

THESIS

EVALUATING THE SUCCESS OF ARKANSAS DARTER TRANSLOCATIONS IN
COLORADO: AN OCCUPANCY SAMPLING APPROACH

Submitted by

Matthew C. Groce

Department of Fish, Wildlife, and Conservation Biology

In partial fulfillment of the requirements for the degree of

Master of Science

Colorado State University

Fort Collins, Colorado

Spring 2011

Master's Committee:

Department Head: Kenneth R. Wilson

Advisor: Kurt D. Fausch

Larissa L. Bailey
N. LeRoy Poff

ABSTRACT

EVALUATING THE SUCCESS OF ARKANSAS DARTER TRANSLOCATIONS IN COLORADO: AN OCCUPANCY SAMPLING APPROACH

Like many fishes native to western Great Plains streams, the Arkansas darter *Etheostoma cragini* has declined, apparently in response to changes in flow regimes and habitat fragmentation. I investigated the effectiveness of translocation as a management strategy to conserve this threatened species in the Arkansas River basin of southeastern Colorado. I used a multiscale design to sample darters and several attributes of their habitat at the local 10-m site scale, the 3.25-km translocation segment scale, and the 10-km riverscape scale, in all 19 streams where darters were previously translocated. I used multistate occupancy estimation, based on two consecutive dipnetting surveys, to determine habitat characteristics correlated with site occupancy and detectability of Arkansas darters. Darters were present in 11 of 19 streams, although 5 were completely dry when visited. Darters had reproduced in 10 of the 11 streams (one criterion in the state recovery plan), and 6 streams also met a second criterion for abundance (>500 individuals). However, populations in only two streams unequivocally met the third criterion of being self-sustaining, because the other four streams had been stocked annually with hatchery-reared darters. Detectability of darters at sites where water was present was high for both age groups, 91% for age-0 darters and 76% for age-1

darters, and was a function of Julian date (age-0) and habitat depth (age-1). Residual stream temperature (a site-scale variable) and the total length of available habitat (a riverscape-scale variable) were the strongest predictors of site occupancy for both age groups. The models were useful in identifying fragmentation by a road culvert as a potential impediment to success in another stream where conservation biologists have proposed translocating darters. These models can be used to guide habitat conservation and land management practices that seek to conserve, protect, and restore current and future critical habitat for Arkansas darters.

Matthew C. Groce
Department of Fish, Wildlife, and Conservation Biology
Colorado State University
Fort Collins, CO 80523
Spring 2011

ACKNOWLEDGEMENTS

I have greatly enjoyed my time at Colorado State University (CSU) and wish to thank the faculty, staff, and graduate students of the Department of Fish, Wildlife, and Conservation Biology for their help and support.

I wish to thank my advisory committee members, Dr. Larissa Bailey and Dr. N. LeRoy Poff, for their help and advice during my time at CSU. I would especially like to express my gratitude to my major professor, Dr. Kurt Fausch, for the advice, support, and encouragement that he has given me while studying under his direction. He carefully read and commented on many drafts, helping me polish my writing skills. More importantly, he served as a mentor for me during my time at CSU. I could not be more grateful for his help and involvement at every stage in the project.

I am also very grateful to the Colorado Division of Wildlife (CDOW) for providing funding for this research. My grant was administered by Harry Crockett, and I received considerable logistical support from CDOW employees Casey Cooley, Gary Dowler, Paul Foutz, Doug Krieger, Jim Melby, and Jim Ramsay, for which I am thankful. In addition, Bruce Rosenlund and Chris Kennedy (USFWS); Rick Bunn, Rick Day, April Estep, and Jim McDermott (US Army, Fort Carson); and several private landowners provided information and access to field sites. Donna Crown (Triple Crown Ranch), John Sanderson (The Nature Conservancy) and Louis Martin (Brett Gray Ranch) provided access to Horse Creek and Steels Fork of Horse Creek. Additional financial support came from the Cutthroat Chapter of Trout Unlimited Memorial Research Fellowship, the Gregory L. Bonham Memorial Scholarship, and the Freda T. Roof Memorial General Scholarship.

I thank Dr. Larissa Bailey for all her help and insightful comments with the study design, modeling, and writing involved with my research. Additional programming was provided by Jim Hines, and Gary White gave statistical advice. Kevin Bestgen, Harry Crockett, Jeff Duda, and Jeff Falke provided constructive reviews of my thesis and manuscript. Finally, this study could not have been completed without the hard work and assistance in the field from Will Stacy and Rebecca Harris.

Finally, I wish to thank Rebecca Harris and my family, Leslie, Scott, and Lisa Groce, for the love, encouragement, and emotional support they have given to me through the years.

TABLE OF CONTENTS

Introduction.....	1
Field methods.....	4
Study streams	4
Study segments, reaches, and sampling sites	6
Habitat measurements	10
Statistical modeling of Arkansas darter occupancy	13
Occupancy estimation and modeling	13
Model covariates for conditional darter occupancy	14
Candidate models and model selection	16
Occupancy predictions	17
Goodness of fit and spatial autocorrelation.....	18
Results.....	19
Success of Arkansas darter translocations	19
Models of Arkansas darter occupancy	21
Occupancy predictions	23
Spatial autocorrelation of sample sites.....	24
Discussion.....	25
Translocation success	25
Influence of habitat on occupancy and translocation success	28
Use of models for conservation.....	29
References.....	32
Tables.....	37
Figures.....	48

Introduction

Many native fish populations of western Great Plains streams are declining in response to rapid environmental change. The cumulative threats from degraded and fragmented habitats, primarily from dewatering caused by groundwater mining, dams, and surface diversions for irrigation, are imminent and pervasive throughout the region (Labbe and Fausch 2000; Scheurer et al. 2003; Dodds et al. 2004). For example, of the 19 fish species which make up the native ichthyofauna in the Arkansas River basin of southeast Colorado, more than 40% are either extirpated ($n=3$), state endangered ($n=3$), state threatened ($n=1$), or a state species of special concern ($n=1$), and several of these are the focus of conservation and recovery efforts (Nesler et al. 1999; CDOW 2007; Hubert and Gordon 2007). Although this fish assemblage is well-adapted to the naturally harsh environment of the western Great Plains, ongoing changes to hydrologic regimes, water temperatures, and channel configurations, aggravated by climate change, are exacerbating already degraded conditions and causing further endangerment (Falke et al. 2010, in press).

The Arkansas darter *Etheostoma cragini* is a good example of a declining native fish species in Colorado's plains streams. This darter typically inhabits cool, slow-moving, clear, spring-fed streams with abundant aquatic rooted vegetation and sandy bottoms. Originally broadly distributed in Arkansas River tributaries in Colorado, Kansas, Oklahoma, Missouri, and Arkansas (Moss 1981; Miller 1984; Taber et al. 1986; Labbe and Fausch 2000; Krieger et al. 2001), the species has declined and now occurs in fragmented populations throughout its range. Extensive fish surveys by the Colorado Division of Wildlife (CDOW) from 1979 to 1982 and 1993 to 1996 showed apparent

reductions in abundance and range, leaving populations scattered in fragments of habitat throughout the foothills transition zone and plains portions of the basin (Loeffler et al. 1982; Miller 1984; Nesler et al. 1999; Krieger et al. 2001). The ongoing decline prompted the CDOW to list the Arkansas darter as a threatened species in Colorado in 1975 (CDOW 2006), and in 1991 it was proposed as a candidate for protection under the federal Endangered Species Act (USFWS 2009). Populations of Arkansas darters are currently listed as vulnerable in Missouri (MDC 2010), threatened in Kansas (KDWP 2004; Haslouer et al. 2005), and a Species of Special Concern in Arkansas (Hargrave and Johnson 2003) and Oklahoma (ODWC 2010).

One management strategy to conserve species at risk of extinction is to move them to suitable unoccupied habitats within their native range with the goal of establishing new populations. This practice is termed translocation, or reintroduction (Armstrong and Seddon 2007; Rahel et al. 2008; George et al. 2009), and is one of the main management options for restoration of imperiled species (World Conservation Union 1987; Tenhumberg et al. 2004). It is often used to reduce the risk of extinction by establishing, re-establishing, or supplementing a population. However, success rates for translocations of birds, mammals, and fish are generally less than 50% (Griffith et al. 1989; Harig and Fausch 2002; Sheller et al. 2006). The number of individuals released, proximity of the site to the core of the species' historical distribution, and habitat quality are primary factors that influence translocation success, with the last most often cited as the leading cause of translocation failure.

Evaluating factors that contribute to the success or failure of translocated populations is critical to improving future conservation and recovery efforts (George et

al. 2009). In turn, evaluating translocation success requires unbiased techniques that can be used to estimate species occurrence and relative abundance. A main source of error in many evaluations is sampling that fails to detect the species of interest when it is present (i.e., imperfect detectability, $p < 1$), which can bias estimates of habitat occupancy and relative abundance, as well as the effects of predictor variables (MacKenzie et al. 2006). This may be particularly important for small fishes that are rare or difficult to detect, such as Arkansas darters. Perfect detection (i.e., $p = 1$) is almost never attained (Gu and Swihart 2004), but statistically rigorous methods have been developed to estimate the probability of detecting a species at occupied sites based on multiple site visits (MacKenzie et al. 2002, 2006). These occupancy models have been extended to include multiple states (e.g., different categories of relative abundance), and can incorporate the influence of habitat and other covariates on detection and site occupancy probabilities (Royle 2004; Royle and Link 2005; Nichols et al. 2007; MacKenzie et al. 2009; Falke et al. 2010). This class of models is particularly useful when species are distributed heterogeneously among habitats at multiple spatial scales, which is common when sampling stream fishes (Fausch et al. 2002; Torgersen et al. 2006; Isaak et al. 2007). Occupancy estimation is well suited to evaluate translocation success, but has not been used for this purpose for any fish species.

Fish conservation biologists have used translocation as a management strategy to conserve Arkansas darters in plains streams of eastern Colorado since 1980. Wild broodstocks were used as source populations for early translocations until 1999 (Krieger et al. 2001). Since 2002, hatchery-reared darters propagated by the CDOW at the Native Aquatic Species Restoration Facility in Alamosa, CO have been used for new

translocations, as well as supplemental stocking of one stream segment where wild darters were previously translocated. The current Arkansas darter recovery plan for Colorado (Krieger et al. 2001) established the following criteria for recovery success to ensure the viability, health, and genetic integrity of a translocated population: (1) the population is represented by at least 500 individuals; (2) the population has produced at least two year-classes by natural reproduction; and (3) the population is self-sustaining and does not depend on recruitment from other areas for year-to-year survival.

The two goals of my research were to evaluate the success of these Arkansas darter translocations in Colorado based on the three recovery criteria, and to assess what factors contribute to success. I sampled all translocation streams using a multiscale design to determine whether darters had persisted at the translocation site or within the adjacent stream segment, and used new multistate occupancy estimation methods to relate darter occurrence at sampling sites to habitat and biotic factors that could account for translocation success or failure. My approach allowed me to model separately the two processes that lead to translocation failure, namely lack of suitable wet habitat, or absence of the species in habitat that was wet and apparently suitable. Moreover, I analyzed whether darter occupancy at wet sites was related more to local-scale habitat or biotic factors, or riverscape-scale habitat features, and use these results to infer which are most important to promote persistence and hence translocation success.

Field methods

Study streams — During summer 2009, I sampled all 19 streams where Arkansas darters were translocated (Figure 1), and used a multiscale sampling design to measure fish occupancy and habitat features that could explain occupancy. I evaluated the success

of wild Arkansas darters translocated during 1980 to 1999 in flowing water systems (e.g., streams, canals, and ditches; $n=12$), including those with associated ponds (Table 1). I also evaluated translocations made during 2002 to 2008 of hatchery-reared darters into stream sites ($n=7$), including one previously planted with wild darters (Table 2). Sampling of these latter streams was completed before stocking occurred in July 2009, so age-0 darters captured were from natural reproduction. Translocations were made at multiple locations in two streams. I considered three locations in Big Sandy Creek that were less than 5 km apart to be a single translocation, and two locations in Vista del Rio that were 12 km apart as separate translocations. Translocation streams that were stocked with hatchery-reared darters were surveyed a mean of 7.3 years (range: 4 – 12, but see below) after initial translocations, whereas streams that were stocked with wild darters were surveyed a mean of 14.8 years (range: 11 – 29) after initial translocations. This was judged to be long enough for natural reproduction to occur and numbers to increase, or for the population to decline or die out. One stream (Horse Creek) was sampled the summer after translocation with hatchery-reared darters in October 2008. These data were included because the translocation was judged unsuccessful.

Translocation streams were typically small, shallow, low-gradient streams or ditches with silt or sand substrate and abundant rooted aquatic vegetation, but lacking distinct pool-riffle morphology (Table 3). The 19 streams were of three general types, arrayed from east to west (Figure 1): natural intermittent channels or constructed ditches in the floodplain of the Arkansas River in southeastern Colorado that conveyed irrigation seepage back to the river ($n=8$), typical intermittent plains streams ($n=2$), and streams in the foothills transition zone between the Rocky Mountains and the Great Plains in south

central Colorado ($n=9$). Study streams had simple fish assemblages common to plains streams in eastern Colorado, but about half had been invaded by nonnative fishes. In addition to Arkansas darters, five native fish species and two non-native species were captured. Of the five native species, central stoneroller *Campostoma anomalum* were abundant and found in 10 streams, fathead minnow *Pimephales promelas*, northern plains killifish *Fundulus kansae*, and sand shiner *Notropis stramineus* were common and captured in 3 to 8 streams each, and white sucker *Catostomus commersoni* was rare and captured in only 1 stream. Among nonnative fish, western mosquitofish *Gambusia affinis* were also abundant and found in 9 streams, and common carp *Cyprinus carpio* were uncommon and found in 3 streams.

Study segments, reaches, and sampling sites — Sampling was designed to account for three post-translocation scenarios (1) fish did not persist, possibly owing to a lack of suitable habitat or from biotic interactions with nonnative species; (2) fish survived and reproduced within or near the initial translocation site, and may have also emigrated to other reaches; or (3) fish did not persist locally, but emigrated from the original translocation site to other reaches where they survived and reproduced. I considered the last scenario plausible because many stream fish, including those in the western Great Plains, are capable of moving long distances from release sites (Labbe and Fausch 2000; Fausch et al. 2002; Scheurer et al. 2003). In addition, I expected that movement of small fish like darters might be directional with greater downstream than upstream movements from translocation sites.

To investigate these potential scenarios, I used a multiscale systematic sampling design, with more sample locations near the translocation site and fewer farther away. A

3.25-km stream segment (henceforth the translocation segment; Figure 2) was defined around a central 250-m stream reach where fish were initially transplanted (the translocation reach). To assess whether darters had moved and established populations elsewhere, sampling to determine darter presence (occupancy sampling, see below) was conducted in four 62.5-m study reaches laid out systematically in each of five sampling strata, including the 250-m translocation reach, in two 500-m reaches adjacent to the translocation reach, and in two 1000-m reaches farthest from the translocation reach. In total, occupancy surveys were conducted in up to 20 study reaches within the translocation segment. I did not sample reaches upstream of barriers to fish movement (e.g., impassible culverts, water diversion structures). In addition, when proceeding downstream, further sampling was not conducted in two streams (Deadman Ditch and Montgomery Ditch) which entered large, swiftly-flowing irrigation canals, because I assumed any darters that entered them would be swept away and unable to colonize reaches farther downstream in the translocation segment. Some sites could not be sampled because landowners denied access ($n=16$), or because thick emergent cattails (*Typha*) prevented dipnetting or trapping ($n=4$). In total, 336 sites were visited and sampled, including both wet and dry sites in the 19 streams.

Translocation reaches were located using information from Krieger et al. (2001) and CDOW biologists who performed the initial translocations. Study reaches were laid out by pacing along one bank, after calibration of strides against measured distances, being careful to follow the sinuous contours of the bank. This method is as accurate as distances measured along stream channels (± 1 m per 50 m; Fausch, unpublished data). I initially planned to sample deep, vegetated pools, but most translocation segments

consisted of relatively homogeneous habitat. Instead, I assumed that darters that moved from the translocation site would occupy the best available habitat of nearby reaches, and so focused sampling in those places in each 62.5-m study reach. Maintaining a constant study reach length prevented bias that could have been caused by selecting the best available habitat from longer reaches in more distal sampling strata. Within each study reach, I selected a sampling site (termed site hereafter) that was approximately two to four channel widths long and had either deep water, complex habitat structure, or both, if available. In narrower streams the sites were at the longer end of this range to maintain a similar area sampled.

Sampling to determine Arkansas darter occupancy and minimum abundance —I conducted occupancy surveys during mid-May through late August 2009 to assess darter persistence and movement in translocation segments. Following a single-season occupancy sampling scheme (MacKenzie et al. 2006), each site was surveyed on two consecutive days during which sites were assumed closed to changes in occupancy state. Previous research (Labbe and Fausch 2000) and pilot sampling indicated that dip netting and minnow trapping were the most effective methods of capturing Arkansas darters, whereas electrofishing proved ineffective due to high water conductivity ($>1000 \mu\text{S}/\text{cm}$; Table 3). In the first two translocation segments sampled, dip netting was conducted for the first survey, followed by minnow traps fished overnight for the second. However, analysis showed that the detection probability with minnow traps was only about 20-30% of that with dip nets for age-0 and age-1 and older darters, so all subsequent segments were sampled with two dip netting surveys. In the first translocation segment sampled, Vista del Rio Ditch 2, darters were captured at no new sites with minnow traps, so there

was no state uncertainty (see below). In the second, Deadman Ditch, the single darter detected was captured in a minnow trap.

Dip netting surveys were conducted by a two-person crew, each using a long-handled 3.2-mm mesh dip net with a 30-by-30-cm frame. Sites were sampled for 10 minutes each on both surveys, taking care to sample all available microhabitats. After the first dipnetting survey at each site, all darters were counted, measured for total length (nearest mm), and released near their capture site. Length-frequency histograms were then plotted to distinguish age-0 darters (mean total length: 27 mm, range: 15 – 41 mm) from age-1 and older fish (mean total length: 45 mm, range: 32 – 66 mm). Other fish species captured during the first survey at each site were identified and counted. On the second survey, only detection or non-detection of darters in each age class was recorded at each site.

In addition to occupancy sampling, I attempted to estimate minimum fish abundance to determine whether translocated populations met the recovery criterion of supporting at least 500 individuals (Krieger et al. 2001). If occupancy surveys failed to capture darters in the translocation segment, or if captures were relatively low (<50 individuals), minimum abundance was not estimated. In those instances, I assumed that the translocation segment was unable to support more than a small population of darters and assigned it an “unsuccessful” rating. If occupancy sampling revealed >500 individuals, this recovery criterion for abundance was met, and no further sampling was conducted. If I captured between 50 and 500 darters, further sampling was conducted within the translocation segment to establish whether >500 individuals were present. Sampling to assess abundance was conducted using dip nets or minnow traps in a ~150-m

reach determined from occupancy surveys to have the highest fish abundance, and continued until 500 fish were captured or this goal appeared infeasible because fish abundance was low (one stream, Big Sandy Creek). In two cases, this sampling was conducted on an additional date after occupancy surveys were completed, so reaches were selected >100 m away from those where occupancy was estimated to minimize chances of recapturing the same fish.

Habitat measurements — Recent studies of stream fishes demonstrate that factors operating at both local and landscape scales interact to influence fish–habitat relationships and fish occurrence (Torgersen et al. 2006; Isaak et al. 2007). Therefore, habitat variables hypothesized to contribute to darter occurrence and persistence (i.e., translocation success) were measured at both the local site scale and at the larger riverscape scale using low-altitude flights (Fausch et al. 2002; Falke et al., in press).

Local-scale in-stream habitat was measured immediately after fish sampling was completed using protocols developed in the Great Plains ecoregion (Labbe and Fausch 2000; Scheurer et al. 2003; Falke et al. 2010) and for a similar study on trout translocation success (Harig and Fausch 2002). Each site was georeferenced with a Garmin Rino 530 Global Positioning System (GPS; Garmin International Inc., Olathe, Kansas, USA), and detailed measurements of site dimensions were made by: (1) measuring length along the longest axis, (2) dividing the length evenly into three perpendicular transects, (3) measuring wetted width at the midpoint of each transect, and (4) measuring depth at three positions located at one-sixth, one-half, and five-sixths of each width transect. Visual estimates were made of the proportion of each site covered by five categories of aquatic vegetation or other habitat structure (rooted aquatic vegetation,

emergent aquatic vegetation, algae, tumbleweed, and woody debris). Streambed substrate was also visually estimated, but not reported because it was nearly always composed of fine materials such as mud, clay, or silt.

At each site, conductivity and water temperature were measured using a YSI Model 85 multi-meter (Yellow Spring Instruments, Inc., Yellow Springs, Ohio). Conductivity (μS ; adjusted for elevation and temperature) was measured at mid-depth, and temperature (nearest 0.1°C) was measured at the surface and at the stream bottom just above the substrate. Bottom temperatures were used in further analysis, because these measure groundwater inputs and are often the coolest temperatures available to fishes in plains streams, which can exceed 34°C at the surface during summer (Labbe and Fausch 2000; Scheurer et al. 2003). Because stream temperatures were highly variable ($\text{SD} = 3.31$, range: $13 - 30^\circ\text{C}$) and varied both daily and seasonally, I normalized temperatures by calculating residual values from two nonlinear regressions of bottom temperature ($^\circ\text{C}$) as a function of time of day, and day of year (i.e., Julian date). A set of four linear and quadratic candidate models were fit to the data for all sites in all streams for the diurnal period of heating (0730 to 1730 h) and afterwards as streams began cooling (1730 to 2030 h), and the best model (below) for each case was selected using Akaike's Information Criterion (AIC; Burnham and Anderson 2002):

before 1730 h:

$$T_{\text{predicted},i} = -88.93 + 1.32(\text{JD}) - 0.0036(\text{JD})^2 - 45.35(t) + 47.59(t)^2$$

after 1730 h:

$$T_{\text{predicted},i} = -574.00 + 3.54(\text{JD}) - 0.010(\text{JD})^2 + 76.05(t) - 514.40(t)^2$$

where $T_{\text{predicted},i}$ is the predicted temperature ($^{\circ}\text{C}$) at sample site i , JD is Julian date, and t is time (24 h). Then, given the actual measured temperature at site i ($T_{\text{measured},i}$; $^{\circ}\text{C}$), the residual temperature ($^{\circ}\text{C}$) is calculated as:

$$\text{TEMP}_i = T_{\text{measured},i} - T_{\text{predicted},i}$$

This measure indicates whether a site was relatively warm (positive residual) or relatively cool (negative residual) compared to the mean across all streams, after adjusting for time of day and day of year. I caution, however, that the models presented here may not yield accurate predictions in other geographic regions, and may vary somewhat among years even in this region.

Two riverscape-scale characteristics, which set the overall physical habitat template for darters in each translocation stream, were measured over a 10-km segment centered on the translocation reach using low-altitude flights. Percent wetness is the proportion of the 10-km segment with a wetted channel measured during the period of lowest water (18 September 2009). Available habitat is the total length (km) of habitat accessible to the translocated darters during this period. This included all wetted stream channel downstream from barriers to upstream movement (e.g., road culverts and diversion structures), but excluded dry reaches. During field sampling of the 3.25-km translocation segments, I found that all roads encountered had impassible culverts with vertical drops >20 cm, so I designated all roads as barriers to upstream movement. Moreover, Ficke et al. (2006) found that Arkansas darters were unable to ascend even a 10-cm step and were rarely able to hold position at 16 cm/s so it is apparent that they would be unable to ascend any culverts during high flows when these steps might be

passable. In addition, the two stream segments described above that were downstream from large canals were excluded. Aerial surveys of each stream were conducted from a fixed-wing aircraft at low-altitude, 200 to 300 m above the stream channel. A GPS was used to map locations of culverts and other barriers to movement, and transitions among flowing (all pools connected), intermittent (disconnected pools), and dry stream reaches. Surveys of three streams were done on the ground due to flight restrictions over Fort Carson.

Statistical modeling of Arkansas darter occupancy

Occupancy estimation and modeling — I modeled site occupancy of darters using a single-season multistate occupancy model incorporating covariates measured at three spatial scales (Nichols et al. 2007; MacKenzie et al. 2009). I fit separate models for detections of age-0 and age-1 fish, and also modeled the influence of habitat depth and season (Julian date) on probability of detection for both groups. Since my interest was in both the availability of habitat and the important features of suitable habitat that influenced darter occupancy, observations at each site were classified as one of three states: dry and thus unoccupied by darters (0), wet but no darters detected (1), or wet and darters detected (2). Data sets were created for each age group and were used to estimate the probability that site i contained potential (wet) habitat (ψ_i^1); the probability that darters occurred at site i , given that it was wet (ψ_i^2); and the probability of detecting darters at site i during survey t ($p_{i,t}^2$) given the site was wet and occupied (i.e., in true state 2, referred to as $\delta_{i,t}$ in Nichols et al. 2007). The unconditional probability that site i was wet and occupied by darters was $\psi_i^{1*2} = \psi_i^1 \times \psi_i^2$ (Nichols et al. 2007).

An underlying assumption of my occupancy modeling is that sites were closed to changes in occupancy (e.g., darters were either present or absent on both days) during the two-day survey period (MacKenzie et al. 2006). In other words, during the time between sampling events, I assumed that the population of darters at an occupied site did not go locally extinct via death or movement, and that unoccupied sites were not colonized by other darters. For each site, a detection history (h_i) for each age class of Arkansas darters was compiled; for example, if age-0 fish were not captured in the first survey of a wet site but were captured in the second survey, the corresponding detection history for site i would be $h_i = 12$. In this case, there is no uncertainty about the true state of the site (wet and occupied, true state = 2). However, if darters were not observed on either survey (i.e., $h_i = 11$), then two occupancy states are possible: the site could be occupied (true state 2) or not (true state 1), given that it is wet.

Model covariates for conditional darter occupancy — I selected eight covariates that previous research suggested might influence darter occupancy and persistence at sites in translocation segments. Local site-scale covariates included residual temperature ($TEMP_i$) and the percent area with vegetative or woody structure that might shelter darters (i.e., not bare substrate; VEG), because previous research indicated that Arkansas darters prefer cool, spring-fed streams with abundant aquatic vegetation (Moss 1981; Taber et al. 1986; Loeffler and Krieger 1994; Labbe and Fausch 2000). I also considered a “biotic resistance” hypothesis, which addressed the possibility that darter occupancy at the site level may be reduced by biotic interactions with nonnative species. I used the number of western mosquitofish *Gambusia affinis* captured at each site as a metric of biotic resistance because they were common at translocation streams, and are known to

be voracious nonnative predators or competitors responsible for the decline or disappearance of other small fishes in similar habitats (see Pyke 2008 for a review).

Two segment-scale covariates and their interaction were used to address the possibility of movement into nearby habitats after fish were translocated. If fish moved, occupancy might depend on the distance from the translocation site (DIST; absolute value of the upstream or downstream distance from the initial translocation site to the midpoint of the 62.5-m study reach), direction (DIR; a categorical variable distinguishing sites downstream versus upstream of the translocation site), and their interaction (INT). I considered three possibilities, that: 1) distance could influence darter occurrence, but with no difference between upstream and downstream sites (i.e., same slope and intercept), 2) there was an additive difference in the effect of distance between upstream and downstream sites (same slope but different intercepts), and 3) there was an interaction, indicating that the effect of distance differed between upstream and downstream sites.

At the riverscape-scale, I hypothesized that darter persistence, and hence occupancy, might be influenced by the relative wetness of the 10-km segment centered on the translocation segment (% wetness, WET), and the amount of stream habitat available for darters to colonize (HAB). Finally, I also suspected that persistence and occupancy could be influenced by whether wild or hatchery darters were used to establish translocated populations (HAT). This covariate was a surrogate for a suite of differences. Translocations with hatchery-propagated darters were conducted within the previous seven years (2002-2008) and involved repeated stockings totaling thousands of individuals, whereas translocations with wild darters were conducted more than a decade before my sampling using single releases of relatively few fish (Table 2). Overall, the

translocation streams sampled encompassed a broad range of conditions for each covariate (Table 3).

Candidate models and model selection — I developed *a priori* candidate models that contained sets of covariates that are biologically relevant for estimating the probability, or proportion, of wet sites (ψ_i^1) and explaining occupancy of Arkansas darters at wet sites (ψ_i^2). I reasoned that variation in the probability of apparently suitable (wet) habitat among sites could be adequately modeled as a function of a single covariate, the percent wetness of the 10-km reach surrounding the translocation reach (WET). Next, focusing on factors that may influence darter occupancy at wet sites, I developed 15 models using only the four types of covariates described above, as well as a null model with no covariates (intercept only), a global model with all eight covariates, and a set of models with a mixture of covariate types (Tables 4 and 5). For example, three models were developed with riverscape-scale covariates only, including either percent wetness, available habitat (HAB), or both (models M9-M11, Tables 4 and 5). Three mixture models were used to test, for example, whether darter occupancy was best described by percent wetness, available habitat, and whether wild or hatchery darters were translocated (M15). Preliminary analysis showed that when conditional darter occupancy was modeled as a function of counts of western mosquitofish the relationship was positive, suggesting that both species occur in similar habitats. This was opposite my hypothesis, so I excluded this covariate from further consideration.

In addition to the occupancy covariates, I hypothesized that detection probabilities could be influenced by two covariates that also vary among sites. Age-0 darters might be more difficult to detect earlier in the season when they are smaller, and detectability of

both age groups of darters might be lower at deeper sites. Rather than fit all possible combinations of conditional occupancy and detection probability structures, I used my most general occupancy structure (M1, the global model) to fit four models with different detection probability structures for each age group. Specifically, detection probability was modeled as a function of Julian date (DATE) or site-specific depth (DEPTH), as an additive function of both date and depth (DATE+DEPTH), or as constant among all sites (.). This initial analysis revealed that Julian date (DATE) was an important variable determining detectability for age-0 darters, whereas depth (DEPTH) was important for age-1 fish. These covariate structures were used in all subsequent models (Tables 4 and 5).

I used an information-theoretic approach (Burnham and Anderson 2002) to evaluate all models. Model selection and multimodel inference were used to find the most parsimonious set of independent variables to estimate conditional occupancy state and detectability for both age groups. I used Akaike's information criterion adjusted for small sample size (AIC_c) and Akaike weights (w_i) to compare candidate models simultaneously. Based on the results of my *a priori* models presented above, I considered an additional set of five exploratory models evaluated post-hoc (M16-M20) to refine a subset of covariate comparisons. I used model averaging to account for model selection uncertainty when reporting real parameter estimates and to provide model-based predictions (see next section). All analyses were conducted using the multistate occupancy parameterization in Program MARK (White and Burnham 1999).

Occupancy predictions — To demonstrate the usefulness of my results for guiding management decisions, I collected habitat covariate information on a stream segment

where biologists from CDOW and The Nature Conservancy have proposed translocating Arkansas darters. In mid-July 2010 I measured the length of total available habitat, and the depth and bottom water temperature at 20 evenly-spaced sites along the headwaters of Steels Fork of Horse Creek. I used these data to predict site occupancy for each age group of darters, after converting water temperatures to residuals using my nonlinear regression equations.

Goodness of fit and spatial autocorrelation — An underlying assumption of occupancy models is that species occurrence and detection are independent among sites, so that the presence or detection of darters at a given site is not influenced by presence or detection at an adjacent site. My design involved sampling spatially distinct sites over two days during summer low flows, so it is unlikely that the same darters would have been detected at multiple sites. Moreover, there is no goodness-of-fit (GOF) test for most occupancy models, including the multistate model. The parametric bootstrap GOF test developed by MacKenzie and Bailey (2004) for the basic, single-season occupancy model (i.e., the simple two-state model) represents the only method commonly used in occupancy analyses, and in limited simulations, this method had moderate to excellent power to detect lack of independence and estimate a corresponding overdispersal parameter, \hat{c} .

To address the potential for lack of independence among sites (i.e., possible spatial autocorrelation), I tested model fit using the parameteric bootstrap method implemented in program PRESENCE (MacKenzie and Bailey 2004). Since the state of dry sites was observed without error, I reasoned that poor fit would most likely result from models of conditional darter occupancy. Accordingly, dry sites were eliminated

from the GOF evaluation and a simple, single-season model was used with the appropriate global structure for each age group. Using these same data sets, I also evaluated spatial autocorrelation using a first-order Markov model recently developed by Hines et al. (2010). This model allows the probability that a site is occupied to differ based on whether the previous upstream site was occupied (θ'), or not (θ). The new model explicitly accounts for spatial autocorrelation and allowed me to estimate both site-level (θ' and θ) and stream-level occupancy (ψ) of darters and verify the estimated relationships to the chosen habitat characteristics. Using the most influential habitat covariates from the multistate analyses, I constructed three models for both age groups which assumed independent (random) occupancy probabilities ($\theta' = \theta$) and three more models that modeled site-specific occupancy as an additive first-order Markov process (i.e., site occupancy exhibits spatial dependence and is non-random).

Results

Success of Arkansas Darter Translocations — In 5 of the 19 streams the entire 3.25-km translocation segment was completely dry, so fish sampling and habitat measurements were not conducted at any sites, but flights of the 10-km segment were made to measure the two riverscape-scale variables. Of the 14 wetted streams, darters were not detected at any of the wet sites in 3 streams. Occupancy surveys established darter presence in the remaining 11 translocation segments (Tables 1 and 2), including 5 of 12 streams where only wild darters were translocated and all but 1 of the 7 streams where hatchery-reared darters were translocated. In some streams, Arkansas darter populations were established from introductions of relatively few wild fish (e.g., 34

individuals in 1980 for Lytle Pond; Table 1), whereas another failed to support high numbers of darters despite repeated stockings of hatchery-propagated individuals (e.g., a total of 1,094 individuals were stocked in Deadman Ditch from 2005 to 2008; Table 2).

Of the 11 translocation streams where darters were present, only two met all criteria for translocation success set out in the CDOW recovery plan (Tables 1 and 2). In six streams with darters, initial occupancy sampling or additional sampling revealed >500 individuals and so met the first criterion for translocation success. Darters were captured in low numbers in four translocation segments (<50 total), including in Deadman Ditch where only one darter was captured. Abundance was not estimated for these streams and translocations were considered “unsuccessful” to date. For one stream (Big Sandy Creek), both occupancy and additional sampling (20 minnow trap nights) for abundance was conducted in deep or heavily vegetated habitat that likely hindered capture efficiency. Sampling yielded only 229 darters, although further effort might yield the additional fish required to meet the minimum abundance criterion.

Most streams with darters met the second recovery criterion of natural reproduction supporting multiple age classes, because both age-0 and age-1 and older darters were captured in 10 of the 11 streams. Two streams into which only wild darters were translocated, Brackett Creek and Lytle Pond, also met the third recovery criterion of a self-sustaining population not depending on outside demographic support. In contrast, four streams met the other two criteria but continued to receive annual stocking of hatchery-reared darters, so it was unclear whether the populations were self-sustaining. Likewise, for the five streams with low abundance (<500 captured), it is unknown whether the populations were self-sustaining, or will eventually die out.

Models of Arkansas Darter Occupancy — Model selection revealed that total habitat available for translocated darters and relative bottom water temperature (i.e., the residuals from the regressions that account for season and time of day) had the strongest influence on Arkansas darter occupancy at wet sites within translocation streams. For age-0 darters, the model including these two covariates was demonstrably better than other models and carried the most weight (Table 4; M16, $w_i=40\%$). The second and third ranked models also included these two covariates but incorporated an additional covariate, either percent wetness (M14, $w_i=19\%$) or translocation type (M17, $w_i=15\%$). Inspection of the measure of fit $[-2\log(L)]$ for these two models shows that they are similar to the simpler model with only two primary covariates (M16), indicating that the additional variables contributed little explanatory power (i.e., an example of lurking covariates, Burnham and Anderson 2002, p.131). The model with total available habitat alone ranked fourth (M10, $w_i=13\%$). Together, these model results provide clear evidence of the importance of temperature and available habitat for occupancy of age-0 darters.

Water temperature and, to a lesser degree, available habitat were also important for explaining occupancy of age-1 darters. The four top models differed by less than 2.0 AIC units (Table 5), indicating model selection uncertainty and suggesting that several models may be reasonable for the collected data. Similar to age-0 results, a model that related conditional occupancy to bottom water temperature and available habitat (Table 4; M16, $w_i=15\%$), ranked high, but a simpler model with only water temperature was the top ranked model (M3, $w_i=24\%$), indicating the importance of local temperature. Adding additional covariates to these two primary model structures failed to improve model fit, based on the log likelihood [e.g., vegetative structure (M5, $w_i=9\%$), or percent wetness

(M14, $w_1=9\%$)], again indicating that these additional variables provided little explanatory power.

Model-averaged estimates of beta coefficients and unconditional standard errors from both age groups suggested a negative relationship between conditional occupancy and the residual of bottom water temperature (age-0: $\hat{\beta} = -0.09$, $\widehat{SE} = 0.04$; age-1: $\hat{\beta} = -0.07$, $\widehat{SE} = 0.03$), indicating that occupancy was higher for cooler sites with lower relative temperature. In addition, model parameters for available habitat were positive in all models, indicating that occupancy was greater at sites in streams with more habitat available to translocated darters (age-0: $\hat{\beta} = 0.31$, $\widehat{SE} = 0.06$; age-1: $\hat{\beta} = 0.02$, $\widehat{SE} = 0.03$), although the relationship was not precise for age-1 darters. In contrast, distance, direction, vegetation, and translocation type (wild vs. hatchery) were uninformative parameters and were interpreted as having little, if any, ecological effect that could explain occupancy of translocated Arkansas darters at sites with wet habitat. For example, darters readily colonized stream segments both upstream and downstream from the translocation sites. Of the 11 streams where darters were present, darters colonized the farthest upstream or downstream site sampled in six and seven cases, respectively (Tables 1 and 2). In 11 of the 22 cases, they colonized $\geq 1,375$ m from the translocation site.

Model-averaged parameter estimates for the probability that a site was wet ($\widehat{\psi^1}$) depended on the percent wetness of the surrounding 10-km reach, and was 0.79 ($\widehat{SE} = 0.04$) at the mean percent wetness value of 0.57 (including all 336 wet and dry sites). The probability that a site was occupied given that it was wet ($\widehat{\psi^2}$) was 0.46 ($\widehat{SE} = 0.04$) for both age groups (using mean covariate values). Therefore, the unconditional

probability of site occupancy ($\widehat{\psi}^1 \times \widehat{\psi}^2$) was 0.36 ($\widehat{SE} = 0.04$) for both groups, suggesting that darters occupied approximately one third of all sites visited and sampled in translocation segments (including dry sites). Overall, detectability (\widehat{p}_i^2) was high for both age groups, 0.91 ($\widehat{SE} = 0.03$) for age-0 fish and 0.76 ($\widehat{SE} = 0.05$) for age-1 fish, reported at mean Julian date and depth, respectively.

Using my model-averaged parameter estimates for the effect of bottom water temperature and available habitat, I predicted the conditional probability of site occupancy for each age group under three different temperature regimes: an average site (residual temperature of 0°C), a site with among the warmest temperatures (residual temperature of +4°C), and a site with among the coolest (-4°C; Figure 3). For age-0 darters, conditional occupancy reaches 50% at about 4.1 km of available habitat for a site of average temperature, but is expected to increase to 58% at sites that have 4°C colder bottom temperature. For age-1 darters, the effect of available habitat is weaker, but still evident, with predicted occupancy reaching 50% at about 9 km of available habitat, and increasing to 57% in sites that have 4°C colder bottom temperature. Likewise, the models indicate that sites with less available habitat, or warmer temperatures, are less likely to be occupied.

Occupancy Predictions — Habitat characteristics were measured at 20 sites in Steels Fork of Horse Creek to assess whether darters would likely persist and occupy sites if translocated. My sampling found an impassible culvert which separates the stream into a downstream segment 1.7 km long and an upstream segment 2.1 km long. Therefore, I assumed that darters translocated in the upstream segment could colonize downstream and access 3.8 km of habitat, but that darters translocated downstream would

have only 1.7 km of available habitat, unless the culvert was removed. Using the habitat information collected at each site, I predicted site occupancy of both age-0 and age-1 darters under two scenarios: 1) translocation occurred either upstream or downstream of the culvert, or 2) the culvert was removed before translocation occurred, connecting the two segments. My model predicts an increase in mean conditional probability of occupancy for age-0 darters downstream from the culvert from ~40% to ~60% when the culvert is removed, reflecting the importance of available habitat (Figure 4). For age-1 darters, the mean site occupancy in the downstream segment increases slightly from 52% to 56%, on average, when the culvert is removed, showing the lesser sensitivity to available habitat for this age group. Additional variation in site occupancy resulted from variation in groundwater inputs along the segment which changed site-specific residual temperatures (range: -4.57 to -1.04°C).

Spatial Autocorrelation of Sample Sites — I found no evidence of lack-of-fit of the global model using the Mackenzie and Bailey (2004) parametric bootstrap GOF test for age-0 darters ($\chi^2 = 0.38$, $P = 0.94$, $\hat{c} = 0.13$) or age-1 darters ($\chi^2 = 0.42$, $P = 0.91$, $\hat{c} = 0.15$), suggesting no substantial departures from model assumptions. These results would not raise questions about the assumption of independence among sites. In contrast, the new Markovian spatial-dependence models strongly suggested that wet sites were more likely to contain darters if the preceding upstream site was occupied (Table 6). For each of the three pairs of models (with and without spatial dependence) for both age groups, the model which includes spatial dependence always ranked higher (i.e., lower AIC). Models that assumed spatial independence (i.e., models where site-specific occupancy was independent of the state of the previous upstream site) were not supported and do not

contribute to the model weight. Still, the direction and magnitude of the relationships between site occupancy and the habitat covariates were consistent with the previous multistate occupancy analysis for both age groups. These results indicate that parameter estimates remain relatively unbiased even if the assumption of independence among sites is violated, although precision may be somewhat overstated (McCullagh and Nelder 1989, MacKenzie and Bailey 2004).

Discussion

Translocation success — My data indicate that Arkansas darters were present, and met two of the recovery criteria, minimum abundance (>500 individuals) and reproduction (at least two age classes), in 6 of 19 (32%) of the streams where they were translocated. This is similar to success rates for translocation programs involving other fish species (e.g., cutthroat trout; Harig and Fausch 2002) and across other animal taxa (Griffith et al. 1989; Wolf et al. 1998; Fischer and Lindenmayer 2000). However, of these six streams, only two, those that were established from early stockings of wild fish (Lytle Pond and Brackett Creek), also met the third recovery criterion of producing self-sustaining populations. The other four had been stocked annually with hatchery-propagated darters the previous 4 to 7 years, which prevented determining whether these populations were self-sustained. Nevertheless, there was evidence in all these streams that darters were spawning, because age-0 darters were detected before additional stocking occurred in 2009. I suggest that fishery managers cease stocking in all or some of these sites to determine whether hatchery propagation is an important variable that explains translocation success and whether translocated populations will persist for at

least two generations (which will require about 4 years to determine), or eventually die out.

Darters were present at low densities in five other streams, leaving the future of these populations in doubt. In three streams stocked with wild fish, fewer than 50 individuals were captured after 12 to 19 years, so I classified them as unsuccessful although they were self-sustaining. Based on my habitat measurements and the supported models, failure to meet recovery criteria at Cottonwood Springs, Mary Ellen Springs, and Vista del Rio may be related to a combination of inadequate available habitat and warm temperatures. Although the darter population in Big Sandy Creek apparently remained relatively small even after stocking efforts in 2005 and 2007, a large wild self-sustaining darter population was present in the headwaters much farther upstream (Labbe and Fausch 2000). A single darter was captured in 1 of the 16 sites sampled at the final stream, Deadman Ditch, but this did not indicate successful reproduction and I assumed that this translocation had been unsuccessful to date.

For the three streams where no darters were detected at any of the sampled wet sites (Montgomery Ditch, Williams Creek, Horse Creek; Tables 1 and 2), I used site-specific detection probabilities to determine how likely it was that I failed to detect darters of each age group at a given number of occupied sites within each stream. For any occupied site i , the probability of missing darters over k sampling occasions is $(1 - p_i)^k$, where p_i is the detection probability as before. Based on the observed distribution of darters in other translocation streams, I assumed that in any successful translocation darters would have colonized at least $n = 4$ wet sites, such as the adjacent sites in the 250-m translocation reach. Given this, the probability of failing to detect darters in any of

these four occupied sites on the $k = 2$ sampling occasions can be calculated as $\prod_{i=1}^4 (1 - p_i)^2$. For example, in four adjacent wet sites within the translocation segment of Horse Creek, detection probabilities for age-1 darters (based on depth) were estimated at 0.97, 0.99, 0.84, and 0.95. Therefore, the probability that darters *were* present at all four sites, but were not detected, is miniscule, and is calculated as $\prod_{i=1}^4 (1 - p_i)^2 = (1 - 0.97)^2 \times (1 - 0.99)^2 \times (1 - 0.84)^2 \times (1 - 0.95)^2 = 9.14 \times 10^{-12}$. Among the three streams, values for both age classes ranged from this low value to 5.93×10^{-5} . Thus, my sampling protocol ensured that it was highly unlikely that I failed to detect darter persistence in translocation streams with apparently suitable wet habitat.

My data indicate that Arkansas darters were able to disperse and colonize suitable habitat over long distances, both upstream and downstream of the original translocation site. I initially hypothesized that distance from the translocation site would be an important variable explaining conditional site occupancy, and that darters would be more likely to move downstream than upstream. My analysis did not support this hypothesis, but suggested that if continuous wet habitat is available, darters can colonize long stream segments upstream and downstream and reproduce there. My findings corroborate previous work that showed stream fishes, including small bodied plains fish such as the Arkansas darter, are capable of moving long distances along the riverscape (Gowan et al. 1994; Labbe and Fausch 2000; Scheurer et al. 2003; Falke et al. 2010).

My results also suggest that translocated Arkansas darters are spatially clustered among sites within streams. Given the movement described above, and the spatial heterogeneity of suitable habitat along stream networks (Isaak et al. 2007; Falke et al., in press), it is not surprising that fishes like darters are also patchily distributed. To my

knowledge, this work represents one of the first attempts to address the issue of spatial autocorrelation in stream fish populations. The Markovian spatial dependence model represents a different way of viewing a network of occupied sites, focusing on the spatial hierarchy of multiple sample sites within a stream. Techniques for investigating the degree of spatial autocorrelation are a valuable addition to the suite of modeling tools now available for occupancy estimation.

Influence of habitat on occupancy and translocation success — Occupancy analysis showed that darters were more prevalent at sites where bottom temperatures were cooler than average, and at sites in less fragmented streams with longer segments available for colonization. Although residual water temperature was measured at the local scale, it also may indicate groundwater inputs that promote persistence at the segment scale. For example, Labbe and Fausch (2000) found that overwinter survival of wild Arkansas darters was high in a long spring-fed pool of upper Big Sandy Creek where groundwater inputs moderated winter temperatures, whereas survival was very low in adjacent reaches with little groundwater where pools froze to the bottom. Likewise, groundwater inputs would prevent summer drying during dry years, and thereby enhance translocation success. Studies of natural or translocated salmonid populations isolated in headwater fragments above movement barriers also show that persistence is greater in longer stream segments (Harig and Fausch 2002; Morita and Yamamoto 2002; Young et al. 2005), corroborating my finding that darters are more likely to persist and occur at sites in streams with longer segments of habitat available for colonization.

This multiscale analysis of Arkansas darter occupancy and stream habitat showed that both local-scale and riverscape-scale variables played an important role in

determining occupancy and translocation success. These results are similar to other recent studies showing the importance of spatial ecology for predicting stream fish populations (e.g., Scheurer et al. 2003; Torgersen et al. 2006; Falke and Fausch 2010; see Fausch 2010 for a review). My findings also support the theory that stream fishes respond to habitat features at multiple spatial scales, that habitat features can interact across scales, and that many site-scale variables may be of lesser importance in explaining stream fish distributions (Fausch et al. 2002; Isaak et al. 2007; Falke and Fausch 2010).

I developed my models by sampling all available translocation streams, but this was nevertheless a modest sample ($n=19$ streams, 5 of which were dry) so interpretations based on them should be made with caution. The relationships with available habitat may also be biased by stocking of hatchery darters, which may have supported populations in shorter translocation segments that might otherwise have been extirpated. If so, the predicted relationship of occupancy with available habitat would likely be steeper for age-1 darters, and perhaps also for age-0 darters (Figure 3), and this variable would be more important than reported here. Finally, although I detected no negative relationship between nonnative western mosquitofish and Arkansas darter, these or other nonnative species could have important detrimental effects. For example, Labbe and Fausch (2000) reported that wild Arkansas darters were vulnerable to predation by nonnative northern pike *Esox lucius*, which greatly reduced their distribution and abundance in a 13-km segment of the headwaters of Big Sandy Creek.

Use of models for conservation — This research identified habitat attributes that were correlated with occupancy and persistence of translocated Arkansas darter populations in Colorado's plains streams. In addition to identifying two important habitat

features, cool water and sufficient length of stream habitat, fish conservation biologists can use these models for three main goals: 1) to seek new sites where translocations would most likely be successful, and predict success at sites where translocations are planned, 2) to analyze reasons why a translocation was unsuccessful and failed to meet recovery criteria, and 3) to identify factors that may place current translocated populations at risk.

As an example of the first goal of predicting translocation success, I measured stream habitat at Steels Fork of Horse Creek where translocating darters has been proposed. I used the habitat data collected across sites to predict site occupancy, and identified a road culvert as an impediment to persistence and translocation success, especially for age-0 darters. Likewise, biologists could evaluate similar stream habitat information in other segments where translocations of darters are being considered to determine where success is most likely.

Second, my predictive models and multiscale surveys of habitat enable managers to analyze potential reasons that translocations were not successful. For example, it appears that failure to meet recovery criteria at some streams (e.g., Deadman Ditch, Mary Ellen Spring, Montgomery Ditch, and Williams Creek) may be related to an inadequate amount of available habitat (range: 1.7-2.9 km), whereas at others higher than average temperatures may play a role (Big Sandy Creek and Vista Del Rio 1; residual temperature 2.1-2.9°C higher than average).

Third, my results suggest that current translocated populations may be at risk if translocation segments do not provide cool temperatures at the local scale (often via groundwater inputs), and sufficient habitat at the riverscape-scale. Human land uses that

either increase stream temperatures (e.g., by removal of in-stream or streamside vegetation) or reduce the total length of available habitat (e.g., by constructing new bridges, culverts, or water diversion structures that fragment stream habitats) may jeopardize translocated populations of darters. My models provide support for managers who seek to implement habitat conservation and land management practices that protect and restore relatively long unfragmented segments of cooler streams.

Translocation is one tool that fish conservation biologists use to slow or reverse declines in populations of native plains fish species. Translocations to establish new populations in suitable habitats will likely remain a useful short-term strategy for increasing the number of populations of at-risk species and thereby spread the risk of extinction among them (den Boer 1968). However, it is clear that effective conservation efforts will require a landscape approach in aquatic as well as terrestrial systems (Reeves et al. 1995; Gido et al. 2010; Hoagstrom et al., in press). The models developed here can be used to develop habitat conservation and land management practices that seek to conserve, protect, and restore current and future critical habitat for Arkansas darters.

References

- Armstrong, D. P., and P. J. Seddon. 2008. Directions in reintroduction biology. *Trends in Ecology and Evolution* 23:20–25.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information theoretic approach*. Springer-Verlag, New York.
- CDOW (Colorado Division of Wildlife). 2006. Colorado's comprehensive wildlife conservation strategy and wildlife action plans. < http://wildlife.state.co.us/NR/rdonlyres/D26A4806-8776-4460-831E-AA654EC7DDED/0/CWCS_FinalReport2006.pdf >. Accessed January 23, 2009.
- CDOW (Colorado Division of Wildlife). 2007. Endangered, threatened, and species of special concern. < <http://wildlife.state.co.us/WildlifeSpecies/SpeciesOfConcern/Fish/FishOfConcern.htm> >. Accessed January 23, 2009.
- den Boer, P. J. 1968. Spreading the risk and stabilization of animal numbers. *Acta Biotheoretica* 18:165–194.
- Dodds, W. K., K. B. Gido, M. R. Whiles, K. M. Fritz, and W. J. Matthews. 2004. Life on the edge: the ecology of Great Plains prairie streams. *BioScience* 54:205–216.
- Falke, J. A., K. R. Bestgen, and K. D. Fausch. 2010. Streamflow reductions and habitat drying affect growth, survival, and recruitment of brassy minnow across a Great Plains riverscape. *Transactions of the American Fisheries Society* 139:1566-1583.
- Falke, J. A., and K. D. Fausch. 2010. From metapopulations to metacommunities: linking theory with empirical observations of the spatial population dynamics of stream fishes. *American Fisheries Society Symposium* 73:207-233.
- Falke, J. A., K. D. Fausch, R. Magelky, A. Aldred, D. S. Durnford, L. K. Riley, and R. Oad. in press. The role of groundwater pumping and drought in shaping ecological futures for stream fishes in a dryland river basin of the western Great Plains, USA. *Ecohydrology*.
- Fausch, K. D. 2010. A renaissance in stream fish ecology. *American Fisheries Society Symposium* 73:199-206.
- Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience* 52:483–498.
- Ficke, A. D. 2006. Fish barriers and small plains fishes: fishway design recommendations and the impact of existing instream structures. Master's thesis, Colorado State University, Fort Collins, Colorado.

- Fischer, J. and D. B. Lindenmayer. 2000. An assessment of the published results of animal relocations. *Biological Conservation* 96:1–11.
- George, A. L., B. R. Kuhajda, J. D. Williams, M. A. Cantrell, P. L. Rakes, and J. R. Shute. 2009. Guidelines for propagation and translocation for freshwater fish conservation. *Fisheries* 34:529–545.
- Gido K. B., W. K. Dodds, M. E. Eberle. 2010. Retrospective analysis of fish community change during a half-century of landuse and streamflow changes. *Journal of the North American Benthological Society* 29:970–987.
- Gowan, C., M. K. Young, K. D. Fausch, and S. C. Riley. 1994. Restricted movement in resident stream salmonids: a paradigm lost? *Canadian Journal of Fisheries and Aquatic Sciences* 51:2626–2637.
- Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. *Science* 245:477–480.
- Gu, W., and R. K. Swihart. 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biological Conservation* 116:195–203.
- Hargrave, C. W., and J. E. Johnson. 2003. Status of Arkansas darter, *Etheostoma cragini*, and Least darter, *E. Microperca*, in Arkansas. *The Southwestern Naturalist* 48:89–92.
- Harig, A. L., and K. D. Fausch. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. *Ecological Applications* 12:535–551.
- Haslouer, S. G., M. E. Eberle, D. R. Edds, K. B. Gido, C. S. Mammoliti, J. R. Triplett, J. T. Collins, D. A. Distler, D. G. Huggins, W. J. Stark. 2005. Current status of native fish species in Kansas. *Transactions of the Kansas Academy of Science* 108:32–46.
- Hines, J. E., J. D. Nichols, J. A. Royle, D. I. MacKenzie, A. M. Gopalaswamy, N. Samba Kumar and K. U. Karanth. 2010. Tigers on trails: occupancy modeling for cluster sampling. *Ecological Applications* 20:1456–1466.
- Hoagstrom, C. W., J. E. Brooks, and S. R. Davenport. in press. A large-scale conservation perspective considering endemic fishes of the North American plains. *Biological Conservation*.

- Hubert, W. A., and K. M. Gordon. 2007. Great Plains fishes declining or threatened with extirpation in Montana, Wyoming, or Colorado. Pages 3-13 in M. J. Brouder and J. A. Scheurer, editors. Status, Distribution, and Conservation of Native Freshwater Fishes of Western North America. American Fisheries Society, Symposium 53, Bethesda, Maryland.
- Isaak, D. J., R. F. Thurow, B. E. Rieman, and J. B. Dunham. 2007. Chinook salmon use of spawning patches: Relative roles of habitat quality, size, and connectivity. *Ecological Applications* 17:352–364.
- KDWP (Kansas Department of Wildlife and Parks). 2004. Threatened and endangered species: Arkansas darter. < <http://www.kdwp.state.ks.us/news/Other-Services/Threatened-and-Endangered-Species/Threatened-and-Endangered-Species/Species-Information/ARKANSAS-DARTER> >. Accessed July 30, 2010.
- Krieger, D., T. Nesler, C. Bennett, G. Dowler, and J. Melby. 2001. Arkansas darter (*Etheostoma cragini*) recovery plan. Colorado Division of Wildlife, Denver.
- Labbe, T. R., and K. D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecological Applications* 10:1774–1791.
- Loeffler, C., and D. Krieger. 1994. Arkansas darter *Etheostoma cragini* recovery plan. Colorado Department of Natural Resources, Division of Wildlife, Colorado Springs.
- Loeffler, C., D. L. Miller, R. Shuman, D. Winters, and P. Nelson. 1982. Arkansas River threatened fishes survey. Federal Aid Performance Report SE-8-1, Colorado Division of Wildlife, Denver, Colorado, USA.
- MacKenzie, D. I., and L. L. Bailey. 2004. Assessing fit of site occupancy models. *Journal of Agricultural, Biological and Ecological Statistics* 9:300–318.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy when detection probabilities are less than one. *Ecology* 83:2248–2255.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Academic Press, New York.
- MacKenzie, D. I., J. D. Nichols, M. E. Seamans, and A. J. Gutierrez. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology* 90:823–835.

- McCullagh, P., and J. A. Nelder. 1989. Generalized Linear Models, Second Edition. Chapman and Hall, London.
- Miller, D. L. 1984. Distribution, abundance, and habitat of the Arkansas darter *Etheostoma cragini* (Percidae) in Colorado. *Southwestern Naturalist* 29:496–499.
- MDC (Missouri Department of Conservation). 2010. Missouri species and communities of conservation concern. < mdc4.mdc.mo.gov/Documents/145.pdf >. Accessed July 30, 2010.
- Morita, K., and S. Yamamoto. 2002. Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. *Conservation Biology* 16:1318–1323.
- Moss, R. 1981. Life history information for the Arkansas darter (*Etheostoma cragini*). Kansas Nongame Wildlife Advisory Council, Contract No. 38, Pratt, KS.
- Nesler, T. P., C. Bennett, J. Melby, G. Dowler, and M. Jones. 1999. Inventory and status of Arkansas River Native Fishes in Colorado. Colorado Division of Wildlife Final Report, Colorado Springs.
- Nichols, J. D., J. E. Hines, D. I. MacKenzie, M. E. Seamans, and R. J. Gutierrez. 2007. Occupancy estimation with multiple states and state uncertainty. *Ecology* 88:1395–1400.
- ODWC (Oklahoma Department of Wildlife Conservation). 2010. Oklahoma's threatened and endangered species. < <http://www.wildlifedepartment.com/endanger.htm> >. Accessed July 30, 2010.
- Pyke, G. H. 2008. Plague minnow or mosquito fish? A review of the biology and impacts of introduced *Gambusia* species. *Annual Review of Ecology, Evolution, and Systematics* 39:171–91.
- Rahel F. J., B. Bierwagen, and Y. Taniguchi. 2008. Managing aquatic species of conservation concern in the face of climate change and invasive species. *Conservation Biology* 22:551–561.
- Reeves, G. H., L. E. Benda, K. M. Burnett, P. A. Bisson, and J. R. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. *American Fisheries Society Symposium* 17:360–370.
- Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60:108–115.

- Royle, J. A., and W. A. Link. 2005. A general class of multinomial mixture models for anuran calling survey data. *Ecology* 86:2505–2512.
- Scheurer, J. A., K. D. Fausch, and K. R. Bestgen. 2003. Multiscale processes regulate brassy minnow persistence in Great Plains river. *Transactions of the American Fisheries Society* 132:840–855.
- Sheller, F. J., W. F. Fagan, and P. J. Unmack. 2006. Using survival analysis to study translocation success in the Gila topminnow (*Poeciliopsis occidentalis*). *Ecological Applications* 16:1771–1784.
- Taber, C. A., B. A. Taber, and M. S. Topping. 1986. Population structure, growth and reproduction of the Arkansas darter, *Etheostoma cragini*. *Southwestern Naturalist* 31:207–214.
- Tenhumberg, B., A. J. Tyre, K. Shea, and H. P. Possingham. 2004. Linking wild and captive populations to maximize species persistence: optimal translocation strategies. *Conservation Biology* 18:1304–1314.
- Torgersen, C. E., C. V. Baxter, H. W. Li, and B. A. McIntosh. 2006. Landscape influences on longitudinal patterns of river fishes: spatially continuous analysis of fish–habitat relationships. American Fisheries Society, Symposium 48, Bethesda, Maryland.
- USFWS (U.S. Fish and Wildlife Service). 2009. Species assessment and listing priority assignment form. http://ecos.fws.gov/docs/candforms_pdf/r6/E06H_V01.pdf. Accessed July 30, 2010.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–138.
- Wolf, C. M., T. Garland, and B. Griffith. 1998. Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts. *Biological Conservation* 86:243–255.
- World Conservation Union (IUCN). 1987. IUCN position statement on translocation of living organisms: introductions, reintroductions and re-Stocking. Report of the Species Survival Commission in collaboration with the Commission on Ecology, and the Commission on Environment policy, Law and Administration to IUCN, Gland, Switzerland.
- Young, M. K., P. M. Guenther-Gloss, and A. D. Ficke. 2005. Predicting cutthroat trout (*Oncorhynchus clarkii*) abundance in high-elevation streams: revisiting a model of translocation success. *Canadian Journal of Fisheries and Aquatic Sciences* 62:2399–2408.

Table 1. Characteristics of translocations of wild Arkansas darters during 1980-1999 in 12 streams in the Arkansas River basin. Data from the 2009 sampling of these translocation segments include the number of wet sites sampled, the number of sites at which darters were detected, the total number of darters captured, which of three criteria in the Colorado Division of Wildlife recovery plan were met (X; see Introduction), and maximum distances upstream (US) and downstream (DS) from translocation sites at which darters were captured (NC = not captured in a given direction).

Translocation stream	Translocation		No. wet sites	No. sites darters detected	No. darters captured	Recovery criteria met (X)			Max. distance captured (m)	
	Date	No. fish				>500 darters	≥2 year classes	Self-sustaining	DS	US
Brackett Creek	07/01/98	40	14	13	533 ^a	X	X	X	1,625	1,625
Carrizo Springs	05/27/97	50	Dry	-	-	-	-	-	-	-
	05/11/99	20								
Cottonwood Springs	1990	75-100	6	4	45	-	X	unknown	NC	500
	1991									
Little Spring	10/01/95	112	Dry	-	-	-	-	-	-	-
Lytle Pond Inlet	07/03/80	34	3	3	516	X	X	X	0 ^b	250 ^b
Mary Ellen Springs	1995	95	15	3	14	-	X	unknown	1,375 ^b	NC
	1995	146								
Montgomery's Ditch	06/18/97	50	16	0	0	-	-	-	-	-
Pueblo Reservoir Tributary 1	05/22/97	45	Dry	-	-	-	-	-	-	-
	05/27/97	25								
	07/13/98	27								

Pueblo Reservoir Tributary 2	05/19/97	50	Dry	-	-	-	-	-	-	-
	05/29/97	42								
	07/07/98	25								
	07/08/98	21								
Turkey Spring	1990	unknown	Dry	-	-	-	-	-	-	-
Vista del Rio Ditch 1	07/09/97	50	20	15	42	-	X	unknown	1,625	1,625
Williams Creek	06/12/97	50	11	0	0	-	-	-	-	-

^a Includes additional sampling on a second date to reach the recovery criterion of ≥ 500 darters.

^b Darters were captured at the farthest site sampled in this direction (upstream or downstream). They either could not move beyond because of barriers to fish movement, or sites could not be sampled because access to property was denied or the habitat could not be sampled (see text).

Table 2. Characteristics of ongoing translocations of hatchery Arkansas darters since 2002 in seven streams in the Arkansas River basin. Data from the 2009 sampling of these translocation segments includes the number of wet sites sampled, the number of sites at which darters were detected, the total number of darters captured, which of three criteria in the Colorado Division of Wildlife recovery plan were met (X; see Introduction), and the maximum distances upstream (US) and downstream (DS) from translocation sites at which darters were captured (NC = not captured in a given direction).

Translocation stream	Translocation		No. wet sites	No. sites darters detected	No. darters captured	Recovery criteria met (X)			Max. distance captured (m)	
	Date	No. fish				>500 darters	≥2 year classes	Self-sustaining	DS	US
Big Sandy Creek	07/09/97 ^a	150	28	19	229 ^b	-	X	-	500	1,625
	06/06/05	1,120								
	08/05/07	600								
Buffalo Creek	08/08/02	301	15	15	500 ^b	X	X	unknown	1,375 ^c	625 ^c
	06/03/05	500								
	08/03/06	200								
	09/05/07	169								
	10/28/08	225								
	07/10/09	300								
Deadman Ditch	06/03/05	500	16	1	1	-	-	-	375	NC
	08/03/06	200								
	09/05/07	169								
	10/28/08	225								
	07/10/09	300								

Horse Creek	10/15/08	1,157	17	0	0	-	-	-	-	-
	10/02/09	905								
Vista del Rio Ditch 2	08/08/02	301	16	15	500 ^b	X	X	unknown	1,625	125 ^c
	07/17/03	300								
	07/20/04	363								
	06/03/05	500								
	08/03/06	139								
	09/05/07	169								
	10/28/08	299								
	07/10/09	300								
West May Valley Ditch	08/08/02	301	20	19	554	X	X	unknown	1,625	1,375
	07/17/03	300								
	07/20/04	350								
	06/03/05	500								
	08/03/06	200								
	09/05/07	170								
	10/28/08	225								
	07/10/09	400								

Wild Horse Creek	09/19/02	1,622	16	15	500 ^b	X	X	unknown	1,625	500
	07/17/03	1,600								
	07/20/04	360								
	06/03/05	736								
	08/03/06	400								
	09/05/07	170								
	10/28/08	225								
	07/10/09	973								

^a Initial stocking was performed with wild fish.

^b Sampling continued, in one case on an additional date, until the recovery criterion of ≥ 500 darters were captured or this goal appeared infeasible

^c Darters were captured at the farthest site sampled in this direction (upstream or downstream). They either could not move beyond because of barriers to fish movement, or sites could not be sampled because access to property was denied or the habitat could not be sampled (see text).

Table 3. Habitat characteristics of 14 streams in the Arkansas River basin where translocations of wild or hatchery Arkansas darters were made during 1980-2008. Habitat characteristics were not measured in five streams that were completely dry. Data are means and standard deviations (SD) of habitat variables for all wet sites in each translocation stream. See text for description of habitat variables.

Habitat characteristic	Mean	SD	Range
Width (m)	3.4	1.17	1.5 – 5.8
Depth (m)	0.27	0.10	0.11 – 0.50
Bottom temperature (°C)	19.4	3.31	13.1 – 30.0
Residual temperature (°C)	-0.3	1.77	-3.7 – 4.1
Conductivity (µS/cm)	2,395	1,378.9	327 – 4,354
% Vegetative structure	70	20.1	31 – 96
% Wetted	76	26.2	23 – 100
Available habitat (km)	4.7	2.38	1.7 – 8.6

Table 4. A series of 15 *a priori* multiple-state occupancy models used to estimate occupancy probabilities of age-0 Arkansas darters in 19 translocation streams ($n=336$ sites). Models for this *a priori* analysis address hypotheses concerning translocation type (wild or hatchery) and habitat features at three spatial scales (site-, segment-, and riverscape-scale), separately and in combinations (mixture). Five additional exploratory models were analyzed post-hoc, to refine covariate comparisons (see text). Detection probabilities were modeled as a function of Julian date. The probability that a site was wet (ψ^1) was modeled as a function of the percent wetted habitat within the riverscape (10 km). Conditional darter occupancy probability (ψ^2) was modeled with combinations of covariates. The number of model parameters (K), $-2 \log$ likelihood [$-2\log(L)$], AIC_c values, difference in AIC_c compared to the top model, and Akaike weights (w_i) for candidate models are reported. The “best approximating” model to estimate occupancy of age-0 Arkansas darters (M16) is shown in italics.

Model type	Model name	Ψ^1 covariates ^a	Ψ^2 covariates ^a				Detection covariate ^b				Age-0 model results					
											<i>K</i>	-2log(<i>L</i>)	AIC _c	ΔAIC _c	<i>w_i</i>	
Global	M1	WET	TEMP	VEG	DIST	DIR	INT	WET	HAB	HAT	DATE	13	602.98	630.14	6.07	0.02
Null	M2	WET									DATE	5	638.80	648.99	24.92	0.00
Site-	M3	WET	TEMP								DATE	6	635.61	647.88	23.81	0.00
	M4	WET		VEG							DATE	6	635.86	648.12	24.05	0.00
	M5	WET	TEMP	VEG							DATE	7	633.08	647.43	23.36	0.00
Segment-	M6	WET			DIST						DATE	6	638.02	650.29	26.22	0.00
	M7	WET			DIST	DIR					DATE	7	637.06	651.41	27.34	0.00
	M8	WET			DIST	DIR	INT				DATE	8	636.02	652.47	28.40	0.00
Riverscape-	M9	WET						WET			DATE	6	638.32	650.58	26.51	0.00
	M10	WET							HAB		DATE	6	614.11	626.37	2.30	0.13
	M11	WET						WET	HAB		DATE	7	613.40	627.75	3.68	0.06
Trans.	M12	WET								HAT	DATE	6	630.14	642.40	18.33	0.00
Mixture	M13	WET			DIST			WET	HAB		DATE	8	612.90	629.36	5.29	0.03
	M14	WET	TEMP					WET	HAB		DATE	8	609.13	625.58	1.51	0.19
	M15	WET						WET	HAB	HAT	DATE	8	613.12	629.57	5.50	0.03

Exploratory	M16	WET	TEMP			HAB		DATE	7	609.72	624.07	0.00	0.40	
	M17	WET	TEMP			HAB		HAT	DATE	8	609.54	625.99	1.92	0.15
	M18	WET	VEG					HAT	DATE	7	629.01	643.36	19.29	0.00
	M19	WET	DIST					HAT	DATE	7	629.57	643.92	19.85	0.00
	M20	WET	VEG			DIST			HAT	DATE	8	628.47	644.93	20.86

^a DIST = absolute distance from translocation site, DIR = direction, INT = distance x direction interaction, TEMP = residual temperature, VEG = vegetative cover, WET = percent of 10 km wetted, HAB = available habitat (10 km) , HAT = hatchery/wild translocations.

^b DATE = Julian date.

Table 5. A series of 15 *a priori* multiple-state occupancy models that were used to estimate occupancy probabilities of age-1 Arkansas darters in 19 translocation streams ($n=336$ sites). Models for this *a priori* analysis address hypotheses concerning translocation type (wild or hatchery) and habitat features at three spatial scales (site-, segment-, and riverscape-scale), separately and in combinations (mixture). Five additional multistate occupancy models were analyzed post-hoc, to refine covariate comparisons (see text). Detection probabilities were modeled as a function of depth. The probability that a site was wet (ψ^1) was modeled as a function of the percent wetted habitat within the riverscape (10 km). Conditional darter occupancy probability (ψ^2) was modeled with combinations of habitat covariates. The number of model parameters (K), -2 log likelihood [-2log(L)], AIC_c values, difference in AIC_c compared to the top model, and Akaike weights (w_i) for candidate models are reported. The “best approximating” model to estimate occupancy of age-1 Arkansas darters (M3) is shown in italics.

Model type	Model name	Ψ^1 covariates ^a	Ψ^2 covariates ^a				Detection covariate ^b	Age-1 model results								
								K	-2log(L)	AIC _c	Δ AIC _c	w_i				
Global	M1	WET	TEMP	VEG	DIST	DIR	INT	WET	HAB	HAT	DEPTH	13	617.06	646.41	9.21	0.00
Null	M2	WET									DEPTH	5	629.34	639.53	2.33	0.07
Site-	M3	WET	TEMP								DEPTH	6	624.93	637.20	0.00	0.24
	M4	WET		VEG							DEPTH	6	629.07	641.34	4.14	0.03
	M5	WET	TEMP	VEG							DEPTH	7	624.80	639.15	1.95	0.09
Segment-	M6	WET			DIST						DEPTH	6	629.18	641.45	4.25	0.03
	M7	WET			DIST	DIR					DEPTH	7	629.11	643.46	6.26	0.01
	M8	WET			DIST	DIR	INT				DEPTH	8	627.33	643.79	6.59	0.01
Riverscape-	M9	WET						WET			DEPTH	6	628.51	640.77	3.57	0.04
	M10	WET							HAB		DEPTH	6	628.50	640.76	3.57	0.04
	M11	WET						WET	HAB		DEPTH	7	627.07	641.42	4.23	0.03
Trans.	M12	WET								HAT	DEPTH	6	628.37	640.64	3.44	0.04
Mixture	M13	WET			DIST			WET	HAB		DEPTH	8	626.87	643.33	6.13	0.01
	M14	WET	TEMP					WET	HAB		DEPTH	8	622.65	639.11	1.91	0.09
	M15	WET						WET	HAB	HAT	DEPTH	8	626.19	642.65	5.45	0.02

Exploratory	M16	WET	TEMP			HAB		DEPTH	7	623.77	638.12	0.92	0.15
	M17	WET	TEMP			HAB	HAT	DEPTH	8	623.19	639.64	2.45	0.07
	M18	WET	VEG			HAT		DEPTH	7	628.29	642.64	5.45	0.02
	M19	WET	DIST			HAT		DEPTH	7	628.26	642.62	5.42	0.02
	M20	WET	VEG DIST			HAT		DEPTH	8	628.19	644.64	7.45	0.01

^a DIST = absolute distance from translocation site, DIR = direction, INT = distance x direction interaction, TEMP = residual temperature, VEG = vegetative cover, WET = percent 10 km wetted, HAB = available habitat (10 km) , HAT = hatchery/wild translocations.

^b DEPTH = mean depth.

Table 6. Model selection statistics for three pairs of models fit to age-0 (top) and age-1 (bottom) Arkansas darter detection data collected from wet sites in translocation streams in southeastern Colorado. Pairs of models include those that modeled spatial dependence as a first-order Markov process ($\theta + \theta'$) and those that assume local (site) occupancy is an independent, random process ($\theta = \theta'$). Statistics include the number of model parameters (K), -2 log likelihood [-2log(L)], AIC, Δ AIC, and AIC weight (w_i). The “best approximating” model is shown in italics.

Model ^a	Model No.	K	-2log(L)	AIC	ΔAIC	w _i
Age-0 darters						
$\psi(WET), \theta + \theta' (HAB), p(DATE)$	1	7	262.60	276.60	0.00	0.73
$\psi(WET), \theta = \theta' (HAB), p(DATE)$		6	286.67	298.67	22.07	0.00
$\psi(WET), \theta + \theta' (TEMP), p(DATE)$	2	7	272.17	286.17	9.57	0.00
$\psi(WET), \theta = \theta' (TEMP), p(DATE)$		6	320.15	332.15	55.55	0.00
$\psi(WET), \theta + \theta' (TEMP + HAB), p(DATE)$	3	8	262.60	278.60	2.00	0.27
$\psi(WET), \theta = \theta' (TEMP + HAB), p(DATE)$		7	286.63	300.63	24.03	0.00
Age-1 darters						
$\psi(WET), \theta + \theta' (HAB), p(DEPTH)$	4	7	287.51	301.51	0.00	0.59
$\psi(WET), \theta = \theta' (HAB), p(DEPTH)$		6	296.52	308.52	7.01	0.00
$\psi(WET), \theta + \theta' (TEMP), p(DEPTH)$	5	7	290.04	304.04	2.53	0.16
$\psi(WET), \theta = \theta' (TEMP), p(DEPTH)$		6	328.62	340.62	39.11	0.00
$\psi(WET), \theta + \theta' (TEMP + HAB), p(DEPTH)$	6	8	287.14	303.14	1.63	0.25
$\psi(WET), \theta = \theta' (TEMP + HAB), p(DEPTH)$		7	318.25	332.25	30.74	0.00

^a WET = percent wetted, TEMP = residual temperature, HAB = available habitat, DEPTH = mean depth

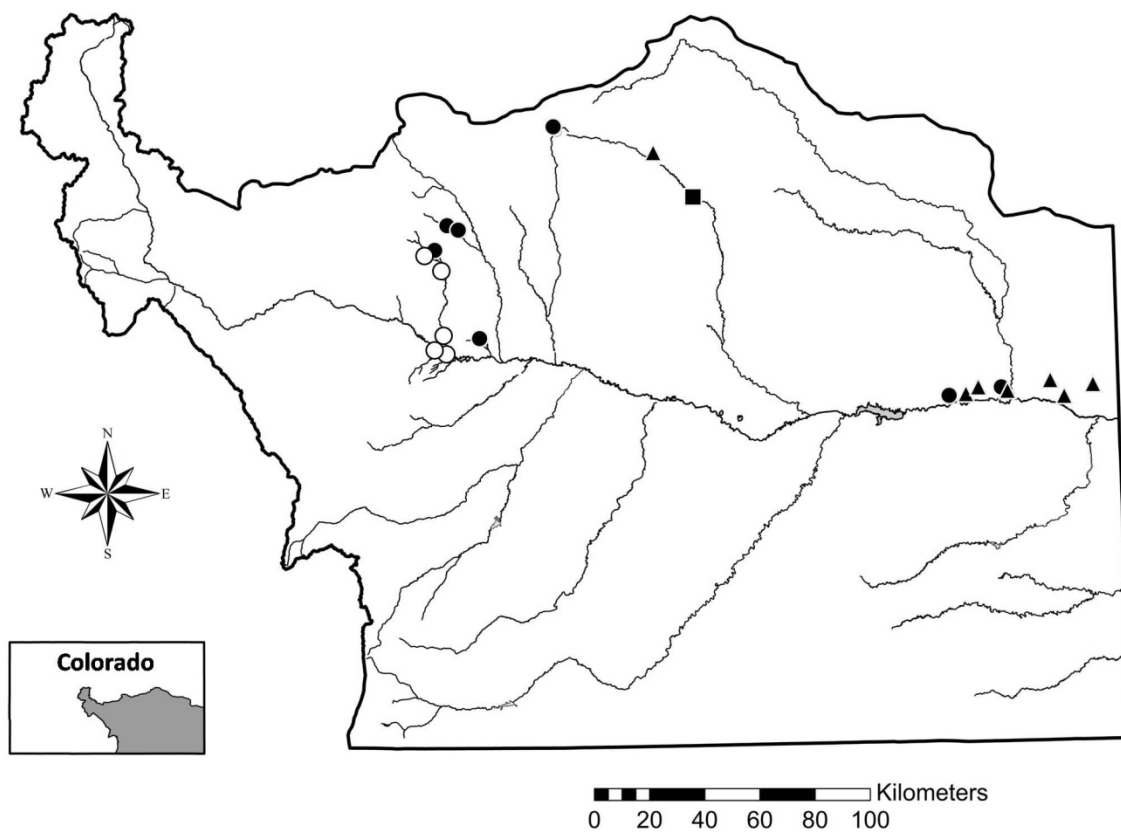


Figure 1. Location of the 19 study streams where Arkansas darter were translocated in the Arkansas River basin in southeastern Colorado. Streams received translocations of either wild (circles; $n=12$) or hatchery-propagated (triangles; $n=7$) darters. Five streams that received wild darters were dry when sampled and are shown as open circles. The square shows Steels Fork of Horse Creek, where habitat was measured to estimate the potential for success of a future translocation.

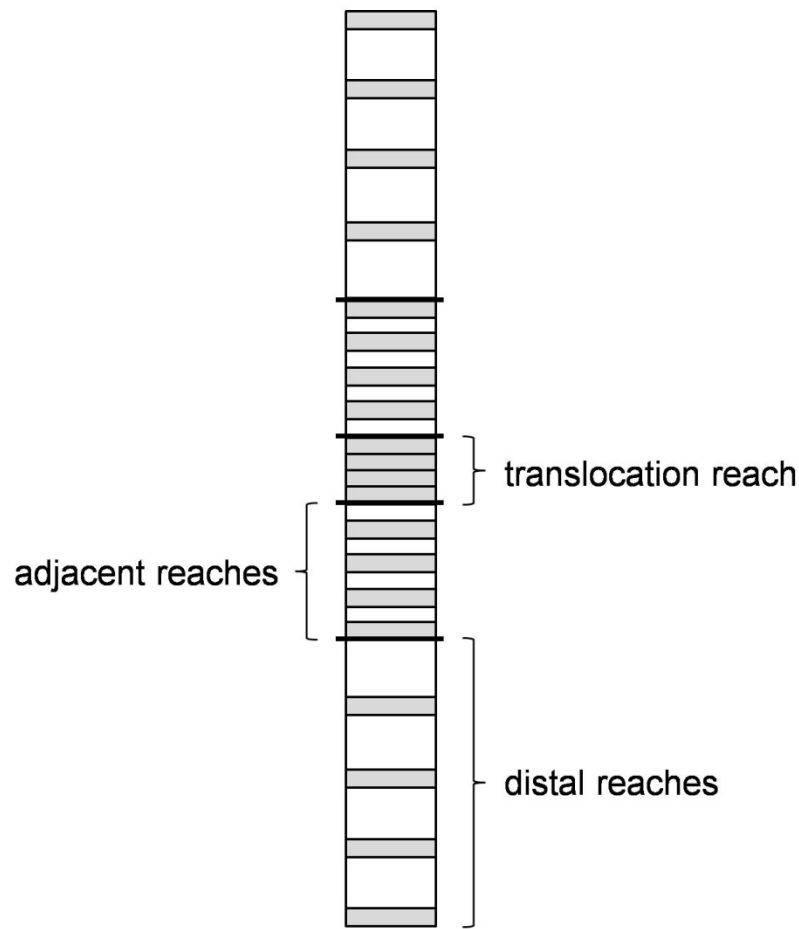


Figure 2. Design of study reaches for translocation streams. After locating the translocation site, a 3.25-kilometer translocation segment was centered on this location, and divided into five reaches: a central 250-m translocation reach, two adjacent 500-m reaches, and two distal 1000-m reaches. Each reach was further subdivided into four equal parts (62.5 m in the translocation reach, 125 m in adjacent reaches, and 250 m in the distal reaches). Study reaches were defined as the final 62.5 m of each (shaded), and study sites were selected in the best available habitat in each study reach (see text). A total of up to 20 sites were sampled in each translocation stream.

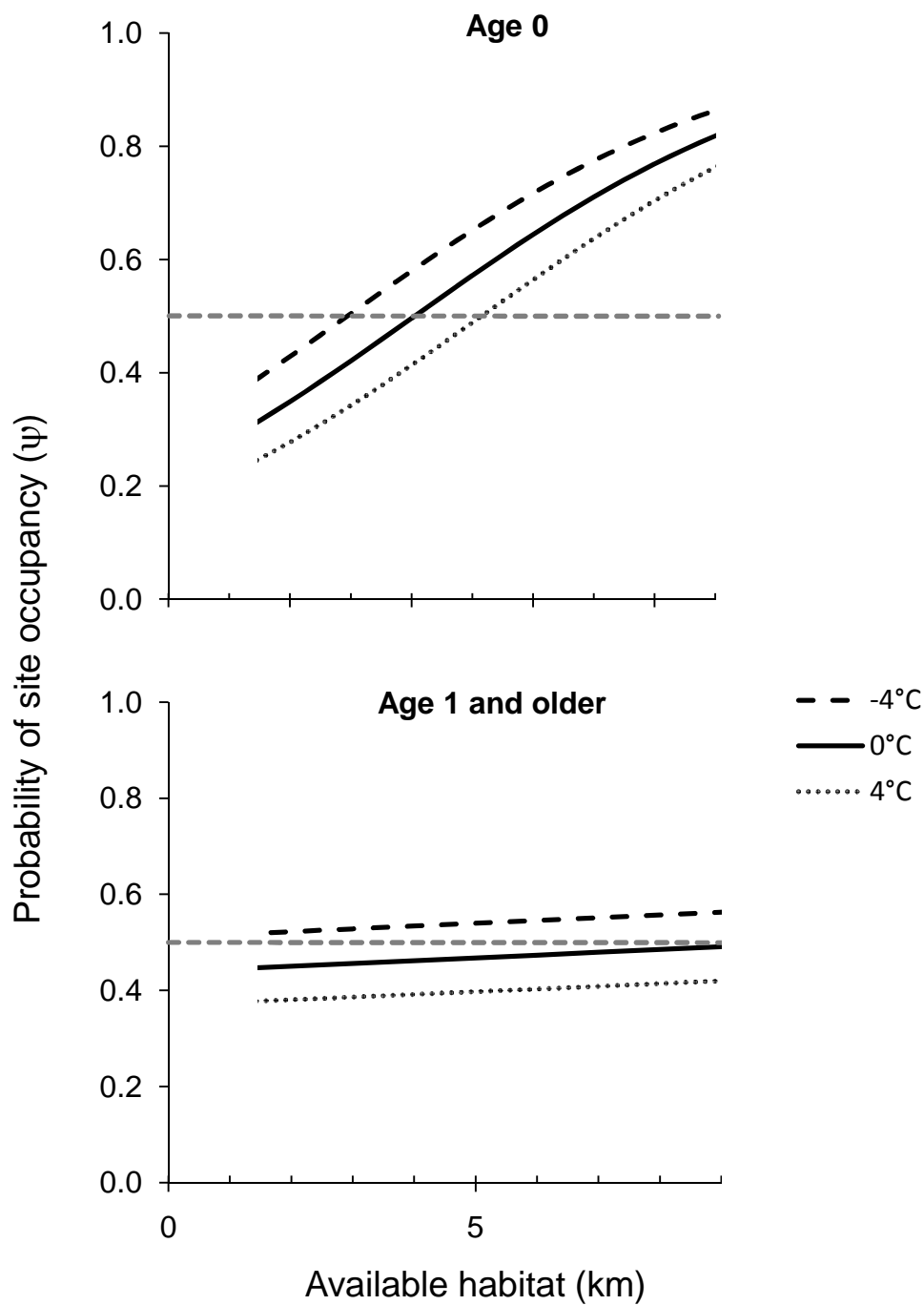


Figure 3. Predicted probability of occupancy for Arkansas darter translocated into streams in the Arkansas River basin, Colorado as a function of available habitat (km) and three values of the residual of stream bottom temperature ($^{\circ}\text{C}$). Curves are model-averaged predictions showing predicted conditional site occupancy probability ($\hat{\psi}^2$) of age 0 (top) and age 1 and older (bottom) darters, and are truncated near the limits of the data. The horizontal dashed line signifies 50% site-occupancy, a level of potential interest to managers.

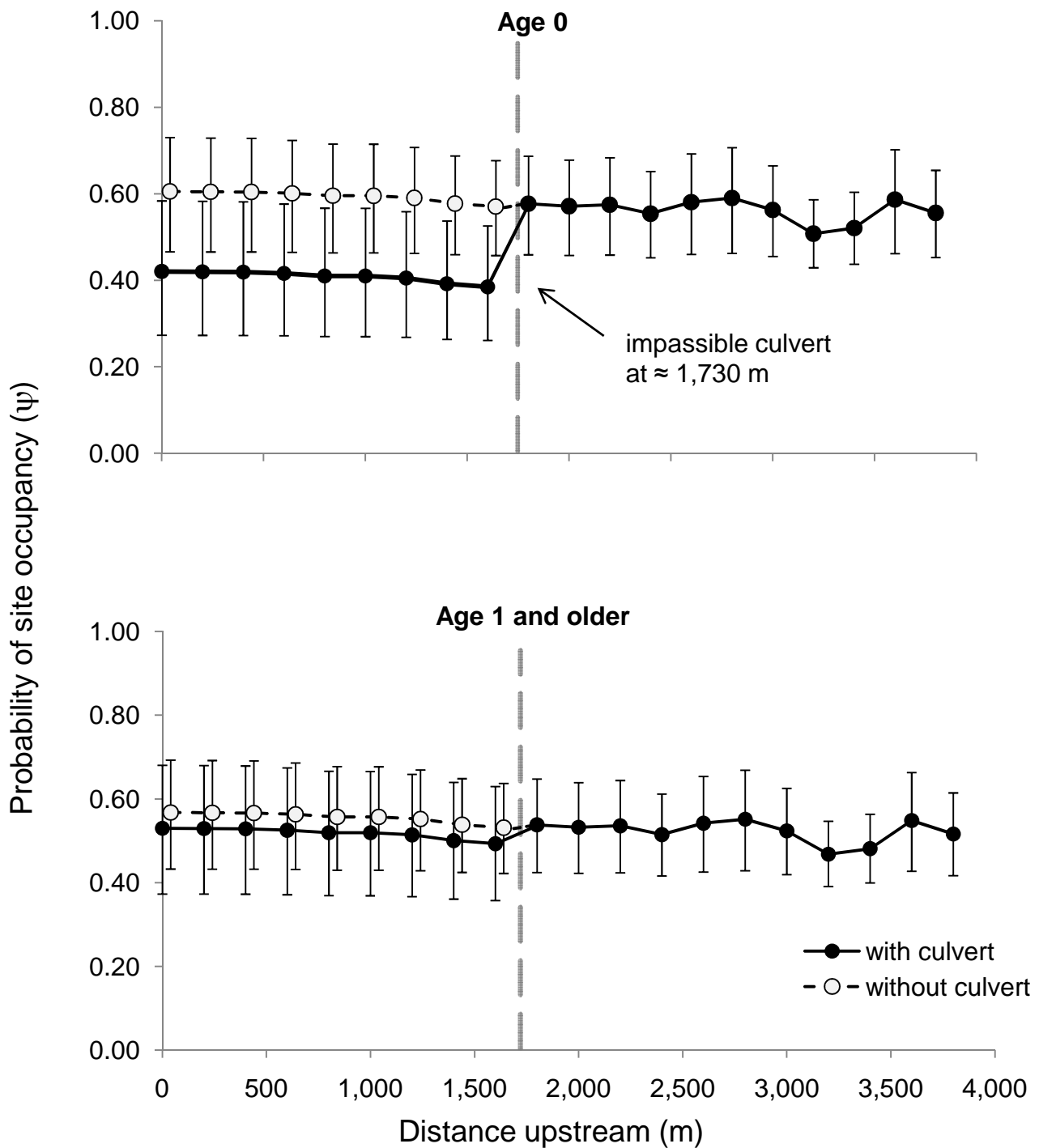


Figure 4. Predicted probability of conditional site occupancy for translocated Arkansas darters in a 3.8-km segment of Steels Fork of Horse Creek, Colorado. An impassible culvert is present in the stream channel at about 1.7 km. This information was used in conjunction with the length of total available habitat, and depth and bottom water temperature measured at 20 equally-spaced sites, to predict site occupancy of age-0 (top) and age-1 and older (bottom) darters under two scenarios: 1) translocation with the existing culvert in place (solid lines), and 2) translocation after the culvert is removed (dashed lines).