

FRAGMENTATION IN STREAM NETWORKS: QUANTIFICATION, CONSEQUENCES,
AND IMPLICATIONS TO DECLINE OF NATIVE FISH FAUNA

by

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B.S., Texas State University-San Marcos, 2006
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Abstract

Habitat fragmentation and loss threaten global biodiversity, but organism responses to changing habitat availability are mediated by structural properties of their habitats. In particular, organisms inhabiting dendritic landscapes with hierarchically arranged branches of habitat tend to have limited access to some patches even in the absence of fragmentation. Consequently, organisms inhabiting dendritic landscapes such as streams respond strongly to fragmentation. Using a combination of meta-analysis, field observations, and ecological network modeling I show that stream fishes respond to fragmentation in predictable ways. First, I addressed how dams and stream dewatering have created a mosaic of large river fragments throughout the Great Plains. Using a geographic information system and literature accounts of population status (i.e., stable, declining, extirpated) for eight “pelagic-spawning” fishes, I found stream fragment length predicted population status (ANOVA, $F_{2,21} = 30.14$, $P < 0.01$) and explained 71% of reported extirpations. In a second study, I applied a new measure of habitat connectivity (the Dendritic Connectivity Index; DCI) to 12 stream networks in Kansas to test the DCI as a predictor of fish response to fragmentation by road crossings. Results indicated fish communities in stream segments isolated by road crossings had reduced species richness (alpha diversity) and greater dissimilarity (beta diversity) to segments that maintained connectivity with the network, and the DCI predicted patterns in community similarity among networks ($n = 12$; $F_{1,10} = 19.05$, $r^2 = 0.66$, $P < 0.01$). Finally, I modeled fish distributions in theoretical riverscapes to test for mechanistic linkages between fragmentation and local extirpations. Results suggested the number of small fragments predicted declines in patch occupancy, and the magnitude of change in occupancy varied with dispersal ability (“high” dispersers responded more strongly than “low” dispersers). Taken together, these works show context-dependencies in fish responses to fragmentation, but a unifying theme is that small fragments contribute to attenuated biodiversity. Moreover, the predictable manner in which stream fish react to fragmentation will aid in biodiversity conservation by revealing potential responses to future scenarios regarding changes to habitat connectivity.

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Approved by:

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Preface

The contents of this dissertation represent concepts and approaches developed in collaboration with my major professor and members of my dissertation committee. Although the work is my own, the chapters are presented in third person for the sake of peer-reviewed publication. Chapter 2 is published with Keith Gido as a coauthor in the journal *Fisheries*, volume 36, issue number 8, on pages 371-383. Chapter 3 is currently in press in the journal *Ecological Applications* with Keith Gido as a coauthor. Chapter 4 is formatted for publication in the journal *Ecological Modelling* with Keith Gido, Caterina Scoglio, and Ola Al-Ta' Ani as coauthors.

Chapter 1 - Stream Fragmentation as a Major Environmental Problem

Humans have altered biological and ecological processes and influenced the abundance and distribution of organisms on a global scale (Dudgeon et al., 2006; Vörösmarty et al., 2010). Among anthropogenic environmental alterations, habitat fragmentation and loss have impacted virtually all ecosystems on Earth (Vitousek et al., 1997; Lindenmayer and Fischer, 2006). Stream systems are particularly vulnerable to fragmentation because of the variety of ecosystem goods and services freshwaters provide to humans and the necessity to alter the flow of water in the process of obtaining such goods and services (Zimmerman et al., 2008). Consequently, most of the world's large river systems are now fragmented by dams that alter river flow regimes and contribute to habitat loss and imperilment for a variety of stream organisms (Bunn and Arthington, 2002; Nilsson et al., 2005). Geographically referenced global distributions of 6,862 dams housed in the Global Reservoirs and Dams Dataset (GRanD; Lehner et al., 2011) provide some insight into magnitude of the environmental problem dams pose (Figure 1.1.). Furthermore, not all structures are geographically referenced or catalogued, and estimates suggest more than 16.7 million impoundments >0.01 hectares in size exist on a global scale (Lehner et al., 2011).

Human structures that fragment streams imperil freshwater organisms by severing dispersal routes and disrupting naturally occurring (meta)population and (meta)community processes. Migratory species that require intact dispersal corridors across broad spatial scales are most sensitive to fragmentation because large stream segments or connectivity with marine environments are necessary for full expression of life history (Morita and Yamamoto, 2002; Dudley and Platania, 2007). For potamodromous species that migrate within freshwater, barriers block dispersal routes and cause population extirpations when source-sink dynamics or rescue effects no longer occur (Winston et al., 1991; Luttrell et al., 1999). For diadromous species that migrate between freshwater and marine ecosystems, barriers block access to vital nursery habitats required for successful recruitment (Hall et al., 2011; Hitt et al., 2012). Fish biodiversity declines are also related to fragmenting structures other than dams, mainly in the form of road crossings characterized by outflows perched above stream beds or culverts that

divert water through engineered structures that create water velocities greater than the swimming capability of most fish (Norman et al., 2009; Nislow et al., 2011). Fragmentation caused by road crossings is therefore an unintentional consequence of infrastructure constructed primarily for transportation through terrestrial settings (Gibson et al., 2005); however, the magnitude of fragmentation caused by road crossings can be extensive (Forman and Alexander, 1998; Poplar-Jeffers et al., 2009). For example, in the state of Kansas more than 20,000 road crossings that are not regulated by federal or state entities exist where road networks interface with stream networks (Figure 1.2) and building evidence suggest such crossings are capable of disrupting dispersal of many fish (Bouska and Paukert, 2009). Consequently, although stream fragmentation has recently received increasing attention (reviewed in Fullerton et al., 2010), the extent of fragmentation combined with our limited understanding of how fragmentation influences stream fish (Branco et al., 2011; Pépino et al., 2012) suggests additional research regarding the effects of fragmentation is necessary for the conservation of declining aquatic biodiversity (Dudgeon et al., 2006).

Given the ecological impairment dams and other barriers can cause in stream ecosystems (Baxter, 1977), there is emerging interest in removing barriers to enhance conservation and management of freshwater biodiversity and ecosystems (Poff and Hart, 2002). However, because fragmenting structures are so common and widely distributed, and resources for removal of barriers are often limited, mitigation approaches must utilize prioritization methods that are most likely to maximize benefits and reduce costs (Kemp and O'Hanley, 2010; O'Hanley, 2011). Assessing fragmentation at increasingly broader spatial scales that incorporate riverine landscape or riverscape perspectives have emerged as a viable option for enhancing freshwater fish conservation (Fausch et al., 2002), and multiple approaches for measuring connectivity within riverscapes have recently been developed (Fullerton et al., 2010). Although such approaches seem promising for enhancing the distribution and abundance of species that respond negatively to fragmentation (Cote et al., 2009), few empirical applications currently exist (Bourne et al., 2011). Thus, application of riverscape-scale measures of habitat and population connectivity is a developing area of research with potential to contribute to the conservation of multiple freshwater organisms as well as the ecosystem goods and services provided by those organisms (Erős et al., 2012).

To address these research needs, this dissertation describes multiple research approaches including meta-analysis, field observations, and ecological modeling aimed at developing predictions regarding fish response to changes in riverscape connectivity across multiple spatial and temporal scales. In Chapter 2, I address the extirpation of a reproductive guild of Great Plains fishes that have indicated extensive declines during the past 50 years. I use a meta-analysis approach regarding population status of eight species to relate population persistence to features of riverine landscapes, in particular the size of stream fragments between barriers, to determine the appropriate spatial scale at which conservation initiatives should be implemented. In Chapter 3, I use stream fish community structure samples taken from 12 dendritic ecological networks (stream networks) throughout eastern Kansas that vary in the number of road crossings that fragment networks to assess relationships between habitat connectivity and metapopulation dynamics. I relate network-scale measures of habitat connectivity to patterns in fish biodiversity to assess the efficiency of using broad-scale measures of habitat connectivity to prioritize barriers for removal in order to enhance the abundance and distribution of stream fish. In Chapter 4, I use a riverscape modeling approach to assess the effects of barrier number, barrier permeability, network architecture, and fish dispersal ability on measures of network-scale habitat connectivity. By using an iterative and replicated approach to modeling fish dispersal and habitat connectivity I identify context-dependences that should be taken into account when broad-scale measures of habitat connectivity are implemented to prioritize barriers for removal. Finally, in Chapter 5, I summarize conclusions drawn from my research and discuss the implications they have for the conservation of stream-dwelling fish and freshwater biodiversity.

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Figure 1.1 Distribution, number, and size of dams globally, in North America, and in the Great Plains. Symbols represent dam heights in meters (m) and the Great Plains ecoregion is outlined in black. Data are from Lehner et al. (2011).

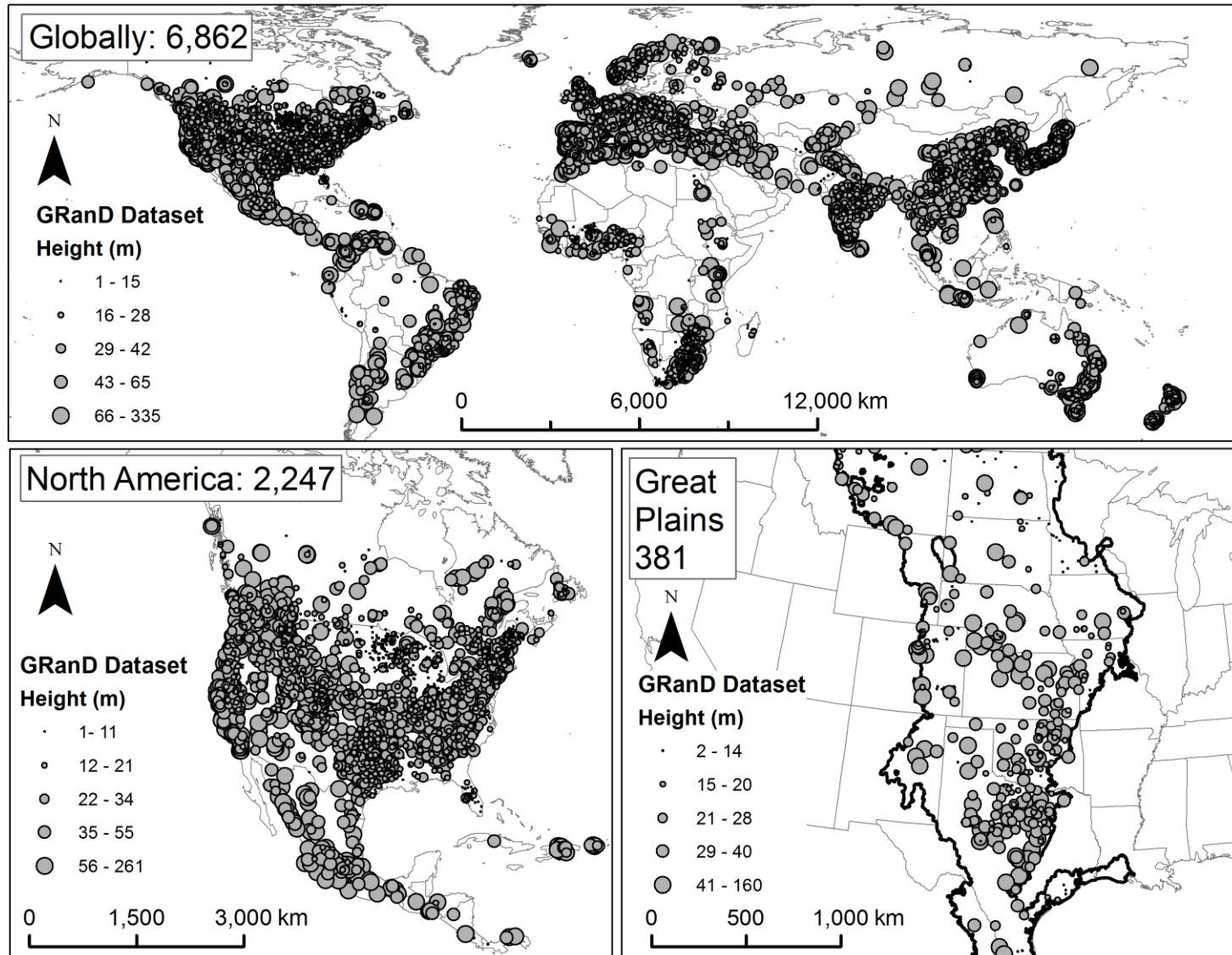
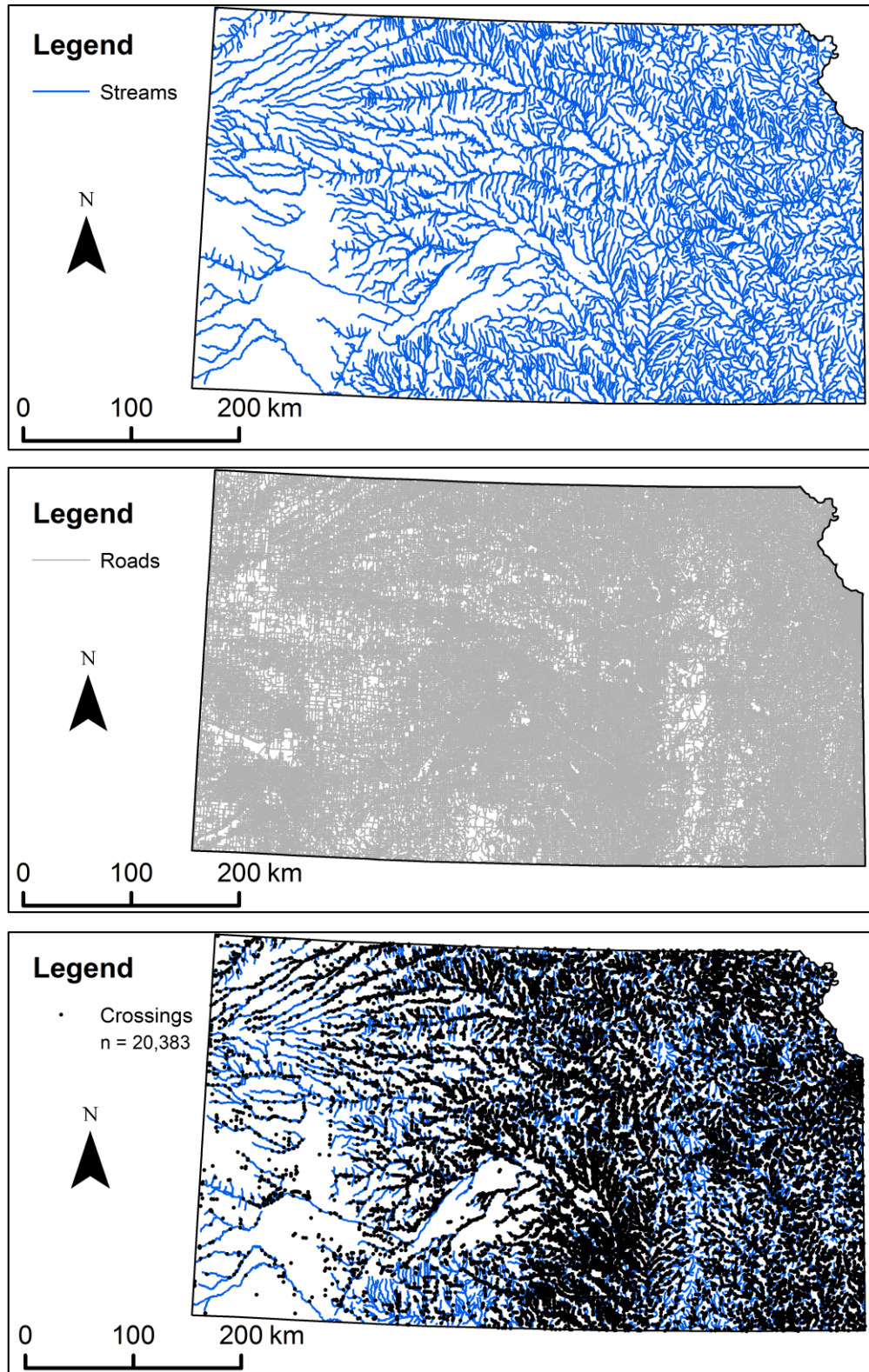


Figure 1.2 Distribution of stream networks, road networks, and road-stream crossings in Kansas. Small streams are not shown for clarity but were included among crossings.



Chapter 2 - Stream Fragmentation Thresholds for a Reproductive Guild of Great Plains Fishes

Abstract

Impoundments, diversion dams, and stream dewatering have created a mosaic of large river fragments throughout the Great Plains of central North America. Coincident with these habitat changes are massive declines in the distribution and abundance of Great Plains fishes belonging to the “pelagic-spawning” reproductive guild. We analyzed longitudinal fragment lengths (measured in river km) and literature accounts of population status for eight species from this guild across 60 fragments to derive thresholds in stream length associated with extirpations. Fragment length predicted population status ($F_{2,21} = 30.14$, $P < 0.01$), with lengths averaging 136 ± 21 rkm for extirpated, 226 ± 69 rkm for declining, and 458 ± 137 for stable populations. Fragment length explained 71% of reported extirpations and estimated thresholds in fragment length explained 67% of variation in population persistence. Our findings provide insight into appropriate spatial scales for conducting riverscape conservation approaches that address the hierarchical effects of fragmentation on stream-dwelling fishes.

Introduction

Humans have altered biological and ecological processes and influenced the abundance and distribution of organisms on a global scale (Dudgeon et al. 2006; Vorosmarty et al. 2010). In particular, groundwater depletion and impoundment of surface waters have compromised the connectivity of many freshwater ecosystems, constraining the ability of stream organisms to use these habitats (Nilsson et al. 2005). These alterations have imperiled freshwater organisms worldwide, most notably organisms dependent upon streams and rivers for long-term persistence (Lytle and Poff 2004; Nilsson et al. 2005). Although the importance of preserving entire riverscapes has recently been recognized as a viable conservation strategy (Fausch et al. 2002), there is limited information on the spatial scale necessary to preserve biodiversity in lotic systems.

Within the coterminous United States, 85% of large rivers are fragmented by impoundments that divide streams longitudinally, alter flow regimes, and reduce transport of

sediments (Hughes et al. 2005). Extensive stream fragmentation, combined with other anthropogenic disturbances (e.g., degradation of water quality, introduction of non-native species), contributes to the imperiled status of nearly 40% of North American freshwater and diadromous fishes (Jelks et al. 2008). Among these imperiled fishes, small-bodied minnows (family Cyprinidae) that dispense passively drifting eggs and larvae into large flowing streams have declined during the past 60 years. These pelagic-spawning fishes decline in association with human alterations to streams, specifically stream fragmentation (Platania and Altenbach 1998; Luttrell et al. 1999). For example, peppered chub (*Macrhybopsis tetranema*) is now extirpated from 90% of its historical range and persists in only two isolated Arkansas River fragments separated by >400 km (Luttrell et al. 1999). Similarly, the federally threatened Arkansas River shiner (*Notropis girardi*) is now extirpated from 80% of its historical range and is currently found in only two isolated fragments of the Arkansas River Basin (Wilde 2002). Documented extirpations of these and other pelagic-spawning cyprinid species coincide with a period of extensive fragmentation of North American rivers from 1950 to 1970 (Cross et al. 1985; Luttrell et al. 1999; Gido et al. 2010).

Reduced stream connectivity is particularly detrimental to pelagic-spawning fishes because of their unique reproductive ecology. Pelagic-spawning cyprinids dispense gametes into pelagic zones of flowing streams. Immediately following spawning, water osmotically enters cell membranes and causes eggs to swell and become semi-buoyant (in physical terms, slightly negatively buoyant; Bottrell et al. 1964). These semi-buoyant eggs remain suspended within the water column at current velocities above 0.01 m/s, drift for 24-28 hours before hatching, and drifting for an additional 2-3 days as developing larvae. During the drift period, individuals presumably become displaced great distances downstream (>140 km) from parent localities before complete development of a gas bladder and the onset of exogenous feeding, which allow larval individuals to exit the drift (Moore 1944; Platania and Altenbach 1998). The extent to which larval individuals continue to drift is largely unknown (Durham and Wilde 2008). Consequently, large river fragments (>100 km) are required by drifting eggs and larvae (collectively referred to as ichthyoplankton; *sensu* Dudley and Platania 2007) to allow time to develop before being deposited in impounded downstream habitats. Downstream transport is of particular concern because high mortality rates occur among ichthyoplankton deposited within downstream reservoirs, owing to suffocation within anoxic sediments or predation from

lacustrine species (Platania and Altenbach 1998; Dudley and Platania 2007; Pompeu et al. In Press). Spatial dynamics of adult pelagic-spawning cyprinids also are disrupted by stream fragmentation (Luttrell et al. 1999; Bonner 2000). During adult stages, some pelagic-spawning cyprinids are capable of moving upstream on the order of 50 km in <72 h (Bestgen et al. 2010) and are presumed to make upstream migrations to recolonize upstream areas (Cross et al. 1985; Bonner 2000). Thus impoundments also act as barriers to adult dispersion and preclude source-sink dynamics as well as rescue effects (Winston et al. 1991). Stream fragmentation therefore carries the potential to negatively alter the spatial dynamics of pelagic-spawning cyprinids via interruption of dispersal in space (i.e., in downstream and upstream directions) and time (i.e., during ichthyoplankton and adult life stages; Dudley and Platania 2007; Pompeu et al. In Press).

Stream fragmentation might provide a mechanistic pathway useful in predicting population declines among imperiled Great Plains pelagic-spawning cyprinids. Within the Great Plains region of North America, pelagic-spawning cyprinids historically dominated vertebrate assemblages within prairie rivers (Cross and Moss 1987; Gido et al. 2010). Documentation of reproductive strategies and egg types place four broadly distributed imperiled Great Plains cyprinids in this guild: Arkansas River shiner (Moore 1944), peppered chub (Bottrell et al. 1964), plains minnow (*Hybognathus placitus*) (Platania and Altenbach 1998), and sturgeon chub (*Macrhybopsis gelida*) (Hoagstrom et al. 2006). Similarities in morphology, larval drift catches, and available (although limited) information on reproductive strategy suggest potential for an additional four that either broadcast drifting eggs or have an obligatory drifting larval stage: the shoal chub (*Macrhybopsis hyostoma*) (Eisenhour 2004), silver chub (*Macrhybopsis storeriana*) (Simon 1999), flathead chub (*Platygobio gracilis*) (Cross et al. 1985; Durham and Wilde 2008), and prairie chub (*Macrhybopsis australis*) (Eisenhour 2004). Numerous proposed drivers exist for the declines of these species, including alterations in streamflow timing and magnitude (Taylor and Miller 1990), poor recruitment associated with reduced streamflows (Wilde and Durham 2008), changes to instream habitat including substrate compaction and channel homogenization (Cross and Moss 1987), introduction of non-native taxa, and changes in water quality (Gido et al. 2010). However, reported declines transcend a spatial scale ranging over 20° of latitude and have occurred within 13 regionally distinct North American ecoregions (as defined by Jelks et al. 2008) where all of the above drivers may not be operating. A unifying theme among reported declines is that stream fragmentation is capable of disrupting pelagic-

spawning cyprinid life history (as described above) and might represent a primary regulator of species decline. Effects of fragmentation are seemingly not equal among all pelagic-spawning cyprinids, as evidenced by differential levels of extirpation and persistence of guild members within similarly sized fragments (Platania and Altenbach 1998). Consequently, the need exists to identify species-specific threshold levels of fragmentation that might explain declines among numerous fishes across large spatial and temporal scales.

We examined the relationship between stream fragmentation and reported declines among eight species of imperiled Great Plains pelagic-spawning cyprinids. Specifically, we sought to (1) compile literature accounts for the occurrence and status of pelagic-spawning cyprinids within fragmented streams; (2) determine the relationship between population status and stream fragment length; and (3) estimate minimum fragment lengths associated with population persistence. Our test of the extent to which stream fragmentation has imperiled these fishes provides a framework that can be used by managers to select habitats needed to conserve populations of these highly threatened fishes.

Methods

Study Area

The North American Plains comprise a semi-arid region that was historically dominated by grassland, prairie, and steppe biomes that span from Alberta, Canada to the Rio Grande Basin, Mexico. The plains are bordered to the west by the Rocky Mountains and to the east by the Mississippi River. Consequently, most large-order plains rivers flow west to east within three major basins: the Missouri River, Arkansas River, and Red River basins (Matthews and Zimmerman 1990). These river basins occur in two major plains regions, the Great Plains and Osage Plains (collectively referred to as the Great Plains hereafter) and span the majority of 10 states: Montana, North Dakota, South Dakota, Wyoming, Nebraska, Colorado, Kansas, Oklahoma, New Mexico, and Texas. Additionally, southern portions of the Great Plains are drained by river basins that empty directly into the Gulf of Mexico, including the Brazos, Colorado, San Antonio Bay, Nueces, and Rio Grande basins. Throughout this region, portions of large prairie rivers characterized by low gradients, sandy bottoms, relatively high turbidity, and lying within the coterminous United States were chosen based on inhabitation by pelagic-spawning cyprinids and availability of historical ichthyofauna data.

Evaluating Extent of Stream Fragmentation

Stream fragments were included based on occurrence of instream barriers, historical inhabitation by targeted species, and availability of historical fish assemblage data. Upstream and downstream limits of fragments were defined by one of four instream barriers to fish movement: (1) dams associated with impoundments, hydroelectric energy generation, or water diversions, (2) lentic environments created at upstream extents of reservoirs, (3) stream desiccations occurring as a consequence of anthropogenic water withdrawals, and (4) the upstream natural distribution of targeted species. Distribution of dams was evaluated using the National Inventory of Dams (NID) compiled by the United States Army Corp of Engineers and through inspection of aerial photography. Areas of stream desiccation were identified during reviews of literature pertaining to distributions of Great Plains fishes (e.g., Cross et al. 1985; Luttrell et al. 1999), and the period of time for which dewatered streams occurred was quantified using United States Geological Survey (USGS) streamflow data. Streamflow data were downloaded from USGS gauges for the period following most major alterations to flow regime associated with groundwater withdrawals (1969-2009; Milly et al. 2005; Gido et al. 2010) and discharge values (mean annual and monthly median) were quantified and compared to available historical data (pre-1968) using Indicators of Hydrologic Alteration (IHA; Richter et al. 1996). Whereas stream desiccations are likely semi-permeable barriers, they were included because of the substantial period of the year in which movement was precluded (Luttrell et al. 1999) and because pelagic-spawning cyprinids typically do not occupy ephemeral streams (Cross et al. 1985). When barriers isolated populations in upstream segments, extent of target species natural distributions within upstream reaches were based on accounts in Lee et al. (1980) following the methods of Dudley and Platania (2007).

Stream lengths between barriers were quantified in river kilometers (rkm) using the stream layer associated with the National Hydrography Dataset (NHD) from the USGS. Stream lengths were measured along the main-channel, excluding oxbows or parallel secondary channels. When data were available, all adjoining main-stem fragments within a basin were targeted. We excluded mainstem sections of the Missouri and Mississippi rivers because of large differences in stream size and relatively sparse historical data. Stream fragment length was then used as a continuous variable to test for species-specific changes in population status and fragment length thresholds in population persistence.

Historical Changes in Fish Assemblages

We reviewed literature accounts regarding the contemporary (1969-2009) and historical (pre-1968) occurrence of eight target species within each fragment. Species were included if found in at least four stream fragments and occurrences were not limited to mainstem Mississippi or Missouri rivers. Confirmed and suspected pelagic-spawning cyprinids targeted throughout the Great Plains were the plains minnow, Arkansas River shiner, sturgeon chub, peppered chub, flathead chub, shoal chub, silver chub, and prairie chub. In general, these species inhabit perennial Great Plains prairie streams where their distributions are limited to mainstem habitats including shallow, braided, and sandy shoals and backwaters where historical (pre-1968) seining data were commonly collected.

Because of differences in sampling methodologies and purposes among published studies, data were used to define four coarse levels of population status: stable, declining, extirpated, and rare. Stable status indicated populations with no reduction in abundance (e.g., density, relative abundance, rank abundance) or distribution (e.g., area inhabited, presence/absence among sampling sites) through time, despite monitoring over a 20 year period. Declining (or depleted) status indicated populations with reductions in either abundance or distribution among sampling periods spread over a period of at least 20 years. Extirpated (or undetectable) status indicated populations not detected within a given fragment in at least 20 years despite continued monitoring. Rare status indicated species that were historically reported within fragments with low frequency or in low abundance; rare occurrences were not included in statistical analyses. Thirty-three published and unpublished accounts were used in describing population statuses of target species. These accounts were partitioned among species-specific descriptions (n = 6; e.g., Luttrell et al. 1999), regional reviews of numerous species-specific accounts (n = 5; e.g., Eisenhour 2004), unpublished assemblage data specific to one or more fragments (n = 4; e.g., G. Wilde, Texas Tech University, unpublished data), and published accounts specific to one or more fragments included in this study (n = 18; e.g., Hoagstrom et al. 2011).

Data Analysis

We used stream fragment length as a continuous independent variable to test the hypothesis that the status of populations occurring within larger fragments are more likely to be stable. A single-factor analysis of variance (ANOVA) was used to test for differences in mean stream lengths for fragments with stable, declining, or extirpated populations of each species. We used a Bonferroni adjustment to control for experiment-wise error associated with conducting ANOVAs for eight species ($\alpha = 0.05/8 = 0.006$). Post-hoc multiple comparisons among the three population types were conducted within species using Fisher's Least Significant Differences (LSD; $\alpha = 0.006$). Additionally, we tested for differences in population status among grand means of fragment lengths for all species combined (i.e., mean fragment lengths for each population status were combined among species) using an ANOVA and Fisher's LSD.

Initial observations indicated many species did not persist in shorter fragment lengths, supporting published accounts of pelagic-spawning cyprinid extirpations in shorter fragments of the Rio Grande Basin of New Mexico (Dudley and Platania 2007). Accordingly, we tested for minimum thresholds in fragment length associated with population status of each species using Classification Tree Analysis (CTA; De'ath and Fabricius 2000). We asked if thresholds existed for species persistence (i.e., extant populations) and local extinction, which might lend insight into the minimum possible fragment length needed to maintain pelagic-spawning cyprinid populations. For extinction threshold analysis, declining and stable populations of species were combined to represent fragments capable of supporting persistence of pelagic-spawning species, although we acknowledge declining populations may in fact be related to fragment length (Dudley and Platania 2007; this study).

Finally, we used polynomial logistic regression to model fragment length (predictor variable) against extirpations within pelagic-spawning assemblages (i.e., all pelagic-spawning species within a fragment) for each fragment (response variable) to assess the relationship between fragmentation and extirpation at the guild level. The coefficient of determination was calculated using the Nagelkerke R^2 value (Nagelkerke 1991). We then regressed our estimated thresholds in fragment length (predictor variable) against the percent of extant populations (response variable) for each species to quantify the relationship between fragment thresholds and population persistence.

Results

Within the Great Plains region of North America, 60 stream fragments met the requirements for inclusion in our study (Figure 2.1). The length of these fragments ranged from 38 to 705 rkm (Table 2.1). Barriers to fish dispersion included 36 dams associated with water diversions, hydroelectric generation, and reservoir storage, 39 lower bounds defined by impounded water, 21 upper bounds defined by upstream extent of pelagic-spawning cyprinid natural distributions, and six localized regions where water withdrawals resulted in reduced discharges and stream desiccation. Streamflows were reduced by 48-83% among fragments associated with stream dewatering, which generally resulted in discharge values of $0 \text{ m}^3/\text{s}$ throughout pelagic-spawning cyprinid reproductive seasons (May-August) as well as most of the year (up to 310 days; Table 2.2).

Population status of confirmed or suspected pelagic-spawning cyprinids consisted of 57% extirpated, 21% declining, and 22% stable populations ($n = 157$ observations among species). Among 90 extirpations, 8 occurred in the northern region of the Great Plains (Montana, North Dakota, South Dakota, Wyoming), 45 in the central (Nebraska, Colorado, Kansas), and 37 in the southern (New Mexico, Texas, Oklahoma). Among species, the plains minnow occurred in the greatest number of fragments ($n = 48$) and the narrowly distributed prairie chub occurred in the fewest ($n = 4$). Three stream fragments exhibited extensive dewatering and various levels of fragmentation because of temporal variation in stream desiccations between barriers; these included the Arkansas River and upper reaches of the Cimarron River in southwestern Kansas (i.e., fragment ID numbers 33, 40, 41; Cross et al. 1985; Luttrell et al. 1999). We initially retained these fragments in our study because they represented historical occurrences of species, but in each case fragmentation was confounded by loss of a definable fragment length. Among remaining fragments ($n = 57$), stream lengths differed according to population status for plains minnow ($F_{2,42} = 24.92$, $P < 0.01$, Bonferroni adjusted), Arkansas River shiner ($F_{2,13} = 24.97$, $P < 0.01$), sturgeon chub ($F_{2,9} = 11.45$, $P = 0.03$), flathead chub ($F_{2,23} = 14.40$, $P < 0.01$), shoal chub ($F_{2,13} = 15.23$, $P < 0.01$), and silver chub ($F_{2,11} = 98.71$, $P < 0.01$). ANOVA could not be conducted for peppered chub or prairie chub because of rare occurrences of persistent populations, but the association between population status and fragment length was consistent with other species (Figure 2.2). Grand mean rkm lengths differed ($F_{2,21} = 30.14$, $P < 0.01$)

among all species combined and averaged (\pm SD) 136 (\pm 21) for extirpated, 226 (\pm 69) for declining, and 458 (\pm 137) for stable populations.

Fragment length thresholds associated with localized extirpations varied by species. Classification Tree Analysis (CTA) produced models that significantly differed from random ($\alpha = 0.05$), successfully classified populations as extant or extirpated (as measured by Cohen's Kappa, κ), and produced estimated minimum thresholds in fragment length (rkm) associated with population persistence for plains minnow (115 rkm, $P < 0.01$, $\kappa = 0.81$), Arkansas River shiner (217 rkm, $P = 0.01$, $\kappa = 0.77$), sturgeon chub (297 rkm, $P = 0.01$, $\kappa = 0.79$), flathead chub (183 rkm, $P < 0.01$, $\kappa = 0.85$), shoal chub (103 rkm, $P < 0.01$, $\kappa = 0.75$), and silver chub (203 rkm, $P < 0.01$, $\kappa = 0.8$). Model calculation of minimum threshold lengths were not possible for peppered chub or prairie chub because each of these species included only one declining and one stable population. For both species, the median fragment length between declining and extirpated population statuses was used to estimate the minimum threshold necessary for population persistence, resulting in threshold estimates of 205 rkm for peppered chub and 128 rkm for prairie chub. These estimates combined with CTA results produced minimum length thresholds ranging from 103 to 297 rkm, below which species-specific extirpations occurred.

When pelagic-spawning cyprinid assemblages were considered, and the proportion of species extirpated from assemblages regressed against stream fragment length, differential thresholds in persistence contributed to a logistic relationship (Figure 2.3a). This pattern was characterized by 100% extirpation of pelagic-spawning assemblage members within fragments <103 rkm, variable percentages in extirpation among fragments ranging 103-297 rkm, and no reported extirpations among fragments >297 rkm in length. Stream fragmentation explained 71% (Nagelkerke $R^2 = 0.71$, $P < 0.01$) of pelagic-spawning assemblage member extirpations within the 57 stream fragments included in our analysis (excluding fragment ID numbers 33, 40, and 41). Similarly, estimated minimum thresholds in fragment length for the eight species included in our analysis explained 67% ($R^2 = 0.67$, $P < 0.01$) of the variation in the number of extant populations (Figure 2.3b).

Discussion

Fragmentation Drives Imperilment

Pelagic-spawning cyprinid assemblages inhabiting fragmented streams throughout the Great Plains represent a disappearing guild of fishes, as evidenced by high imperilment rates and conservation listings at state, regional, and national levels (Jelks et al. 2008). Reported reductions in abundance and distribution include extirpation from 45% of its historical range for the sturgeon chub (Rahel and Thel 2004), 55% for shoal chub (Luttrell et al. 1999), 80% for Arkansas River shiner (Wilde 2002), and 90% for peppered chub (Luttrell et al. 1999). Our findings supported extirpation from a majority (i.e., >50%) of fragments included in this study for the flathead chub (61%), silver chub (64%), and sturgeon chub (75%), and values that closely match previously reported extirpations for the Arkansas River shiner (79%) and peppered chub (88%). Similar extirpations have occurred among six species of pelagic-spawning cyprinids in the Rio Grande and Pecos River basins of New Mexico and Texas, where the Rio Grande shiner *Notropis orca* and Rio Grande bluntnose shiner *Notropis simus simus* are now extinct and remaining species are restricted to river fragments >100 kilometers in length (Dudley and Platania 2007). Two species of pelagic-spawning cyprinids endemic to the Brazos River of Texas, the sharpnose shiner *Notropis oxyrhynchus* and smalleye shiner *Notropis buccula*, are now restricted to approximately one-third of their historical range because of stream fragmentation and associated effects of reservoirs (Durham and Wilde 2009a). These reported patterns of decline are evident across a large spatial extent (i.e., the entire Great Plains), include multiple taxonomic levels (i.e., 4 genera, 16 species, 2 subspecies; Platania and Altenbach 1998; Durham and Wilde 2009a; this study), span 13 North American ecoregions, and collectively include 8% of the imperiled freshwater cyprinids in North America (Jelks et al. 2008). Consequently, pelagic-spawning cyprinids represent a substantial challenge for conservation of biodiversity in North America.

Though previous studies have formulated a number of reasons for observed declines, our synthesis of declines suggests imperilment of pelagic-spawning cyprinids is a direct consequence of stream fragmentation. This pattern is seemingly driven by instream barriers precluding upstream migration of adults (Luttrell et al. 1999) as well as reduced downstream dispersion and recruitment of drifting ichthyoplankton (Dudley and Platania 2007). Throughout the Great

Plains, we found estimated minimum thresholds in fragment length varied among eight species, but were consistently >100 rkm in length. Suspected pelagic-spawning shoal chub exhibited the shortest threshold in longitudinal length (103 rkm), which was consistent with Platania and Altenbach's (1998) conclusion that the speckled chub (*Macrhybopsis aestivalis*) (once synonymous with shoal chub; Eisenhour 2004) require relatively shorter stream lengths for completion of life history. Our estimated minimum thresholds for Arkansas River shiner and peppered chub (217 and 205 rkm, respectively) were consistent with Bonner and Wilde's (2000) conclusion that the Canadian River between Ute and Meredith reservoirs (220 rkm) represents the near minimum length required for completion of their reproductive cycles. Furthermore, our estimated minimum threshold of 297 rkm for sturgeon chub resembled the apparent minimum stream length necessary for persistence of the closely related sicklefin chub (*Macrhybopsis meeki*) (i.e., 301 rkm; Deiterman and Galat 2004).

Our results contradict the findings of Medley et al. (2007) and Widmer et al. (2010) who suggest that given the appropriate habitat complexity, reproduction and recruitment of pelagic-spawning fishes is possible in stream fragments <100 rkm. However, the above studies were based only on modeling the retention of artificially manufactured eggs and did not consider the many factors that long stream fragments can play in the success of these species (Zymonas and Propst 2009). A notable oversight of these studies is the potential for an obligate drifting larval stage, which might contribute to the need for increased longitudinal distances within fragmented streams given drifting might not cease at the end of the egg developmental phase. The extent to which larval individuals continue to drift is unknown for many of the species included in this study, but high abundances during drift sampling suggests drift frequently occurs among larval pelagic-spawning fishes (Simon 1999; Durham and Wilde 2008). The paucity of data related to reproductive mechanisms for suspected pelagic-spawning fishes and for patterns in larval drift among all species in this study suggests future research into declining Great Plains cyprinids is necessary. However, conservation approaches aimed at mitigating massive declines of poorly studied species necessitate management actions based on the best available biological data (Richter et al. 2003). Imperilment associated with stream fragmentation provides a parsimonious mechanism that links widely dispersed literature accounts of decline among eight highly imperiled Great Plains fishes, and likely provides a framework for future investigations related to potential conservation approaches.

The Hierarchical Effects of Fragmentation

Stream fragmentation produces a hierarchy of environmental changes that imperil stream-dwelling fishes through direct and indirect pathways. Notable environmental changes associated with construction of large instream barriers include alteration of downstream flow regimes, water temperatures, and channel morphologies (Poff et al. 1997). Direct consequences of altered flow regimes include removal of high flow pulses that cue synchronization of spawning, increase spawning intensity, and maintain eggs in suspension long enough for hatching (Moore 1944; Bottrell et al. 1964). Reductions in mean annual discharge negatively affect some pelagic-spawning species because recruitment of age-0 individuals is directly dependent upon discharge (Wilde and Durham 2008; Durham and Wilde 2009b). Throughout the Great Plains, we found extirpation of pelagic-spawning cyprinids occurred to the highest extent in the central and southern Great Plains regions, where notable reductions in discharge have occurred since at least the 1970s (Cross et al. 1985; Gido et al. 2010). In these cases, reductions in discharge likely contributed to declines and extirpations by inducing both fragmentation and negative effects on reproductive success. For example, groundwater withdrawals in western Kansas have contributed to dry streams during 70-99% of pelagic-spawning cyprinid reproductive seasons (May-August), providing limited opportunity for spawning and successful recruitment (Aguilar 2009). Projected changes in climate suggest this region of the Great Plains will undergo further reductions in stream discharge associated with variation in precipitation and evapotranspiration cycles (Milly et al. 2005). Consequently, the possibility exists for reductions in discharge, both related to anthropogenic withdrawal and climate change, to contribute to an increase in declines and extirpations among Great Plains pelagic-spawning cyprinids in this region (Taylor 2010). This conclusion is consistent with the findings of a recent large-scale literature review that found alteration to magnitude of discharge was detrimental to many fluvial organisms, notably fishes (Poff and Zimmerman 2010).

Indirect effects of instream barriers such as deep storage reservoirs alter downstream thermal regimes and channel morphologies. Reservoirs that release water from the hypolimnion contribute to cooler tail-water temperatures, and effects extend many kilometers downstream (Edwards 1978). Development rates of drifting eggs and larvae are prolonged during cooler water temperatures, contributing to the need for further downstream transport before free-swimming larval stages are reached. Similarly, sustained high flows associated with reservoir

releases contribute to increased downstream transport through homogenization of habitat (e.g., deep, incised channels) and increased rate of flow (Dudley and Platania 2007). Our analysis did not include measurements of water temperature or channel morphology, two factors that might be manipulated more easily than removal of large impoundments or diversion dams to facilitate pre-larval development within stream fragments (Widmer et al. 2010). However, our findings across a diversity of streams with regional variation in temperature and channel morphology suggest that fragment lengths <100 rkm were correlated with extirpation of pelagic-spawning cyprinids in areas upstream of impoundments, where habitat complexity is not altered by reservoir management. This patterned occurred for seven fragments in which 100% of pelagic-spawning cyprinids were extirpated, suggesting mitigation of extirpation through restoration of habitat complexity should not discount overall fragment length. Additional support for the importance of long river fragments for all eight species included in this study is the occurrence of declining populations within intermediate-length fragments. These declines might be related to time-lag effects associated with reduced reproductive success ultimately arising from changes in flow regime (Perkin and Bonner 2010) or possibly because fragment lengths (i.e., patch sizes) are no longer large enough to support historical population sizes (Aló and Turner 2006).

Mitigation Potential and Broader Implications

Future approaches targeting enhanced conservation of Great Plains pelagic-spawning cyprinids, as well as a diversity of stream-dwelling organisms, will likely require restoration or preservation of connectivity within stream systems. In particular, the use of fishways that allow passage in an upstream direction for a wide range of fishes (Prchalová et al. 2006) are likely of great conservation value. However, a paucity of empirical data exists pertaining to the passage of small-bodied cyprinids through fishways, though existing evidence suggests passage is possible (Prchalová et al. 2006; Bestgen et al. 2010). The greater challenge will ultimately involve the downstream passage of drifting ichthyoplankton, especially through large reservoirs (Agostinho et al. 2007; Pompeu et al. In Press). We are unaware of initiatives aimed specifically at allowing the downstream transport of ichthyoplankton through reservoirs in fragmented river systems, which is perhaps the greatest challenge associated with conservation of pelagic-spawning cyprinids. Additional conservation options for mitigating the effects of fragmentation include management of flow regimes that target recruitment of native fishes (Propst and Gido

2004), release of epilimnetic water to minimize thermal alterations (Dudley and Platania 2007), and management of instream habitat complexity to facilitate increased heterogeneity (Widmer et al. 2010). Ecological benefits of these mitigation approaches hold potential for improving the conservation status of many diadromous and freshwater fishes not included in this study (Jelks et al. 2008) as well as riparian vegetation forms, unionid mussels, and aquatic invertebrates (Lytle and Poff 2004). Unregulated, interconnected river systems have driven the adaptation and evolution of fluvial organisms and preservation of stream communities will ultimately require trade-offs between ecological needs of streams and human needs associated with freshwater resources (Richter et al. 2003; Lytle and Poff 2004; Limburg et al. 2011). Restoration approaches targeting improvement at riverscapes scales hold potential for successful species and ecosystem preservation; however, such approaches are limited by the ability to identify appropriate spatial scales at which to implement management actions (Fausch et al. 2002). Our findings suggest providing connectivity at spatial scales on the order of hundreds of rkm is likely necessary for the preservation of at least one diverse functional group of stream-dwelling organisms in the Great Plains, which is consistent with recent calls for improving connectivity within streams across the globe (e.g., Nilsson et al. 2005; Agostinho et al. 2007; Dudley and Platania 2007).

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Figure 2.1 Distribution of North American Great Plains stream fragments included in analyses. Fragment numbers correspond with descriptions in Table 2.1.

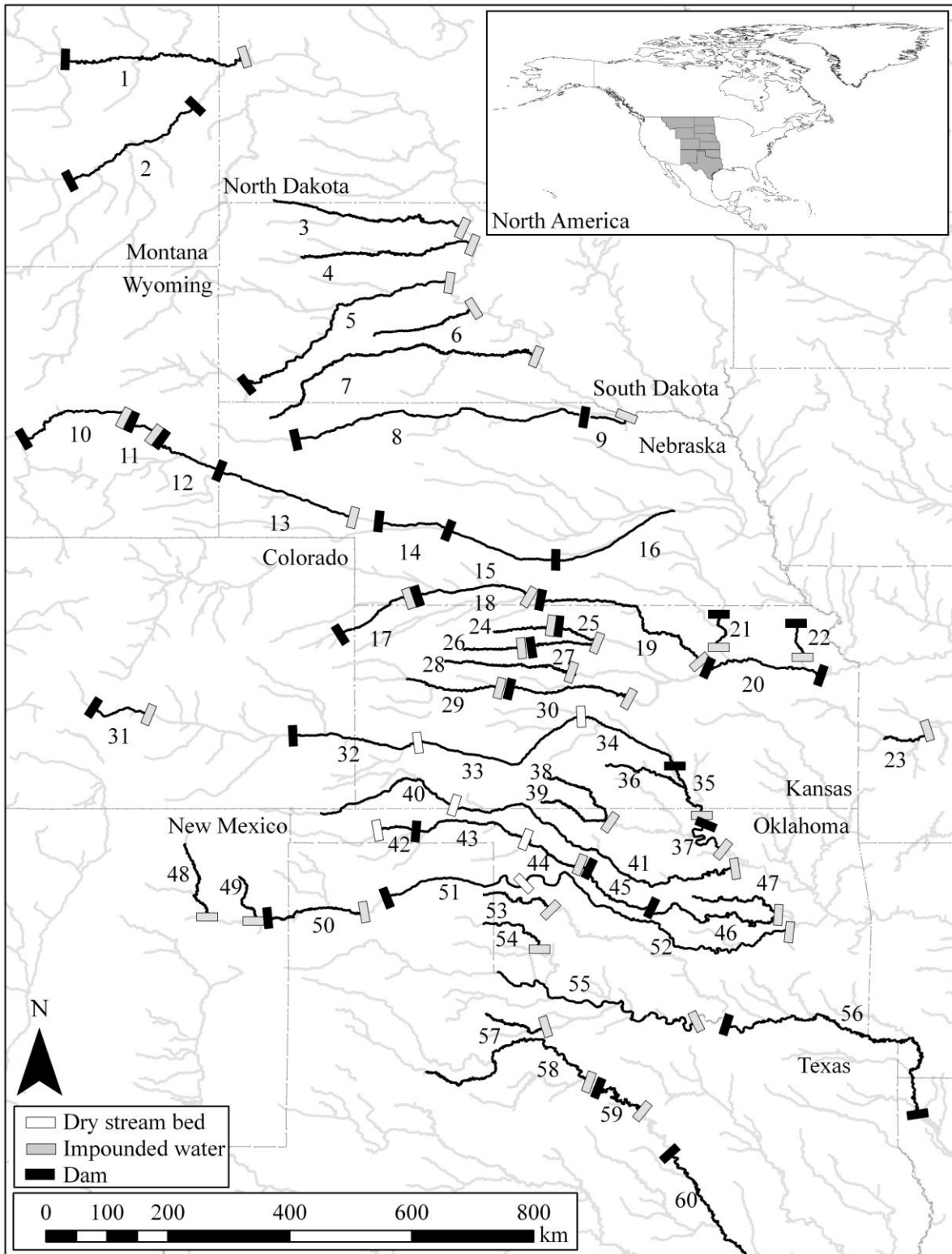


Figure 2.2 Mean (\pm SD) stream fragment lengths (river kilometers, rkm) for confirmed (left column), suspected (right column), and combined (bottom, center) Great Plains pelagic-spawning cyprinid populations according to population status: extirpated (E), declining (D), and stable (S). Lowercase letters represent statistical differences among statuses (see text for statistical procedures).

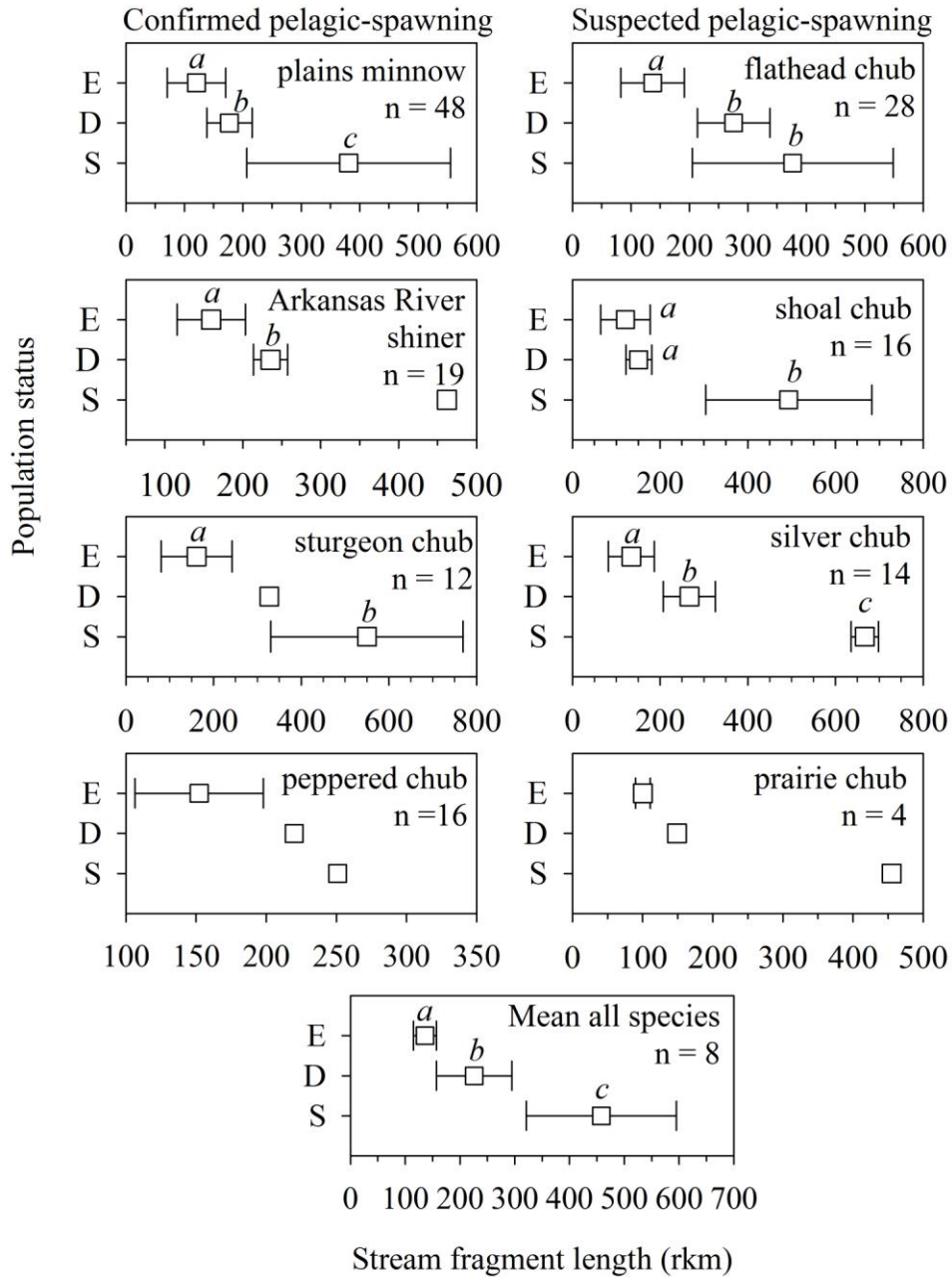


Figure 2.3 (a) Proportion of species extirpated from Great Plains pelagic-spawning cyprinid assemblages as a function of stream fragment length measured in riverine km (rkm; x-axis log-scaled). (b) Percent of extant populations for eight Great Plains pelagic-spawning species as a function of the estimated minimum threshold (rkm) necessary for persistence.

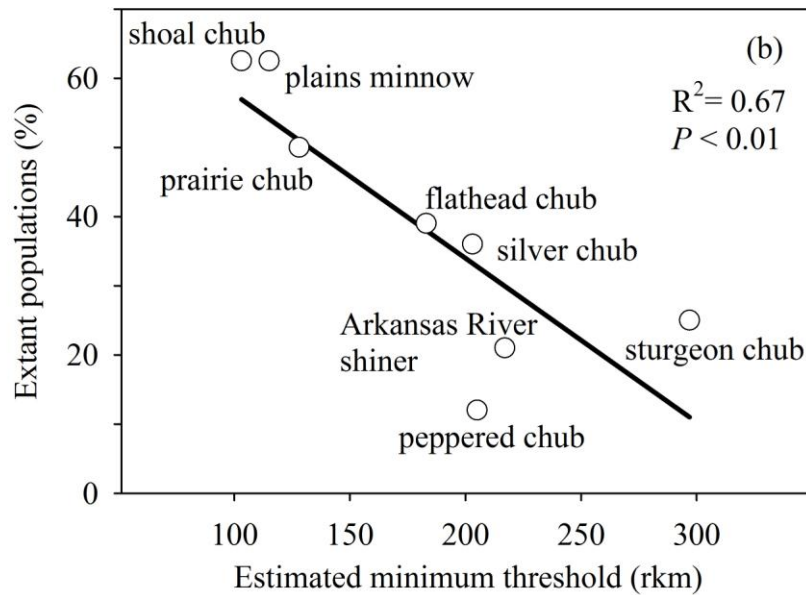
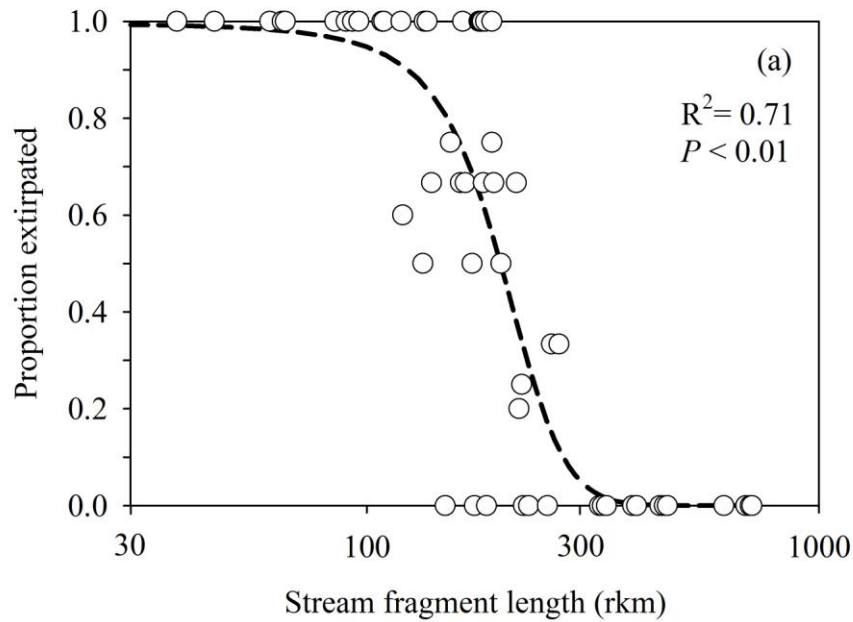


Table 2.1 Description, length (riverine km), and population status (S, stable; D, declining; E, extirpated; R, rare) of eight Great Plains fishes (1, Plains minnow; 2, Flathead chub; 3, Sturgeon chub; 4, Silver chub; 5, Shoal chub; 6, Peppered chub; 7, Arkansas River shiner; 8, Prairie chub) within 60 stream fragments. Full citations for works referenced within the table are available upon request or see Perkin et al. (2010).

No.	Fragment Description	Length	1	2	3	4	5	6	7	8	References
1	Yellowstone R. between Fort Peck Dam and upper reaches of Lake to Sakakawea	327	S	D	D						18, 19, 33
2	Yellowstone R. between Cartersville Dam and Intake Dam	266	S	S	E						18, 19, 33
3	Mainstem Grand R. of South Dakota upstream of Lake Oahe	256	S	S	E						29, 30, 33
4	Mainstem Monroe R. of South Dakota upstream of Lake Oahe	387	S	S							30, 33
5	Cheyenne R. between Angostura Dam and upper reaches of Lake Oahe	395	S	S	S						30, 31, 33
6	Mainstem Bad R. of South Dakota upstream of Lake Sharpe	184	S	S							29, 30, 33
7	Mainstem White R. of South Dakota upstream of Lake Francis Case	705	S	S	S						30, 33
8	Niobrara R. between Box Butte Dam and Spencer Dam	445		S							26, 29
9	Niobrara R. between Spencer Dam and upper reaches of Lewis and Clark Lake	65	E	E	E	E					11, 26, 33
10	North Platte R. between Alcova Dam and upper reaches of Glendo Res.	228	S	D							12, 33
11	North Platte R. between Glendo Dam and upper reaches of Guernsey Res.	46	E	E	E						11, 26, 33
12	North Platte R. between Guernsey Dam to WY/NE diversion dam	96	E	E	E						11, 26, 33
13	North Platte R. between WY/NE diversion dam and upper reaches of McConaughy Res.	198	S		E						11, 12, 33
14	North Platte R. between Kingsley Dam and Diversion dam at North Platte, NE	96	E	E							12, 33
15	Platte R. North Platte diversion dam to weir dam near Elm Creek, NE	133	D	E	E		D				11, 14, 26, 33
16	Platte R. between weir dam near Elm Creek, NE and Columbus, NE	217	S	D	E	D	D				11, 14, 26, 33
17	Republican R. between dam at Bonny, CO and upper reaches of Swanson Res.	136		E							4, 26
18	Republican R. between Trenton Dam and upper reaches of Harlan County Res.	181		E		E	D				4, 11, 33
19	Republican R. between Harlan County Dam and upper reaches of Milford Res.	332	S	D		D	S				4, 26, 33
20	Kansas R. between Milford Dam and Bowersock Dam	177	E	E	E	E	E				4, 6, 11, 33

Table 2.1 Continued

No.	Fragment Description	Length	1	2	3	4	5	6	7	8	References
21	Big Blue R. between Marysville Dam and upper reaches of Tuttle Creek Res.	66					E				23
22	Delaware R. between Mission Lake Dam and upper reaches of Perry Lake	61		E		E	E				4
23	Osage R. upstream of upper reaches of Truman Res.	85				E	E				16, 20
24	North Fork Solomon R. upstream of upper reaches of Kirwin Res.	109	E								4, 22, 33
25	North Fork Solomon R. between Kirwin Dam and upper reaches of Waconda Res.	93	E								4, 22, 33
26	South Fork Solomon R. between Hoxie, KS and upper reaches of Webster Res.	90	E								4, 22, 33
27	South Fork Solomon R. between Webster Dam and upper reaches of Waconda Res.	134	E								4, 22, 33
28	Saline R. upstream of upper reaches of Wilson Res.	189	E			E					4, 15, 33
29	Smokey Hill R. between Wallace County Kansas and upper reaches of Cedar Bluff Res.	173	D								15, 33
30	Smokey Hill R. between Cedar Bluff Dam and upper reaches of Kanopolis Res.	222	D								15, 33
31	Arkansas R. between Salida, CO and dam at Florence, CO	119		E							26
32	Arkansas R. between John Martin Dam and Lakin, KS	179		E				E			5, 20, 33
33	Arkansas R. between Lakin, KS and Great Bend, KS	290	E	E				E	E		5, 20, 27, 28, 33
34	Arkansas R. between Great Bend, KS and weir dam at Wichita, KS	178	E	E		E		E	E		5, 20, 27, 28, 33
35	Arkansas R. between weir dam at Wichita, KS and upper reaches of Kaw Res.	153	D			E	E		E		5, 20, 27, 28, 33
36	Ninnescah/Arkansas rivers between Cairo, KS and upper reaches of Kaw Res.	251	D			D		S	D		4, 28, 33
37	Arkansas R. between Kaw Dam and upper reaches of Keystone Lake	120	D			E	S	E	E		20, 25, 27, 33
38	Mainstem Medicine Lodge R. upstream of upper reaches of Great Salt Plains Lake	165	D					E	E		5, 33
39	Mainstem Salt Fork Arkansas R. upstream of upper reaches of Great Salt Plains Lake	163	E					E	E		5, 33
40	Cimarron R. between Castaneda, OK and just East of Liberal, KS	277	E	E				E	E		5, 33
41	Cimarron R. between just East of Liberal, KS and Keystone Lake	434	D					E	D		5, 20, 33
42	North Canadian R. between Pony Creek confluence and Optima Dam	38	E					E	E		7, 9, 20, 33
43	North Canadian R. between Optima Dam and Fort Supply (Wolf Creek Confluence)	191	D					E	E		7, 9, 20, 33
44	North Canadian R. between Fort Supply and upper reaches of Canton Lake	139	D					E	E		7, 9, 20, 33
45	North Canadian R. between Canton Dam and Overholser Dam, Oklahoma City	161	D					E	E		7, 9, 20, 33

Table 2.1 Continued

No.	Fragment Description	Length	1	2	3	4	5	6	7	8	References
46	North Canadian R. between Overholser Dam and upper reaches of Urika Res.	339							R		9, 33
47	Deep Fork R. upstream of upper reaches of Lake Eufaula	183					E		E		9, 20, 33
48	South Canadian R. upstream of upper reaches of Conchas Lake	180	E	E					E		8, 33
49	Ute Creek between Gladstone, NM to upper reaches of Ute Res.	189	D	E				E	E		17, 33
50	South Canadian R. between Ute Dam and upper reaches of Lake Meredith	220	D	E				D	D		21, 33
51	South Canadian R. between Sanford Dam and Roger Mills County, OK	214	D	R				E	E		1, 21, 33
52	South Canadian R. between Roger Mills County, OK and Urika Res.	462	S				S	R	S		1, 9, 20, 25, 33
53	Washita R. upstream of upper reaches of Foss Res.	93								E	24, 33
54	North Fork of the Red R. upstream of upper reaches of Altus Res.	108	E							E	10, 33
55	Upper Red R. between Prairie Dog Town Fork and upper reaches of Lake Texoma	455	S							S	13, 33
56	Red R. between Denison Dam and Dam at Shreveport, LA	689	S			S	S				25, 33
57	North Fork Wichita R. between Truscott, TX and upper reaches of Lake Kemp	149	D							D	2, 33
58	Brazos R. between McMillan Dam and upper reaches of Possum Kingdom Res.	616	S				S				2, 33
59	Brazos R. between Morris Sheppard Dam to upper reaches of Lake Waco	171	E				D				3
60	Brazos R. downstream of Waco Dam to Gulf of Mexico	645				S	S				32

1: Gene Wilde, Texas Tech University, unpublished data; **2:** Fran Gelwick, Texas A&M University, unpublished data; **3:** Jack Davis, Brazos River Authority, unpublished data; **4:** Keith Gido, Kansas State University, unpublished data; **5:** Cross et al. (1985); **6:** Cross and Moss (1987); **7:** Pigg (1987); **8:** Sublette et al. (1990); **9:** Pigg (1991); **10:** Winston et al. (1991); **11:** Hesse et al. (1993); **12:** Lynch and Roh (1996); **13:** Taylor et al. (1996); **14:** Chadwick et al. (1997); **15:** Eberle et al. (1997); **16:** Pflieger (1997); **17:** Pittenger and Schiffmiller (1997); **18:** Patton et al. (1998); **19:** Helfrich et al. (1999); **20:** Luttrell et al. (1999); **21:** Bonner and Wilde (2000); **22:** Eberle et al. (2002); **23:** Gido et al. (2002); **24:** Eisenhour (2004); **25:** Miller and Robison (2004); **26:** Rahel and Thel (2004a); **27:** Rahel and Thel (2004b); **28:** Haslouer et al. (2005); **29:** Hoagstrom et al. (2006); **30:** Hoagstrom et al. (2007a); **31:** Hoagstrom et al. (2007b); **32:** Runyan (2007); **33:** Hoagstrom et al. (2010).

Table 2.2 Fragment number, United States Geological Survey (USGS) gauge number, flow period, and historical (pre-1968) and contemporary (1969-2009) values for mean annual flow (M.A.F.; m³/s), median number of zero flow days, and median monthly flow values (m³/s) for cyprinid reproductive seasons (May-August) for stream fragments associated with dewatering and desiccation.

Fragment number	USGS gauge	Flow period	Historical						Contemporary					
			M.A.F.	Zero days	May	June	July	August	M.A.F.	Zero days	May	June	July	August
33 ^a	7139000	1938-2009	5.68	0	0.40	0.76	0.40	0.31	2.97	211	0.00	0.00	0.00	0.00
34 ^a	7141220	1999-2009	NA	NA	NA	NA	NA	NA	3.76	119	0.01	0.02	0.15	0.00
41 ^a	7155590	1971-2009	NA	NA	NA	NA	NA	NA	0.23	310	0.00	0.00	0.00	0.00
42 ^b	7232500	1932-1993	0.84	2	0.14	0.07	0.09	0.05	0.15	186	0.04	0.00	0.00	0.00
44 ^b	7234000	1938-2009	2.79	72	0.86	0.80	0.46	0.03	0.5	60	0.32	0.13	0.00	0.00
52 ^b	7228000	1938-2009	11.65	0	0.35	2.34	0.60	0.37	1.94	0	1.46	1.20	0.32	0.27

^aDesiccations associated with reduced species distributions (Cross et al. 1985)

^bDesiccations and dewatering associated with reduced species distributions (Pigg 1991)

Chapter 3 - Fragmentation Alters Stream Fish Community Structure in Dendritic Ecological Networks

Abstract

Effects of fragmentation on the ecology of organisms occupying dendritic ecological networks (DENs) have recently been described through both conceptual and mathematical models, but few hypotheses have been tested in complex, real-world ecosystems. Stream fishes provide a model system for assessing effects of fragmentation on the structure of communities occurring within DENs, including how fragmentation alters metacommunity dynamics and biodiversity. A recently developed habitat availability measure, the Dendritic Connectivity Index (DCI), allows for assigning quantitative measures of connectivity in DENs regardless of network extent or complexity and might be used to predict fish community response to fragmentation. We characterized stream fish community structure in 12 DENs in the Great Plains, USA during periods of dynamic (summer) and muted (fall) discharge regimes to test the DCI as a predictive model of fish community response to fragmentation imposed by road crossings. Results indicated fish communities in stream segments isolated by road crossings had reduced species richness (alpha diversity) relative to communities that maintained connectivity with the surrounding DEN during summer (mean \pm SD number of species: fragmented = 8.1 ± 3.5 , unfragmented = 10.5 ± 2.4 , $p < 0.01$) and fall (fragmented = 7.0 ± 4.0 , unfragmented = 10.8 ± 2.7 , $p < 0.01$). Furthermore, isolated communities had greater dissimilarity (beta diversity) to downstream sites not isolated by road crossings during summer (15% greater dissimilarity, $p < 0.01$) and fall (14%, $p = 0.04$). Finally, dissimilarity among communities within DENs decreased as a function of increased habitat connectivity (measured using the DCI) for summer ($r^2 = 0.64$, $p < 0.01$) and fall ($r^2 = 0.57$, $p = 0.03$), suggesting communities within highly connected DENs tend to be more homogeneous. Our results indicate that the DCI is sensitive to community effects of fragmentation in riverscapes and might be used by managers to predict ecological responses to changes in habitat connectivity. Moreover, our findings illustrate that relating structural connectivity of riverscapes to functional connectivity among communities might aid in maintaining metacommunity dynamics and biodiversity in complex dendritic ecosystems.

Introduction

Recent advances in community ecology have emphasized the relationship between ecological network structure and patterns and processes occurring within ecosystems (Brown and Swan 2010, Auerbach and Poff 2011). In particular, streams are unique in that they are constrained dendritic ecological networks (DENs) generally characterized by bifurcating branches of habitat that decrease in size and increase in number with greater distance from the base of the network (Dodds and Rothmann 2000). Examples of DENs include linear or fractal-like systems such as caves or streams with hierarchically structured patches of habitat that house multi-species communities linked by dispersal (Grant et al. 2007, Grant 2011). The framework by which multiple communities are linked by dispersal of organisms is the basis of the metacommunity concept as defined by Leibold et al. (2004), in which environmental heterogeneity, species-environment relationships, and dispersal patterns are used to describe community assembly processes. Local community composition is dependent upon local abiotic and biotic conditions as well as regional species pools; however, in streams, location within DENs and connectivity among network segments (patches) is an important abiotic constraint that can be a primary driver of community composition (Labonne et al. 2008, Thornbrugh and Gido 2010, Brown et al. 2011, Finn and Poff 2011). Taken together, these findings suggest spatial distribution of habitat patches and dispersal of organisms among patches (i.e., the principles of metacommunity theory, Leibold et al. 2004) aid in synthesizing complex dynamics in DENs (Brown et al. 2011). However, real-world applications of metacommunity dynamics in the context of DENs are rare (Brown et al. 2011) and existing knowledge was derived largely from theoretical models (e.g., Goldberg et al. 2010, Padgham and Webb 2010) with little empirical support (but see Falke and Fausch 2010 and Peres-Neto and Cumming 2010). Validating models of metacommunity dynamics in DENs with empirical data will assist in understanding how human-mediated alterations to dendritic networks threaten biodiversity as well as aid in directing conservation actions (Falke and Fausch 2010, Grant 2011).

Fragmentation of streams causes concern for the long-term persistence of species (Fagan 2002, Perkin and Gido 2011) as well as the goods and services provided by those ecosystems (Srivastava and Vellend 2005, Lecerf and Richardson 2010). Connectivity of stream networks is impacted most by the first few barriers introduced to a system, which contrasts most non-dendritic networks that are resistant to fragmentation caused by low numbers of barriers (Cote et

al. 2009). Furthermore, simulations suggest structural modifications to streams such as changes in patch quality and accessibility are additive, causing non-interactive reductions in fish populations as patch quality and accessibility diminish (Padgham and Webb 2010). However, as noted by Padgham and Webb (2010), most analyses of DEN properties to date are theoretically modeled and potentially of limited usefulness in predicting population- or community-level responses to altered connectivity in real-world DENs (Urban et al. 2009). Models predicting metapopulation extinction risk or metacommunity dynamics in DENs are inherently simplified and generally require additional biological information (e.g., dispersal capabilities, network topology) before being applicable to real-world networks because of the complex nature of ecosystems and inability of models to incorporate all realistic parameters (Padgham and Webb 2010, Auerbach and Poff 2011, Grant 2011). Because of these issues, natural experiments that encompass a diversity of network topologies and entire communities might prove useful in predicting consequences of anthropogenic environmental modifications to complex ecosystems (Hitt and Roberts 2012).

Habitat availability measures that relate structural landscape connectivity to functional connectivity among metapopulations or metacommunities within DENs allow for testing the effects of fragmentation on the ecology of organisms inhabiting complex ecosystems. Structural connectivity is defined as the adjacency or proximity of patches within a landscape and is a measure of the degree to which patches are connected without regard to organism behavior or interpretation of the landscape (Taylor et al. 1993). Alternatively, functional connectivity is conceptually defined as the degree to which a landscape impedes or facilitates movement of organisms among patches (Bélisle 2005). The Dendritic Connectivity Index (DCI) developed by Cote et al. (2009) measures structural connectivity of riverine landscapes regardless of the spatial extent or complexity of networks. The DCI considers stream networks as branching lines of continuous habitat in which the absence of barriers yields a DCI value of 100. As barriers are introduced, the number, placement, and permeability of barriers are considered so that the DCI value of a given system declines from 100, and the rate of decline can vary depending upon life history attributes of the stream organisms being considered (i.e., diadromous: moving between freshwater and marine systems; potamodromous: migrating within freshwater systems; Cote et al. 2009). Permeability of barriers is of concern because most stream obstacles do not completely thwart organism dispersal, that is, structures are considered semi-permeable. For

example, Norman et al. (2009) found fish passage at road crossings that exhibited rapid drops in elevation at their outflow, commonly known as perching, was limited to periods of storm runoff when elevated discharges caused water levels to inundate perches. Alexandre and Almeida (2010) found changes in habitat caused by a series of perched crossings resulted in spatially segregated fish communities associated with each crossing so that upstream sites generally had fewer native species, and Nislow et al. (2011) showed that species richness in stream segments upstream of perched crossings was reduced to at least half the number of fishes occurring immediately downstream. These examples illustrate the negative effects of fragmentation on the availability of habitat to fishes in stream networks and the capacity of semi-permeable barriers to mimic larger obstacles (e.g., impoundments; Winston et al. 1991, Luttrell et al. 1999) in disrupting dispersal pathways of fishes (Alexandre and Almeida 2010). However, such examples lack network-scale analysis of barriers (i.e., the cumulative effect of multiple barriers occurring within a network) and do not allow predictive ability regarding ecological responses to fragmentation across riverine landscapes (Fausch et al. 2002). Consequently, examining the performance of habitat availability indices such as the DCI is now a key area of research required for further significant progress in our understanding of the relationship between network structure and community ecology (Erős et al. 2012).

In this study, we use dendritic stream networks and stream fish community samples taken throughout these networks to test for changes in community assembly associated with fragmentation of DENs caused by road crossings. Perched road crossings present semi-permeable barriers characterized by rapid elevation changes or channelized sections with swift current velocities that selectively exclude fishes with slow critical swimming speeds (e.g., Leavy and Bonner 2009), limited leaping ability (e.g., Ficke et al. 2011), or are otherwise disinclined to pass culverts (e.g., Alexandre and Almeida 2010). Barriers to fish movement invoked by road crossings was the impetus for development of the DCI (Cote et al. 2009), and to our knowledge we present the first empirical assessment of the DCI associated with biodiversity patterns in stream fish communities. We show that fragmented communities exhibit lower species richness and increased dissimilarity to communities that maintain connectivity with the surrounding DEN using geo-referenced data for perched road crossings, DENs composed of 2nd and 3rd order streams, and stream fish community data collected from multiple points within 12 replicates of DENs. Furthermore, we show that dissimilarity among communities (an indirect measure of

interrupted functional connectivity) within DENs is negatively correlated with structural connectivity measured using the DCI.

Materials and Methods

Dendritic Ecological Networks and Fragmentation

We evaluated the distribution and topology of stream DENs using a version of the National Hydrology Database (NHD; U.S. Geological Survey, USGS) modified for the Kansas Aquatic Gap program (e.g., Oaks et al. 2005). We selected DENs composed of 2nd and 3rd order streams defined using the Strahler classification system (Strahler 1957) because our primary interest was fragmentation imposed by perched road crossings that occur most frequently within these stream classes (Figure 3.1). Within each DEN, we sampled stream fish communities at three locations designated as (1) a 3rd order stream site from which fish species were expected to disperse upstream, (2) an unfragmented 2nd order stream site with no instream barriers that would thwart dispersal from the 3rd order site, or (3) a fragmented 2nd order stream site separated from the source site by at least one perched road crossing (Figure 3.2a; Figure 3.3). Stream organisms, especially fishes can disperse upstream into adjacent streams during reproductive seasons and such dispersal has implications for local community assembly (Schlosser 1987, Hitt and Angermeier 2006, Grant 2011). For each DEN, unfragmented and fragmented 2nd order stream sampling locations were placed so that distances from the source sampling site were approximately equal. For replication, we selected three DENs composed of streams in close proximity to control for variation in abiotic parameters such as landuse and precipitation as well as biotic parameters such as regional species pools (Figure 3.2b). We then selected four 8-digit USGS hydrologic unit codes (HUCs) in the eastern portion of Kansas (Lower Big Blue, 10270205; Middle Kansas, 10270102; Lower Cottonwood, 11070203; Upper Verdigris, 11070101) that generally correspond with the Flint Hills Ecoregion where uplands are grazed by cattle and river valleys are row crop agriculture (Figure 3.2 c and d). Because of the relatively small size of watersheds included in this study (3rd order catchments) and proximity of sampling sites (<10 km apart), landuse changes were not expected to influence unfragmented and fragmented sampling sites differently within DENs.

We initially used the geographic information systems (GIS) layer produced by the Kansas Department of Transportation (KDOT) for the abundance and distribution of road crossings

potentially characterized by perched outflows capable of blocking fish dispersal. We then used a GIS approach to select three DENs in close proximity with similar topologies (i.e., number of bifurcations) and variation in number and placement of perched road crossings. We estimated average stream width (m) observed during fish community sampling (see below) as a measure of patch size. During field sampling we surveyed all crossings to ensure perches existed. When perches (if present) were inundated by water and therefore did not constitute a barrier to fish dispersal, we removed the barrier from our GIS database. We also evaluated stream corridors to ensure the absence of natural barriers that might confound connectivity measures by walking sections between sampling sites and inquiring with local landowners. To our knowledge no natural barriers to dispersal were present in the study DENs. Because of discrepancies between perched crossings in the initial KDOT GIS layer and those identified during field sampling, the number of unfragmented and fragmented sites was not always balanced within each DEN, although both classifications existed within each HUC (Table 3.1).

We quantified connectivity at the DEN scale using the DCI. Networks were defined as 3rd order streams and all 2nd order tributaries, including tributaries that were not sampled for fish community data, but excluding all 1st order streams because most dry during the year. In all cases, the downstream limit of DENs was the confluence with a 4th order or larger stream. Barriers consisted of all perched road crossings that existed within DENs and were uniformly assigned a permeability value of 0.5 (where 0 = impassible and 1 = completely passable). Although permeability of crossings might be a function of perch height and local hydrologic regimes (Norman et al. 2009, Bourne et al. 2011), we used a value of 0.5 because Cote et al. (2009) found that the DCI yields informative structural connectivity measures even in the absence of specific permeability values for each barrier and because we generally encountered box culverts with perched outflows as barriers (i.e., low-head dams were absent from DENs included in our study system and only one corrugated crossing, which also exhibited perching, was observed). We used the potadromous component of the DCI (i.e., DCI_p) that assumes fishes are not obligated to disperse beyond the lowest levels of DENs (i.e., long distance migrations to the ocean, Cote et al. 2009). This approach includes dividing the total stream network length (measured in stream km) into sections isolated by barriers, then computing a weighted average of connectivity within (permeability = 1) and among (permeability = 0.5) all sections so that greater DCI values correspond with isolation of a smaller fraction of the riverscape (see Cote et al. 2009

and Bourne et al. 2011 for detailed calculation methods). All DCI calculations were conducted in statistical program R version 2.12.1 (R Development Core Team, Vienna, Austria) using source code obtained from David Cote (Parks Canada).

Fish Community Sampling

Stream fish communities were sampled during summer and fall of 2010. Summer sampling was conducted during May and June when Great Plains prairie stream discharges are characterized by flashy pulses with potential to inundate road crossing perches, whereas fall sampling was conducted during September and October when prairie streams typically have muted hydrographs with few pulses (Dodds et al. 2004). At each site, a combination of single-pass electrofishing (Smith-Root® LR-24 backpack electrofisher) and seining (4.6 m by 1.8 m, 3.2 mm mesh) was conducted for 150-300 m of stream following the standardized methods of McMahon et al. (1996) to obtain representative samples of communities within stream reaches. All fishes collected were identified to species, enumerated, and released in the case of large-bodied specimens or retained for laboratory identification in the case of small-bodied specimens. In the field, length and width of habitats sampled were measured to calculate area sampled and estimate fish densities. Each site was visited twice (once during each season) with the exception of sites that dried during the fall and were not sampled a second time (n = 4, Table 3.1). We also visited road crossings within each DEN and surveyed perch heights (cm) using standard survey equipment to verify presence of barriers included in the KDOT GIS layer. Based on the occurrence of perched road crossings (heights 4-102 cm) within DENs, we determined that our summer collections included 12 source, 13 unfragmented, and 13 fragmented communities and fall collections included 12 source, 12 unfragmented, and 10 fragmented communities. The 72 total samples retained excluded four sites (one unfragmented and three fragmented) that dried during fall and a single site that was dominated by groundwater discharge surfacing upstream of the sampling area, which contributed to notably cooler water temperatures, narrow channel widths, and reduced species richness relative to surrounding streams.

Community Composition Within and Among DENs

We evaluated differences in community composition among unfragmented and fragmented sampling sites using distance matrices (Bray and Curtis 1957) as a measure of beta diversity (i.e., biodiversity changeover between sites; greater distance indicates greater beta

diversity) and species richness as a measure of alpha diversity (i.e., biodiversity at a single site). Proportional densities (i.e., density of each species/density of all species encountered) were calculated (fish/m²) for species within each community and imported into the statistical program Primer 6 (Primer-E, Ivybridge, United Kingdom). Because densities of common and rare species varied by two orders of magnitude, we fourth-root transformed data before analyzing to reduced skewness of distributions (Somerfield et al. 1995). We then used the transformed data and the resemblance function in Primer 6 to construct a non-metric Bray-Curtis distance matrix among all communities sampled. We developed pair-wise measures of dissimilarity for all source and unfragmented or fragmented comparisons by multiplying distance measures by 100 to yield values between 0 (i.e., no dissimilarity) and 100 (completely dissimilar). Because habitat isolation and size tend to align along general gradients associated with stream fish community composition (Angermeier and Schlosser 1989, Lonzarich et al. 1998), we tested for differences in distance between unfragmented and fragmented communities from source communities as well as stream size (width in m). For each potentially confounding effect we used linear regression to test for either isolation by distance (i.e., stream distance vs. dissimilarity between sites) or a species-area relationship (i.e., stream width vs. species richness at each site). We then directly compared stream distances from source sites for unfragmented and fragmented sites using a two tailed t-test ($\alpha = 0.05$) and stream widths among source, unfragmented, and fragmented sites using a single factor analysis of variance (ANOVA, $\alpha = 0.05$) followed by Fisher's Least Significant Difference (LSD) multiple comparisons. We hypothesized that communities occurring upstream of perched crossings (i.e., fragmented sites) would show increased dissimilarity to source sites (i.e., greater beta diversity) as well as lower species richness (attenuated alpha diversity) relative to unfragmented sites because of reduced dispersal through perched crossings. We then tested for differences in dissimilarity and species richness between unfragmented and fragmented sites using a two tailed t-test and ANOVA.

We assessed the relationship between structural and functional connectivity to evaluate the effects of fragmentation on metacommunity structure in DENs. We measured structural connectivity at the scale of DENs and deemed patches isolated when perched road crossings occurred using the spatially implicit DCI to produce quantitative measures of connectivity for each DEN. We estimated functional connectivity as the degree of dissimilarity among communities. Thus, increased connectivity throughout the riverscape would contribute to high

faunal similarity and low beta diversity (assuming organisms are moving optimally; Bélisle 2005). We hypothesized that reduced structural connectivity would cause a reduction in functional connectivity among communities because of the lack of alternative routes within stream DENs (Grant et al. 2007). To test this hypothesis we evaluated the relationship between structural and functional connectivity using linear regression and plotting mean dissimilarity among all pair-wise comparisons within a DEN as a function of the DCI. We then considered how structural connectivity related to functional connectivity among HUCs by evaluating the coefficient of determination among DCI values and mean dissimilarity values for all 12 DENs included in the study.

Results

Stream Fish Community Structure

Stream fish community collections produced 47 species representing 30 genera and 11 families (Table 3.2). Gamma diversity measured across DENs and seasons was 19 in the Lower Big Blue HUC, 25 in the Middle Kansas HUC, 22 in the Lower Cottonwood HUC, and 30 in the Upper Verdigris HUC, and alpha diversity at sampling sites was generally similar during summer and fall (Table 3.1). Among all sites, drainage distance from source sampling sites was on average (\pm SD) 5.68 (2.23) km for unfragmented sites, 5.88 (2.20) km for fragmented sites, and distance distributions did not significantly differ ($t = 0.23$, $df = 24$, $p = 0.82$). Third order stream sites had widths ranging from 3.9 to 8.5 m, whereas 2nd order sites ranged from 2.2 to 6.2 m for unfragmented sites and from 1.5 to 6.2 m for fragmented sites. Whereas widths differed among 2nd and 3rd order streams (ANOVA, $F_{2,69} = 22.88$, $p < 0.01$), post-hoc Fisher's LSD comparisons indicated unfragmented and fragmented sites had similar widths ($p = 0.78$). Sites exhibited a general reduction in stream width from summer to fall (paired t-test, $t = 5.86$, $df = 33$, $p < 0.01$) as discharges declined and four 2nd order sites dried entirely (Table 3.1).

Community Response to Fragmentation

Regression analysis of drainage distance (km) between source-unfragmented or source-fragmented sites as the independent variable and dissimilarity between communities as the dependent variable indicated no isolation by distance at the spatial extent of our study (Figure 3.4 2). There was no relationship between drainage distance (km) and dissimilarity during summer

($n = 26$, $F_{1,25} = 0.32$, $r^2 = 0.02$, $p = 0.57$) or fall ($n = 22$, $F_{1,21} = 0.86$, $r^2 = 0.04$, $p = 0.36$). However, dissimilarity was on average 15% lower for source-unfragmented community comparisons relative to source-fragmented community comparisons during summer ($t = 3.22$, $df = 24$, $p < 0.01$; Figure 3.4a) and 14% lower during fall ($t = 2.18$, $df = 20$, $p = 0.04$; Figure 3.4b), indicating significantly greater similarity among source-unfragmented communities.

Regression analysis of stream width (m) as the independent variable and species richness as the dependent variable indicated a species-area relationship at the spatial extent of our study (Figure 3.5). There was a positive relationship between stream width (m) and alpha diversity (species richness) in source and unfragmented sampling sites for summer ($n = 26$, $F_{1,23} = 5.51$, $r^2 = 0.19$, $p = 0.03$) and fall ($n = 25$, $F_{1,22} = 5.23$, $r^2 = 0.19$, $p = 0.03$). Fragmented sites were excluded from regression analysis because of the potential for confounding effects of barriers on alpha diversity. During summer, mean (\pm SD) species richness was 14.2 (3.6) for source, 10.5 (2.5) for unfragmented, and 8.1 (3.5) for fragmented sampling sites, and richness values differed significantly among sampling site types (ANOVA, $F_{2,35} = 11.22$, $p < 0.01$). During fall, mean (\pm SD) species richness was 13.6 (2.8) for source, 10.8 (2.7) for unfragmented, and 7 (4.1) for fragmented sampling sites, and richness values differed significantly among sampling site types (ANOVA, $F_{2,31} = 11.60$, $p < 0.01$). Despite similarities in stream width between unfragmented and fragmented sites, mean species richness was significantly greater in unfragmented relative to fragmented sites during summer (Fisher's LSD, $p < 0.05$; Figure 3.4a) and fall (Fisher's LSD, $p < 0.05$; Figure 3.4b).

Variability in alpha and beta diversity among stream fish communities at unfragmented and fragmented 2nd order stream sites was associated with patterns in species occurrences. Sixteen species occurred in approximately equal numbers of unfragmented and fragmented streams, including seven in Cyprinidae, three in Ictaluridae, four in family Centrarchidae, and one in Percidae (Table 3.2). Five species from different families (Fundulidae, Poeciliidae, Atherinidae, Centrarchidae, and Percidae) occurred in a greater number of fragmented streams. Fifteen species had reduced occurrences or were absent altogether in fragmented streams, including seven in the family Cyprinidae, two in Catostomidae, one in Ictaluridae, two in Centrarchidae, and three in Percidae. Commonly occurring species (i.e., occurred in >30 of 72 collections) that indicated approximately equal occurrences in unfragmented and fragmented streams included central stoneroller (*Campostoma anomalum*), redfin shiner (*Lythrurus umbratilis*), bluntnose

minnow (*Pimephales notatus*), creek chub (*Semotilus atromaculatus*), black bullhead (*Ameiurus melas*), green sunfish (*Lepomis cyanellus*), bluegill sunfish (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), and orangethroat darter (*Etheostoma spectabile*). Intermediately common species (i.e., occurred in >15 of 72 collections) that indicated absence or reduced occurrence at fragmented sites included red shiner (*Cyprinella lutrensis*), common shiner (*Luxilus cornutus*), sand shiner (*Notropis stramineus*), suckermouth minnow (*Phenacobius mirabilis*), fathead minnow (*Pimephales promelas*), white sucker (*Catostomus commersonii*), slender madtom (*Noturus exilis*), longear sunfish (*Lepomis megalotis*), and orangespotted sunfish (*Lepomis humilis*).

Community Composition and Connectivity at the Scale of DENs

Regression analysis predicting beta diversity among sites within DENs as a function of DCI indicated a relationship between structural and functional connectivity (Figure 3.6). Mean dissimilarity among sites decreased as DCI increased among DENs for summer ($n = 12$, $F_{1,10} = 19.05$, $r^2 = 0.66$, $p < 0.01$; Figure 3.6a) and fall ($n = 8$, $F_{1,6} = 10.09$, $r^2 = 0.63$, $p = 0.02$; Figure 3.6b). Sites that dried during fall were in the Middle Kansas (i.e., two sites in the Dry Creek DEN, one site in the Mulberry Creek DEN) and Lower Cottonwood (one site in the Bruno Creek DEN, one site in the Coyne Creek DEN) 8-digit HUCs, and these DENs were removed from regression analysis for fall. Although pair-wise comparisons could still be conducted for the remaining sites within excluded DENs, mean dissimilarity values might be skewed because contributions from communities at dried sites no longer existed. Following removal of DENs in which sites dried, the relationship between DCI and dissimilarity was driven largely by the small DCI value for the Snake Creek DEN in the Upper Verdigris 8-digit HUC. Consequently, we tested the relationship between DCI and all available measures of dissimilarity for fall, acknowledging seasonal patterns in dissimilarity for four DENs were likely confounded by extirpated communities from dried sites, and we still detected a relationship ($n = 12$, $F_{1,10} = 5.15$, $r^2 = 0.34$, $p = 0.04$).

Discussion

Our findings empirically show that structural connectivity influences community structure of stream fishes at both local and network scales. We found communities in fragmented stream sections had reduced alpha diversity (lower species richness) as well as

increased beta diversity (greater dissimilarity) compared to communities that maintained connectivity with the surrounding DEN. These patterns were not explained by isolation because of drainage distance or variation in 2nd order stream patch size, rather community disparity coincided with occurrence of barriers that impeded dispersal routes. We also found that structural connectivity measured at the scale of DENs using the DCI predicted reduced dissimilarity among communities, presumably because of increased dispersal and colonization of 2nd order streams, and consequently augmented alpha diversity in less fragmented DENs. Our findings support network connectivity as a mediator of ecological processes occurring within complex dendritic ecosystems and promote the need for improved connectivity to enhance conservation of metacommunity dynamics and biodiversity in DENs.

Metacommunity Response to Fragmentation in DENs

Altered dispersal routes in an upstream direction, or toward the extremities of DENs, have direct implications for metacommunity dynamics. Brown and Swan (2010) suggested dispersal among headwater streams is generally low for aquatic organisms confined to within-branch movement, but rates of dispersal increase with proximity to the base of dendritic stream networks. Thus, metacommunities in headwater reaches are structured by species-sorting processes (i.e., species occupy patches of highest suitability), whereas the influence of mass-effects (i.e., strong dispersal among all species allows for persistence even in poorly suited patches) increases with proximity to the base of the network (see Leibold et al. 2004 for further details of metacommunity paradigms). In the context of stream-dwelling fish communities, 2nd and 3rd order streams likely occur within the transitional zone between strong species sorting in 1st order headwater streams and mass-effect-dominated dynamics in 3rd order and greater streams (Hitt and Angermeier 2006). We found evidence that species associated with small streams (as classified by Goldstein and Meador 2004) showed little response to fragmentation in our study system (e.g., redbfin shiner, southern redbelly dace *Phoxinus erythrogaster* and creek chub, western mosquitofish *Gambusia affinis*, orangethroat darter) whereas other species characteristic of a range of stream sizes, including small-bodied and early maturing cyprinids (e.g., red shiner *Cyprinella lutrensis*, sand shiner, and suckermouth minnow) exhibited reduced occurrence or were absent altogether from fragmented streams (Table 3.2). These observations are consistent with previous findings that suggest early maturing fishes with small body size disperse upstream

from larger adjacent streams to colonize communities in 2nd and 3rd order streams (Schlosser 1987, Hitt and Angermeier 2006). For example, we detected an absence of stream species such as sand shiner but relatively little change in occurrence of generalist species such as creek chub, bluntnose minnow, and green sunfish in fragmented communities (Goldstein and Meador 2004), which reflect findings by Falke and Gido (2006) among streams isolated by impounded water upstream of large reservoirs. We also found a general reduction of red shiner and an absence of Topeka shiner *Notropis topeka* in fragmented streams, two species known to be extirpated from fragmented streams because of reduced dispersal (Adams et al. 2000, Matthews and Marsh-Matthews 2007, Franssen 2011). Spatial extent over which stream fish complete their life history varies (Schlosser 1991), and can range from dispersal on scales ranging 10-100 m (e.g., Fletcher et al. 2004) to hundreds of km (e.g., Perkin and Gido 2011). Although existence of obligate potamodromy among many Great Plains small-bodied fishes is poorly studied, thwarted dispersal and attenuated mass effects caused by instream obstructions generally explain reduced alpha diversity and increased beta diversity among fragmented communities in prairie streams (Winston et al. 1991, Perkin and Gido 2011).

Metacommunities fragmented by barriers distributed throughout DENs become isolated communities in which dispersal linkages to processes operating at regional scales are severed and local composition is determined largely by local drivers (e.g., Angermeier and Winston 1998, Mathews and Robison 1998). Existing theoretical models have linked small and isolated populations or communities within DENs to reduced population size and increased extinction risk among organisms (Labonne et al. 2008, Padgham and Webb 2010, Grant 2011), a pattern consistent with our findings. Fishes dependent upon processes occurring at broader spatial scales (e.g., cyprinids; catostomids) were either absent or occurred at low abundances within fragmented communities and support reduced dispersal as the primary cause for altered community composition in fragmented stream reaches. On the other hand, species characteristic of smaller headwater reaches indicated little response to fragmentation and occurred in nearly equal numbers of unfragmented and fragmented communities. These differential levels of persistence are likely related to functional or life history attributes of fishes, which might allow for persistence of certain guilds through a suite of mechanisms (e.g., competition, predation, or suitability of available resources). In the absence of dispersal, isolated communities likely diverged from communities that maintained connectivity with the surrounding DEN because of

biological (e.g., predation or competition) or non-biological (e.g., desiccation of streams) processes. Matthews and Marsh-Matthews (2006) found seven initially identical isolated mesocosm fish communities diverged over the course of approximately one year despite control of abiotic factors (e.g., water availability, habitat mosaics), suggesting biological interactions might be contributing to stream fish community structure. Disrupted connectivity between 2nd and 3rd order streams might also thwart predator-prey transitions among stream sizes during periods of hydrologic stability when biotic interactions are expected to contribute largely to community composition (Creed 2006). Lastly, we observed drying among three fragmented communities included in this study to the extent that all fish were completely extirpated, suggesting influence of abiotic factors cannot be ruled out in natural setting such as Great Plains streams that commonly endure harsh fluctuations in hydrology (Dodds et al. 2004). Although dispersal for a diversity of fish species is negatively affected by the presence of perched culverts at road crossings (e.g., Norman et al. 2009, Alexandre and Almeida 2010, Nislow et al. 2011), altered ecological interactions and occurrence of abiotic processes within fragmented communities likely contributed, in part, to variability in community composition and patterns in biodiversity.

Structural Connectivity Predicts Functional Connectivity

We can think of at least three reasons for the strong relationship we observed between DCI and community dissimilarity within DENs, each of which are not necessarily mutually exclusive. First, dispersal corridors are singular and linear in stream networks and disruption to structural connectivity eliminates routes for organisms confined to within-branch movement (Grant et al. 2007). Functional connectivity must then be reduced given the strong dependency of fishes on aquatic corridors for dispersal (Padgham and Webb 2010). Secondly, the occurrence of strong mass-effects within streams at the spatial extent of our study would lead to a disruption of community mixing within and among non-headwater streams caused by perched culverts at road crossings. In fragmented sections, biological (e.g., competition, predation) and non-biological (e.g., local extinctions during desiccations) processes might be altered because fishes are not able to mix with other sections. This pattern would explain the greater levels of community disparity we observed in highly fragmented DENs relative to DENs with greater connectivity, and perhaps would contribute to incremental increases in similarity among

communities as connectivity increased. Finally, perched culverts included in this study were constructed during the 1950s-1980s according to dates stamped on the structures (J. Perkin, personal observation) and fish communities might have responded to the presence of culverts well before our study was conducted given the resiliency of Great Plains stream communities (Dodds et al. 2004). Inundation of perches during summer high flows likely allowed for temporary dispersal of fishes into perennial 2nd order streams (e.g., Bouska and Paukert 2009, Norman et al. 2009), but given prairie stream fishes are generally resistant to downstream displacement during floods (Franssen et al. 2006) communities in upstream segments might have been resistant to colonization (Hitt and Roberts 2012). Although evidence exists for stream fish communities being invadable (Angermeier and Winston 1998), colonization of upstream reaches is generally lower relative to downstream reaches (Gotelli and Taylor 1999). By this account, community similarity and functional connectivity among stream segments might be rigid despite ephemeral increases in structural connectivity caused by flood pulses. Regardless of the mechanism, our findings promote the use of the DCI as a habitat availability measure with potential for significant contribution toward understanding ecological processes in fragmented riverscapes (Erős et al. 2012).

Fragmentation and Conservation of Biodiversity in DENs

Habitat loss and fragmentation are primary threats to aquatic biodiversity and action is required to conserve rare and declining organisms that increasingly constitute the majority of biodiversity in stream networks on a global scale (Nilsson et al. 2005, Dudgeon et al. 2006, Jelks et al. 2008, Cote et al. 2009). Building evidence suggests alterations to connectivity have ecological and evolutionary consequences for aquatic communities (Falke and Gido 2006, Franssen 2011, this study) and network connectivity in DENs is emerging as a central theme in conserving biodiversity (Erős et al. 2011, Erős et al. 2012). Examples of diminished connectivity negatively affecting freshwater biodiversity exist for regions around the world (e.g., Morita and Yamamoto 2002, Alexandre and Almeida 2010, Fullerton et al. 2010), and illustrate the critical need for synthesizing effects of fragmentation in stream DENs regardless of topology or spatial scale (Fausch et al. 2002, Erős et al. 2012). In particular, intermediate spatial scales incorporating stream reaches or segments ranging from 10² to 10⁴ m have been largely ignored in the context of stream fish conservation research. According to Fausch et al. (2002), these are the

scales at which anthropogenic alterations to streams most strongly conflict with the life history needs of stream-dwelling fishes. We found evidence for fragmentation of DENs contributing to altered community composition among Great Plains stream fishes at the spatial scale of our study (i.e., 10^2 – 10^4 m), illustrating the utility of the DCI for researching stream mosaics at ecologically meaningful scales (*sensu* Fausch et al. 2002). Cote et al. (2009) suggested the DCI could be applied to networks as large as the entire Mississippi drainage basin or as small as a single tributary reach, which allows for directly addressing the challenge of variability in network topology when assessing connectivity across spatial scales (Fullerton et al. 2010). An advantage of applying the DCI to measure habitat connectivity over the spatial extent of a species' life span is the scale-independent nature of networks that can be modeled as well as the improved ability to incorporate species-specific dispersal capabilities with regard to barrier permeability.

Our understanding of long-term responses among stream organisms to fragmentation of dendritic stream networks is temporally limited. Assemblage level responses to fragmentation of large rivers on time scales ranging 30-60 years suggest time-lag effects on demography of stream-dwelling organisms might cause prolonged responses to current levels of fragmentation (Taylor et al. 2008, Perkin and Bonner 2011), which might constitute extinction debts in many systems (Tilman et al. 1994, Strayer et al. 2004). Prioritizing barriers for remediation based on contemporary responses to fragmentation might attenuate long-term ecological effects caused by reduced connectivity, and a diversity of approaches have been developed to measure connectivity in stream networks (Fullerton et al. 2010). Our findings suggest relating functional connectivity of stream fish communities in DENs to structural connectivity measured with minimal biological data (here, the DCI with uniform barrier permeability of 0.5) might be a fruitful approach to prioritizing specific barriers for remediation in order to achieve desired connectivity of metapopulations or communities (*sensu* Cote et al. 2009). However, to ensure remediation approaches reach maximum potential improvement to connectivity, additional detail pertaining to barrier permeability is needed before prioritization (Bourne et al. 2011). Similarly, predictive scenarios for reducing connectivity to control spread of invasive species (e.g., Jackson and Pringle 2010) might also be applied to network management in order to assess the role of connectivity in mediating ecological processes at relevant spatial scales in complex, dendritic ecosystems.

Conclusions

Stream fragmentation imposed by semi-permeable barriers is a global pattern contributing to the reduced abundance and distribution of stream organisms and constitutes a major environmental problem. Mitigation approaches for developing improved fish passage structures in place of perched or otherwise impermeable obstacles indicate success in terms of allowing local improvements to organism dispersal. Cost-benefit analysis and prioritization of barriers that yield maximum gains in structural connectivity is now possible with advances in habitat availability measures such as the DCI (Cote et al. 2009). However, evaluating benefits of improved structural connectivity requires some ability to predict potential ecological outcomes before action is taken, such as the potential for increased dispersal of organisms throughout stream networks. Our findings suggest that improvements to structural connectivity are likely to equal associated improvements in the abundance and distribution of organisms confined to within-stream dispersal (e.g., fishes).

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Figure 3.1 Relative frequency of non-state road crossings (grey bars) and stream segments (black lines and dots) among stream orders within 8-digit hydrologic unit codes (HUCs) for Lower Big Blue (10270205), Middle Kansas (10270102), Lower Cottonwood (11070203), and Upper Verdigris (11070101). We tested whether crossings were uniformly distributed among stream orders by comparing the relative frequency of stream orders and occurrence of non-state crossings for each HUC. Number (*N*) of crossings in each HUC is listed along with differences (*D*) and significance values for Kolmogorov-Smirnov tests for differences in expected (proportion of stream segments obtained from geographic information system) and observed distributions of road crossings among stream orders classified using the Strahler classification system (Strahler 1957).

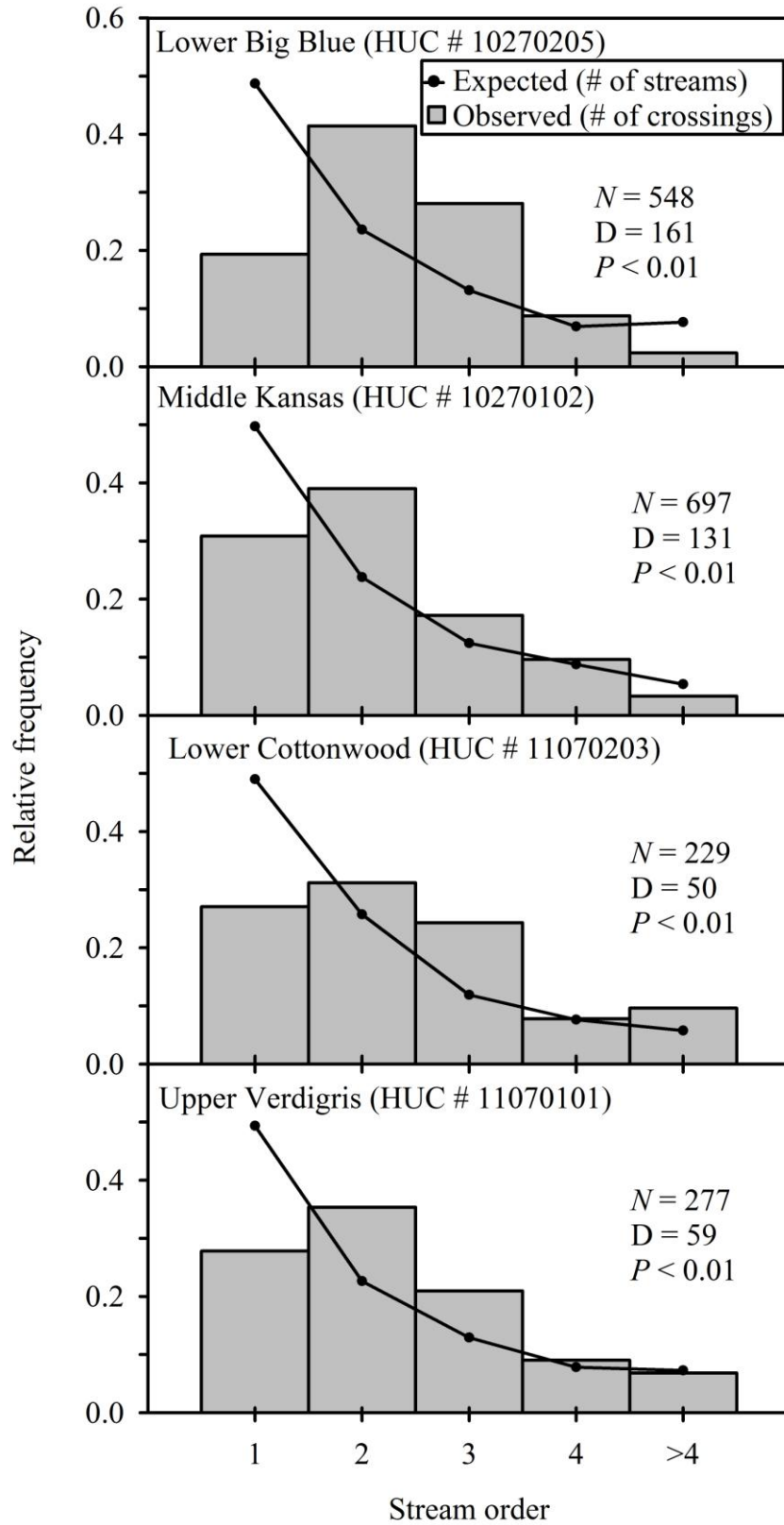


Figure 3.2 (a) Little Sandy Creek dendritic ecological network (DEN) composed of a third-order stream and second-order tributaries (first order streams are shown as dashed lines) with three fish sampling sites (white circles): (1) a source community in a 3rd order stream, (2) an unfragmented community in a 2nd order stream, and (3) a fragmented community in a 2nd order stream isolated by a perched road crossing (solid line). (b) Streams, fish sampling sites, and 14-digit U.S. Geological Survey (USGS) hydrologic unit codes (HUCs) associated with three DENs within the Upper Verdigris 8-digit HUC (USGS # 11070101). (c) Distribution of four 8-digit USGS HUCs in which three DENs were sampled, 14-digit HUCs associated with DENs are shown. (d) Kansas is located in the central contiguous United States. See Figure 3.3 for detailed illustrations of 12 DENs included in study.

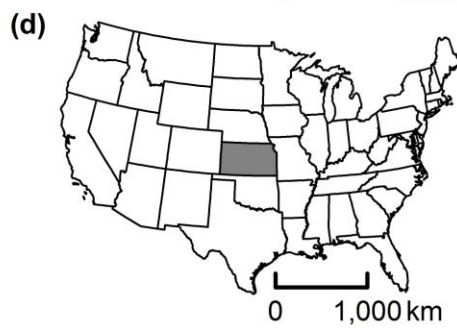
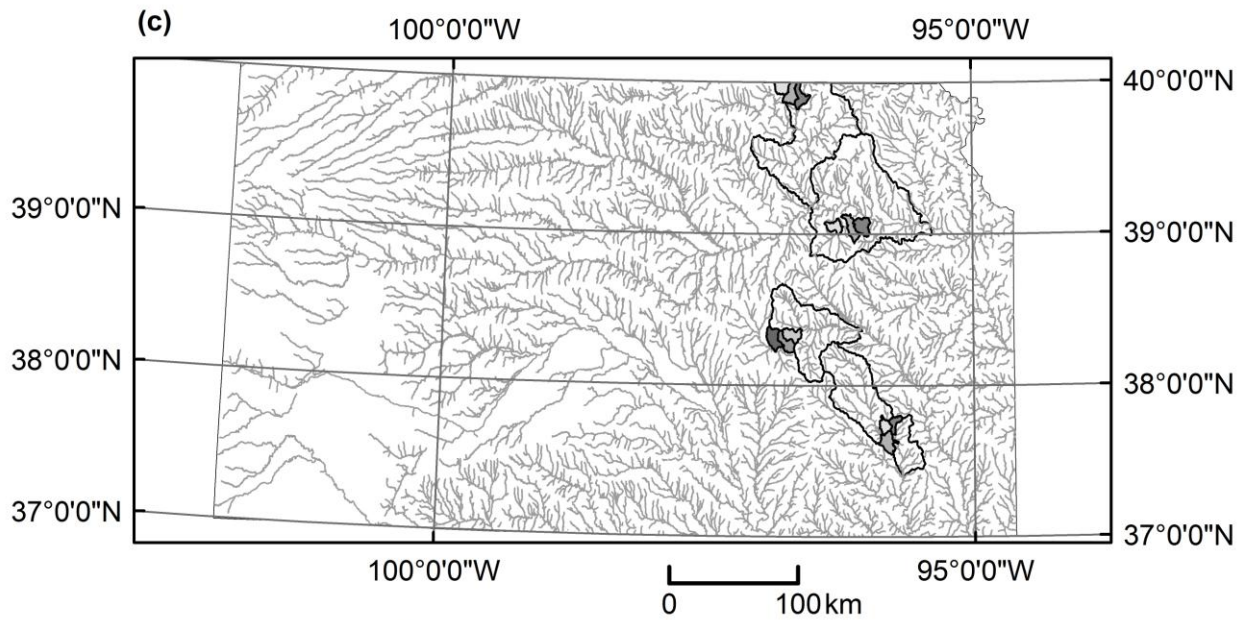
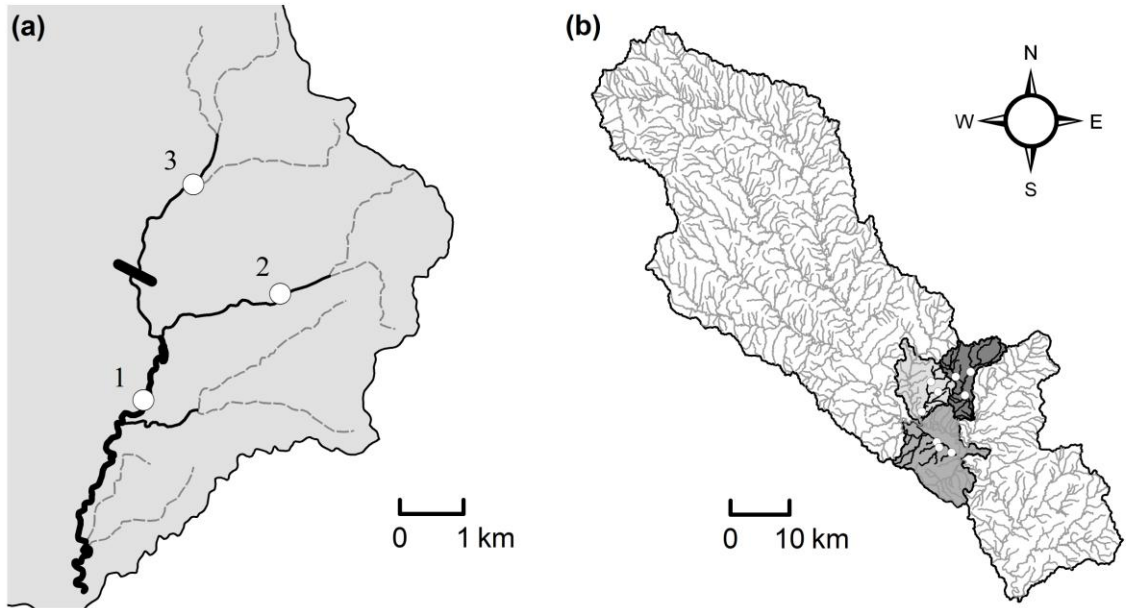


Figure 3.3 Great Plains Dendritic Ecological Networks (DENs) illustrating 2nd and 3rd order stream networks (gray solid lines), 1st order tributary streams not included in network analysis (dashed gray lines), fish sampling locations (black circles; source = S, unfragmented = U, fragmented = F), and road crossings characterized by perched outflows (black dashes). Dendritic Connectivity Index (DCI) values are given for each DEN. Panels correspond with 8-digit U.S. Geological Survey hydrologic unit codes, including the Lower Big Blue (10270205, panels a-c), Middle Kansas (10270102, panels d-f), Lower Cottonwood (11070203, panels g-i), and Upper Verdigris (11070101, panels j-l).

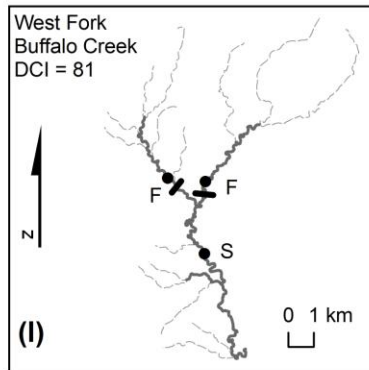
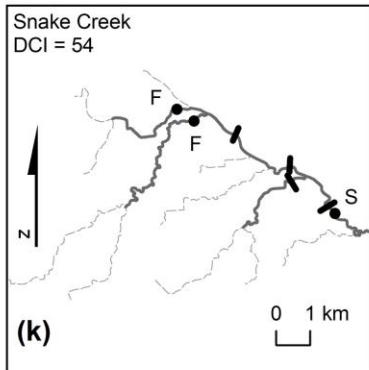
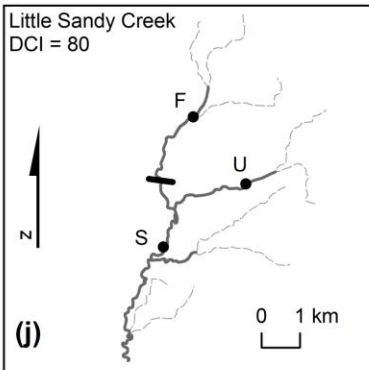
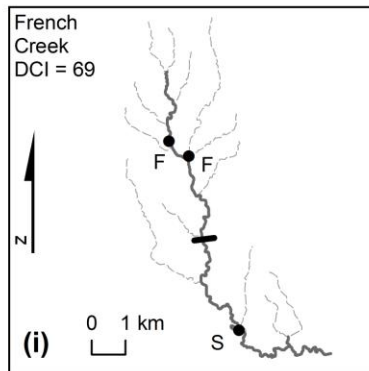
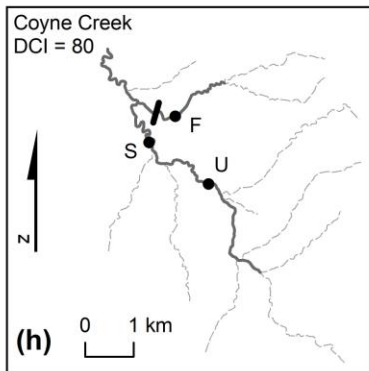
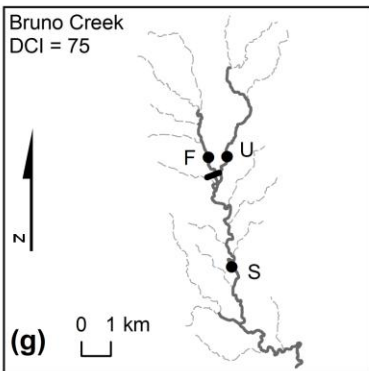
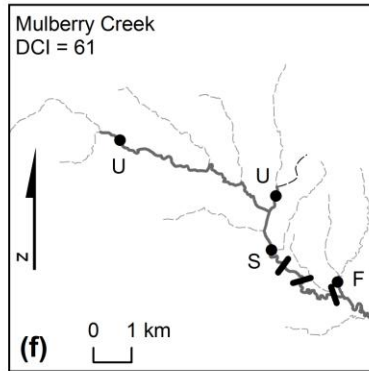
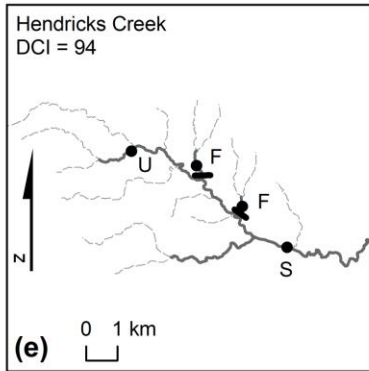
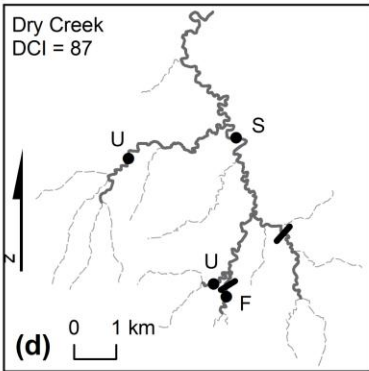
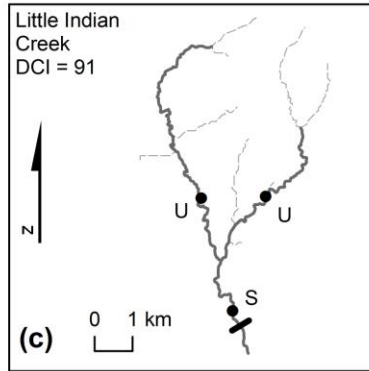
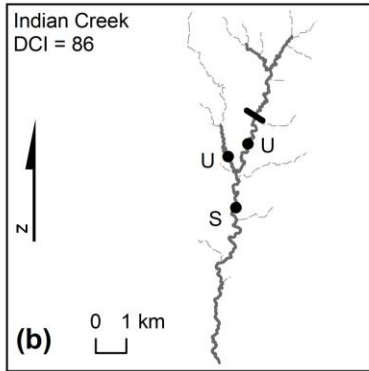
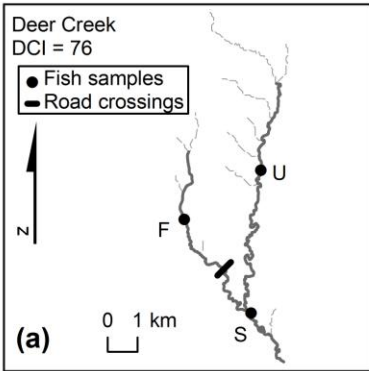


Figure 3.4 Relationship between drainage distance from source sampling sites and dissimilarity to source sampling site communities for 2nd order stream fish communities sampled in Kansas streams during (a) summer and (b) fall of 2010. Inserts illustrate mean (\pm SD) dissimilarity among source-unfragmented (“Unfrg”; black triangles) versus source-fragmented (“Frag.”; grey boxes) sampling sites for summer and fall; letters *a* and *b* indicated differences in dissimilarity between unfragmented and fragmented sites detected during t-test analysis.

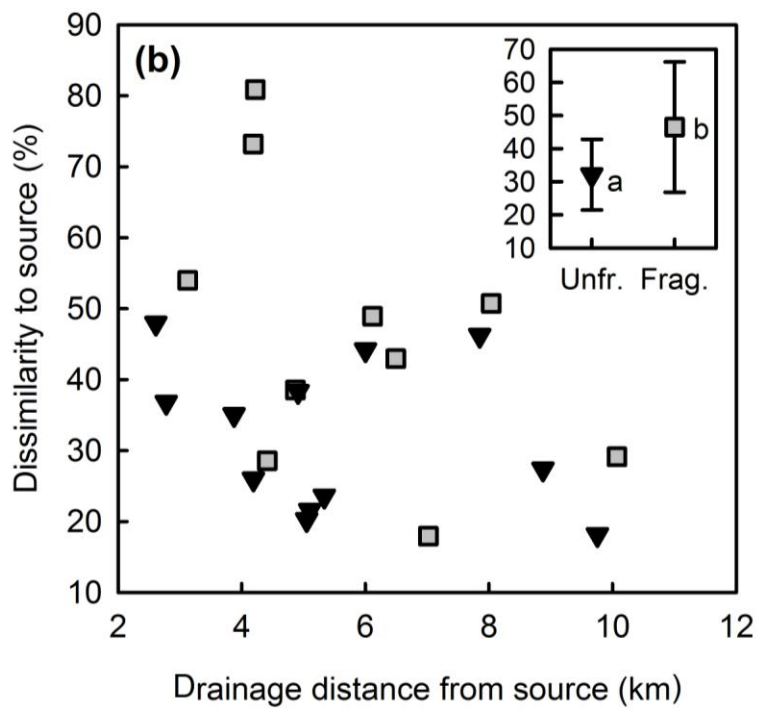
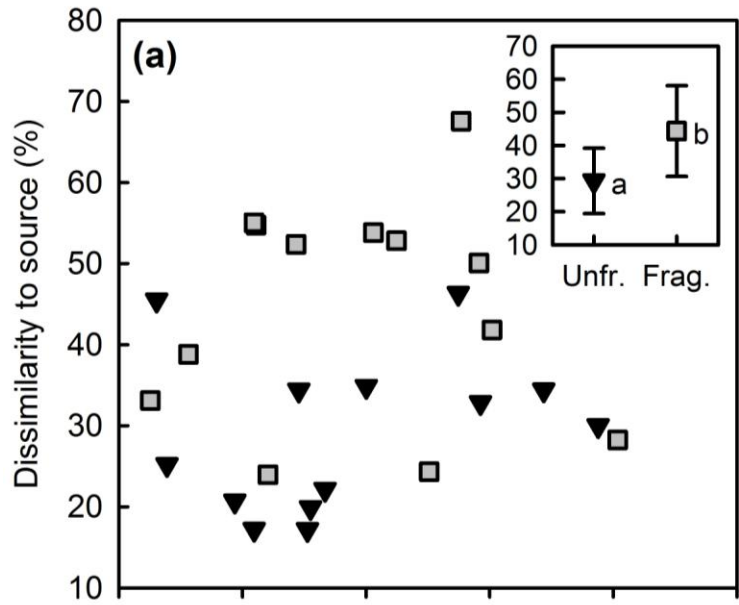


Figure 3.5 Relationship between stream width and species richness among Great Plains stream fish communities in Kansas sampled during (a) summer and (b) fall of 2010. Inserts illustrate mean (\pm SD) species richness according to 3rd order source (“Sour.”, white circles), 2nd order unfragmented (“Unfr.”, black triangles), and 2nd order fragmented (“Frag.”, grey boxes) sampling sites; letters *a*, *b*, and *c* indicated difference in species richness detected during analysis of variance and post-hoc testing. Regression models illustrate the relationship between stream width and species richness for source and unfragmented sampling sites to avoid confounding effects of barriers among fragmented sampling sites.

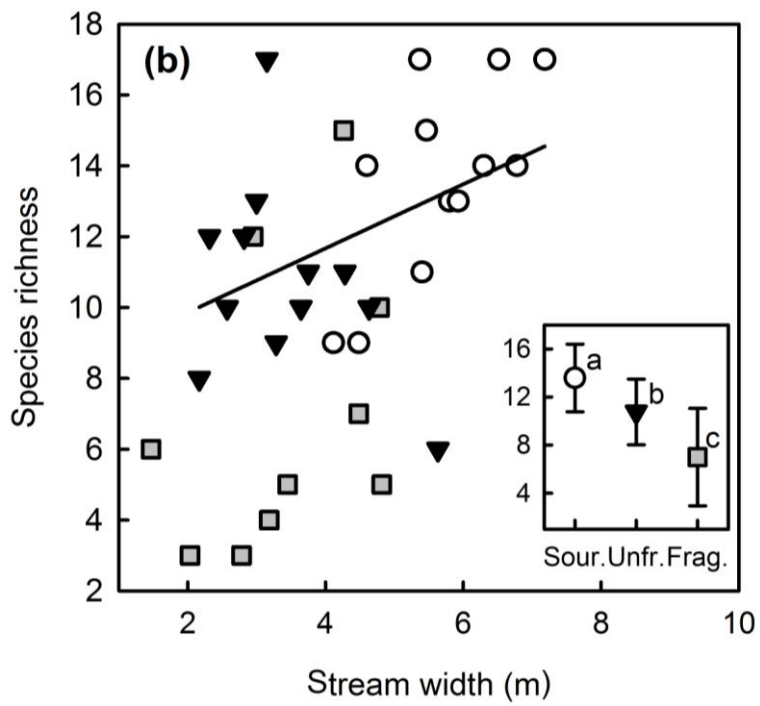
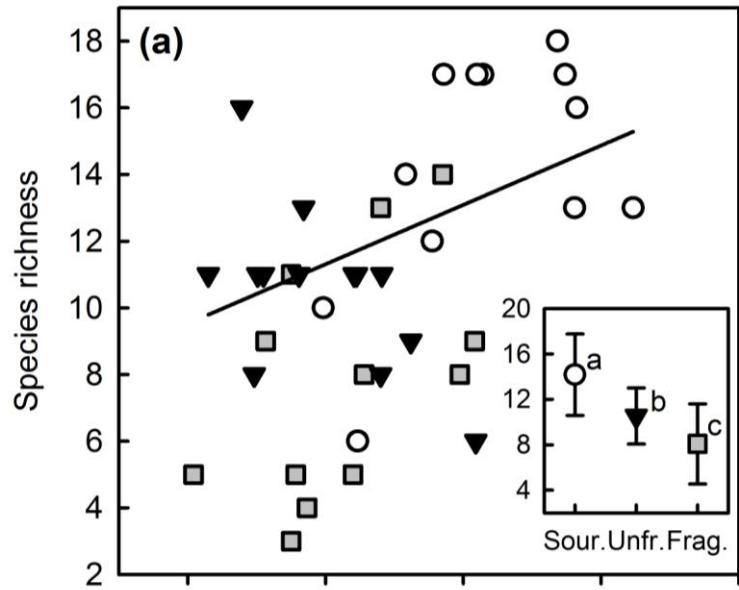


Figure 3.6 Relationship between Dendritic Connectivity Index (DCI) and mean dissimilarity among stream fish communities within dendritic ecological networks (DENs) of Kansas sampled during (a) summer and (b) fall of 2010. Drying of sites and subsequent exclusion of associated DENs reduced sample size during fall; error bars around points represent ± 1 standard deviation from the mean dissimilarity among sampling sites.

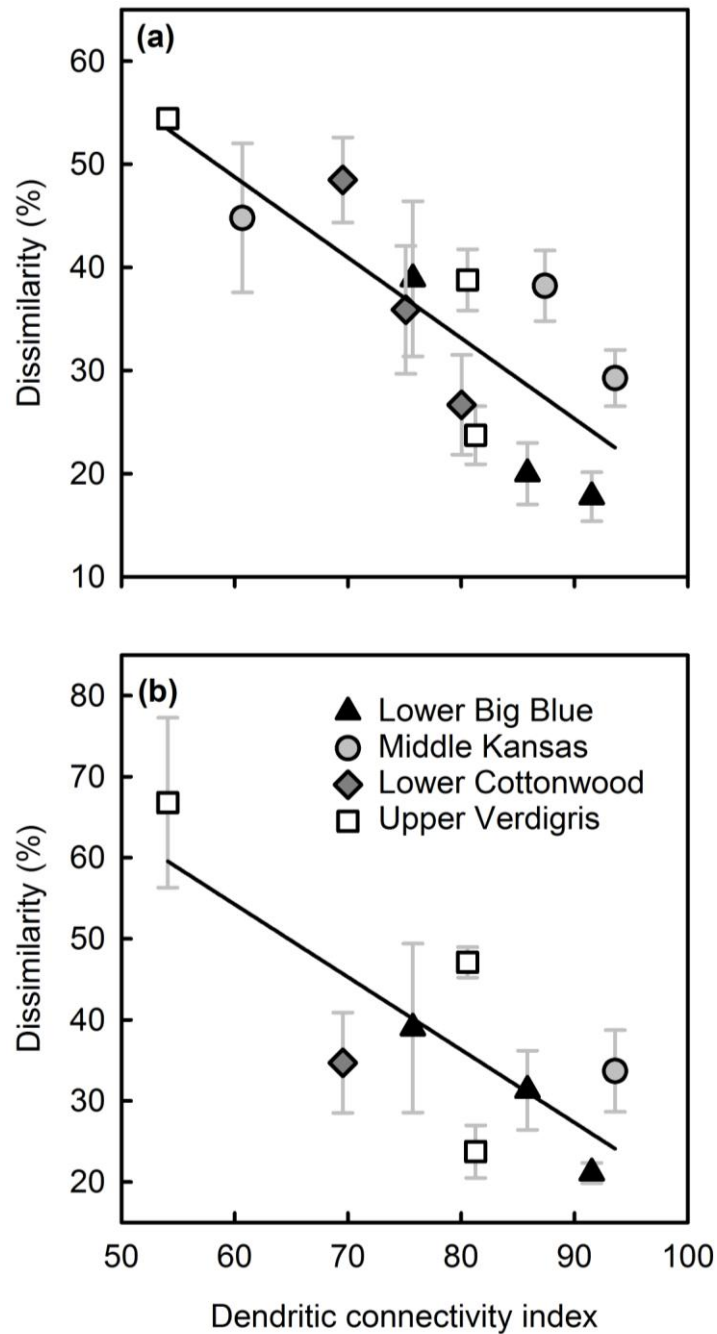


Table 3.1 Site and dendritic ecological network (DEN) description, community status, gamma diversity (all species collected during both seasons and at all sites and DENs; bolded values in Richness columns), alpha diversity (species richness), and mean and standard deviation stream width for sampling sites in four 8-digit hydrologic unit codes (HUCs) in eastern Kansas sampled during summer and fall of 2010. Site 2 in the lower Cottonwood HUC, Bruno Creek DEN was dominated by groundwater discharge, was not sampled during fall, and was excluded from analyses. Sites that were dry during fall are shown as “-“. Mean stream widths were calculated by averaging widths measured at each geomorphic unit (i.e., riffle-pool sequences; 5-6 observations per stream). Average stream widths were narrower during fall (4.22) compared to summer (4.87), excluding the four dry sites (paired t-test; $t = 5.86$, $df = 33$, $p < 0.01$).

Hydrologic Unit Code (HUC) DEN and site description	Community Status	Summer			Fall		
		Richness	Mean width	SD width	Richness	Mean width	SD width
Lower Big Blue (HUC # 10270205)		19			19		
Deer Creek DEN		17			17		
Deer Creek Site 1	Unfragmented	11	3.10	0.89	13	3.15	1.15
Deer Creek Site 2	Fragmented	5	2.08	0.61	6	1.47	0.46
Deer Creek Site 3	Source	17	6.28	2.28	17	5.93	1.87
Indian Creek DEN		15			15		
Indian Creek Site 1	Unfragmented	11	2.30	0.53	8	2.17	0.65
Indian Creek Site 2	Unfragmented	13	3.68	0.75	12	2.32	0.91
Indian Creek Site 3	Source	12	5.55	1.09	14	4.60	0.70
Little Inidan Creek DEN		14			14		
Little Indian Creek Site 1	Unfragmented	11	4.45	2.14	11	3.75	1.66
Little Indian Creek Site 2	Unfragmented	11	3.62	1.17	10	2.57	0.67
Little Indian Creek Site 3	Source	10	3.97	0.97	9	4.11	1.10

Table 3.1 Continued

Hydrologic Unit Code (HUC) DEN and site description	Community Status	Summer			Fall		
		Richness	Mean width	SD width	Richness	Mean width	SD width
Middle Kansas (HUC # 10270102)		25			25		
Dry Creek DEN		20			20		
Dry Creek Site 1	Fragmented	11	3.53	1.29	-	-	-
Dry Creek Site 2	Unfragmented	11	4.82	1.15	11	4.28	1.25
Dry Creek Site 3	Unfragmented	8	4.78	0.98	-	-	-
Dry Creek Site 4	Source	17	5.72	1.34	17	5.37	1.80
Hendricks Creek DEN		16			16		
Hendricks Creek Site 1	Fragmented	5	3.57	1.22	5	3.45	1.27
Hendricks Creek Site 2	Fragmented	9	3.13	1.02	12	2.95	1.00
Hendricks Creek Site 3	Unfragmented	11	3.02	1.06	13	3.00	0.98
Hendricks Creek Site 4	Source	13	7.62	1.84	14	6.30	1.82
Mulberry Creek DEN		18			18		
Mulberry Creek Site 1	Fragmented	3	3.47	0.61	-	-	-
Mulberry Creek Site 2	Unfragmented	16	2.78	0.60	12	2.82	0.91
Mulberry Creek Site 3	Unfragmented	8	2.97	0.87	9	3.28	1.33
Mulberry Creek Site 4	Source	17	6.20	2.09	17	6.52	2.12
Lower Cottonwood (HUC # 11070203)		22			22		
Bruno Creek DEN		17			17		
Bruno Creek Site 1	Unfragmented	9	5.24	0.93	10	4.63	1.86
Bruno Creek Site 2*	Fragmented	5	3.30	0.31	-	-	-
Bruno Creek Site 3	Source	16	7.65	2.41	13	5.80	2.58
Coyne Creek DEN		8			8		
Coyne Creek Site 1	Unfragmented	5	6.18	2.37	6	5.63	2.19
Coyne Creek Site 2	Fragmented	6	4.18	0.85	-	-	-
Coyne Creek Site 3	Source	6	4.47	0.75	9	4.48	2.55
French Creek DEN		17			17		
French Creek Site 1	Fragmented	4	3.73	1.23	4	3.18	2.17
French Creek Site 2	Fragmented	8	5.95	2.53	5	4.82	2.33
French Creek Site 3	Source	14	5.17	1.76	11	5.40	1.98

Table 3.1 Continued

Hydrologic Unit Code (HUC) DEN and site description	Community Status	Summer			Fall		
		Richness	Mean width	SD width	Richness	Mean width	SD width
Upper Verdigris (HUC # 11070101)		30			30		
Little Sandy Creek DEN		16			16		
Little Sandy Creek Site 1	Fragmented	9	6.17	2.03	7	4.48	1.09
Little Sandy Creek Site 2	Unfragmented	11	4.42	0.97	10	3.64	1.18
Little Sandy Creek Site 3	Source	13	8.47	1.41	17	7.18	2.89
Snake Creek DEN		23			23		
Snake Creek Site 1	Fragmented	8	4.56	0.57	8	2.78	1.66
Snake Creek Site 2	Fragmented	11	3.50	0.65	11	2.03	1.32
Snake Creek Site 3	Source	17	7.48	1.33	14	6.78	1.61
West Fork Buffalo DEN		21			21		
West Fork Buffalo Site 1	Fragmented	13	4.80	1.65	10	4.27	2.35
West Fork Buffalo Site 2	Fragmented	14	5.70	1.51	15	4.78	1.88
West Fork Buffalo Site 3	Source	18	7.37	3.28	15	5.47	3.00

*Only groundwater dominated site, excluded from analysis

Table 3.2 Fish families, genera, and species collected from U.S. Geological Survey 8-digit hydrologic unit codes (HUCs), total number of samples in which species occurred (source, unfragmented, and fragmented during summer and fall), and four categories of occurrence (approximately equal at unfragmented and fragmented sites, greater occurrence at fragmented sites, reduced occurrence or absent at fragmented sites, or rare occurrences [<3]) based on percent occurrence in unfragmented (“Unfr.”) and fragmented (“Frag.”) Great Plains streams where each species occurred during summer and fall of 2010. Percent occurrence was calculated for species by dividing the number of unfragmented or fragmented streams in which the species was detected by the total number of 2nd order streams for each HUC in which the species occurred. Abbreviations for HUCs are Lower Big Blue (LB; HUC # 10270205), Lower Cottonwood (LC; HUC # 11070203), Middle Kansas (MK; HUC # 10270102), and Upper Verdigris (UV; HUC # 11070101).

Family	Genus and species	HUCs	Total Occurrences	Summer		Fall	
				Unfragmented	Fragmented	Unfragmented	Fragmented
Approximately Equal Occurrence							
Centrarchidae	<i>Lepomis cyanellus</i>	LB, LC, MK, UV	70	100.0	92.3	100.0	90.0
Centrarchidae	<i>Lepomis macrochirus</i>	LB, LC, MK, UV	34	53.8	30.8	41.7	40.0
Centrarchidae	<i>Micropterus salmoides</i>	LB, LC, MK, UV	35	53.8	46.2	58.3	40.0
Centrarchidae	<i>Pomoxis annularis</i>	LB, UV	7	0.0	0.0	16.7	16.7
Cyprinidae	<i>Campostoma anomalum</i>	LB, LC, MK, UV	68	100.0	92.3	100.0	80.0
Cyprinidae	<i>Lythrurus umbratilis</i>	LC, MK, UV	31	50.0	50.0	42.9	44.4
Cyprinidae	<i>Notemigonus crysoleucas</i>	MK, UV	7	33.3	44.4	20.0	0.0
Cyprinidae	<i>Notropis percobromus</i>	MK	4	0.0	0.0	0.0	0.0
Cyprinidae	<i>Phoxinus erythrogaster</i>	MK	11	60.0	50.0	25.0	100.0
Cyprinidae	<i>Pimephales notatus</i>	LB, LC, MK, UV	37	23.1	38.5	41.7	40.0
Cyprinidae	<i>Semotilus atromaculatus</i>	LB, LC, MK	53	100.0	87.5	100.0	100.0
Ictaluridae	<i>Ameiurus melas</i>	LB, LC, MK, UV	36	53.8	53.8	58.3	40.0
Ictaluridae	<i>Ameiurus natalis</i>	LB, LC, MK, UV	28	23.1	23.1	50.0	20.0
Ictaluridae	<i>Ictalurus punctatus</i>	MK, UV	6	16.7	11.1	0.0	0.0
Percidae	<i>Etheostoma spectabile</i>	LB, LC, MK, UV	65	100.0	84.6	91.7	70.0
Percidae	<i>Percina caprodes</i>	LC, MK, UV	8	12.5	0.0	0.0	11.1

Table 3.2 Continued

Family	Genus and species	HUCs	Total Occurrences	Summer		Fall	
				Unfragmented	Fragmented	Unfragmented	Fragmented
Greater Occurrence at Fragmented Sites							
Atherinidae	<i>Labidesthes sicculus</i>	UV	4	0.0	20.0	0.0	0.0
Centrarchidae	<i>Lepomis gulosus</i>	UV	3	0.0	20.0	0.0	0.0
Fundulidae	<i>Fundulus notatus</i>	UV	6	0.0	40.0	0.0	40.0
Percidae	<i>Etheostoma gracile</i>	UV	4	0.0	40.0	0.0	20.0
Poeciliidae	<i>Gambusia affinis</i>	LC, MK, UV	8	0.0	16.7	0.0	22.2
Absent or Reduced Occurrence at Fragmented Sites							
Catostomidae	<i>Catostomus commersonii</i>	LB, MK	16	40.0	0.0	55.6	0.0
Catostomidae	<i>Moxostoma erythrurum</i>	LC, MK, UV	15	12.5	16.7	57.1	11.1
Centrarchidae	<i>Lepomis humilis</i>	LB, LC, MK, UV	15	30.8	7.7	16.7	0.0
Centrarchidae	<i>Lepomis megalotis</i>	LC, MK, UV	17	37.5	8.3	28.6	11.1
Cyprinidae	<i>Cyprinella lutrensis</i>	LB, LC, MK, UV	36	46.2	30.8	50.0	20.0
Cyprinidae	<i>Luxilus cardinalis</i>	LC	9	100.0	0.0	100.0	0.0
Cyprinidae	<i>Luxilus cornutus</i>	LC, MK	18	71.4	28.6	50.0	25.0
Cyprinidae	<i>Notropis stramineus</i>	LB, LC, MK	19	41.7	0.0	45.5	0.0
Cyprinidae	<i>Notropis topeka</i>	LB, MK	8	20.0	0.0	11.1	0.0
Cyprinidae	<i>Phenacobius mirabilis</i>	LB, LC, MK, UV	19	23.1	7.7	16.7	0.0
Cyprinidae	<i>Pimephales promelas</i>	LB, LC, MK	23	50.0	25.0	54.5	40.0
Ictaluridae	<i>Noturus exilis</i>	MK	15	60.0	25.0	100.0	50.0
Percidae	<i>Etheostoma flabellare</i>	LC	9	50.0	0.0	100.0	0.0
Percidae	<i>Etheostoma nigrum</i>	LB, MK	10	20.0	0.0	22.2	0.0
Percidae	<i>Etheostoma whipplei</i>	UV	4	100.0	20.0	100.0	20.0

Table 3.2 Continued

Family	Genus and species	HUCs	Total	Summer		Fall	
			Occurrences	Unfragmented	Fragmented	Unfragmented	Fragmented
Rare Occurrences							
Catostomidae	<i>Carpiodes carpio</i>	LB	2	20.0	0.0	0.0	0.0
Catostomidae	<i>Ictiobus niger</i>	UV	1	0.0	0.0	0.0	0.0
Catostomidae	<i>Minytrema melanops</i>	UV	2	0.0	0.0	0.0	0.0
Centrarchidae	<i>Micropterus punctulatus</i>	UV	1	0.0	0.0	0.0	0.0
Clupeidae	<i>Dorosoma cepedianum</i>	LC, UV	2	0.0	0.0	0.0	0.0
Cyprinidae	<i>Cyprinus carpio</i>	LB, UV	2	0.0	0.0	0.0	0.0
Cyprinidae	<i>Pimephales vigilax</i>	UV	1	0.0	0.0	0.0	0.0
Ictaluridae	<i>Noturus flavus</i>	LC	1	0.0	0.0	0.0	0.0
Lepisosteidae	<i>Lepisosteus osseus</i>	UV	1	0.0	20.0	0.0	0.0
Percidae	<i>Percina maculata</i>	MK	1	0.0	0.0	0.0	0.0
Sciaenidae	<i>Aplodinotus grunniens</i>	UV	2	0.0	20.0	0.0	0.0

Chapter 4 - Simulating Fish Dispersal in Stream Networks Fragmented by Road Crossings

Abstract

Organisms inhabiting stream ecosystems are vulnerable to the effects of habitat fragmentation because of the inherent importance of connectivity among habitat patches in these hierarchically structure riverscapes. Fragmentation caused by crossings at road-stream interfaces contributes to extensive alteration of stream organism distributions. We used principles of graph theory to developed three artificial riverscapes and test for network-scale changes in simulated fish dispersal caused by barriers that resembled the properties of road crossings (semi-permeable; numerous within a single network). Fish occupancy of nodes (habitat patches) declined in the presence of a single barrier when barrier permeability was <0.5 , and fish with high dispersal indicated greater declines in occupancy than fish with low dispersal. Probability of extirpation (emigration without return) from nodes was greatest for nodes that mimicked headwater stream segments and extirpation probability was generally greater near the upstream extent of riverscapes. We used a network-scale measure of habitat connectivity (the dendritic connectivity index; DCI) to measure changes in occupancy across all nodes and found the DCI predicted declines in occupancy when a greater number of barriers were added to the riverscape. Declines in occupancy were driven by threshold responses of fish to the occurrence of small fragments (≤ 3 nodes), and the number of small fragments increased with greater numbers of barriers in riverscapes. Our simulations identified three important properties of stream fish dispersal that are likely relevant to natural systems: (i) species dispersal affinities determine response to fragmentation; (ii) fragments that are too “small” for organism persistence drive declines in riverscape occupancy; and (iii) measurement of structural (habitat) connectivity used to draw inference on functional (population) connectivity require knowledge of organism dispersal affinity and dispersal-mediated response to barrier positioning.

Introduction

Habitat fragmentation and loss threaten global biodiversity and cause concern for the long-term persistence of numerous organisms (Dudgeon et al., 2006; Lindenmayer and Fischer, 2006). However, the manner in which organisms respond to landscape-scale changes in habitat

availability is mediated by structural properties of the habitats required for species persistence (Grant et al., 2007). For example, many terrestrial organisms interact with lattice networks of habitat patches arranged so that multiple dispersal routes exist between any two patches, whereas organisms inhabiting dendritic networks characterized by hierarchically arranged branches of habitat tend to have limited access to many patches even in the absence of fragmentation (Labonne et al., 2008; Cote et al., 2009; Padgham and Webb, 2010; Neeson et al., 2012). Consequently, organisms inhabiting dendritic landscapes such as streams tend to respond strongly to fragmentation (Fagan, 2002).

Stream fragmentation is associated with range reductions and local extinctions of fish species on a global scale. Anthropogenic barriers to fish movement include large and small dams as well as road crossings over small tributaries (Morita and Yamamoto, 2002; Alexandre and Almedia, 2010; Lehner et al., 2011). Road networks that overlap with stream networks present a global form of anthropogenic fragmentation to stream ecosystems and disrupt fish dispersal (Forman and Alexander, 1998; O’Hanley, 2011). Unlike large dams, structures that allow water to flow under or over roads that are characterized by rapid drops in elevation at their outflow (referred to as *perching*) represent barriers to dispersal with fluxes in permeability associated with stream flow (Norman et al., 2009; Nislow et al., 2011). Perched road crossings are common features on contemporary landscapes, far out-numbering dams, and partially blocking fish passage at 53% to 97% of crossings within a single watershed (Gibson et al., 2005; Poplar-Jeffers et al., 2009).

The manner in which fish respond to fragmentation is mediated by their dispersal ability or behavior, and fish that tend to disperse over greater distances tend to respond more strongly to fragmentation (Pépin et al., 2012). Given that fish dispersal can vary widely even within a single community (e.g., Albanese et al. 2008) and that fish dispersal changes with age or size (e.g., Skalski and Gilliam 2000), the potential for fish to interact with barriers distributed throughout a watershed can also vary depending on the spatial scale of investigation (Schlosser, 1991). Consequently, network-scale measures of habitat connectivity that incorporate the impacts of multiple barriers are emerging as a central theme in freshwater fish conservation (i.e., riverscape approaches *sensu* Fausch et al., 2002) with significant potential for developing robust predictions of fish response to fragmentation across a range of spatial scales (Bourne et al., 2011; Erős et al., 2011; Perkin and Gido, 2012).

Network-scale measures of habitat connectivity that identify particular barriers contributing most to fragmentation of riverine landscapes or riverscapes (hereafter *riverscape* and *network* are used interchangeably) and attenuated habitat availability can be used to guide conservation or management actions (Faucsh et al., 2002). Multiple approaches for quantifying habitat availability have recently been developed (see reviews: Fullerton et al., 2010; Kemp and O’Hanley, 2010) and include prioritizing barriers for remediation based on barrier permeability and maximizing fragment sizes (i.e., portion of a network isolated by one or more barriers; Cote et al., 2009) or maximizing the size of the single largest stream fragment in a riverscape (O’Hanley, 2011). Approaches targeting particular fragment sizes or maximizing fragment size in general seem most appropriate for enhancing the conservation of stream fish given reported relationships between species richness or population viability and stream fragment length (Bain and Wine, 2010; Perkin and Gido, 2011). Among recently developed measures involving fragment size is the *dendritic connectivity index* (DCI; Cote et al., 2009), which considers the fraction of stream network length isolated by a barrier (i.e., fragment) and computes the weighted average probability of movement within (permeability = 1) and among (permeability < 1) all fragments; among-fragment movement probability is dependent upon the number and assigned permeability of individual barriers in the network (see Cote et al., 2009 for additional details). The DCI is a quantitative measure of connectivity that can be assigned to stream networks regardless of their overall size or the number of barriers present and allows for transcending spatial scales while addressing the interactions among multiple barriers (Fullerton et al., 2010; O’Hanley, 2011). Accordingly, network-scale measures of habitat availability such as the DCI can enhance conservation of organisms that respond negatively to fragmentation of stream networks by prioritizing removal of barriers that maximize fish distributions (Bourne et al., 2011; O’Hanley, 2011; Erős et al., 2012; Perkin and Gido, 2012).

Modeling approaches for testing relationships among fish population persistence and stream network properties allow for assessing the utility of new connectivity measures with relatively few data requirements. Riverscape models have recently illustrated the relative effects of habitat accessibility versus quality on simulated fish distributions (Padgham and Webb, 2010), effects of network structure and organism movement bias (upstream or downstream) on metapopulation persistence (Grant, 2011), and the effect of network structure on species-specific responses to the distribution of habitats (Neeson et al., 2011; 2012). In the context of habitat

fragmentation, similar riverscape models can be combined with principles of graph theory to test network-scale relationships between habitat connectivity and population persistence (Urban and Keitt, 2001; Lookingbill et al., 2010). In particular, stream networks based on realistic riverscapes can be generated as in a neutral landscape model approach (e.g., With, 1997; Gardner and Urban, 2007) and combined with individual-based (Neeson et al., 2011) or transition-matrix-based (Padgham and Webb, 2010) dispersal models to simulate fish interaction with riverscape features. By simulating fragmentation, relationships between structural connectivity (i.e., physical relations among nodes) and functional connectivity (i.e., the manner in which the riverscape impedes or facilitates movement of individuals or populations) can reveal the utility of network-scale measures of habitat connectivity (Taylor et al., 1993; Urban and Keitt, 2001; Zetterberg et al., 2010; Rayfield et al., 2011). Whereas such approaches are well developed in terrestrial settings (e.g., Andersson and Bodin, 2009), examining the performance of patch-based graphic approaches as well as network-scale habitat availability measures in freshwater ecosystems requires additional research (Erős et al., 2012).

The goal of this study was to evaluate how network-scale dispersal of fish responded to habitat fragmentation using a patch-based graphic modeling approach. Specific objectives were to: (i) develop alternative stream networks that resembled the architecture of real-world riverscapes using patch-based graphs; (ii) evaluate responses in simulated fish dispersal to the presence of semi-permeable barriers across a range of network architectures, fish dispersal abilities, and barrier permeability values; and (iii) assess whether habitat availability measured at the network scale using the DCI is useful for predicting fish response to changes in connectivity.

Methods

In this study we used graph theory to visualize a stream network as a series of linked nodes and used simulated fish dispersal to test relationships between habitat connectivity and fish population distributions measured at the scale of stream networks (Figure 4.1). We first developed three riverscapes that resembled realistic hierarchical structuring of habitat patches in stream networks using nodes (habitat patches) and edges (dispersal corridors). Second, we simulate fish dispersal for relatively high and low dispersal (i.e., “high” dispersal is approximately twice as much as “low”) using a transition matrix approach to track network-scale occupancy of nodes in the absence of fragmentation (i.e., a neutral condition; sensu With, 1997).

We began by assuming all nodes were initially occupied by an equal portion of a population and used a Markovian random walk model to represent movement of fish throughout each riverscape. Third, we fragmented riverscapes by randomly placing up to five barriers with various permeability values (0.5, 0.05, and 0.00; where 1 is completely passable and 0 is completely impassable) among links and recorded the percent of nodes occupied after 156 iterations (i.e., model convergence in the neutral case). Finally, we calculated the DCI for all barrier insertions as a measure of network-scale habitat connectivity and explore mechanistic factors involved with the observed relationships between the DCI and riverscape occupancy.

Development of Riverscapes

We adopted the approach of generating distributions of nodes in theoretical riverscapes based on topological patterns of stream channel networks observed in nature (Kirchner, 1993). To begin, we used 15 nodes that represent stream segments (i.e., the section of stream between two confluences; Neeson et al., 2011) based on previous analyses of stream networks (Fagan, 2002). Nodes were then arranged using Horton's Laws regarding stream channel network architecture (Horton, 1945; Labonne et al., 2008). Horton's Laws describe patterns in the number and size of stream segments according to the Strahler (1957) ordering system, in which the smallest of headwater stream channels are first-order stream segments, two first-order segments meet to form a second-order stream segment, two second-order segments meet to form a third-order stream segment, and so on. The first of Horton's Laws is the bifurcation ratio (R_B), which describes the number of streams of a particular order in a network:

$$R_B = \frac{N_w}{N_{w+1}} \quad (1)$$

where N_w is the number of streams of order w . The R_B ranges from 3 to 5 among natural stream channel networks and exhibited a modal value of roughly four in simulations conducted by Kirchner (1993). Horton also developed the length ratio (R_L), which describes the distribution of stream lengths in a network:

$$R_L = \frac{L_w}{L_{w-1}} \quad (2)$$

where L_w is the mean length for streams of order w . The R_L ranges from 1.5 to 3 among natural stream channel networks and exhibited a modal value of roughly two during simulations conducted by Kirchner (1993). Stream channel networks also exhibit random patterns in

elongation or compaction, described as the relative amount of stream between the most upstream headwater and the outlet of the network (Kirchner 1993). Although recent studies suggest other measures of network structure are useful when constructing large networks (e.g., network diameter; Neeson et al., 2011), here we focus on the R_B and R_L for characterizing channel structure because of the small size of networks generated (i.e., only 15 nodes) and use of Horton's Laws in similar studies of network connectivity (Labonne et al., 2008).

We constructed three riverscapes represented as patch-based graphs (Erős et al., 2012) so that nodes were arranged in a manner consistent with bifurcating stream networks that conform to Horton's Laws of stream channel networks (i.e., R_B within 3-5, R_L within 1.5-3; Kirchner, 1993; Grant et al., 2007). For simplicity, we assumed all nodes were of equal size and quality (homogeneous node resolution), but differed in their spatial arrangement in a manner consistent with the topology of third-order stream channel networks. Riverscapes included in this study were characterized by $R_B = 4$ (calculated using N_w = number first-order streams), $R_L = 1.5$ (calculated using L_w = length of third-order stream), and relatively compact (Figure 4.2; Riverscape A); $R_B = 3.5$, $R_L = 2$, and intermediate compaction (Figure 4.2; Riverscape B); and $R_B = 3$, $R_L = 2.5$, and relatively elongated (Figure 4.2; Riverscape C). Whereas alternative architectures were possible within the constraints listed above, as a starting point we conducted analyses on only these three networks (*sensu* Fagan 2002). These theoretical riverscapes constitute constrained networks that mimic the spatial scale at which dispersal and fragmentation are known to influence fish community composition (i.e., third-order stream networks; Hitt and Angermeier, 2008; Perkin and Gido, 2012).

Dispersal Model Description

Our model depicted riverscapes as constrained networks (*sensu* Padgham and Webb, 2010) defined by 15 nodes. Edges defined the dendritic topology of nodes and describe each as headwater, confluence, second- or third-order channel unit, or the base of the network (Figure 4.2, middle column). We assumed directional variability among links (i.e., heterogeneous link resolution) consistent with a patch-base graphic Model type II from Erős et al. (2012).

Dispersal among nodes (i.e., link resolution) was constrained by discrete transition probabilities that defined the ability of fish to move to adjacent reaches in upstream (u) and downstream (d) directions (Figure 4.3a). We again followed the conceptual framework of

Padgham and Webb (2010) that emphasizes such connectivities are generally involved in landscape-scale measures of species movement (Bélisle, 2005) and habitat connectivity (Cote et al., 2009). However, the model differed from that of Padgham and Webb (2010) in that perceptual range of fish was limited to only immediately adjacent nodes rather than network-scale knowledge (Figure 4.3b). Local knowledge is likely more biologically relevant for organisms forming dispersal decisions in the absence of enhanced perception of entire networks (e.g., olfactory cues from distant upstream nodes; Neeson et al., 2011). Because dispersal ability of organisms can influence their response to fragmentation, and high dispersing organisms generally respond more strongly than low dispersers (e.g., Funk et al., 2004; Pépino et al., 2012), the model included two levels of dispersal. We began with transition probability values based on mark-recapture rates for stream fish documented by Norman et al. (2009). Mean weekly transition probabilities for movement from one stream segment to the immediately adjacent segment in upstream (u) and downstream (d) directions were calculated across study sites for benthic (“low” dispersal, $u = 0.07$; $d = 0.05$; Figure 4.3c) and water column (“high” dispersal, $u = 0.12$, $d = 0.11$; Figure 4.3d) fish (see Norman et al., 2009). These values resulted in an upstream movement bias for both high and low dispersal, which is consistent with previously reported patterns of organism dispersal in ecological networks (Grant, 2011). We assumed initial occupation of each node (Fagan, 2002) by an even portion of the population (i.e., 1/15) and used a Markovian random walk model based on a transition matrix (Padgham and Webb, 2010) to simulate iterative time steps of transition probabilities (Ching and Ng, 2006). This approach resulted in biased random movements (i.e., a biased random walk) among nodes so that the decision regarding dispersal in the subsequent iteration depended on the current distribution among nodes and occurred independently of the decision in the previous iteration (Codling et al., 2008). We used a context-dependent number of iterations ($n = 156$) based on model convergence in the neutral case (i.e., no barriers present) for both high and low dispersal and replicated scenarios 1000 times for each of the three riverscapes.

Fragmentation of Riverscapes

We simulated fragmentation of riverscapes by inserting up to five semi-permeable barriers at randomly assigned locations. Previous assessments of fish passage through perched road crossings suggest permeability values are generally less than or equal to 0.5 (Bourne et al.,

2011; Anderson et al., 2012), thus we used a range of permeability values (i.e., 0.5, 0.05, 0.00) in our simulation of fragmentation to assess how barrier permeability influenced connectivity measures. Furthermore, although permeability values are rarely equal among barriers within a network (e.g., Anderson et al., 2012), we assumed uniform permeability within each simulation to gain a better understanding of the importance of barrier location (and consequently fragment size) without confounding effects of variability in permeability. To simulate fragmentation, we began with addition of a single barrier randomly placed at one of 14 possible locations in each riverscape (labeled A-N in Figure 4.2) and replicated this process 1000 times for each barrier permeability value (i.e., 0.5, 0.05, and 0.00). Next, we inserted barriers at two randomly selected locations and repeated the previous process, followed by insertion of three, four and five barriers.

Our last step was to evaluate the impact of barrier additions on functional (i.e., the manner in which riverscapes facilitate or impede fish dispersal; Taylor et al., 1993) and structural (i.e., physical connectivity among nodes) connectivity of riverscapes. To estimate functional connectivity, we began with the addition of a single barrier and multiplied barrier permeability (0.5, 0.05, or 0.00) by the upstream transition probability for the corresponding location in the transition matrix. This process resulted in the probability of transition through a fragmented node in an upstream direction being reduced according to the permeability of the newly inserted barrier; while movement in a downstream direction remained unaltered (assuming fish were capable of downstream dispersal over perches). We estimated network-scale functional connectivity by considering each node as occupied or unoccupied, where occupied nodes contained at least 1% of the population after 156 iterations and unoccupied nodes contained <1%. The sum of all occupied nodes divided by the total number of nodes in the riverscape (i.e., 15) was then multiplied by 100 to estimate percent of riverscape occupied. We also calculated the probability of extirpation (here *extirpation* refers to emigration without return to the extent that <1% of the population occurred in a node) for specific nodes in the presence of a range of barriers using the fraction of replications ($n = 1000$) that resulted in extirpation for each scenario.

To estimate structural connectivity, we used the potamodromous component of the DCI (as opposed to the anadromous component; see Cote et al, 2009). Calculation of the DCI involves dividing stream networks into fragments separated by barriers and characterized by known longitudinal lengths, then calculating the probability of fish movement between all fragments in the network. Here we use the term *fragment* to define the total number of stream

nodes (segments) that remain connected after barrier addition (i.e., fragments are made up of connected nodes). The DCI is calculated as:

$$DCI = \sum_{i=1}^n \sum_{j=1}^n c_{ij} \frac{l_i}{L} \frac{l_j}{L} \times 100 \quad (3)$$

where l is the length of fragments i and j , c_{ij} is the connectivity between fragments i and j , and L is the length of all the segments in the network (Cote et al., 2009). The index is rescaled to a maximum value of 100 with the final multiplication factor. Since nodes in our stream networks had a uniform unit length, we estimated fragment size using the number of isolated nodes based on barrier locations in the transition matrix (i.e., fragmented nodes corresponded with those for which dispersal was altered in the transition matrix). For this process we used the same randomly drawn barrier locations used for simulated fragmentation in the context of functional connectivity, so that responses to altered structural connectivity were related to the same barrier locations as functional connectivity. We began by calculating the DCI for riverscapes containing only one barrier to assess how barrier location influenced DCI measurements, and then extended calculations to scenarios for addition of two through five barriers. To assess relationships between structural and functional connectivity, we used regression and plotted DCI as the independent variable and riverscape occupancy as the dependent variable and calculated the coefficient of determination. Data were \log_{10} transformed before analysis to address skewness in distributions.

Effect of Barrier Location

We evaluated the effect of barrier location on patterns in riverscape occupancy and DCI estimates by comparing estimates to known locations of a single barrier. This approach linked barrier locations with declines in habitat availability and declines in occupancy. We first combined all simulations during which a barrier was placed at one of 14 possible locations (labeled A-N in Figure 4.2) for each riverscape, dispersal level, and barrier permeability scenario. Effect of barrier location on node occupancy was evaluated by plotting the mean (\pm standard deviation) percent of nodes occupied across the 1000 replications computed for each scenario. Effect of barrier location on DCI calculations was evaluated by computing the index for each barrier location in the riverscape. This approach allowed for addressing if greater declines in structural connectivity (habitat availability) were equal to greater declines in functional connectivity (node occupancy) based on barrier placement.

The structure of riverscapes developed during this study resulted in specific numbers of nodes being isolated when a single barrier was in place (i.e., 1, 3, 4, 5, 10, 11, 13, and 14 nodes). This pattern was driven by barriers being placed on headwaters (first-order nodes; one node isolated), mid-order reaches (second-order nodes; 3, 4 or 5 nodes isolated) and “mainstems” (third-order nodes; 1, 10, 11, 13, or 14 nodes isolated) of each riverscape. We compared the number of nodes in which fish became extirpated to the number of isolated nodes caused by a single barrier to evaluate the occurrence of thresholds in fish response to fragmentation. We interpreted a threshold as a disproportionately large change in extirpation over a relatively small change in the number of isolated nodes. Thresholds were evaluated for each riverscape assuming all dispersal and barrier permeability scenarios.

Change in Fragment Size Distributions

We investigated changes in fragment size distributions as a function of the number of barriers present in the riverscape. Although riverscapes consisted of 15 linked nodes in the absence of fragmentation, the number and placement of barriers added contributed to an increased number of smaller fragments. Because of this pattern, we characterized how the frequency distribution of fragment sizes varied with the number of barriers present. Barrier locations were randomized and replicated 1000 times for 1-5 barriers in each riverscape. To illustrate patterns in changing size distributions caused by an increasing numbers of barriers, we plotted mean (\pm standard deviation) frequencies of fragment size classes among the three riverscapes for one through five barriers. Initial results suggested fish of both dispersal levels indicated threshold responses in occupancy when three or fewer nodes were isolated by a single barrier (see Results). Consequently, we assessed the relationship between the number of small habitat fragments (i.e., ≤ 3 nodes) present in a riverscape and the percentage of nodes occupied. This approach allowed for assessing fish response to the number of small fragments in a riverscape regardless of the number of barriers present.

Results

Fish Response to Barriers

Upstream bias in transition probabilities resulted in a greater percent of populations at the upstream extent of riverscapes and complete riverscape occupancy in the absence of

fragmentation. At a barrier permeability value of 0.5, neither high nor low dispersing fish indicated a change in riverscape occupancy regardless of the number of barriers present in the riverscape (Table 4.1). When barrier permeability was reduced to 0.05, low dispersing fish declined as barriers were introduced and reached approximately 77% occupancy (averaged across 1000 simulations) when five barriers were present; whereas, high dispersing species declined to 56% occupancy. When barrier permeability was reduced to 0.00, low dispersing species declined to approximately 59% occupancy averaged across riverscapes when five barriers were present; whereas, high dispersing species declined to approximately 38%. Addition of barriers characterized by permeability 0.05 and 0.00 resulted in an increase in probability of extirpation among nodes, and nodes nearer the upstream extent of riverscapes tended to endure a greater extent of extirpation (Figure 4.4). There was a general pattern of greater decline in occupancy as riverscapes became more elongated, so that Riverscape C generally exhibited the greatest decline in occupancy because of fragmentation.

Network-Scale Measurement of Habitat Connectivity

The DCI explained 37-69% of variation in occupancy among riverscapes, dispersal levels, and barrier permeability values (Figure 4.5). Percent riverscape occupancy and DCI, averaged by numbers of barriers, were strongly positively related (overlaid in Figure 4.5). Variation among DCI estimates was least in the presence of a greater number of barriers; however, variation among occupancy estimates was least when few barriers were in place. The DCI captured more variation in occupancy for the high than low dispersal fish, as well as for barrier permeability 0.00 relative to 0.05. There was little variability among the three riverscapes in terms of the amount of variation in occupancy explained by the DCI.

Effect of Barrier Location

Barrier location affected estimates of occupancy and the DCI differently. Declines in occupancy were consistently observed among scenarios with barriers on first-order nodes (Figure 4.6). Fragmented first-order nodes nearer to the upstream extent of riverscapes indicated declines in occupancy every time a barrier was in place (i.e., no variability) associated with extirpation of the single isolated node or 7% of the riverscape; the exception being for the low dispersal level and barrier permeability 0.05, for which little variability occurred. Fragmented second-order nodes near the upstream extent of riverscapes exhibited greater declines in

occupancy relative to those nearer to the base of the network, associated with isolation of three upstream nodes (i.e., one second-order and two first-order nodes) or 20% of the riverscape. For high dispersal and barrier permeability 0.00, occupancy declined to approximately 80% when a single barrier fragmented upstream second-order nodes. Fragmentation caused by barriers on third-order nodes generally caused little decline in occupancy, the only case being the scenario in which a barrier was placed at either of the upstream third-order nodes of Riverscape C for high dispersal and barrier permeability 0.00.

Contrary to patterns observed for occupancy, the greatest declines in DCI caused by a single barrier were associated with locations on second- and third-order nodes. In particular, large magnitude declines in DCI were caused by barriers at nodes near the center of riverscapes (i.e., upstream third-order or downstream second-order nodes). The DCI declined to approximately 87 across both permeability values when a single node was isolated, including all first-order nodes and the case for riverscapes B and C when the downstream-most third-order node was fragmented. Variability in barrier permeability (0.05 or 0.00) caused little change in DCI values.

Relationships between fragment size and the proportion of upstream nodes from which fish became extirpated in the presence of only a single barrier were indicative of threshold responses. When fragment sizes were small (i.e., ≤ 3 nodes), the proportion of extirpated upstream nodes was high; however, as fragment size increased beyond three, extirpations declined rapidly or were absent (Figure 4.7). For the low dispersal scenario when barrier permeability was 0.05, fish were extirpated from single, isolated upstream nodes approximately a third of the time across riverscapes. This case resulted from few extirpations when a single upstream node was fragmented near the upstream extent of riverscapes, but relatively greater extirpations from single isolated upstream nodes nearer the base of riverscapes. Among all other scenarios, when a single upstream node was isolated fish became extirpated. Similarly, when three upstream nodes were isolated, fish were extirpated from some fraction of the riverscape (except for the case of low dispersal and barrier permeability 0.05). The greatest extent of extirpation from three fragmented upstream nodes was for the high dispersal scenario when barrier permeability was 0.00, in which fish were extirpated from all three nodes nearly 90% of the time.

Changes in Fragment Size Distributions

Distributions of fragment sizes became biased toward smaller size classes when a greater number of barriers were in place (Figure 4.8). When a single barrier was inserted, the distribution of fragment sizes was symmetrical and an equal number of relatively large and small fragments occurred among riverscapes. However, introduction of additional barriers caused distributions to become increasingly skewed towards small fragments with ≤ 3 nodes. This pattern resulted in the proportion of small fragments present in riverscapes increasing as one (38%), two (53%), three (63%), four (70%), and finally five (77%) barriers were inserted among riverscapes.

Increases in the number of small fragments in riverscapes contributed to declines in occupancy (Figure 4.9). When zero small fragments were present in riverscapes, either because of the absence of barriers (i.e., neutral condition) or because existing barriers did not isolate small fragments, occupancy was on average greater than 98% for all dispersal levels and barrier permeability values (Table 4.2). Increases in small fragments, brought on by either changes in barrier locations or increases in the number of barriers present in the riverscape, caused steady declines in occupancy. The number of small fragments possible in a riverscape was determined in part by the number of barriers, and although sample sizes for simulations involving zero through five small fragments were high (>600 replications), the number of times six small fragments occurred in a riverscape was generally low (0-9 replications). This was driven by the fact that in order to achieve six small fragments, five barriers must be placed so that three or fewer nodes are isolated by each barrier, and the probability of this happening was low using random barrier insertions. Consequently, we focus on the maximum case of five small fragments occurring in riverscapes. When barrier permeability was 0.05, low dispersing fish declined to approximately 75% occupancy across riverscapes when five small fragments were present; whereas, high dispersing species declined to approximately 57% occupancy. When barrier permeability was 0.00, low dispersing fish declined to approximately 61% occupancy across riverscapes when five small fragments were present; whereas, high dispersing species declined to approximately 40% occupancy.

Discussion

Modeling habitat connectivity and fish dispersal in three hypothetical riverscapes identified specific properties of fragmented riverscapes that could lead to species declines. These properties include: (i) extirpations occur most among “smaller” fragments; (ii) barriers with lower permeability cause greater extirpations; and (iii) specific barrier locations are associated with greater levels of extirpation. Though context-dependencies exist for each property, results suggest that habitat connectivity measured at the network scale predicts fish response to multiple barriers in a riverscape. Moreover, the dispersal level of fish interacts with barrier permeability and location to determine the threshold size for “small” fragments within which populations do not persist. We believe these properties have implications for the ecology of stream fish in real-world riverscapes and hold relevance for management of biodiversity in fragmented riverscapes.

Models Reveal Properties of Fragmented Riverscapes

Our modeling approach required several key assumptions that contributed directly to the observed patterns in species declines. Key model assumptions included: biased upstream movement for both dispersal levels; fish were not lost from the network; downstream dispersal was not interrupted by the presence of a barrier; all barriers within a simulation had equal permeability; and nodes had uniform quality. The most apparent pattern was the disappearance of fish from small fragments in our riverscapes, which was related to movement out of the fragment in a downstream direction and limited reentry in an upstream direction. This result occurred because of our assumption that movement was biased in an upstream direction (the case for many organism in stream networks; Grant, 2011) but became biased in a downstream direction when a barrier was present and local upstream transition probability was reduced by at least half (i.e., barrier permeability <0.5). Thus, extirpations from small fragments were not related to fish being lost from the network (e.g., because of node-specific demographic rates or extinction probabilities; Labonne et al., 2008; Grant, 2011), but instead were related to accumulations in larger fragments nearer the center or downstream portions of riverscapes. Second, accumulation in larger, centrally located fragments was most evident when barrier permeability was lower. Based on our model assumptions, barriers with permeability values greater than 0.50 posed little threat to riverscape-scale occupancy, though declines did occur at

permeability 0.10 (results not shown) and lower even when only a single barrier was in place. This pattern was driven by the manner in which barriers “reflected” fish and caused them to transition downstream rather than upstream (Rodríguez, 2010), and barriers with lower permeability reflected a greater proportion of fish. Finally, declines in occupancy were driven by probability of extirpation being highest among upstream nodes that corresponded with greater fish abundances in the absence of fragmentation (i.e., the neutral condition). Consequently, node-specific responses to fragmentation were greatest among upstream nodes and followed the hierarchical structuring of habitats in riverscapes. By this account, although we assumed equal quality among nodes prior to their arrangement, an intrinsic quality based on their location within the riverscape emerged with respect to patterns in occupancy prior to and following fragmentation.

Emergent properties are common in hierarchically structured landscapes such as streams and highlight the potential for riverscape patterns (e.g., architecture, connectivity) to influence ecological processes such as organism dispersal at broad scales (Grant et al., 2007). Although habitat connectivity and quality have the potential to interact and cause variable responses in fish occupancy throughout a riverscape, previous work suggests such interactions are minor (Padgham and Webb, 2010) and supports our assumption of homogenous node quality in favor of emphasizing responses to changing connectivity. Despite homogenous node quality, we found patterns in extirpation were not equal among all nodes and that headwaters emerged as most susceptible to extirpation when riverscapes were fragmented. This pattern was exacerbated by the addition of multiple barriers that fragmented a greater portion of the riverscape. In this context, interplay between shifts in node connectivity and fish occupancy occurred at the riverscape scale, which likely explains the success of the DCI in predicting fish response to fragmentation. Habitat connectivity measured using the DCI predicted 30-50% of variation in fish distribution for low dispersal and 50-70% of variation for high dispersal. Because we assumed homogeneity in barrier permeability within simulations, lower DCI values should be interpreted as a greater splitting of the riverscape, either through barrier arrangement (i.e., contributing to variability within the number of barriers) or barrier number (i.e., contributing to variability among the number of barriers). The greatest variation in DCI estimates occurred for the single barrier scenario, when the barrier could produce a greater range of fragment sizes. As additional barriers were inserted, the range of potential fragment sizes declined and DCI values

were restricted accordingly. On the contrary, variability in estimates in riverscape occupancy increased as barrier number increased, likely as an artifact of increased model convergence time when multiple barriers slowed dispersal. Consequently, we believe the mechanism by which the DCI predicted changes in occupancy was the threshold response by fish caused by isolation of small fragments, so that highly predictable declines in occupancy occurred when 1-3 nodes were isolated. This pattern resulted in a near-linear decline in riverscape occupancy as the number of small fragments in the riverscape increased, and higher dispersal resulted in a greater extent of extirpation because greater transition probability resulted in a greater likelihood of fish encountering a barrier.

Dispersal Ability Determines Response to Fragmentation

High dispersing fish species respond to fragmentation of river networks to a greater extent than do relatively sedentary fish. In our study, the high dispersal level indicated greater declines in occupancy relative to the low dispersal level regardless of riverscape architecture, barrier permeability, or barrier number. This is in part because dispersal events incorporating greater distances (i.e., higher transition probabilities) stand a better chance of encountering barriers and either moving to adjacent stream sections or being reflected by a barrier (Rodríguez, 2010). Thus fish that depend on dispersal over greater distances for population regulation tend to respond strongly to fragmentation (Pépin et al., 2012). For example, Hitt and Angermeier (2008) found fish in families Catostomidae and Cyprinidae dispersed over distances of at least six to eight stream km in the James River drainage, Virginia, USA. The authors concluded that habitat connectivity was therefore important for local persistence of these fish, at least at a spatial scale of up to 10 stream km. It is not surprising then that catostomids and cyprinids indicated strong responses to fragmentation in Kansas, USA stream networks measured at comparable spatial scales (i.e., up to 10 stream km), or that species in these families tended to become locally extirpated when barriers were in place downstream (Perkin and Gido, 2012). Furthermore, fish that indicated little response to fragmentation of Kansas streams were similar to those with low dispersal rate according to Norman et al. (2009), including stonerollers (genus *Campostoma*) and darters (genus *Etheostoma*); whereas, fish that indicated local declines or extirpations upstream of perched road crossings were similar to those with high dispersal rates (genera *Cyprinella* and *Notropis*; Perkin and Gido, 2012). These patterns illustrate how appropriate matches in the

spatial extent at which (i) fish interact with riverscapes and (ii) habitat connectivity is measured can enhance conservation of stream fish (Fausch et al., 2002). However, addressing such context-dependencies and determining appropriate spatial scales for network measures of connectivity can be challenging (Erős et al., 2012; Geheber and Piller, 2012).

Threshold Responses to Fragmentation

Non-linear responses by fish to stream fragmentation might be a useful method for determining the appropriate spatial scales at which to measure network connectivity. In realistic river networks, extirpations are generally due less to dispersal out of fragments as in our model (but see Aló and Turner, 2005; Agostinho et al., 2007) and more so to altered demographic rates within fragments. Altered demographic rates can result in threshold responses in population persistence and thresholds are therefore a feature in real-world ecological networks (Dewhurst and Lutscher, 2009). Fish extirpations from cool and warm water stream systems in North America provide examples. Brook trout *Salvelinus fontinalis* is a cool-water species with high dispersal during the reproductive season and reproductively viable populations are now extirpated from small stream fragments in the Fishkill Creek network of New York, USA (Bain and Wine, 2010). The apparent mechanism for extirpation involves inadequate habitat availability for reproduction among stream fragments less than 3.2 km in length (Bain and Wine, 2010), and such threshold responses to fragmentation are reported by other authors (Letcher et al. 2007). Similarly, warm-water, pelagic-spawning cyprinids in rivers throughout the Plains of North America are now extirpated from many stream fragments <100 stream km in length, though species-specific thresholds can be greater (Dudley and Platania, 2007; Perkin and Gido, 2011). The mechanism for these extirpations is again related to the absence of appropriate reproductive habitat in shorter fragments and loss of source-sink dynamics or rescue effects (Winston et al., 1991; Luttrell et al., 1999). In fact, Dudley and Platania (2007) specifically prioritized stream fragments in the Rio Grande drainage that are currently <100 stream km but would exceed this threshold with the removal of a single barrier. These examples suggest using network-scale measures of fragmentation in which reconnection of fragments less than the estimated threshold required for persistence are prioritized might contribute to increases in targeted species distributions.

Prioritizing specific fragment sizes that have ecological relevance rather than simply removing barriers to obtain maximum fragments sizes represents a paradigm shift in the current approach to barrier prioritization (Fullerton et al., 2010). In the absence of additional information, barriers are prioritized so that the maximum amount of stream length is reconnected by removal of the minimum number of barriers (Cote et al., 2009; Kemp and O’Hanley, 2010), and models specifically targeting reestablishment of a single, large fragment of stream have been developed (O’Hanley, 2011). For such models, when organism interpretation of a riverscape is not taken into account, increases in structural connectivity might not equal increases in functional connectivity (and vice versa). For example, Branco et al. (2011) found fish in four Portugal streams indicated little response to reduced longitudinal connectivity, likely because residual fragment sizes were large enough to allow completion of life history for even potamodromous species that are expected to respond strongly to fragmentation. Similarly, limited dispersal among targeted fish species or high permeability of barriers can contribute to weak relationships between structural and functional connectivity for stream-dwelling fish populations (Pépin et al., 2012). Thus species interpretation of barriers should be taken into account when barriers are prioritized for removal because highly permeable barriers might pose little threat to functional connectivity (Bourne et al., 2011) or because barrier locations do not interrupt fish life cycles (Hudman and Gido, In Review). Because both measures of connectivity (structural and functional) are scale and target dependent (Crooks and Sanjayan, 2006) an unavoidable context-dependent element must be included in network-scale assessments of organism response to fragmentation (Erős et al., 2012).

Conclusions

Fragmentation of riverscapes disrupts the abundance and distribution of numerous stream fish species, but the magnitude of fish response can vary among species and systems (e.g., Alexandre and Almeida, 2010; Branco et al., 2011; Andersson et al., 2012). Our findings suggest fish response to stream fragmentation is mediated by dispersal affinity as well as the permeability and distribution of barriers throughout a riverscape so that declines are greatest when dispersal is high and barrier permeability is low (Pépin et al., 2012). Because road crossings are common in contemporary landscapes (Gibson et al., 2005), methods for measuring network-scale connectivity and prioritizing barrier removal to enhance habitat connectivity have

recently been developed (Kemp and O’Hanley, 2010; Fullerton et al., 2010). However, maximizing structural connectivity with the ultimate goal of enhancing functional connectivity should be directed by specific goals for restoration because there might be little ecological benefit (e.g., Palmer et al., 2010) to maximizing structural connectivity if there is little response in fish abundance and distribution (Fausch et al., 2002). Knowledge of organism-specific threshold responses to fragmentation might therefore provide a greater ecological benefit if barrier prioritization methods are adapted to target specific fragment lengths in riverscapes with the goal of maximizing the number of fragments capable of supporting the organism of interest.

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Figure 4.1 Flow chart of operations used to test relationships between fish distributions and fragmentation in simulated riverscapes. Gray boxes represent the combination of multiple steps to obtain an output. Perm. refers to barrier permeability (where 1 is completely passable and 0 is completely impassible); DCI is the *dendritic connectivity index* described by Cote et al. (2009).

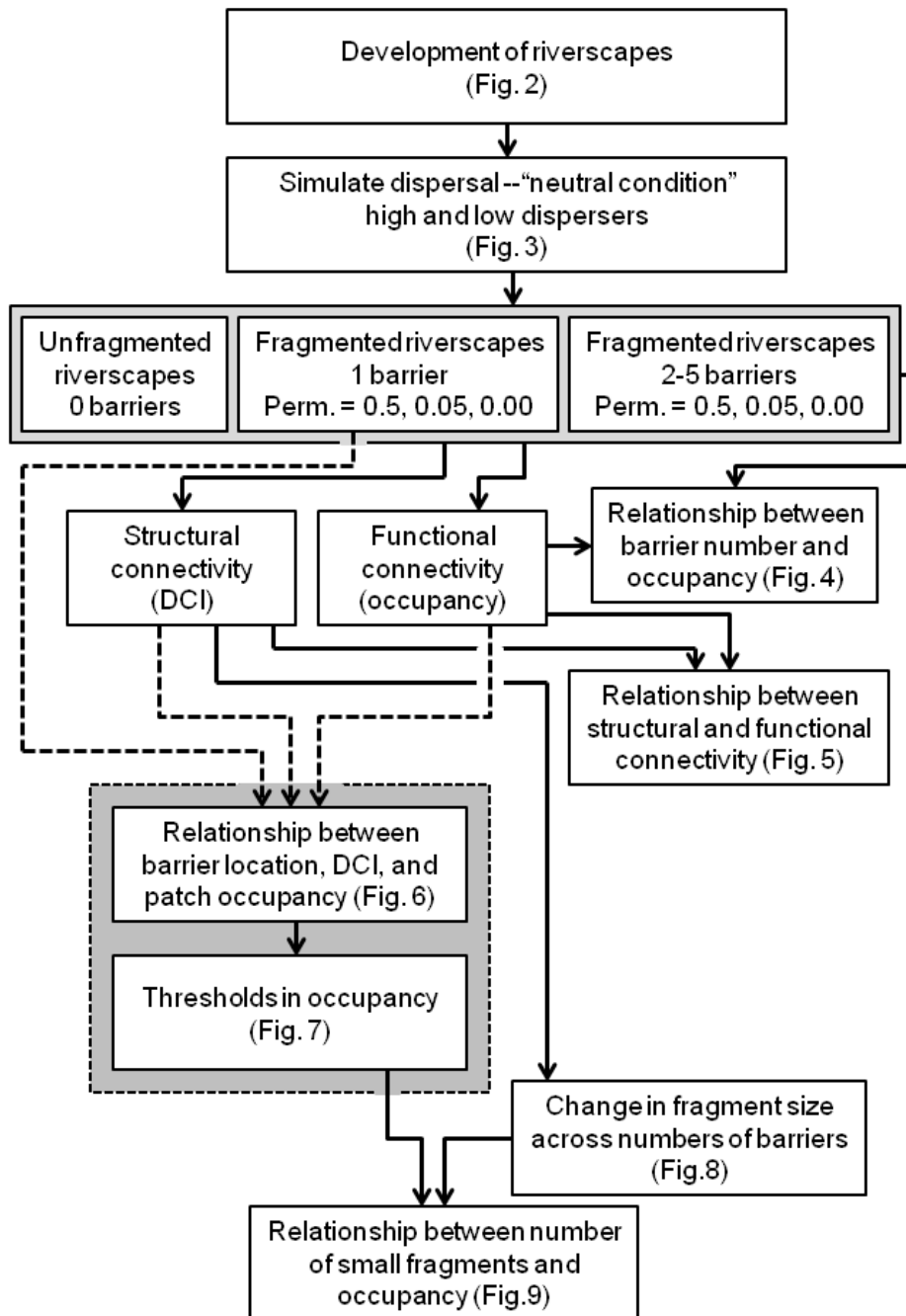


Figure 4.2 Simulated riverscapes included in study. Proceeding from left to right stream sections between confluences were converted to nodes (numbered circles) linked by dispersal pathways (lines; see description by Erós et al., 2012) on which barriers were randomly placed (lettered bars). Nodes are illustrate as first-order stream segments (black circles), second-order stream segments (gray circles), and third-order stream segments (white circles) according to the Strahler (1957) stream ordering system.

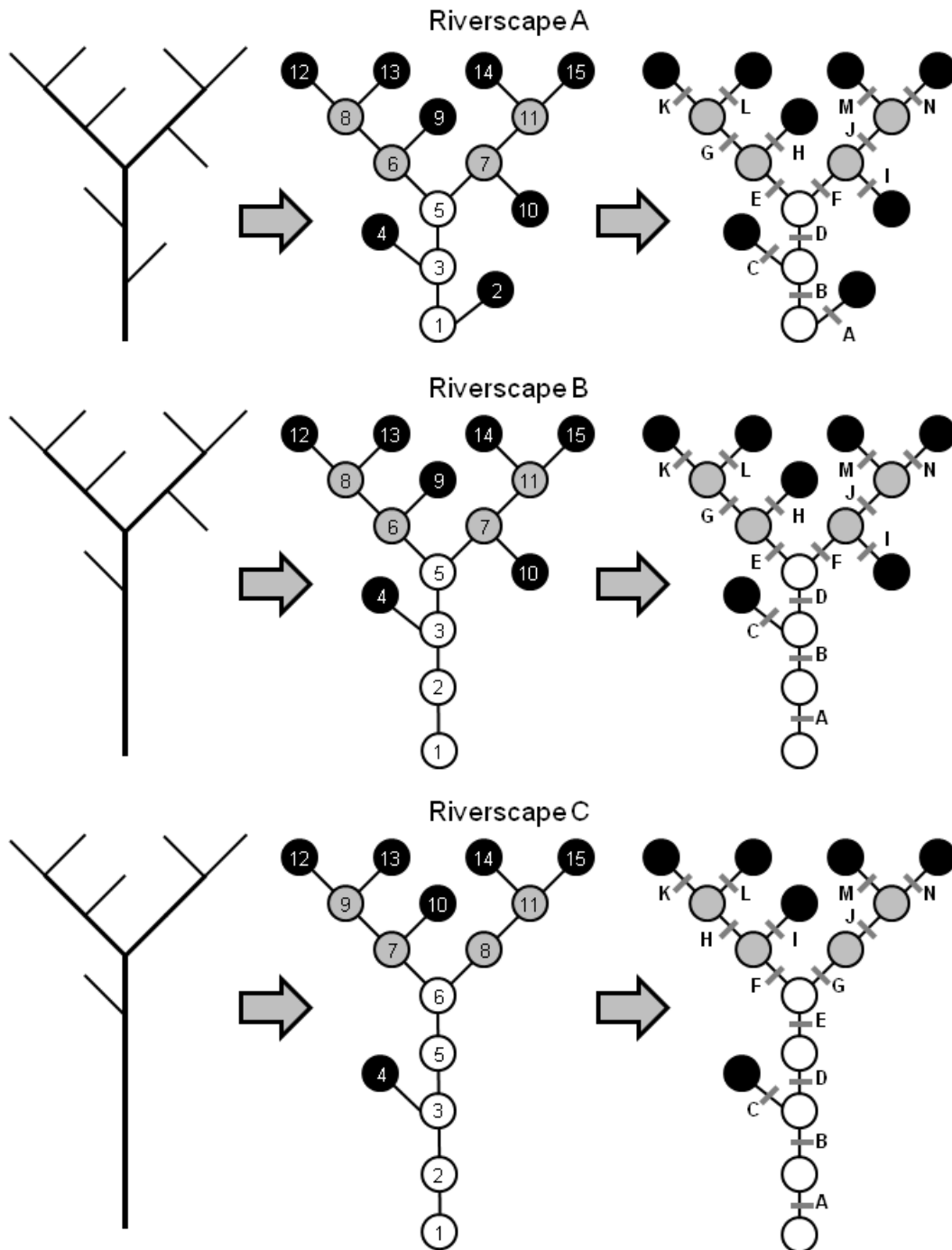


Figure 4.3 Basis for calculation of transition probabilities for network (a) versus local (b) knowledge of riverscapes as well as applied probabilities (invoking local knowledge) for low (c) and high (d) dispersing fish.

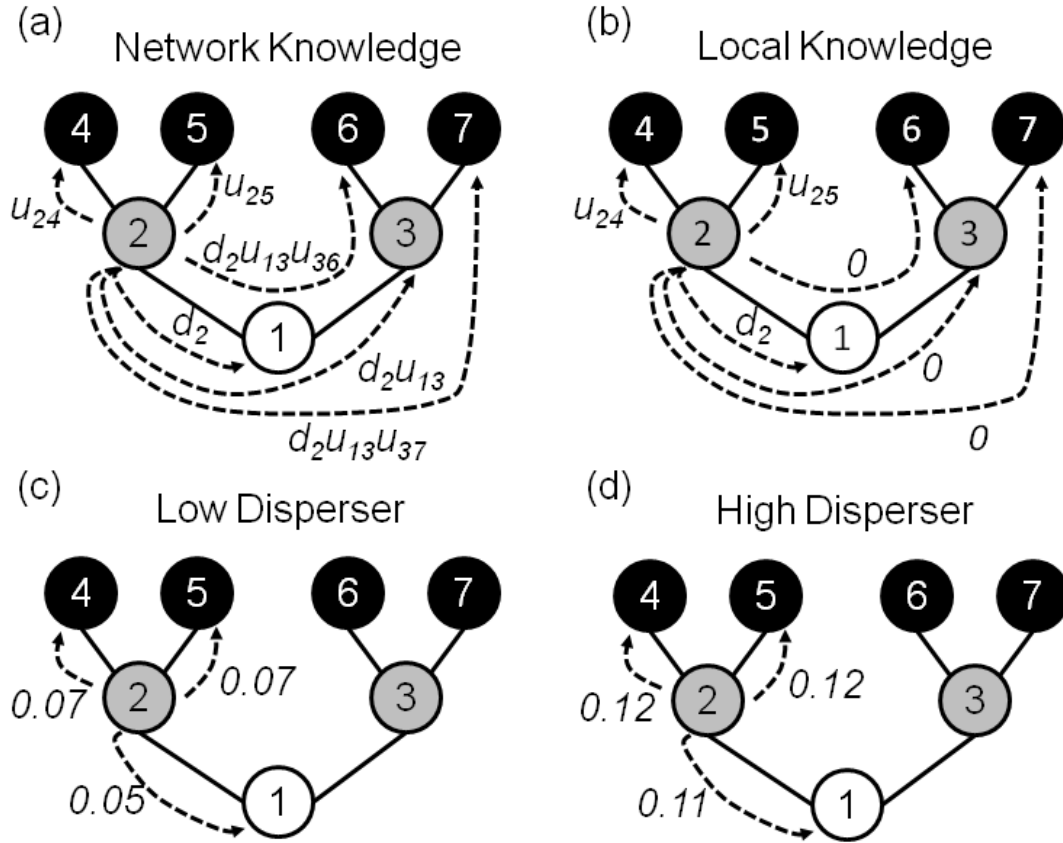


Figure 4.4 Percent of fish distributed among nodes (gray line) during the neutral condition (i.e., no barriers) and change in probability of extirpation after the addition of one (open circles), three (open down triangles), or five (shaded up triangles) barriers for three riverscapes assuming low (upper six panels) and high (lower six panels) dispersal and two barrier permeability values ($P = 0.05$ and $P = 0.00$). Node locations are numbered 1-15 for each riverscape (see Figure 4.2 for reference). For clarity, values for two and four barrier scenarios are excluded and points are slightly jittered among node identifications.

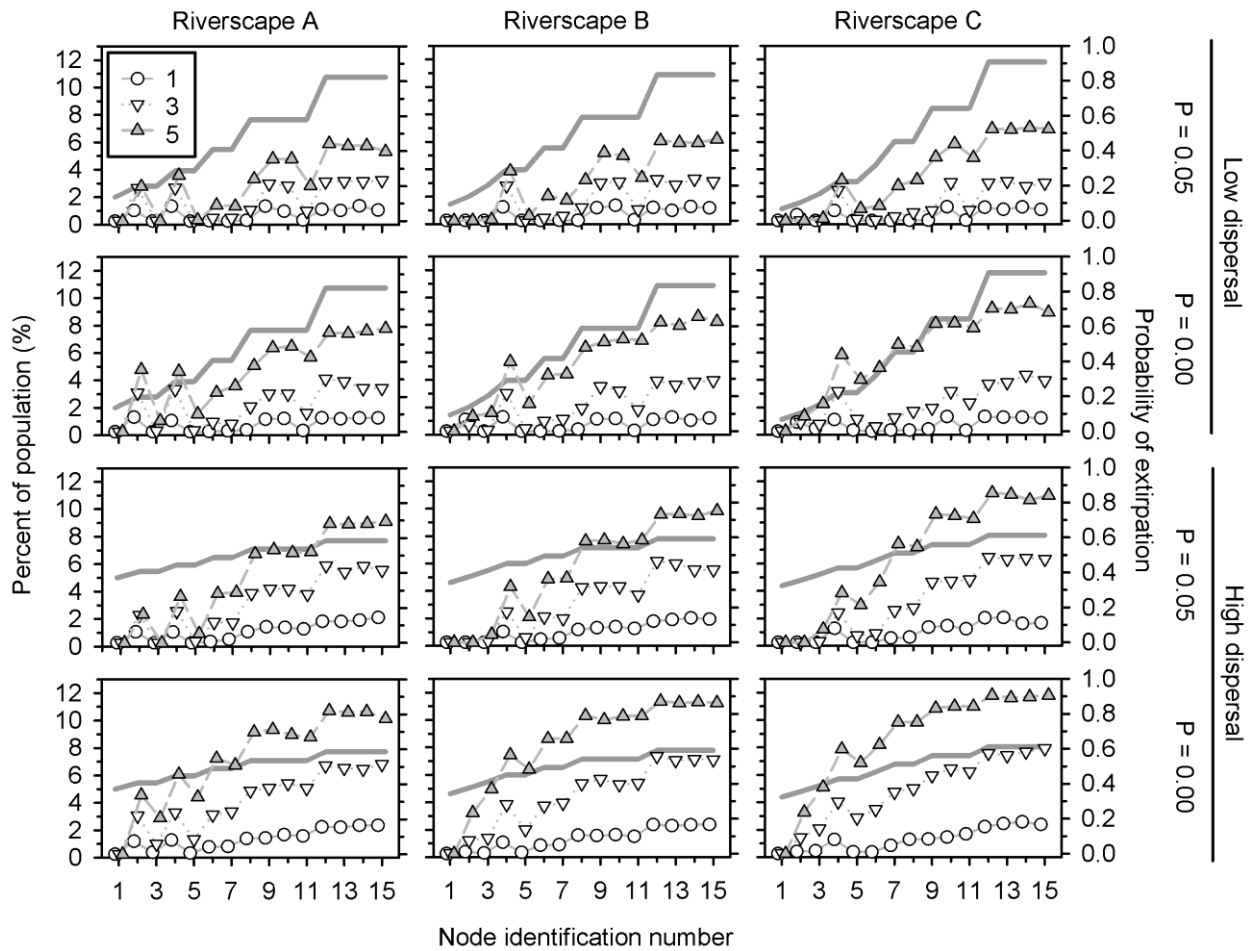


Figure 4.5 Relationship between the dendritic connectivity index (DCI) and percent of riverscape occupied for fish species with low (upper six panels) and high (lower six panels) dispersal ability in three riverscapes assuming two barrier permeability values (0.05 and 0.00). Gray points represent scatter plots (N = 6000) for replicated (n = 1000) addition of 0-5 barriers. Central tendencies are illustrated with the dark gray regression line (coefficient of determination for logarithmic data are given). White points are means (standard deviation) for DCI versus occupancy relationships for each number of barriers.

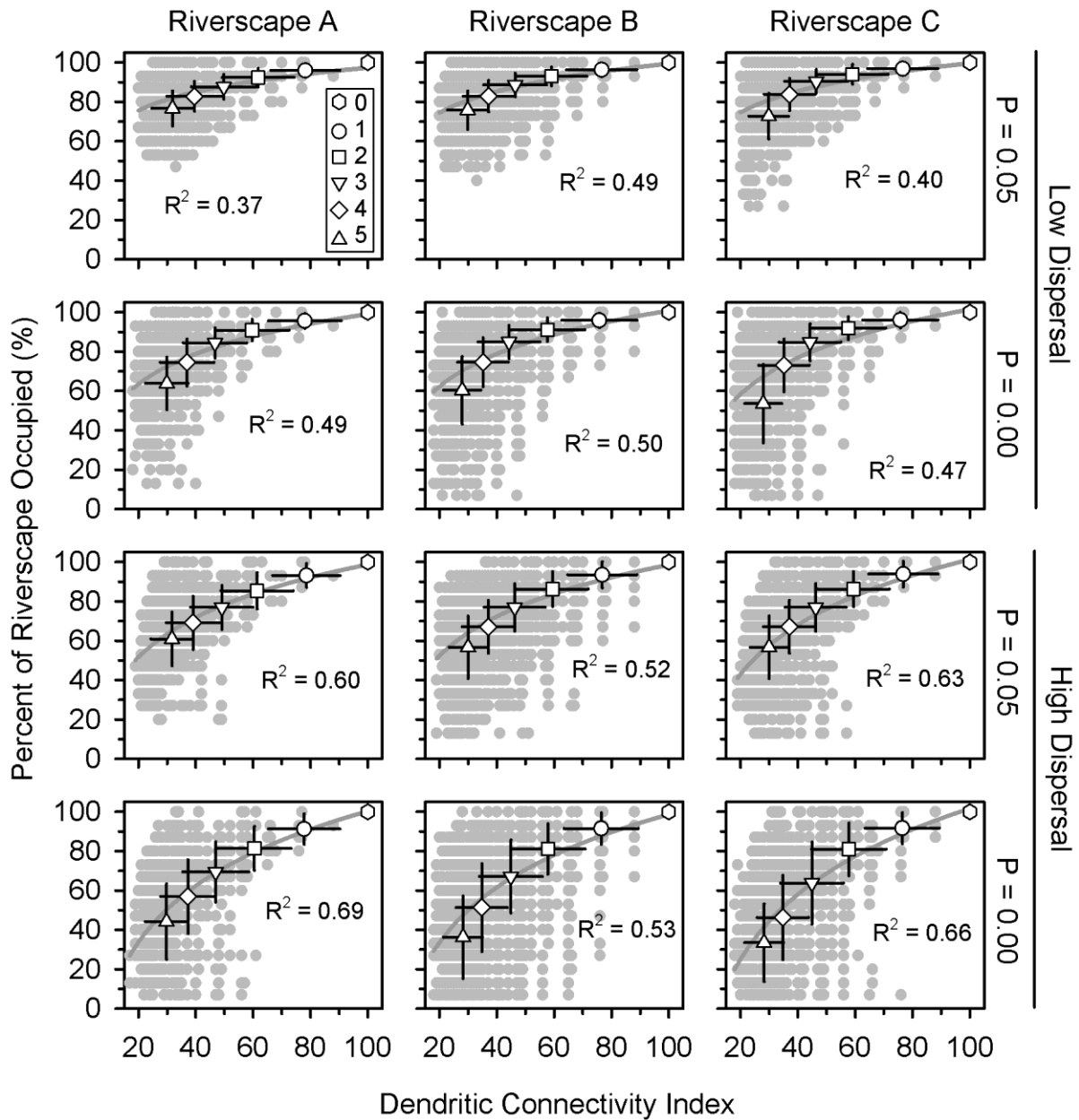


Figure 4.6 Relationships between barrier locations (see Figure 4.1 for reference) and percent of riverscape occupied (bars) as well as dendritic connectivity index (DCI; points) for fish species with low (upper six panels) and high (lower six panels) dispersal ability in three riverscapes assuming two barrier permeability values (0.05 and 0.00). Bars represent mean (standard deviation) of occupancy estimates for 1000 iterations during which barriers were randomly placed at one of 14 locations (A-N) and are color-coded by first- (black), second- (gray), and third-order (white) stream segments. Points represent DCI values related to placing a barrier at each of the 14 locations; only one DCI value is produced when a single barrier is in place (i.e., no error bars are presented).

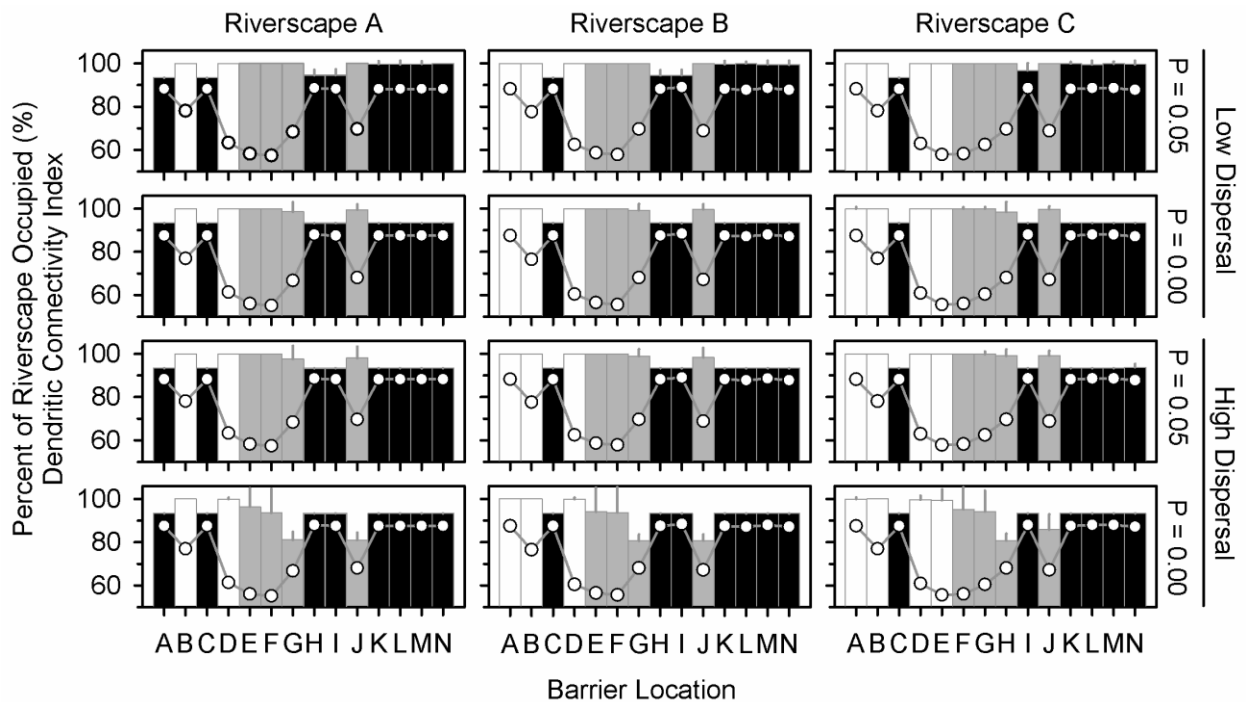


Figure 4.7 Relationship between isolated fragment size and the proportion of upstream nodes from which fish become extirpated for low (upper panel) and high (lower panel) dispersal ability and barrier permeability 0.00 (gray) and 0.05 (white) when a single barrier was placed in riverscapes. Bars represent means (standard deviations) among riverscapes A, B, and C.

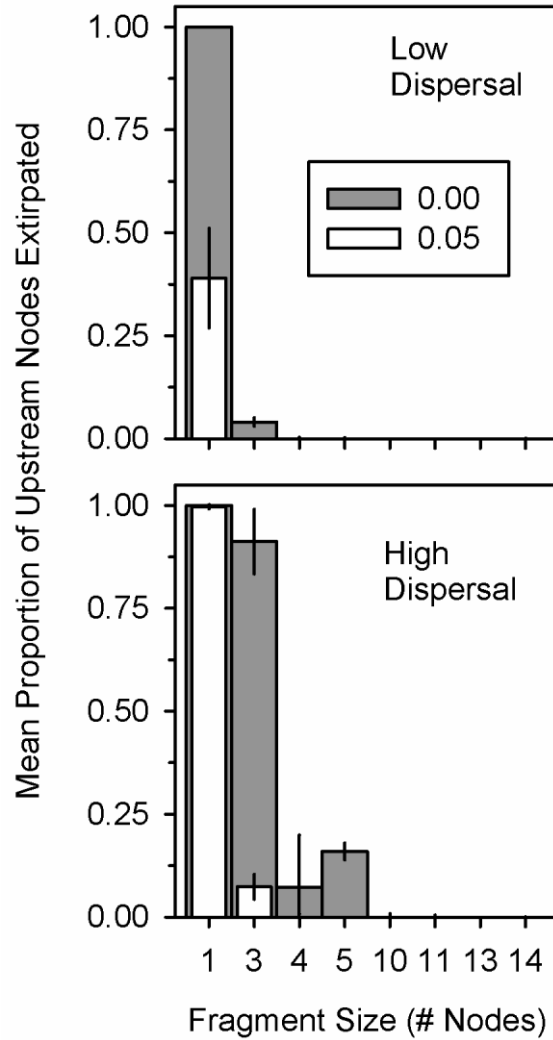


Figure 4.8 Change in frequency distribution of fragment sizes when 1-5 barriers are introduced to riverscapes. Bars illustrated means (standard deviations) for riverscapes A, B, and C.

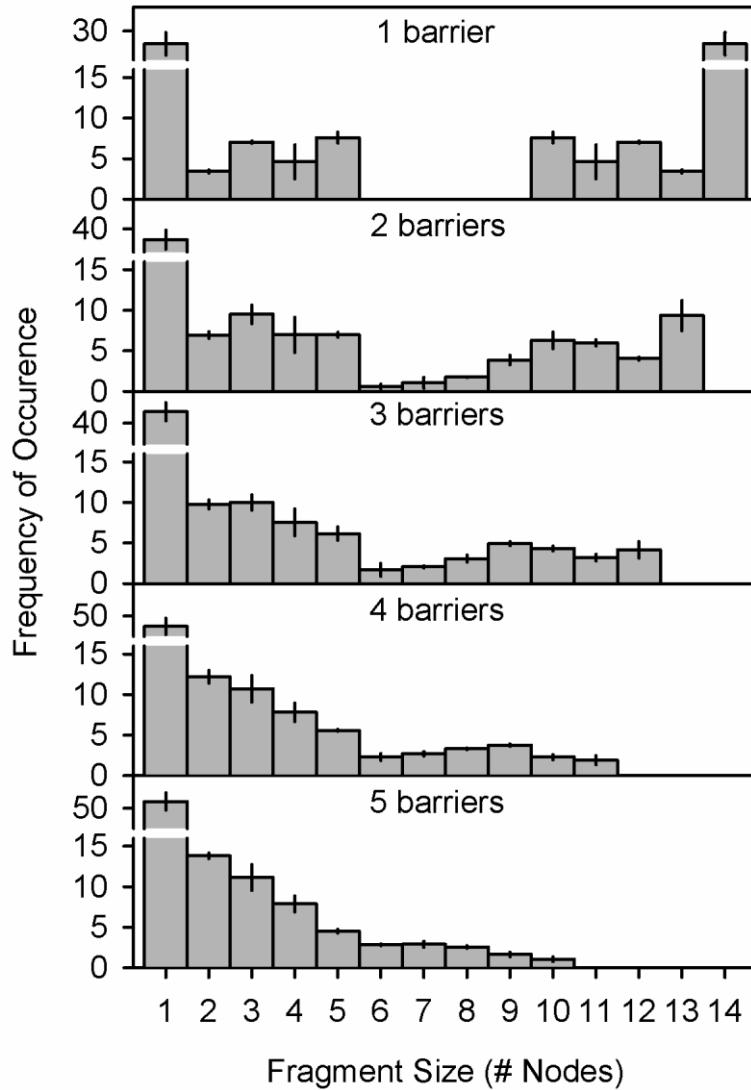


Figure 4.9 Relationship between number of small fragments (≤ 3 nodes) and percentage of riverscape occupied for fish species with low (gray points) and high (black points) dispersal ability for three riverscapes assuming two barrier permeability values (0.05 and 0.00).

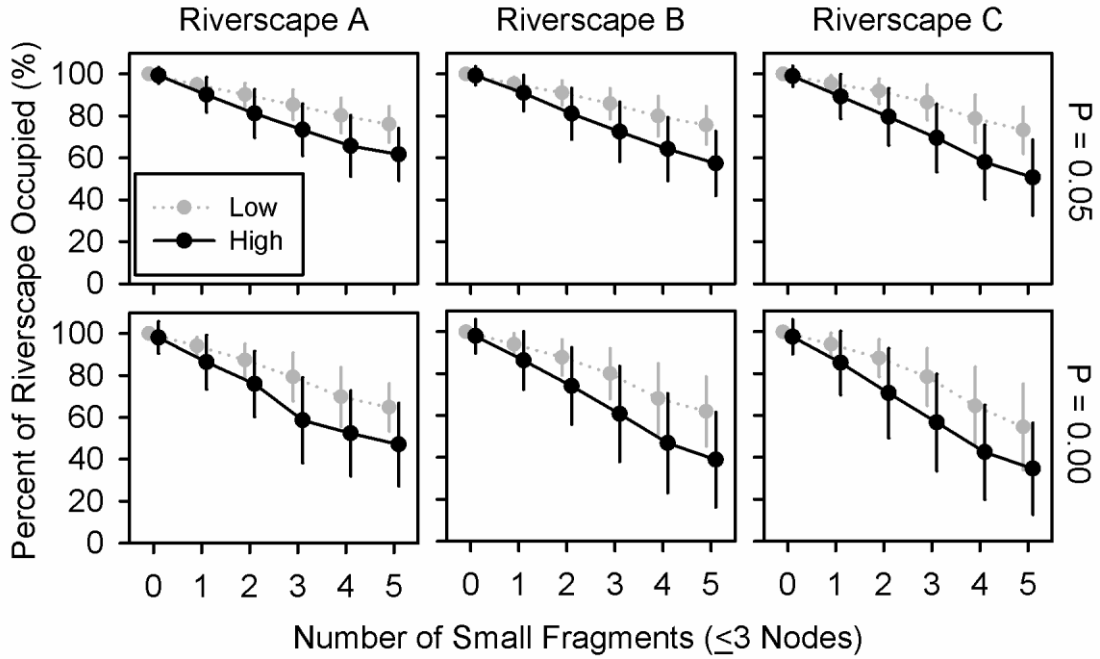


Table 4.1 Mean and standard deviation for percentage of riverscape occupied by simulated fish with low and high dispersal ability in the presence of zero through five barriers among riverscapes.

Barrier Number	Riverscape A				Riverscape B				Riverscape C			
	Low dispersal		High dispersal		Low dispersal		High dispersal		Low dispersal		High dispersal	
	\bar{x}	sd	\bar{x}	sd	\bar{x}	sd	\bar{x}	sd	\bar{x}	sd	\bar{x}	sd
Permeability = 0.5												
0	100	0	100	0	100	0	100	0	100	0	100	0
1	100	0	100	0	100	0	100	0	100	0	100	0
2	100	0	100	0	100	0	100	0	100	0	100	0
3	100	0	100	0	100	0	100	0	100	0	100	0
4	100	0	100	0	100	0	100	0	100	0	100	0
5	100	0	100	0	100	0	100	0	100	0	100	0
Permeability = 0.05												
0	100	0	100	0	100	0	100	0	100	0	100	0
1	96	4	93	6	96	3	93	7	97	3	94	7
2	92	5	85	9	93	5	86	9	94	5	86	10
3	88	6	77	11	89	6	77	12	90	6	76	13
4	83	8	69	14	83	8	67	13	84	8	62	16
5	77	9	61	14	76	10	57	16	73	12	50	17
Permeability = 0.00												
0	100	0	100	0	100	0	100	0	100	0	100	0
1	96	4	91	8	96	4	91	8	96	4	92	8
2	91	6	81	11	91	6	81	13	92	6	81	13
3	84	8	69	15	85	8	67	19	85	9	64	21
4	74	12	57	19	75	13	51	22	73	13	46	22
5	64	13	44	19	60	17	36	21	54	20	33	20

Table 4.2 Sample size, mean, and standard deviation for percentage of riverscape occupied by simulated fish with low and high dispersal ability in the presence of zero through six small fragments (i.e., ≤ 3 nodes) among riverscapes.

Fragment Number	Riverscape A						Riverscape B						Riverscape C					
	Low dispersal			High dispersal			Low dispersal			High dispersal			Low dispersal			High dispersal		
	<i>N</i>	\bar{x}	SD	<i>N</i>	\bar{x}	SD	<i>N</i>	\bar{x}	SD	<i>N</i>	\bar{x}	SD	<i>N</i>	\bar{x}	SD	<i>N</i>	\bar{x}	SD
Permeability = 0.05																		
0	1,259	100	0	1,249	99	4	1,228	100	0	1,254	99	4	1,354	100	1	1,330	99	5
1	1,134	95	3	1,157	90	8	1,160	95	3	1,123	91	9	1,147	95	4	1,185	89	11
2	1,035	90	5	1,050	81	12	1,057	91	6	1,081	81	12	1,053	92	6	1,028	80	14
3	1,011	85	7	993	73	12	988	86	7	988	72	14	946	86	8	957	69	16
4	929	80	8	901	66	15	949	80	9	862	64	15	891	79	11	885	58	18
5	631	76	9	647	62	12	614	76	9	692	57	15	604	73	11	606	51	18
6	1	67	0	3	47	0	4	65	18	0	-	-	5	71	14	9	38	7
Permeability = 0.00																		
0	1,243	100	1	1,232	98	8	1,254	100	1	1,253	98	8	1,341	100	1	1,335	98	8
1	1,185	94	4	1,169	86	13	1,156	94	5	1,167	86	14	1,173	94	5	1,167	85	15
2	1,036	87	8	1,027	76	16	1,059	88	9	1,042	74	18	1,026	87	9	1,048	71	21
3	993	79	12	992	59	20	1,006	80	12	946	61	23	966	78	14	958	57	23
4	917	70	14	963	52	20	892	68	17	971	47	24	887	64	19	881	42	23
5	624	65	11	615	47	20	629	62	17	617	39	23	600	55	21	608	35	22
6	2	40	28	2	20	9	4	68	19	4	22	17	7	43	19	3	36	15

Chapter 5 - Conclusions

Connectivity among stream ecosystems is now compromised on a global scale. These structural alterations have profound consequences for stream fishes that require dispersal throughout riverscapes for persistence, and many fishes are now imperiled as a direct consequence of attenuated habitat connectivity. In light of this profuse problem, conservation actions directed toward reestablishing connectivity among populations and communities are emerging. Because of the large number of barriers on streams, mitigation approaches must prioritize maximum gains in connectivity while minimizing costs in terms of allocating limited resources to removal of barriers. This paradigm has driven the development of cost-benefit analyses in which the cost of barrier removal is weighted against gains in the amount of stream length or area reconnected following barrier removal. However, the extent to which gains in stream length or area are likely to equal improved status of fish that respond negatively to fragmentation is largely untested.

Chapters in this dissertation provide evidence for a positive relationship between connected stream length and fish biodiversity, but multiple context-dependencies must be considered when barrier prioritizations are made. In Chapter 2 I found that Great Plains fishes which disperse over great distances indicated threshold responses to the length of stream available between barriers, and the size of stream required for persistence can be very large (>100 km). The occurrence of such thresholds suggests gains in habitat connectivity (i.e., stream length) that fall below the threshold required for species persistence might not equal associated gains in distribution, unless the removal of the barrier connects a source population in a large fragment (length > threshold) with a smaller, previously unoccupied fragment (length < threshold). In Chapter 3 I found that network-scale measures of habitat connectivity predicted changes in fish biodiversity, so that greater connectivity resulted in more similar communities with higher species richness. Because the measure of network-scale connectivity was the DCI with a uniform barrier permeability of 0.5, smaller DCI values should be interpreted as a greater dividing of the network into smaller fragments. These findings suggest, at least at the spatial scale of third-order stream networks, that a greater number of small fragments in the network resulted in local extirpations for a subset of species while others indicated little response to fragmentation. This concept was further supported by findings from Chapter 4, in which

simulated fish with greater dispersal ability responded strongly to riverscape fragmentation and the extent of extirpation was related to the number of small fragments in the riverscape. Taken together, these studies indicate that measures of habitat connectivity that include riverscape perspectives have potential to enhance conservation of freshwater biodiversity, especially when approaches target specific conservation objectives that include consideration of ecologically meaningful processes (e.g., the scale at which dispersal is important to population persistence).

This work significantly contributes to our understanding of the effects of altered habitat connectivity on stream fish by identifying three key processes that mediate fish response to fragmentation. First, fragmentation does not affect all fish equally and species with greater dispersal affinities respond to fragmentation more strongly than fish that disperse to a lesser extent. Second, fish response to fragmentation can resemble threshold patterns in persistence so that below some level of connectivity, predictable declines occur. Third, reestablishing habitat connectivity through the process of prioritizing barriers for removal is likely to be most successful when ecological information (e.g., dispersal ability of targeted species) is incorporated in to conservation planning.