DISSERTATION

EFFECTS OF GROUNDWATER WITHDRAWAL AND DROUGHT ON NATIVE

FISHES AND THEIR HABITATS IN THE ARIKAREE RIVER, COLORADO

Submitted by

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Fish, Wildlife, and Conservation Biology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

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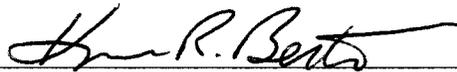
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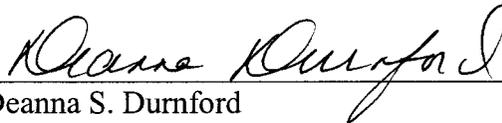
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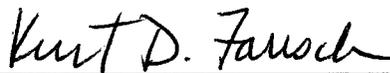
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ABSTRACT OF DISSERTATION

EFFECTS OF GROUNDWATER WITHDRAWAL AND DROUGHT ON NATIVE

FISHES AND THEIR HABITATS IN THE ARIKAREE RIVER, COLORADO

Great Plains streams are harsh environments for fishes, and are increasingly

degraded by human-caused impacts, including overuse of groundwater. Plains stream

fishes are in decline, due in part to interactions between natural drought and

anthropogenic stream drying. To address these issues, in a collaborative study we

developed a model of groundwater and surface water that predicted fish habitat quantity

within the Arikaree River basin in eastern Colorado into the future, based upon three

scenarios of land and water use (e.g., irrigation pumping). We found that under the status

quo of pumping, > 60% of remaining refuge habitats in the wettest segment of river will

be dry in 35 years, and will be isolated in a 1-km fragment along the river. Loss of

critical habitats due to stream dewatering, and subsequent negative effects on native

fishes, are not unique to eastern Colorado but are in fact widespread across the western

Great Plains. Secondly, to set this research in context, I conducted a review of

metapopulation and metacommunity research in the stream fish literature. Stream fish

populations and communities are spatially structured at multiple scales, and easily

fragmented. To date, this spatial structure has not been incorporated into stream fish

population and community models. However, recent research in this area should improve

our understanding of processes that regulate stream fish assemblages. Next, I developed

a spawning phenology for Arikaree River fishes and found that cumulative growing

season degree days had the strongest effect on hatching initiation. Occupancy by larvae of most species was related to local scale spawning habitat characteristics (e.g., habitat size and type). Among years, colonization and extinction rates for individual species differed in segments that were fed by groundwater, versus those that were not, and were influenced by climate variability among years. Last, I investigated when and where the threatened brassy minnow, *Hybognathus hankinsoni*, spawns, and what environmental factors influence growth and survival of this species within and among years. Interannual variability in climate, and the hydrologic context of segments along the riverscape, had a strong influence on habitat availability and recruitment of brassy minnow in the Arikaree River.

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INTRODUCTION

Habitat fragmentation and loss are the most important factors causing population

declines and extirpations of species worldwide (Vitousek et al. 1997), especially in

aquatic ecosystems (Ward 1998; Dudgeon et al. 2006). For stream fishes, connections

among spawning, rearing, and refuge habitats at the riverscape scale are critical for

successful recruitment and population persistence (Schlosser and Angermeier 1995;

Fausch et al. 2002). Stream habitat fragmentation has become a critical issue across the

western Great Plains of North America, because widespread groundwater mining for

agricultural irrigation has contributed to significant declines in groundwater levels

(Gutentag et al. 1984; Robson and Banta 1995; McGuire et al. 2003). Moreover, recent

drought and climate change have exacerbated the effects of pumping on groundwater and

surface water resources.

Water is a valuable commodity in the semi-arid Great Plains. Yuma County,

located in eastern Colorado, is one of the top three corn producing counties in the United

States, with over 41 million bushels produced in 2008 (NASS 2009). However, corn and

other irrigated crops need water, and surface water and precipitation are not enough to

meet crop requirements. As a result, 90% of the corn produced in Yuma County is

irrigated using groundwater pumped from the underlying High Plains aquifer. Since the

early 1960's, pumping for irrigated agriculture has averaged over 400 million m^3 of

groundwater extracted per year in Yuma County. During that same time period, mean

annual flows in three groundwater dependent streams in the region, the North Fork

Republican, Arikaree, and South Fork Republican rivers, have declined precipitously.

Harsh environmental conditions are the rule, not the exception, in most Great Plains stream habitats, and life history strategies of native plains stream fishes have become adapted to cope with these variable environments (Matthews 1988; Dodds et al. 2004). However, despite these adaptations, native fish populations across the Great Plains are declining range wide (Cross and Moss 1987, Fausch and Bestgen 1997; Hubert and Gordon 2007). In the Arikaree River, many native fish species have been extirpated: three since the 1940's (flathead chub *Platygobio gracilis*, stonecat *Noturus flavus*, and river shiner *Notropis blennius*; Metcalf 1966), two since the late 1970's (plains minnow *Hybognathus placitus* and suckermouth minnow *Phenacobius mirabilis*; Cancalosi 1980), and two other species that occurred in the early 2000's (red shiner *Cyprinella lutrensis* and sand shiner *Notropis stramineus*; Scheurer et al. 2003) but were not detected in the intensive sampling described here during 2005-2007. Several of these species were collected historically in the lower portion of the Arikaree River that no longer flows during any season. Of the nine native species that remain, brassy minnow *Hybognathus hankinsoni* is a state threatened species in Colorado, and orangethroat darter *Etheostoma spectabile* is a state species of special concern (CDOW 2007). It is likely that loss of critical habitats due to hydrologic alteration resulting from overuse of groundwater resources is largely responsible for these declines and extirpations.

Herein, I summarize the results of a three-year (2005-2007) field study of the effects of groundwater pumping and drought on spawning, rearing, and refuge habitats of native plains fishes along the Arikaree River basin, eastern Colorado. Sampling of fish and habitat was conducted within three 6.4-km river segments which represented a gradient in intermittency from perennial (upstream segment) to intermittent (middle

segment) to mostly dry (downstream segment). Additionally, habitat connectivity data were collected, and groundwater modeling was conducted, at the scale of the entire river basin. Chapter 1 details the results of a collaborative study linking groundwater and fish habitat data to develop a model of groundwater and surface water that predicts declines in habitat quantity within the Arikaree Basin into the future, based upon three scenarios of land and water use (e.g., increased irrigation pumping). We found that under the status quo of pumping, > 60% of the remaining refuge pool habitats in the wettest segment of river will be dry in 35 years, and nearly all will be isolated in a 1-km fragment of the upstream segment. This will be all that remains of what was once at least 110 km of flowing river habitat. The loss of critical habitats due to stream dewatering and subsequent negative effects on native fishes are not unique to eastern Colorado, but are in fact widespread across the western Great Plains.

Chapter 2 is a literature review of metapopulation and metacommunity research in stream fish ecology. I found that although stream fish ecologists have considered metapopulation concepts, little of this research has explicitly incorporated space into models. Likewise, metacommunity research in stream fish ecology is in its infancy. However, the concepts and tenets of this body of theory are promising for furthering our understanding of processes that regulate stream fish assemblages.

In Chapter 3, I describe sampling of larval fishes and develop a spawning phenology for Arikaree River fishes. I compared dates of hatching initiation to environmental factors that may serve as spawning cues, and investigated patterns in spawning habitat use by larvae within and among years. Cumulative growing season degree days had the strongest effect on initial hatching dates. Within a year, high

abundance of larvae of most species was related to habitat size (e.g., area and depth) and habitat type, although spatial location (i.e., segment in which larvae occurred) also influenced abundance of some species. Among years, colonization and extinction rates for individual species differed in segments that were fed by groundwater, versus those that were not, and were influenced by among-year climate variability.

Finally, Chapter 4 details the results of my study of where and when the state-threatened brassy minnow spawn, and what environmental factors influence growth and survival of larvae of this species within and among years. Overall, I found that interannual variability in climate, and the hydrologic context of segments along the riverscape, have a strong influence on habitat availability and recruitment of brassy minnow in the Arikaree River. I end this chapter with insights into the life history of brassy minnow in Great Plains streams, and make recommendations for conserving this species in the context of further human-caused loss of habitats and connectivity across the Arikaree River riverscape.

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CHAPTER 1: The Role of Groundwater Pumping and Drought in Shaping

Ecological Futures for Stream Fishes in a Western Great Plains River Basin

Forward

The research presented in this chapter resulted from an unique, interdisciplinary effort among graduate students and faculty from the Department of Fish, Wildlife, and Conservation Biology (FWCB) , and the Department of Civil and Environmental Engineering (CEE) at Colorado State University. The project was a close collaboration among stream fish ecologists, groundwater hydrologists, and agricultural irrigation engineers. Each collaborator played an important role in the design, implementation and analysis of this research.

The majority of field data collection, analysis and writing were performed by two graduate students, Jeff Falke (FWCB), and Robin Magelky (CEE). Over three years, Jeff collected data in the field on fish habitats, habitat connectivity, and alluvial groundwater levels. Jeff also compiled data on historical fish assemblages, streamflow, and drought. Robin obtained historical and current groundwater level and well data, and information on the hydrogeology and surface geology of the Arikaree River basin. Jeff created all maps, figures, and tables, and calculated streamflow decline over time for Republican River tributaries. Robin developed and conducted the MODFLOW and water balance groundwater modeling, building on previous work by Angela Squires (Squires 2008), Linda Riley (Riley 2009), and Ryan Banning (*unpublished data*), and wrote methods and results detailing those efforts. The other portions of the manuscript were written by Jeff.

Drs. Kurt Fausch (FWCB), Deanna Durnford (CEE), and Ramchand Oad (CEE) provided advice, comments and revisions to the chapter text, and project administration.

Abstract

Across the western Great Plains, groundwater pumping for irrigated agriculture is depleting regional aquifers that sustain stream flow for native fishes. Simultaneously, the region has undergone a multi-year drought since 2000 that further reduced stream flow and increased water demands by agriculture. We first measured fish habitat quantity and connectivity in the Arikaree River in eastern Colorado at multiple spatial scales during spring and summer 2005-2007 to investigate habitat loss for imperiled native fishes. At the basin scale, monthly low-altitude flights showed that flowing reaches were reduced from 65 to <15 km by late summer, and long permanently dry segments in the lower basin now prevent recolonization. At the river segment scale, stream drying occurred rapidly during summer in three 6.4-km segments, but varied among segments along the river due to hydrogeology. At the local scale, refuge pool habitats dried rapidly during summer, and most either dried completely or lost more than half their volume, becoming disconnected from other pools by late summer. Based on our empirical fish habitat data, and historical groundwater and stream flow data, we then constructed a MODFLOW groundwater model to predict how pumping will affect groundwater stage and fish habitat under three future scenarios. With status quo pumping, refuge pools in the wettest segment are reduced by half in 25 years (by 2035), and nearly all those remaining by 2045 are isolated in an upstream 1-km fragment of the original 110 km of river habitat. Results were identical after removing three nearby alluvial wells. Likewise, the current policy of retiring wells within a 4.8-km band around the river to meet an interstate water compact resulted in only 55% of pools remaining in 35 years (2045), nearly all isolated in a 1.7-km fragment upstream. A water balance model indicated that maintaining current

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alluvial groundwater levels and refuge pools for fishes would require at least a 75%

reduction in groundwater pumping, which is not economically or politically feasible.

Given widespread streamflow declines, ecological futures are bleak for stream fishes in

the Western Great Plains, and managers will be challenged to conserve native fishes

under current groundwater pumping regimes.

Introduction

Habitat fragmentation and loss are the most important factors causing population declines and extirpations of species worldwide (Vitousek et al. 1997), especially in aquatic ecosystems (Ward 1998; Dudgeon et al. 2005). Streams are the most easily fragmented aquatic habitats, because of their linear and hierarchical structure (Fagan 2002; Campbell-Grant et al. 2007), and connectivity is quickly lost as habitats become increasingly fragmented (Bunn and Arthington 2002; Wiens 2002). For stream fishes, these connections among spawning, rearing, and refuge habitats at the riverscape scale are critical for successful recruitment and population persistence (Schlosser and Angermeier 1995; Fausch et al. 2002). Stream habitat fragmentation has become a critical issue across the western Great Plains of North America, because widespread groundwater mining for agricultural irrigation has contributed to significant declines in groundwater levels (Gutentag et al. 1984; Robson and Banta 1995; McGuire et al. 2003). Streams in this region depend on groundwater input to maintain base flows and connections among habitats important for the persistence of stream fish populations (Winter 2007). Moreover, recent drought has exacerbated the effects of pumping on groundwater and surface water resources.

Harsh environmental conditions are the rule, not the exception, in most Great Plains stream habitats, and life history strategies of native plains stream fishes have become adapted to cope with these variable environments (Matthews 1988; Dodds et al. 2004). However, despite these adaptations, native fish populations across the Great Plains are declining range wide (Cross and Moss 1987, Fausch and Bestgen 1997). For example, of 37 species native to the Platte, Arkansas, and Republican river basins in

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eastern Colorado, 20 have become either extirpated, endangered, threatened, or a species of concern in Colorado (Fausch and Bestgen 1997; CDOW 2007; Hubert and Gordon 2007). Cross and Moss (1987) attributed the decline of native fishes in the western Great Plains to habitat loss, including overuse of groundwater resources. However, to our knowledge, no study has quantified the linkages between groundwater pumping, loss of connectivity, and stream fish habitat.

The ability to forecast future ecosystem states is critical for conservation of native species. Carpenter (2002) presented a framework for evaluating "ecological futures", defined as an emerging process-based decision making tool to anticipate future scenarios with respect to environmental change. He suggested that ecological forecasting should: 1) be simple, but contain enough complexity to address alternate future states, 2) focus on an ecosystem service subject to management, 3) be set in a socio-economic framework, and 4) be applicable at temporal scales meaningful to managers. Furthermore, Baker et al. (2004) suggested that this process should 1) characterize the current and historical landscape in terms of trajectory of change to date, 2) develop two or more scenarios for future conditions, and 3) evaluate effects of these changes to specific resource endpoints. The utility of such forecasts hinges on choosing appropriate ecosystem attributes that can be predicted with a minimum amount of uncertainty based on ecological and socio-economic factors (Clark et al. 2001). By framing an analysis using these guidelines, relevant and useful information can be provided to inform both management and policy decisions.

The purpose of this paper is to consider what will be required to conserve native stream fishes over the long term in a western Great Plains river basin subject to persistent

agricultural groundwater pumping and multi-year droughts. We frame our analysis by considering alternative future scenarios (i.e., ecological futures, sensu Carpenter 2002) based on the status quo of the current pumping regime and climate, as well as scenarios incorporating varying levels of groundwater conservation, to assess what must be done to ensure a sustainable future for these fishes. Specifically, our goals were to 1) measure the spatial and temporal distribution of fish habitat quantity and connectivity across spatial scales in a Great Plains river basin, 2) develop water balance and groundwater models for the basin and, 3) link groundwater dynamics to fish habitat to project fish habitat loss (i.e., drying) into the future based on pumping and drought scenarios.

Conceptual model of ecological futures

The conceptual model we developed predicts that under current pumping regimes, habitat for stream fishes in groundwater dependent Great Plains headwater streams is not sustainable (linear decline and extinction threshold; Figure 1.1). Under these conditions, groundwater stage will decrease until the entire stream dries completely, and fishes will be extirpated from the basin. However, the rate of decline in groundwater stage and fish habitat is currently unknown. For example, it may be non-linear owing to increased irrigated corn production for ethanol, so that the rate of decline accelerates and hastens extinction. Conversely, with improved water conservation practices, such as reduced pumping, more efficient crop systems, or artificial recharge, groundwater levels and fish habitats could be sustained into the future at a level above a conservation threshold that allows long-term persistence of fish populations. The shaded areas around the conservation and extinction thresholds represent uncertainty resulting from variability in climate, agricultural irrigation demands, and fish population dynamics.

Environmental setting

Our research was conducted in the Arikaree River basin in eastern Colorado (Figure 1.2). The Arikaree River is one of three principle tributaries of the Republican River, located at the headwaters of the Kansas River basin. Surficial geology of the basin consists mainly of areas of highly permeable dune sand and Peorian loess underlain by the Ogalalla formation of the High Plains Aquifer (Weist 1964). The river channel flows through alluvial deposits consisting of unconsolidated gravel, sand, silt, and clay. The alluvium is in turn underlain by the groundwater-bearing Ogalalla formation in the upper portion of the basin, and low permeability Pierre shale in the lower portion (Figure 1.3).

The xeric climate in eastern Colorado causes mean pan evaporation (152 cm/year) to exceed mean precipitation (44 cm/year), resulting in little net recharge of the aquifer over most of the year (Robson and Banta 1995). Important periods of recharge may occur after snowmelt or during episodes of heavy precipitation when evapotranspiration rates are low. Where the aquifer head is higher than the streambed, discharge occurs into the stream channel. However, evapotranspiration from phreatophytes, and to a lesser extent from upland vegetation, is also an important component of the hydrologic cycle (Wachob 2006).

Land use in the Arikaree basin is predominantly agricultural (NASS 2007). Primary crops produced are corn (50%), wheat (30%), and alfalfa (< 10%). Most corn is irrigated by large center-pivot systems that apply groundwater to circles 400 m in diameter. Pumping typically begins in early June and ceases in early September, but varies annually with climate, and coincides with riparian evapotranspiration (Riley 2008).

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The High Plains Aquifer underlies 451,000 km^2 of the western Great Plains

ecoregion (Figure 1.2), and is the major source of groundwater that contributes to stream

flows and agricultural irrigation in this semi-arid region. Since the early 1960's the total

area irrigated with groundwater from this aquifer increased rapidly, from 8,500 km^2 in

1949 to 55,000 km^2 in 1980 (Gutentag et al. 1984). In eastern Colorado, over 4,000 high

capacity wells were installed and currently irrigate over 3,000 km^2. Groundwater levels

have declined 8 m or more (Robson and Banta 1995) over 5,200 km^2 in this region

(McGuire et al. 2003). By 1990, over 21×10^9 m^3 (17 million acre-feet) of groundwater

had been removed in eastern Colorado (Van Slyke and Joliet 1990), and by 2002 the rate

of groundwater stage decline was approximately 0.3 m per year (CDNR 2002).

Estimated groundwater used for irrigation within the Colorado portion of the Arikaree

basin was approximately 82×10^6 m^3 (67,000 acre-feet) in 2007 (Riley 2008).

Western Great Plains streams depend on groundwater to maintain base flows and

connect habitats important for persistence of stream fish populations (Labbe and Fausch

2000). Since the advent of intensive groundwater withdrawal for agricultural irrigation in

the early 1960's, mean annual discharge in western Great Plains headwater tributaries has

declined precipitously (Szilagyi 1999). For example, in the Arikaree River, Colorado,

mean annual discharge declined 60% from 0.71 ($\pm$ 0.06 SE) m^3/sec during 1932-1965, to

0.29 ($\pm$ 0.02 SE) m^3/sec during 1966-2006 (t-test, $t = 2.02$, $P < 0.001$; Figure 1.4).

Additionally, variability in mean annual flows has also declined by half ($\sigma = 0.32$, 1932-

1965; $\sigma = 0.15$; 1966-2006). Peak flows in the Arikaree typically occur in May and June,

from a combination of groundwater recharge of the alluvial aquifer and spring

precipitation (Figure 1.5). Low flows occur in late summer through winter months.

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Mean monthly flows have decreased drastically since the advent of intensive groundwater mining in the 1960s.

Drought conditions are relatively frequent in Great Plains basins (Figure 1.6; Schubert et al. 2004), and flows in eastern Colorado plains streams have been recently affected by a major drought that began in 2000 (NDMC 2008). Historically, flows in the Arikaree River resumed after intense droughts, even when the stream gauge recorded no flow during up to 25% of days in a given year. However, the proportion of days without flow has increased during the current drought (2000 – 2007) to almost 80%. This suggests that due to the cumulative effects of groundwater withdrawal and drought, the river may have lost the ability to recover from drought, and is at a critical threshold.

Plains fish habitats and assemblages

Most plains fish species are small-bodied, short-lived, and reach maturity at an early age (Fausch and Bestgen 1997). Early maturation and high vagility allow for rapid recolonization of habitats that were previously unavailable due to floods or droughts (Labbe and Fausch 2000; Bestgen et al. 2003; Scheurer et al. 2003). Therefore, connectivity among habitats is critical for plains stream fish population persistence because it: 1) permits movement among spatially discrete complementary habitats (e.g., spawning and rearing habitats), 2) allows for demographic support of sink habitats where mortality exceeds natality (i.e., rescue effect; Brown and Kodric-Brown 1977), and 3) provides corridors critical for recolonization of habitats. Plains streams are harsh environments for fishes, and dynamic patterns of wetting and drying of habitats are typical (Matthews 1988; Dodds et al. 2004). In intermittent reaches, habitats dry down to isolated pools during summer, which serve as refuge habitats for fishes until

opportunities for movement occur when flow resumes and refugia become re-connected to upstream and downstream habitats (Labbe and Fausch 2000; Scheurer et al. 2003). As a result, plains stream fish assemblages are composed of highly vagile species adapted to cope with these extremes in flow, temperature, and physical habitat (Fausch and Bestgen 1997).

The Arikaree River supports a relatively intact native fish assemblage, compared to nearby basins such as the North and South Forks of the Republican River (Nesler 2004). However, of 16 species native to the basin, 2 have not been collected since the 1940's (flathead chub *Platygobio gracilis* and stonecat *Noturus flavus;* Metcalf 1966) and three others (plains minnow *Hybognathus placitus*, river shiner *Notropis blennius*, and suckermouth minnow *Phenacobius mirabilis*) have not been found since an extensive survey of the basin in the late 1970's (Cancalosi 1980). Largemouth bass (*Micropterus salmoides*) is the only non-native species recorded from the Arikaree River (Scheurer et al. 2003), but this species was not detected during intensive sampling from 2005-2007 (J. Falke *unpublished data*). Off-channel ponds may provide a source for repopulation of this species. Eleven extant native fishes include central stoneroller *Campostoma anomalum*, red shiner *Cyprinella lutrensis*, sand shiner *Notropis stramineus*, fathead minnow *Pimephales promelas*, creek chub *Semotilus atromaculatus*, white sucker *Catostomus commersonii*, black bullhead *Ameiurus melas*, plains killifish *Fundulus zebrinus*, and green sunfish *Lepomis cyanellus* (Scheurer et al. 2003; J. Falke *unpublished data*). Brassy minnow (*H. hankinsoni*) is classified as a threatened species by the state of Colorado, and orangethroat darter (*Etheostoma spectabile*) is a species of special concern (CDOW 2007).

Methods

Study area

Our study area was restricted to the lower half of the Arikaree River basin because reaches with the potential for perennial streamflow occur only in the lower 110 km of the basin (Scheurer et al. 2003; Figure 1.2). We measured groundwater and fish habitats at the segment and channel unit scales within three 6.4-km segments in the lower basin identified by Scheurer et al. (2003). Our study segments were selected to represent a gradient in intermittency, from the more perennial upstream segment, to the intermittent middle segment, to the downstream segment which is almost completely dry by early summer. The upstream segment is located within The Nature Conservancy's (TNC) Fox Ranch, and long reaches sustain flow in all but the driest of conditions. It is characterized by alternating runs and deep, persistent pools. Beaver (*Castor canadensis*) activity increased after 2001 and created large pools in some reaches. The middle segment is made up of State Trust Lands in conservation easement administered by the Colorado Division of Wildlife (CDOW), and is largely intermittent most of the year. The upper half has deep, well developed pools and an extensive gallery forest of riparian cottonwood (*Populus deltoides*), whereas the lower half is wide and shallow with mostly sand substrate and no riparian canopy. The downstream segment flows through private lands (approximately 2/3) and the CDOW Simmons State Wildlife Area (approximately 1/3) and is nearly dry most of the year. A few pools persist at its upper end in some years. However, a perennial tributary, Black Wolf Creek, enters the middle of this segment and often sustains a short reach of flowing habitat in the main channel downstream.

Habitat connectivity

Our sampling of fish habitats focused on quantifying connectivity among habitats and the distribution and abundance of refuge pools at the basin and segment scales over the course of summer drying. Connectivity was classified into three categories: flowing (all pools connected), intermittent (disconnected pools), and dry. At the basin scale, low-altitude flights were conducted 200-300 m above the stream channel in May 2005, and monthly from May through July 2006, and May through October 2007. Each flight surveyed approximately 110 km of the Arikaree River, from Cope, CO downstream to its confluence with the North Fork Republican River, and included all segments in which flow occurred. Stream reaches were visually classified by connectivity category and their boundaries marked using a Garmin GPSmap 60 Global Positioning System (GPS; Garmin International Inc., Olathe, Kansas, USA) during flights. A Geographic Information System (GIS) line layer was then created with reaches classified by connectivity type using ArcGIS ver. 9.1 (Environmental Systems Research Institute, Redlands, California, USA).

At the segment scale, connectivity was measured twice a month from May through August in 2005, and weekly from late May to mid August in 2006 and 2007. During each survey, each entire segment was traversed on foot, and the presence of water was recorded throughout. Boundaries of reaches in the three different connectivity classes were georeferenced with the GPS and a GIS layer was produced of each segment. Lengths of flowing, intermittent, and dry reaches (km) at the basin and segment-scales were calculated using ArcGIS.

Groundwater and pool habitats

We installed six groundwater monitoring wells in the upstream segment in August 2005 to investigate the relationship between groundwater stage and refuge pool depth. The wells were spaced evenly along the length of the segment, approximately 10 m from the stream channel. The well casings consisted of three 0.9 m sections of 5-cm diameter PVC pipe. The lower section of casing was slotted (0.6-cm spacing, 0.05-cm slot width) to allow groundwater to enter the well and had a conical PVC cap. Pressure-based HOBO U20 water level loggers (Onset Corp., Bourne, Massachusetts, USA) were installed in each well and recorded groundwater stage hourly with a precision of ±0.5 cm.

Fish habitat (pools) was censused during the period of lowest water levels in late July each year (2005-2007). Surveys were also conducted in August 2006, to compare drydown between July and August. All pools in each segment were identified and georeferenced. For each pool we measured (m) length, width at the midpoint, and maximum depth, and used these measurements to estimate their surface area (m^2) and volume (m^3).

In summer 2007, we monitored maximum pool depth (cm) at 10 locations along the upstream segment to gather data on drawdown of pools for our groundwater model. We chose deep pools that were close to the groundwater monitoring wells and distributed throughout the segment. Pool maximum depth (cm) was recorded weekly from March through August 2007, and periodically through October 2007, from fixed stage gauges installed in each pool.

Water balance model

We developed a water balance model for the High Plains and alluvial aquifers within our study area to compare hydrologic storage, inputs, and outputs between pre-development (pre-1958, before pumping) and current (2007) conditions, and to estimate parameters for our more complex groundwater model (see below). A water balance model is based on a water conservation equation, and quantifies water inputs and outputs to a control volume for a system in equilibrium:

$$\Delta S = Q_{in} + R - ET - Q_{out}$$

where ΔS is the change in groundwater storage (m^3) within the control volume, Q_{in} is the total inflow of streamflow and groundwater (m^3/year), R is recharge to the aquifer (cm/year), ET is water lost to evapotranspiration due to phreatophytes (m^3/year), Q_{out} is streamflow, groundwater flow, and groundwater pumping out of the control volume (m^3/year).

A significant assumption of the pre-development water balance is that the change in groundwater storage over time is negligible (i.e., $\Delta S = 0$) . That is, the groundwater table recovers after each growing season, and there is no long term change in storage volume. The regional control volume used for our water balance model includes both the High Plains Aquifer and the alluvial aquifer (Squires 2007).

As a groundwater-fed stream, water levels and flow within the Arikaree River are directly determined by the water balance in the surrounding High Plains Aquifer and the alluvial aquifer in which the stream is incised. When precipitation falls in the area, a portion recharges the High Plains Aquifer, eventually flowing to the alluvial aquifer and discharging to the river. Along that path, water is lost from the subsurface to the

atmosphere through evapotranspiration and irrigation pumping, particularly in the riparian corridor along the Arikaree River where the water table is closest to the land surface. The water balance model for the aquifer and stream system was evaluated using estimates of the total inflow to, and outflow from, the aquifer to develop an initial estimate of aquifer fluxes, as well as to develop a general estimate of the impact of pumping. The water balance model does not account for spatial or temporal variability in parameters such as recharge, evapotranspiration, and pumping, but provides an important initial step in understanding and modeling the aquifer and river hydrologic system.

Pre-development groundwater flow into and out of the control volume was estimated from a 1958 groundwater contour map (Weist 1964). Stream outflow was estimated from the USGS stream gauge 06821500 at Haigler, NE (waterdata.usgs.gov). For the High Plains Aquifer, the recharge was initially estimated to be about 7% of the average precipitation of 44 cm/yr from 1951 to 2006, or approximately 2.9 cm/yr (Scanlon et al. 2006; Squires 2007). For the alluvial aquifer, recharge was estimated to be approximately 6.3 cm/yr, or 15% of the average precipitation of 44 cm/yr, based on a lysimeter study in the alluvium along the South Platte River in nearby Morgan County, Colorado (Willard Owens Consultants 1988). Groundwater flux from the aquifer to the alluvium and the total evapotranspiration in the alluvium were calculated so that the change in storage in each control volume was zero for pre-development, pseudo-equilibrium conditions.

Based on the results of the predevelopment water balance model, a second water balance model was developed assuming current irrigation pumping rates. The groundwater flux and the yearly water table declines were evaluated for the condition

where water is taken from storage. Based on the loss of storage, we estimated an average yearly decline in the groundwater levels of 0.25 m/yr in the High Plains Aquifer, assuming an apparent specific yield (*Sya*; unitless) of 0.17 (Squires 2007). Moreover, the average decline in groundwater levels measured in seven wells south of the Arikaree River from 1965 to 2007 was 0.27 m/yr (SE = 0.01, range 0.21-0.31; CDSS 2007), similar to the estimate based on change in storage. Finally, we used our post-development water balance model to estimate the percent reduction in pumping that would be needed to maintain current alluvial groundwater levels and fish habitats. This was done by reducing the amount of irrigation pumping (Q_{out}) until the change in storage (ΔS) equaled zero.

Groundwater model

   Groundwater system conceptualization—Our initial investigation into the geology and groundwater dynamics in the Arikaree River basin showed that the regional (High Plains) and alluvial aquifers become hydraulically disconnected just downstream of our upstream study segment. In the upper portion of our study area, the alluvium is hydraulically connected to the High Plains Aquifer and groundwater flows into the alluvium, providing base flow and maintaining habitat for fishes during dry conditions (Figure 1.3). However, downstream of our upstream segment, the river channel and the alluvial aquifer are instead underlain by a layer of impermeable Permian shale bedrock. Consequently, the alluvium in downstream segments is disconnected from the regional aquifer, receives only alluvial and surface flow from upgradient, and fish habitats are maintained only by flow from upstream reaches supplemented by episodic precipitation events. Moreover, groundwater pumping for irrigation from the regional aquifer has

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reduced groundwater levels, leading to reduced input of groundwater from the regional

aquifer to the alluvium upstream. Therefore, groundwater and stream flow from

upstream to downstream has been reduced, and consequently fish habitat has declined

markedly in the middle and downstream segments over time (Scheurer et al. 2003; Falke

unpublished data). Given the high incidence of drying in these segments (Scheurer et al.

2003), it appeared likely that habitat to sustain viable populations of native fishes like

brassy minnow and orangethroat darter would persist primarily in the upstream segment.

Likewise, decline of the remaining habitat in the middle segment would likely precede

that in the upstream segment. Therefore, we chose to model only the upper portion of our

study area (Figure 1.3) where the alluvial aquifer is hydraulically connected to the High

Plains Aquifer, and where core habitats for fishes are most likely to persist into the

future.

Model design—A numerical groundwater model was constructed using

MODFLOW-2000, a block-centered finite-difference code for simulating groundwater

flow systems (Harbaugh et al. 2000). The MODFLOW model is a widely used, well-

documented, and verified groundwater flow model (Anderson and Woessner 1992).

Simulations were run with the following packages (Hill 1990; Harbaugh et al. 2000) :

Basic (BAS6), Block-Centered Flow (BCF6), General Head Boundary (GHB6), Drain

(DRN6), Stream (STR6), Recharge (RCH6), Evapotranspiration (EVT6), Constant Head

(CHD6), and Solver (PCG26). Pre- and post-processing, including finite grid

development, were performed using Visual MODFLOW version 4.0 (Waterloo

Hydrogeologic Inc., Waterloo, Ontario, Canada).

Within our model domain (Figure 1.3), grid spacing of 201 m (0.4 km^2 each) resulted in 17,326 active cells. The model was constructed with general head boundaries to the north and south representing the groundwater divides between the Arikaree River Basin and the North and South Forks of the Republican River. For both the High Plains Aquifer and the alluvium, the eastern and western boundaries were constructed as general head boundaries representing aquifer water levels. The eastern model boundary just north of the Arikaree River was represented as a drain element to incorporate the small intermittent tributary in this area. The Arikaree River was represented in the model using the STR6 package, to enable stream routing of water through the model domain. Precipitation recharge was modeled using the RCH6 package, and evapotranspiration in the riparian areas was modeled using the EVT6 package.

The rate of evapotranspiration for the riparian areas of 86 cm/yr determined by Squires (2007) was applied for the growing season. Apparent specific yield for the High Plains Aquifer and alluvium were set to 0.17 and 0.125, respectively, based on previous modeling studies (RRCA 2003; Squires 2007). The number of irrigation wells and their spatial position on the landscape within our model domain were obtained from the Colorado Decision Support System (CDSS 2007) and pumping rates for individual wells were assumed to be 60% of their rated capacities (Fardal 2003).

Model calibration and sensitivity— The model was calibrated using an iterative process, by first calibrating a steady-state model to pre-development water levels, and then refining the calibration to best match historical trends in water levels from the pre-development condition to the present. The steady-state model was calibrated to match the 1958 water table contour map of Weist (1964), which represented pre-development

conditions. The model was calibrated by adjusting hydraulic conductivity, including the conductance term in the GHB6 package and recharge rates, to minimize the root mean squared error (RMSE) of the modeled water levels when compared to the 1958 contours. The water level output from the steady state model was then passed to a transient model for calibration to the 1958 to 2007 period. Within the model domain, historical groundwater level measurements were available for eight wells in the High Plains Aquifer and one in the alluvial aquifer (CDSS 2007), allowing a second, more refined calibration to water level declines to be performed. The goal of this calibration was to minimize the RMSE of the modeled water levels when compared to the 1958 contours and the 1958 to 2007 water level records. The final model parameters for the alluvium and High Plains Aquifer are shown in Table 1.1. The RMSE for the final transient calibration was 2.5 meters, which is 2.7% of the range in measured water levels across the study area.

We performed a sensitivity analysis on two parameters that are likely to influence our steady state model results. The first parameter, recharge, was varied by increasing and decreasing base values up to 50%. The results of the sensitivity analysis on recharge indicated that a good calibration was achieved given the other input parameters, and that the model is more sensitive to larger rates of recharge (Figure 1.7). The model is much less sensitive to changes in the second parameter, the rate of evapotranspiration. Relative sensitivities of recharge and evapotranspiration are different because of their proximity to boundary conditions and the area to which they are applied. Evapotranspiration stresses are limited to the area near the stream, whereas recharge is applied across the entire model domain.

Model scenarios

We used the MODFLOW model to predict groundwater levels for three scenarios to evaluate the impact of future water use on alluvial water levels and pool depths. These transient prediction scenarios were constructed in the same manner as the historical transient model, with two stress periods per year representing the pumping season and the non-pumping season. To prevent drying out of model cells in areas of significant pumping, the pumping rate for all wells located more than one mile from the river was averaged over the year, rather than focused during the pumping season. The purpose of this modification was to reduce problems with the aquifer becoming desaturated near wells, which would cause wells to be removed from the model calculations, resulting in reduced future pumping and artificially decreasing the predicted impact on the river. There was no observable trend in the 1958 to 2007 average rainfall data, so we used the average rainfall for this period (44 cm/yr) to estimate precipitation for future scenarios.

The three future scenarios we modeled were as follows. For the status quo scenario (SQ), the current number of wells and pumping rates were continued into the future. For the alluvial well removal scenario (AW), the three wells that were located directly in the alluvium within our model domain were removed, whereas all wells in the High Plains Aquifer continued pumping (Figure 1.3). For the third scenario (TM), we removed all wells within our model domain identified by the Colorado State Engineers Office (CDWR 2007) as being within a 4.8 km (three mile) band of the river from the Fox Ranch downstream. These removed wells represented 18% of the wells in the model domain and 19% of the total pumping volume in the SQ scenario. The TM scenario is based on the current policy of the Colorado State Engineers Office to curtail

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pumping and restore flows to the river for delivery downstream to Kansas. Water level declines in the alluvium along the upstream segment were then predicted for each scenario.

We evaluated the results of modeling the three future scenarios by calculating the number of refuge pools remaining in August (at the maximum drydown each year) along the upstream segment from 2007-2045. For our initial state, we set the pool surface elevation in August 2007 and shallow alluvial groundwater elevation in that same month to be equal. Due to the close relationship between pool stage and groundwater stage during summer months (see Results), we assumed that future pool depths would correspond to alluvial water table levels. Based on pool locations and depths measured in 2007, we considered a pool to be dry when the alluvial groundwater table dropped below the maximum pool depth. Subsequently, we calculated the percentage and spatial location of pools remaining over time under each scenario.

Trends in discharge for other tributaries

We quantified trends in mean annual discharge over time for all Republican River tributaries in Colorado, Nebraska, and Kansas for which USGS streamflow data was available. For this analysis we calculated the slope for calendar year vs. mean annual discharge (m^3/sec) for each stream, as well as the range and number of years included in the analysis. Calculations were conducted using SPSS version 11.0 (SPSS Inc., Chicago, IL).

Results

Climate and drought

Drought conditions that started in 2000 continued during 2005-2007 (Figure 1.6), although mean annual flows in 2005 were the highest since 2001 (0.05 m^3/sec). Total annual precipitation for 2005 of 53.2 cm measured at Idalia, CO (CoAgMet 2008) was the highest since 1995, and above the long term mean for 1895-2005 (mean = 44.3 cm; SD = 8.8). Total annual precipitation in 2006 and 2007 (32.8 cm and 33.0 cm, respectively) was well below the long term mean, and both years ranked among the lowest 10% over the period of record. The average flow declined in 2006 to 0.02 m^3/sec, the third lowest mean annual flow over the period of record (1933-2007), and remained low in 2007 (0.04 m^3/sec). However, abundant snowfall in December 2006 (30-45 cm; NOAA 2008) contributed to relatively higher flows in the basin in spring 2007 (see basin scale connectivity, below).

Habitat connectivity

Basin scale—We quantified seasonal patterns in connectivity at the basin scale by low altitude flights 12 times from May 2005 through October 2007. Each flight surveyed approximately 110 km of the Arikaree River, and included all segments in which flow occurs. During all spring surveys, flows in the Arikaree River began 30-35 km downstream from Cope, CO (Figure 1.2). During the single survey in May 2005, flow began 35 km downstream and continued for 43 km. The channel downstream from that point was dry for 25 km to the confluence with the Pioneer Canal, which diverts flow from the North Fork Republican River into the Arikaree River. Flow resumed here and continued 7 km to the confluence of the Arikaree with the North Fork Republican River.

In May 2006, more of the river channel length was dry throughout the basin than in 2005. Flows again began about 35 km downstream of Cope, but continued only for 28 km, followed by a set of intermittent reaches along the middle segment for 6 km, and then flowing reaches for 10 km. Downstream, the river was mostly dry to the confluence with the Pioneer Canal, and then flowed 7 km to the confluence. In June 2006, the flowing reaches declined whereas intermittent and dry reaches increased. By July 2006, only one 11-km flowing reach remained, centered on the upstream segment, and no flows were present below the Pioneer Canal to the confluence during this dry period.

During March through May 2007, the Arikaree River flowed continuously from 30 km downstream of Cope for 59-63 km (Figure 1.8), below which was a 10-14-km long dry segment. Flows resumed below the Pioneer Canal as during the spring in the other two years. The number of intermittent and dry reaches increased rapidly in July, as in 2006. By September 2007, only 15 km of consecutive flowing reaches remained upstream of the confluence with the Pioneer Canal, centered on the upstream segment. By October 2007, this flowing reach had increased slightly to 17 km. The Pioneer Canal contributed flow at the downstream end of the river throughout the surveys in 2007.

Segment scale—Twenty-six segment-scale connectivity surveys were conducted in each of the three river segments during summers 2005-2007 (2005, n = 7 surveys; 2006, n = 9; 2007, n = 10) for a total of 78 connectivity surveys. For clarity of presentation, and because different numbers of surveys were conducted each year, we plotted only the final survey of each summer month across years (Figure 1.9). In 2005, flow persisted in the upstream segment throughout the summer, except for one 0.5-km reach that was intermittent in July. Flow persisted in the middle segment until the end of

June but a large portion of the segment became dry by the end of July, and another 36% was intermittent, distributed throughout the segment. Half of the downstream segment was dry by the end of June, and by the end of July 2005 the segment was completely dry.

The year 2006 was extremely dry, and this was reflected in patterns of drying across the three segments (Figure 1.9). During spring and summer 2006, the upstream segment flowed consistently until late June, after which dry and intermittent reaches increased in proportion, and by the end of July only about 10% of the segment was flowing. In the middle segment, dry reaches were present by late May (about 30% of the segment), and increased to cover about 70% of the segment by late August. The downstream segment was completely dry during all 2006 surveys.

In 2007, all segments had relatively high proportions of flowing reaches during late spring and early summer (Figure 1.9). However, by the end of the summer, connectivity patterns across segments were similar to those in 2006. The upstream segment flowed through the end of June, after which about 60% of the segment became intermittent by August, with a short (<5%) dry reach present. The middle segment flowed through the end of June 2007, after which reaches quickly dried and became intermittent, and by the end of August more than 60% of the segment was dry. The downstream segment flowed through the end of May, was 80% dry in June, and completely dry thereafter. Overall, patterns in connectivity at the segment scale reflected both the connections of the segment to the alluvial groundwater aquifer (see below for a detailed description of groundwater dynamics in the basin) and climate variability from year to year.

Groundwater and pool habitats

We censused the total amount of refuge pool habitat within each of the three

segments during late July, during the period of lowest connectivity, from 2005-2007

(Table 1.2). No pools were ever present in the downstream segment during any of the

surveys. In 2006, we censused refuge pools twice, once in late July, and once in late

August. We observed a marked decrease in the number of pools in the upstream segment

and the total volume of pool habitat in both segments over this short period. In late July

2006, there were 180 pools present in the upstream segment, but by late August 56 (30%)

had dried completely. Of the 124 pools that remained, about half (N = 57) dried to less

than 50% of their late-July volumes. Overall, the upstream segment contained more than

an order of magnitude more pool volume than the middle segment during the driest

portion of the summer 2005-2007, and the largest refuge pools had much greater volume.

Alluvial water table elevation (m) was directly related to pool depth (cm) across

six pairs of wells and pools in the upstream segment from April through October 2007.

As water table elevation declined during the summer, pool depths also declined. Spikes

in water table elevation were due to precipitation events, and were not reflected in pool

depths (Figure 1.10). We tested the correlation between mean daily groundwater table

elevation and measured pool depth for that day (n = 14 pairs for each well/pool). Pearson

correlation coefficients ranged from 0.81 to 0.99 ($P<0.05$) for all six pairs, and these

observations indicated that the dynamics of pool stage were directly related to alluvial

groundwater in the Arikaree River.

Model scenarios

    Status quo scenario—Under the status quo of current pumping rates in the

Arikaree River basin, our model predicted that 50% of the 218 pools in the upstream

segment will be dry by 2035, about 25 years in the future (Figure 1.11). Pools in the

middle and downstream segments also would be permanently dry by this time. However,

by 2045 most pools that remain are located within a 1-km reach near the downstream end

of the upstream segment and many are created by beaver dams (Figure 1.12).

    Alluvial well removal scenario—Removal of two alluvial wells upstream and one

downstream of the Fox Ranch (Figure 1.3) had no effect on increasing pool persistence in

our model (Figures 1.11 and 1.12). The trajectory of pools remaining over time was

virtually identical to that of the status quo scenario. Although removing actively

pumping alluvial wells will generally increase stream flows, the vertical separation of the

water levels in the alluvium from the bottom of the stream, coupled with the distance of

the three upstream alluvial wells from the study area, limits the effectiveness of this

scenario.

    Three mile band—Under the three mile band scenario, about 65% of pools remain

in 2035, but by the end of our modeling timeframe in 2045 only about 55% of the pools

that were in the upstream segment in 2007 remain (Figure 1.11). However, similar to the

other two scenarios, most of these remaining pools are located within only 1.7 km of the

upstream segment (Figure 1.12), and would most likely constitute the only habitat refuge

in 105 km upstream from the Pioneer Ditch. Additionally, average depth of the

remaining pools decreased 32% from 67 cm (± 1.8 SE) to 46 cm (± 2.1 SE) during the

period 2007 to 2045.

Conservation scenario—The results of our conservation water balance model indicate that at least a 75% reduction in irrigation pumping within our model domain is needed to reach equilibrium conditions (Δ Storage = 0), where the High Plains Aquifer and the alluvium water levels are no longer declining (Table 1.3). We also found that stream flow into and out of our control volume had declined due to pumping. However, compared to groundwater flow, streamflow constituted a very small proportion of the water balance. Overall, for water levels to recover and sustain more pools than found during August 2007, a reduction greater than 75% would be required for a prolonged period of years.

Trends in annual discharge

All 11 Republican River tributaries with streamflow data showed significant, negative linear trends ($P<0.001$) in discharge over time (Table 1.4). This analysis confirms that the effects of groundwater pumping and drought are not restricted to the Arikaree River basin, but are widespread across Republican River tributaries.

Discussion

We combined empirical field data on stream fish habitat with groundwater modeling scenarios to show that ecological futures are bleak for fishes in western Great Plains streams, including the Arikaree River. Frequent surveys of connectivity and persistence of refuge pools, both at the segment scale on foot and at the riverscape scale using low-altitude flights, showed that these habitats dried substantially each summer during 2000-2007, a period of recent drought (Fardal 2003; Scheurer et al. 2003; Fausch et al. 2004; Griffin 2004). The most recent flights in 2007 showed that only 15 km of

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connected stream habitat persisted through the driest period of the summer within a 105-km segment that originally flowed at least seasonally. Coupling measured pool depths in the most perennial river segment to a state-of-the-art groundwater model allowed us to forecast habitat at this summer minimum into the future, and to create a spatially explicit map of the pools remaining. Our results show that refuge habitats for fishes in the Arikaree River are not sustainable under any of the three ecological futures modeled. Under the current pumping regime, half of the pools remaining at low water in 2007 are projected to be completely dry within 25 years, and after 30 years nearly all of the remaining refuge pools for fish will be concentrated in less than 1 km of river. Moreover, at this low groundwater stage, this is likely to be the only set of connected pools remaining in the entire 105 km of the Arikaree River above the Pioneer Ditch. Likewise, even under the scenario in which wells within 4.8 km (3 miles) of a large segment of the river are retired, a similar fate will occur within 35 years.

Reducing refuge habitats for fishes by continued pumping will hasten the extirpation of rare fishes in the Arikaree River. Isolating fishes in short stream fragments and forcing them to subsist in drying pools during the summer increases the chances that random factors like a severe drought will extirpate these populations from the basin (Rieman and McIntyre 1995; Lande 1998; McElhany et al. 2000). Reduced depth and volume of pools can also lead to decreased fitness and increased mortality of fishes in these shallow habitats due to degraded water quality (e.g., high temperatures, low dissolved oxygen, freezing in winter), increased parasitism rates (Medeiros and Maltchik 1999), and increased predation from terrestrial and avian predators (Power 1987).

Once populations are extirpated, long, permanently dry segments of river currently present in the lower basin effectively prevent any chance of recolonization from adjacent basins. Connectivity is important to provide demographic support of sink populations, and recolonization after catastrophes (Neville et al. 2006). Habitat alteration and loss of connectivity are likely key factors in the extirpation of five fish species from the basin since the 1940s. For example, one extirpated species, plains minnow, produces semi-bouyant eggs that drift downstream and hatch quickly. Successful reproduction by this species requires periodic high flows and long stretches of unfragmented stream habitats (Taylor and Miller 1990; Dudley and Platania 2007). These conditions are now scarce or absent in the Arikaree River, and will continue to decline into the future.

Our analysis rests on coupling a modern groundwater model with a multi-scale analysis of fish habitat dynamics. Results of our transient groundwater model were based on several assumptions. The first was that current irrigation pumping rates within the Arikaree River basin will continue during the period we forecasted (2007-2045). Since large-scale agricultural irrigation began in Yuma County during the 1960s, the volume of groundwater used for irrigation has been relatively constant since 1975 (Figure 1.4), so we have no reason to believe that rates will differ in the future. The second assumption was that the apparent specific yield (Sya) of the regional aquifer within our model domain was 0.17. Apparent specific yield is an important model parameter defined as a unitless ratio of the volume of water released from storage (e.g., pumped) in a saturated unconfined aquifer to the change in the volume of water below the water table. Squires (2007) modeled Sya for our study area, and compared the results to empirically estimated values developed for similar systems. She found the values to be similar, so we are

confident that this value is a reasonable estimate of the true *Sya* in our study area. The third assumption was that irrigation wells within our study area do not pump at their maximum rated capacity. Through surveys of irrigators and published values, Fardal (2003) estimated that irrigation systems within our study area pump at about 60% of their rated capacity, due to declining efficiency over time and the variable cost of electricity used to power the pumps. We considered this estimate of pumping rates to be a more realistic estimate than simply applying the maximum rated capacity to each irrigation well. Moreover, if pumping rates are higher, then fish habitat would decline faster. Our final assumption, which was used for our scenario modeling, was that future pool depths would coincide with water table levels. This assumption was based on the highly significant relationships between pool depths and alluvial groundwater table levels measured during summer (2007). Strong hydrologic connectivity between alluvial aquifers and rivers is common in sand-bedded streams that are primarily groundwater-fed (Winter 2007). As long as stream reaches remain "gaining" rather than "losing", this assumption should hold. Finally, we evaluated the sensitivity of our model to two potentially influential parameters, riparian evapotranspiration rate and aquifer recharge, and found that any error in these parameter estimates would be of minor influence on our model results, within the range of possible conditions. Therefore, given that our modeling framework is based on reasonable assumptions and robust to changes in key parameters, we judge that declines in fish habitat that we project for the Arikaree River are accurate for the three scenarios modeled.

Our water balance model showed pumping would need to be reduced by at least 75% to maintain the current, depleted state of aquatic habitat in the Arikaree River basin.

Given the socioeconomic importance of agriculture in this region, this reduction is most likely an unrealistic goal. However, our technique is broadly applicable to other systems where declining groundwater levels are affecting aquatic habitats. Our two-stage modeling approach (water balance and transient groundwater models) provides useful tools to quantify, 1) the amount of pumping needed to maintain alluvial groundwater levels and fish habitats in Great Plains streams and, 2) the spatial distribution of well retirements needed to help reach a conservation threshold. Combined, these model outputs allow managers to easily ascertain the amount and location of pumping that needs to be reduced to meet conservation goals. An interdisciplinary approach such as the one we provide will continue to be critical for plains fish conservation due to declining groundwater and fish habitats across the western Great Plains (Table 1.4).

Declining alluvial groundwater levels due to irrigation pumping will have negative effects that extend beyond the aquatic ecosystem in these Great Plains basins. Riparian gallery forests are a critical component of stream-riparian ecosystems in the Great Plains, providing stable stream banks, cooler stream temperatures from shading, and habitat for many terrestrial species (Rood et al. 2003). Phreatophytes (e.g., riparian trees and grasses) that depend on shallow alluvial groundwater for growth and persistence are the most vulnerable vegetation elements to reduced groundwater levels (Rood and Mahoney 1990; Friedman et al. 1998), and complete collapses of riparian gallery forests due to stream dewatering have occurred in the West (Rood and Mahoney 1995). Reductions in riparian canopy can lead to increased stream temperatures, causing negative effects on fishes and other aquatic organisms (e.g., high water temperatures and low dissolved oxygen; Whitledge et al. 2006). More broadly, valuable economic and

cultural human activities that depend on riparian habitats (e.g., recreation, livestock grazing) will also be degraded by the collapse of riparian gallery forests. Overall, declining alluvial groundwater levels will have far-reaching, negative effects across both terrestrial and aquatic ecosystems in the Arikaree River basin.

What can be done to decrease the decline of groundwater levels in the Arikaree Basin, and conserve fishes and their habitats into the future? Our water balance suggested pumping within our study area would need to be reduced by at least 75% to maintain alluvial groundwater levels and fish habitats, and even more reduction would be required to reverse the downward trend of groundwater stage over time. Two possible solutions are, 1) reducing water use by changing from crops with high water requirements (e.g., irrigated corn and alfalfa) to those that require less water (e.g., dryland corn or winter wheat), or increasing irrigation efficiencies, and, 2) increasing water availability through artificial aquifer recharge or trans-basin diversions. However, changing crops may prove to be difficult to implement because of the current increase in farm revenues generated from growing corn for biofuel (see below). Likewise, although artificial aquifer recharge or trans-basin water diversion would supplement river flows, it would involve risk. Concerns related to trans-basin water transfer include facilitating introduction of non-native species, alteration of hydrologic regimes in both basins, and habitat alteration (Davies et al. 1992; Meador 1992). By any measure, conserving fish diversity and habitats that currently exist in the Arikaree should be a top priority.

Habitat loss and fragmentation due to declining groundwater levels may be influenced by two factors we did not explicitly incorporate into our model scenarios. The first is the increasing demand for, and profitability of, corn for biofuels (Hill et al. 2006;

Tilman et al. 2006). Although no new well permits have been allowed in Yuma County

since the 1970s, it is possible that fields with old wells that have been set aside for

conservation or converted to dryland agriculture could be brought back online, increasing

irrigated area and groundwater use in the basin. More irrigation pumping within the

Arikaree River basin can only exacerbate the decline in groundwater and fish habitats

that our models predict. Secondly, in general the western Great Plains ecoregion is

predicted to become warmer and drier in the future due to global climate change.

Specifically, recent climate models for northeast Colorado predict more extreme weather

events (e.g., droughts), increased average temperatures in winter and spring, and

decreased overall precipitation (Joyce et al. 2001; Ojima and Lackett 2002). These

changes are predicted to result in increased irrigation water demand, higher rates of

evapotranspiration, and intensified competition for water resources. Although we

detected no changes in precipitation patterns over the past 100 years in the Arikaree River

basin, climate change may be driving the current major drought. Regardless, climate

change can only add variability to groundwater and fish habitat declines, and hence drive

fishes to extinction sooner than our projections.

Conclusion

Our analysis shows that declines in streamflow due to groundwater pumping are

not restricted to the Arikaree River, but are in fact widespread across the western Great

Plains. A significant negative trend in mean annual streamflow over time is present in all

11 Republican River headwaters for which data were available in eastern Colorado,

western Nebraska, and western Kansas, including the Arikaree River (Table 1.4).

Extirpation and population declines of stream fish species are widespread across this

region (Fausch and Bestgen 1997; Haslouer et al. 2005; Hubert and Gordon 2007), and our results indicate that with continued over-use of groundwater resources we can expect further losses of stream fish habitats. This will lead to declining and more fragmented populations, and local extinctions similar to those we found in the Arikaree River. Ultimately, species inhabiting these primarily east-west drainages will shrink eastward and decline in range and abundance (cf. Matthews and Zimmerman 1990), becoming more imperiled as groundwater declines and climate change continue. Managers across the Great Plains will be challenged to address these issues, and should consider what options are available to conserve native plains fishes in these basins.

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Tables

Table 1.1. Model parameters for regional High Plains and alluvial aquifers within the lower Arikaree River basin, Colorado. Recharge values are 15% and 25% of precipitation for the High Plains and alluvial aquifers, respectively.

Model parameter	Units	High Plains aquifer	Alluvial aquifer
Hydraulic conductivity	m/d	152.0	9.1
Recharge	cm/yr	6.3	10.5
Apparent specific yield (Sya)	unitless	0.17	0.125

Table 1.2. Number and volume (m^3) of refuge pools censused along two 6.4-km

segments of the Arikaree River, CO during summer 2005-2007.

| Survey | Segment | N | Pool volume (m^3) | | |
			Total	Mean (SE)	Range
July 2005	US	172	6095	20.5 (3.4)	1-433
	MS	35	556	15.9 (3.1)	2-68
July 2006	US	180	4235	23.5 (3.1)	1-253
	MS	27	321	11.9 (4.9)	1-51
August 2006	US	124	2809	15.6 (2.8)	1-207
	MS	27	197	7.3 (3.1)	1-32
July 2007	US	218	7532	34.7 (9.4)	1-502
	MS	31	321	17.9 (3.3)	2-91

Table 1.3. Results of three water balance model scenarios for the lower portion of the Arikaree River basin, CO (see Figure 1.2). Inputs from surface flow (SF_{in}), groundwater flow (Q_{in}), and aquifer recharge (R), and outputs from riparian evapotranspiration (ET), surface flow (SF_{out}), groundwater flow (Q_{out}), and irrigation pumping (Q_w) are shown. All units are volumes in ha-m/yr x 10^3. The change in storage (Δ Storage) represents the difference in groundwater volume within the model per year. Pre-development conditions were before irrigation pumping began (pre-1965), whereas post-development conditions describe the period after pumping began (1965-2007). Under the conservation model scenario, irrigation pumping must be reduced by 75% to reach equilibrium (Δ Storage = 0).

Water balance model	Inputs			Outputs				Δ Storage
	Q_{in}	SF_{in}	R	ET	Q_w	Q_{out}	SF_{out}	
Pre-development	2.39	0.23	5.32	3.02	0	2.60	2.32	0
Post-development	2.39	0.11	5.32	3.02	8.02	2.60	1.1	-6.92
Conservation	2.39	0.03	5.32	3.02	2.02	2.39	0.31	0

Table 1.4. Trends in mean annual discharge (m³/sec) over time (year) for 11 Republican River tributaries in Colorado, Nebraska, and Kansas. Slope of the linear regression of year vs. mean annual discharge, number of years in the analysis, range of years with flow records, and the USGS gauge number are shown. All slopes were significantly less than zero ($P<0.001$).

Stream	Slope	Number of years	Range of years	Gauge number
Rock Creek, NE	-0.128	67	1941-2007	6824000
Buffalo Creek, NE	-0.110	67	1941-2007	6823500
South Fork Republican River, NE	-1.475	70	1938-2007	6827500
Frenchman Creek, NE	-2.025	57	1951-2007	6835500
Driftwood Creek, NE	-0.342	61	1947-2007	6836500
Red Willow Creek, NE	-0.338	46	1962-2007	6838000
Sappa Creek, KS	-3.119	61	1947-2007	6845110
North Fork Republican River, CO	-0.464	71	1936-2007	6823000
Arikaree River, NE	-0.780	75	1933-2007	6821500
Beaver Creek, KS	-1.139	61	1947-2007	6846500
Prairie Dog Creek, KS	-1.858	64	1930-2007	6848500

Figures

Conservation

Extinction

Time

(Groundwater level or amount of fish habitat)

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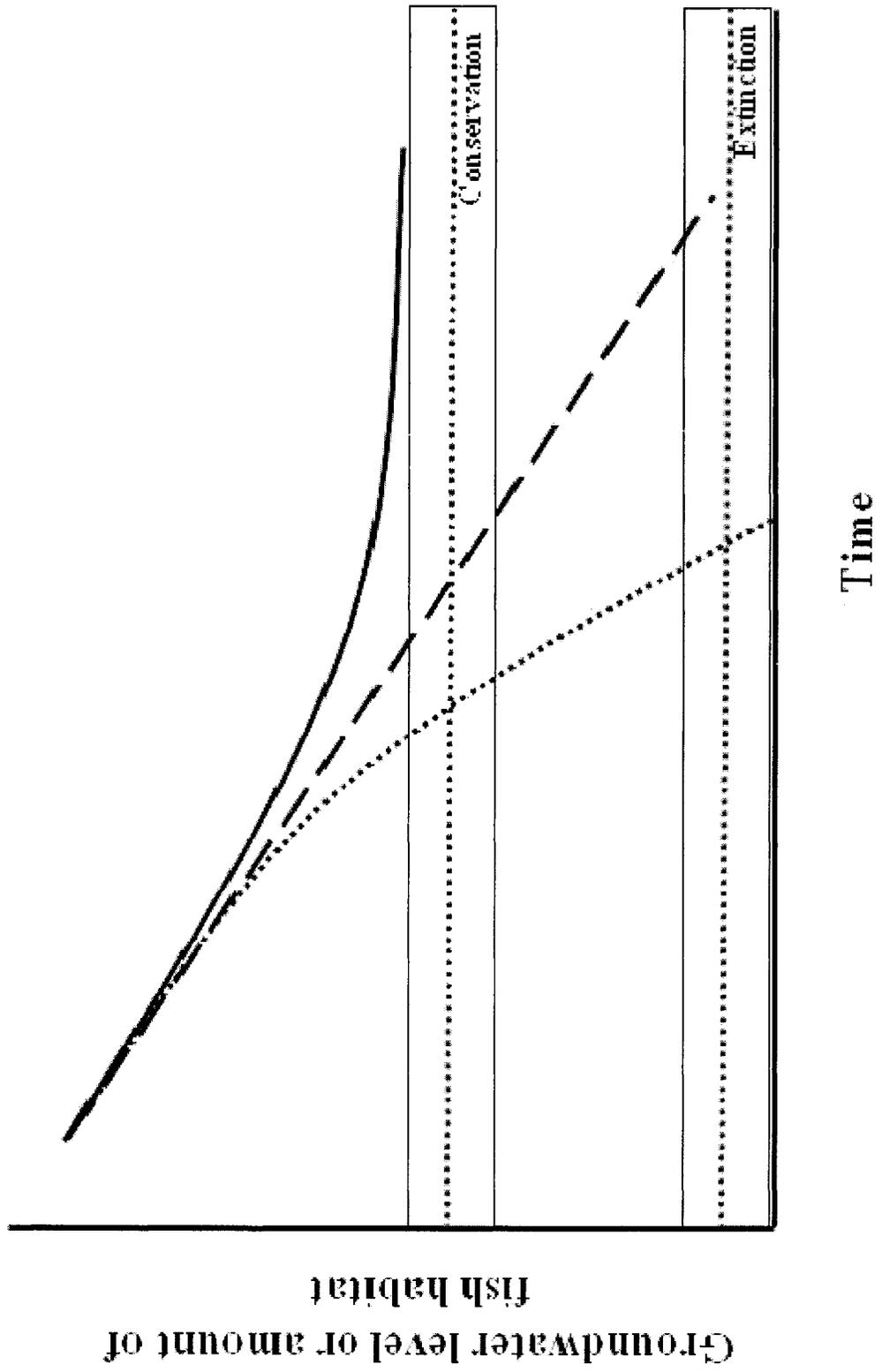
Figure 1.1. Expected ecological futures (i.e., changes through time in alluvial groundwater table level and stream fish habitat) in a groundwater dependent Great Plains river. We predict that under current pumping regimes, fish habitat is not sustainable. However, the rate of decline (e.g., dashed line or dotted curve) is unknown. When groundwater level drops below the river bed elevation, fish habitats will dry completely, represented by the extinction threshold. The light bar indicates variability attributable to climate fluctuations and fish population dynamics around this threshold. Our goal is to suggest a scenario under which fish habitats can persist over time indefinitely (solid line), above a conservation threshold (dark bar).

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A) High Plains Aquifer
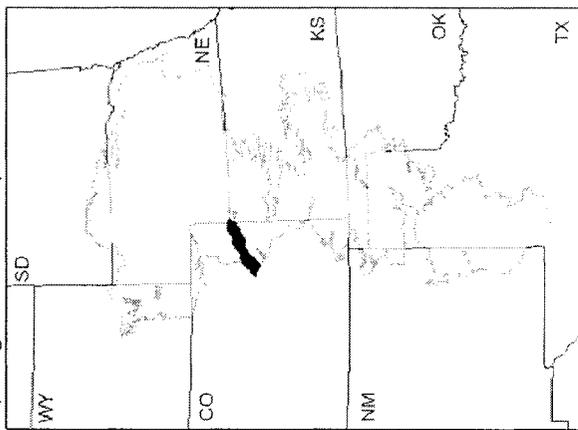
B) Arikaree River Basin

103° W

40° N

0   20   40   80
Km
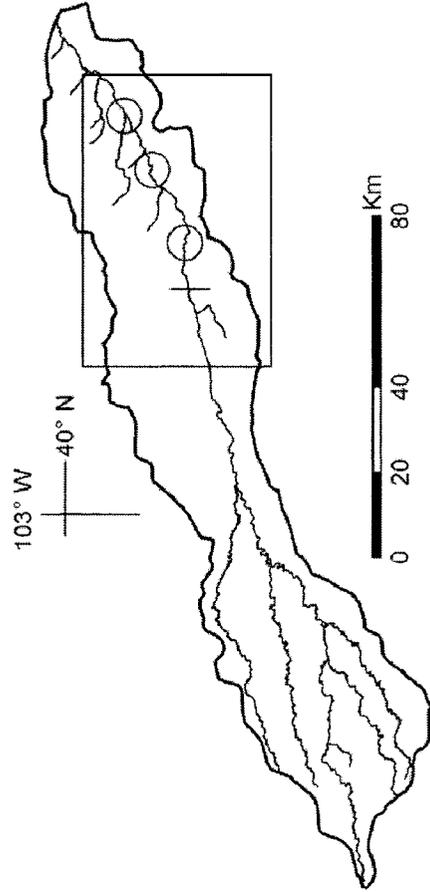
C) Modeled area
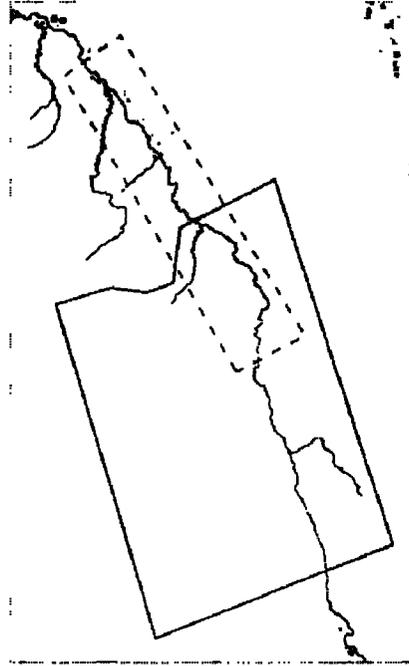
Surficial geology

☐ Dune Sand

☐ Peorian Loess

☐ Ogallala Formation

■ Alluvium

55
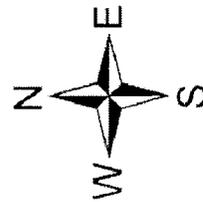
Figure 1.2. Map of our study area illustrating the location of the Arikaree River basin in eastern Colorado (inset) on the western edge of the High Plains Aquifer (shaded area). At the river basin scale, fish habitat and groundwater level data were collected along three 6.4-km segments (circled; US = upstream segment, MS = middle segment, DS = downstream segment). Solid stream reaches flow seasonally, whereas dashed reaches are dry. The locations of the town of Cope, Colorado, and tributaries to the Arikaree River (Black Wolf Creek and Pioneer Ditch) are labeled. The black box outlines the area within which our groundwater model domain is located (see Figure 1.3).
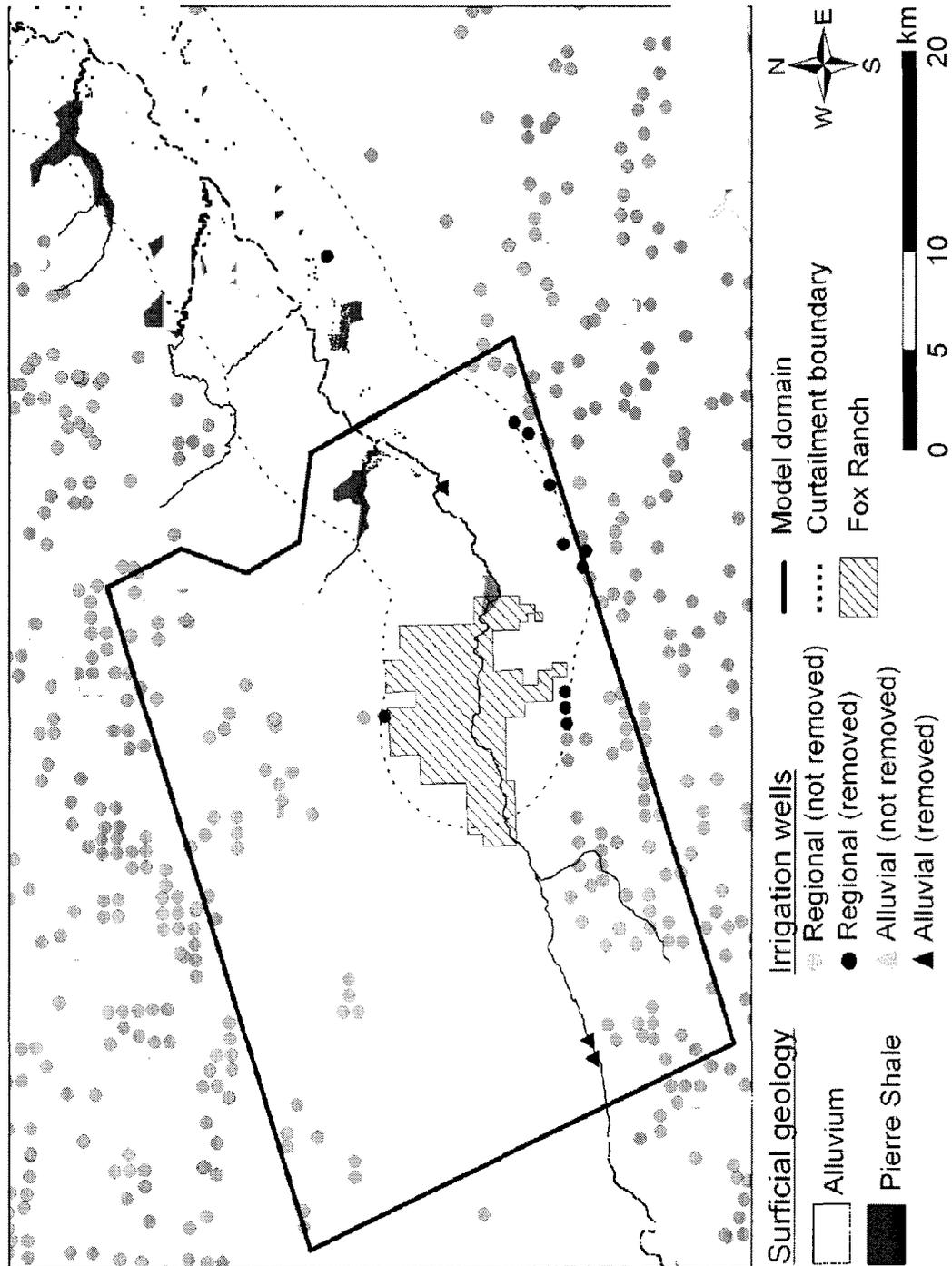
Figure 1.3. Map of the lower Arikaree River basin (outlined in Figure 1.2), showing the domain of our MODFLOW groundwater model (polygon). The model domain extends from the groundwater divides with the South Fork Republican River (shown at lower right) to the south, and the North Fork Republican River to the north. Also shown are major surficial geologic units (see legend; Weist 1964), the Fox Ranch, and locations of irrigation wells within the study area (CDSS 2007). The alluvium upstream from the Fox Ranch is narrow and not shown. Grey circles are wells pumping from the regional aquifer that were not removed in our model scenarios (see text), whereas black circles are wells that fell within the curtailment zone (dashed area) and were removed. Grey triangles are alluvial irrigation wells that were not removed in our model scenarios, whereas black triangles are alluvial wells that fell within the curtailment zone and were removed.
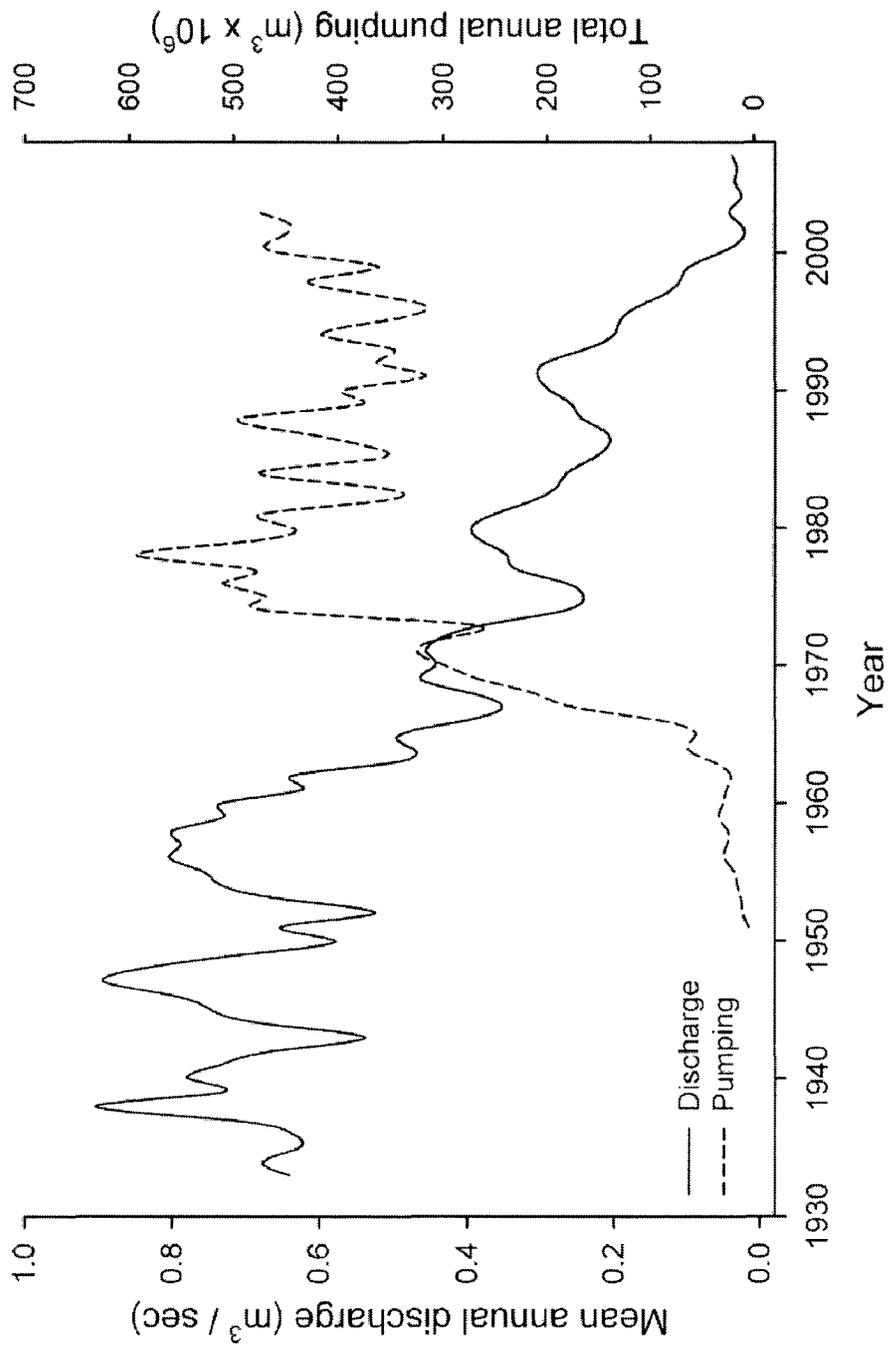
Figure 1.4. Five year running means of annual discharge for the Arikaree River in eastern Colorado from 1932-2005 (left y-axis; solid line; USGS gauge #6821500, Haigler, NE) and the estimated amount of groundwater pumped for irrigation in Yuma County, Colorado from 1950-2005 (right y-axis; dashed line; Davis and Richrath 2005). The Arikaree River and its associated aquifers are located in the southern half of Yuma County, Colorado.

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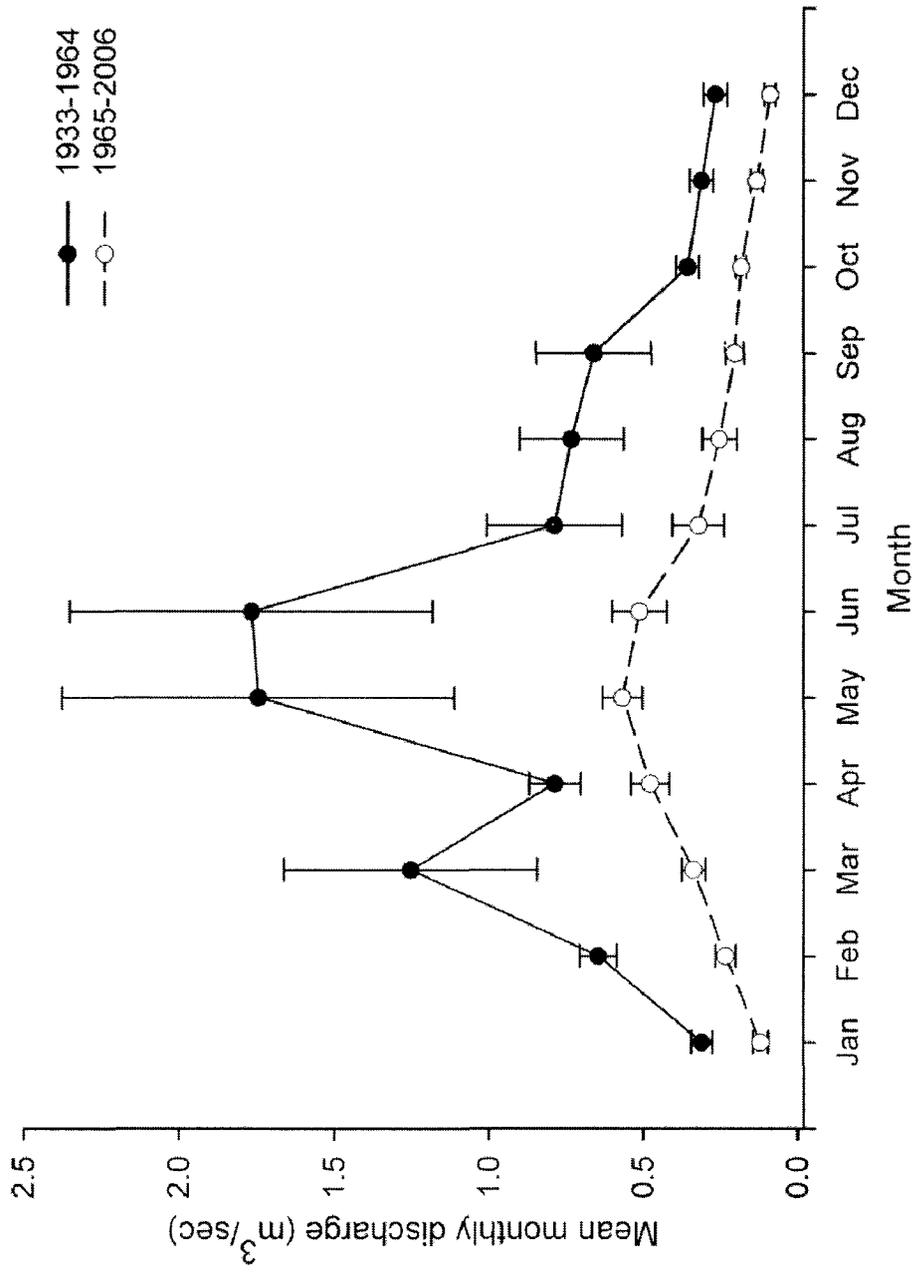
Figure 1.5. Mean monthly discharge ($\pm$ 1 SE) for the Arikaree River in eastern Colorado from 1933-1964 (solid line) and 1965-2006 (broken line) measured near its confluence at Haigler, NE (USGS gauge #6821500).
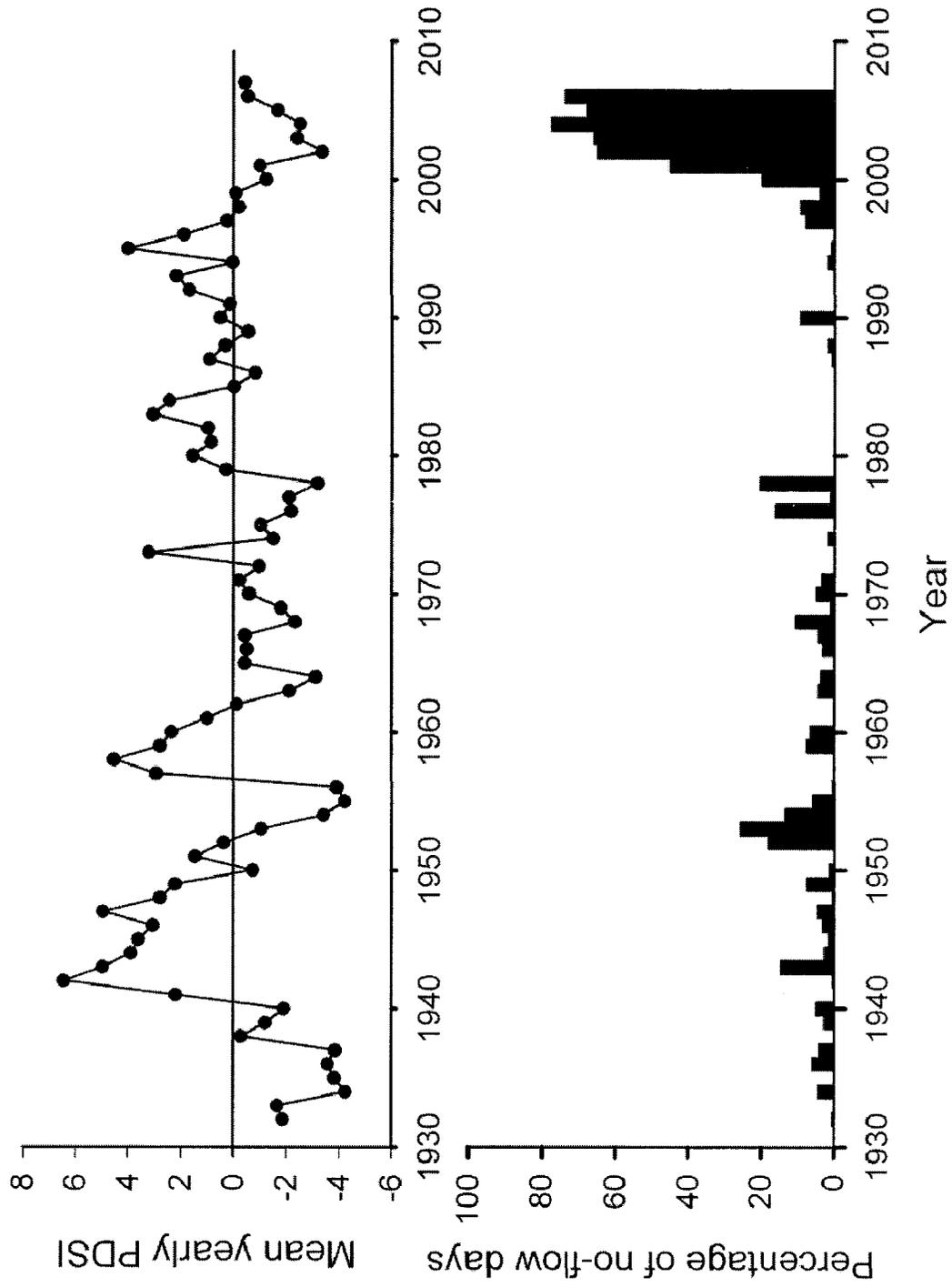
Figure 1.6. Relationship between drought and river flows for the Arikaree River in eastern Colorado from 1931 to 2007. Top panel is the mean Palmer drought severity index (PDSI; Palmer 1965) over time (NOAA 2007). The PDSI incorporates air temperature, precipitation, and soil moisture. More negative values indicate harsher drought conditions. Lower panel is the percentage of days in a year the Arikaree River had no flow near its confluence at Haigler, NE (USGS gauge #6821500). No-flow days were defined as days where flow was below the detection limit of 0.028 m^3/sec.

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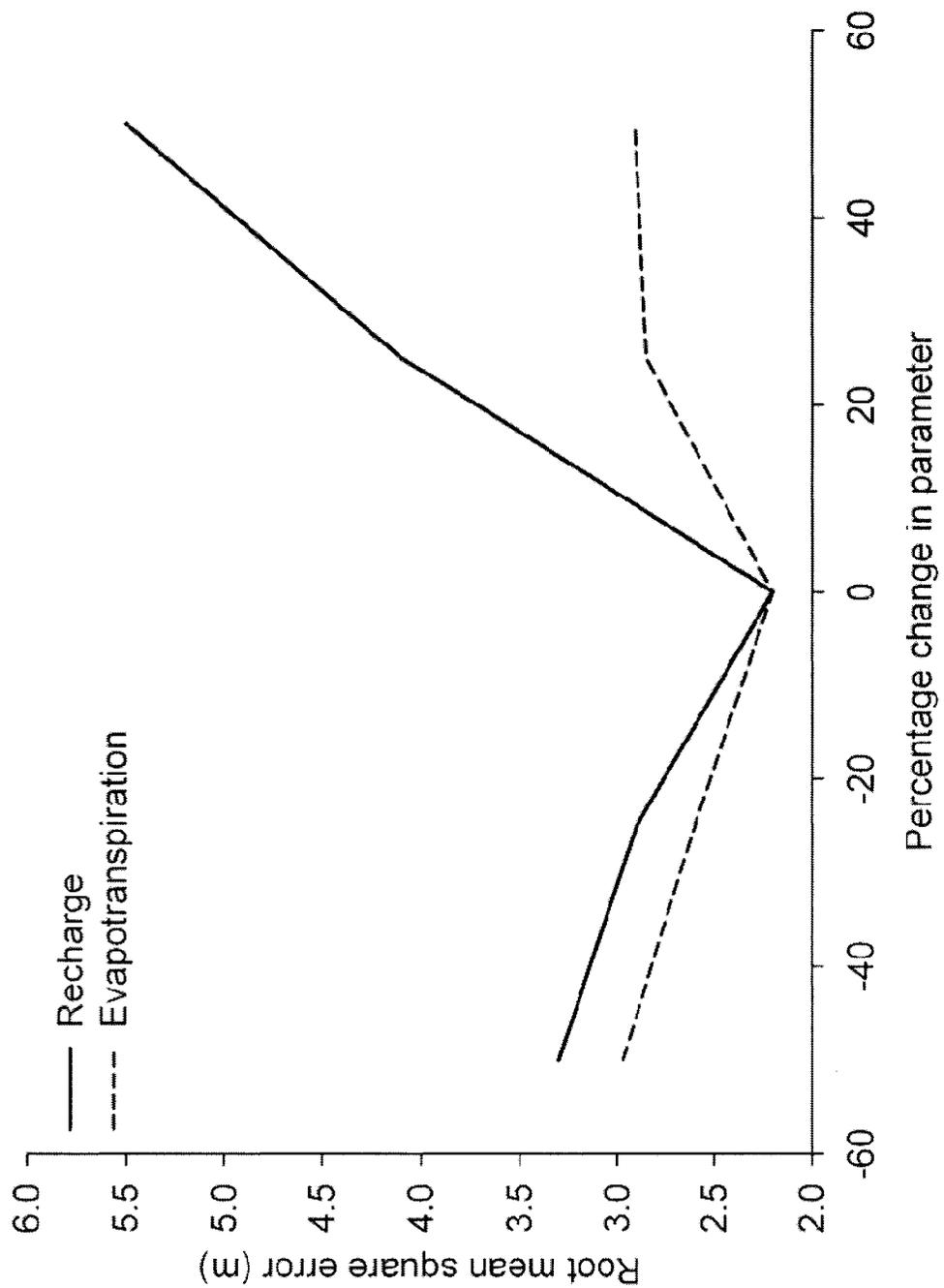
Figure 1.7. Sensitivity of the MODFLOW groundwater model to changes in two key parameters, recharge and evapotranspiration. The root mean square error (RMSE; y-axis) for the groundwater table level (m) is plotted as a function of the percentage change in the parameter (x-axis).

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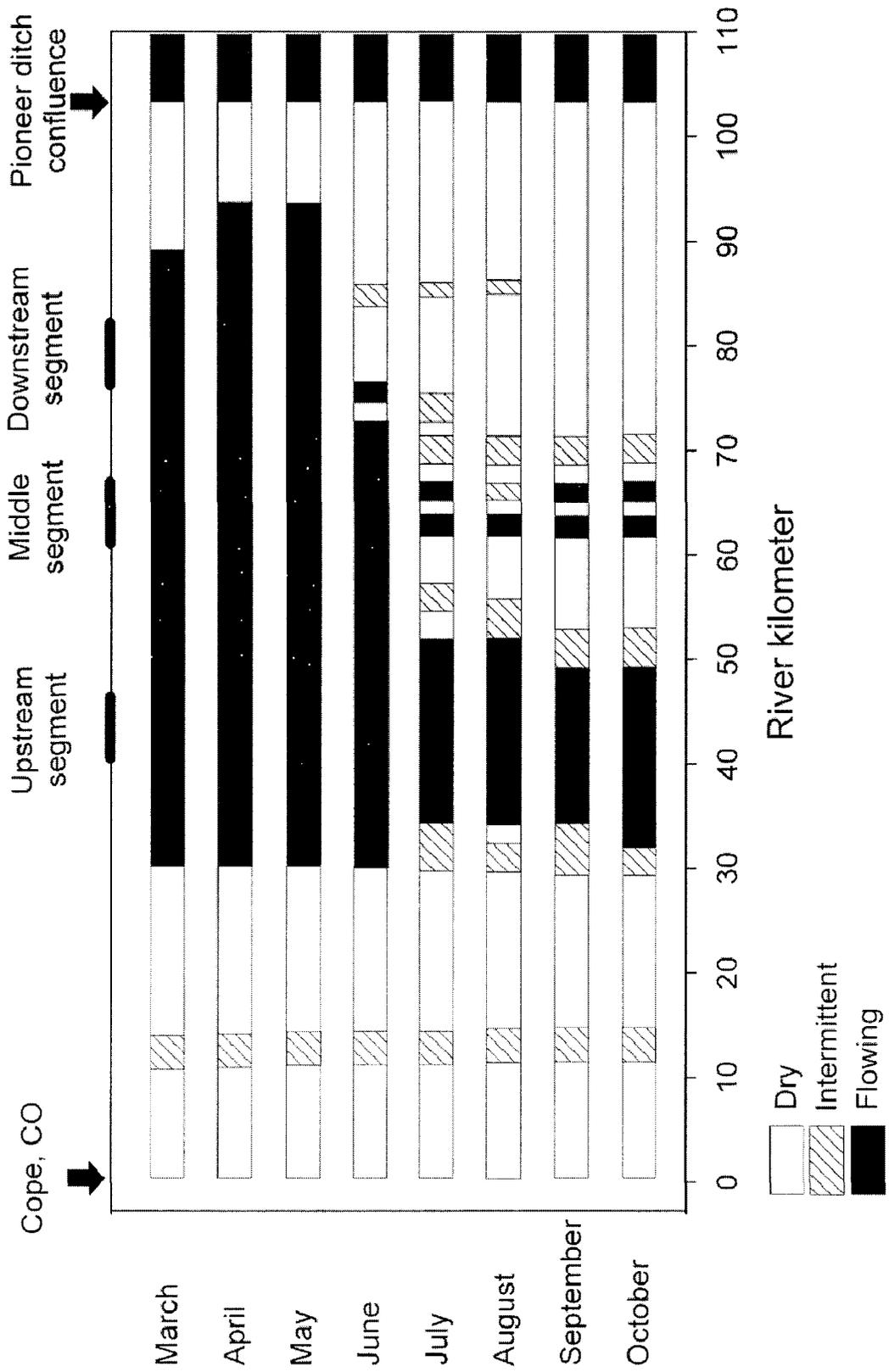
Figure 1.8. Among-habitat connectivity measured at the basin scale from low-altitude flights over the Arikaree River, CO during

2007. Survey month is on the y-axis, and river kilometer is on the bottom x-axis (flow is from left to right). Black bars represent

flowing reaches, hatched bars are intermittent reaches, and open bars are dry reaches. The position of Cope, CO, the Pioneer

diversion canal, and three 6.4-km study segments are indicated along the top x-axis.

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Upstream segment

		Flowing / Intermittent / Dry
2005	May	
	June	
	July	
	August	
2006	May	
	June	
	July	
	August	
2007	May	
	June	
	July	
	August	

Middle segment

2005	May
	June
	July
	August
2006	May
	June
	July
	August
2007	May
	June
	July
	August

Downstream segment

2005	May
	June
	July
	August
2006	May
	June
	July
	August
2007	May
	June
	July
	August

Segment connectivity (%)

■ Flowing
Intermittent
Dry
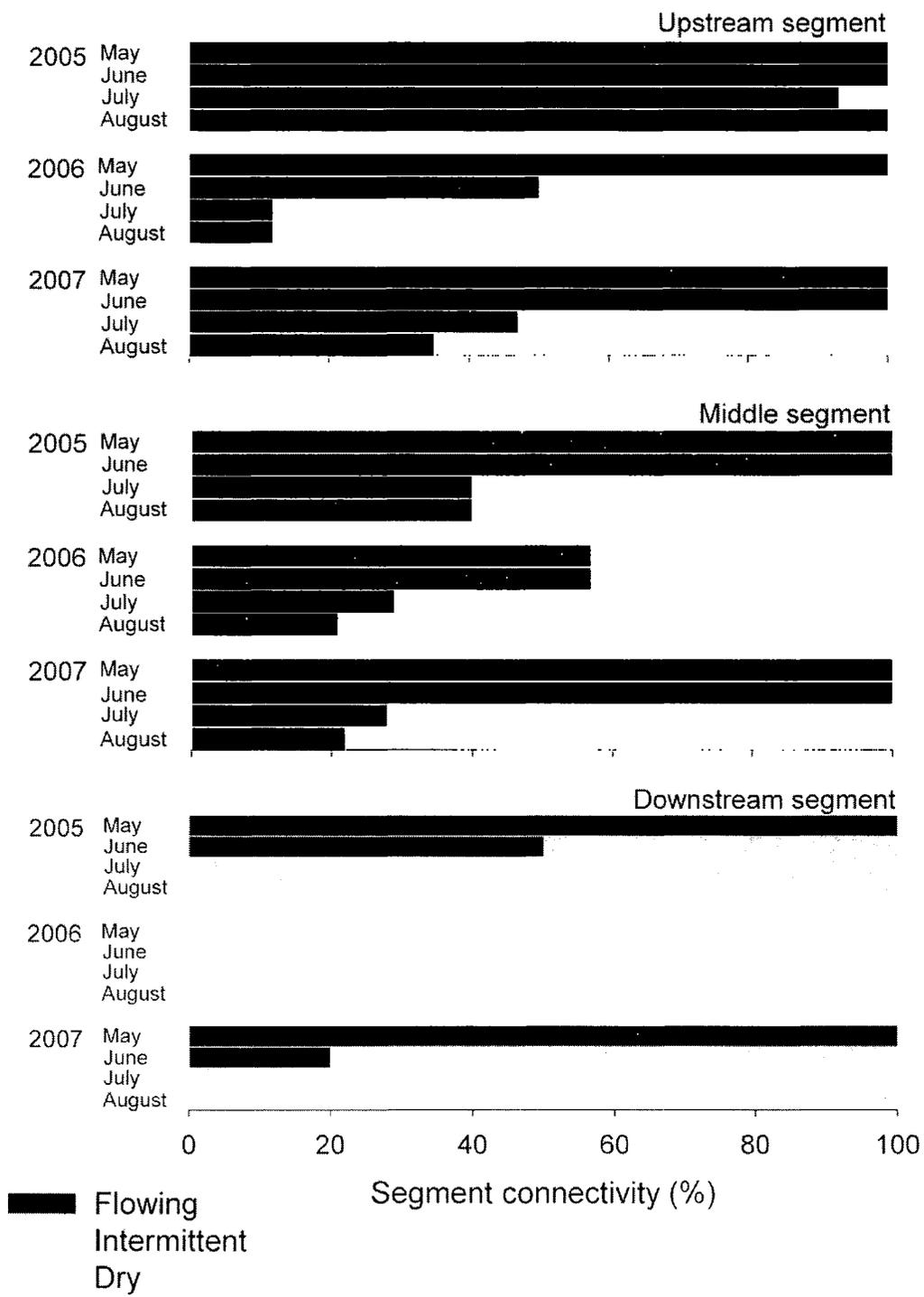
Figure 1.9. Among-habitat connectivity measured at the segment scale from foot surveys during summer months from 2005-2007 along three 6.4-km segments of the Arikaree River, CO. Survey month and year are on the y-axis, and the percent of the segment in each connectivity class (flowing, intermittent, and dry) is on the x-axis.

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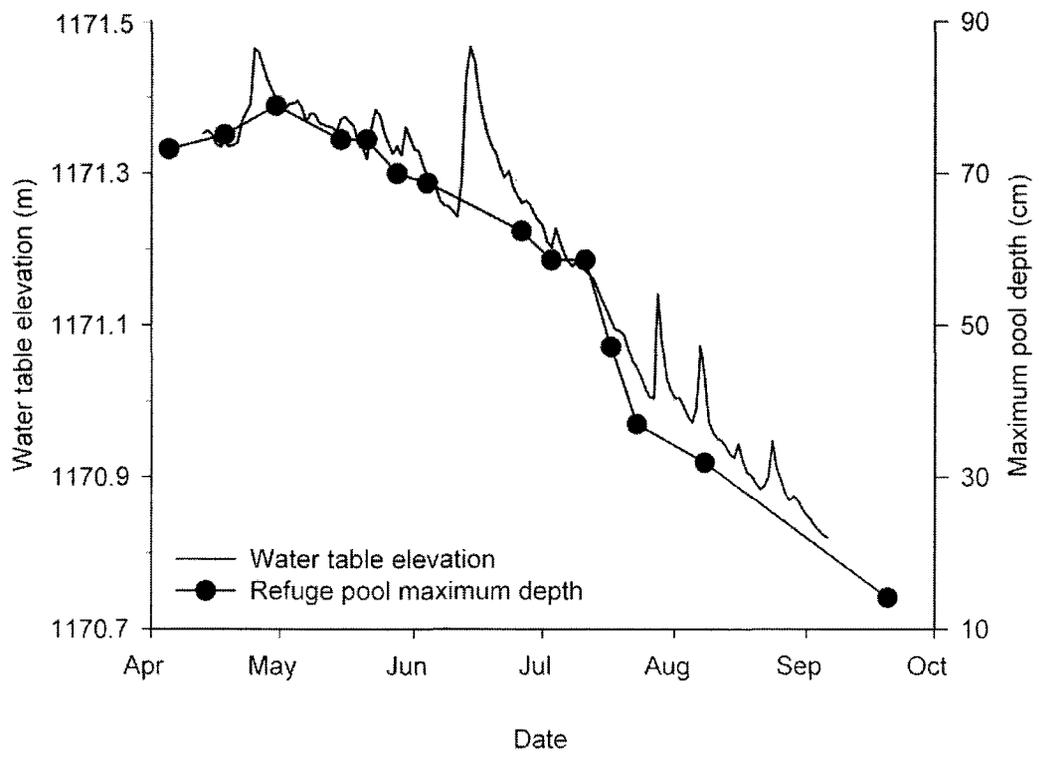
Figure 1.10. Relationship between alluvial groundwater table level (meters above sea level; right y-axis) and maximum pool depth (cm; left y-axis) for a typical pool of the six pools monitored in the upstream segment from April through late September 2007. Groundwater stage was measured hourly from a groundwater monitoring well, and pool depth weekly from a fixed stage gauge located in a nearby stream pool.
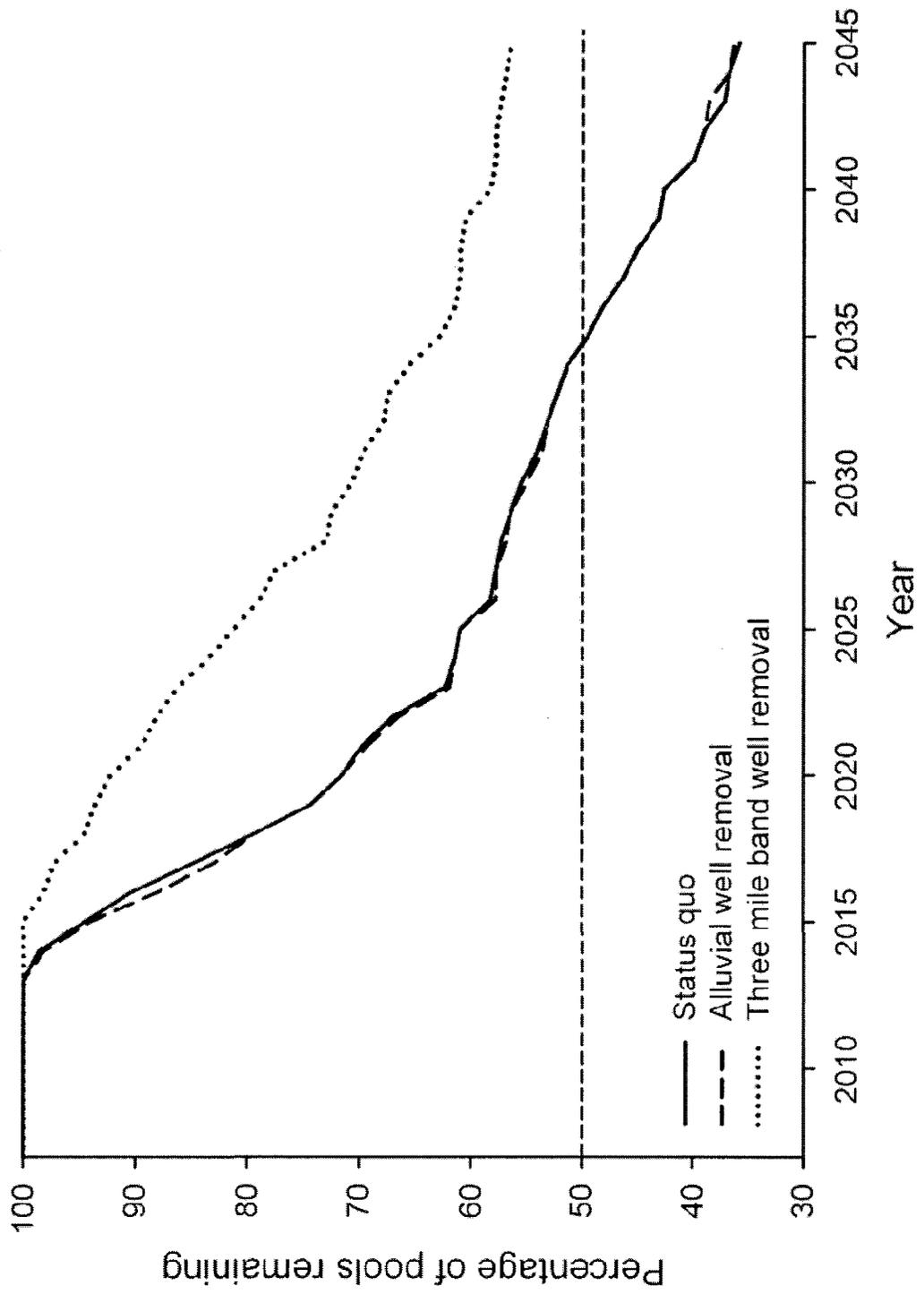
Figure 1.11. The percentage of refuge pools remaining over time under three scenarios of groundwater pumping for irrigation along a 6.4-km segment of the Arikaree River, CO. The status quo scenario (solid line) represents continued current (2007) irrigation pumping rates. Under the alluvial well removal scenario (dashed line), irrigation wells pumping from the alluvial aquifer are removed. The dotted line represents a scenario where wells within a specific three mile band of the river are taken out of service (see text and Figure 1.3).

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Baseline (2007)

Status quo (2045)

Alluvial well removal (2045)

Three mile band well removal (2045)

0   0.5   1   2
Km

N
W E
S

75
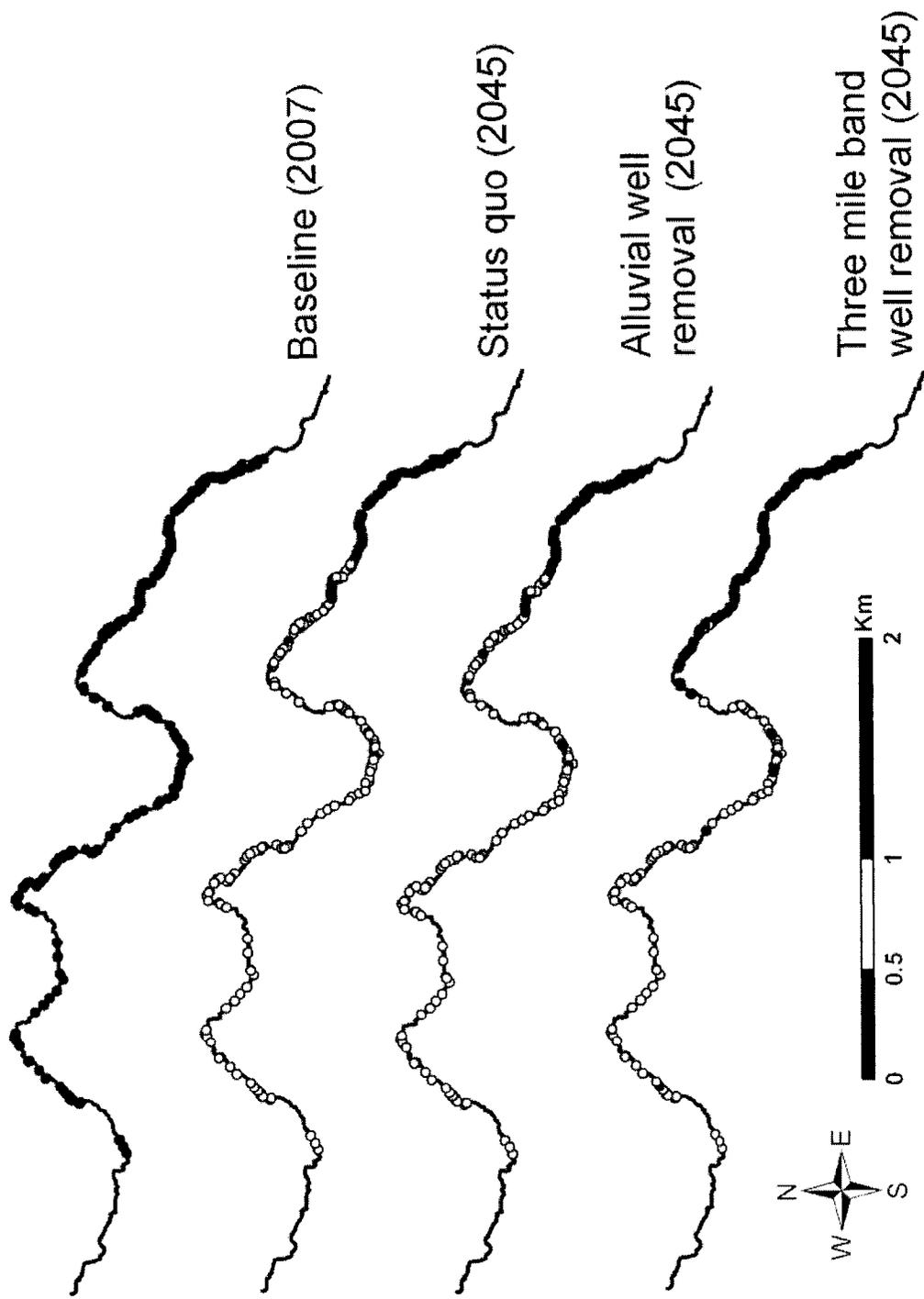
Figure 1.12. Projected persistence of refuge pools in August 2045 under three scenarios of irrigation pumping along a 6.4-km segment (our upstream segment; Figure 1.2) of the Arikaree River, CO, compared to baseline conditions in August 2007. Solid circles represent extant pools, and open circles dry pools. See text for description of the three scenarios modeled.

Chapter 2: From Metapopulations to Metacommunities: Linking Theory with Empirical Observations of the Spatial Population Dynamics of Stream Fishes

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, I 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, I suggest that stream fish ecologists should incorporate space into models, and recognize that metapopulation types may change across scales. Second, I considered metacommunity theory, which addresses how tradeoffs 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 I used data from my research in a Great Plains stream to test the utility of these paradigms. I 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, I 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 multi-species 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 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 (Schlosser and Angermeier 1995; Rieman and McIntyre 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 and 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 non-salmonid 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 (Liebold 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, 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.

My objectives in this chapter are to review and synthesize what is known about stream fish metapopulations and metacommunities, and provide a simple test of metacommunity models using empirical data for Great Plains stream fishes in the western

U.S. Specifically, I 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, I 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, I used data from my own research to evaluate how dispersal opportunity and habitat heterogeneity affect community structure across scales in a Great Plains stream fish metacommunity. I also evaluated what metacommunity model best fits these data.

Metapopulation dynamics in stream fish populations

Methods

I reviewed the literature on stream fish ecology to evaluate empirical evidence for metapopulation dynamics. I included only primary research papers that dealt with lotic fishes and included the term "metapopulation" or "source-sink" in the title, abstract, or keywords. I used the Web of Science © database as the primary method of identifying these papers. My 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 Hanksi and Simberloff (1997). Spatially

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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 GIS landscape models. In these models, migration depends on distance but is usually restricted to adjacent patches. The final model type, spatially realistic models, are 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 outlying patches (e.g., patch size, patch quality). The most well known is the incidence function model (Hanksi 1994).

In addition to the type of metapopulation model used in each study, I 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 2.1).

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 sub-populations had independent dynamics (Hanski and Simberloff 1997; Gotelli 2001). 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 2.1B; 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 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 is relaxed. In fact, high dispersal among habitat patches and vastly different types of habitats characterize the patchy population model (Figure 2.1A), 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

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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 2.1C; 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, increase the rate of extinction among subpopulations, few of which are recolonized (Figure 2.1D; 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 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. Finally, if there is a core area that contains different critical habitats with high

dispersal among them, 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

I 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 2.1). All papers were published since 1995 and the majority (n = 20) were published after 2000. In contrast, a search for the term "metapopulation" alone in the Web of Science © database returned >3000 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 (n = 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. I considered these papers to be strictly observational. 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, OK, and found that

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colonization 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 (non-spatial) 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 recommended 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 the papers I reviewed (Table 2.1). 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, non-equilibrium 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 my 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) present 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 my 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 < 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, I 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, 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 2.2).

Patch dynamics—The patch dynamics model builds on the equilibrium theory of island biogeography (MacArthur and Wilson 1967; Figure 2.2A). This paradigm predicts that regional co-existence is maintained by a tradeoff between competitive and dispersal ability among members of the community (Hutchinson 1951; Hastings 1980; Tilman 1994). For co-existence 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

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(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 habitats, and that community structure may change along environmental gradients (Whittaker 1972; Liebold 1998; Figure 2.2B). This model allows for dispersal by member species but occurrence is determined mainly by local abiotic conditions (e.g., habitat configuration) 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 2.2C). 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 so that, on average, 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 2.2D). 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 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 (Liebold 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 I 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 I support.

The only paper I 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 were 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, I 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 I 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

My 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, NE (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 others 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 (*Chapter 1*). 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. My 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. I 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 I expect that if the species-sorting model was most applicable to the Arikaree metacommunity, that 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, I would conclude that the mass effects model may be more appropriate. If neither environmental or spatial factors explain significant variation, I 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, I 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, I predicted that the Arikaree River fish metacommunity would conform most closely to the mass effects model.

Data collection

My data collection focused on evaluating both local scale habitat characteristics and regional dispersal opportunity for Arikaree River fishes. I 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 two 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. I 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 two weeks after the census), I 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 I 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, 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 °C) was recorded with a digital

thermometer (Cooper-Atkins Corp., 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, I evaluated spatial factors that may explain variation in the Arikaree River fish assemblage. At the same time as habitat sampling each year, I measured among-habitat connectivity as the length of flowing, intermittent, and dry reaches along each 6.4-km segment. I georeferenced the start and end of each connectivity class (flowing, intermittent, dry) and created a GIS line layer with reaches classified by connectivity. I also divided each of the two segments into relatively homogeneous reaches based on geomorphology and patterns of drying. Geomorphology and drying were evaluated using USGS topographic maps and maps of monthly within-segment habitat connectivity collected from 2000-2007 (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, I 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.

I sampled fishes from the pools that were previously surveyed for detailed habitat measurements within two 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

I 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 me to test for the effects of one set of explanatory variables while holding the other set constant. Consequently, I was able to evaluate the relative influence of spatial versus environmental factors on variation in fish assemblage structure.

I began my statistical analyses by calculating separate CCAs to determine which environmental and spatial variables in each set best explained variation in the fish assemblage data. I tested all variables for multicollinearity using pair-wise 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 my 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.

I tested 11 pool habitat variables using CCA for inclusion into my 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 my field data, so I

calculated the percent of the pool that was composed of sand substrate (SAND). I

adjusted pool temperature measurements taken at different times of day by calculating

residuals from a regression of pool ambient surface temperature (°C) versus time of day

(e.g., 1240 h). 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 I 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, I 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). I also included

the longitudinal position of the pool along the riverscape (LONG) and the distance to the

nearest pool (DISTBW). My final spatial variable indicated the amount of flowing water

habitat surrounding a focal pool at three different spatial scales. From my connectivity

maps and georeferenced pool locations, I 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.

I 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∩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 my Arikaree River fish metacommunity to one of the four MC paradigms, I 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 2.2), 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 more sandy 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 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 2.3a and 2.3b). For example, white sucker and

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creek chub were associated with large, deep pools with low conductivity, whereas green

sunfish and black bullhead were associated with turbid, silty pools (Figure 2.3a; 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, central stoneroller, and creek chub were associated with

wet reaches (high 1000M), whereas white sucker was associated with pools located close

together (low DISTBW) and pools that were not isolated (Figure 2.3b). Fathead minnow

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). 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∩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 variance components were

significant I 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, I conclude that mass effects most likely dominate metacommunity dynamics in this system.

I found that regional-scale spatial factors (e.g., distances among habitats, longitudinal position, habitat isolation) were important in structuring stream fish assemblages in pools along the Arikaree River. My 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. My 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 use of spawning habitats in Idaho, spatial factors such as habitat size and connection to other habitats were more important than habitat 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 2.1c). Within "source" areas, all habitats (spawning, rearing, 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 non-refuge) or that the metapopulation was considered at too fine a spatial scale. In my 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 I build the case for accepting a hybrid metapopulation model for a Great Plains stream fish with which I am 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 TL (*Chapter 4*). 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 my key (see *Distinguishing among metapopulation types* above), I 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 non-equilibrium 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 more harsh 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, 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 may be aggregated in reaches with high groundwater connectivity (J. Falke, *unpublished data*). 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 2.1C). 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. Sub-populations 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 2.1). 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. 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 non-equilibrium 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 Liebold 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. Much of the variation in stream availability results from seasonal flow variability, and any model of stream fish metacommunity dynamics should explicitly incorporate flow.

I 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 2.4), and illustrate this concept using my Great Plains fish assemblage. In spring, species-sorting metacommunity dynamics may dominate, because individual species show strong preferences for specific spawning habitats. 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 ability to disperse quickly from spawning to refuge habitats is critical. Therefore, I 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 probably 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. I suggest that metacommunity theory 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, I predict that this emerging body of research could be valuable not only for basic research in stream fish ecology, but also multi-species conservation and management.

Acknowledgements

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Tables

Table 2.1. 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), non-equilibrium (NE), or not defined (ND).

Reference	Title	Keywords	Abstract	Species	Model type	Metapopulation structure
Chaumot et al. (2006)	N	N	Y	*Cottus gobio*	SRM	NE
Cooper and Mangel (1998)	Y	N/A	Y	*Oncorhynchus kisutch*	SEM	SS
Crozier and Zabel (2006)	N	N	Y	*Oncorhynchus tshawytscha*	SEM	NE
Dunham and Rieman (1999)	Y	Y	Y	*Salvelinus confluentus*	SEM	Range[1]
Dunham et al. (2002)	N	N/A	Y	*Salvelinus confluentus, Oncorhynchus clarkii henshawi*	SEM	ND
Fagan (2002)	Y	N	Y	*Oncorhynchus gilae*	SIM	ND
Fagan et al. (2005)	N	Y	N	Sonoran Desert fishes (21 spp.)	SIM	ND
Gagen et al. (1998)	Y	N	N	*Noturus lachneri*	OBS	SS
Garant et al. (2000)	N	Y	Y	*Salmo salar*	OBS	NE
Gilliam and Fraser (2001)	N	N	Y	*Rivulus hartii*	OBS	SS
Gotelli and Taylor (1999)	Y	Y	Y	Cimarron River fishes (36 spp.)	SIM	CL
Hilderbrand (2003)	N	N	Y	*Oncorhynchus clarkii*	SEM	SS

Reference				Species		
Isaak et al. (2007)	N	Y	N	*Oncorhynchus tshawytscha*	SRM	SS
Isaak et al. (2003)	N	N/A	Y	*Oncorhynchus tshawytscha*	SIM	PM
Koizumi and Maekawa (2004)	Y	N	Y	*Salvelinus malma*	SEM	ND
Labbe and Fausch (2000)	N	Y	N	*Etheostoma cragini*	SIM	SS
Labonne and Gaudin (2006)	N	N/A	Y	*Zingel asper*	SRM	SS
Luttrell et al. (1999)	N	N/A	Y	*Macrohybopsis tetranema*, *Macrohybopsis hyostoma*	OBS	SS
Matsubara et al. (2001)	Y	N	Y	*Odontobutis obscura*	SEM	SS
McMahon and Matter (2006)	N	Y	N	*Cyprinodon macularis*	OBS	SS
Morita and Yamamoto (2002)	N	N/A	Y	*Salvelinus leucomaenis*	SEM	SS
Neville et al. (2006)	N	Y	Y	*Oncorhynchus clarkii henshawi,*	OBS	NE
Policansky and Magnuson (1998)	Y	Y	Y	*Oncorhynchus* spp.	OBS	ND
Rieman and Dunham (2000)	Y	Y	Y	*Salvelinus confluentus,* *Oncorhynchus clarkii henshawi,* *Oncorhynchus clarkii lewisi*	OBS	ND
Rieman and McIntyre (1995)	N	N/A	Y	*Salvelinus confluentus*	SEM	SS
Schlosser and Angermeier (1995)	N	N/A	Y	*Oncorhynchus tshawytscha,* *Semotilus atromaculatus*	OBS	SS, PM
Schlosser (1998)	N	Y	N	*Semotilus atromaculatus*	OBS	SS
Shepard et al. (2005)	N	N/A	Y	*Oncorhynchus clarkii lewisi*	OBS	NE
Slack et al. (2004)	N	Y	Y	*Etheostoma rubrum*	OBS	SS
Winston et al. (1991)	N	N/A	Y	*M. aestivalis, Hybognathus placitus,* *Notropis bairdi, N. potteri*	OBS	SS
Young (1999)	Y	N/A	Y	*Oncorhynchus* spp.	OBS	NE

[1] Range: A range of metapopulation types was found.

Table 2.2. Mean (SE) values for environmental and spatial variables used to partition variation in the stream fish assemblage of the Arikaree River, CO across two 6.4-km stream segments and two 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 2006	Upstream segment 2007	Middle segment 2006	Middle segment 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)
1000 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

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Figures

B) Segment scale
(100-1000 m)
Source-sink model

D) Region scale
(100+ km)
Nonequilibrium model

A) Reach scale
(1-100 m)
Patchy Population model

C) Basin scale
(1-100 km)
Hybrid model

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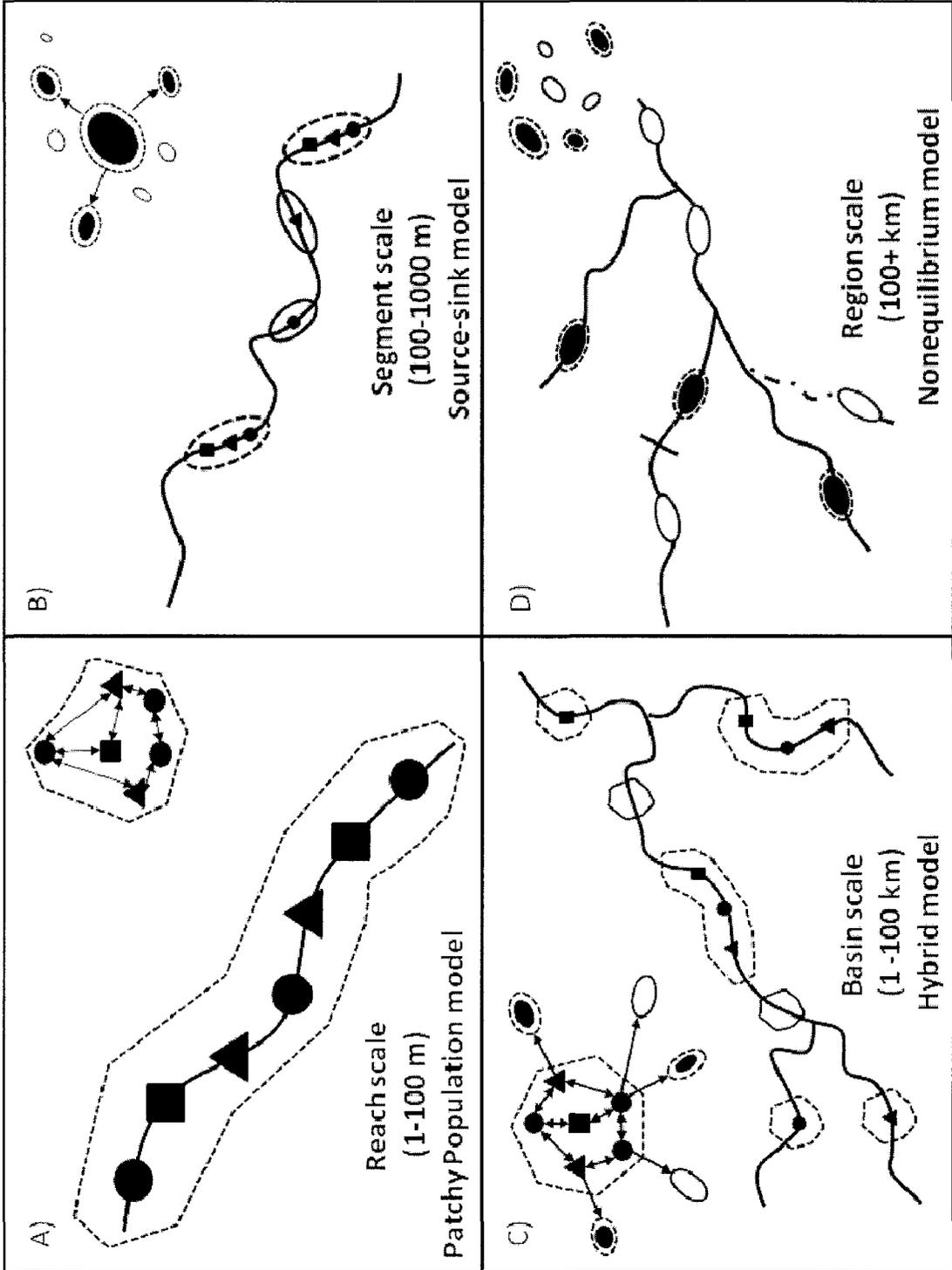
Figure 2.1. A conceptual model of metapopulation types for stream fishes across spatial scales in riverscapes. Symbols represent habitat patches that are occupied (solid) or vacant (open). Arrows show dispersal among patches, and dashed lines indicate boundaries of "populations". Filled shapes (e.g., triangles) represent different habitat types (e.g., spawning, rearing, refuge) within patches that are required for stream fish to carry out their life history (not shown at the Region scale), and 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). 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.

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B) Species Sorting model

D) Neutral model

A)
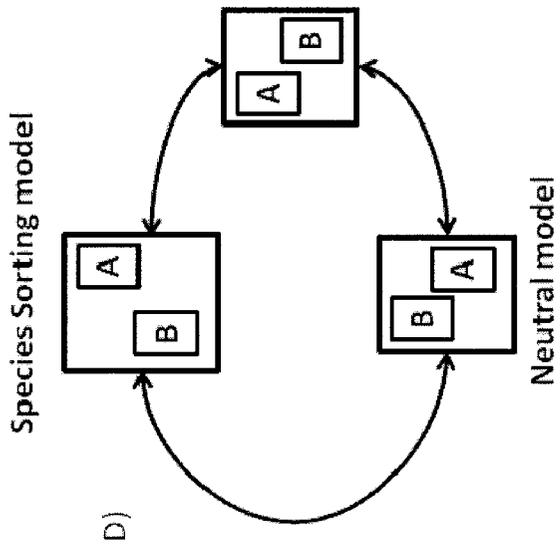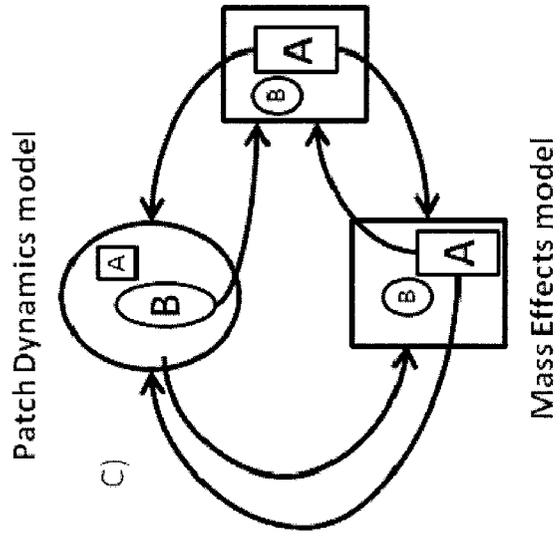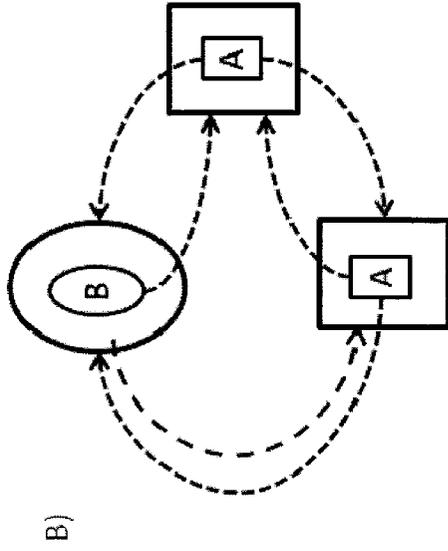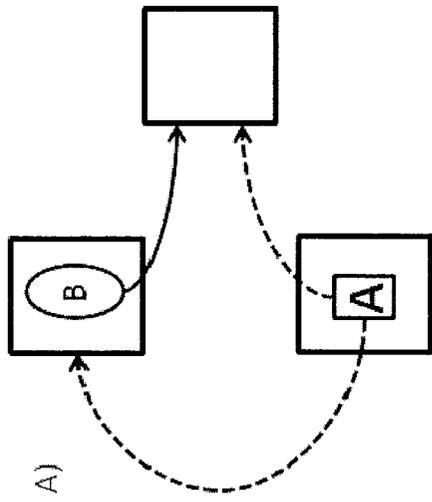
C) Patch Dynamics model

Mass Effects model

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Figure 2.2. 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 sub-dominant 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 (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 speciation.

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A) ENVIRONMENT

B) DISPERSAL/SPACE
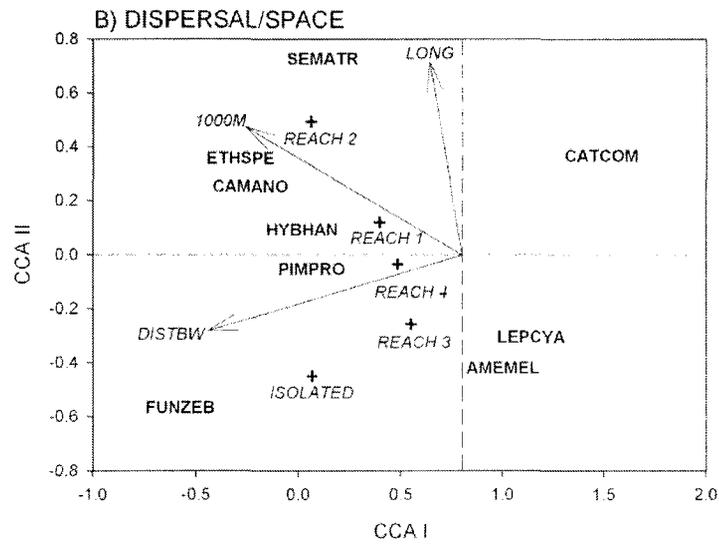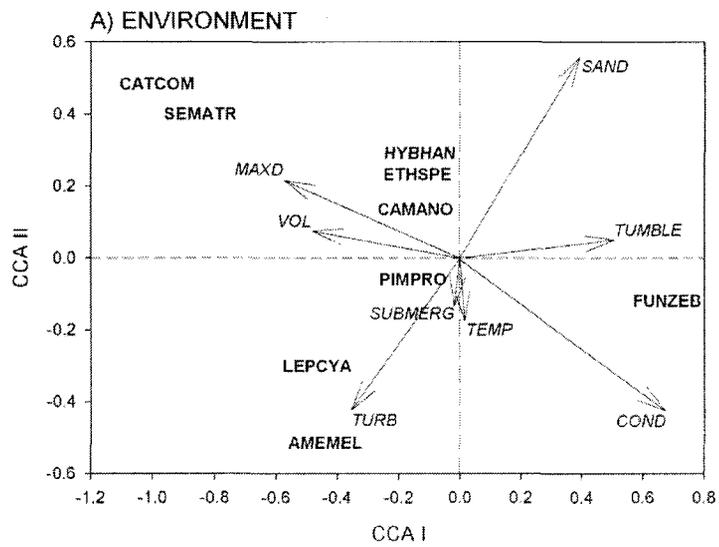
Figure 2.3. Two canonical correspondence analyses of fish assemblage data across 104 pool habitats located along the Arikaree River, CO. Top panel (A) shows the results of fish assemblage vs. environmental factors, and the lower panel (B) shows fish assemblage versus spatial factors. Codes for environmental 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.

Spawning habitat
(Spring/Early Summer)
Species-sorting

Overwinter habitat
(Winter)
Neutral or Patch dynamics

Refuge habitat
(Late Summer/Fall)
Mass effects
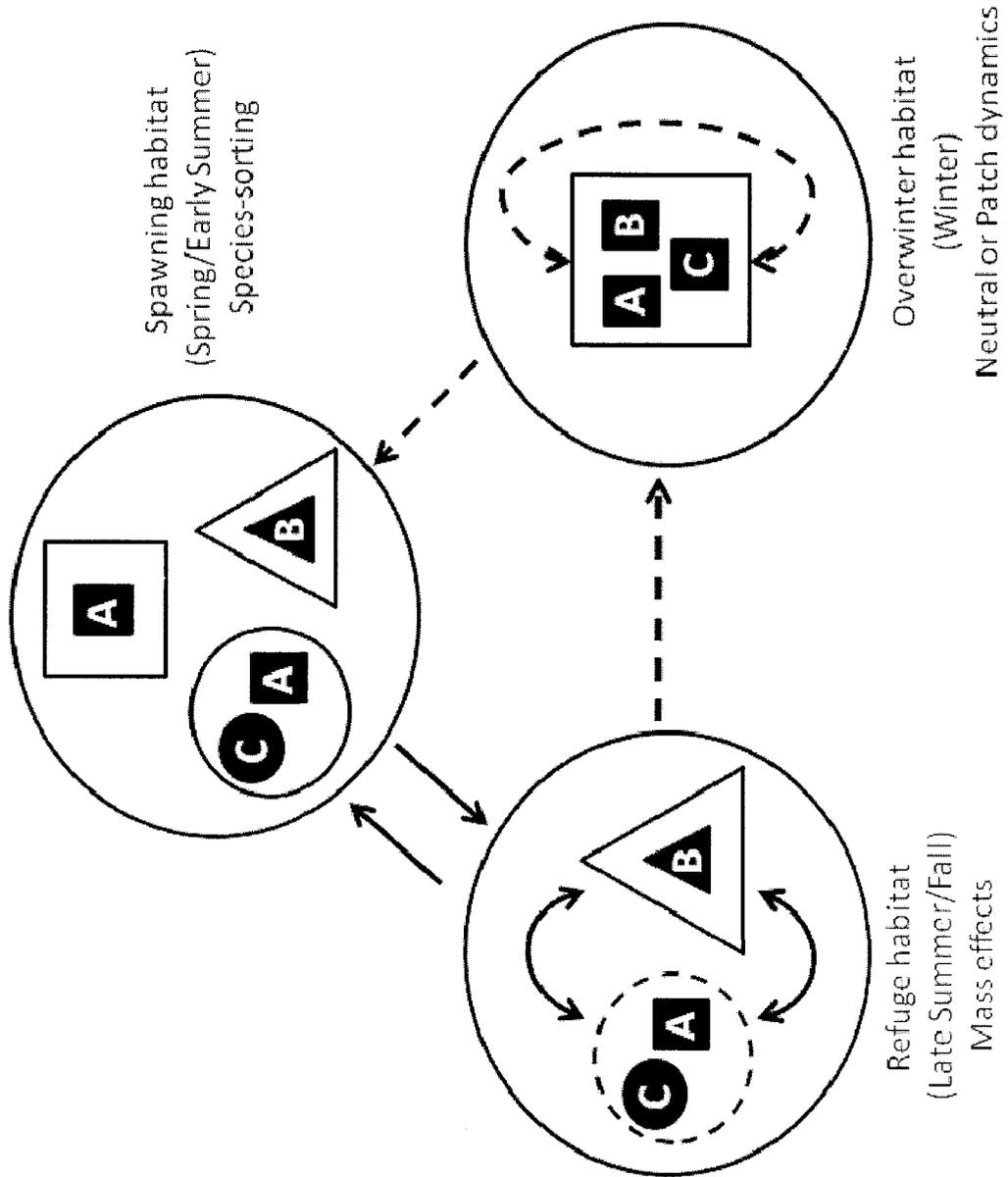
Figure 2.4. Theoretical model of Great Plains stream fish metacommunity dynamics with emphasis on habitat heterogeneity, movement, and seasonal flow variation for three species, A-C (modified from Schlosser and Angermeier 1995; Leibold et al. 2004). Arrows connect seasonal macrohabitats (large open circles: spawning, summer refuge, 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 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 square). 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.

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CHAPTER 3: Habitat Use and Phenology of an Assemblage of Larval Fishes in a Great Plains Stream: Effects of Drought and Habitat Drying Across Years

Abstract

Great Plains streams are harsh, dynamic environments for fishes and are increasingly degraded by human-caused impacts, including groundwater extraction. Although well adapted to harsh conditions, plains stream fishes are in decline, due in part to interactions between natural and anthropogenic stream drying. Effects of these factors on early life stages may serve as a bottleneck regulating their populations. To address these issues, I sampled larval fish and characterized spawning habitat from 2005 to 2007 in three 6.4-km segments of the Arikaree River, CO along a gradient of intermittency. I developed a spawning phenology by estimating the initiation of hatching for the six most abundant fishes using an inverse prediction procedure based on larval length over time and known size at hatching, and compared my estimates to environmental factors that may serve as spawning cues. Cumulative growing season degree days had the strongest effect on initial hatching dates. Additionally, I modeled larval occupancy, abundance, and detectability for the six species as a function of spawning habitat characteristics using multiple-state occupancy models. High abundance of larvae of most species was related to habitat size (e.g., area and depth) and habitat type, although spatial location (i.e., segment in which larvae occurred) also influenced abundance of some species. Detectability of larvae differed among species, and was influenced by habitat depth and larval size. Results of my modeling indicate that multiple samples from individual habitats within a season are needed to adequately detect and predict occupancy by larval plains fishes. Finally, I used an integrated model of habitat suitability and occupancy to investigate colonization and extinction among years for each species. Colonization and extinction rates for individual species differed in segments that were fed by groundwater,

versus those that were not, and were influenced by among-year climate variability. Temporal availability of spawning habitats of adequate size and distribution are critical for successful recruitment in plains fishes. Therefore, conservation efforts should focus on sustaining flows in these systems that maintain a sufficient density of spawning habitats above critical size thresholds needed for successful spawning.

Introduction

Streams on the Great Plains of North America are harsh environments for fishes (Matthews 1988; Dodds et al. 2004), and all life stages are subject to extremes in physiochemical conditions such as habitat drying during summer (Scheurer et al. 2003), and freezing in winter (Labbe and Fausch 2000). Great Plains fishes are well adapted to the harsh environmental conditions and tolerate extremes in physiochemical conditions, including high temperatures and hypoxia (Gee et al. 1978, Smale and Rabeni 1995; Smith and Fausch 1997). Most are small-bodied, short-lived, and reach maturity at an early age (Fausch and Bestgen 1997). Additionally, most plains fishes are generalists in habitat use and feeding habits, and can take advantage of resources that fluctuate in availability (Goldstein and Meador 2004; Frimpong and Angermeier *in press*), which allows them to occupy and thrive in a heterogeneous array of habitats (Matthews and Hill 1980, Fausch and Bramblett 1991).

Over the past 100 years, plains streams have been highly altered by humans (Fausch and Bestgen 1997). These alterations have exacerbated the harsh environmental conditions and caused declines in populations of native fishes range-wide owing to a combination of factors including construction of impoundments (Bonner and Wilde 2000; Falke and Gido 2006), habitat fragmentation and groundwater depletion (Dudley and Platania 2007; *Chapter 1*), and habitat alteration and loss (Cross and Moss 1987). For example, in Colorado 20 of 38 fish species native to the western Great Plains are extirpated or listed as endangered, threatened, or of special concern by the state.

Successful recruitment is vital for maintaining populations of the remaining Great Plains fishes, yet the environmental conditions that influence successful spawning in

these species are little studied. For example, spawning cues in fishes native to Great Plains streams are poorly understood. Exceptions include the red shiner *Cyprinella lutrensis*, which are cued by thermal regime (Gale 1986), and the guild of fishes that broadcast semi-buoyant eggs (e.g., Rio Grande silvery minnow *H. amarus,* plains minnow *H. placitus,* Arkansas River shiner *Notropis girardi*), cued by spikes in spring flows (Taylor and Miller 1990). However, successful recruitment by these latter species requires periodic high flows and long stretches of unfragmented stream habitats, which are becoming rare in plains streams (Taylor and Miller 1990, Scheurer et al. 2003, Dudley and Platania 2007). Many plains fishes may be able to spawn throughout the summer, as evidenced by the presence of postovulatory follicles in smalleye shiner *N. buccula* from April through September (Durham and Wilde 2008), for example. However, reproductive potential, output, and recruitment are most likely highest early in the reproductive season, owing to increasingly harsh environmental conditions as summer progresses (Bonner 2000; Durham and Wilde 2005, 2008). Additionally, interactions among environmental factors (e.g., flow and thermal regime, photoperiod) that serve as cues may be important. As a result, quantifying the relationship between environmental conditions and initiation of spawning is vital for understanding recruitment dynamics in Great Plains stream fishes.

Early life is a critical period for fishes when bottlenecks limiting recruitment to reproductively-mature life stages may occur (Ludsin and DeVries 1997; Bystrom et al. 1998; Halpern et al. 2005). Therefore, accurate, unbiased estimation of habitat occupancy and relative abundance of fish larvae in spawning habitats is important for understanding both the basic ecology of species as well as evaluating population vital

rates and conservation status. A main source of error in many sampling and monitoring programs is caused by imperfect detection (i.e., detectability < 1), which can bias estimates of habitat occupancy and relative abundance, as well as estimates of the effects of predictor variables (Tyre et al. 2003; Gu and Swihart 2004). Recently, statistically rigorous methods have been developed to estimate the probability of detecting a species based on multiple site visits (MacKenzie et al. 2003, 2006). These methods allow for more reliable inference into the factors and processes that influence species occurrence, colonization, and extinction dynamics. These models have been extended to incorporate multiple states (e.g., absent, present at low abundance, present at high abundance), as well as the influence of detectability and habitat covariates on those states (Royle and Nichols 2003; Nichols et al. 2007; MacKenzie et al. 2009). This class of model is particularly appealing when species are distributed heterogeneously among habitats, and there is high variance among replicate samples, both of which are common in early life stages of fishes (Hilden and Urho 1988; Cyr et al. 1992).

Spawning and rearing habitats in Great Plains streams are extremely dynamic, and may fluctuate in abundance and spatial location from year to year, potentially causing low spawning habitat fidelity in plains fishes (Matthews 1998, Dodds et al. 2004; *Chapter 1*). However, early maturation and high mobility in plains fishes may also allow rapid recolonization of habitats that were previously unavailable due to floods or droughts. Several investigators have reported rapid recolonization within a season (see Labbe and Fausch 2000; Scheurer et al. 2003), but the effects of interannual variation in climate on extirpation and recolonization rates of plains fishes may also be important and have yet to be measured. Understanding the response of plains fishes to habitat drying

within and across years, and their ability to recolonize and successfully spawn in previously dewatered reaches, will be useful for setting conservation priorities given further habitat degradation and global climate change (Ficke et al. 2007; *Chapter 1*)

To address gaps in knowledge of the phenology, spawning habitat relationships, detectability, and colonization/extinction dynamics of Great Plains stream fishes, I sampled larval fishes across three years in the Arikaree River, Colorado, a harsh, intermittent western Great Plains stream. Specifically, my objectives were to, 1) develop a phenology for larval fishes in the Arikaree and compare spawning timing to environmental factors that may act as cues, 2) investigate how habitat characteristics influence occupancy and relative abundance of larvae in spawning habitats, and 3) assess colonization and extinction rates of larval fishes among years and compare these to climate variation. To address the second objective, I also evaluated sampling gear efficacy and quantified factors that influence detectability of larval plains fishes, and use this information to suggest improved sampling methods.

Study area

My study area was restricted to the lower half of the Arikaree River basin, CO because segments with the potential for perennial streamflow and fish habitats occur only in the lower 110 km of the basin (Scheurer et al. 2003; *Chapter 1*; Figure 3.1). I sampled larval fishes and spawning habitats within three 6.4-km segments studied by Scheurer et al. (2003). These study segments were selected to represent a gradient in intermittency, from the more perennial upstream segment, to the intermittent middle segment, to the downstream segment which dries almost completely by early summer. The upstream

segment is located within The Nature Conservancy's (TNC) Fox Ranch, and long reaches sustain flow in all but the driest periods. It is characterized by alternating runs and deep, persistent pools. Beaver *Castor canadensis* activity increased after 2001 and created large pools in some reaches of this segment. The middle segment is made up of State Trust Lands in conservation easement administered by the Colorado Division of Wildlife (CDOW) and is largely intermittent most of the year. Its upper portion has deep, well developed pools and an extensive gallery forest of riparian cottonwood *Populus deltoides* whereas its lower portion is wide and shallow with mostly sand substrate and no riparian canopy. The downstream segment flows through private lands (approximately 2/3) and the CDOW Simmons State Wildlife Area, and is dry most of the year. A few pools persist at its upper end in some years. However, a perennial tributary, Black Wolf Creek, enters the middle of this segment and often sustains a short reach of flowing habitat in the main channel downstream.

Methods

In the third weeks of May 2005 and 2006, and the last week of March 2007, potential spawning and rearing habitats in each segment were identified and georeferenced using a Global Positioning System. Each habitat was then sampled semi-weekly through the second week of July. These habitats were classified into backwater and channel margin types. Backwaters were relatively large, deep, off-channel habitats connected to the main channel but with little or no flow. Channel margin habitats were relatively small, shallow, flowing areas along the main channel where higher stream flows in spring inundated terrestrial vegetation. For backwater habitats, during each

sampling occasion, I measured surface area, maximum depth, conductivity, and ambient water temperatures at the surface and just above the substrate. Surface area was quantified by (1) measuring length along the longest axis of the backwater, (2) dividing the length evenly into three perpendicular transects, and (3) measuring width at the midpoint of each transect. Area (m^2) was calculated as the average width times length. Maximum depth of each backwater was measured with a stadia rod (cm), and conductivity (μS) was measured using a Yellow Springs Instruments Systems Inc. model 85 multimeter. Ambient surface and bottom water temperature (nearest 0.1 °C) were recorded with a digital thermometer (Cooper-Atkins Corp., Versatuff Plus 396). Additionally, hourly temperature measurements were taken across years using thermographs (Onset Corp., HOBO Water Temp Pro v1) installed in backwater and main channel habitats (upstream segment, N = 7; middle segment, N = 3; downstream and Black Wolf Creek, N = 1 each; Figure 3.1). Additionally, during the first week of habitat sampling in 2007, area and maximum depth were estimated once for all channel margin habitats, as described above for backwater habitats.

Larval fishes were sampled along with spawning habitats throughout spring and early summer 2005-2007 (see above). Fish were sampled in spawning and rearing habitats previously identified along the three study segments and Black Wolf Creek. In 2005, larvae were collected using aquarium dipnets (20 cm x 16 cm; 250 μm-mesh) during daytime spawning habitat surveys. In shallow backwaters (< 30 cm maximum depth) in 2006, larvae were collected using dipnetting as above. In deeper backwaters in 2006 (>30 cm maximum depth), larvae were sampled at night using quatrefoil-type light traps (design modified from Kilgore 1994). Four 4-mm entrance slots allowed larvae to

enter an inner chamber that consisted of four 7.5-cm diameter Plexiglas tubes that were

14 cm long. Traps were suspended from a 6-cm thick Styrofoam ring attached to the top

of the trap and floated at the water surface. Upon retrieval, trap contents were flushed

into the lower part of the trap that consisted of a 1.5-L bowl (Rubbermaid Corp.,

TakeAlongs) containing two holes covered with a fine mesh screen that allowed water to

drain. Larval fishes were attracted using a 15-cm yellow 12-hour Cyalume light stick

suspended inside the trap (Extreme Glow Corp, 6" Lightstick). Traps were deployed in

fixed positions within backwaters at dusk for approximately 2 hours. Laboratory

experiments indicated light traps were effective over an area of at least 28 m^2 (Chapter 4).

Therefore, multiple traps were used in backwaters with areas greater than 28 m^2.

In 2007, both sampling methods were used, allowing me to compare sampling

bias and efficiency between dipnetting and light trapping using a paired sampling

approach in each backwater habitat. Light traps were set in backwaters for approximately

2 hours at dusk as described previously, and the following day dipnetting was conducted

in each backwater prior to habitat surveys. Channel margin habitats were sampled using

dip nets only. During 2007, effort was standardized so that dipnetting sampling effort

was 15 min for backwaters, and 5 min for channel margin habitats, which had smaller

area. Larval fishes sampled were preserved in 100% ethanol, except for orangethroat

darter *Etheostoma spectabile* collected by dipnetting. Orangethroat darter is a species of

special conservation concern in Colorado, and were easily identifiable by sight, so they

were counted and released. In the laboratory, all other larvae were identified to species,

enumerated, and measured for total (TL) and standard length (SL) to the nearest 0.01 mm

using digital calipers.

Statistical analysis

Phenology

I used an inverse prediction procedure (Zar 1996) to estimate the initial date of hatching and develop a phenology for larval fishes in the Arikaree River using data collected in 2007. I assumed that the largest individuals collected in each week hatched first and were the oldest. For each species captured in each weekly sample, I calculated the 90th percentile SL. I then fit linear regression models of the 90th percentile SL as a function of capture date for each species. I determined the mean SL at hatching for each species from published literature, and then rearranged the linear regression model for each species to solve for the date that corresponded to this estimated mean length at hatching. I also calculated the standard deviation for my point estimates of hatching date (Zar 1996). I considered the endpoint of spawning for each species to be the week in which I last collected larvae within 1 mm SL of their respective mean hatching length.

I compared these estimates of hatching date and hatching duration for each species with continuous data on environmental conditions that might cue spawning. Photoperiod was calculated as the number of minutes of daylight, starting January 1st 2007 (NOAA 2008). I characterized the thermal regime by both the average daily temperature across my 11 thermographs, and cumulatively as growing season degree days (GSDD) based on those same data. The GSDD were calculated by summing the average daily temperature (°C) from January 1 to the estimated hatching date for each species. Additionally, I compared initial hatching dates to patterns in groundwater stage and stream flow. Because of the strong influence of groundwater on stream flows in the Arikaree, groundwater stage is an accurate proxy for river stage in this system (*Chapter*

1). I plotted the average alluvial groundwater stage over time (m; above sea level) from six monitoring wells located in the upstream segment, and mean daily discharge (m³/sec) from USGS gauge 6821500 located at the downstream end of the Arikaree River.

Larval occupancy, abundance, and spawning-habitat relationships

For each fish species, I modeled the relationship between 1) occupancy and 2) relative abundance of larvae in backwater and channel margin habitats, and environmental characteristics of those habitats, to evaluate what factors best predict high abundances (i.e., successful spawning) of larvae. I also simultaneously modeled the influence of habitat depth and larval size on the probability of detection (i.e., detectability) for each species. I used the single season multiple-state models of Nichols et al. (2007) for larval fish and spawning habitat data collected in 2007, the most extensive survey. I used the same nomenclature and parameterization as Nichols et al. (2007). States were classified as: not detected = 0, detected at low abundance = 1, and detected at high abundance = 2 (see below for critera). Parameters estimated were: the probability that spawning habitat *i* was occupied by larvae (ψ_i^1); the probability that larvae occurred at high abundance, given occupancy (ψ_i^2); the probability that occupancy is detected for habitat *i* during week *t*, given the habitat is occupied (ρ_{it}^1); the probability that occupancy is detected for habiat *i* during week *t*, given that larvae occur at high abundance (ρ_{it}^2); and the probability that high abundance of larvae is found, given detection of occupancy in habitat *i* , during week *t*, with high abundance (δ_{it}). The unconditional probability that a habitat was occupied at high abundance was $\psi_i^{1*2} = \psi_i^1 \psi_i^2$.

Counts of larvae in individual spawning habitats were categorized among occupancy states as follows. First, for each species, I calculated catch-per-unit effort (c/f_{it}) as the number of fish collected per minute in each habitat i during each week t. Because estimates of relative abundance were similar between the two sampling gears (see Results) in habitats where both dipnetting and light trapping were conducted, estimates were pooled for both gears for that occasion. I reasoned that pooling data from the two sampling gears would improve occupancy estimates, especially for the rare sampling occasions where a species was detected with one gear but not the other. Next, to classify samples into low or high abundance, I plotted the frequency of c/f_{it} for each species to look for natural groupings. Distributions for all species were right-skewed, indicating that larvae often occurred at low relative abundance, and less often at higher abundance. Therefore, I classified a species as being present at low abundance when c/f_{it} was < 1.0 fish per minute, and high abundance if ≥ 1.0. Across species, this resulted in a mean of 0.85 (0.03 SE) percent of observations being classified as state 1, and 0.15 (0.03 SE) percent of observations being classified as state 2.

An assumption of occupancy modeling is that sites are closed to changes in occupancy during the season (MacKenzie et al. 2006). I defined the season for each species as the period in which I expected larvae to be present in a habitat, potentially at high abundance. For a given species, I reasoned that the season began on the date I estimated that hatching began (see Results), and ran until habitat shifts due to ontogeny, or high mortality due to increasingly unsuitable environmental conditions, reduced occupancy and abundance estimates in spawning habitats. This period varied from 3 to 6 weeks among species. An example detection history $h_i = 01221$ for habitat i indicates

nondetection during week 1, detection at low abundance during week 2, detection at high abundance in weeks 3 and 4, and detection at low abundance in week 5. The potential for state misclassification under the Nichols et al. (2007) framework extends in only one direction. That is, possible true states for a species not detected (observed state = 0), are 0, 1 or 2, whereas possible true states for a species detected at low abundance (observed state = 1), are 1 or 2. Therefore, I assumed that if a species was detected at high abundance (observed state = 2) then there was no uncertainty (i.e, true states could not be 0 or 1). Additionally, the lowest observed state has the greatest uncertainty. As a result, for the example detection history above, there is no uncertainty about true abundance level or occupancy status during the season, because high abundance (observed state = 2) was observed at least once during the sampling period.

I modeled the probability of occupancy at low and high abundance, and detectability, based on characteristics of individual spawning habitats at two scales, local and segment. Local scale covariates included habitat area (continuous, Area), habitat depth (continuous, Depth), a quadratic version of habitat depth (continuous, $Depth^2$), and habitat type (categorical, backwater or channel margin). I included the quadratic depth term to account for the possibility that the probability of occupancy or high abundance might be greatest at a moderate depth. For example, adults might avoid spawning in habitats that were too shallow (i.e., habitat is unsuitable), and too deep (i.e., higher predation risk). Segment scale covariates included the segment in which the habitat was located (categorical, Segment), reach water temperature (continuous, GSDD), and persistence of the habitat (categorical, Pers). The GSDD was the cumulative number of growing season degree days (see above for calculation) for the reach in which the

spawning habitat was located, to the end of the last week of sampling. This covariate was included because I anticipated that high abundance of larvae of some species might be influenced by thermal characteristics at the reach scale. Finally, I classified each habitat as to whether it dried by the end of my spawning habitat surveys or not (dry or wet; Pers). Although habitats never dried within the period I modeled for any species, many dried by the end of my surveys (see Results). I felt that inclusion of this variable might potentially explain avoidance of a particular habitat by an individual species.

I modeled detectability as dependent on both time and state ($\rho_{it}^s = \rho_t$, $s = 1, 2$; $t = 1,..n$), where n is the number of weeks included in a model for an individual species, and i is an individual spawning habitat. This allowed me to investigate patterns in my ability to detect larvae at low and high abundance throughout the sampling period. Habitat depth was included as a covariate to model its potential influence on detection. After developing models, I compared my estimates of ρ_{it}^s to the mean size of larvae collected during week t to investigate the relationship between detectability and larval size. Finally, I developed a model where detectability was state but not time dependent ($\rho_i^s = \rho_t$, $s = 1, 2$) to estimate an overall probability of capture (and SE) for each species at low and high abundance, and allow comparison among species.

I used an information-theoretic approach to find the most parsimonious set of independent variables to predict occupancy state and detectability for each species (Burnham and Anderson 2002). First, I developed 11 *a priori* candidate models that contained sets of explanatory variables that were of biological significance (Table 3.1). I included models with local (M2-M6) and segment (M7, M8) scale covariates, combinations of local and segment scale covariates (M9, M10), a null model with no

covariates (M1), and a global model that included all covariates (M0). All models were run as dependent on time and state, and with and without depth as a covariate for detectability. I used Akaike's information-criterion (AIC) to select the best approximating model by comparing each of the candidate models simultaneously. The AIC scores were adjusted for bias due to a small sample size (AIC_c), and Akaike weights (w_i) were calculated. Thus, the model with the lowest AIC_c and the highest w_i was considered the best model. All analyses were conducted using the multiple state occupancy estimation procedure in Program MARK (White and Burnham 1999).

Spawning habitat, colonization, and extinction dynamics among years

I used multi-season joint habitat suitability and occupancy models to model the dynamics of spawning habitat availability and larval fish occurrence from 2005 to 2007 (MacKenzie et al. 2006, 2009). Fifty-nine spawning habitats were modeled for this period. Models were formulated for each species separately. I estimated annual transition probabilities among three states (*m*) of spawning habitats: spawning habitats that were dry in a given year (denoted 0, hence *m* = 0), spawning habitats that were wet but unoccupied (*m* = 1), and spawning habitats that were wet and occupied (*m* = 2). I followed the parameterization of MacKenzie et al. (2009): $\psi_{t+1}^{[m]} R_{t+1}^{[m]}$, where $\psi_{t+1}^{[m]}$ is the probability of a spawning habitat being wet in year *t*+1 given that it was in state *m* in year *t*. Likewise, $R_{t+1}^{[m]}$ is the probability that a spawning habitat was occupied in year *t* + 1, given that it was in state *m* in year *t*. An example detection history (h_i) for larval fish of a given species in a single spawning habitat over the three years is h_i = 221 000 122, where the species was detected in suitable (i.e., wet) habitat during the first two weeks of the first year, then not detected in the final week, although the habitat was suitable. In the

second year, the species was never detected because the habitat was unsuitable (i.e., dry). In the third year, habitat was suitable in all weeks, but the species was not detected in the first week. Nevertheless, it was detected in the final two weeks.

My objectives with this analysis were to quantify the dynamics of spawning habitats and evaluate the relative importance of available habitat to the distribution of larvae. I constructed models to address multiple hypotheses about spawning habitat suitability and larval fish habitat use. I modeled spawning habitat suitability ($\psi_{t+1}^{[m]}$) as either dependent on conditions the previous year, or independent of previous suitability (i.e., dynamic), to investigate if some sites are consistently more likely to be wet than others, or alternatively, that previous conditions do not matter. I assumed that occupancy state did not affect habitat dynamics, so for the dependent model m: 0, 1=2, and for the dynamic model m: 0=1=2. Additionally, I investigated whether spawning habitat use ($R_{t+1}^{[m]}$) by larvae in year t +1 was dependent on occupancy and availability in year t, under three scenarios, where the probability a spawning habitat was occupied: 1) depended on its previous state (m: 0,1,2), 2) depended only on whether it was wet or dry the previous year (m: 0=1, 2), or 3) did not depend on the previous state (m: 0=1= 2). I considered the first two scenarios to indicate site fidelity for a species, and the last to represent random habitat use. Based on these hypotheses, I constructed a balanced set of six candidate models where dynamic ($\psi_{t+1}^{[0=1=2]}$) or dependent ($\psi_{t+1}^{[0,1=2]}$) habitat suitability was paired with each of the three occupancy scenarios: $R_{t+1}^{[0,1,2]}$, $R_{t+1}^{[0=1,2]}$, and $R_{t+1}^{[0=1=2]}$. From these parameters, colonization (γ) and extinction (ε) probabilities, and the probability a habitat remained wet and occupied between years (η) were derived (MacKenzie et al. 2003, 2006, 2009).

I also expected that spawning habitat suitability would be influenced by the hydrology of the segment in which the habitat occurred. Initially I considered models that included a categorical covariate representing whether a habitat was located in the upstream, middle, and downstream segments, or Black Wolf Creek. Unfortunately sample sizes were too small to produce reliable estimates for the four segments. As a result, I categorized the segments based on groundwater inflow (*Chapter 1*) and combined the upstream segment with Black Wolf Creek, and the middle segment with the downstream segment. Therefore, I estimated transition probabilities (i.e., colonization and extinction) for habitat suitability in relatively wet, and relatively dry, reaches of the Arikaree River. Likewise, I was unable to model conditional occupancy ($R_{t+1}^{[m]}$) as a function of these locations. However, based on the results of my multiple state models (see Results), species occurrence dynamics did not appear to be strongly influenced by segment, so I felt justified in not including segment as a covariate for occupancy in these models.

Finally, I tested whether detectability (δ) was heterogeneous for each species using three alternative detection structures, where 1) δ was constant across the three years, indicated by (.), 2) that δ varied from year to year but not within sampling occasions (*YEAR*), and 3) that δ varied among sampling occasions (i.e., within years) but not among years (*OCC*). I tested each detection structure for each of my six hypotheses, resulting in a total of 18 models in my candidate model set, for each species. All analyses were performed using the multiple season, multiple state procedure in Program PRESENCE (Hines 2008).

Results

Environmental variability among years in the Arikaree River sets the context for potential variation in spawning and recruitment of fishes. Drought conditions that started in 2000 continued during 2005-2007, although mean annual flows in 2005 (0.05 m^3/sec) were the highest since 2001. Total annual precipitation for 2005 of 53.2 cm measured at Idalia, CO (CoAgMet 2008) was the highest since 1995, and above the long-term mean for 1895-2005 (mean = 44.3 cm; SD = 8.8), but the previous years of drought reduced its effect. Total annual precipitation in 2006 and 2007 (32.8 cm and 33.0 cm, respectively) was well below the long term mean, and both years ranked among the lowest 10% over the period of record. The average flow declined in 2006 to 0.02 m^3/sec, the third lowest mean annual flow over the period of record (1933-2007), and remained low in 2007 (0.04 m^3/sec), although abundant snowfall in December 2006 (30-45 cm; NOAA 2008) contributed to relatively higher flows in spring 2007.

I collected a total of 17,353 larval and juvenile fishes representing nine species across the three years of sampling (Appendix C). Fathead minnow (27%), brassy minnow (26%), and green sunfish (23%) dominated the samples numerically, followed by plains killifish (10%), central stoneroller (10%), and creek chub (4%). Orangethroat darter (1%) and black bullhead (<1%) were rarely collected, and white sucker was extremely rare with only 10 individuals captured across all three years. Green sunfish was collected in only two backwater habitats during one week at the end of sampling in 2006 and 2007. As a result I excluded this species from my phenology and occupancy analyses. Additionally, black bullhead and white sucker were extremely rare, and were excluded from all further analyses.

I tested the rank correlation of the relative abundances of larval fishes among years using the non-parametric Spearman's rho statistic in SPSS® ver 11.0 (SPSS Inc. 2001). Individuals of each species were pooled across segments within a year. I found that rank abundance between 2005 and 2007 was highly correlated ($r_S = 0.912$, $P < 0.001$). In contrast, rank abundance of larval fishes collected in 2006 was not correlated with 2005 or 2007 ($r_S = 0.134$, $P = 0.737$; $r_S = 0.383$, $P = 0.308$, respectively). These results indicate that the larval fish assemblage differed in composition during the hot, dry conditions of 2006 relative to the more benign temperature and flow conditions during early summer in 2005 and 2007. I investigate these patterns further in my multiple season joint habitat suitability-occupancy analyses below.

Sampling bias comparisons

I tested the efficacy of dip netting vs. light trapping in backwater habitats using paired sample data collected in 2007, with the overall goal of comparing sampling bias between the two gears. Four kinds of bias were tested: whether 1) one gear collected larvae, regardless of species, better than the other; 2) one gear consistently captured a species and the other did not (i.e., species bias); 3) the length structure within a species differed between gears (i.e., size selectivity); and 4) relative abundance estimates (measured as catch-per-unit-effort) differed between gears.

My paired comparison of dipnetting and light trapping in backwater habitats across six weeks in spring 2007 suggested that the two gears produced similar results when sampling larval fish communities in plains stream habitats. Of the 128 samples (64 dipnet and 64 light trap), larval fish were collected in only six samples with dip nets but not with light traps. Conversely, in only eight samples were larvae collected with light

traps but then not with dipnetting, and all eight of these occasions were during the first week of sampling in early April. Species making up > 5% of the total abundance collected using both gears included central stoneroller, brassy minnow, fathead minnow, creek chub, and green sunfish. Eighty-five percent of green sunfish larvae were collected using light traps, and most were captured in one backwater during one sampling night. Rank abundance of species captured by the two gears was highly correlated ($r_S = 0.810$, $P = 0.015$). Therefore, both gears performed well in capturing larval fishes in backwater habitats in the Arikaree River.

I tested species bias by calculating the number of samples in which the five most abundant species were collected using one gear but not the other, using a chi-square test for independence. Based on my results I accepted the null hypothesis that the samples were independent ($X^2 = 1.23$, $P = 0.873$, df = 4). This indicates that the two gears performed similarly in capturing larval fish species in backwater habitats.

Size bias between the two gears was tested for the four most abundant species, for which adequate length-frequency data were available. The number of weeks included in the analysis was five for brassy minnow, four for central stoneroller and fathead minnow, and one week for creek chub. I tested for equality of the shape of the length-frequency distributions and medians of the distributions for each species between the two gears using two-sample Kolmogorov-Smirnov and Mann-Whitney's U tests, respectively. There were no significant differences for the shape or the medians of the length-frequency distribution for any species in any week (All $P > 0.13$). Therefore, no size bias was detected between the two gears for the four most common species collected.

Finally, I compared the catch-per-unit effort (c/f; number of fish/min), estimated using the two gears for each species. I calculated the c/f for each species in each paired dipnet and light trap sample and used linear regression to model the relationship between the two. I found a significant, positive linear relationship ($r^2 = 0.54$, $P = 0.003$) between the c/f of species collected using dipnetting and light trapping during the same sampling period. This suggests that across species the relative abundances of larval fishes captured are correlated among gears (i.e., many larvae are collected using dipnets when many are collected using light traps). Based on my results, and because the same effort was used for each gear on each sampling occasion, I summed the c/f for each species collected using dip nets and light traps in the same sample as an overall estimate of c/f (number of fish/min) for individual samples collected in backwater habitats in 2007.

Spawning habitat availability

Fifty-nine individual spawning habitats were surveyed within the three segments and Black Wolf Creek, across the three years of study (backwaters, N = 16; channel margin, N = 43; Figure 3.1). No backwater habitats were ever present in the downstream segment or Black Wolf Creek. Backwater habitats were clustered in the lower half of the upstream segment, and the upper one-third of the middle segment. The number and total area of backwater habitats varied among years, and corresponded to climate conditions. Total backwater area in the upstream and middle segments during late May was lowest in the dry conditions of 2006 (670 m^2), compared to 2005 (1140 m^2) and 2007 (1820 m^2) . Higher winter precipitation during December 2006 contributed to the large area of available spawning habitat during spring and early summer 2007. Total backwater area in 2007 in the upstream (880 m^2) and middle segments (940 m^2) was about twice, and

three times, the amount available in 2006 (460 m^2 and 210 m^2), respectively. The number

of channel margin habitats was also fewest in 2006 (N = 15) due to low water conditions,

compared to 2005 (N = 23) and 2007 (N = 37).

Phenology and environmental cues

The six most abundant fish species in the Arikaree River began spawning at

distinct times during spring, and were apparently cued by rising temperature. No

differences were detected among segments (ANCOVA, all *P* > 0.36), so I combined

estimates across segments for each species. Therefore, my phenology can be

characterized as being for the Arikaree River basin as a whole (Table 3.2). Size at

hatching for each species was estimated from published literature, except for brassy

minnow, which I quantified in the laboratory during an otolith microstructure validation

(Chapter 4). I estimated that the first species to hatch was orangethroat darter starting

April 17th (SD = 4.5 days). Fish within 1 mm of hatching size (5.0 mm SL; Simon and

Wallus 2006) were collected through May 23rd, indicating about a one month spawning

period for this species. Creek chub began hatching April 19th (SD = 6.7 days), and

spawned through May 16th. Brassy minnow and central stoneroller had similar initial

(April 25th, SD = 4.7 days, and April 24th, SD = 1.7 days, respectively) and final (May

23rd) hatching date estimates. Fathead minnow had the longest period of spawning, with

hatching estimated to have begun on April 30th (SD = 7.4 days) and lasted through the

end of sampling in mid-July. Plains killifish was the last species to initiate spawning, not

starting until May 10th (SD = 4.7 days) and ending on about June 13th. Overall, the

spawning period of all six species overlapped for at least a week. Orangethroat darter

and creek chub overlapped almost entirely, and brassy minnow and central stoneroller

had nearly identical spawning periods. Clearly, mid-April through early-June is a critical spawning period for fishes in the Arikaree River.

I investigated the relationship between my estimates of hatching initiation for the six species, and environmental factors that might serve as cues to spawning (Figure 3.2). Other than plains killifish, which initiated hatching just after a spike in streamflow and groundwater stage in late April, no other species appeared to be cued by stream flows. Instead, photoperiod and water temperatures are the most likely factors to initiate spawning in the other five species. Orangethroat darter and creek chub were early spawners, and initiated spawning at <600 GSDD (Table 3.2). Intermediate spawners were central stoneroller, brassy minnow, and fathead minnow. These species initiated spawning between 660 and 740 GSDD. Plains killifish, the latest species to spawn in the Arikaree River, did not initiate spawning until GSDD were about 900.

Occupancy, abundance, and detection of larvae in spawning habitats

The probability that a spawning habitat was occupied by larvae, regardless of abundance $(\hat{\psi}^1)$, varied from 0.62 ($\pm$ 0.08 SE) for plains killifish, to 0.94 ($\pm$ 0.29) for central stoneroller (Table 3.3). The unconditional probability that a spawning habitat was occupied by larvae at high abundance $(\hat{\psi}^{1*2})$ ranged from 0.23 ($\pm$ 0.06) for plains killifish to 0.65 ($\pm$0.07) for central stoneroller. Brassy minnow and fathead minnow had relatively high probabilities of occupancy (0.89 and 0.93, respectively), but were present in high abundance in only about half of spawning habitats. As expected, when imperfect detection was accounted for, modeled estimates of occupancy and occupancy at high abundance were higher than naïve estimates of those parameters.

For five of the six species (central stoneroller, orangethroat darter, brassy minnow, fathead minnow, and creek chub; Table 3.4), most best-supported models included only local-scale covariates (habitat area, depth, and/or type), indicating that these characteristics provided the best description of occupancy state, given the data for those species. Occupancy state of plains killifish was best explained primarily by segment scale covariates (habitat type and segment). The best supported model for creek chub was the null model (no covariates on occupancy), although there was substantial support for a model that included habitat depth.

Habitat area or depth, and habitat type (i.e., backwater or channel margin) were present in the top three models for four of the six species (Table 3.4). Central stoneroller occupied relatively large, shallow, channel margin habitats at high abundance. Orangethroat darter was predicted to be at high abundance in relatively small, shallow, channel margin habitats. Conversely, high abundances of brassy minnow were predicted to be found in large, deep, backwater habitats. Segment was an important predictor of high abundance for plains killifish and fathead minnow. Larvae of these two species were most likely to be found at high abundance in the middle and downstream segments. Overall, the direction of effects and covariates contained in the top models differed among species, indicating that larvae of each species was present at high abundance in spawning habitats characterized by different attributes. This was a higher level of spawning habitat specialization than I predicted, based on general habitat preferences of adults during summer and winter (*Chapter 2*).

Spawning habitat area was an important predictor of high larval abundance for five of the six species, although the direction of effects differed (Table 3.4; Figure 3.3).

For example, brassy minnow larvae are predicted to occur at high abundance in larger

spawning habitats. I predicted a 50% probability of high abundance of brassy minnow

larvae in backwaters with areas of approximately 25 m^2. The probability of high

abundance of central stoneroller larvae in spawning habitats also increased with

spawning habitat area, although the slope of the relationship was more gradual than for

brassy minnow. Conversely, high abundance of orangethroat darter and creek chub

larvae declined with area, indicating that adults of these species preferred to spawn in

smaller habitats. Overall, habitat size was an important predictor of high abundances of

larvae.

My ability to detect larvae in spawning habitats, and to detect them at high

abundance, varied among species (Table 3.3). Creek chub had the lowest overall

detection probability ($\hat{p}$ = 0.26), whereas brassy minnow had the highest ($\hat{p}$ = 0.87).

Overall detectability of high abundance of larvae, given occupancy ($\hat{\delta}$), ranged from

0.43 for brassy minnow to 0.93 for orangethroat darter. The relationship between

detectability and time also varied among species (Figure 3.4). Detectability of central

stoneroller and orangethroat darter was lowest early in the spawning season, when larvae

were very small, and late, when larvae were large, matching my predictions. However,

detectability of plains killifish, brassy minnow, and fathead minnow generally increased

and remained high, indicating that small larvae of those species were more difficult to

detect, but larger larvae were not. Detectability of creek chub larvae was highest early in

the sampling period, and declined rapidly thereafter, corresponding to the period when

larger individuals were present. Detectability for three of the six species (central

stoneroller, brassy minnow, and fathead minnow; Table 3.4; Figure 3.5) declined with

increasing spawning habitat depth. The probability of detecting central stoneroller larvae declined rapidly at depths > 60 cm, whereas detectability of brassy minnow and fathead minnow larvae remained high (>60%) in habitats as deep as 80 cm.

Spawning habitat, colonization, and extinction dynamics among years

My joint habitat suitability-occupancy models suggested that the probability of a habitat being wet was dynamic from year to year (Table 3.5). Models that included $\psi_{t+1}^{[0=1=2]}$ were ranked first across all six species. However, there was some evidence for the alternative hypothesis that suitability in year t + 1 depended on suitability in year t, as models including $\psi_{t+1}^{[0=1,2]}$ were ranked second and contributed substantial AIC weight for four of the six species. Similarly, the dynamic occupancy $(R_{t+1}^{[0=1=2]})$ hypothesis was included in the top models for five of six species. Only spawning habitat occupancy by plains killifish was dependent on the previous occupancy state.

Similar to the results of my single-season models, detectability varied within a year for most species, probably due to larval growth. With the exception of fathead minnow, the variable indicating that detection structure varied among occasions (*OCC*), was included in all top models. In contrast, either constant detectability across years (.) or variation among years (*YEAR*) were included in fathead minnow top models. Regardless of which detection structure was true, detectability of fathead minnow was very high across years (δ>0.8). Model averaged estimates of δ for each species are included in Appendix D.

Across all species, extinction rates (ε) were very high (0.52 to 0.98) during the transition from the moderate climate conditions of 2005 to the dry climate conditions of 2006 (period 1), and were higher in segments not fed by groundwater (Table 3.6).

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Colonization (γ) during this period was very low or absent, and ranged from <0.01 to 0.16. In contrast, during the transition from 2006 to 2007 (i.e., dry year to wet year; period 2), extinction rates were lower (0.10-0.62), and colonization rates were higher (0.05 to 0.66). Additionally, the probability that a habitat stayed wet and occupied (η) was low from 2005 to 2006 (0.02 to 0.48), but increased from 2006 to 2007 (0.37 to 0.84). With respect to individual species, central stoneroller, brassy minnow, fathead minnow, and creek chub were good colonists during the transition to a wet year (period 2), compared to plains killifish and orangethroat darter for which colonization ability appeared low regardless of habitat suitability. Clearly, climate was an important factor that influenced habitat suitability and colonization and extinction rates of plains fish larvae in spawning habitats.

Discussion

I developed a method for estimating the initiation of hatching based on the change in larval length over time, using inverse prediction models. From these estimates I constructed a phenology for spawning fishes in the Arikaree River. To my knowledge, no other spawning phenologies exist for western Great Plains stream fish communities, although there are some data for the southern Great Plains (Durham and Wilde 2005), and dryland streams in Australia (King et al. 2004). I found that all species initiated spawning in spring, and with the possible exception of fathead minnow, had discrete spawning periods. At the level of families, my estimates of the order of spawning among species were similar to those made in other temperate stream ecosystems (e.g., Floyd et al. 1984), where the phenology was percids, cyprinids, cyprinodontids, then centrarchids.

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The initiation of hatching for most species was influenced by rising water temperatures from winter to spring. In plains streams such as the Arikaree River, water temperatures are moderated by groundwater. As groundwater input declines in the future due to irrigation pumping (*Chapter 1*), species may spawn sooner due to earlier spring warming, putting them at a disadvantage because prey resources may not match up. None of the six species analyzed in my spawning phenology were cued by spikes in stream flow. This is not surprising because species that are known to be influenced by flow spikes (e.g., plains minnow) are already extirpated from the Arikaree River (*Chapter 1*). Altered thermal regimes and increased habitat fragmentation can only have more negative effects on plains fishes in the future.

I found that estimates made using the inverse prediction models were very similar to estimates made from directly aging larvae from otoliths. For example, my estimate for the initiation of hatching in brassy minnow was April 25th (± 4.8 days) using the inverse prediction models, and the first date of hatching from daily ring counts was about April 21st (Chapter 4). Knowledge of spawning phenology and environmental factors that serve as cues is valuable for species conservation, especially in Great Plains streams where flow regimes modified by water extraction and impoundments may have negative impacts on spawning and recruitment. In the Arikaree River, larvae that are spawned later are likely to be most vulnerable to habitat drying (Chapter 4).

Local-scale spawning habitat characteristics accurately predicted high abundances of plains fish larvae, and habitat size (i.e., area or depth) and habitat type were the most important factors across species. This specialization was surprising, and was more than I expected, given the generalized habitat preferences of adult plains fishes during other

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parts of the year (Taylor et al. 1993; *Chapter 2*). This finding underscores the importance of temporal variation in habitat use by plains stream fishes, and the need to conserve all habitat types required by them to carry out their life histories (Fausch et al. 2002). For example, I found that brassy minnow required large, deep, backwater habitats for successful spawning. These results imply that there may be a threshold of habitat size for successful spawning by these species. Managers will be challenged to maintain habitats of adequate size, as well as connections among habitats, with increased anthropogenic stream drying in the future.

Overall, I detected no difference in species of larval fish captured, their size distribution, or their relative abundance (*c/f*) between dip netting and light trapping. This suggests that both methods allow robust measures of presence and relative abundance of larval fishes in plains streams. However, an order of magnitude more individuals were collected using dip netting versus light trapping. If large sample sizes are needed for analyses, dip netting would be a superior method for sampling larval fishes in plains stream habitats. Conversely, if negative impacts to population levels (e.g., rare species) from sampling are a concern, then light trapping may be a better alternative. Overall, I felt my estimates of larval occupancy in spawning habitats were improved by using both gears in tandem.

I was able to produce unbiased estimates of occupancy states for larvae of six species of plains fishes in spawning habitats, based on multiple site visits. These estimates accounted for imperfect detection, which is rarely incorporated into studies of larval fish ecology. To my knowledge, these are the first estimates of the influence of fish size and habitat characteristics on detectability of fish larvae in streams.

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Specifically, I found that habitat depth and fish size influenced the probability of detection of larvae in spawning habitats, and that detectability was heterogeneous among species and varied over time. Generally, detectability did not peak during the same week among species. For example, the highest detectability of creek chub larvae was early in the sampling period, whereas the highest probability of detecting plains killifish larvae was late in the sampling period. This indicates that to accurately quantify the occupancy state of larvae at the assemblage level, multiple site visits over time are needed. Additionally, I found that detectability of three species declined in deeper habitats. However, detectability of these species remained relatively high (>0.7) across the majority of the range of depths (< 70 cm) encountered in spawning habitats in the Arikaree River. Only two spawning habitats sampled were > 70 cm maximum depth. I suggest that sampling effort may need to be adjusted (i.e., increased) in deeper spawning habitats to adequately detect the presence of larvae of central stoneroller, brassy minnow, and fathead minnow.

I found that the suitability of spawning habitats was very dynamic among years in the Arikaree River. In other words, the probability that a habitat was wet or dry in a given year was independent of whether it was wet or dry the previous year. These results are concurrent with observations of refuge habitat availability among years (*Chapter 1*). However, there was also some support for the hypothesis that occupancy by larvae was influenced by habitat suitability the previous year, particularly for brassy minnow. For this species, mixed results may have occurred because backwater habitats were persistent among years, but confounded because larvae were also found (at low abundance) in dynamic, marginal habitats (i.e., channel margins). Unfortunately, including a covariate

that identified habitats by type in my multi-season analysis was not an option, due to

small sample sizes. Likewise, the influence of habitat suitability in the previous year on

larval occupancy may have differed among years (i.e., differed between wet and dry

years), but my sample sizes were too small to parameterize models that test for that

effect. However, I suggest that this line of research is interesting and important, and

should be pursued in the future when more years of data may be available.

Climate variability had strong effects on habitat suitability and habitat use by

larvae during 2005-2007. Occupancy of larvae in spawning habitats was lower in the

extremely dry conditions of 2006 despite habitats being suitable and available. This

could result from several mechanisms. Adults could have avoided spawning in some

apparently suitable (i.e., wet) habitats in 2006 because environmental conditions (e.g.,

high temperatures, low dissolved oxygen) were degraded by the harsh climatic

conditions. Alternatively, spawning may have occurred in those habitats but larvae did

not survive to be captured during my surveys, due to lethal physiochemical conditions or

lack of food resources. Lastly, some of these habitats may not have been accessible to

spawning adults, because dry reaches were present and presumably limited dispersal,

especially in the middle segment during 2006 (*Chapter 1*). Regardless of the mechanism,

my results suggest that occupancy of spawning habitats during drought years is

influenced by more than just the availability of habitat.

Recolonization was rapid from the dry conditions of 2006 to the wet conditions of

2007, though some species were better colonizers than others. The ability of plains fishes

to quickly recolonize previously dry habitats is an adaptive response to the dynamic

habitat conditions. My results concur with Fausch and Bramblett (1991), who found that

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fathead minnow was among the best at colonizing upstream in arroyos that flash flood and then go intermittent in a southern Colorado basin. I also found that brassy minnow quickly recolonized previously unsuitable habitats. In contrast, orangethroat darter, a species of conservation concern in Colorado, was a poor colonist. The Arikaree River basin is the last refugia for this species in Colorado, and as a result its populations may be particularly susceptible to the negative impacts of drought years.

I modeled the impact of one severely dry year followed by a relatively wet year, but the effects of consecutive, very dry years on colonization and extinction rates in Great Plains stream fishes remain to be quantified. I suggest that sampling protocols that use larval fish data from multiple site visits and across years will allow managers to accurately estimate and potentially predict effects of habitat drying on spawning and recruitment in an unbiased manner. This information will be especially valuable in light of increased human-caused stream drying from overappropriation of groundwater and surface water resources (*Chapter 1*), and the impacts of global climate change (Xenopoulos et al. 2005; Ficke et al. 2007). Early life stages are critical periods that influence recruitment and ultimately population persistence in Great Plains stream fishes, and managers will be challenged to keep plains streams flowing into the future to avoid further declines in native fishes.

Acknowledgements

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Tables

Table 3.1. Candidate models for multiple-state occupancy models used to estimate occupancy of larval fishes in the Arikaree River, Colorado, in 2007. Models were formulated to address hypotheses at two spatial scales (Local and Segment), separately and in combinations (Mixture). Models were fit with the covariates for occupancy, and with and without detection covariates. See text for description of covariates.

Model type	Model name	Occupancy covariates							Detection covariates	
		Area	Depth	Depth^2	Habitat	GSDD	Segment	Pers.	Depth	Time
Global	M0	Area	Depth	Depth^2					Depth	Time
Null	M1								Depth	Time
Local	M2	Area							Depth	Time
	M3		Depth						Depth	Time
	M4		Depth	Depth^2					Depth	Time
	M5				Habitat				Depth	Time
	M6	Area	Depth		Habitat				Depth	Time
Segment	M7						Segment		Depth	Time
	M8					GSDD	Segment	Pers.	Depth	Time
Mixture	M9	Area	Depth		Habitat	GSDD	Segment	Pers.	Depth	Time
	M10				Habitat		Segment		Depth	Time

Table 3.2. Estimates of the initiation of hatching for six fish species collected in the Arikaree River, CO during spring 2007. Coefficients of determination (r^2), x-axis intercepts (β_0) and standard deviation in parentheses, the slope (β_1) of each model, the estimated hatching date, growing season degree days (GSDD; cumulative °C) for that date, and the size at hatching (mm) based on published literature are presented.

Species	Model			Estimated hatching date	GSDD	Size at hatch (mm)	Reference
	r^2	β_0	β_1				
orangethroat darter	0.97	108 (4.0)	0.22	April 17	571	5.0	Simon and Wallus (2006)
creek chub	0.97	110 (6.7)	0.38	April 19	595	5.8	Buynak and Moore (1979)
central stoneroller	0.99	115 (1.7)	0.52	April 24	662	5.7	Reed (1958); Buynak and Moore (1980)
brassy minnow	0.96	116 (4.8)	0.40	April 25	671	4.0	Falke and Fausch (*unpublished data*)
fathead minnow	0.96	121 (7.4)	0.33	April 30	741	3.6	Snyder et al. (1977)
plains killifish	0.94	131 (4.7)	0.33	May 10	893	5.7	Koster (1948)

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Table 3.3. Naïve estimates based on raw data ($\tilde{\psi}^1$, $\tilde{\psi}^2$, $\tilde{\psi}^{1*2}$), and parameter estimates ($\hat{\psi}^1$, $\hat{\psi}^2$, $\hat{\psi}^{1*2}$, $\hat{\rho}$, $\hat{\delta}$) with standard errors. Estimates are from top multiple-state occupancy models, fit to abundance data for larval Great Plains stream fish from 45 spawning habitats in the Arikaree River, CO in 2007. See text for parameter descriptions.

Species	$\tilde{\psi}^1$	$\tilde{\psi}^2$	$\tilde{\psi}^{1*2}$	$\hat{\psi}^1$	$\hat{\psi}^2$	$\hat{\psi}^{1*2}$	$\hat{\rho}$	$\hat{\delta}$
central stoneroller	0.76 (n/a)	0.62 (n/a)	0.47 (n/a)	0.94 (0.29)	0.69 (0.22)	0.65 (0.07)	0.64 (0.06)	0.73 (0.05)
orangethroat darter	0.47 (n/a)	0.22 (n/a)	0.10 (n/a)	0.63 (0.16)	0.51 (0.12)	0.42 (0.16)	0.38 (0.08)	0.93 (0.07)
plains killifish	0.60 (n/a)	0.22 (n/a)	0.13 (n/a)	0.62 (0.08)	0.37 (0.10)	0.23 (0.06)	0.83 (0.03)	0.64 (0.12)
brassy minnow	0.87 (n/a)	0.47 (n/a)	0.40 (n/a)	0.89 (0.05)	0.57 (0.09)	0.50 (0.08)	0.87 (0.03)	0.43 (0.05)
fathead minnow	0.91 (n/a)	0.44 (n/a)	0.40 (n/a)	0.93 (0.04)	0.53 (0.09)	0.49 (0.09)	0.74 (0.05)	0.49 (0.08)
creek chub	0.80 (n/a)	0.56 (n/a)	0.44 (n/a)	0.82 (0.04)	0.65 (0.09)	0.53 (0.15)	0.26 (0.03)	0.63 (0.07)

Table 3.4. Results of multiple-state occupancy models for larvae of six species of Great Plains stream fish in the Arikaree River in 2007. Model results for each species are ranked by AIC$_c$ (w_i = Akaike weight), from best to worst. Direction of effects for each covariate is indicated by + (positive) or - (negative). The global model for each species (M0) is presented for reference. Covariate acronyms are: CM = channel margin habitat, BW = backwater habitat, MS = middle segment, DS = downstream segment, DRY = habitats dried. See Table 3.1 for a description of the models.

| | Occupancy | | | | | | Detection | Model results | | | |
| | Local Scale | | | Segment Scale | | | | | | | |
Model	Area	Depth	Habitat	GSDD	Segment	Persistence	Depth	K	AICc	ΔAICc	w_i
central stoneroller											
M6	(+)	(-)	(CM)				(-)	20	310.69	0.00	0.76
M2	(+)						(-)	16	313.52	2.83	0.18
M5			(CM)				(-)	16	317.38	6.69	0.03
M0								30	415.04	109.89	<0.01
orangethroat darter											
M3		(-)						17	225.79	0.00	0.63
M2	(-)							17	228.51	2.71	0.16
M5			(CM)					17	229.04	3.32	0.12
M0								30	360.75	134.95	<0.01
plains killifish											
M5			(CM)		(MS/DS)			15	180.79	0.00	0.63
M8				(+)	(MS/DS)	(DRY)		17	182.86	2.07	0.22
M7					(MS/DS)			14	184.68	3.89	0.09
M0								30	250.74	69.94	<0.01

Table 3.4. (cont.)

		Occupancy						Detection	Model results			
		Local Scale			Segment Scale							
	Model	Area	Depth	Habitat	GSDD	Segment	Persistence	Depth	K	AICc	ΔAICc	w_i
Fathead minnow	M10			(CM)		(MS)		(-)	20	363.71	0.00	0.73
	M2		(+)					(-)	16	366.06	2.36	0.22
	M5			(CM)				(-)	16	370.14	6.44	0.03
	M0								30	462.41	98.71	<0.01
Creek chub	M1								11	223.81	0.00	0.72
	M3		(+)						13	226.09	2.28	0.23
	M2	(-)							13	231.50	7.69	0.02
	M0								30	288.96	65.15	<0.01

Table 3.5. Model selection of joint habitat suitability-occupancy models for larvae of six fish species in the Arikaree River, CO, during 2005-2007. Model results for each species are ranked by AIC_c (w_i = Akaike weight), from best to worst. See text for model descriptions.

Species	No. parameters	-2*Log-likelihood	AIC_c	ΔAIC_c	w_i
central stoneroller					
$\psi^{[0=1=2]} R^{[0=1=2]} \delta(OCC)$	13	572.97	598.97	0	0.3466
$\psi^{[0,1=2]} R^{[0=1=2]} \delta(OCC)$	14	571.88	599.88	0.91	0.2199
$\psi^{[0=1=2]} R^{[0=1,2]} \delta(OCC)$	15	570.97	600.97	2.00	0.1275
$\psi^{[0,1=2]} R^{[0=1,2]} \delta(OCC)$	16	569.80	601.80	2.83	0.0842
orangethroat darter					
$\psi^{[0=1=2]} R^{[0=1=2]} \delta(OCC)$	12	308.97	332.97	0	0.4706
$\psi^{[0,1=2]} R^{[0=1=2]} \delta(OCC)$	13	307.89	333.89	0.92	0.2971
$\psi^{[0=1=2]} R^{[0=1,2]} \delta(OCC)$	14	308.29	336.29	3.32	0.0895
$\psi^{[0,1=2]} R^{[0=1,2]} \delta(OCC)$	15	307.23	337.23	4.26	0.0559
brassy minnow					
$\psi^{[0=1=2]} R^{[0=1=2]} \delta(OCC)$	13	576.44	602.44	0	0.2451
$\psi^{[0=1=2]} R^{[0=1,2]} \delta(OCC)$	15	572.84	602.84	0.40	0.2007
$\psi^{[0,1=2]} R^{[0,1,2]} \delta(OCC)$	17	569.32	603.32	0.88	0.1579
$\psi^{[0,1=2]} R^{[0=1=2]} \delta(OCC)$	14	575.36	603.36	0.92	0.1547
$\psi^{[0,1=2]} R^{[0=1,2]} \delta(OCC)$	16	571.66	603.66	1.22	0.1332
$\psi^{[0,1=2]} R^{[0,1,2]} \delta(OCC)$	18	568.08	604.08	1.64	0.1080
plains killifish					
$\psi^{[0=1=2]} R^{[0,1,2]} \delta(OCC)$	16	338.61	370.61	0	0.5062
$\psi^{[0,1=2]} R^{[0,1,2]} \delta(OCC)$	17	336.66	370.66	0.05	0.4937
fathead minnow					
$\psi^{[0=1=2]} R^{[0=1=2]} \delta(.)$	10	478.34	498.34	0	0.2519
$\psi^{[0=1=2]} R^{[0=1=2]} \delta(YEAR)$	12	475.22	499.22	0.88	0.1622
$\psi^{[0,1=2]} R^{[0=1=2]} \delta(.)$	11	477.26	499.26	0.92	0.1590
$\psi^{[0,1=2]} R^{[0=1=2]} \delta(YEAR)$	13	474.14	500.14	1.80	0.1024
creek chub					
$\psi^{[0=1=2]} R^{[0=1=2]} \delta(OCC)$	12	336.83	360.83	0	0.4857
$\psi^{[0,1=2]} R^{[0=1=2]} \delta(OCC)$	13	335.43	361.43	0.60	0.3598
$\psi^{[0=1=2]} R^{[0=1,2]} \delta(OCC)$	14	336.75	364.75	3.92	0.0684
$\psi^{[0,1=2]} R^{[0=1,2]} \delta(OCC)$	15	335.35	365.35	4.52	0.0507

Table 3.6. Model averaged extinction (ε) and colonization probabilities, their components, and the probability of staying wet and occupied (η) for 59 spawning habitats in the Arikaree River, CO, from 2005-2006 (period 1), and 2006-2007 (period 2). Probabilities are shown for six plains stream fish species along river segments fed by groundwater or not. Dry or Wet describes spawning habitat suitability in year $t-1$, and whether it was occupied (O) or unoccupied (U) by each species.

| | Extinction | | | | | | Colonization | | | | | |
| | Dry | | Wet(U) | | (ε) | | Dry>Wet(O) | | Wet(U)>Wet(O) | | Wet(O)>Wet(O) (η) | |
	1	2	1	2	1	2	1	2	1	2	1	2
Groundwater fed segments												
central stoneroller	0.39	0.00	0.41	0.31	0.79	0.31	0.18	0.66	0.21	0.69	0.23	0.75
orangethroat darter	0.39	0.00	0.51	0.62	0.90	0.62	0.08	0.37	0.10	0.38	0.08	0.37
plains killifish	0.37	0.00	0.21	0.20	0.59	0.20	0.33	0.79	0.34	0.07	0.41	0.80
brassy minnow	0.39	0.00	0.13	0.10	0.52	0.10	0.27	0.77	0.06	0.86	0.48	0.84
fathead minnow	0.39	0.00	0.18	0.20	0.57	0.20	0.38	0.77	0.43	0.80	0.43	0.80
creek chub	0.34	0.00	0.56	0.28	0.91	0.28	0.08	0.70	0.09	0.73	0.09	0.72
Segments not fed by groundwater												
central stoneroller	0.83	0.00	0.11	0.31	0.94	0.31	0.04	0.66	0.06	0.69	0.06	0.75
orangethroat darter	0.83	0.00	0.14	0.62	0.97	0.62	0.02	0.37	0.03	0.38	0.02	0.37
plains killifish	0.82	0.00	0.06	0.20	0.88	0.20	0.08	0.79	0.02	0.07	0.12	0.80
brassy minnow	0.83	0.00	0.04	0.10	0.87	0.10	0.07	0.77	0.09	0.86	0.13	0.84
fathead minnow	0.83	0.00	0.05	0.20	0.88	0.20	0.09	0.77	0.12	0.80	0.12	0.80
creek chub	0.83	0.00	0.15	0.28	0.98	0.28	0.02	0.70	0.02	0.73	0.02	0.72

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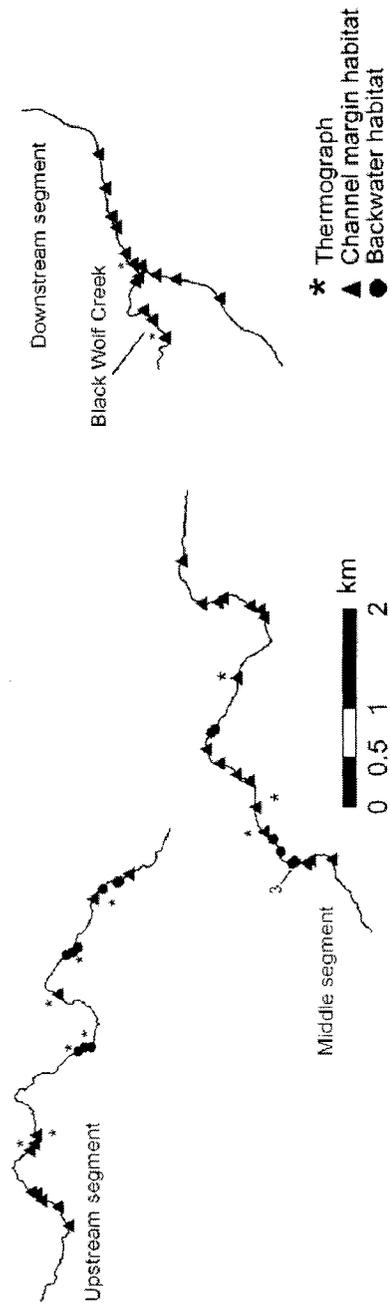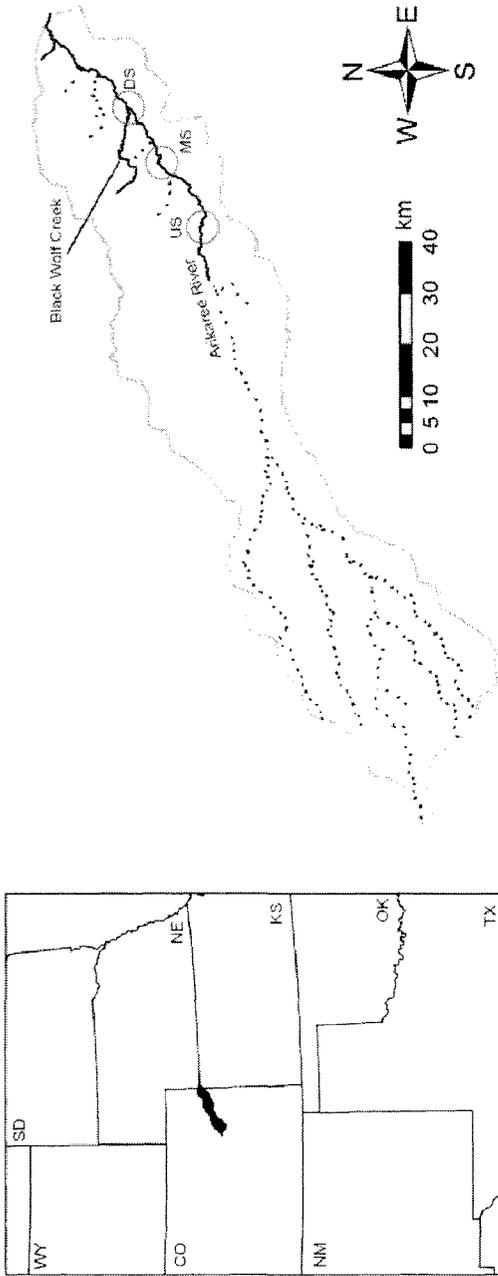
Figures

Figure 3.1: Study area in the Arikaree River basin in northeastern Colorado (top left panel), and the location of three 6.4-km study segments (US = Upstream segment; MS = Middle segment; DS = Downstream segment) and Black Wolf Creek (top right panel). Solid lines in the lower basin illustrate where the potential for perennial stream flow remains (based on Falke et al. *in review*). In the lower panel the locations of 59 spawning habitats and 12 thermographs sampled across three years in the three segments are shown. A cluster of 3 backwaters in the upper middle segment are indicated.

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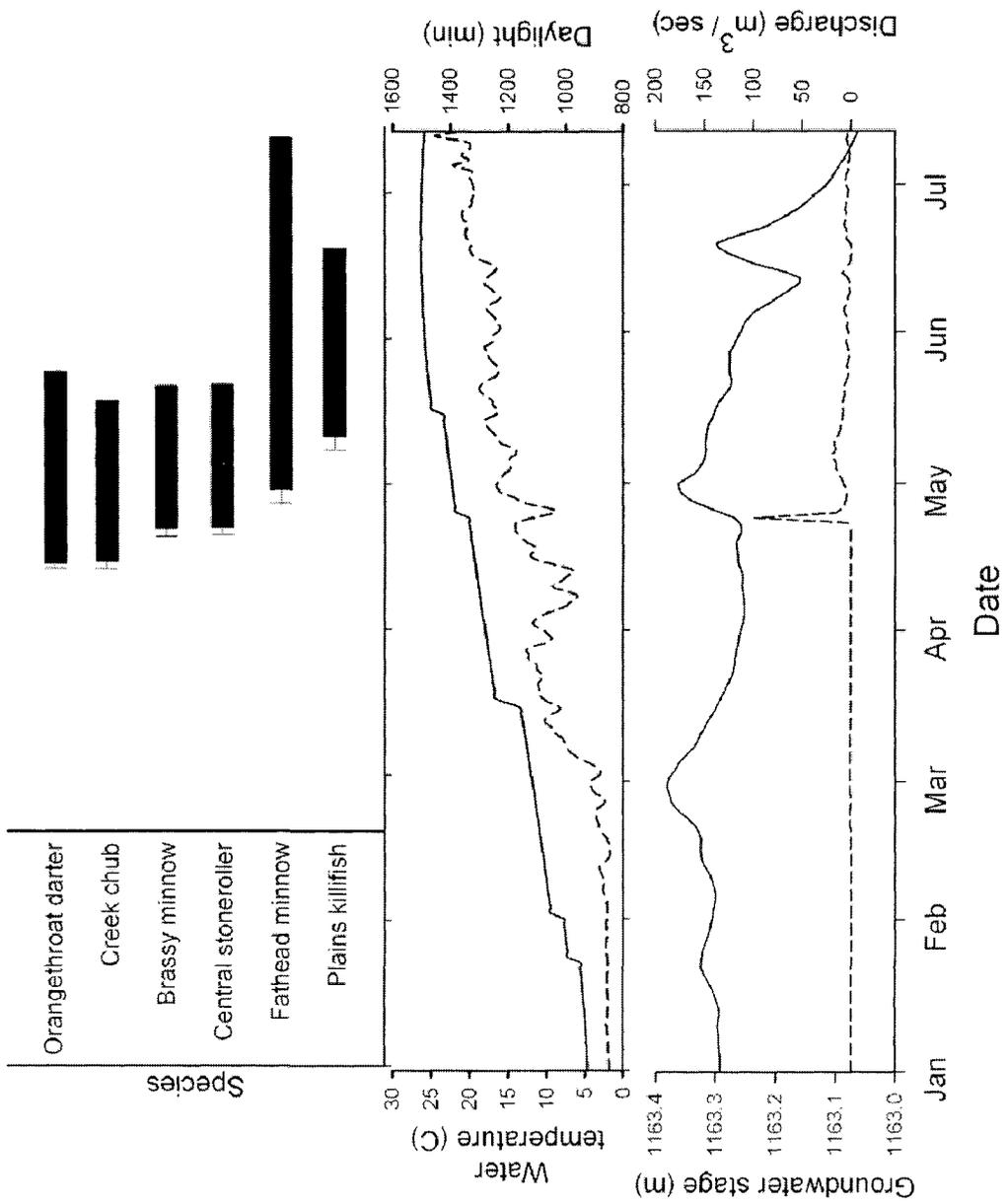
Figure 3.2: Spawning phenology for six plains fish species in the Arikaree River, Colorado. Top panel is the date of hatching initiation for each species ($\pm$ 1 SD), and the estimated duration of hatching. In the middle panel are mean water temperature collected across 12 thermographs (dashed line) and cumulative photoperiod (minutes of daylight; solid line). Lower panel is alluvial groundwater stage in the upstream segment (see Figure 3.1; meters above sea level; solid line), and daily discharge from USGS gauge 6821500 (m^3 / sec; dashed line). All data are from 2007.
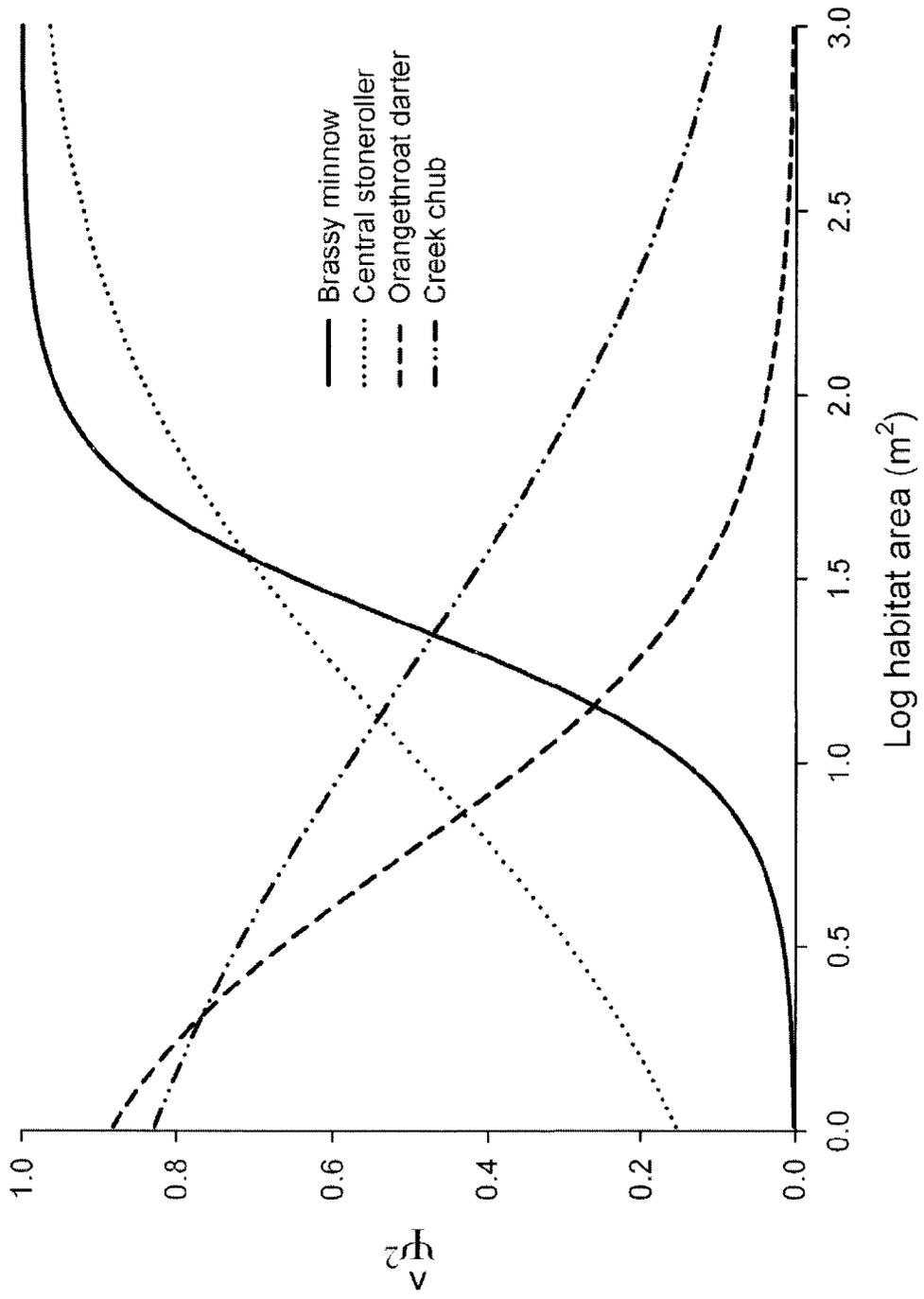
Figure 3.3: Probability of occupancy at high abundance ($\hat{\psi}^2$) of larvae of four plains fish species across 45 spawning habitats in the

Arikaree River, Colorado in 2007 as a function of spawning habitat area (m^2).
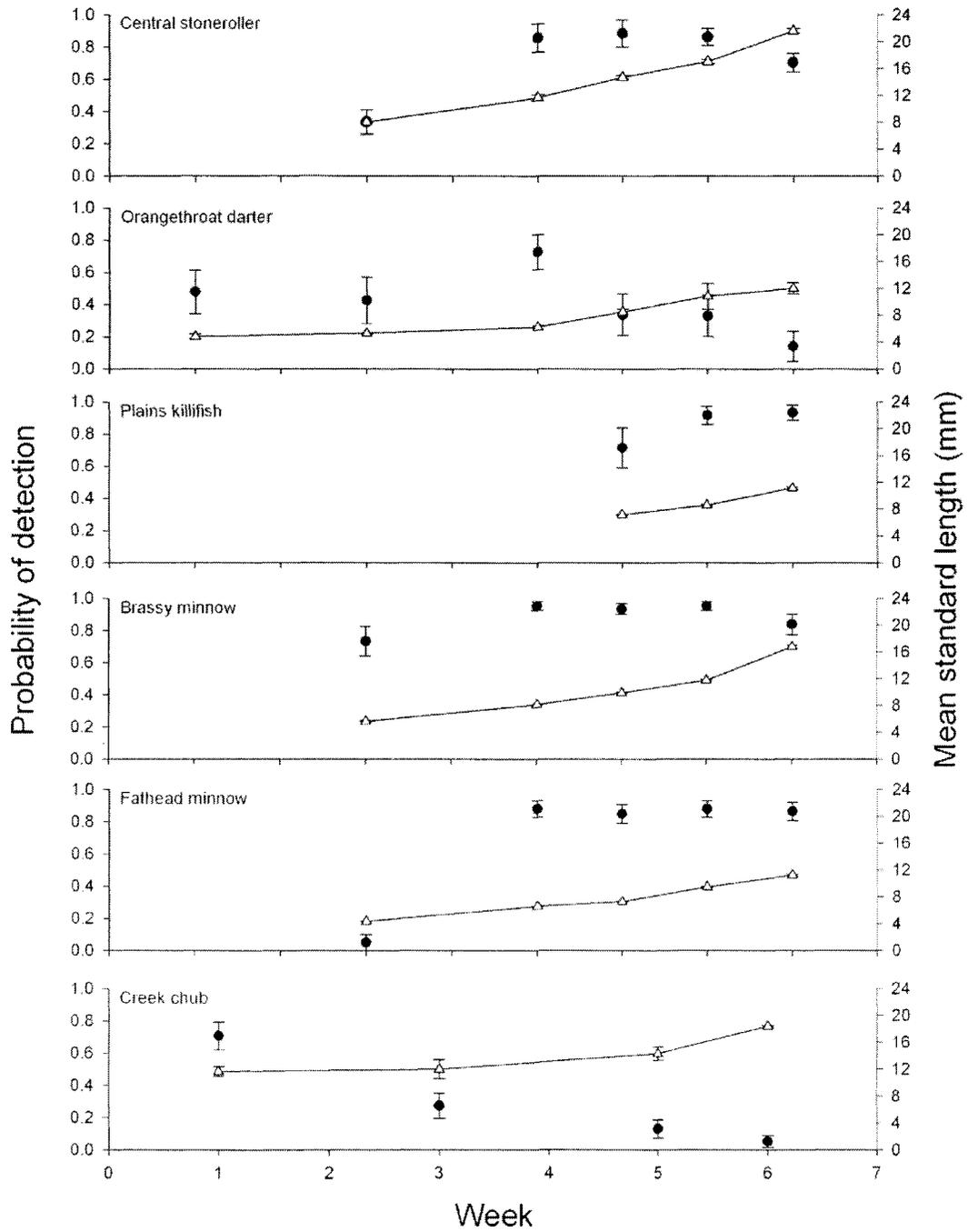
Figure 3.4: Probability of detection of larvae of six plains fish species (circles; left y-axis) and mean standard length (mm; triangles; right y-axis) in spawning habitats in the Arikaree River, Colorado across six weeks of sampling during late spring to early summer 2007.
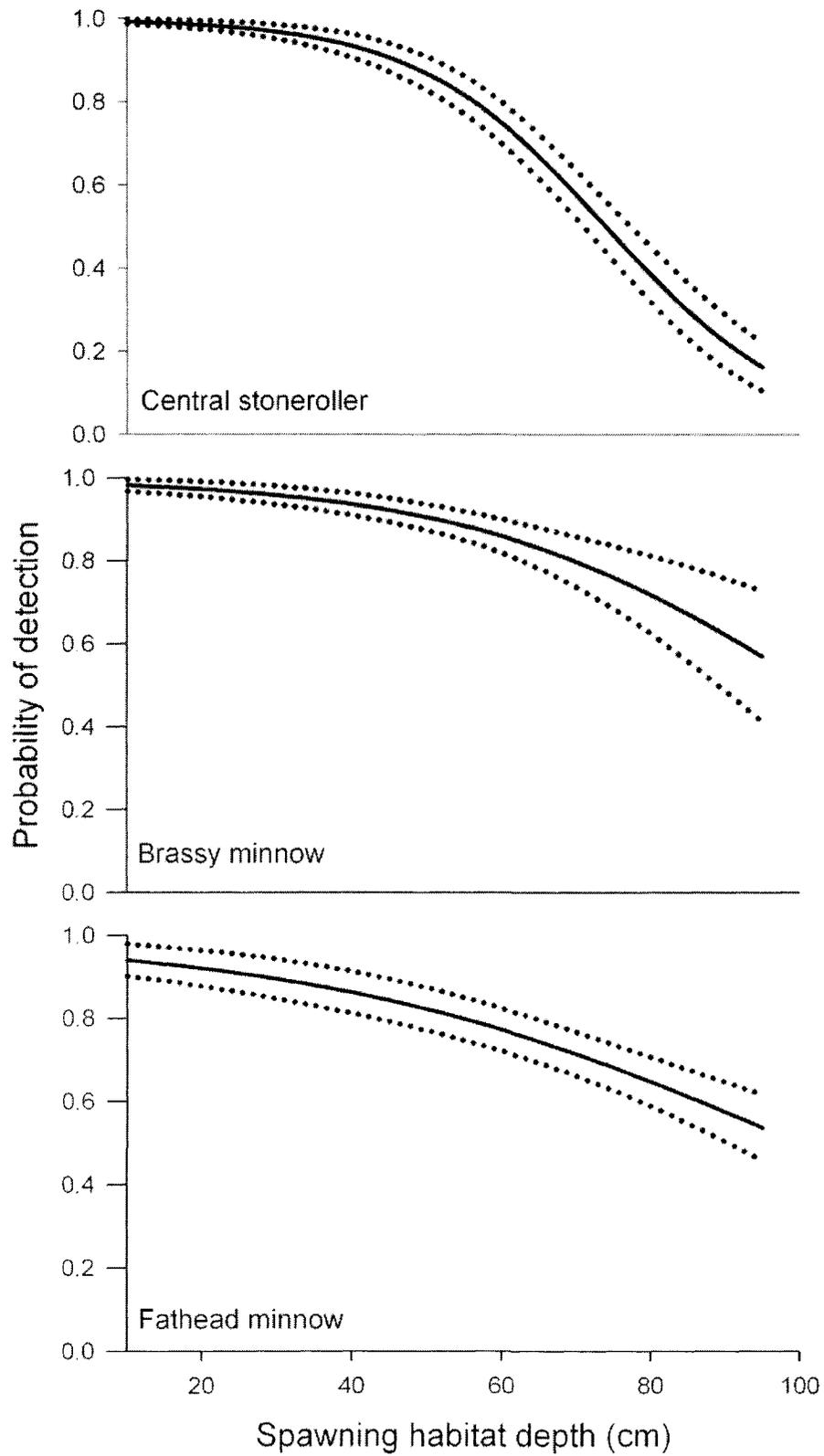
Figure 3.5: Probability of detection of larvae of three species of plains stream fish as a function of spawning habitat depth. Dotted lines represent 90% confidence intervals.

Chapter 4: Effects of habitat drying on growth, survival, and recruitment of brassy minnow *Hybognathus hankinsoni* across a Great Plains riverscape

Abstract

Groundwater pumping for irrigated agriculture is a major disturbance in Great Plains streams, altering hydrologic regimes and fragmenting habitats for fishes. Early life stages of fishes are particularly sensitive to altered flow regimes, and the larval stage may serve as a bottleneck that limits recruitment to reproductively-mature life stages. I investigated how growth and survival of brassy minnow *Hybognathus hankinsoni* larvae in the Arikaree River, Colorado, varied among three long river segments that differed in hydrology, and how climate influenced drying rates of spawning and rearing habitats, across three years. Based on otolith increment analysis, I found that brassy minnow spawned in backwater habitats within a discrete period from mid-April to late May. Timing of spawning and relative growth of larvae were influenced by climate and the hydrologic context of the river segment. Brassy minnow spawned earlier in warmer, drier years, and growth rates were lower compared to wet years. Similarly, survival of larvae was higher in wet years vs. dry years. At the scale of individual cohorts of larvae, survival was higher in spawning habitats that were larger, dried slower, and for cohorts that hatched in the middle of the spawning period. Overall, we found that interannual variability in climate, and the hydrologic context of segments along the riverscape, have a strong influence on habitat availability and recruitment of brassy minnow in the Arikaree River. I suggest that conservation efforts should focus on maintaining spawning, rearing, and refuge habitats that are critical to brassy minnow population persistence. Effective conservation will require explicit consideration of the unique adaptations of these organisms to harsh environments, and the understanding that these adaptations can only protect these fish populations above a certain threshold in human-caused disturbance.

Introduction

Water abstraction for human use is a major problem affecting rivers and streams worldwide, and has resulted in losses of natural flow periodicity, increased risk of drought, and severed upstream-downstream linkages (Benke 1990; Malmqvist and Rundle 2002). For stream fishes, this has resulted in habitat loss and reduced dispersal opportunities among habitats. Successful reproduction and survival of early life stages of stream fishes are strongly influenced by hydrologic variability (Starret 1951; Schlosser 1985; Mion et al. 1998). As a result, early life history stages of fish are particularly sensitive to altered hydrologic regimes (Scheidegger and Bain 1995; Freeman et al. 2001; Bestgen et al. 2006).

Water withdrawals are an especially important issue in Great Plains streams where water diversions and agricultural irrigation pumping are widespread (Gutentag et al. 1984; McGuire et al. 2003; *Chapter 1*). Across the High Plains aquifer that underlies much of the Great Plains, pumping has caused high rates of groundwater decline, resulting in reduced flows in streams that are hydrologically connected to groundwater. Although adapted to harsh conditions common to Great Plains streams, native fishes are often near the threshold of their physicochemical tolerance (Matthews 1985; Matthews and Zimmerman 1990). Additionally, habitat loss and fragmentation have lead to declining populations of these fishes (Fausch and Bestgen 1997; Hubert and Gordon 2007; *Chapter 1*). Therefore, knowledge of factors that influence recruitment, growth, and survival in the context of drying habitats is important for conserving these species.

Groundwater is a key for fish persistence in dryland streams because it maintains base flows and connections among habitats along the riverscape. Furthermore,

groundwater moderates stream water temperatures, keeping habitats cooler during summer, and preventing them from freezing completely in the winter (Labbe and Fausch 2000; Schuerer et al. 2003). Previously, I found that persistence of spawning habitats was increased in groundwater-fed river segments through years of variable climatic conditions (*Chapter 3*). However, the specific mechanisms that control spawning, growth, and survival of early life stages in groundwater-fed habitats in plains streams is unknown.

Spawning and early life history stages in fishes are critical periods that may serve as bottlenecks that limit recruitment to reproductively-mature life stages (May 1973; Ludsin and DeVries 1997; Halpern et al. 2005). In streams, characteristics of the physical environment such as discharge, water temperature, and precipitation have been shown to be important mechanisms limiting survival of larval fishes (Crecco and Savoy 1984; Mion et al. 1998; Leach and Houde 1999). There is some evidence that survival of larval Great Plains fishes varies among years, rivers, and species (Wilde and Durham 2008). However, little is known of the relative importance of environmental factors operating across broad spatial scales that may influence survival of larval fishes in Great Plains streams.

The brassy minnow *Hybognathus hankinsoni* is listed as a threatened species in Colorado because its distribution and population levels are declining (Scheurer 2001; CDOW 2007), and populations are likely to decline more in the future (*Chapter 1*). The decline in brassy minnow in the Great Plains of eastern Colorado could be due to recruitment failure brought on by habitat fragmentation and loss owing to altered hydrology. Population dynamics of this species are known to differ among segments

with different hydrology in western Great Plains streams (Scheurer et al. 2003; *Chapter 3*). Additionally, there is evidence that brassy minnow use multiple habitat types for spawning and early rearing, juvenile and adult growth, and refuge during harsh periods (Scheurer et al. 2003). However, basic early life history and spawning habitat requirements are poorly understood for this species, and the factors that influence population regulation at the larval stage are likewise unknown.

The goals of this study were to quantify when and where brassy minnow spawn and rear, and investigate how growth and survival of larvae vary among river segments that differ in hydrology, and among years that differ in climate, in the Arikaree River, Colorado, a Great Plains stream. My specific objectives were to 1) measure the rate of spawning habitat drying and investigate the importance of shallow alluvial groundwater for maintaining those habitats, 2) determine the period of hatching and population age structure, 3) explore how relative growth and survival of larvae were influenced by hydrology and climate, and 4) examine what environmental factors influenced survival among cohorts of larval brassy minnow. Finally, based on these results, I discuss implications for brassy minnow recruitment in Great Plains streams in the future as anthropogenic habitat drying continues (*Chapter 1*) and spawning and rearing habitat availability and suitability decrease.

Methods

Study area—The study area was restricted to the lower half of the Arikaree River basin, Colorado because segments with the potential for perennial streamflow and fish habitats occur only in the lower 110 km of the basin (Figure 4.1). I sampled larval fishes

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and spawning habitats within three 6.4-km segments selected to represent a gradient in intermittency, which are described in detail in Scheurer et al. (2003) and *Chapter 1*. The upstream segment is perennial, with long reaches that sustain flow in all but the driest periods and is characterized by alternating runs and deep, persistent pools. Beaver *Castor canadensis* have created large pools in some reaches. The middle segment is largely intermittent most of the year. Its upper portion has deep, well developed pools, whereas the lower portion is wide and shallow, with sand substrate. The downstream segment dries almost completely by early summer, although a few pools persist upstream in some years. In addition, a perennial tributary, Black Wolf Creek, often sustains a short reach of flowing habitat in the middle of this segment (Figure 4.1).

Sampling backwater and refuge pool habitats—I investigated the effects of seasonal drying on spawning habitats for brassy minnow along the three study segments and in the lower 1 km of Black Wolf Creek during spring and summer 2005-2007. In late May 2005 and 2006, and late March 2007, potential spawning and rearing habitats in each segment were identified, classified into backwater and channel margin habitats, and georeferenced using a Global Positioning System. Each habitat was then surveyed semi-weekly through the first or second week of July. Backwaters were relatively large, deep, off-channel habitats connected to the main channel but with little or no flow. Channel-margin habitats were relatively small, shallow, flowing areas at margins of the main channel where higher spring flows inundated terrestrial vegetation. In backwater habitats during each sampling occasion I measured surface area, maximum depth, conductivity, and ambient water temperatures at the surface and just above the substrate. Surface area was quantified by (1) measuring length along the longest axis of the backwater, (2)

dividing the length evenly into three perpendicular transects, and (3) measuring width at the midpoint of each transect. Area (m^2) was calculated as the average width times length. Maximum depth was measured with a stadia rod (cm), and conductivity (μS) was measured using a Yellow Springs Instruments Systems Inc. model 85 multimeter. Ambient surface and substrate water temperature (nearest 0.1 °C) was recorded with a digital thermometer (Cooper-Atkins Corp., Versatuff Plus 396). Additionally, water temperature was measured hourly during 2007 (Jan-Aug) using thermographs (Onset Corp., HOBO Water Temp Pro v1) installed in backwater and main channel habitats (upstream segment, n = 7; middle segment, n = 3; downstream and Black Wolf Creek, n = 1).

Pool habitats for juvenile and adult fishes along the entire upstream and middle segments were censused in late July of each year. In the upstream segment, a subset of pools (N = 31 of 172 in 2005, N = 29 of 180 in 2006, N = 19 of 218 in 2007) were randomly selected from two pool size categories (small and large). In the middle segment, all pools were sampled in all years (N = 9 in 2005, N = 27 in 2006, N = 29 in 2007).

In August 2005 (Figure 4.1), I installed six groundwater monitoring wells spaced evenly along the upstream segment to investigate the relationship between groundwater stage and spawning habitat size. The wells were approximately 10 m from the stream channel, and consisted of three 0.9 m sections of 5 cm (diameter) PVC pipe. The lower section of well casing was slotted (0.5 cm spacing, 0.03 cm slot width) to allow groundwater to enter the well. A conical PVC cap was fit to the bottom of each well

casing. Depth to groundwater (cm) was measured using a steel tape during spawning habitat surveys.

Sampling larval and adult fishes—Larval brassy minnow were sampled semi-weekly beginning in late May 2005 and 2006, and late March 2007, and ending the first or second week of July, in spawning and rearing habitats previously identified. In 2005, larvae were collected from both channel margins and backwaters using aquarium dipnets (20 cm x 16 cm; 250 μm-mesh) during daytime spawning habitat surveys. In 2006 and 2007, in shallow backwaters (< 30 cm maximum depth) larvae were collected using dipnetting, whereas in deeper backwaters larvae were sampled at night using floating quatrefoil-type light traps (design modified from Kilgore 1994). Four 4-mm entrance slots allowed larvae to enter an inner chamber that consisted of four 7.5-cm diameter Plexiglas tubes 14 cm long. Traps were attached at the top to a 6-cm thick Styrofoam ring and contained yellow glow sticks to attract fish larvae. Upon retrieval, trap contents were flushed into a lower plastic bowl from which water drained through screened holes. Traps were deployed at fixed locations in backwaters at dusk for approximately 2 h. Laboratory experiments (see below) indicated light traps were effective over an area of at least 28 m^2, so multiple traps were used in backwaters > 28 m^2. A paired comparison using data collected in 2007 showed that estimates of brassy minnow size structure and relative abundance collected using the two gears were similar, so I pooled data collected using both gears for 2007 (*Chapter 3*).

I sampled young-of-year and adult brassy minnow in refuge pools within study segments in August of 2005 through 2007 to quantify recruitment and population structure. No pools were present in the downstream segment during any adult fish

sampling. Brassy minnow were collected using three-pass depletion seining (4.8-mm mesh), except in 2005 when two passes were made per pool. Pools were blocked at both ends using block nets (with the same mesh) to prevent fish movement. All seining passes were conducted from upstream to downstream. All brassy minnow were enumerated separately for each pass, a subsample of the total number collected in each segment were measured to TL and FL (mm), and all fish were released unharmed.

Light trap validation—I tested the efficacy of the light trap design in capturing larval fishes in a controlled laboratory experiment (Foothills Fishery Facility, Colorado State University). I released a known number of four-day-old fathead minnow (*Pimephales promelas*) larvae (N = 30; approximately 5 mm SL) at fixed distances away from a light trap, and counted the number captured in the trap after 2 h. Two fiberglass raceways (3.0 m x 0.45 m) were painted matte black to simulate the dark substrate in Arikaree River backwater habitats, and to reduce reflection that could interfere with larval attraction. Impermeable plastic dividers were used to create four release distances: adjacent (0.75 m), short (1.5 m), medium (2.25 m), and long (3.0 m). For all treatments, the light trap was placed midway between the end of the raceway and the first partition (ca. 0.37 m from the partition). Experiments were conducted at dusk. Two replicates of each treatment were conducted over four days total.

Validation of deposition and frequency of brassy minnow otolith daily rings— Knowledge of the date of first otolith increment deposition, and the frequency of increment deposition, are critical factors in reducing bias in the back calculation of age from otolith microstructures (Campana and Nielson 1985). I validated my estimates of hatching dates for field collected brassy minnow by spawning and rearing brassy minnow

in the laboratory and evaluating otolith increment deposition over time. I collected

sexually mature brassy minnow adults using minnow traps from a pond on the Foothills

Campus of Colorado State University. These fish were progeny of fish originally

collected from the Arikaree River. Only fish that showed secondary sexual

characteristics (males with yellow pigmented fins, females with distended abdomens)

were retained. I spawned the fish manually in the laboratory by dry-stripping eggs from

females and combining them with milt from 1-2 males in a petri dish, after which a few

milliliters of water were added. The eggs adhered firmly to the petri dish after

fertilization (J. Falke, *personal observation*), so I did not transfer them to another

medium. They water hardened in about 1 h, and hatched in approximately three days. I

split the larvae into two batches, and continued to rear them under two temperature

regimes. The first was constant at ambient room temperature (20 °C), whereas the

second fluctuated between 18 and 24 °C on a diel cycle. The second treatment was

conducted to facilitate identification of daily rings, which are thought to be accentuated

by diel temperature fluctuations (Bestgen and Bundy 1998). Larvae in both treatments

were reared under a natural photoperiod (14.5 h light : 9.5 h dark). They were initially

fed a diet of ground flake food, and then switched to newly hatched brine shrimp

(*Artemia* spp.) once the larvae were large enough to capture these prey items. For both

treatments, I recorded embryo development, measured growth of larvae, and preserved a

series of four fish per day from each treatment in 100% ethanol. For each preserved

specimen, I measured TL (mm) and SL (mm), extracted otoliths, recorded the date of first

increment deposition, and counted daily rings as described below.

Larval brassy minnow age and growth—I measured length-at-age, hatching date, and relative growth for larval brassy minnow collected in the field during 2005-2007. After measuring TL and SL using digital calipers (±0.01 mm) , right and left sagittal otoliths were dissected from fish and stored in a drop of immersion oil on a standard microscope slide. A compound light microscope at 40X magnification was used to count daily rings on right otoliths. Two readers made independent estimates of the total number of otolith daily rings for each otolith. Estimates were compared, and those that exceeded 10% difference were discarded. Final ages for individual larvae were the average of the two estimates.

Statistical analyses—I compared hatching dates, growth, and survival of brassy minnow larvae among segments and across years and related them to habitat drying. I estimated the rate of drying for individual backwater habitats in the upstream and middle segments each year from the slope of a linear regression of backwater area (m^2) vs. time (days). I then compared mean backwater drying rates among segments and years using ANOVA. If differences were detected, I used Tukey's HSD for multiple comparisons.

I used catch curves to estimate survival rates for brassy minnow larvae collected in the three years (Essig and Cole 1986). The catch curves were calculated from the descending limb of increment-frequency histograms. Daily survival rate (S) was calculated as $S = e^{-Z}$, where e is the base of natural logarithms and Z is the slope of the catch curve. To compare survival among years, all larvae collected across segments within a year were combined. I then evaluated differences in S among years using ANCOVA (for $\alpha < 0.05$). If differences were detected, I used Tukey's HSD for multiple comparisons to evaluate in which year S differed.

In a previous study, I found that brassy minnow larvae occupied backwater spawning habitats at high abundance, whereas they were found at low abundance in channel margin habitats (*Chapter 3*). Therefore, I modeled the influence of backwater spawning habitat characteristics on survival of cohorts of brassy minnow collected in 2007. Following age assignment (see *Results-Hatching date distributions*), I categorized larvae to cohorts based on an overall hatching date distribution. Hatching dates for 98% of larvae were between 16 April and 21 May 2007. Subsequently, I split this 36-d period into three 12-d periods, and assigned larvae into cohorts (early, middle, or late). I then calculated daily survival rates for each cohort in each backwater using catch curves as above.

I modeled cohort survival as a function of a mixture of backwater habitat characteristics and cohort specific predictors. Values for survival were transformed by calculating the arcsine of their square root. Backwater characteristics were rate of drying across weeks (see above; RATE), and backwater area (AREA) and maximum depth (DEPTH) during the first week of habitat sampling. I also included the abundance of larvae (total number collected in a respective backwater across all weeks; ABUN) to investigate density dependence. Cohort-specific predictors were mean hatching date (MHD) for the cohort, and cumulative growing season degree days (GSDD). The GSDD were calculated by summing the average daily temperature (°C) from January 1 to the mean hatching date. Temperature data was derived from the thermograph nearest to each backwater (Figure 4.1). I also included a quadratic term for MHD and GSDD because I hypothesized survival might be lower early or late in spawning period. Finally, I included a categorical variable identifying the segment (upstream or middle) in which the

cohort hatched. I constructed a set of 22 *a priori* candidate models that contained sets of explanatory variables that were of biological significance (Burnham and Anderson 2002). I used Akaike's information-criterion (AIC) to select the best approximating model by comparing each of the candidate models simultaneously. The AIC scores were adjusted for bias due to small sample size (AIC_c), and Akaike weights (w_i) were calculated. Thus, the model with the lowest AIC_c and the highest w_i was considered the best approximating model. All analyses were conducted using Proc GLM in SAS ver. 9.0 (SAS Institute).

Results

Habitat availability and drying

There was a major drought on the eastern plains of Colorado beginning in 2000 (*Chapter 1*), and drought conditions persisted past 2007, the final year of my study. Precipitation and flows were highest for 2005 (53.2 cm and 0.05 m^3/sec, respectively), lowest during 2006 (32.8 cm and 0.02 m^3/sec), and intermediate during 2007 (33.0 cm and 0.04 m^3/sec). However, abundant snowfall in December 2006 contributed to relatively higher flows in spring 2007 (*Chapter 1*). These higher flows were reflected in the amount and drying rate of spawning habitat during 2007 (see below).

Fifty-nine individual spawning habitats were measured in the three segments and Black Wolf Creek, during the 3-yr study (backwaters, N = 16; channel margins, N = 43; Table 4.1). No backwater habitats were ever present in the downstream segment or Black Wolf Creek. Backwater habitats were clustered in the lower half of the upstream segment, and the upper one-third of the middle segment. The number and total area of backwater habitats varied among years, and corresponded to climate conditions. Total

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backwater area was lowest in the dry conditions of 2006, but higher winter precipitation during December 2006 resulted in the highest total backwater area during spring and early summer 2007. Total backwater area in the upstream and middle segments in 2007 was about twice, and more than four times, the amount available in 2006 in those segments, respectively.

I found that many backwater and channel margin habitats dried completely by mid-July in all segments and years (Table 4.1). Due to their shallow, ephemeral nature, most (50-100%) channel margin habitats dried by the end of sampling each year. Fewer backwater habitats dried completely, and fewer dried in the upstream segment than in the middle segment (0-25 % vs. 33-80%). Backwaters in the middle segment dried faster than those in the upstream segment when all three years were combined ($F = 12.88$, $P = 0.001$ by oneway ANOVA). Among years, backwaters dried fastest in 2007 when the two segments were combined (vs. 2005; $P = 0.031$; vs. 2006, $P = 0.045$). There was no difference in the rate of backwater drying between 2005 and 2006 ($P = 0.931$). Across segments and years, the rate of drying was highest in the middle segment in 2007. Although the total area of backwater habitat available was highest during spring 2007 in the middle segment, this area dried rapidly.

I compiled hourly temperatures from January through July 2007 for five backwaters and six main channel habitats in the upstream and middle segment, and Black Wolf Creek (Figure 4.2). In the upstream segment, main channel and backwater habitat thermal regimes were similar throughout this period. In the middle segment, backwater and main channel temperatures were similar through the end of April, after which temperatures in one backwater remained stable, and cooler than temperatures at two main

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channel sites. The highest recorded temperatures occurred in Black Wolf Creek in late June through July.

Groundwater and spawning habitat

I found that backwater habitats in the upstream segment were fed by groundwater, and generally dried as groundwater levels declined during spring and early summer 2006. Additionally, the relationship between backwater spawning habitat area and shallow near-channel groundwater stage reflected patterns of reach-scale habitat connectivity. I pooled the area for two to four backwaters near each of four wells and compared the percent backwater area remaining to the groundwater stage for five consecutive weeks. I also recorded the connectivity (flowing = connected pools, intermittent = disconnected pools, dry = dry channel) of the reach in which the well and backwaters were located during the final week of sampling. No backwaters were located near the two most upstream wells, and there were no dry reaches during these weeks in the upstream segment. In three intermittent reaches, backwater area and groundwater stage declined linearly over time (Figure 4.3). The percent of backwater area remaining at the end of June was 27%, 15%, and 57% of the original area in these reaches. Conversely, in a flowing reach groundwater stage and backwater area increased over time, the latter to 123% of the original spawning habitat area at the beginning of June. I attribute this increase to beavers, which began to impound flow as flows decreased during June. This probably caused hydraulic head to be higher in the stream than in the banks, and resulted in an increase in shallow groundwater levels.

Light trap validation

I found no significant differences in the number of larval fathead minnow collected in light traps among release distances ($F_{3,7}$ = 3.11, P = 0.151 by oneway ANOVA). Overall, light traps captured two-thirds of the available larvae (mean = 20 fish/trap, SE = 0.94). These data indicate that the light trap design was effective at capturing larval fishes to at least 3 m, or within a circle of area = 28 m^2.

Validation of deposition and frequency of brassy minnow otolith daily rings

Otoliths of brassy minnow larvae reared in the lab corresponded well with known ages. However, increments in otoliths of larvae reared at constant, ambient temperature (20 °C), were difficult to distinguish, similar to results reported for Colorado pikeminnow *Ptychocheilus lucius* reared under ambient conditions in the laboratory by Bestgen and Bundy (1998). Therefore, I analyzed only brassy minnow larvae raised in the fluctuating thermal regime, which was more similar to natural conditions. I extracted otoliths, measured standard length (mm) and otolith diameter (μm), and counted increments for 47 individuals reared in the laboratory that ranged in age from 1 to 30 d. Fish were approximately 4.0 mm SL at hatching, and fish that were 1 d old had one clear increment, indicating that the first daily ring in brassy minnow is deposited on the day of hatching. Overall, I found that increments in these larvae were easy to distinguish, and blind increment counts were nearly identical to known age (r = 0.97). Linear regressions between known standard length (SL) as a function of age (SL = 3.409 + 0.319 (age), r^2 = 0.94; SE of intercept = 0.171; SE of slope = 0.012), known otolith diameter (OD) as a function of age (OD = 5.972 + 1.867 (age), r^2 = 0.98; SE of intercept = 0.638; SE of slope = 0.045), and standard length as a function of otolith diameter (SL = 2.377 + 0.171

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(OD), $r^2 = 0.97$; SE of intercept = 0.144; SE of slope = 0.005) were highly significant (all

$P < 0.001$). These results indicate that counts of daily rings in field collected brassy

minnow larvae provide accurate and precise estimates of age.

Hatching date distributions

A total of 4,505 individual brassy minnow larvae were captured during three

years of sampling, and >85% were captured in the upstream and middle segments (Table

4.2). Brassy minnow were not captured in Black Wolf Creek in 2005, or in the

downstream segment in 2006 when it was entirely dry during sampling. A total of 514

brassy minnow larvae were aged, including all larvae collected in 2005 (N = 191) and

2006 (N = 168), and a subsample of larvae collected in 2007 (N = 155). For 2007, I

randomly selected two individuals from each segment and Black Wolf Creek within each

1-mm length class from 4 to 35 mm SL. There were few large individuals, so some

length classes from each segment had fewer than two fish. Increments on otoliths from

fishes greater than 17 mm SL were difficult to read, so they were ground and polished

using standard techniques. The subsampling in 2007 enabled us to develop an age-length

relationship which I used to assign ages to the rest of the fish collected. Based on

ANCOVA, the slope of the standard length vs. estimated age (days) relationships was

different in Black Wolf Creek than in the upstream, middle, and downstream segments

($F = 337.67$, $P < 0.01$), so I fit two equations, one for Black Wolf Creek (EQ 1), and the

other for the other three segments (EQ2):

EQ 1: Age = 2.757 (SL) – 9.81, (N = 37, $r^2 = 0.95$)

EQ 2: Age = 2.159 (SL) – 4.49, (N = 118, $r^2 = 0.94$)

I then used these equations to assign ages to all other brassy minnow larvae based on their lengths.

Across segments and years, the majority of brassy minnow larvae hatched between mid-April and late May (Figure 4.4). A subset of larvae hatched in early-June in the downstream segment and Black Wolf Creek in 2007. Brassy minnow spawned earlier, especially in the upstream segment and Black Wolf Creek, during the hot, dry conditions of 2006, compared to 2005 and 2007.

The age estimates and length-frequency histograms provide two lines of evidence for larval transport into the downstream segment. During 2005, five brassy minnow larvae were collected in channel margin habitats in the downstream segment that were wet for only two weeks, following a precipitation event. These five larvae were estimated to have hatched before the habitats became available (i.e., before the rainstorm), indicating that they must have hatched elsewhere. The most likely source was upstream habitats because the larvae were too small to be mobile (mean SL = 10.1 mm). Secondly, in 2007, the peak of hatching in the downstream segment was about a week earlier than in Black Wolf Creek, even though this tributary provided most of the flow that created the habitat in the main river, and the two locations were < 1 km apart. Habitat conditions in the downstream segment are most likely not conducive for brassy minnow spawning (i.e., no backwater habitats available). These results suggest that larvae collected in the downstream segment were a mixture of individuals originating in Black Wolf Creek and those that drifted from upstream habitats.

Survival of brassy minnow larvae

Survival of brassy minnow larvae differed among years under variable climate conditions. To make comparisons among years, I pooled fish collected in all segments, and used only the subsample of fish that were aged for 2007. Therefore, these can be considered estimates of survival for brassy minnow larvae within the Arikaree River basin as a whole. Estimates of daily survival (S, 1/d) were 0.894, 0.839 and 0.897 for 2005, 2006, and 2007, respectively, which were different among years ($F = 158.63$, $P <$ 0.001 by ANCOVA). Survival was significantly lower in 2006 than in 2005 or 2007 (all $P < 0.001$), based on Tukey's HSD post-hoc comparisons. No difference in survival rates between 2005 and 2007 could be detected ($P = 0.286$).

Influence of spawning habitat characteristics on cohort survival

The rate of backwater drying, initial area and depth, and the linear and quadratic terms for GSDD had the most influence on survival of cohorts of brassy minnow (Table 4.3). However, there was considerable support ($w_i > 0.05$) for three other models, one of which included the linear and quadratic terms for mean hatching date. To account for this uncertainty, I model averaged parameter estimates and variances from the top four models (Burnham and Anderson 2002), and made inference based upon these estimates (Table 4.4). Survival was predicted to be higher in backwaters that dried slower, and were initially larger and deeper. Survival was also higher for cohorts that hatched in the middle of the spawning period (Figure 4.5), and at a moderate number of GSDD (median = 810). Surprisingly, models including the covariate indicating the segment in which a backwater was located were not included in top models. Nevertheless, a simple t-test comparing arcsine of the square root-transformed mean cohort survival between the two

segments showed that survival was higher in the upstream segment than in the middle

segment (t = -2.55, P = 0.03, d.f. = 11).

Brassy minnow ontogeny

Backwater habitats most likely become unsuitable rearing habitats past a certain

point, due to habitat drying, deteriorating environmental conditions (e.g., high

temperature and low dissolved oxygen), and depletion of food resources. I hypothesized

that brassy minnow larvae would move from backwaters to main channel habitats at

some size threshold to avoid habitat desiccation and reduced growth and survival in

backwater habitats. I calculated the change in mean CPUE of brassy minnow larvae in

backwater and channel margin habitats in the upstream segment from mid-April to late

July 2007 (Figure 4.6). Brassy minnow CPUE increased quickly in backwater habitats

during spawning in early May. Thereafter, CPUE declined in backwaters and increased

in channel margin habitats. After the first of June, CPUE of brassy minnow was higher in

channel margin habitats than in backwater habitats. According to my hatching date

estimates and relative growth estimates (see below), these larvae would be from 30-40

days old and 17 to 22 mm SL during this habitat transition.

Relative growth in backwater habitats

Relative growth of brassy minnow larvae differed among years with different

climate conditions. I defined relative growth as the change in mean standard length

estimated using larvae grouped in 5-d age increments. These values were calculated for

brassy minnow larvae in backwater habitats in the middle and upstream segments for

2005 to 2007. To make comparisons among years, I used only the subsample of fish that

were aged for 2007. I included only fish up to 40 days old, or the age by which I

predicted that habitat switching had occurred (see above). The slopes of mean SL as a function of age were significantly different among years ($F = 158.63$, $P < 0.001$ by ANCOVA), and the growth rate each year was significantly different from the others (all $P \leq 0.05$ by Tukey's HSD). The slopes can be interpreted as growth rates (mm /d), and were 0.30 (± 0.03 SE), 0.25 (± 0.03 SE), and 0.41 mm/d (± 0.02 SE) for 2005, 2006, and 2007, respectively.

Size structure in August

Based on length-frequency histograms, size structure of brassy minnow populations varied among years, and likely was influenced by survival of age-0 fish to late-summer, and adults over winter (Figure 4.7). The histograms indicated that age-0 fish were approximately <55 mm FL, and age-1 and older fish were >55 mm FL in August each year. Young-of-year fish were relatively abundant in 2005 and 2007 during August, but were at low abundance in 2006, in both segments. Low survival (see above) during the larval stage in 2006 likely contributed to a low number of YOY in August during this year. In 2005, many age-1 and older fish were present in the upstream segment, but few were detected in the middle segment. However, during 2006 adult fish were present at high relative abundance in both segments. Survival of age-0 brassy minnow from 2005 to 2006 was likely high. Relative abundance of adults in 2007 was low in both segments, indicating that survival between 2006 and 2007 was low, for both the few age-0 fish that survived from spring to summer 2006, and the adults that were present in August 2006.

Discussion

Life history of brassy minnow in Great Plains streams

Here I synthesize information on the life history of brassy minnow in Great Plains streams, and use it to integrate the findings from my research in the Arikaree River, Colorado. The data generated from this work allowed me to describe much about the life history of brassy minnow that was previously unknown.

Embryos and larvae in backwaters—Brassy minnow prefer to spawn in shallow, vegetated backwater habitats in Great Plains streams (Copes 1975; Scheurer et al. 2003; *Chapter 3*). Spawning is not initiated by any obvious hydrologic cues; instead it most likely commences once water temperature exceeds a critical threshold. I found that brassy minnow initiate spawning at about 670 cumulative growing season degree days (*Chapter* 3). I found that thermal conditions are typically met by mid-April in the Arikaree River, and that brassy minnow spawn within a discrete period that lasts one month. However, the distribution of hatching dates is strongly unimodal, and larvae that hatch in the middle of the spawning period survive better than those hatched early or late.

Brassy minnow eggs are adhesive, and adults likely attach them to vegetation or other structure in spawning habitats. Presumably this is an evolutionary adaptation to keep embryos aerated and away from the potentially smothering silt substrate common in low velocity backwater habitats. Eggs develop quickly, and brassy minnow larvae hatch within 3 d at 4.0 mm SL. Rapid incubation and fast growth of larvae are reproductive adaptations to life in harsh, unpredictable environments (Fausch and Bestgen 1997), and brassy minnow in Great Plains streams fit these criteria well.

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Dispersing age-0— Dispersal of age-0 brassy minnow from backwaters to rearing habitats may result from one of two possible mechanisms: 1) active dispersal once a certain size is reached (ontogenic habitat shift), or 2) passive dispersal due to high flow events. Active dispersal may occur owing to declining resources in backwaters caused by intra/inter-specific competition. I found a clear pattern in the decline of brassy minnow abundance in backwater habitats over time, and an increase in channel margin habitats. Once in the main channel, age-0 brassy minnow may be subject to downstream displacement due to poor swimming ability. If the backwater is located near a pool refugium, this may be ameliorated. However, in river segments with few pools (e.g., middle and downstream segments) the dispersal stage may be prolonged, and early life stages may be subject to starvation or predation while they range about looking for suitable refugia.

Age-0 fish may also be passively dispersed by high flow events. Depending on the magnitude of discharge, larvae may be displaced far downstream, possibly into unsuitable habitat. I found larvae in ephemeral habitats in the downstream segment during spring 2005, which apparently had been displaced from upstream. The lower reaches of the Arikaree River are harsh environments, prone to dry quickly, and some are permanently dry (*Chapter* 1). Therefore, larvae displaced into these habitats most likely suffer high mortality from desiccation or starvation. Regardless of mechanism, this dispersal stage is critical for recruitment of age-0 brassy minnow.

Growth and refugia—When young brassy minnow leave backwaters, the growth and refuge pool habitats to which they migrate can differ significantly in their characteristics, and physicochemical attributes of these habitats often deteriorate as

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summer progresses (Scheurer et al. 2003; *Chapter 1*; *Chapter 2*). For convenience, pools can be stratified into two categories: refuge and growth (sensu Schlosser and Angermeier 1995). However, in reality pools exist along a continuum between the two. In growth pools, physicochemical conditions are suitable for growth, and resources are abundant. These pools are common in the upstream segment, and are large, deep, and well connected to similar habitats (*Chapter 2*). Negative effects of abiotic factors may be minimal in growth pools, but high temperatures and low oxygen concentrations may occur during the heat of summer even in these relatively benign habitats. In the middle and downstream segments, age-0 brassy minnow may be relegated to pools of poorer quality due to low connectivity among habitats. In these refuge pools, juvenile brassy minnow may be more susceptible to high temperatures, low dissolved oxygen, and drought effects such as desiccation. Additionally, these pools are typically more shallow, increasing the risk of avian or mammalian predation (sensu Power 1987). As a result, both biotic and abiotic factors are probably important sources of mortality for juvenile brassy minnow in refuge pools during summer.

Overwinter habitat for brassy minnow—Overwinter mortality may be particularly high in plains streams, because shallow pools are subject to freezing to the bottom (Labbe and Fausch 2000). Brassy minnow need to have stored enough energy as fat to last them the winter (cf. Coleman and Fausch 2007). Entering winter, the amount of available energy may depend on habitat quality during the summer and fall. Therefore, fish that spend the summer in refuge pools may be in relatively poor condition entering winter, compared to fish in growth pools. Growth pools are typically deeper and more connected to groundwater, decreasing the chance of freezing to the bottom. However, growth pools

typically have abundant aquatic vegetation, which may result in low dissolved oxygen concentrations under the ice when plant material decomposes during winter.

Spawning habitat drying

Spawning and rearing habitat availability, physical characteristics, and rate of drying were strongly influenced by the hydrologic context of the segment, and interannual climate variation. In the two study segments that supported backwaters for spawning and rearing, backwater habitat area was highest in 2007 and 2005, both years with relatively wet spring seasons, whereas backwater area was much lower in the extremely dry conditions of 2006. However, the rate of backwater drying was fastest in both segments during 2007. The power to detect differences in drying rates among years was probably reduced by the small sample size in 2006, especially in the middle segment. Regardless, the large amount of habitat available in the middle segment at the beginning of 2007 dried rapidly, and 60% of backwaters in this segment dried completely even in the relatively high flows of spring 2007.

The most extreme habitat conditions were found in the downstream segment and Black Wolf Creek. Spawning and rearing habitats in the downstream segment were highly ephemeral, and were inundated for only two weeks following a precipitation event in 2005, and not at all in 2006. However in 2007, habitats in the downstream segment were available from early spring through mid-June, and brassy minnow larvae were found throughout these habitats. Overall, the spatial and temporal distribution of spawning habitats was patchy, with long reaches not containing habitat one year but having it the next (e.g., 2006 vs. 2007, downstream segment), indicating that source-sink population dynamics could potentially be important in the Arikaree River basin (*Chapter*

2). Clearly, the variable nature of spawning habitat availability across space and through time plays an important role in spawning and recruitment of brassy minnow in the Arikaree River.

Assumptions of the catch curve analysis

The catch curves I used to estimate survival of brassy minnow larvae across years and in individual backwaters in 2007 are based on several fairly restrictive assumptions. These include that mortality rate is constant with age, larvae recruit to the sampling gear at a similar size, detectability is equal across size, and for larvae, that increment counts correspond to actual age in days (Robson and Chapman 1961; Ricker 1975; Essig and Cole 1986). Recruitment to the sampling gear was likely not an issue, because I captured larvae that were as young as one day old. Detectability was heterogeneous with larval size, but was high (> 0.8) across the range of sizes I modeled in the catch curve analysis (*Chapter 3*). Additionally, based on otolith increment validation, increment counts corresponded nearly exactly to actual age of larvae. Mortality rate was likely not constant across ages, because larvae are susceptible to different mortality factors from the early to late larval periods. Nevertheless, my objective was to use survival rates generated from the catch curves in a relative, not absolute, sense. As a result, violation of this assumption of constant mortality made in catch curves analysis was unlikely to have introduced a strong bias in my conclusions.

Brassy minnow survival and recruitment

Larval survival in backwaters—Survival of brassy minnow larvae in backwater habitats is likely influenced by complex interactions among habitat drying, water temperature, and habitat size. I found that the rate of habitat drying was an important

predictor of survival of cohorts of brassy minnow larvae. Larvae spawned late in the spawning period are more likely to be trapped in rapidly drying spawning habitats as connections with the main channel are severed. Also, physicochemical conditions (e.g., water temperature and dissolved oxygen) are harsher in smaller drying habitats late in the spawning period. As a result, the rate of habitat drying may have direct (e.g., from desiccation) and indirect (e.g., reduced habitat area) effects on larval brassy minnow mortality.

The number of growing season degree days prior to hatching also was an important predictor of larval survival. Temperature controls larval metabolic rates, which directly affects growth, and ultimately condition of larvae (Blaxter 1992). Water temperatures are cooler early in the spawning period, and larval growth rates are slower. Water temperature also influences larval prey resources, because phenology and growth of prey items are also controlled by temperature. As a result, food availability may be lower early in the spawning period. In contrast, cohorts hatched late in the spawning period, when water temperatures are high, may quickly deplete endogenous energy stores (i.e., yolk), or may not be able to consume enough prey to meet energetic costs. Survival of larvae that hatch in the middle of the spawning period is likely higher due to moderate water temperatures, conferring the advantage of adequate growth conditions, abundant prey resources, and low densities of predators.

I found that survival of brassy minnow larvae was higher in backwater habitats that were larger and deeper at the beginning of the spawning period. These results support those of *Chapter 3*, where I found habitat area and maximum depth influenced the occupancy of brassy minnow larvae at high abundance. Selection of large spawning

habitats by adult brassy minnow is likely an evolutionary response to maximize larval survival, because physicochemical conditions in these habitats are more benign, and larval prey resources may be greater (Cushing 1975, 1990). In the Arikaree River, large, deep backwater spawning habitats are associated with groundwater input, and most are located in the upstream segment.

Biotic factors (e.g., competition and predation) are likely less influential to the survival of brassy minnow larvae in Great Plains when compared to the harsh environment conditions to which these larvae are exposed. I found little support for models in which larval survival was a function of the number of brassy minnow larvae collected in a backwater. Additionally, I found that high abundances of brassy minnow larvae were associated with backwater vs. channel margin spawning habitats, the same habitats in which I found survival to be highest (*Chapter 3*). This suggests that density of brassy minnow larvae within the range I measured is not a limiting factor to survival, and that larvae were likely below the carrying capacity in backwater habitats.

Adult survival and recruitment bottlenecks—Survival during early life stages is an important regulator of, and can have a disproportionate effect on (i.e., serves as a bottleneck), long-term population demographics of fishes (May 1973; Houde 1987; Ludsin and DeVries 1997). I found that the proportion of the brassy minnow population composed of young-of-year individuals was very low in 2006, when overall survival of larvae was also low. This was consistent among the upstream and middle segments, indicating that environmental conditions during spawning (i.e., climate) were important mechanisms that regulated brassy minnow population structure. Low survival of larvae and recruitment to the juvenile stage in 2006 likely influenced the low relative proportion

of adults in August 2007. Although abundant snowfall during winter months between 2006 and 2007 increased the distribution and amount of spawning habitat in spring 2007, these harsh winter conditions may have contributed to low overwinter survival of adults, especially in shallow pools in the middle segment. Regardless, low overwinter adult survival was offset by the ability of those few adults to recolonize spawning habitats (*Chapter 3*) and successfully spawn, as evidenced by the high abundance of brassy minnow larvae collected in spring 2007.

Synthesis and conservation implications

Habitat drying is a critical factor that influences growth and survival of brassy minnow in Great Plains streams across all life stages (Scheurer et al. 2003; *Chapter 1*; *Chapter 3*). The quality and quantity of spawning, rearing, and refuge habitats for brassy minnow, and the connections among them, reflect the segments in which those habitats are set (Figure 4.8). Relatively wet, groundwater-fed segments, such my upstream study segment, support relatively large populations and have high recruitment and survival of fishes across life stages. Even during dry years, these segments support backwater spawning habitats that allow for successful recruitment of larvae. When larvae reach a threshold in body size, connections among habitats that persist through summer allow larvae to move to main channel margin habitats, and then to pools that offer suitable conditions for growth. During winter, abundant deep pools offer refuge from freezing conditions (Labbe and Fausch 2000; *Chapter 1*). These wet segments likely serve as source populations that provide demographic support for (i.e., allow for the persistence of) populations in sink habitats (*Chapter 2*).

Intermittent segments, such as my middle segment, may support high recruitment of larvae in some backwaters during the spring, but harsh conditions in the summer and winter may limit survival of age-0 and older fishes (Figure 4.8). In dry conditions, such as those in 2006, few backwater habitats occur or persist. Connections to adjacent channel margin habitats may dry before larvae are large enough to move between these habitat types. Larvae that are successful at moving into the main channel are faced with rapidly drying habitats and may be forced into isolated refuge pools for the summer and winter months, where mortality is likely high and the probability of surviving to spawn the next spring is low. Because a moderate density of high quality spawning backwaters occur in intermittent segments, during high flow years these segments also may provide individuals to support poor quality habitats downstream (i.e., sinks). However, during dry years, low connectivity among spawning and rearing habitats, and long dry reaches, preclude larval transport out of intermittent segments.

Dry segments, such as the downstream segment, are poor quality habitats. In dry years no habitats exist, and even in wet years no backwater habitats in which brassy minnow prefer to spawn are available (*Chapter* 3; Figure 4.8). Channel margins or tributaries (e.g., Black Wolf Creek), may provide some opportunity for spawning, but channel margins quickly dry, recruitment is low, and survival past the larval stage is likely to be very low or nil. Populations in dry segments are mainly supported by input of individuals from upstream populations, and hence fit the classic definition of sink populations.

I have shown that interannual variability in climate, and the hydrologic context of segments along the riverscape, have a strong influence on habitat availability and

recruitment of brassy minnow in the Arikaree River. Droughts are a common occurrence

on the Great Plains and may become more frequent and more intense in the future due to

climate change (Ojima and Lackett 2002; *Chapter 1*). However, droughts are natural

phenomena to which plains fishes have become adapted over evolutionary time. Life-

history adaptations of plains stream fishes allow for them to survive and quickly

repopulate entire segments following droughts and other natural disturbance (*Chapter 3*).

A more pressing concern facing stream fish populations across the western Great

Plains is overuse of groundwater resources by irrigated agriculture (*Chapter 1*).

Periodicity and magnitude of flows in the Arikaree have already been severely reduced

by groundwater pumping. Moreover, groundwater-fish habitat models predict that at

current pumping rates, hydrologic alteration will continue in the future resulting in

further losses of stream fish habitat availability and habitat connectivity. The

implications for brassy minnow populations are that over time, conditions in wet and

intermittent segments will shift to a drier state, resulting in fewer spawning habitats, and

lower recruitment and survival of fishes (Figure 4.8). Conservation efforts should focus

on maintaining spawning, rearing, and refuge habitats that are critical to brassy minnow

population persistence. Effective conservation will require explicit consideration of the

unique adaptations of these organisms to harsh environments, and the understanding that

these adaptations can protect these fish populations only above a certain threshold in

human-caused disturbance.

Acknowledgements

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Tables

Table 4.1. Characteristics of brassy minnow spawning habitat during 2005 to 2007 in three 6.4-km segments and lower Black Wolf Creek in the Arikaree River basin, CO. Numbers of weeks and habitats sampled, total and mean (SE) area of backwater habitats, and the number of habitats (percent of total) that dried during each year are shown.

Segment	Number of weeks	Number of habitats sampled		Backwater area (m^2)		Number of habitats dried	
		CM	BW	Total	Mean	CM	BW
Upstream							
2005	4	5	9	710	64 (21)	5 (100)	2 (22)
2006	5	2	8	460	42 (13)	2 (100)	2 (25)
2007	6	5	9	880	97 (23)	5 (100)	0 (0)
Middle							
2005	4	7	5	430	33 (11)	7 (100)	4 (80)
2006	5	0	3	210	69 (12)	0 (0)	1 (33)
2007	6	14	5	940	188 (59)	14 (100)	3 (60)
Downstream/BWC							
2005	4	10	0	0	-	5 (50)	-
2006	5	5	0	0	-	0 (0)	-
2007	6	10	0	0	-	5 (50)	-

Table 4.2. Number of brassy minnow larvae collected in three 6.4-km segments of the Arikaree River basin and the lower 1 km of Black Wolf Creek from 2005 to 2007. Also shown are the total number of larvae aged from otoliths each year.

Year	Upstream	Middle	Downstream	Black Wolf Creek	Total collected	Aged
2005	103	83	5	0	191	191
2006	42	58	0	68	168	168
2007	1393	2166	151	436	4146	155
Total	1538	2307	156	504	4505	514

Table 4.3. Summary of model selection statistics for the four top models ($w_i > 0.05$) and the global model of survival of 25 cohorts of brassy minnow larvae in 14 backwater spawning habitats in the Arikaree River, CO in 2007. The $L\text{-}L$ is the log-likelihood, AIC_c is Akaike's information criterion adjusted for small sample size, ΔAIC_c is the difference in the AIC_c value for a particular model when compared to the top ranked model, w_i is the AIC_c model weight, and K is the number of parameters including the intercept and residual variance. Also shown are the statistics for the global model. See the text for a description of the covariates.

Model	$L\text{-}L$	AIC_c	ΔAIC	w_i	K
Rate, Area, Depth, GSDD, $GSDD^2$	51.24	-81.90	0.00	0.27	7
Rate, Area, GSDD, $GSDD^2$, MHD, MHD^2	53.26	-81.53	0.37	0.23	8
Rate, GSDD, $GSDD^2$	47.19	-81.20	0.70	0.19	5
Rate, Area, GSDD, $GSDD^2$	48.80	-80.92	0.98	0.17	6
Rate, Area, Depth, Abun, Segment, GSDD, $GSDD^2$, MHD, MHD^2	54.30	-66.29	15.61	<0.01	11

Table 4.4. Model-averaged parameter estimates, unconditional standard errors, and lower and upper 90% confidence limits (CL) for covariates predicting survival of 25 cohorts of brassy minnow larvae in 14 backwater spawning habitats in the Arikaree River, CO in 2007. See the text for a description of the covariates.

| Parameter	Estimate	SE	Lower 90% CL	Upper 90% CL
Intercept	-5.45	3.24	-1.08×10^{1}	-1.33×10^{-1}
Rate	-2.45×10^{-3}	8.63×10^{-4}	-3.87×10^{-3}	-1.04×10^{-3}
Area	1.06×10^{-4}	6.15×10^{-5}	5.42×10^{-6}	2.07×10^{-4}
Depth	4.35×10^{-4}	4.39×10^{-5}	3.63×10^{-4}	5.07×10^{-4}
GSDD	6.12×10^{-3}	2.61×10^{-3}	1.83×10^{-3}	1.04×10^{-2}
$GSDD^{2}$	-9.82×10^{-7}	2.30×10^{-8}	-1.02×10^{-6}	-9.45×10^{-7}
MHD	3.45×10^{-2}	2.88×10^{-3}	2.97×10^{-2}	3.92×10^{-2}
MHD^{2}	-1.36×10^{-4}	4.38×10^{-5}	-2.08×10^{-4}	-6.42×10^{-5}

Figures
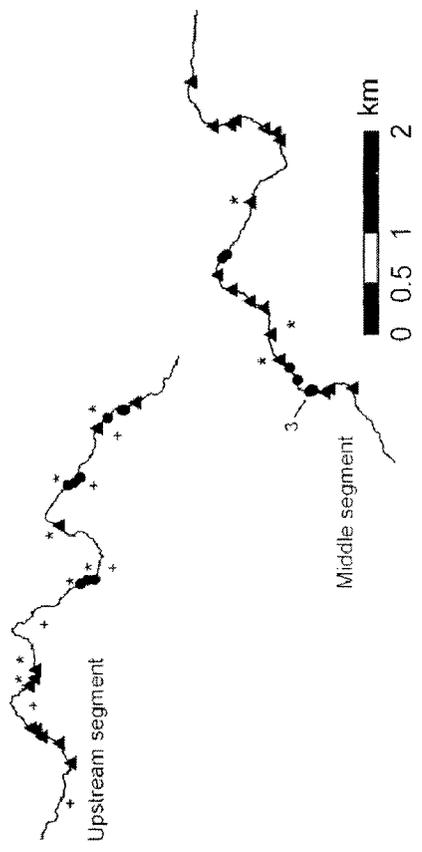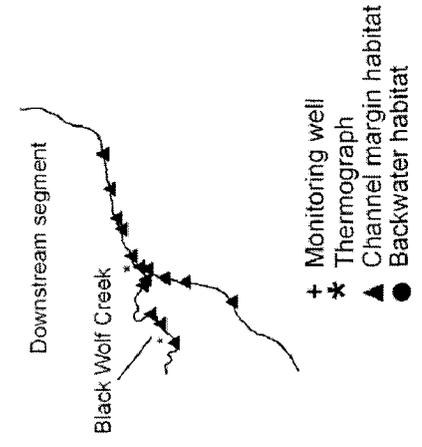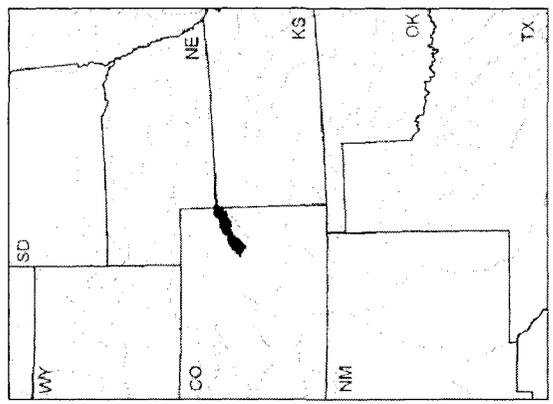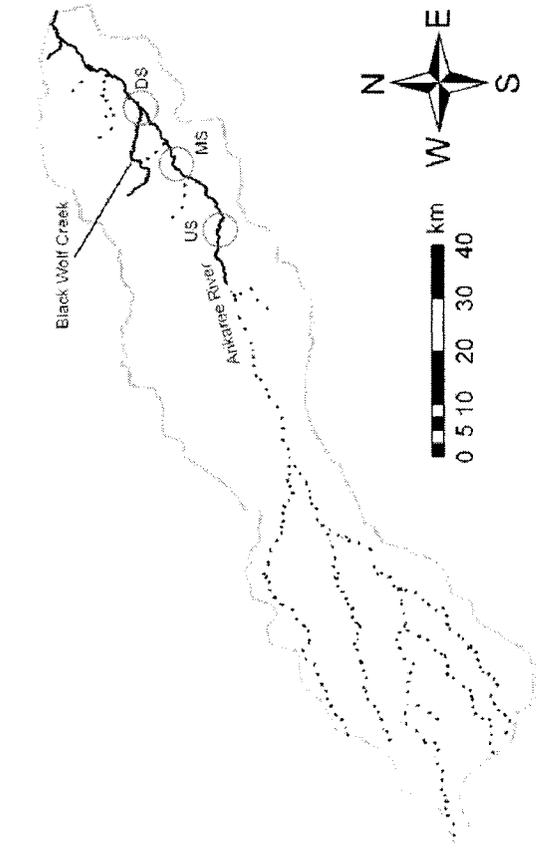
Figure 4.1. Study area in the Arikaree River basin in northeastern Colorado (top left panel), and the location of three 6.4-km study segments (US = Upstream segment; MS = Middle segment; DS = Downstream segment) and Black Wolf Creek (top right panel).

Solid lines in the lower basin illustrate where the potential for perennial stream flow remains (based on Falke et al. *in review*). In the lower panel the locations of 59 spawning habitats and 12 thermographs sampled across three years, and six groundwater wells monitored in one year in the three segments are shown. A cluster of 3 backwaters in the upper middle segment is indicated.

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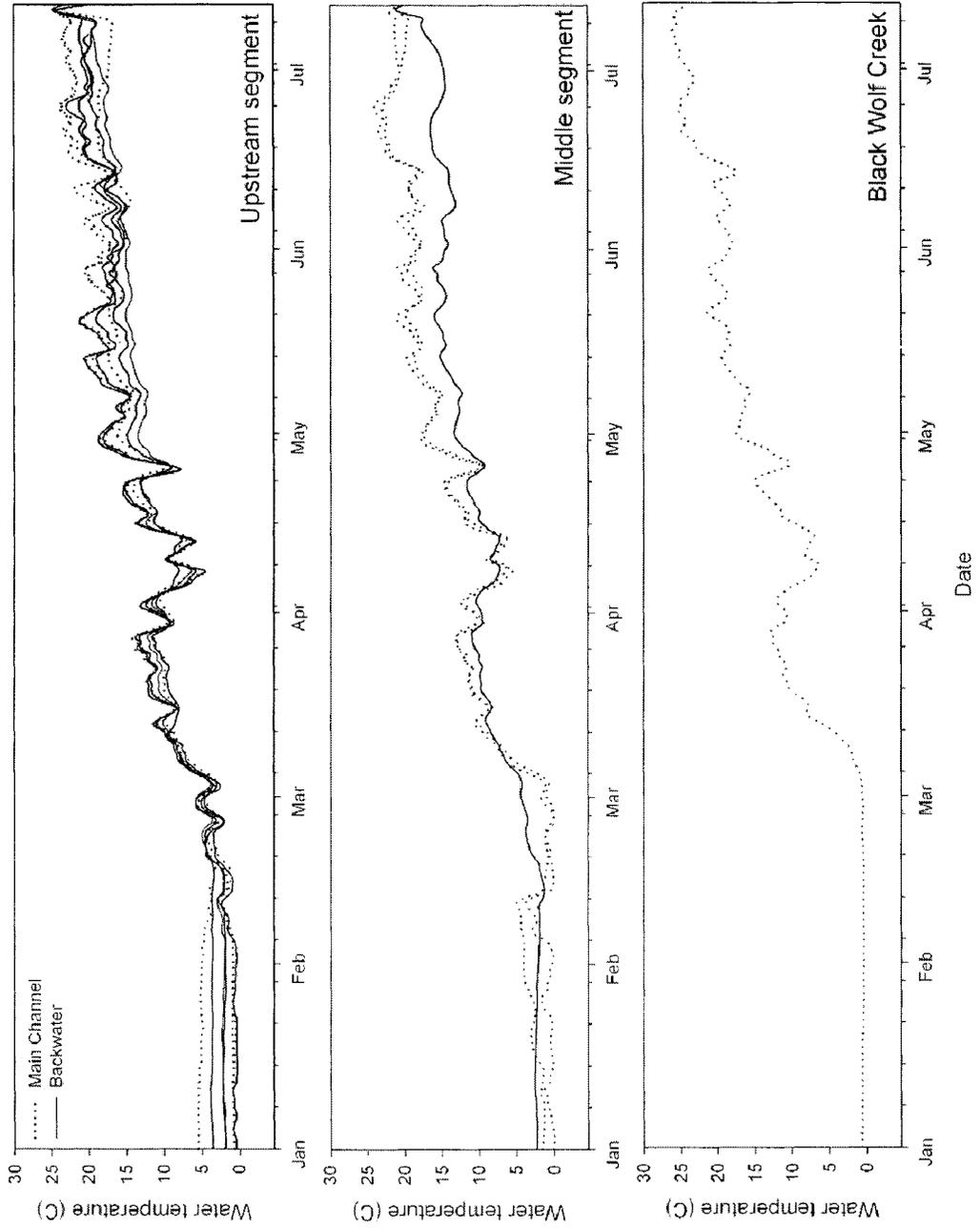
Figure 4.2. Hourly water temperature profiles for main channel (solid lines) and backwater habitats (dotted lines; see Figure 4.1 for a map of thermograph locations) in the upstream (US) and middle segments (MS), and Black Wolf Creek from January through July 2007.
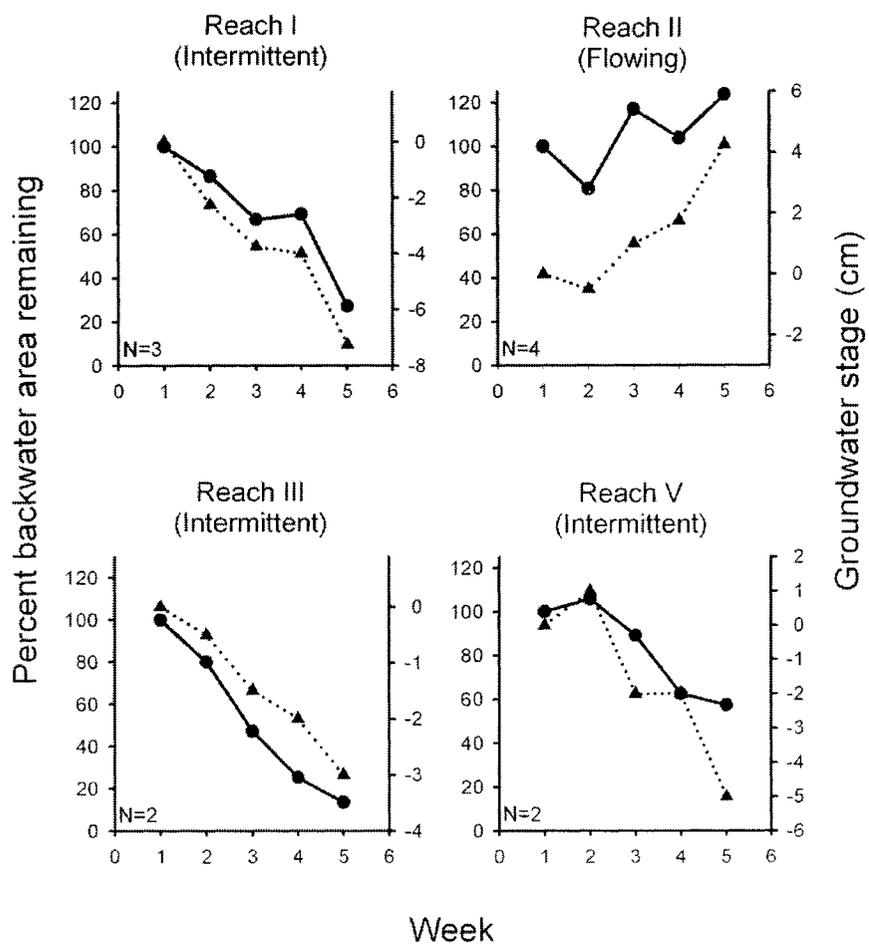
Figure 4.3. Percentage backwater area remaining based on an average for backwaters

(N = 2-4) by reach (solid lines; left y-axis), and relative groundwater stage (cm;

dashed lines; right y-axis) for five consecutive weekly measurements (x-axis) starting

June 1, 2006 in the upstream segment, Arikaree River, CO.

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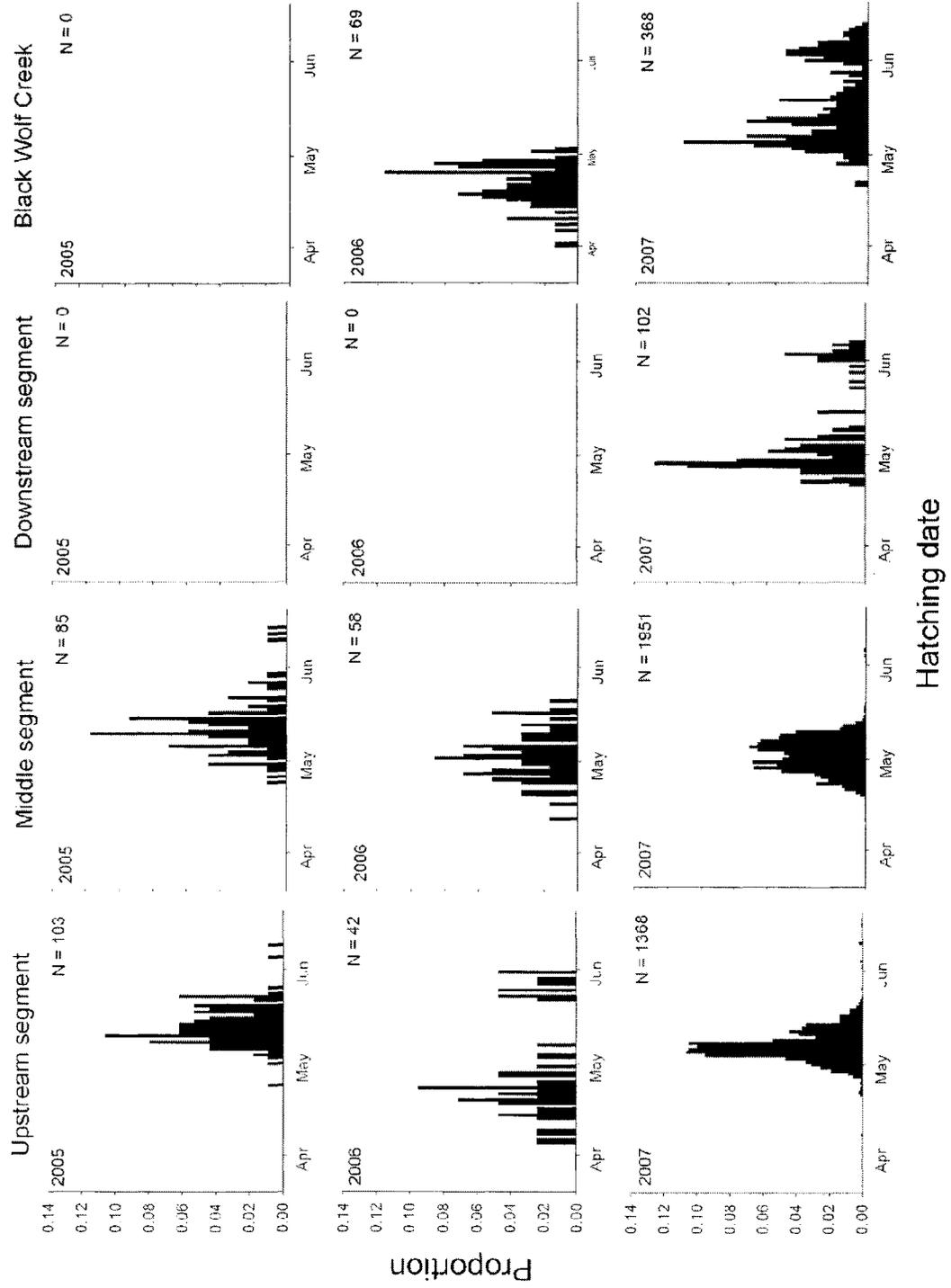
Figure 4.4. Hatching date distributions for brassy minnow larvae collected from the three segments and Black Wolf Creek in the

Arikaree River, Colorado during 2005-2007. Hatching dates for larvae in 2007 were estimated from a subsample of fish (N= 155)

and this distribution was then applied to all fish. Bars represent 1 d.
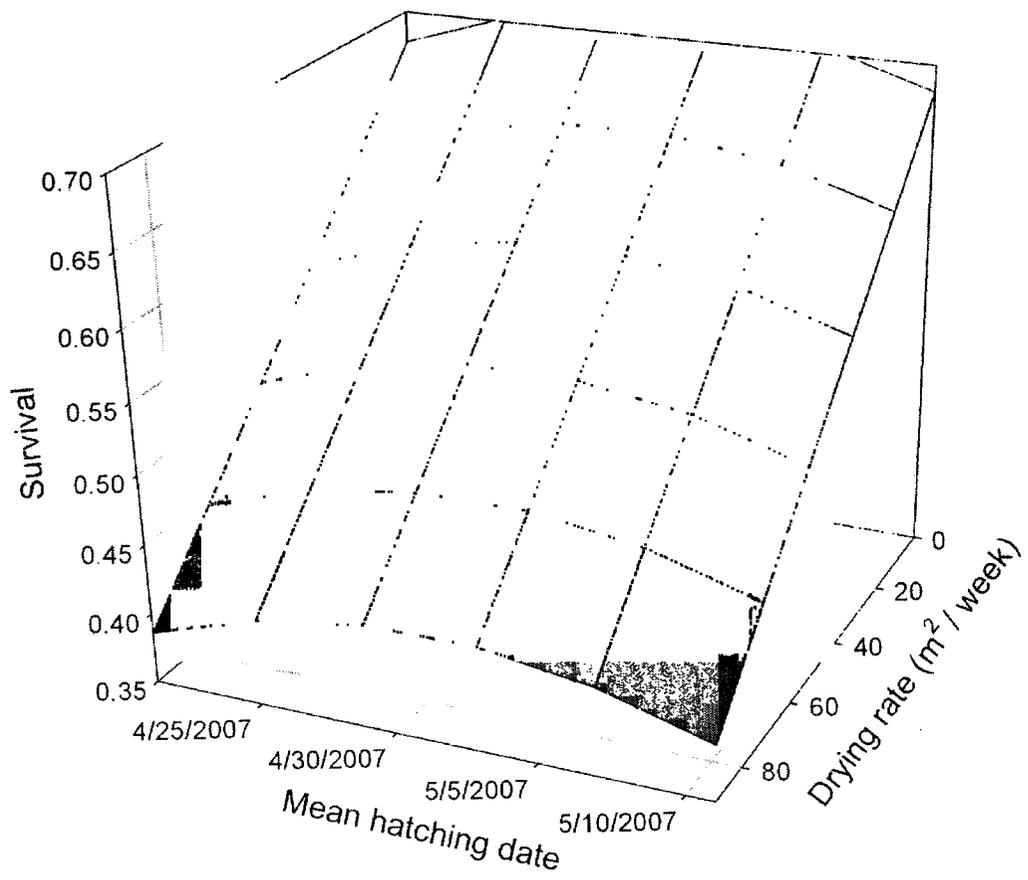
Figure 4.5. Estimated survival of brassy minnow larvae (y-axis) as a function of the rate of backwater habitat drying (m^2 /week; x-axis) and mean cohort hatching date (z-axis). Parameters were estimated using multiple linear regression, and are model-averaged from the top three models ranked using AIC.
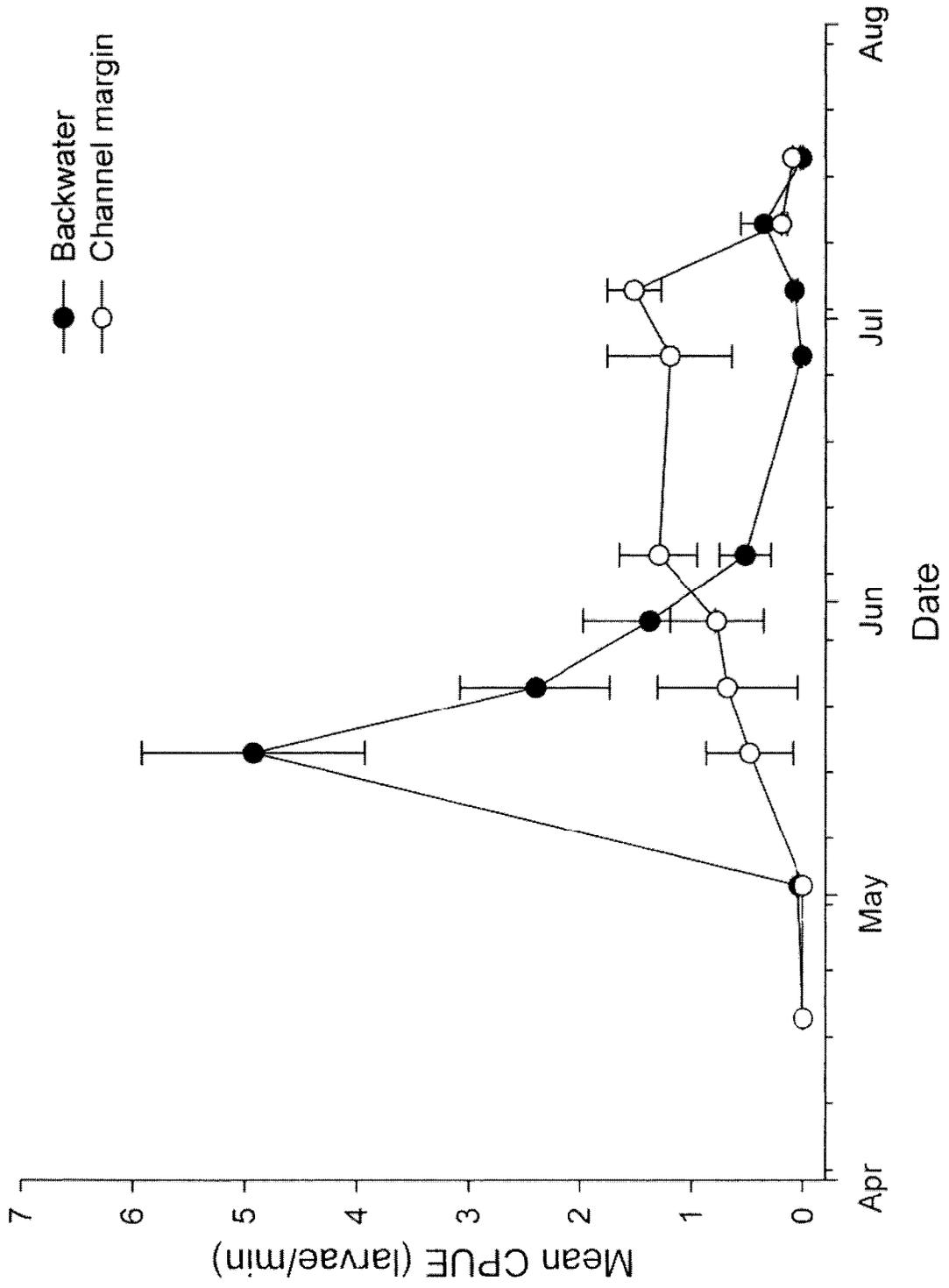
Figure 4.6. Mean catch-per-unit of effort (CPUE; ± 1 SE) of brassy minnow during spring and summer 2007 in backwater (closed circles) and channel margin (open circles) habitats in the upstream segment.

Upstream segment   Middle segment
                  2005
                  2006
                  2007

Fork length (mm)
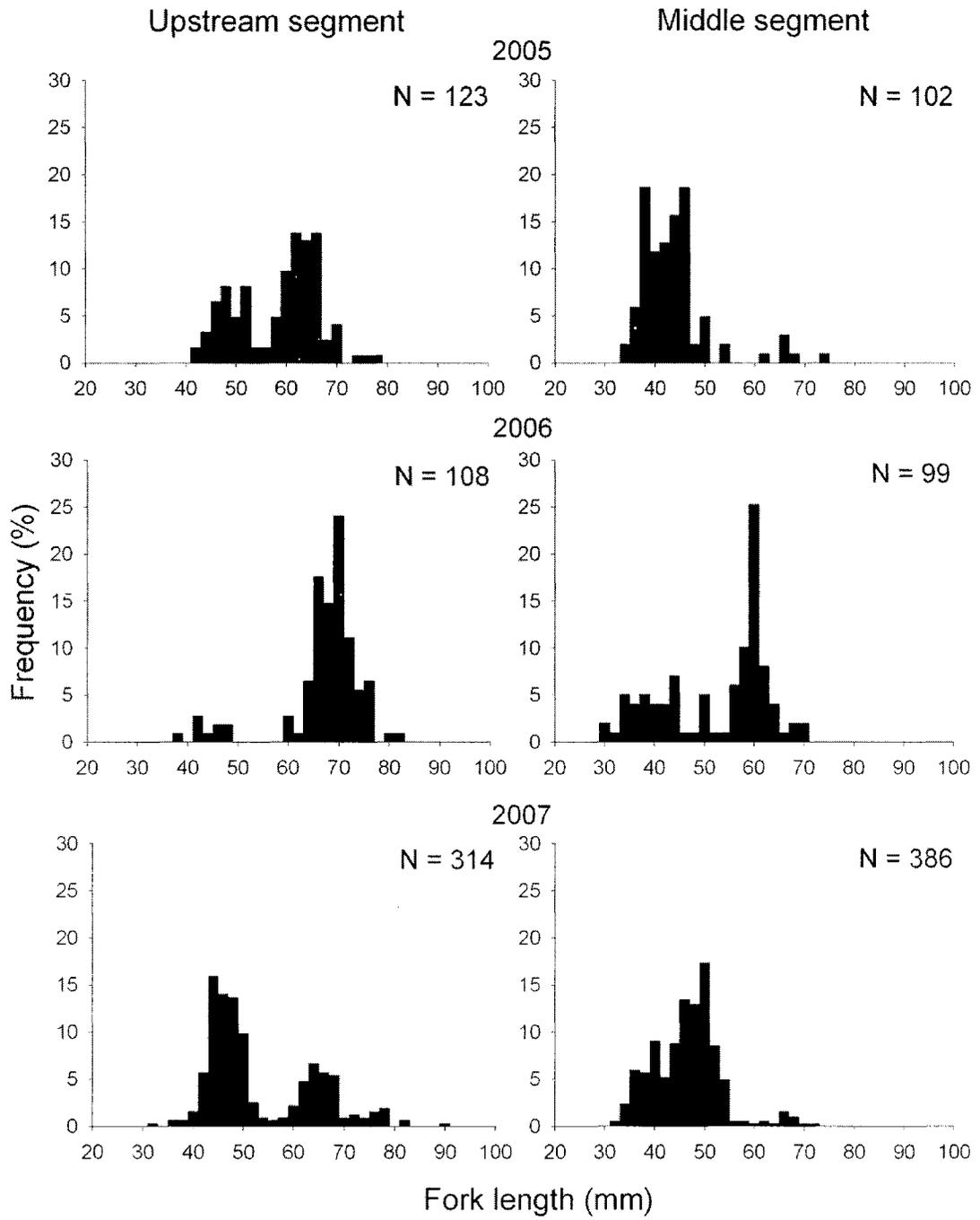
Frequency (%)

Figure 4.7. Length-frequency histograms of adult brassy minnow collected in August

2005 to 2007 in pools in the upstream (left column) and middle (right column)

segments of the Arikaree River, Colorado. Bars represent 2-mm SL classes (e.g., 30-

31, 32-33, etc.).

River segment

Life history stage	Month	Wet	Intermittent	Dry
Spawning/ early rearing	April-May	Many backwaters	Few backwaters	Channel margins only
Age-0 dispersal	Early June	Channel margins persistent	Channel margins drying	Channel margins dry
Age-0 growth and refuge	June-Oct	Many growth pools	Few growth pools Sufficient refuge pools	Most habitat dry
Overwinter	Nov-March	Many refuge pools	Few suitable refuge pools	Most habitat dry
Population viability		High recruitment and survival	High recruitment Moderate to low survival	Low recruitment Very low or no survival
Population type		Source	Source/Sink	Sink

Effects of groundwater pumping, drought and climate change

(Shifts all segments to drier state)

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Figure 4.8. Conceptual model of generalized trends in spawning, rearing, and refuge habitat availability for early life stages of brassy minnow within river segments with differing flow regimes across a Great Plains riverscape. Arrows indicate the direction and relative magnitude of recruitment and survival within these habitats and segments. Also displayed are the population viability and metapopulation type expected to be found within each type of segment. Under groundwater pumping, drought, and climate change, conditions within each segment type are expected to shift to a drier state (i.e., to the right).

Appendices

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	*Ameiurus melas*	AMEMEL
central stoneroller	*Campostoma anomalum*	CAMANO
white sucker	*Catostomus commersonii*	CATCOM
orangethroat darter	*Etheostoma spectabile*	ETHSPE
plains killifish	*Fundulus zebrinus*	FUNZEB
brassy minnow	*Hybognathus hankinsoni*	HYBHAN
green sunfish	*Lepomis cyanellus*	LEPCYA
fathead minnow	*Pimephales promelas*	PIMPRO
creek chub	*Semotilus atromaculatus*	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 (%)	P-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	

Appendix C. The number of larval fish species collected in each segment (US = Upstream segment, MS = Middle segment, DS = Downstream segment, BWC = Black Wolf Creek) in the Arikaree River, CO, during spring and early summer 2005-2007.

Species	2005				2006				2007				Total
	US	MS	DS	BWC	US	MS	DS	BWC	US	MS	DS	BWC	
black bullhead	0	0	0	0	48	0	0	0	0	0	0	0	48
central stoneroller	113	50	0	0	3	34	0	2	416	826	154	79	1677
white sucker	2	0	0	0	0	0	0	0	8	0	0	0	10
orangethroat darter	4	0	0	0	1	4	0	0	62	22	2	0	95
plains killifish	3	108	40	4	12	99	0	311	0	562	557	10	1706
brassy minnow	103	83	5	0	42	58	0	68	1393	2166	151	436	4505
green sunfish	0	0	0	0	3484	2	0	0	7	433	0	2	3928
fathead minnow	134	430	145	115	140	138	0	90	507	1327	742	970	4738
creek chub	30	2	0	0	1	2	0	0	218	359	24	10	646
Total	389	673	190	119	3731	337	0	471	2611	5695	1630	1507	17353

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Appendix D. Model-averaged estimates of detectability across weeks for larvae of six fish species in the Arikaree River, CO from 2005 to 2007. Estimates were produced using multi-year joint habitat suitability-occupancy models (MacKenzie et al. 2006, 2009). Top models for fathead minnow during 2005-2007 indicated detection varied by year (see Table 3.4), but not within a year.

Species	Week				Year		
	1	2	3	4	2005	2006	2007
central stoneroller	0.252	0.629	0.660	0.562			
orangethroat darter	0.820	0.861	0.370				
plains killifish		0.499	0.955	0.955			
brassy minnow	0.667	0.781	0.838	0.483			
fathead minnow					0.818	0.823	0.783
creek chub	0.998	0.429	0.041				