

From Metapopulations to Metacommunities: Linking Theory with Empirical Observations of the Spatial Population Dynamics of Stream Fishes

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Abstract.—Stream fishes carry out their life histories across broad spatial and temporal scales, leading to spatially structured populations. Therefore, incorporating metapopulation dynamics into models of stream fish populations may improve our ability to understand mechanisms regulating them. First, we reviewed empirical research on metapopulation dynamics in the stream fish ecology literature and found 31 papers that used the metapopulation framework. The majority of papers applied no specific metapopulation model, or included space only implicitly. Although parameterization of spatially realistic models is challenging, we suggest that stream fish ecologists should incorporate space into models and recognize that metapopulation types may change across scales. Second, we considered metacommunity theory, which addresses how trade-offs among dispersal, environmental heterogeneity, and biotic interactions structure communities across spatial scales. There are no explicit tests of metacommunity theory using stream fishes to date, so we used data from our research in a Great Plains stream to test the utility of these paradigms. We found that this plains fish metacommunity was structured mainly by spatial factors related to dispersal opportunity and, to a lesser extent, by environmental heterogeneity. Currently, metacommunity models are more heuristic than predictive. Therefore, we propose that future stream fish metacommunity research should focus on developing testable hypotheses that incorporate stream fish life history attributes, and seasonal environmental variability, across spatial scales. This emerging body of research is likely to be valuable not only for basic stream fish ecological research, but also multispecies conservation and management.

Introduction

Stream fishes require multiple habitat types (e.g., spawning, rearing, and refuge) to complete their life cycles (Schlosser and Angermeier 1995). These habitats are often dispersed in space, throughout the riverscape, so that fish must move among habitat patches to carry out

their life history (Schlosser 1991; Fausch et al. 2002). Additionally, streams are linear habitats, arranged in hierarchical dendritic patterns (Fagan 2002; Campbell Grant et al. 2007). As a result, natural and anthropogenic barriers can easily block movements among habitats in such branching networks (Ward 1983; Winston et al. 1991; Morita and Yamamoto 2002). Therefore, the spatial arrangement of habitats

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and the ability to move among them are critical for stream fish persistence and recolonization dynamics. Moreover, incorporating spatial information into models of stream fish populations should improve our understanding of the mechanisms that control their dynamics.

The metapopulation concept has been used by stream fish ecologists to help explain variability in local-scale population dynamics (Rieman and McIntyre 1995; Schlosser and Angermeier 1995). Metapopulations are defined as groups of habitat patches that support local populations, within a matrix that is not suitable habitat. Metapopulation theory states that all local populations eventually go extinct, but that dispersal among them has a quantitative influence on population dynamics, including rescuing them from extinction or allowing for recolonization after extinction (Hanski and Simberloff 1997). Therefore, a metapopulation approach may be well suited for the study of fish population dynamics across the spatially dispersed, heterogeneous habitats common to streams (Schlosser and Angermeier 1995). This approach has most commonly been used in the conservation and management of salmonids (Rieman and Dunham 2000). However, empirical support for metapopulation dynamics in most stream fish populations remains to be quantified, especially for nonsalmonid species.

Because there are strong effects of spatial scale, habitat heterogeneity, and dispersal on stream fish populations, it stands to reason that stream fish communities also may be spatially structured. Recent work has built upon three decades of metapopulation theory to bridge the gap between spatial population structure and spatial community dynamics (Leibold et al. 2004). Metacommunity models attempt to "scale up" the concepts set forth by metapopulation models to the community level. Metacommunity theory holds that biotic interactions (e.g., competition and predation)

and dispersal both vary in strength in different communities and that trade-offs between these two forces can help explain fundamental differences in community structure and the processes that shape it. One tenet of the metacommunity approach is that local communities often do not have discrete boundaries (Holyoak et al. 2005). In fact, patches within which local communities reside are often temporary and vary in position over time. Habitat patches in stream ecosystems may fit this model well, due to variation in their persistence and location seasonally owing to fluctuations in stream flow, and over longer time scales owing to succession after disturbance. However, the relative importance of spatial versus temporal habitat heterogeneity remains to be addressed for stream fish assemblages in the context of metacommunity theory.

Our objectives in this chapter are to review and synthesize what is known about stream fish metapopulations and metacommunities and to provide a simple test of metacommunity models using empirical data for Great Plains stream fishes in the western United States. Specifically, we first conducted a literature review of stream fish metapopulation research to evaluate (1) what empirical evidence exists for stream fish metapopulation dynamics, (2) what types of models have been used to test for metapopulation dynamics in stream fishes and the extent to which these models incorporate space, and (3) what metapopulation type (Harrison 1991; Schlosser and Angermeier 1995) best fits stream fish metapopulations based on a consensus among empirical studies. Second, we reviewed stream fish and metacommunity literature to evaluate (1) what empirical evidence exists for stream fish metacommunity dynamics, and (2) whether four metacommunity paradigms might apply to stream fish communities. Finally, we used data from our own research to evaluate how dispersal opportunity

and habitat heterogeneity affect community structure across scales in a Great Plains stream fish metacommunity. We also evaluated what metacommunity model best fits these data.

Metapopulation Dynamics in Stream Fish Populations

Methods

We reviewed the literature on stream fish ecology to evaluate empirical evidence for metapopulation dynamics. We included only primary research papers that dealt with lotic fishes and included the term “metapopulation” or “source-sink” in the title, abstract, or keywords. We used the Web of Science © database as the primary method of identifying these papers. Our review covers articles published from 1900 to 2008 from all journals included in the Web of Science.

Once located, papers were categorized by the degree to which space was incorporated, based on model types identified in Hanski and Simberloff (1997). Spatially implicit models are the simplest type of metapopulation model and assume all subpopulations are identical and equally connected. No habitat heterogeneity is included in these models, and spatial locations of patches are not incorporated. An example is Levins’ metapopulation model (Levins 1969, 1970). In contrast, spatially explicit models incorporate space or habitat heterogeneity into the model but not necessarily both. Examples are cellular automata, lattice grid, and raster-based geographic information system (GIS) landscape models. In these models, migration depends on distance but is usually restricted to adjacent patches. The final model type, spatially realistic models, is the most complex. These models incorporate both the spatial position of each patch on the landscape and individual attributes of both focal patches and all outly-

ing patches (e.g., patch size, patch quality). The most well known is the incidence function model (Hanski 1994).

In addition to the type of metapopulation model used in each study, we classified whether or not the authors observed or measured metapopulation dynamics in the population and what metapopulation structure was found. Metapopulation structure was categorized among five types defined by Harrison (1991), as modified by Schlosser and Angermeier (1995; Figure 1).

Classic metapopulation.—The concept of a population of populations linked by dispersal (i.e., metapopulation) was first proposed by Richard Levins (1969, 1970). Levins showed that a metapopulation could be maintained by dispersal among several subpopulations in discrete habitat patches. He assumed that all patches were of equal size, patches were the same distance from one another, rates of colonization and extinction were equal, and subpopulations had independent dynamics (Hanski and Simberloff 1997; Gotelli 2001). Some patches can remain vacant at equilibrium in this model type. Although this “classic” metapopulation structure is unrealistic and probably rare, it serves as a null model and a basis on which to build more spatially realistic models of metapopulations.

Source-sink metapopulation.—Several models based on empirical evidence of metapopulation dynamics were proposed by Harrison (1991) and modified for stream fish metapopulations by Schlosser and Angermeier (1995). The first is a modification of the mainland-island concept from island biogeography theory (Figure 1B; MacArthur and Wilson 1967). By relaxing the assumption of the classic metapopulation model that each patch is the same size and has an equal potential for producing migrants, a more realistic model in which patches differ in demography (i.e., survival

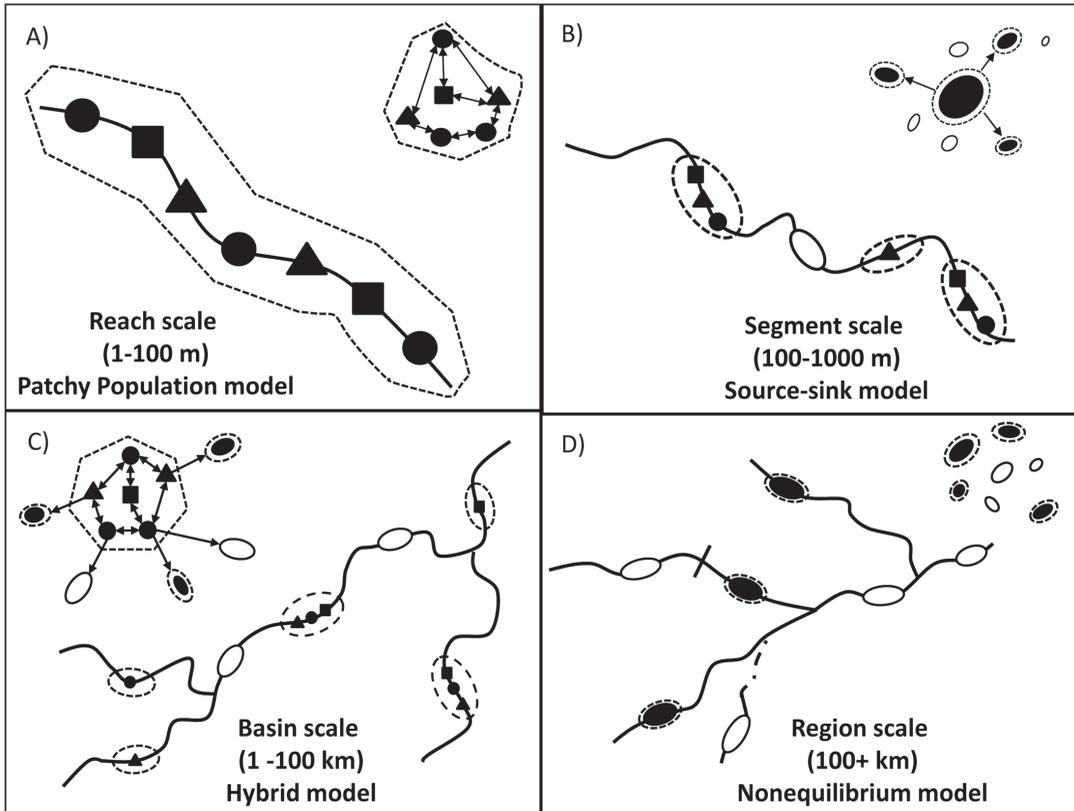


Figure 1. A conceptual model of metapopulation types for stream fishes across four spatial scales in riverscapes. Ovals represent habitat patches that are occupied (filled) or vacant (open). Insets show the most applicable original theoretical metapopulation types defined by Harrison (1991; after Schlosser and Angermeier 1995): (A) patchy population, (B) source-sink, (C) hybrid, and (D) nonequilibrium metapopulation types. Flow is from left to right in all stream networks. Arrows show dispersal among patches, and dashed lines indicate boundaries of "populations." Symbols (e.g., triangles) represent different habitat types (e.g., spawning, rearing, and refuge) within patches that are required for stream fish to carry out their life history (not shown at the region scale). Some habitat patches that contain only a subset of these types may support only sink populations. Upstream and downstream movement that allows rescue and recolonization may be blocked by barriers (perpendicular line) or dry reaches (dot-dashed line).

and/or reproductive rates) can be defined (Pulliam 1988). Source habitats have positive population growth rates (i.e., $\lambda \geq 1.0$), owing to higher survival of adults and juveniles, and reproduction by adults. In contrast, subpopulations in sink habitats are unable to maintain themselves indefinitely (i.e., $\lambda < 1.0$) without significant immigration of individuals from source habitats (e.g., "rescue effect"; Brown and Kodric-Brown 1977).

Patchy metapopulation.—Similar to the classic model, the patchy population model requires that subpopulation dynamics are mostly independent (Harrison 1991). However, the assumptions of identical habitat patches and low dispersal among subpopulations are relaxed. In fact, high dispersal among habitat patches and vastly different types of habitats characterize the patchy population model (Figure 1A) and may result from taxa

that use complementary habitats during different life stages (Dunning et al. 1992; Schlosser and Angermeier 1995). A key characteristic of the patchy metapopulation model is that no patches are ever unoccupied, because of high dispersal rates.

Hybrid metapopulation.—By incorporating both patchy and source-sink population dynamics, a hybrid model can be developed that may be more realistic than either model alone (Figure 1C; Harrison 1991). Within a group of “source” subpopulations, high dispersal among different habitats required for carrying out the species life history leads to persistence over time. In addition, satellite populations may act as sinks, due to the absence of critical habitats required for persistence.

Nonequilibrium metapopulation.—Naturally or anthropogenically fragmented populations may be represented by a nonequilibrium metapopulation model. Low or no dispersal due to reduced connectivity among patches, coupled with deteriorating habitat quality, increases the rate of extinction among subpopulations, few of which are recolonized (Figure 1D; Harrison 1991; Schlosser and Angermeier 1995). A nonequilibrium model often may be most appropriate for a species that shows a regional decline in distribution and abundance due to habitat fragmentation and loss of connectivity.

Distinguishing among metapopulation types.—Based on their different characteristics, a short dichotomous key can be developed to differentiate among the five different metapopulation types. First, if dispersal and colonization among patches is low or nonexistent, then a nonequilibrium metapopulation model fits best. Second, if patches never go extinct, then a patchy metapopulation is appropriate. Third, if habitat patches are identical and their dynamics independent, then a classic metapopulation model fits best. Fourth, if there is a core area that contains different critical habitats with high dispersal among

them, and that never goes extinct, then this is a hybrid metapopulation. Otherwise, a source-sink metapopulation model may fit best, assuming it fits the characteristics defined above for this type.

Results and Discussion

We identified 31 papers in the stream fish ecology primary literature that contained the terms “metapopulation” or “source-sink” in the title, abstract, or keywords (Table 1). All papers were published since 1995 and the majority (20) were published after 2000. In contrast, a search for the term “metapopulation” alone in the Web of Science © database returned more than 3,000 research papers that contained the term in their title, abstract, or keywords. Therefore, papers in the stream fish literature make up less than 1% of the total body of metapopulation research to date.

Metapopulation dynamics for approximately 80 fish species or subspecies were considered among the 31 papers. Fifty-seven of these species were analyzed concurrently in two papers, Fagan et al. (2002) and Gotelli and Taylor (1999), though little species-specific data were provided. However, most papers (24) addressed only one species, and 18 of the 31 papers focused solely on salmonids. Other families represented included Cottidae, Cyprinidae, Cyprinodontidae, Ictaluridae, Odontobutidae, Percidae, and Rivulidae.

Many of the papers (14 of 31) discussed dynamics of the study populations in terms of metapopulation theory, but no specific model was applied. We considered these papers to be strictly observational (Table 1). Five papers used spatially implicit (Levins' type) analyses to model metapopulation dynamics. For example, Gotelli and Taylor (1999) modeled turnover in 36 species native to the Cimarron River, Oklahoma and found that colonization

Table 1. Summary of peer-reviewed literature on stream fish metapopulation ecology from 1995 through 2008. Presence or absence of the terms "metapopulation" or "source-sink" in the title, keywords, or abstract is indicated, along with the species studied. Papers with N/A in the abstract or keywords fields indicate that the journal does not contain these elements. Model type refers to the type of statistical model used: spatially implicit model (SIM), spatially explicit model (SEM), spatially realistic model (SRM), or observational (no modeling conducted; OBS). The type of metapopulation structure reported in the paper is also listed using codes (after Harrison 1991; Schlosser and Angermeier 1995): classic (CL), source-sink (SS), patchy (PM), nonequilibrium (NE), or not defined (ND).

Reference	Title	Keywords	Abstract	Species	Model type	Metapopulation structure
Chaumot et al. (2006)	N	N	Y	Bullhead <i>Cottus gobio</i>	SRM	NE
Cooper and Mangel (1998)	Y	N/A	Y	Coho salmon <i>Oncorhynchus kisutch</i>	SEM	SS
Crozier and Zabel (2006)	N	N	Y	Chinook salmon <i>O. tshawytscha</i>	SEM	NE
Dunham and Rieman (1999)	Y	Y	Y	Bull trout <i>Salvelinus confluentus</i>	SEM	Range ^a
Dunham et al. (2002)	N	N/A	Y	Bull trout, Lahontan cutthroat trout <i>O. clarkii henshawi</i>	SEM	ND
Fagan (2002)	Y	N	Y	Gila trout <i>O. gilae</i>	SIM	ND
Fagan et al. (2005)	N	Y	N	Sonoran Desert fishes (21 species)	SIM	ND
Gagen et al. (1998)	Y	N	N	Ouachita madtom <i>Noturus lachneri</i>	OBS	SS
Garant et al. (2000)	N	Y	Y	Atlantic salmon <i>Salmo salar</i>	OBS	NE
Gilliam and Fraser (2001)	N	N	Y	Giant rivulus <i>Rivulus hartii</i>	OBS	SS
Gotelli and Taylor (1999)	Y	Y	Y	Cimarron River fishes (36 species)	SIM	CL
Hilderbrand (2003)	N	N	Y	Cutthroat trout <i>O. clarkii</i>	SEM	SS
Isaak et al. (2007)	N	Y	N	Chinook salmon	SRM	SS
Isaak et al. (2003)	N	N/A	Y	Chinook salmon	SIM	PM
Koizumi and Maekawa (2004)	Y	N	Y	Dolly Varden <i>Salvelinus malma</i>	SEM	ND
Labbe and Fausch (2000)	N	Y	N	Arkansas darter <i>Etheostoma cragini</i>	SIM	SS
Labonne and Gaudin (2006)	N	N/A	Y	Apron Zingel <i>asper</i>	SRM	SS
Luttrell et al. (1999)	N	N/A	Y	Peppered chub <i>Macrohybopsis tetranema</i> , shoal chub <i>M. hyostoma</i>	OBS	SS
Matsubara et al. (2001)	Y	N	Y	Donko <i>Odontobutis obscura</i>	SEM	SS
McMahon and Matter (2006)	N	Y	N	Desert pupfish <i>Cyprinodon macularius</i>	OBS	SS
Morita and Yamamoto (2002)	N	N/A	Y	Whitespotted char <i>Salvelinus leucomaenis</i>	SEM	SS
Neville et al. (2006)	N	Y	Y	Lahontan cutthroat trout	OBS	NE
Policansky and Magnuson (1998)	Y	Y	Y	<i>Oncorhynchus</i> spp.	OBS	ND
Rieman and Dunham (2000)	Y	Y	Y	Bull trout, Lahontan cutthroat trout, Westslope cutthroat trout <i>O. c. lewisi</i>	OBS	ND

Table 1. Continued.

Reference	Title	Keywords	Abstract	Species	Model type	Metapopulation structure
Rieman and McIntyre (1995)	N	N/A	Y	Bull trout	SEM	SS
Schlosser and Angermeier (1995)	N	N/A	Y	Chinook salmon, creek chub <i>Semotilus atromaculatus</i>	OBS	SS, PM
Schlosser (1998)	N	Y	N	Creek chub	OBS	SS
Shepard et al. (2005)	N	N/A	Y	Westslope cutthroat trout	OBS	NE
Slack et al. (2004)	N	Y	Y	Bayou darter <i>Etheostoma rubrum</i>	OBS	SS
Winston et al. (1991)	N	N/A	Y	Speckled chub <i>Macrohybopsis aestivalis</i> , plains minnow <i>Hybognathus placitus</i> , Red River shiner <i>Notropis bairdi</i> , chub shiner <i>N. potteri</i>	OBS	SS
Young (1999)	Y	N/A	Y	<i>Oncorhynchus</i> spp.	OBS	NE

^a Range: a range of metapopulation types was found.

and extinction probabilities were not correlated with the percentage of sites occupied. Instead, site occupancy was related more to its longitudinal position along the river. These results indicate that for these stream fishes, and probably others, a spatially implicit (nonspatial) approach is inadequate for characterizing metapopulation dynamics. Of the 17 papers that modeled metapopulation dynamics, 9 incorporated space explicitly. Most models were patch-based (see Dunham et al. 2002 for discussion) and were used to predict patch occupancy based on variables such as patch size, longitudinal position along the stream, isolation, and habitat quality. Multiple logistic regression was the most common method used to model occupancy (e.g., Rieman and McIntyre 1995; Dunham and Rieman 1999; Koizumi and Maekawa 2004). Overall, results of these studies indicated that habitats that are larger, less fragmented and isolated, and less degraded are more likely to be occupied by the stream fish species studied.

The realistic incorporation of space into metapopulation models has been recom-

mended for some time (Moilanen and Hanski 1998; Hanski 2001; Ricketts 2001). However, only three papers in the stream fish ecology literature incorporated characteristics of neighboring habitats and their actual spatial relationships to predict occupancy or population parameters of focal habitats in a spatially realistic manner. These spatially realistic modeling techniques included multiple logistic regression with information-theoretic model selection (Isaak et al. 2007) and complex matrix population models that incorporate dispersal and spatial processes (Chaumot et al. 2006; Labonne and Gaudin 2006). These models offer great promise for modeling metapopulation dynamics in complex landscapes, but their use to date, especially in the stream fish ecology literature, is limited.

Metapopulation structure was an important point of discussion in all of the papers we reviewed (Table 1). Only 6 of the 31 papers did not classify their study metapopulations into one of the types identified by Harrison (1991) and Schlosser and Angermeier (1995). Gotelli and Taylor (1999) initially classified

their study metapopulations as classic Levins' type, though their analysis did not support this conclusion. It is not surprising that only one paper classified their metapopulation as the classic metapopulation type; as in other taxa, classic metapopulations are probably rare in nature (Hanski 1996; Harrison and Taylor 1996). The most common metapopulation type reported was source-sink (16 of 31 papers). This also is not surprising, because source-sink metapopulation dynamics are the simplest type that incorporates space. Patchy metapopulations were discussed in only two papers, Schlosser and Angermeier (1995) and Isaak et al. (2003). This is surprising, because the definition of patchy metapopulation types (high dispersal among different habitat types) seems to fit many stream fish metapopulations closely. Finally, nonequilibrium metapopulations were reported by six papers. These stream fish metapopulations were typically in decline across their ranges, and the papers were most commonly oriented toward conservation (e.g., Young 1999; Chaumot et al. 2006; Crozier and Zabel 2006).

Several papers that failed the criteria for inclusion in our review nonetheless analyzed populations using a metapopulation approach or discussed spatial population dynamics of stream fishes in detail. For example, Scheurer et al. (2003) modeled persistence of brassy minnow *Hybognathus hankinsoni* as a function of habitat size, among-habitat connectivity, and flow permanence at the river segment scale. The authors found that brassy minnow were more likely to persist in deeper pools that were connected to other pool habitats and that persistence was higher in a segment with perennial flow. These results are similar to those reported above for other stream fish studies that used spatially explicit models. Similarly, Pichon et al. (2006), Letcher et al. (2007), and Schick and Lindley (2007) presented spatially

realistic models of stream fish population dynamics based on principles from landscape and metapopulation ecology, although the term "metapopulation" was not included in their title, abstract, or keywords. Clearly, some metapopulation-based research on stream fish has been published recently that was not detected by our criteria.

Several patterns are common across research in stream fish metapopulations. The first is that most papers (18 of 31) focused on species in the family Salmonidae, even though salmonids make up less than 4% of fish species native to North America (Froese and Pauley 2008). Rieman and Dunham (2000) reported that salmonid life histories are well suited to a metapopulation approach, due to discrete, complementary habitats, frequent dispersal among habitats, and strong population structuring influenced by natal homing. However, the complexity and diversity of life history strategies in salmonids, and the high degree of intraspecific variability in life history expression (e.g., migration patterns; Hendry and Stearns 2004), makes simple metapopulation types and models unsuitable for characterizing salmonid populations (Rieman and Dunham 2000). In fact, Rieman and Dunham (2000) suggested that metapopulation types of salmonids may vary across a gradient of patch quality, dispersal distance, and interpatch distance (see their Figure 1), as opposed to conforming to a single type. Indeed, we found that most papers in the stream fish metapopulation literature used simple statistical models and classified metapopulations as one of the simplest types, that of a source-sink metapopulation. Many papers were strictly observational and did not explicitly model metapopulation dynamics at all. Although observational studies are important for elucidating general patterns across stream fish taxa, important advances in our knowledge of stream fish population dynamics will occur

only when rigorous studies are specifically designed to evaluate spatial population dynamics and distinguish among metapopulation types. This includes quantifying parameters likely to affect population dynamics in a spatial framework, such as those proposed by Rieman and Dunham (2000).

The future of stream fish metapopulation research clearly lies with measurement and modeling of more spatially realistic variables, such as distance among patches, patch quality (but see Isaak et al. 2007 for an alternative), neighboring patch quality, and connectivity among patches. Additionally, knowledge of the characteristics and costs of dispersal by study species is critical to incorporate into such models (Kareiva 1990; Hendry et al. 2004). Unfortunately, complex spatially realistic population models are difficult to parameterize (Chaumot et al. 2006; Labonne and Gaudin 2006). Moreover, the scales at which stream fish metapopulations operate are often unknown, but are a key to our understanding of these processes, especially if metapopulation types do indeed vary across spatial and temporal scales (Rieman and Dunham 2000).

In conclusion, due to the unique characteristics of stream fish life histories and habitats, a refined theory that helps explain variability in stream fish metapopulation structure and dynamics is warranted. However, formulation of this theory may prove challenging because of the lack of detailed empirical data quantifying spatial population dynamics in stream fishes. For example, variables such as habitat size, location, and connectivity can be easily measured, but patch-specific vital rates (e.g., births, deaths, emigration, and immigration), and the rates and costs of movement among patches, are difficult to measure across the large spatial scales over which stream fishes carry out their life histories (Fausch et al. 2002). Nevertheless, these data are what will be required to evaluate

the efficacy of different metapopulation models in explaining stream fish spatial population dynamics.

Metacommunity Dynamics in Stream Fish Assemblages

A metacommunity is a set of local communities linked by dispersal of one or more species (Hubbell 2001). Therefore, in the simplest configuration, a metacommunity consists of several local communities that comprise a combined regional pool of species. It is the interplay of dispersal and community dynamics within and between these two scales (i.e., local and regional) that is the focus of the metacommunity approach. Four paradigms have been suggested as theoretical models for metacommunity dynamics across taxa (Liebold et al. 2004). Each paradigm differs in the degree to which environmental heterogeneity, biotic interactions, and dispersal processes are incorporated (Figure 2).

Patch dynamics.—The patch dynamics model builds on the equilibrium theory of island biogeography (MacArthur and Wilson 1967; Figure 2A). This paradigm predicts that regional coexistence is maintained by a trade-off between competitive and dispersal ability among members of the community (Hutchinson 1951; Hastings 1980; Tilman 1994). For coexistence to occur, dispersal of strong competitors must be limited so that they do not drive other species to regional extinction. In contrast, inferior competitors must be better at colonizing than dominants when patches open up following disturbance (Caswell 1978; Yodzis 1986). The patch dynamics paradigm is a spatially implicit model; patches are distributed uniformly and habitats are homogeneous.

Species sorting.—The species-sorting model incorporates the ideas that strong niche relationships can occur between species and their

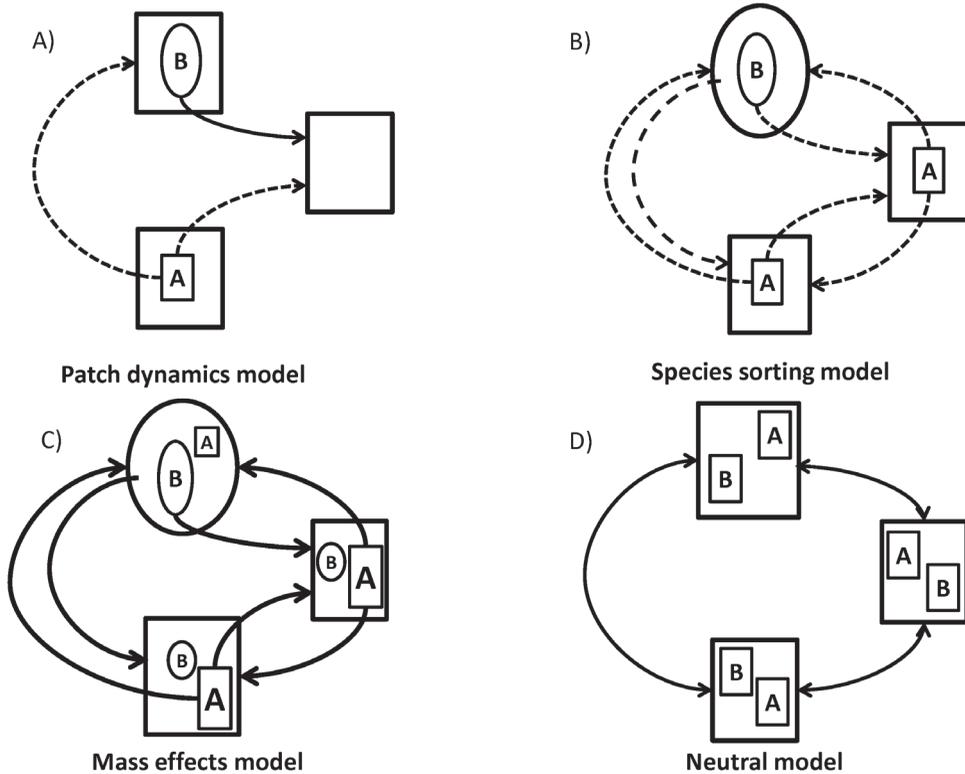


Figure 2. Schematic representation of four metacommunity paradigms for two species, A and B (after Leibold et al. 2004). Arrows represent dispersal among habitat patches; heavy, solid arrows represent rapid dispersal, light, solid arrows moderate dispersal, and dashed arrows represent slow dispersal. Dominant species are indicated by large letters, and subdominant by small letters. Adaptation for specific niches is represented by shapes that match for species and habitat patches. The patch dynamics model (panel A) predicts that species persist by a trade-off between competition and colonization. Species A is a superior competitor, but species B is a better colonizer and can rapidly colonize empty patches. Under the species sorting model (panel B), species are well adapted to particular habitats (niches), and dispersal is slow. In contrast, under the mass effects model (panel C), dispersal is rapid among patches. Species persist in source habitats (larger symbols), to which they are well adapted and disperse to sink habitats (smaller symbols) to which they are not well adapted. Finally, the neutral model (panel D) predicts that all species are in all patches, and some will be lost due to slow random ecological drift, but this will be countered by moderate dispersal and speciation.

habitats and that community structure may change along environmental gradients (Whittaker 1972; Leibold 1998; Figure 2B). This model allows for dispersal by member species, but occurrence is determined mainly by local abiotic conditions (e.g., habitat composition) independent of purely spatial effects. By nature, habitats are heterogeneous under the species-sorting paradigm, so this model would be considered spatially explicit based

on the terms developed for metapopulation models.

Mass effects.—The mass effects paradigm assumes that local community dynamics are strongly affected by dispersal (Shmida and Wilson 1985; Figure 2C). Moderate dispersal among patches that support local communities results in a source-sink dynamic (Holt 1985; Pulliam 1988; Holt 1993) within the metacommunity, where sink populations are

maintained by a rescue effect (Brown and Kodric-Brown 1977). Mass effects models predict that species are different in their competitive abilities in local habitat patches but are similar across the region among all habitat patches, on average, so that none are driven extinct. Habitats are heterogeneous in the mass effects model, so it is spatially explicit. However, spatial processes are predicted to be more important than environmental factors in controlling community composition, so that some species are present in habitat patches in which they could not persist without dispersal from source populations.

Neutral model.—The final metacommunity paradigm is based on neutral theory (Hubbell 2001; Figure 2D). The neutral model assumes that all species are equal in niche relations and dispersal ability. This results in metacommunity dynamics influenced by slow random patterns of compositional change due to random extinction, dispersal, and speciation, termed ecological drift. The neutral model assumes no habitat heterogeneity and moderate dispersal and so is spatially implicit.

Initial tests of metacommunity theory attempted to apply the four paradigms across ecological systems and taxa (Leibold et al. 2004; Cottenie 2005; Holyoak et al. 2005). A few investigators have tested the theory in aquatic systems, but none have specifically tested hypotheses for stream fishes. Therefore, here we briefly review the few applications of metacommunity theory in other aquatic systems.

The most extensive and empirical investigation into metacommunity dynamics in aquatic systems is that of Cottenie and others for zooplankton in a stream-like system of interconnected ponds in Belgium (Cottenie et al. 2003; Cottenie and De Meester 2004, 2005). The authors investigated the relative effects of habitat heterogeneity and dispersal on community structure at the scale of local ponds,

and the “regional” scale over all ponds. Similar to typical stream habitats, connectivity among the ponds was variable depending on the flow into and out of them. The ponds were also heterogeneous in habitat, ruling out the patch dynamics and neutral models. The authors used an integrated observational and experimental approach to investigate whether the mass effects or species-sorting paradigms better characterized this metacommunity. Overall, the authors found that despite high rates of zooplankton dispersal within and among ponds, there was little evidence for pure spatial mass effects (Cottenie and De Meester 2005). Most variation in zooplankton community structure could be explained by environmental variables, conforming closely to the species-sorting model; zooplankton species occurred in the habitats to which they were best adapted.

Mouillot (2007) developed a theoretical perspective for coastal brackish lagoon fish metacommunities based on the four paradigms introduced by Leibold et al. (2004). The author discounted the neutral paradigm as being appropriate for this metacommunity because coastal fish species are not ecologically equivalent. His subsequent discussion focused on how coastal lagoons might be managed differently depending on which metacommunity model fit the best (e.g., patch dynamics, species-sorting, mass effects). He concluded that although it is unlikely that these lagoon habitats would fit only one model best, one paradigm might predominate. He also pointed out that movement beyond “conjecture and speculation” to careful tests of the metacommunity paradigms in real ecosystems is warranted, a conclusion we support.

The only paper we found that addressed stream fish metacommunities was a meta-analysis by Cottenie (2005). The author evaluated 158 published data sets in the ecological literature and used a multivariate variation

partitioning approach to categorize each metacommunity by the relative influence of local habitat heterogeneity and regional dispersal processes. Three of the data sets analyzed (www.epa.gov; Marsh-Matthews and Matthews 2000; Townsend et al. 2003) included 11 stream fish metacommunities. Five classifications resulted: (1) neutral model or patch dynamics, (2) species sorting, (3) species sorting and mass effects, (4) undetermined metacommunity, and (5) no metacommunity dynamics found. Of the 11 stream fish metacommunities, one was classified as neutral or patch dynamics, three as species-sorting, four as species-sorting and mass effects, and three as undetermined metacommunities. These results indicate that at least for the small sample of stream fish metacommunities considered, all showed some form of metacommunity dynamics and most were controlled by strong niche relationships, regional dispersal, or a combination of these.

What metacommunity processes, if any, dominate in stream fish assemblages? The review of metapopulation dynamics showed that source-sink dynamics are widespread across stream fish populations. This is not surprising because high environmental heterogeneity and dispersal among habitats and streams are common in stream fishes (Gowan et al. 1994; Poff 1997). Given this, we might expect patch dynamics and neutral dynamics to be rare in stream fish metacommunities, because in these models patches are assumed to have the same habitats. This leaves the species-sorting and mass effects models, which deal with strong niche relationships and strong dispersal mediating assemblage structure, respectively. However, what is the relative influence of species sorting and mass effects on stream fish assemblage structure, and how might one determine this? In the following section, we attempt to answer these questions for a Great Plains stream fish assemblage using empirical data.

Metacommunity Dynamics in a Great Plains Stream Fish Assemblage *Study System*

Our study system was the Arikaree River, a principle tributary of the Republican River that flows northeast from Colorado into Kansas and has its confluence in southwest Nebraska with the North Fork Republican River near Haigler, Nebraska (see Scheurer et al. 2003 for basin map and study segments). Most of the Arikaree River basin (>96%) is located in Colorado. Eastern Colorado is a semi-arid region, averaging less than 44 cm of rainfall annually. The primary source of flow for the Arikaree is groundwater that originates in the underlying High Plains Aquifer. The flow regime in the Arikaree is predictable across months but variable among years. High flows generally occur in May and June from a combination of groundwater recharge and spring precipitation. Flows decline during summer and are further reduced by pumping shallow alluvial groundwater for irrigation and riparian evapotranspiration (ET). Once pumping and ET cease in the fall, flow resumes and increases gradually until the following spring. This is a harsh environment for fishes because water quality can be poor and flows low in the winter and summer. During summer, water temperatures in shallow habitats can exceed 34°C and dissolved oxygen levels often are less than 0.1 mg/L (Scheurer et al. 2003). Conversely, during winter, shallow habitats can freeze entirely (e.g., Labbe and Fausch 2000). As a result, fishes native to the Arikaree include species tolerant to extremes in environmental conditions.

Fish and Habitat Characteristics

The Arikaree fish assemblage is mainly composed of 11 native species collected since 2000. Most are from the family Cyprinidae, but oth-

ers represent Catostomidae, Centrarchidae, Fundulidae, and Ictaluridae. Mesohabitat types consist of pools connected by shallow runs. In the spring, flooded terrestrial vegetation along the stream margin and in connected backwaters provide spawning habitats. During summer drying, pools become disconnected, and some desiccate entirely. The remaining pools provide important refugia for fishes. As a result, opportunity for fishes to disperse to both spawning and refuge habitats is critical for survival and population persistence. Also, flow permanence varies longitudinally along the river basin depending on inputs of groundwater. During summer drying, flow is highest and most perennial in upstream reaches of the basin and decreases downstream as the alluvium becomes disconnected from the regional aquifer (Falke 2009). This results in a gradient of flow and environmental conditions along the Arikaree riverscape.

Predictions

Significant variation in habitat quality and seasonal dispersal opportunity among habitats makes the Arikaree riverscape an ideal place to test metacommunity theory. Our analyses focused on determining the relative influence of environmental (habitat composition) and spatial (dispersal opportunity) factors in explaining variation in the fish assemblage of the Arikaree River. We used a decision tree developed by Cottenie (2005) to determine metacommunity type based on the results of statistical tests. Metacommunity type was determined by the significance structure of the components of variation (based on $\alpha = 0.05$; see Statistical Methods for details). For example, from metacommunity theory, we expect that if the species-sorting model was most applicable to the Arikaree metacommunity, variation in fish assemblage structure would be best explained by environmental

factors (i.e., local habitat characteristics), whereas spatial variables would not explain significant variation. Conversely, if spatial factors (e.g., regional dispersal opportunity or habitat connectivity) explain variation in the fish assemblage better than local habitat, we would conclude that the mass effects model may be more appropriate. If neither environmental nor spatial factors explain significant variation, we would conclude that (1) patch dynamics or neutral models may be more appropriate, (2) metacommunity dynamics for this system cannot be determined, or (3) no metacommunity dynamics are occurring in this system. Table 1 in Cottenie (2005) presents the decision tree used to evaluate the significance structure and metacommunity types.

Fishes native to the Arikaree riverscape are relatively small-bodied, short-lived, and able to disperse rapidly to recolonize habitats that were previously dry (Scheurer et al. 2003). These fishes also have adaptations that allow them to maximize their reproductive potential in this harsh, dynamic system such as (1) egg placement strategies to avoid smothering or abrasion in shifting substrates, (2) short egg incubation time, and (3) fast larval growth and maturation. Finally, most fishes native to this system feed across trophic levels, so omnivory is prevalent. Because many of these species have similar resource requirements (and presumably habitat requirements), and these habitats are extremely dynamic seasonally, we predicted that local environmental conditions would be less important in explaining fish assemblage structure than the opportunity to move among habitats when environmental conditions deteriorate or resources become limiting. Based on these factors, we predicted that the Arikaree River fish metacommunity would conform most closely to the mass effects model.

Data Collection

Our data collection focused on evaluating both local scale habitat characteristics and regional dispersal opportunity for Arikaree River fishes. We collected these data during the driest period (August) of 2006 and 2007, along two 6.4-km river segments (upstream and middle) identified by Scheurer et al. (2003). These segments vary in environmental conditions and are characterized by differences in stream flows. During these 2 years, the upstream segment was mostly perennial, whereas the middle segment was mostly intermittent.

The minimum unit for the habitat measurements was a pool. Pools along the entire upstream and middle segments were censused in late July of both years. We identified and georeferenced each pool, and measured length (m), width at the midpoint (m), and maximum depth (cm). These measurements allowed estimating maximum surface area (m^2) and volume (m^3) of each pool. Subsequently, in August of each year (about 2 weeks after the census), we conducted a detailed survey to measure local scale habitat characteristics. In the upstream segment, a subset of pools ($N = 29$ of 180 in 2006, $N = 19$ of 218 in 2007) were randomly selected from two pool size categories (small and large) for detailed habitat measurements. In the middle segment, all pools were sampled in both years ($N = 27$ in 2006, $N = 29$ in 2007). Within each pool, we measured pool area, volume, maximum depth, composition and distribution of substrate particles and aquatic vegetation, presence and proportion coverage of woody debris and tumbleweeds, up- and downstream flow connectivity, turbidity, conductivity, and surface temperature. Surface area was quantified by (1) measuring length along the longest axis of the pool, (2) dividing the length evenly into three perpendicular transects, and (3) measuring width at the midpoint of each transect. Pool volume (m^3)

was estimated by making depth measurements (nearest 0.01 m) at three stations located at one-sixth, one-half, and five-sixths of each respective width transect. Pool area, volume, and average depth were calculated after Platts et al. (1983). Additionally, at each depth station, substrate (sand, silt, gravel, and bedrock) and aquatic vegetation (emergent, submergent, or floating) categories were recorded. Maximum depth of each pool was measured with a stadia rod (cm), and conductivity (μS) was measured using a multimeter (YSI Inc., model 85). Ambient surface water temperature (nearest $0.1^\circ C$) was recorded with a digital thermometer (Cooper-Atkins, Versatuff Plus 396). Qualitative estimates of the proportion of pool area covered by each vegetation type (see above for categories) and tumbleweeds were recorded, as well as a count of the number of pieces of small (≤ 4 cm diameter) and large (> 4 cm diameter) woody debris in each pool.

In addition to detailed local habitat measurements, we evaluated spatial factors that may explain variation in the Arikaree River fish assemblage. At the same time as habitat sampling each year, we measured among-habitat connectivity as the length of flowing, intermittent, and dry reaches along each 6.4-km segment. We georeferenced the start and end of each connectivity class (flowing, intermittent, and dry) and created a GIS line layer with reaches classified by connectivity. We also divided each of the two segments into relatively homogeneous reaches based on geomorphology and patterns of drying. Geomorphology and drying were evaluated using U.S. Geologic Survey topographic maps and maps of monthly within-segment habitat connectivity collected from 2000 to 2007 (see Scheurer et al. 2003). Longitudinal position of each pool along the riverscape was determined by measuring the distance from the downstream most boundary of the middle segment upstream to

each pool (m) using GIS. Finally, we measured the distance from each focal pool sampled for detailed habitat conditions to the nearest adjacent pool (m) and recorded whether or not the focal pool was isolated from the adjacent pools upstream and downstream.

We sampled fishes from the pools that were previously surveyed for detailed habitat measurements within 2 weeks of habitat measurements. Fishes were collected with 4.8-mm mesh seines using three-pass depletion sampling. Pools were isolated at their up- and downstream ends with block nets of the same mesh size to prevent emigration of fishes during sampling. All seining passes were conducted from upstream to downstream. All fishes were identified to species and enumerated separately for each pass, and all fishes were released unharmed following processing. Abundance estimates and standard errors for each species within individual pools were estimated using the generalized removal model in Program CAPTURE (White et al. 1982).

Statistical Methods

We used canonical correspondence analysis to partition environmental and spatial variation in the Arikaree River fish data (Palmer 1993; ter Braak and Verdonschot 1995; Legendre and Legendre 1998). Canonical correspondence analysis (CCA) selects a linear combination of explanatory variables to maximize the dispersion of species scores (Jongman et al. 1995). Using this method, partitioning the variation allowed us to test for the effects of one set of explanatory variables while holding the other set constant. Consequently, we were able to evaluate the relative influence of spatial versus environmental factors on variation in fish assemblage structure.

We began our statistical analyses by calculating separate CCAs to determine which environmental and spatial variables in each set

best explained variation in the fish assemblage data. We tested all variables for multicollinearity using pairwise matrices based on Pearson's correlation coefficient. If the correlation coefficient between a pair of variables was greater than 0.8, one of the variables was excluded from our analysis. Variables to be included within each of the two final matrices were evaluated by forward selection (ter Braak and Verdonschot 1995; ter Braak and Smilauer 2002) with a Monte Carlo test ($\alpha = 0.05$). Each CCA was computed using CANOCO 4.5 (ter Braak and Smilauer 2002), and analyses were based on interspecies distances and biplot scaling. All Monte Carlo permutation tests were done under the reduced model with 999 permutations.

We tested 11 pool habitat variables using CCA for inclusion into our environmental matrix: maximum depth (MAXD), volume (VOL), conductivity (COND), turbidity (TURB), small woody debris (SMWOOD), tumbleweeds (TUMBLE), submergent vegetation (SUBMERG), emergent vegetation (EMERG), and floating vegetation (FLOAT). Only sand and silt substrate types were observed in our field data, so we calculated the percent of the pool that was composed of sand substrate (SAND). We adjusted pool temperature measurements taken at different times of day by calculating residuals from a regression of pool ambient surface temperature ($^{\circ}\text{C}$) versus time of day (e.g., 1240 hours). This resulted in a variable (TEMP) that indicated whether a pool was relatively warm (positive residual) or relatively cool (negative residual) compared to others and accounted for the potential influence of groundwater on pool temperature. All environmental variables (excluding TEMP) were transformed to ensure normal distribution. Maximum depth, volume, and conductivity were \log_{10} -transformed, and the other variables (all proportions) were transformed by calculating the arcsine of their square root.

Following transformation, all environmental variables were standardized and centered by calculating their z -scores (mean = 0; standard deviation = 1). After evaluation, eight variables explained significant environmental variation in the fish assemblage among pools: MAXD, VOL, TEMP, TURB, TUMBLE, SUBMER, and SAND. Subsequently, these variables comprised the environmental matrix [E] in subsequent partitioning analyses.

Variables tested for inclusion into the spatial [S] matrix were those we considered might influence dispersal opportunity among habitats for fishes in the Arikaree metacommunity. This CCA was performed as described for [E]. To evaluate species patchiness on the riverscape, we assigned each pool to one of the 11 geomorphic reaches identified across the two study segments. These variables were entered as 11 dummy variables (REACH0 to REACH10). Additional discrete spatial variables included segment in which the pool was located (i.e., upstream or middle; SEGMENT) and whether the pool was isolated from all adjacent habitats (ISOLATED). We also included the longitudinal position of the pool along the riverscape (LONG) and the distance to the nearest pool (DISTBW). Our final spatial variable indicated the amount of flowing water habitat surrounding a focal pool at three different spatial scales. From our connectivity maps and georeferenced pool locations, we calculated the amount of flowing water habitat upstream and downstream from each pool at three scales: 50, 250, and 500 m upstream and downstream (100M, 500M, 1000M, respectively). Finally, z -scores were calculated for all continuous variables (excluding LONG). After evaluation, 8 of the 18 variables explained significant variation in the fish assemblage and were included in the final spatial matrix [S]: 1000M, REACH1, REACH2, REACH3, REACH4, LONG, DISTBW, and ISOLATED.

We partitioned the variation in fish assemblage structure among pools into the following components using partial canonical correspondence analysis (pCCA; following Borcard et al. 1992; Cottenie 2005; Langenheder and Ragnarsson 2007): environmental variation [E]; spatial variation [S]; total explained variation [E+S]; pure environmental variation (proportion variation explained by environmental factors independent of space) [E|S]; pure spatial variation (proportion explained by space independent of environment) [S|E]; the spatial component of environmental influence (variation shared by environment and space; $[E \cap S]$, calculated as $[E] - [E|S]$); and the total amount of unexplained variation ($1 - [E + S]$). These calculations were based on eigenvalues resulting from the pCCA procedure. All results are presented as the proportion of the total explained variation. To classify our Arikaree River fish metacommunity to one of the four MC paradigms, we used the decision tree presented by Cottenie (2005).

Results and Discussion

Mean values of the 19 environmental and spatial variables within a segment were generally similar among years (Table 2), but values differed between segments and reflected the heterogeneity in habitats. Percent sand substrate was higher in the middle segment in 2006, and variables representing aquatic vegetation coverage were usually lower in the middle than upstream segment. Therefore on average, the upstream segment contained siltier, more vegetated pool habitats, whereas pools in the middle segment were sandier and less vegetated. Factors representing water quantity in both environmental and spatial sets (e.g., VOL; 1000M) were usually higher in the upstream than middle segment. Also, more pools were isolated in the middle than in the upstream segments and distance between pools

Table 2. Mean (SE) values for environmental and spatial variables used to partition variation in the stream fish assemblage of the Arikaree River, Colorado across two 6.4-km stream segments and 2 years. Variables in bold explained significant variation and were included in final models ($P < 0.05$). Number of pools included from each year is shown. See text for detailed descriptions of variables.

Variable	Upstream segment		Middle segment	
	2006	2007	2006	2007
Environment				
Maximum depth (m)	0.76 (0.07)	0.76 (0.06)	0.40 (0.03)	0.47 (0.03)
Volume (m³)	12.63 (2.51)	14.96 (3.27)	3.61 (1.24)	7.58 (1.28)
Residual temperature	0.18 (0.24)	-0.05 (0.53)	-0.19 (0.54)	-0.17 (0.43)
Conductivity (µS)	498.55 (16.95)	547.32 (27.11)	753.67 (30.86)	695.45 (28.18)
Turbidity (%)	63.10 (6.28)	61.84 (7.28)	32.96 (5.87)	43.97 (4.75)
Small woody debris (%)	4.66 (2.08)	1.58 (1.58)	3.52 (1.77)	1.03 (0.58)
Tumbleweeds (%)	0.00 (0.00)	0.00 (0.00)	9.44 (2.30)	6.21 (1.73)
Submergent vegetation (%)	27.59 (6.82)	29.74 (4.90)	31.11 (6.37)	23.28 (5.62)
Emergent vegetation (%)	32.41 (4.90)	22.89 (2.82)	10.74 (2.38)	7.93 (1.52)
Floating vegetation (%)	42.76 (7.44)	25.53 (7.95)	1.11 (1.11)	16.38 (4.88)
Sand substrate (%)	25.29 (42.11)	42.11 (7.95)	74.49 (4.47)	49.43 (4.29)
Space				
Segment	-	-	-	-
100 flow (m)	19.38 (6.73)	54.21 (10.55)	32.74 (8.82)	13.07 (5.45)
500 flow (m)	103.10 (27.83)	263.32 (51.18)	148.30 (38.21)	78.41 (17.80)
1,000 flow (m)	195.76 (43.02)	505.32 (87.19)	251.93 (55.14)	195.28 (27.47)
Geomorphic reach	-	-	-	-
Riverscape longitudinal position	-	-	-	-
Distance to nearest pool (m)	24.76 (3.71)	17.47 (3.49)	73.63 (28.20)	36.28 (5.53)
Number isolated	4	10	15	16
Number of pools	29	19	27	29

was higher in the middle segment than the upstream segment. Therefore in general, the upstream segment was wetter and contained more complex habitats than the middle segment, which was drier with simpler habitats spaced farther apart.

Ordination revealed patterns in fish assemblage structure influenced by both environmental and spatial factors (Figure 3A and 3B). For example, white sucker *Catostomus commersonii* and creek chub were associated with large, deep pools with low conductivity, whereas green sunfish *Lepomis cyanellus* and black bullhead *Ameiurus melas* were associated with turbid, silty pools (Figure 3A; see Appendix A for species codes). These habitat associations are similar to those reported for these species (Cross and Collins 1995; Pflieger 1997).

When spatial variables were considered, orangethroat darter *Etheostoma spectabile*, central stoneroller *Campostoma anomalum*, and creek chub were associated with wet reaches (high 1000M), whereas white sucker was associated with pools located close together (low DIST-BW) and pools that were not isolated (Figure 3B). Fathead minnow *Pimephales promelas* was relatively ubiquitous so scores for this species were near the origin in both ordinations.

All components of the variation partitioning (E, S, E|S, S|E and E+S) explained significant ($P < 0.05$) variation in the Arikaree fish assemblage, indicating that metacommunity dynamics do occur in this assemblage. The total amount of variation [E + S] explained in the metacommunity by the environmental and spatial factors was 50.8% (Appendix B).

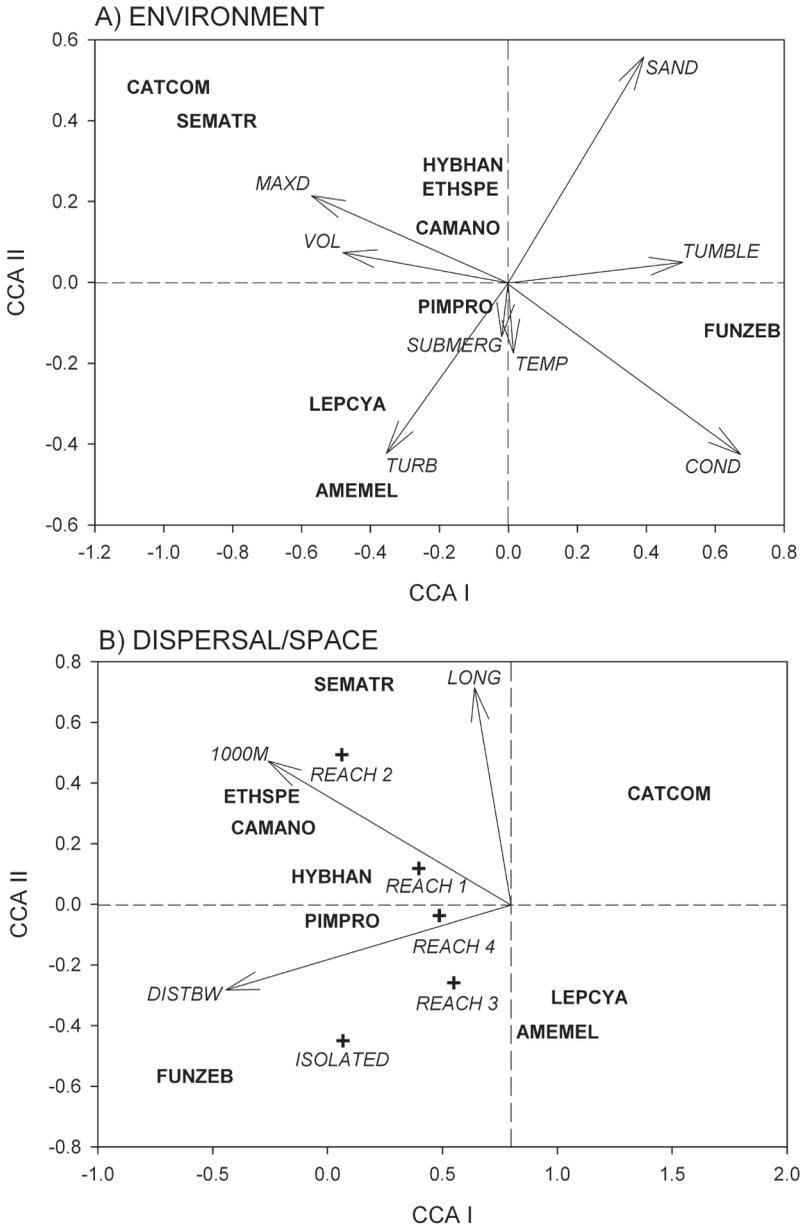


Figure 3. Two canonical correspondence analyses of fish assemblage data across 104 pool habitats located along the Arikaree River, Colorado. The top panel (A) shows the results of fish assemblage versus environmental factors, and the lower panel (B) shows fish assemblage versus spatial factors. Codes for environmental and spatial variables are explained in the text. Species codes are the first three letters of the genus and specific epithet, respectively. Species and codes are listed in Appendix A.

Pure environmental effects accounted for only 6.5% of the variation explained, whereas pure spatial effects accounted for 31.4%. The overlap among environmental and spatial factors

($[E \cap S]$) accounted for 12.9% of the variation in fish assemblage structure. A total of 49.2% of the variation was undetermined. Overall, spatial factors and environmental factors that

were influenced by space explained the majority of variation that could be explained in the Arikaree fish assemblage (44.3% of 50.8%). Because both pure environmental and pure spatial variation components were significant, we cannot rule out that both species-sorting and mass effects dynamics are occurring in this assemblage during this dry portion of the year along the Arikaree riverscape (Cottenie 2005). However, because the majority of variation was explained by spatial factors, we conclude that mass effects most likely dominate metacommunity dynamics in this system.

We found that regional-scale spatial factors (e.g., distances among habitats, longitudinal position, and habitat isolation) were important in structuring stream fish assemblages in pools along the Arikaree River. Our results were not surprising given presumed strong effects of drying within and between habitats on colonization and recolonization dynamics in this system. These results for the entire community agree with those reported by Scheurer et al. (2003) for this system. For example, they found that the probability of brassy minnow persistence in pool habitats was highest in deep pools connected on at least one end to other habitats. Our results show that pool isolation was highly influential in structuring the entire fish assemblage along the Arikaree River and indicate that spatial factors affecting dispersal opportunity (e.g., habitat connectivity and isolation) were more important than habitat quality (i.e., local pool attributes) in shaping this assemblage. Falke and Gido (2006) also showed that a pure spatial factor (distance from a reservoir) was important in explaining stream fish assemblage structure upstream of large reservoirs in Kansas. Finally, Isaak et al. (2007) reported that for Chinook salmon *Oncorhynchus tshawytscha*, use of spawning habitats in Idaho, factors such as habitat size and connection to other habitats were more important than habi-

tat quality. Clearly, there is a strong influence of space on structuring stream fish populations and assemblages, but more research is needed across different ecoregions and stream sizes before generalizations can be made about the relative influence of environmental and spatial factors in determining assemblage structure.

Future Directions

Metapopulations.—Overall, we know that stream fishes require multiple habitat types that are often dispersed across riverscapes to carry out their life histories (Dunning et al. 1988; Schlosser and Angermeier 1995; Fausch et al. 2002). These habitats may vary in quality and quantity across space. Therefore, it makes sense that spatially structured stream fish populations may be best described by a hybrid metapopulation model (Figure 1C). Within “source” areas, all habitats (spawning, rearing, and refuge) required for a species to carry out its life history are available. These habitats are well connected, allowing for population persistence over time. In satellite “sink” areas, some habitat type (e.g., spawning, rearing, refuge) is often missing, leading to extinction of the subpopulation over time without emigration of individuals from the source area. Alternatively, mortality in the sink habitat could be high due to predation. The prevalence of reports of the source-sink model in the stream fish metapopulation literature may be because only certain habitat types were considered (e.g., only refuge and nonrefuge) or because the metapopulation was considered at too fine a spatial scale. In our opinion, most of the metapopulations in those studies might be more accurately classified as the hybrid type. What is an appropriate metapopulation model for stream fishes, and how might one go about categorizing a population to a particular metapopulation type? Below, we build the case for accepting

a hybrid metapopulation model for a Great Plains stream fish with which we are familiar.

Metapopulation theory may be particularly applicable to plains fishes, given the heterogeneous and dynamic nature of the habitats they occupy. The brassy minnow in the Arikaree River is a good example of a species that requires multiple habitat types. They spawn and their larvae rear in shallow vegetated backwaters (Copes 1975; Scheurer et al. 2003). An ontogenic habitat shift occurs when juveniles are about 20 mm total length (Falke 2009). They move to the main channel where they seek pools to continue growth during summer and presumably store energy for winter. These pools vary in habitat quality depending on their location along a river segment. Persistence of brassy minnow in a given pool over the summer is a function of how deep the pool is in June (which determines whether it dries completely by August; Labbe and Fausch 2000) and how connected it is to other pools (Scheurer et al. 2003). If they survive the summer, brassy minnow must seek deep refuge pools in which to overwinter because shallow pools in Great Plains streams can freeze to the bottom during harsh winters (Labbe and Fausch 2000). Therefore brassy minnow require at least three specific habitat types (spawning, rearing, and refuge habitats) within a given year, to reproduce and survive.

This previous research showed that brassy minnow require complementary, heterogeneous habitats, which indicates that a metapopulation model is needed. Which metapopulation model best fits brassy minnow in the Arikaree River basin? Based on our key (see Distinguishing among metapopulation types above), we begin by ruling out the nonequilibrium model. The nonequilibrium model typifies a situation in which there are many local extinctions and infrequent recolonization (Harrison 1991). Along the Arikaree, local

extinctions are common due to harsh environmental conditions (e.g., pool desiccation), but these habitats, or newly created habitats, are quickly recolonized. Therefore, at the scale of in the Arikaree River basin, the nonequilibrium model is probably not appropriate. Likewise, although the patchy-population model is quite attractive for brassy minnow in the Arikaree, given the heterogeneity of habitats and high rate of dispersal among them, extinctions do take place, especially in harsher stream reaches (e.g., middle segment). This model would probably describe well the spatial dynamics of brassy minnow in a given stream reach that contains all required habitats but would describe poorly the dynamics in reaches that do not.

What about the classic metapopulation model? The classic metapopulation model does not allow habitat patches to be heterogeneous and requires that habitats be equally spaced. In contrast, channel units (pools, riffles, runs, and backwaters) in Great Plains streams are the result of the complex interaction between habitat forming events (e.g., intense thunderstorms) and the habitat template represented by variability in geomorphology and groundwater connectivity. For example, spawning and refuge habitats are aggregated in reaches with high groundwater connectivity (Falke 2009). Similarly, the source-sink model is probably too simple because it does not allow for complementary habitats (Pulliam 1988). However, it may be reasonable to assume a source-sink dynamic if the reach scale is being considered, where reaches that contain all habitats required by brassy minnow are "sources" and those that do not are "sinks."

Overall, metapopulation dynamics of brassy minnow within the Arikaree River basin are best described by the hybrid metapopulation model, which incorporates both patchy and source-sink population dynamics

(Figure 1C). Patchy population dynamics occur in core segments (e.g., upstream segment), where spawning, rearing, and refuge habitats are available and well connected and allow high among-habitat dispersal rates. Subpopulations in core habitats do not go extinct. In contrast, downstream segments (e.g., middle segment) may not contain habitats needed for all life stages and act as outlying sinks.

The metapopulation model that best describes the spatial population dynamics of brassy minnow also may change across spatial scales (Figure 1). Within a given reach, persistence depends on availability of complementary habitats and high dispersal ability (connectivity) among those habitats. A patchy metapopulation model would be most appropriate within a reach. At the scale of multiple reaches, where complementary habitats are aggregated within a reach, a source-sink model may be appropriate. At the segment scale, a hybrid model where within-segment dynamics are represented by patchy metapopulation dynamics and among-segment dynamics are represented by source-sink dynamics may be most appropriate. And finally, at a regional scale, given the decline in brassy minnow distribution across its range in eastern Colorado, a nonequilibrium model might be best. This model could account for reduced recolonization potential among basins resulting from permanent reductions in among-basin connectivity due to diversions and reservoirs that create barriers and groundwater pumping that causes reaches to dry permanently.

Metacommunities.—Clearly, the four metacommunity paradigms proposed by Leibold et al. (2004) are a heuristic tool, a starting point for further exploration of how dispersal, habitat heterogeneity, and biotic interactions interact across scales to shape communities. Moving beyond these simple models to testable hypotheses is the next step in understanding

metacommunity dynamics (Mouillot 2007). However, an important intermediate step would be to integrate the four metacommunity paradigms into a model based on actual life history attributes of a real metacommunity and incorporate factors previously established to be important in regulating communities, such as seasonal and environmental variability, across spatial scales. This approach could generate hypotheses to test using empirical research.

Streams are fluctuating environments with seasonal flow dynamics influenced mainly by climate. Although variable across stream ecotypes, flow regimes in temperate streams typically include periods of high and low flows, and fish assemblages in these streams have become adapted to maximize reproductive capacity and survival in these environments (Poff and Ward 1989; Poff 1996). Much of the variation in stream habitat availability results from seasonal flow variability, and any model of stream fish metacommunity dynamics should explicitly incorporate flow.

We predict that the relative importance of habitat heterogeneity and dispersal opportunity in structuring stream fish assemblages changes along a gradient of seasonal variation in flows (Figure 4) and illustrate this concept using our Great Plains fish assemblage. In spring, species-sorting metacommunity dynamics may dominate because individual species show strong preferences for specific spawning habitats (Falke 2009). In the Arikaree River basin, many species use specific habitats only available during spring, such as flooded terrestrial vegetation and off-channel backwaters, and there may be limited movement among them. The end of the spawning season in the Arikaree coincides with drying of shallow habitats. During this period, fishes must move from spawning habitats into summer refugia. Drying can occur rapidly, so the

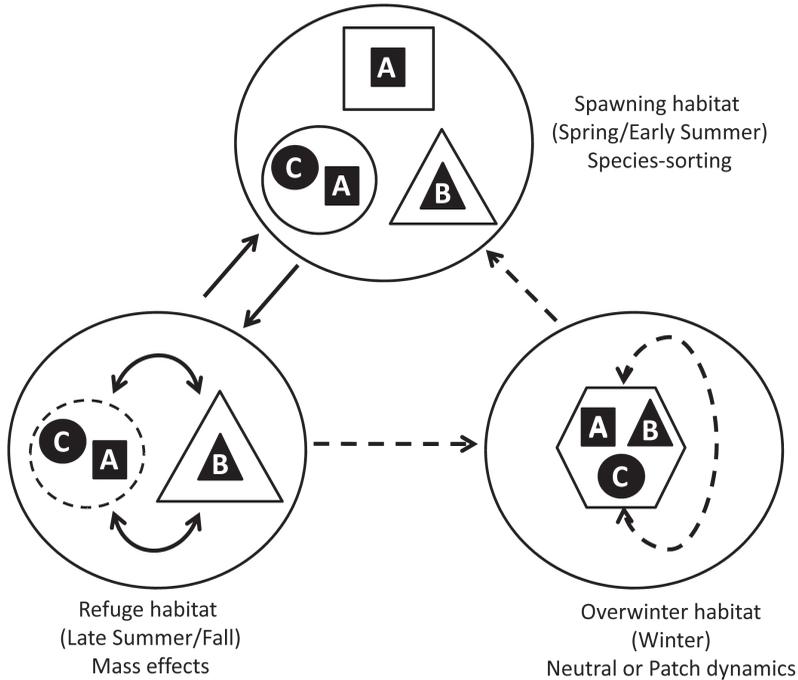


Figure 4. Theoretical model of Great Plains stream fish metacommunity dynamics with emphasis on habitat heterogeneity, movement, and seasonal flow variation for three species, A–C (modified from Schlosser and Angermeier 1995; Leibold et al. 2004). Arrows connect seasonal macrohabitats (large open circles: spawning, summer refuge, and overwinter) and mesohabitats used within seasons (patches: smaller open circles, squares, and triangles). Solid arrows indicate rapid dispersal rates; dashed arrows indicate slower dispersal rates. During spring/early summer, species sort into appropriate spawning habitat patches based on life history requirements (denoted by small filled shape matching larger open shape). However, species A is a generalist that spawns in multiple habitat patch types. Metacommunity dynamics during this period are best described by the species sorting model. Dispersal among patches is restricted during this period. Individuals then quickly move from spring spawning to summer refuge habitat as flow declines. During summer, two habitat types are available, harsh (open circle) and benign (open triangle) refugia. The harsh refugia serve as sink habitats and may dry and re-wet frequently (dynamic habitat persistence represented by dashed border). Dispersal is rapid among harsh and benign refugia (mass effects) but is often impossible due to lost connectivity between habitats. As flows slowly resume into winter, individuals disperse to occupy all habitats (represented by an open hexagon). During winter, habitats are homogeneous, and dispersal among them is low due to cold water temperatures. Metacommunity dynamics during this period are best represented by the patch dynamics or neutral models. Following winter, individuals move slowly to spawning habitats, based on phenology. See text for a full description of metacommunity types.

ability to disperse quickly from spawning to refuge habitats is critical. Therefore, we predict that a transition occurs in metacommunity dynamics from species-sorting to mass effects, in which dispersal dominates. As water quality conditions in refuge habitats degrade due to drying, movement to more suitable refugia may occur,

if pathways among those habitats exist. Finally, during winter, flow in the Arikaree increases and habitats become reconnected. However, during this period, most habitats are fairly homogeneous, and dispersal may be limited due to cold water temperatures. As a result, aspects of the neutral or patch dynamics models prob-

ably better describe stream fish assemblage dynamics during winter flow conditions.

Conclusions

Clearly, spatial factors have an important influence on both population and community dynamics of stream fishes. However, to date, research into how space influences population and community dynamics in stream fishes has been in a formative state. Future metapopulation level research should incorporate space realistically and also consider that metapopulation types may vary across spatial scales. Advances will likely be driven by better methods of estimating habitat-specific demography (e.g., Hines 1994) and costs of movement in terms of growth and mortality. We suggest that metacommunity theory also could be useful in developing hypotheses and experiments to investigate the relative influence of spatial and environmental factors in structuring stream fish assemblages. However, less emphasis should be placed on categorizing assemblages by metacommunity type, as this may vary seasonally, and more on using appropriate statistical methods to partition variation important in structuring assemblages during specific seasons. Finally, we predict that this emerging body of research could be valuable not only for basic research in stream fish ecology, but also multispecies conservation and management.

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Appendix A. Stream fish species common names, scientific names, and codes used in a partial canonical correspondence analysis of fish assemblage data collected in the Arikaree River, Colorado.

Common name	Scientific name	Code
Black bullhead	<i>Ameiurus melas</i>	AMEMEL
Central stoneroller	<i>Campostoma anomalum</i>	CAMANO
White sucker	<i>Catostomus commersonii</i>	CATCOM
Orangethroat darter	<i>Etheostoma spectabile</i>	ETHSPE
Plains killifish	<i>Fundulus zebrinus</i>	FUNZEB
Brassy minnow	<i>Hybognathus hankinsoni</i>	HYBHAN
Green sunfish	<i>Lepomis cyanellus</i>	LEPCYA
Fathead minnow	<i>Pimephales promelas</i>	PIMPRO
Creek chub	<i>Semotilus atromaculatus</i>	SEMATR

Appendix B. Eigenvalues and *P* values for a partial canonical correspondence analysis of stream fishes in the Arikaree River, Colorado. Total inertia = 0.957.

Variation	Eigenvalues	Variation explained (%)	<i>P</i> -value
[E + S]	0.504	50.8	<0.001
[E]	0.186	19.4	<0.001
[S]	0.425	44.4	<0.001
[E S]	0.062	6.5	0.005
[S E]	0.301	31.4	<0.001
[E ∩ S]		12.9	
1 – [E + S]		49.2	

