; Olden chapter). Conservation decisions will have to balance the probabilities that non-natives will disperse into a system if barriers are removed (Clarkson et al., 2012) and the predicted impact of those species (Rahel, 2013). Understanding the latter is particularly complex, as many species invasions are benign, but some are devastating (Vander Zanden et al., chapter). The most comprehensive examples of purposeful fragmentation involve management and conservation of native and endemic inland trout species. For these species, an important threat to persistence is competition and/or hybridization with non-natives, usually introduced rainbow, brown, or brook trout (Fausch et al., 2009). To mitigate this threat, an impassable barrier to upstream movement is typically constructed, followed by

removal of non-native species (Novinger and Rahel, 2003; Fausch et al., 2009). Once non-natives are removed, wild or hatchery-reared natives are repatriated to these fragmented, renovated reaches. The management trade-off is that barrier construction excludes non-natives but necessarily isolates the native population from gene flow, and thereby increases vulnerability to extinction through stochastic demographic events, localized catastrophic disturbance, and inbreeding depression (Roberts et al., 2013). This trade-off extends to co-occurring species, and may disrupt production and linkages of energy and nutrient flow, which further disrupts local fish abundance.

10.7 Future direction and challenges

Fragmentation alone has negative consequences for freshwater fishes, but isolating populations and communities is intensified by other human-mediated disturbances such as increased intensity of drought via climate change, poor water quality, and invasive species (Hoagstrom et al., 2011; Cooke et al., 2012). Both conceptual and mathematical frameworks are available to assess the consequences of fragmentation (e.g., Fausch et al., 2009; Padgham and Webb, 2010). Future efforts to build on these conceptual frameworks should incorporate technological advances as well as inclusion of other potentially important intrinsic and extrinsic factors influencing fish communities. For example, technological advances in mapping aquatic habitats and quantifying barrier permeability will help quantify structural connectivity in fragmented lakes, rivers and streams (Chin et al., 2008; Park et al., 2008). However, it also will be important to test measures of structural connectivity with empirical measurements of dispersal and ultimately population persistence. Such measurements will be facilitated through advances in genetic analyses and advanced tracking methods (e.g., Fraser et al., 2004; Winemiller et al., 2010; Gido and Jackson, 2010).

A potentially important, but understudied source of fragmentation is due to biotic factors that inhibit or promote movement of fishes through natural or artificial corridors. Gilliam and Fraser (2001) noted the pattern of reduced abundance of small fishes in mainstem habitats compared to small tributaries might be caused by predator avoidance in the mainstem. Although predators could fragment habitat for these smaller fishes, dispersal was dependent on intrinsic (body size)

and extrinsic (water level) factors and suggested predation as an agent of fragmentation was complex. More research is needed to identify the role of individual behaviour and biotic interactions in fragmented systems. For example, the construction of instream barriers that alter habitat upstream and downstream might attract predators that inhibit passage, even if the structure itself is passable. The potential of fish-passageways to become “ecological traps” by luring populations to unsuitable habitats needs to be evaluated so that facilities can be properly constructed (Pelicice and Agostinho, 2008, Olden chapter). Although this is of particular concern for impounded waters that create lentic habitats that provide habitat for large predatory fishes (e.g., Gillette et al., 2005), concentrations of fishes below dams can also attract predators, such as sea lions in costal drainages (Keefer et al., 2012). These indirect or unexpected consequences of fragmentation certainly need to be considered when prescribing management recommendations.

Adverse effects of climate change on fish communities (see Heino chapter) also are exacerbated by fragmentation because increases in disturbance frequency and altered thermal regimes will shrink suitable habitat of fishes (Rahel et al., 1996), and barriers will impede movement or escape from potentially inhospitable conditions. Moreover, in arid and semi-arid regions, increased frequency of drying will force fishes downstream into impoundments where they have to contend with lentic habitats and species. Identifying the constraints that climate change will have on fragmented habitats is a necessary area of future research.

Finally, the evolutionary consequences of living in fragmented habitats are not well understood because a number of factors (intrinsic and extrinsic) and forces (e.g., genetic drift, selection and gene flow) are acting simultaneously to shape organism response to altered habitats and reduced connectivity. Historically, the rate at which natural fragmentation reduced connectivity of populations supported increased diversification in evolutionary time (Dias et al., 2012). Recent fragmentation, however, has resulted in rapid loss of connectivity, causing decreased population viability in ecological time and ultimately decreased diversity in evolutionary time. Reductions in genetic diversity and dispersal constraints will create selective environments that are quite different than in connected habitats. Smaller, less mobile individuals might have a selective advantage over larger more mobile individuals (Bain and Wine, 2010). Trophic interactions might change as individuals dependent on movement are unable to access foraging habitats (e.g.,

oceans, large rivers) in a fragmented system. Similarly, reproductive ecology and migration patterns of fishes are likely to change. Movement of migrant individuals will be highly constrained and if there is a trade-off in reproductive success, those individuals might be selected against in fragmented habitats. Comparative landscape genetic studies with multiple species analysed simultaneously are rare for freshwater fishes, but the promise of this approach is well appreciated (Wares, 2002; Urban and Skelly, 2006). One outcome is that intrinsic differences in life history and ecology have important consequences for the distribution of genetic diversity in space and time (e.g., Waples, 1987; Avise, 1992; Tibbets et al., 1996; Turner and Trexler, 1998; Whiteley et al., 2004; Burridge et al., 2008) and that life history can interact with landscape features to determine overall population structure within species (Neville et al., 2006) and differences among species (e.g., Manier and Arnold, 2006; Turner et al., 2006). Current research across species is beginning to identify traits that predict responses to fragmentation, but clearly more research is needed to refine these predictions.

In conclusion, as the human population increases, the need to traverse aquatic habitats with structures that potentially constrain movement of fishes will increase. Major strides have been made to research and effectively design structures to allow dispersal of fishes (e.g., Stuart and Mallen-Cooper, 1999; Pelicice and Agostinho, 2008). Given that the frequency of major dam construction has declined in many countries, and that smaller barriers can be constructed to allow fish passage, current conservation goals should begin a trend of restoring connectivity of aquatic habitats on global, national and watershed scales. Additional advances have been put forward in the literature to prioritize barriers for removal or renovation. These tools consider both the location of barriers in a network of habitats, the permeability of existing barriers and the intrinsic characteristics of the fish populations impacted by those barriers. These cumulative efforts can inform natural resource agencies, but there are still large gaps in understanding the context in which barriers influence dynamics of fish populations and communities. As with many conservation problems, empirical data describing how barriers will influence natural populations lags well behind theoretical expectations. Thus, researchers should embrace emerging technological advances in conservation genetics and our ability to track fish movement to gather critical data on habitat needs and responses of fishes to fragmentation. Using demographic and genetic data in concert (e.g., genetic mark-recapture approaches; relatedness and behavioral

ecology) offers great potential for synthesis and prediction of ecological and evolutionary outcomes of fragmentation on fish populations and communities, and may help overcome shortcomings of each method when used alone (e.g., Kanno et al. 2014).

10.8 Acknowledgements

Financial support for KBG and TFT was provided by the Bureau of Reclamation Water Smart Program. JEW was supported by the Department of Education GAANN scholarship and JSP was supported by the Kansas State University Division of Biology. Thoughtful comments on an earlier draft of this chapter were provided by the Aquatic Journal Club at Kansas State University. We thank Nick Bond and an anonymous reviewer for thoughtful comments that greatly improved the presentation of these materials.

10.9 Suggested Readings

- Bain, M.B. & Wine, M.L. (2010). Testing predictions of stream landscape theory for fish assemblages in highly fragmented watersheds. *Folia Zoologica* **59**, 231-239.
- Erős, T., Olden, J.D., Schick, R.S., Schmera, D. & Fortin, M.J. (2012). Characterizing connectivity relationships in freshwaters using patch-based graphs. *Landscape Ecology* **27**, 303-317.
- Fagan, W.F. (2002). Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology* **83**, 3243-3249.
- Grant, E.H.C., Lowe, W.H. & Fagan, W.F. (2007). Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters* **10**, 165-175.
- Lowe, W. H. & F. W. Allendorf. 2010. What can genetics tell us about population connectivity? *Molecular Ecology* **19**, 3038–3051.
- Nilsson, C., Reidy, C.A., Dynesius, M. & Revenga, C. (2005). Fragmentation and flow regulation of the World's large river systems. *Science* **308**, 405-408.
- O’Hanley, J. R., Wright, J., Deibel, M., Fedora, M. A. & Soucy, C. L. (2013). Restoring stream habitat connectivity: a proposed method for prioritizing the removal of resident fish passage barriers. *Journal of Environmental Management* **125**, 19-27.

- Perkin, J.S. & Gido, K.B. (2012). Fragmentation alters stream fish community structure in dendritic ecological networks. *Ecological Applications* **22**, 2176-2187.
- Rahel, F.J. (2013). Intentional fragmentation as a management strategy in aquatic systems. *BioScience* **63**, 362-372.
- Slatkin, M. (1985). Gene flow in natural populations. *Annual Review of Ecology and Systematics* **16**, 393-430.

10.10 Topic questions

- What intrinsic characteristics (traits) of species make them vulnerable to fragmentation?
- What extrinsic characteristics of waterbodies (streams or lakes) influence how fragmentation affects fish communities?
- How do effect of natural barriers on fish communities compare to human-engineered barriers?
- How do the effect of fragmentation on fish populations change when considered at ecological and evolutionary time scales?
- Are demographic or genetic responses more important predictors of long-term population persistence following fragmentation?
- Why does local species diversity of freshwater fish communities generally decline following fragmentation? Are there scenarios where fragmentation can increase species diversity?
- What factors might limit functional connectivity when structural connectivity is intact?
- What potentially confounding effects, such as habitat degradation, are typically associated with fragmentation?

10.11 Literature

- Aló, D. & Turner, T.F. (2005). Effects of habitat fragmentation on effective population size in the endangered Rio Grande silvery minnow. *Conservation Biology* **19**, 1138-1148.
- Anderson, G.B., Freeman, M.C., Freeman, B.J., Straight, C.A., Hagler, M.M. & Peterson, J.T. (2012). Dealing with uncertainty when assessing fish passage through culvert road crossings. *Environmental Management* **50**, 462-477.
- Agostinho, A.A., Marques, E.E., Agostinho, C.S., Almeida, D.A., Oliveira, R.J. & Melo, J.R.B. (2007). Fish ladder of Lajeado Dam: migrations on one-way routes? *Neotropical Ichthyology* **5**, 121-130.
- Avise, J.C. (1992). Molecular population structure and the biogeographic history of a regional fauna: a case history with lessons for conservation biology. *Oikos* **63**, 62-76.
- Bain, M.B. & Wine, M.L. (2010). Testing predictions of stream landscape theory for fish assemblages in highly fragmented watersheds. *Folia Zoologica* **59**, 231-239.
- Baki, A.B., Zhu, D.Z., Courtice, G., & Rajaratnam, N. (2012). Exploring the potential fish pathways in an experimental rocky ramp type nature-like fish pass. In *9th International Symposium on Ecohydraulics 2012 Proceedings*, Mader H. & Kraml J., editors.
- Beatty, R.J., Rahel, F.J. & Hubert, W.A. (2009). Complex influences of low-head dams and artificial wetlands on fishes in a Colorado River tributary system. *Fisheries Management and Ecology* **16**:457-467.
- Blanchet, S., Rey, O., Etienne, R., Lek, S. & Loot G. (2010). Species-specific responses to landscape fragmentation: implications for management strategies. *Evolutionary Applications* **3**, 291-304.
- Bourne, C.M., Kehler, D.G., Wiersma, Y.F. & Cote, D. (2011). Barriers to fish passage and barriers to fish passage assessments: the impact of assessment methods and assumptions on barrier identification and quantification of watershed connectivity. *Aquatic Ecology* **45**, 389-403.
- Branco, P., Segurado, P., Santos, J.M., Pinheiro, P., & Ferreira, M.T. (2012). Does longitudinal connectivity loss affect the distribution of freshwater fish? *Ecological Engineering* **48**, 70-78.

- Burdick, S.M. & Hightower, J.E. (2006). Distribution of spawning activity by anadromous fishes in an Atlantic slope drainage after removal of a low-head dam. *Transactions of the American Fisheries Society* **135**, 1290-1300.
- Burridge, C.P., Craw, D., Fletcher, D. & Waters, J.M. (2008). Geological dates and molecular rates: fish DNA sheds light on time dependency. *Molecular Biology and Evolution* **25**, 624-633.
- Catalano, M.J., Bozek, M.A. & Pellet, T.D. (2007). Effects of dam removal on fish assemblage structure and spatial distributions in the Baraboo River, Wisconsin. *North American Journal of Fisheries Management* **27**, 519-530.
- Chin, A., Laurencio, L.R. & Martinez, A.E. (2008). The hydrologic importance of small- and medium-sized dams: examples from Texas. *The Professional Geographer* **60**, 238-251.
- Clarkson, R. W., Marsh, P. C. & Dowling, T. E. (2012). Population prioritization for conservation of imperilled warmwater fishes in an arid-region drainage. *Aquatic Conservation of Marine and Freshwater Ecosystems* **22**, 498–510.
- Cooke, S. J., Paukert, C. P. & Hogan, Z. (2012). Endangered river fish: factors hindering conservation and restoration. *Endangered Species Research* **17**, 179-191.
- Corander, J., Waldmann, P., Marttinen, P. & Sillanpää, M.J. (2004). BAPS 2: enhanced possibilities for the analysis of genetic population structure. *Bioinformatics* **20**, 2363-2369.
- Cote, D., Kehler, D.G., Bourne, C. & Wiersma, Y.F. (2009). A new measure of longitudinal connectivity for stream networks. *Landscape Ecology* **24**, 101-113.
- Coutant, C.C. & Whitney, R.R. (2000). Fish behavior in relation to passage through hydropower turbines: a review. *Transactions of the American Fisheries Society* **129**, 351-380.
- Creed, R.P. (2006). Predator transitions in stream communities: a model and evidence from field studies. *Journal of the North American Benthological Society* **25**, 533-544.
- Dias, M.S., Cornu, J.F., Oberdorff, T., Lasso, C.A. & Tedesco, P.A. (2012). Natural fragmentation in river networks as a driver of speciation for freshwater fishes. *Ecography* **35**, 1-7.
- Dudley, R.K. & Platania, S.P. (2007). Flow regulation and fragmentation imperil pelagic-spawning riverine fishes. *Ecological Applications* **17**, 2074-2086.

- Eadie, J.M. & Keast, A. (1984). Resource heterogeneity and fish species diversity in lakes. *Canadian Journal of Zoology* **62**, 1689-1695.
- Englund, G., Johansson, F., Olofsson, P., Salonsaari, J. & Öhman, J. (2009). Predation leads to assembly rules in fragmented fish communities. *Ecology Letters* **12**, 663-671.
- Erős, T., Schmera, D. & Schick, R.S. 2011. Network thinking in riverscape conservation: a graph-based approach. *Biological Conservation* **144**, 184-192.
- Erős, T., Olden, J.D., Schick, R.S., Schmera, D. & Fortin, M.J. (2012). Characterizing connectivity relationships in freshwaters using patch-based graphs. *Landscape Ecology* **27**, 303-317.
- Fagan, W.F. (2002). Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology* **83**, 3243-3249.
- Falke, J.A. & Gido, K.B. (2006). Effects of reservoir connectivity on stream fish assemblages in the Great Plains. *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 480-493.
- Falke, J.A. & Fausch, K.D. (2010). From metapopulations to metacommunities: linking theory with empirical observations of the spatial population dynamics of stream fishes. In *Community ecology of stream fishes: concepts, approaches, and techniques*. K.B. Gido & Jackson, D.A., editors. American Fisheries Society Symposium 73, Bethesda, Maryland. pp 207-234
- Falke, J.A., Fausch, K.D., Magelky, R., Aldred A., Durnford, D.S., Riley, L.K. & Oad, R. (2011). The role of groundwater pumping and drought in shaping ecological futures for stream fishes in a dryland river basin of the western Great Plains, USA. *Ecohydrology* **4**, 682-697.
- Fausch, K.D., Torgersen, C.E., Baxter, C.V. & Li, H.W. (2002). Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience* **52**, 483-498.
- Fausch, K.D., Rieman, B.E., Dunham, J.B., Young, M.K. & Peterson, D.P. (2009). Invasion versus isolation: Tradeoffs in managing native salmonids with barriers to upstream movement. *Conservation Biology* **23**, 859-870.
- Flecker, A.S., McIntyre, P.B., Moore, J.W., Anderson, J.T., Taylor, B.W. & Hall, R.O. Jr., (2010). Migratory fishes as material and process subsidies in riverine ecosystems. In *Community ecology of stream fishes: concepts, approaches, and techniques*. Gido, K.B.

- & Jackson, D.A., editors. American Fisheries Society Symposium 73, Bethesda, Maryland. pp. 559-592
- Forman, R.T. & Alexander, L.E. (1998). Roads and their major ecological effects. *Annual Reviews in Ecology and Systematics* **29**, 207-257.
- Franssen, N. R. (2012). Genetic structure of a native cyprinid in a reservoir-altered stream network. *Freshwater Biology* **57**, 155–165.
- Fraser, D.F., Gilliam, J.F., & Yip-Hoi, T. (1995). Predation as an agent of population fragmentation in a tropical watershed. *Ecology* **76**, 1461-1472.
- Fraser, D.J., Lippe, C. & Bernatchez, L. (2004). Consequences of unequal population size, asymmetric gene flow and sex-biased dispersal on population structure in brook charr (*Salvelinus fontinalis*). *Molecular Ecology* **13**, 67-80.
- Fraser, D.J., Hansen, M.M., Ostergaard, S., Tessier, N., Legault, M. & Bernatchez, L. (2007). Comparative estimation of effective population sizes and temporal gene flow in two contrasting population systems. *Molecular Ecology* **16**, 3866-3889.
- Fullerton, A.H., Burnett, K.M., Steel, E.A., Flitcroft, R.L., Pess, G.R., Feist, B.E., Torgersen, C.E., Miller, D.J. & Sanderson, B.L. (2010). Hydrological connectivity for riverine fish: measurement challenges and research opportunities. *Freshwater Biology* **55**, 2215-2237.
- Gaggiotti, O.E. (2003). Genetic threats to population persistence. *Annales Zoologici Fennici* **40**, 155-168.
- Gibson, R.J., Haedrich, R.L. & Wernerheim, C.M. (2005). Loss of fish habitat as a consequence of inappropriately constructed stream crossings. *Fisheries* **30**, 10-17.
- Gido, K.B. & Brown, J.H. (1999). Invasion of North American drainages by alien fish species. *Freshwater Biology* **42**, 387-399.
- Gido, K.B. & Jackson, D.A., editors. (2010). *Community ecology of stream fishes: concepts, approaches, and techniques*. American Fisheries Society, Symposium 73: Bethesda, Maryland.
- Gillette, D.P., Tiemann, J.S., Edds, D.R. & Wildhaber, M.L. (2005). Spatiotemporal patterns of fish assemblage structure in a river impounded by low-head dams. *Copeia* **2005**, 539-549.

- Gilliam, J.F. & Fraser, D.F. (2001). Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. *Ecology* **82**, 258-273.
- Gilpin, M.E. & Soulé, M.E. (1986). Minimum viable populations: processes of species extinction. In *Conservation Biology: The Science of Scarcity and Diversity*, Soulé, M.E., editor. Sinauer, Sunderland, Massachusetts. pp 19-34.
- Goulding, M. (1980). *The fishes and the forest. Explorations in Amazonian natural history*. University of California Press. Berkeley, California.
- Gowan, C., Young, M.K., Fausch, K.D. & Riley, S.C. (1994). Restricted movement in stream salmonids: a paradigm lost? *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 2626-2637.
- Grant, E.H.C. (2011). Structural complexity, movement bias, and metapopulation extinction risk in dendritic ecological networks. *Journal of the North American Benthological Society* **30**, 252-258.
- Grant, E.H.C., Lowe, W.H. & Fagan, W.F. (2007). Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters* **10**, 165-175.
- Gregory, S., Li, H. & Li, J. (2002). The conceptual basis for ecological responses to dam removal. *BioScience* **52**, 713-723.
- Grossman, G.D., Moyle, P.B. & Whitaker, J.O. (1982). Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage – a test of community theory. *American Naturalist* **120**, 423–454.
- Hart, D.D., Johnson, T.E., Bushhaw-Newton, K.L., Horwitz, R.J. Bednarek, A.T., Charles, D.F., Kreeger, D.A. & Velinsky, D.J. (2002). Dam removal: challenges and opportunities for ecological research and river restoration. *BioScience* **52**, 669-681.
- Haas, T.C., Blum, M.J. & Heins, D.C. (2010). Morphological responses of stream fish to water impoundment. *Ecology Letters* **6**, 803-806.
- Hershey, A.E., Gettel, G.M., McDonald, M.E., Miller, M.C., Mooers, H., O'Brien, W.J., Pastor, J., Richards, C. & Schuldt, J.A. (1999). A geomorphic-trophic model for landscape control of Arctic lake food webs. *BioScience* **49**, 887-897.

- Hitt, N.P. & Angermeier, P.L. (2008). Evidence for fish dispersal from spatial analysis of stream network topology. *Journal of the North American Benthological Society* **27**, 304-320.
- Hitt, N.P., Eyler S. & Wofford, J.E.B. (2012). Dam removal increases American eel abundance in distant headwater streams. *Transactions of the American Fisheries Society* **141**, 1171–1179.
- Hoagstrom, C.W., Brooks, J.E. & Davenport, S.R. (2011). A large-scale conservation perspective considering endemic fishes of the North American plains. *Biological Conservation* **144**, 21–34.
- Horwitz, R.J. (1978). Temporal variability patterns and the distributional patterns of stream fishes. *Ecological Monographs* **48**, 307-321.
- Hudman, S.P. & Gido, K.B. (2013). Multi-scale effects of impoundments on genetic structure of creek chub (*Semotilus atromaculatus*) in the Kansas River basin. *Freshwater Biology* **58**, 441-453.
- Hugueny, B., Movellan, A. & Belliard, J. (2011). Habitat fragmentation and extinction rates within freshwater fish communities: a faunal relaxation approach. *Global Ecology and Biogeography* **20**, 449-463.
- Humphries, P., King, A.J. & Koehn, J.D. (1999). Fish, flows and flood plains: links between freshwater fishes and their environment in the Murray-Darling River system, Australia. *Environmental Biology of Fishes* **56**, 129–151.
- Jackson, C.R., & Pringle, C.M. (2010). Ecological benefits of reduced hydrologic connectivity in intensively developed landscapes. *BioScience* **60**, 37–46.
- Jackson, D.A., Peres-Neto, P.R. & Olden, J.D. (2001). What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 157-170.
- Jaeger, K.L. & Olden, J.D. (2012). Electrical resistance sensor arrays as a means to quantify longitudinal connectivity of rivers. *River Research and Applications* **28**, 1843-1852.
- Jager, H.I. (2006a). Chutes and ladders and other games we play with rivers. I. Simulated effects of upstream passage on white sturgeon. *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 165-175.

- Jager, H.I. (2006b). Chutes and ladders and other games we play with rivers. II. Simulated effects of translocation on sturgeon. *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 176-185.
- Jager, H.I., Chandler, J.A., Lepla, K.B. & Winkle, W.V. (2001). A theoretical study of river fragmentation by dams and its effect on white sturgeon populations. *Environmental Biology of Fishes* **60**, 347-361.
- Kanno, Y., Letcher, B. H., Coombs, J. A., Nislow, K. H. & Whiteley, A. R. 2014. Linking movement and reproductive history of brook trout to assess habitat connectivity in a heterogeneous stream network. *Freshwater Biology* **59**, 142–154.
- Keefer, M.L., Stansell, R.J., Tackley, S.C., Nagy, W.T., Gibbons, K.M., Peery C.A. & Caudill, C.C. (2012). Use of radiotelemetry and direct observations to evaluate sea lion predation on adult pacific salmonids at Bonneville Dam. *Transactions of the American Fisheries Society* **141**, 1236-1251.
- Kemp, P.S. & O’Hanley, J.R. (2010). Procedures for evaluating and prioritizing the removal of fish passage barriers: a synthesis. *Fisheries Management and Ecology* **17**, 297-322.
- Kingsford, R.T. (2000). Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia. *Austral Ecology* **25**, 109-127.
- Lamphere, B.A. & Blum, M.J. (2012). Genetic estimates of population structure and dispersal in a benthic stream fish. *Ecology of Freshwater Fish* **21**, 75–86.
- Lande, R. (1993). Risk of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist* **142**, 911-927.
- Letcher, B.H., Nislow, K.H., Coombs, J.A., O’Donnell, M.J. & Dubreuil, T.L. (2007). Population response to habitat fragmentation in a stream-dwelling brook trout population. *PLoS ONE* **2**, e1139.
- Leslie, A.J. Jr., Van Dyke, J.M., Nall, L.E. & Miley, W.W. II. (1982). Current velocity for transport of grass carp eggs. *Transactions of the American Fisheries Society* **111**, 99-101.
- Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**, 237-240.
- Liermann, C.R., Nilsson, C., Robertson J. & Ng, Y. (2012). Implications of dam obstruction for global freshwater fish diversity. *BioScience* **62**, 539-548.

- Lowe, W.H. & Allendorf, F.W. (2010). What can genetics tell us about population connectivity? *Molecular Ecology* **19**, 3038-3051.
- Lowe-McConnell, R.H. (1987). *Ecological studies in tropical fish communities*. Cambridge University Press. New York.
- Luttrell, G.R., Echelle, A.A., Fisher, W.L. & Eisenhour, D.J. (1999). Declining status of two species of the *Macrhybopsis aestivalis* complex (Teleostei: Cyprinidae) in the Arkansas River Basin and related effects of reservoirs and barriers to dispersal. *Copeia* **1999**, 981-989.
- MacArthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton, NJ. Princeton University Press.
- Magoulick, D.D. & Kobza, R.M. (2003). The role of refugia for fishes during drought: a review and synthesis. *Freshwater Biology* **48**, 1186-1198.
- Mahlum, S., Cote, D., Wiersma, Y.F., Kehler, D. & Clarke, K.D. (2014). Evaluating the barrier assessment technique derived from FishXing software and the upstream movement of brook trout through road culverts. *Transactions of the American Fisheries Society* **143**, 39-48.
- Manel, S., Schwartz, M.K., Luikart, G. & Taberlet, P. (2003). Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology and Evolution* **18**, 189-197.
- Manier, M.K. & Arnold, S.J. (2006). Ecological correlates of population genetic structure: a comparative approach using a vertebrate metacommunity. *Proceedings of the Royal Society- Biological Sciences* **273**, 3001-3009.
- Matthews, W.J. & Marsh-Matthews, E. (2007). Extirpation of red shiner in direct tributaries of Lake Texhoma (Oklahoma-Texas): a cautionary case history from a fragmented river-reservoir system. *Transactions of the American Fisheries Society* **136**, 1041-1062.
- McRae, B.H., Dickson, B.G., Keitt, T.H. & Shah, V.B. (2008). Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* **89**, 2712-2724.
- Morita, K.S. & Yokota, A. (2002). Population viability of stream-resident salmonids after habitat fragmentation: a case study with white-spotted charr (*Salvelinus leucomaenis*) by an individual based model. *Ecological Modelling* **155**, 85-94.

- Morita, K., Yamamoto, S. & Hoshino, N. (2000). Extreme life-history change of white-spotted charr (*Salvelinus leucomaenis*) after damming. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 1300-1306.
- Morrissey M.B. & de Kerckhove, D.T. (2009). The maintenance of genetic variation due to asymmetric gene flow in dendritic metapopulations. *American Naturalist* **174**, 875 – 889.
- Moyle, P. B., Li, H. W. & Barton B.A. (1986). The Frankenstein effect: impact of introduced fishes on native fishes in North America. In *Fish Culture in Fisheries Management*, Stroud, R. H., Editor. American Fisheries Society, Bethesda, Maryland. pp. 415-426.
- Mullen, L.B., Woods, H.A., Schwartz, M.K., Sepulveda, A.J. & Lowe, W.H. (2010). Scale-dependent genetic structure of the Idaho giant salamander (*Dicamptodon aterrimus*) in stream networks. *Molecular Ecology* **19**, 898-909.
- Musil, J., Horky, P., Slavik, O., Zboril, A. & Horka, P. (2012). The response of the young of the year fish to river obstacles: functional and numerical linkages between dams, weirs, fish habitat guilds and biotic integrity across large spatial scale. *Ecological Indicators* **23**, 634-640.
- Neary, V.S. (2012). Binary fish passage models for uniform and nonuniform flows. *River Research and Applications* **28**, 418-428.
- Neeson, T.M., Wiley, M.J., Adlerstein, S.A. & Riolo, R.L. (2011). River network structure shapes interannual feedbacks between adult sea lamprey migration and larval habitation. *Ecological Modelling* **222**, 3181-3192.
- Neville, H.M., Dunham, J.B. & Peacock, M.M. (2006). Landscape attributes and life history variability shape genetic structure of trout populations in a stream network. *Landscape Ecology* **21**, 901-916.
- Nilsson, C., Reidy, C.A., Dynesius, M. & Revenga, C. (2005). Fragmentation and flow regulation of the World's large river systems. *Science* **308**, 405-408.
- Nislow, K.H., Hudy, M., Letcher, B.H. & Smith, E.P. (2011). Variation in local abundance and species richness of stream fishes in relation to dispersal barriers: implications for management and conservation. *Freshwater Biology* **56**, 2135-2144.

- Norman, J.R., Hagler, M.H., Freeman, M.C. & Freeman, B.J. (2009). Application of a multistate model to estimate culvert effects on movement of small fishes. *Transactions of the American Fisheries Society* **138**, 826-838.
- Novinger, D.C. & Rahel, F.J. (2003). Isolation management with artificial barriers as a conservation strategy for cutthroat trout in headwater streams. *Conservation Biology* **17**, 772–781.
- O'Hanley, J.R. (2011). Open rivers: barrier removal planning and the restoration of free-flowing rivers. *Journal of Environmental Management* **92**, 3112-3120.
- O'Hanley, J.R. & Tomberlin, C. (2005). Optimizing the removal of small fish passage barriers. *Environmental Modelling and Assessment* **10**, 85-98.
- O'Hanley, J. R., Wright, J., Deibel, M., Fedora, M. A. & Soucy, C. L. (2013). Restoring stream habitat connectivity: a proposed method for prioritizing the removal of resident fish passage barriers. *Journal of Environmental Management* **125**, 19-27.
- Olden, J.D., Jackson, D.A. & Peres-Neto, P.R. (2001). Spatial isolation and fish communities in drainage lakes. *Oecologia* **127**, 572-585.
- Padgham, M. & Webb, J.A. (2010). Multiple structural modifications to dendritic ecological networks produce simple responses. *Ecological Modelling* **221**, 2537-2545.
- Pelicice, F.M. & Agostinho, A.A. (2008). Fish-passage facilities as ecological traps in large neotropical rivers. *Conservation Biology* **22**, 180-188.
- Pepino, M., Rodriguez, M.A. & Magnan, P. (2012). Fish dispersal in fragmented landscapes: a modelling framework for quantifying the permeability of structural barriers. *Ecological Applications* **22**, 1435-1445.
- Perkin, J.S. & Gido, K.B. (2011). Stream fragmentation thresholds for a reproductive guild of Great Plains fishes. *Fisheries* **36**, 371-383.
- Perkin, J.S. & Gido, K.B. (2012). Fragmentation alters stream fish community structure in dendritic ecological networks. *Ecological Applications* **22**, 2176-2187.
- Perkin, J.S., Gido, K.B., Al-Ta' Ani, O. & Scoglio, C. (2013). Simulating fish dispersal in stream networks fragmented by multiple road crossings. *Ecological Modeling* **257**, 44– 56.
- Piry, S., Alapetite, A., Cornuet, J.M., Paetkau, D., Baudouin, L. & Estoup, A. (2004). GENECLASS 2: A software for genetic assignment and first-generation migrant detection. *Journal of Heredity* **95**, 536-539.

- Poissant, J., Knight, T.W. & Ferguson, M.M. (2005). Nonequilibrium conditions following landscape rearrangement: the relative contribution of past and current hydrological landscapes on the genetic structure of a stream-dwelling fish. *Molecular Ecology* **14**, 1321–1331.
- Poplar-Jeffers, I.O., Petty, J.T., Anderson, J.T., Kite, S.J., Strager, M.P. & Fortney, R.H. (2009). Culvert replacement and stream habitat restoration: Implications from brook trout management in an Application Watershed, U.S.A. *Restoration Ecology* **17**, 404-413.
- Pringle, C.M., Naiman, R.J., Bretschko, G., Karr, J.R., Oswood, M.W., Webster, J.R., Welcomme, R.L. & Winterbourn, M.J. (1988). Patch dynamics in lotic systems: the stream as a mosaic. *Journal of the North American Benthological Society* **7**, 503-524.
- Pringle, J.M., Blakeslee, A.M.H., Byers J.E. & Roman, J. (2011). Asymmetric dispersal allows an upstream region to control population structure throughout a species' range *Proceedings of the National Academy of Sciences, U.S.A* **108**, 15288-15293.
- Quist, M.C. & Spiegel, J.R. (2012). Population demographics of catostomids in large river ecosystems: effects of discharge and temperature on recruitment dynamics and growth. *River Research and Applications* **28**, 1567-1586.
- Rahel, F.J. (2013). Intentional fragmentation as a management strategy in aquatic systems. *BioScience* **63**, 362-372.
- Rahel, F.J., Keleher, C.J. & Anderson, J.L. (1996). Potential habitat loss and population fragmentation for cold water fish in the North Platte River drainage of the Rocky Mountains: response to climate warming. *Limnology and Oceanography* **41**, 1116:1123.
- Reid, S.M., Wilson, C.C., Mandrak, N.E. & Carl, L.M. (2008). Population structure and genetic diversity of black redhorse (*Moxostoma duquesnei*) in a highly fragmented watershed. *Conservation Genetics* **9**, 531-546.
- Rieman, B.E. & Dunham, J.B. (2000). Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. *Ecology of Freshwater Fish* **9**, 51-64.
- Roberts, J.H. & Angermeier, P.L. (2007). Movement responses of stream fishes to introduced corridors of complex cover. *Transactions of the American Fisheries Society* **136**, 971-978.

- Roberts, J.J., Fausch, K.D., Peterson, D.P. & Hooten, M.B. (2013). Fragmentation and thermal risks from climate change interact to affect persistence of native trout in the Colorado River basin. *Global Change Biology* **19**, 1383-1398.
- Rodriguez, M.A. (2002). Restricted movement in stream fish: the paradigm is incomplete, not lost. *Ecology* **83**, 1-13.
- Rolls, R.J., Leigh, C. & Sheldon, F. (2012). Mechanistic effects of low-flow hydrology on riverine ecosystems: ecological principles and consequences of alteration. *Freshwater Science* **31**, 1163-1186.
- Roni, P., Beechie, T., Schmutz, S. & Muhar, S. (2012). Prioritization of watersheds and restoration projects. In *Stream and watershed restoration: a guide to restoring riverine processes and habitats*, Roni, P. & Beechie, T., editors. John Wiley & Sons, Chichester, United Kingdom. pp. 189-214.
- Scheffer, M., Van Geest, G.J., Zimmer, K., Jeppesen, E., Søndergaard, M., Butler, M.G., Hanson, M.A., Declerck, S. & De Meester, L. (2006). Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. *Oikos* **112**, 227-231.
- Schlosser, I.J. (1982). Fish community structure and function along two habitat gradients in a headwater stream. *Ecological Monographs* **52**, 395-414.
- Schlosser, I.J. & Angermeier, P.L. (1995). Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. *American Fisheries Society Symposium* **17**, 392-401.
- Sethi, S.A., Selle, A.R., Doyle, M.W., Stanley, E.H. & Kitchel, H.E. (2004). Response of unionid mussels to dam removal in Koshkonong Creek, Wisconsin (USA). *Hydrobiologia* **525**, 1-3.
- Shurin, J.B., Cottenie, K. & Hillebrand, H. (2009). Spatial autocorrelation and dispersal limitation in freshwater organisms. *Oecologia* **159**, 151-159.
- Skalski, G.T., and Gilliam, J.F. (2000). Modeling diffusive spread in a heterogeneous population: a movement study with stream fish. *Ecology* **81**, 1685-1700.
- Slatkin, M. (1985). Gene flow in natural populations. *Annual Review of Ecology and Systematics* **16**, 393-430.
- Smith, J.M. (1981). Macroevolution. *Nature* **289**, 13-14.

- Stanley, E.H. & Doyle, M.W. (2003). Trading off: the ecological removal effects of dam removal. *Frontiers in Ecology and the Environment* **1**, 15-22.
- Sterling, K.A., Reed, D.H., Noonan, B.P. & Warren, M.L. (2012). Genetic effects of habitat fragmentation and population isolation on *Etheostoma raneyi* (Percidae). *Conservation Genetics* **13**, 859-872.
- Stuart, I.G. & Mallen-Cooper, M. (1999). An assessment of the effectiveness of a vertical-slot fishway for non-salmonid fish at a tidal barrier on a large tropical/subtropical river. *Regulated Rivers: Research and Management* **15**, 575-590.
- Storfer, A., Murphy, M.A., Spear, S.F., Holderegger, R. & Waits, L.P. (2010). Landscape genetics: where are we now? *Molecular Ecology* **19**, 3496-3514.
- Taylor, P.D., Fahrig, L., & Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos* **68**, 571–573.
- Tibbets, C.A. & Dowling, T.E. (1996). Effects of intrinsic and extrinsic factors on population fragmentation in three species of North American minnows (Teleostei: Cyprinidae). *Evolution* **50**, 1280-1292.
- Tonn, W.M. & Magnuson, J.J. (1982). Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology* **63**, 1149-1166.
- Tonn, W.M., Magnuson, J.J., Rask, M. & Toivonen, J. (1990). Intercontinental comparison of small-lake fish assemblages- the balance between local and regional processes. *American Naturalist* **136**, 345-375.
- Turner, T.F. & Trexler, J.C. (1998). Ecological and historical associations of gene flow in darters (Teleostei: Percidae). *Evolution* **52**, 1781-1801.
- Turner, T.F., Osborne, M.J., Moyer, G.R., Benavides, M.A. & Alo, D. (2006). Life history and environmental variation interact to determine effective population to census size ratio. *Proceedings of the Royal Society- Biological Sciences* **273**, 3065-3073.
- Turner, T. F. & Robison, H.W. (2006). Genetic diversity of the Caddo Madtom, *Noturus taylori*, with comments on factors that promote genetic divergence in fishes endemic to the Ouachita highlands. *Southwestern Naturalist* **51**, 338-345.
- Urban, M.C. & Skelly, D.K. (2006). Evolving metacommunities: Toward and evolutionary perspective on metacommunities. *Ecology* **87**, 1616-1626.

- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushing, C.E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 130-137.
- Waits, E.R., Bagley, M.J., Blum, M. J., McCormick, F. H. & Lazorchak, J.M. (2008). Source–sink dynamics sustain central stonerollers (*Camptostoma anomalum*) in a heavily urbanized catchment. *Freshwater Biology* **53**, 2061–2075.
- Walters, D.M., Zuellig, R.E., Crockett, H.J., Bruce, J.F., Lukacs, P.M. & Fitzpatrick, R.M. (2014). Barriers impeded upstream spawning migration of flathead chub. *Transactions of the American Fisheries Society* **143**, 17-25.
- Wang, J.L., and Whitlock, M.C. (2003). Estimating effective population size and migration rates from genetic samples over space and time. *Genetics* **163**, 429-446.
- Waples, R.S. (1987). A multispecies approach to the analysis of gene flow in marine shore fishes. *Evolution* **41**, 385-400.
- Waples, R.S. (1989). Temporal variation in allele frequencies- testing the right hypothesis. *Evolution* **43**, 1236-1251.
- Ward, J. V., Tockner, K. & Schiemer, F. (1999). Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regulated Rivers: Research and Management* **15**, 125–139.
- Wares, J.P. (2002). Community genetics in the Northwestern Atlantic intertidal. *Molecular Ecology* **11**, 1131-1144.
- Wares, J.P. & Pringle, J. M. (2008). Drift by drift: effective population size is limited by advection. *BMC Evolutionary Biology* **8**, 235.
- Warren, M.J.Jr. & Pardew, M.G. (1998). Road crossings as barriers to small-stream fish movement. *Transactions of the American Fisheries Society* **127**, 637-644
- Welcomme, R.L. (1979). *The fisheries ecology of floodplain rivers*. Longman, London.
- Whiteley, A.R., Spruell, P. & Allendorf, F.W. (2004). Ecological and life history characteristics predict population genetic divergence of two salmonids in the same landscape. *Molecular Ecology* **13**, 3675-3688.
- Whitlock, M.C. & McCauley, D.E. (1990). Some population genetic consequences of colony formation and extinction- genetic correlations within founding groups. *Evolution* **44**, 1717-1724.
- Wiens, J.A. (2002). Riverine landscapes: taking landscape ecology into the water. *Freshwater Biology* **47**, 501-515.

- Wilson, G.A. & Rannala, B. (2003). Bayesian inference of recent migration rates using multilocus genotypes. *Genetics* **163**, 1177-1191.
- Winemiller, K.O, Flecker, A.S. & Hoeinghaus, D.J. (2010). Patch dynamics and environmental heterogeneity in lotic ecosystems. *Journal of the North American Benthological Society* **29**, 84-99.
- Winston, M.R., Taylor, C.M. & Pigg, J. (1991). Upstream extirpation of four minnow species due to damming of a prairie stream. *Transactions of the American Fisheries Society* **120**, 98-105.
- Wunderlich, R.C., Winter, B.D. & Meyer, J.H. (1994). Restoration of the Elwah River ecosystem. *Fisheries* **19**, 11-19.
- Woodford, D.J. & McIntosh, A.R. (2010). Evidence of source-sink metapopulations in a vulnerable native galaxiid fish driven by introduced trout. *Ecological Applications* **20**, 967-977.
- The World Commission on Dams. (2000). *Dams and Development: A New Framework for Decision-Making*. London: EarthScan Publications.
- Wright, S. (1939). The distribution of self-sterility alleles in populations. *Genetics* **24**, 538-552.
- Wright, S. (1978). *Evolution and the Genetics of Populations, Volume 4: Variability Within and Among Natural Populations (Evolution and the Genetics of Populations)*. University of Chicago Press.

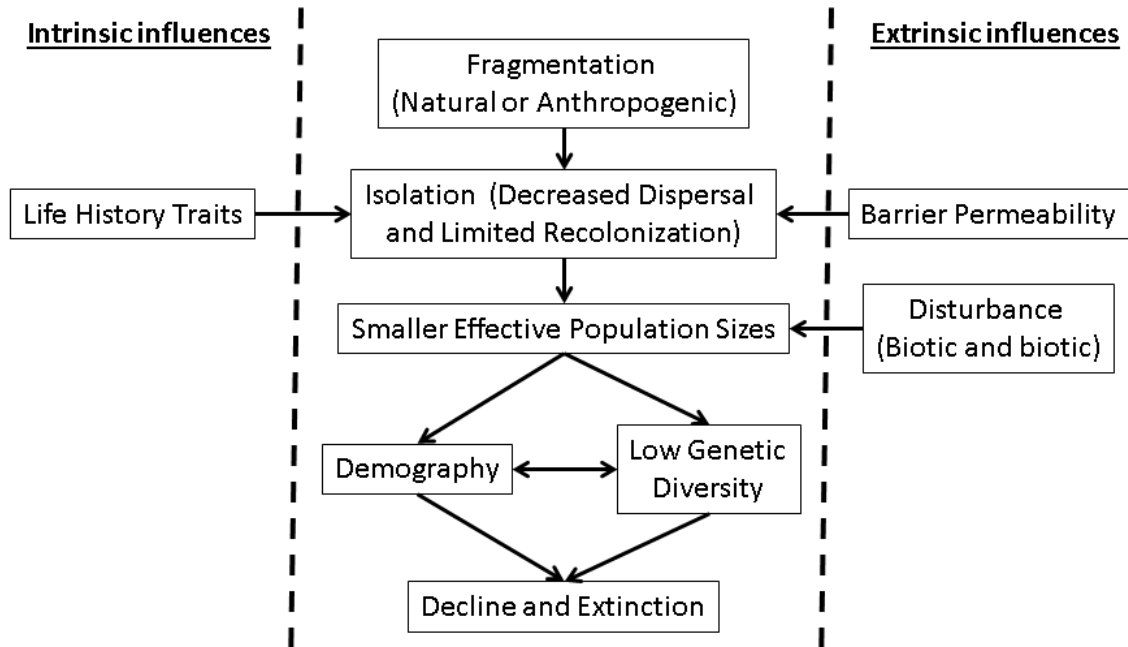


Figure 10.1. Conceptual model describing factors driving decline and extinction of species following fragmentation. Both intrinsic and extrinsic factors can regulate the degree of isolation following fragmentation. Small populations also are more prone to stochastic disturbance events and low genetic diversity can reduce reproductive performance and the ability of a population to adapt to altered conditions.

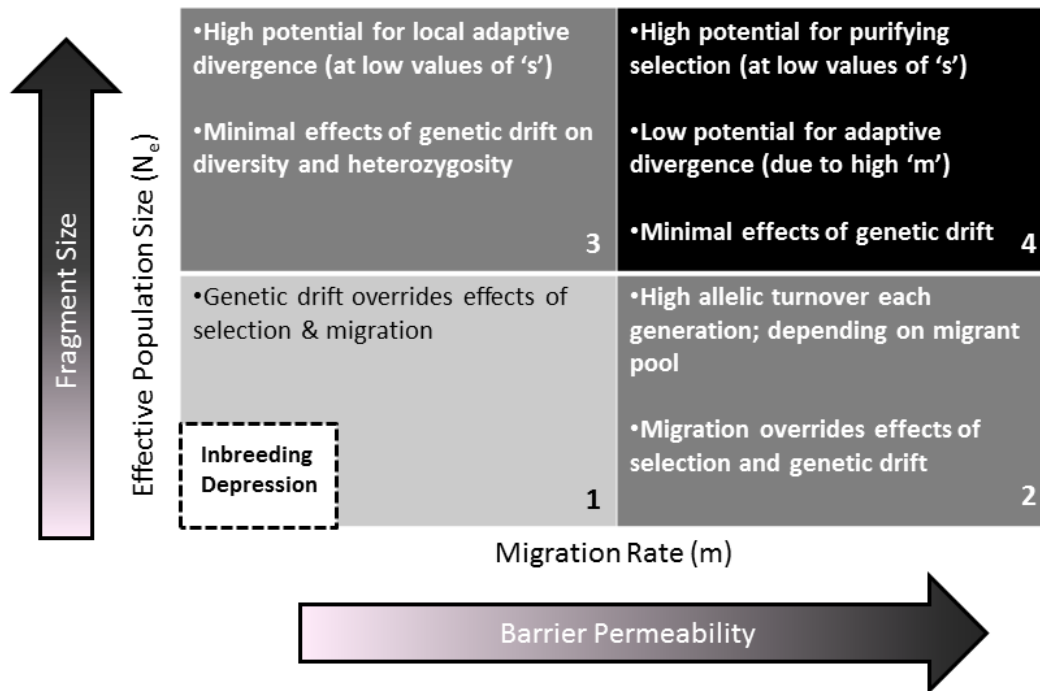


Figure 10.2. A conceptual model of evolutionary response to fragmentation. Three parameters are tracked in the model. The x-axis tracks increasing barrier permeability and the genetic effective migration rate (m). The y-axis tracks fragment size and the genetic effective population size (N_e) of a fragmented subpopulation. Numbers in the lower right-hand corner of each cell identify quadrants that facilitate discussion, but we envision a continuous gradient of m and N_e as barrier permeability and fragment size increase. The selection coefficient (s) is tracked in each quadrant. At maximum values of permeability and fragment size in quadrant 4, the fragmented subpopulations approach panmixia. At minimum values in quadrant 1, fragmented populations are subject to genetic drift and inbreeding. Diversifying natural selection across subpopulations is predicted to be more likely in quadrant 3 because of low gene flow but large N_e . Gene flow resists divergent selection in quadrant 4 unless the selection coefficient is very large.

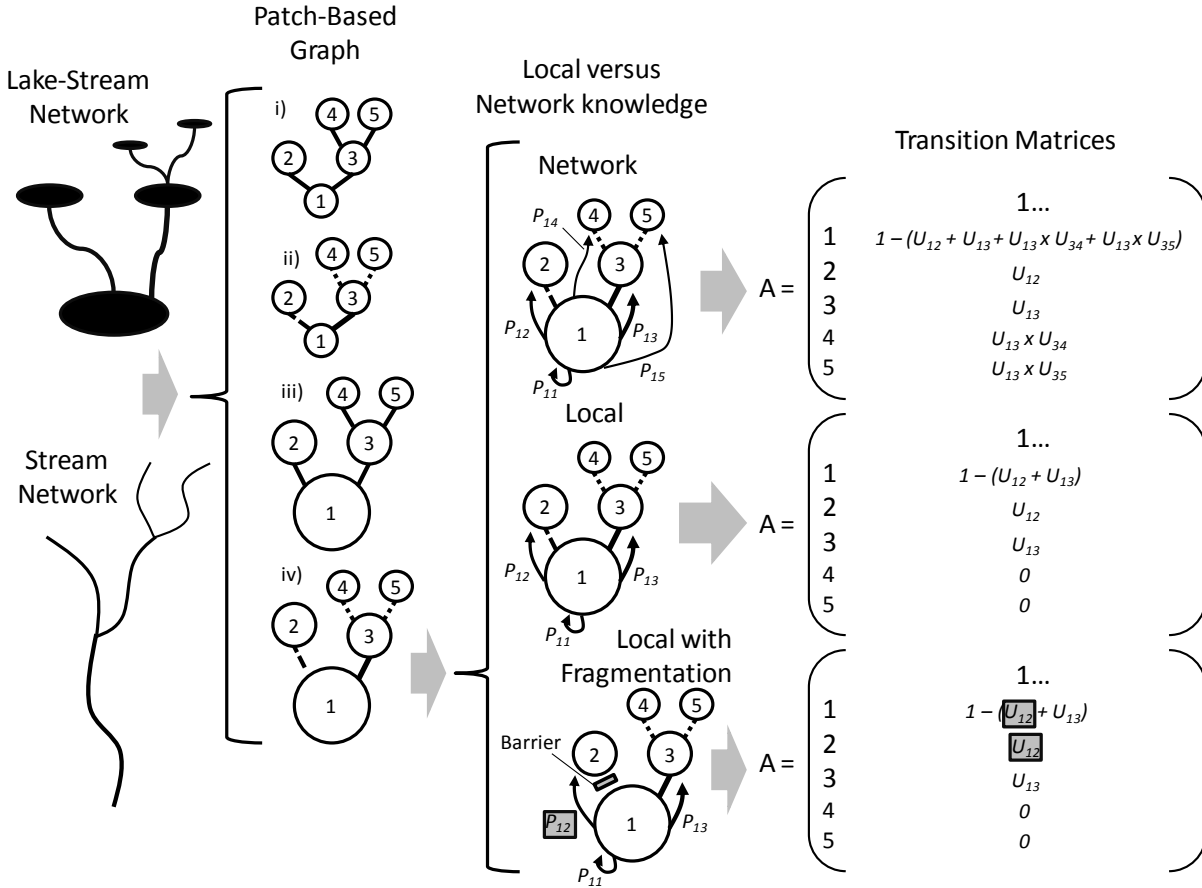


Figure 10.3. Conceptual diagram illustrating use of patch-based graph theory to model fish dispersal in fragmented lake-stream and stream networks. Lakes or the longitudinal length of stream between confluences are considered as patches (Erős et al., 2011), which can be converted into patch-based graphics assuming (i) homogeneous node and link resolution (i.e., nodes = circles of equal size, links = lines of equal character), (ii) homogeneous node resolution and heterogeneous link resolution, (iii) homogeneous link resolution and heterogeneous node resolution, and (iv) heterogeneous node and link resolution (Erős et al., 2012). Within patch-based graphics, fish dispersal can be limited to local or network knowledge during simulations using spatially explicit transition probabilities (P_{xx}) between patches (Padgham and Webb, 2010; Neeson et al., 2011). Fragmentation is modelled by adjusting transition probabilities within deterministic matrices to incorporate barrier location, barrier permeability, and node quality (Padgham and Webb, 2010). For transition matrices, only transition probabilities and portions of matrices associated with dispersal from node 1 are shown for brevity.

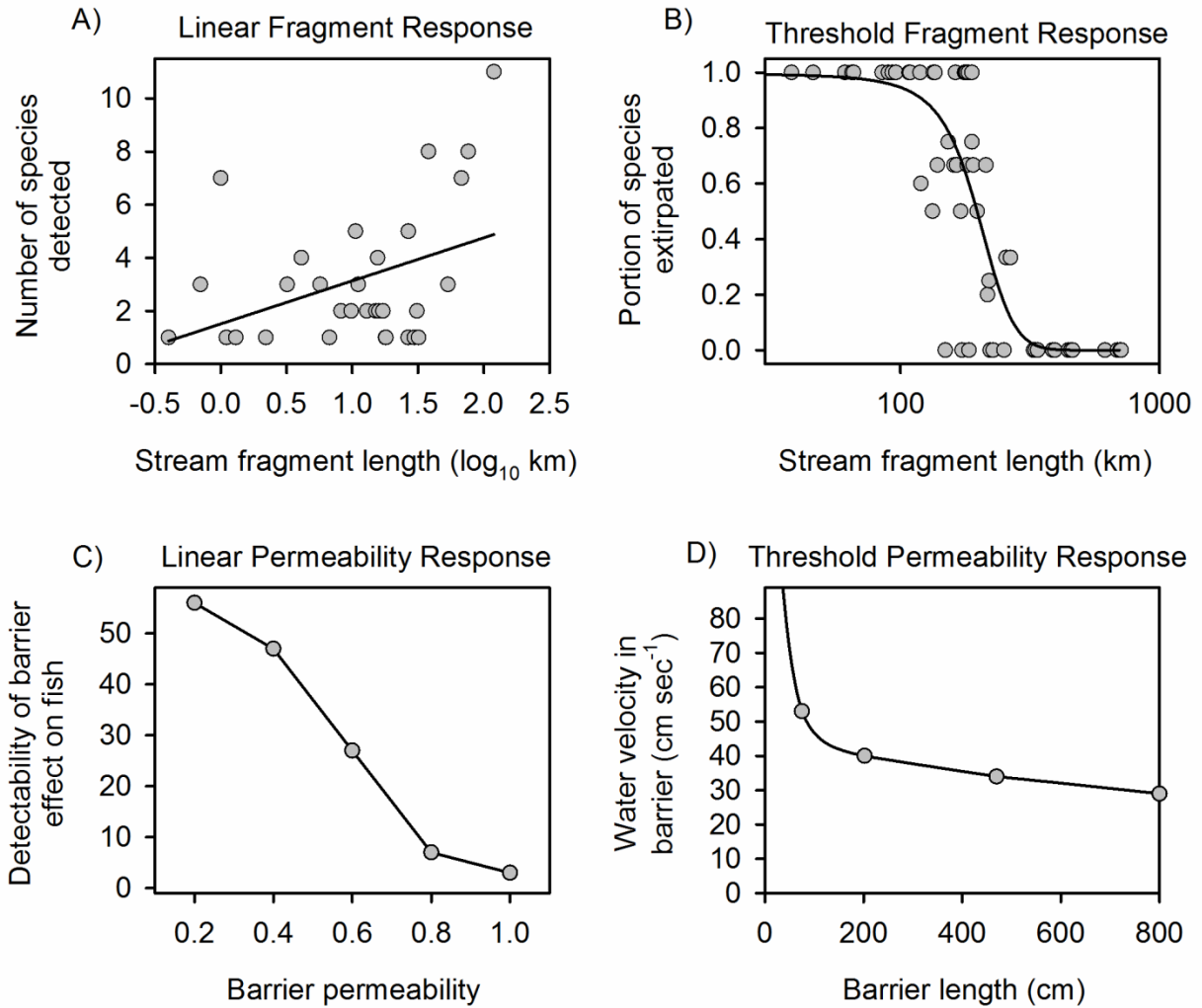


Figure 10.4. Empirical examples of fish responses to fragmentation. These examples illustrate a linear response to fragment length by fish communities in streams of New York (A; Bain and Wine, 2010), a threshold response to fragment length by pelagic-broadcast spawning fish communities in the Great Plains (B; Perkin and Gido, 2011), a linear response in the power to detect effect of a barrier on fish dispersal across a range of permeability values (C; Pepino et al., 2012), and an exhaustion-threshold (i.e., length a fish can swim at a given water velocity before exhaustion) response by fish to the water velocity flowing through a barrier of particular length (D; Neary, 2012).

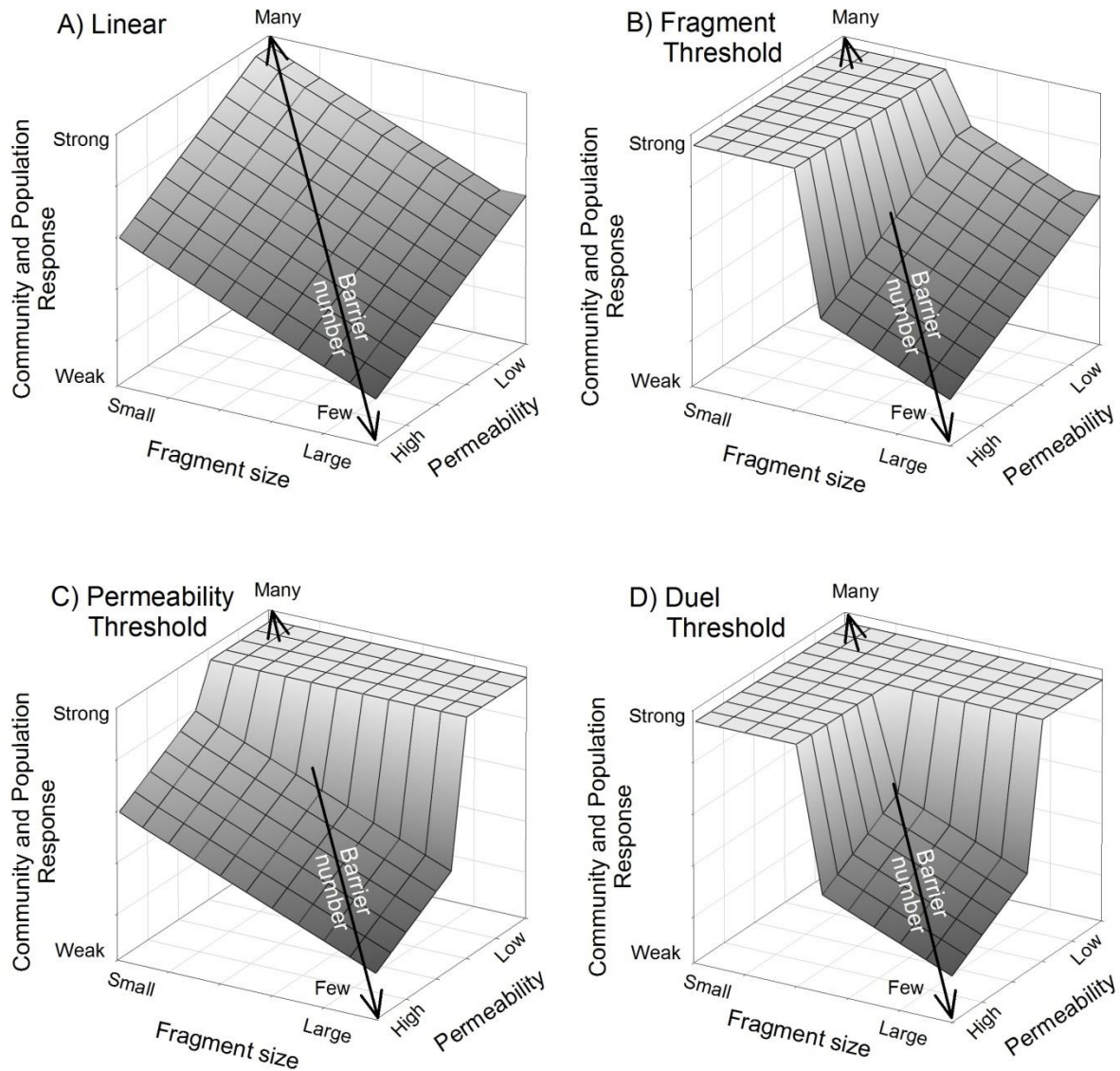


Figure 10.5. Conceptual models describing potential fish community or population responses to changes in stream habitat connectivity. (A) Responses are strongest among watersheds characterized by many barriers with low permeability and consequently small fragment sizes. Alteration to community structure might be greater than expected based on the number of barriers alone because fish interpretations of riverscapes result in threshold responses to (B) fragment size or (C) barrier permeability. (D) In real-world riverscapes, low permeability among many barriers contributes to smaller fragment sizes so that communities effectively respond to barrier number, position (contributing to fragment size), and permeability.