SRP16739

Ecology, 93(4), 2012, pp. 858–867
© 2012 by the Ecological Society of America

Colonization and extinction in dynamic habitats: an occupancy approach for a Great Plains stream fish assemblage

Jeffrey A. Falke,[1,3] Larissa L. Bailey,[1] Kurt D. Fausch,[1] and Kevin R. Bestgen[1,2]

[1]*Colorado State University, Department of Fish, Wildlife, and Conservation Biology, Fort Collins, Colorado 80523-1474 USA*
[2]*Colorado State University, Larval Fish Laboratory, Department of Fish, Wildlife, and Conservation Biology, Fort Collins, Colorado 80523-1474 USA*

Abstract. Despite the importance of habitat in determining species distribution and persistence, habitat dynamics are rarely modeled in studies of metapopulations. We used an integrated habitat–occupancy model to simultaneously quantify habitat change, site fidelity, and local colonization and extinction rates for larvae of a suite of Great Plains stream fishes in the Arikaree River, eastern Colorado, USA, across three years. Sites were located along a gradient of flow intermittency and groundwater connectivity. Hydrology varied across years: the first and third being relatively wet and the second dry. Despite hydrologic variation, our results indicated that site suitability was random from one year to the next. Occupancy probabilities were also independent of previous habitat and occupancy state for most species, indicating little site fidelity. Climate and groundwater connectivity were important drivers of local extinction and colonization, but the importance of groundwater differed between periods. Across species, site extinction probabilities were highest during the transition from wet to dry conditions (range: 0.52–0.98), and the effect of groundwater was apparent with higher extinction probabilities for sites not fed by groundwater. Colonization probabilities during this period were relatively low for both previously dry sites (range: 0.02–0.38) and previously wet sites (range: 0.02–0.43). In contrast, no sites dried or remained dry during the transition from dry to wet conditions, yielding lower but still substantial extinction probabilities (range: 0.16–0.63) and higher colonization probabilities (range: 0.06–0.86), with little difference among sites with and without groundwater. This approach of jointly modeling both habitat change and species occupancy will likely be useful to incorporate effects of dynamic habitat on metapopulation processes and to better inform appropriate conservation actions.

Key words: Great Plains, USA; groundwater; intermittent streams; joint habitat occupancy modeling; metapopulations; species occurrence; stream fishes.

Introduction

Over the past several decades, empirical and theoretical research on spatially structured populations has increased our understanding of dynamics of species in landscapes where suitable habitat is fragmented by natural and anthropogenic processes (Hanski and Ovaskainen 2000, Ricketts 2001, Hanski and Gaggiotti 2004). Generally, habitat quality is viewed as the primary determinant of species distribution and persistence (e.g., Lande 1987, Scott et al. 2002), and as such, metapopulations are more likely to persist in landscapes with many well-connected patches of high-quality habitat (Dunham and Rieman 1999, Koizumi and Maekawa 2004). Metapopulation models often estimate local colonization and extinction probabilities based upon a snapshot of species occurrence, or by monitoring a set of patches over time (e.g., Stelter et al. 1997, Clinchy et al. 2002), but nearly all metapopulation models assume a static (habitat) landscape. However, habitat conditions can rapidly change via a variety of processes including succession, natural disturbance, and human activities, and many rare terrestrial and aquatic species incorporate periodic habitat variation or disturbance events in their life histories (e.g., Reeves et al. 1995, Breininger et al. 2010). In such systems, habitat dynamics in spatially discrete patches are often a main driver of colonization and extinction processes (Harrison and Taylor 1997, Thomas and Hanski 2004, Wilcox et al. 2006). Indeed, the metapopulation literature contains multiple appeals for simultaneous consideration of both habitat and species occupancy dynamics (e.g., Lande 1987), and the ability to separate these processes should provide an explicit link between spatial population dynamics and species conservation.

Dryland streams on the Great Plains of western North America are prime examples of extremely dynamic ecosystems, with a broad range of hydrologic conditions

Manuscript received 18 August 2011; revised 10 November 2011; accepted 14 November 2011. Corresponding Editor: E. G. Cooch.

[3] Present address: Department of Fisheries and Wildlife, Oregon State University, c/o U.S. EPA Western Ecology Division, 200 SW 35th Street, Corvallis, Oregon 97333 USA. E-mail: jeffrey.falke@oregonstate.edu

(e.g., intermittency, flooding) occurring both within and among years (Matthews 1988, Dodds et al. 2004). Interannual climate variation in these semiarid systems strongly influences hydrology, which controls habitat suitability and connectivity, factors critical for the persistence of obligate aquatic organisms (Fisher et al. 1982, Diaz et al. 2008, Falke et al. 2010*a*). The hydrologic regimes of many Great Plains streams have also been heavily altered by anthropogenic impacts such as groundwater mining, diversions, and reservoirs (Bonner and Wilde 2000, Falke and Gido 2006, Falke et al. 2011). These impacts have greatly increased habitat intermittency and drying (Graf 2006, Gido et al. 2010), creating the potential for a highly variable habitat mosaic. In such dynamic ecosystems, biological understanding and conservation efforts will be improved by simultaneous modeling of the proportion of suitable habitat and species occurrence among suitable patches. In our system, we considered a site "unsuitable" if it was dry during our annual study period, and "suitable" if it remained wet, because the presence of water is a minimal requirement for a site to support fish.

Many Great Plains stream fishes require non-substitutable, complementary habitats (e.g., spawning, rearing, and refuge; Dunning et al. 1992, Schlosser 1995) to complete their life histories. These habitats are distributed heterogeneously across the riverscape and their suitability may vary with time (Falke and Fausch 2010). Although the intra-annual dynamics of plains stream fishes have been explored (e.g., Scheurer et al. 2003), it is currently unknown whether these species use the same spawning locations annually or exploit available habitat regardless of its previous history of habitat suitability or spawning occurrence. Such spawning habitat fidelity has strong implications for habitat conservation, given anthropogenic impacts and inherently variable climate and hydrology in plains streams.

High dispersal ability among local habitats is a common trait of many Great Plains stream fishes (Fausch and Bestgen 1997), as would be expected for organisms that inhabit spatiotemporally variable environments (McPeek and Holt 1992). However, their dispersal ability is strongly moderated by both life history traits (e.g., body size, swimming ability) and characteristics of the physical environment that block movement opportunities (e.g., stream intermittency, barriers; Winston et al. 1991, Bonner and Wilde 2000, Hoagstrom et al. 2008). High rates of local extinction may be balanced by traits such as early maturation and high mobility, which allow for rapid colonization of habitats that were previously unavailable due to floods or droughts. However, the relative ability of different species to colonize or recolonize habitats is currently unknown (but see Gotelli and Taylor 1999), but important for understanding metapopulation dynamics.

We used dynamic multistate occupancy models to simultaneously estimate habitat and species dynamics for a suite of Great Plains stream fishes. These integrated habitat suitability–occupancy models (MacKenzie et al. 2009, 2011, Martin et al. 2010) allow for imperfect species detection, a reality that, if ignored, may cause substantial bias in parameters estimated with traditional metapopulation models (Moilanen 2002, MacKenzie et al. 2006). We focused on occurrence of larval fish, which are relatively immobile organisms, in readily identifiable spawning habitats (patches; Falke et al. 2010*a*). As such, occurrence of larvae represents the ability of adults to colonize or recolonize potential spawning habitat patches. Our research sought to answer the following three questions: (1) Is habitat persistence a function of conditions the previous year (e.g., Markovian), or a strictly random process? (2) Do some or all species use the same spawning habitat from year to year, provided habitat remains suitable (i.e., is site fidelity prominent)? (3) Does ability to recolonize patches following disturbance (e.g., habitat drying) differ among species? Though little is known about the relative colonization abilities of our suite of fish species, we expected species-specific differences based on life history characteristics (e.g., dispersal ability and body size). For example, brassy minnow (*Hybognathus hankinsoni*) and fathead minnow (*Pimephales promelas*) have been documented to quickly colonize previously dry habitats (Fausch and Bramblett 1991, Scheurer et al. 2003). Given available habitat, we expected those two species to have higher colonization rates and lower extinction rates compared to a smaller bodied, more sedentary species such as the orangethroat darter (*Etheostoma spectabile*).

Materials and Methods

Study area

Larval fishes and potential spawning habitats were sampled from the Arikaree River (102°51′49″ W, 39°38′50″ N), located in the shortgrass prairie ecosystem of the High Plains ecoregion (Omernik 1987) of northeastern Colorado, USA. Stream flow is variable, but consistently highest during spring and early summer. Current land use is primarily rangeland and row crops irrigated with groundwater. Associated pumping from the underlying High Plains Aquifer has dried the headwaters so that only the lower 110 km of river now has the potential to support fish (Falke et al. 2011).

We examined dynamics of stream habitat and larval fish occupancy among three previously studied 6.4-km river segments that vary along a gradient of flow intermittency (see Scheurer et al. [2003] and Falke et al. [2011] for detailed reach and site descriptions, respectively). Briefly, the upstream segment is well connected to the High Plains Aquifer, and is characterized by alternating runs and deep, persistent pools where flow is sustained under all but the driest conditions. Habitats in the middle segment are normally connected by flows during winter and spring, but are often isolated during summer months owing to hydraulic disconnection from the aquifer and pumping from nearby

irrigation wells. The downstream segment is mostly ephemeral owing to pumping, and is dry most of the year except for a few, isolated pools that persist in some years. A perennial, groundwater-fed tributary, Black Wolf Creek, enters the middle of this segment and usually sustains a short reach of flowing habitat in the main channel downstream.

Survey methods

Fish and habitat surveys started mid-May in 2005 and 2006, and the last week of March 2007, and continued every other week through mid-July each year. All potential spawning habitats (backwaters or channel margins, termed sites hereafter) in each segment were identified and georeferenced using a Global Positioning System (Falke et al. 2010*a*, *b*). 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. Existing literature and our concurrent studies (Falke et al. 2010*a*, *b*), indicated that larvae of all fishes in the Arikaree River could be present and available to be captured during this period. During each survey, habitat state (wet or dry) was assigned for each potential spawning site. At wet sites, fish larvae were sampled using a combination of dipnets (20 × 16 cm; 250-μm mesh) and light traps (design modified from Kilgore 1994, see Falke et al. 2010*b* for details and sampling validation). Dipnetting surveys were conducted during daylight hours in channel margin and backwater sites; light traps were also deployed in backwaters at dusk for ~2 h to sample those larger and deeper areas efficiently. Fish larvae captured were preserved in 100% ethanol and identified in the laboratory, except for easily identified but rare orange-throat darter, which were counted and released.

Spawning habitat and occupancy dynamics among years

We used a habitat–occupancy dynamics model (Martin et al. 2010, MacKenzie et al. 2011) to simultaneously investigate habitat dynamics and larval fish occupancy at sites while accounting for imperfect detection of our target species. Our analyses focused on the potentially large interannual changes in the suitability of habitat at potential spawning sites and the occurrence of larvae at these sites. For each species, sites were classified into one of three possible states during a given survey: dry (and thus unoccupied, denoted 0), wet but species not detected (1), or wet and species detected (2). An example detection history (h_i) for a single site i sampled three times per year for three years is $h_i = 221\,000\,111$. The site was suitable during the first year and the target species was detected during the first two surveys, but not detected in the final survey. In the second year, the site was unsuitable (i.e., dry), and in the third year the site was suitable, but the species was never detected. An important assumption of our joint habitat–occupancy dynamics model is that both habitat and occupancy states were static over surveys from spring to mid-summer within a given year, and we assumed the habitat state (wet or dry) was observed without error.

We fit habitat and detection data for each species separately, using the dynamic multistate model (MacKenzie et al. 2009, Martin et al. 2010), a simplified habitat–occupancy model where only suitable sites can be occupied (MacKenzie et al. 2011). This model contains two focal parameters: $\psi_{t+1}^{[m]}$, the probability a site is wet in year $t+1$ given that it was in state m in year t, and $R_{t+1}^{[m]}$, the conditional probability that a wet site is occupied in year $t+1$, given that it was in state m in year t. Here, m denotes the true state of the site: dry ($m = 0$), wet but unoccupied ($m = 1$), and wet and occupied ($m = 2$). There are two detection probabilities: one associated with correct identification of the habitat state, $p^{[m]} = 1$, (because wet and dry habitat can be observed without error) and δ_{jt}, the probability of detecting larvae of the target species in survey j of year t, given the site was suitable (wet) and occupied ($m = 2$).

Our objectives were to quantify the dynamics of spawning habitats and evaluate the importance of previous habitat and occupancy state to the distribution of fish larvae in a given year. To investigate our first question regarding the persistence of habitat states among years, we fit models where habitat suitability was either dependent on the habitat state the previous year, or independent of previous state suggesting that suitable habitat was randomly available each year. We assumed that larval fish presence did not affect habitat dynamics, so the state-dependent habitat structure contained parameters $\psi_{t+1}^{[0]}$ and $\psi_{t+1}^{[1=2]}$, whereas the random structure assumed $\psi_{t+1}^{[0=1=2]}$. To address our second and third questions regarding site fidelity and recolonization rates among species, we investigated whether larvae presence in suitable habitat in year $t+1$ (i.e., $R_{t+1}^{[m]}$), was dependent on occupancy and habitat suitability in year t. Specifically, we considered models where conditional larval occupancy at a given site, $R_{t+1}^{[m]}$ was (1) dependent on the habitat and occupancy state in the previous year ($R_{t+1}^{[0,1,2]}$), (2) only influenced by larval occupancy in the previous year ($R_{t+1}^{[0=1,2]}$), or (3) a random process ($R_{t+1}^{[0=1=2]}$), where m, again, is habitat and occupancy state at time t. Support for the first two occupancy structures may indicate site fidelity for a species provided estimates of $R_{t+1}^{[2]}$ were greater than those of $R_{t+1}^{[1]}$ and $R_{t+1}^{[0]}$. Support for the third model structure would suggest that larval fish use suitable (wet) habitat randomly regardless of the site's previous habitat or occupancy state. Estimates of $R_{t+1}^{[0]}$ provide a measure of the ability of species to recolonize dry sites, conditional on suitable habitat in year $t+1$.

We also expected that habitat suitability and species occupancy would be influenced by the hydrology of our study segments. We categorized the three segments based on groundwater inflow (see *Study area*; Falke et al. 2010*a*, 2011): Sites in the upstream segment and those

in Black Wolf Creek were groundwater fed and perennial compared to sites in the middle and downstream segments that were not fed by groundwater (i.e., were intermittent). This groundwater covariate was included in $\psi_{t+1}^{[m]}$ structures, but owing to a small sample size we were unable to model conditional occupancy ($R_{t+1}^{[m]}$) as a function of this covariate. However, based on the results of a concurrent study involving multiple occupied states (Falke et al. 2010*b*), species occupancy did not appear to be strongly influenced by segment so exclusion of the groundwater covariate was not considered problematic.

Previous analyses suggested that our two sampling methods (dip nets and light traps) were redundant (Falke et al. 2010*b*), so we pooled the detection data from both methods and modeled species detection probability (δ) using three alternative structures: (1) detection probability was constant across all sampling occasions, $\delta(.)$; (2) detection probability varied annually, but not among sampling occasions within a year, δ(YEAR); and (3) detection probability varied among sampling occasions (i.e., within years) but the pattern was similar among years, δ(OCC). We assumed that detection probability did not vary among sites. Based on these hypotheses, we constructed a balanced set of six habitat–occupancy structures (all combinations of habitat and conditional occupancy dynamics). We paired each habitat–occupancy structure with each detection structure, resulting in a total of 18 candidate models that we fit to habitat and detection data for each species. We used Akaike's information criterion (AIC) to select the best approximating model among our 18 candidate models (Burnham and Anderson 2002). The model with the lowest AIC and the highest Akaike weights (w_i) was considered the best model. To account for model uncertainty, we used model averaging to calculate parameter estimates and standard errors using models with $w_i > 0.05$. All analyses were performed using program PRESENCE (*available online*).[4]

Using the resulting estimates of habitat and occupancy dynamics, we derived overall probabilities of colonization (γ) and extinction (ε) between years. Local extinction occurred when an occupied site in year t became unsuitable the following year ($1 - \psi_{t+1}^{[2]}$), or when the habitat in year t was suitable and occupied, but larvae were not present in year $t+1$ even though the site remained suitable, $\psi_{t+1}^{[2]} \times (1 - R_{t+1}^{[2]})$. Summing these two quantities yields the overall probability of local extinction between years, $\varepsilon_{t+1} = (1 - \psi_{t+1}^{[2]}) + \psi_{t+1}^{[2]}(1 - R_{t+1}^{[2]})$. Colonization probabilities were derived for sites that were dry in year t, $\gamma_{t+1}^{[0]} = \psi_{t+1}^{[0]} \times R_{t+1}^{[0]}$, or wet but unoccupied, $\gamma_{t+1}^{[1]} = \psi_{t+1}^{[1]} \times R_{t+1}^{[1]}$. Standard errors for these derived parameters were approximated using the delta method.

[4] http://www.mbr-pwrc.usgs.gov/software.html

Results

Environmental variability among years in the Arikaree River sets the context for potential variation in habitat suitability and associated spawning of fishes. Fifty-nine sites were identified within the study area and sampled all three years (backwaters, $N = 16$; channel margins, $N = 43$). The number of wet habitats varied each year, and corresponded to flow and climate conditions. Annual precipitation and mean flow at a discharge gauge downstream 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; Falke et al. 2011). However, water levels in the study area in spring 2007 were higher than in other years owing to abundant snowfall in December 2006 (Falke et al. 2010*a*).

We collected a total of 17 353 larval fishes representing nine species across all sites during the three years of sampling. Fathead minnow (27% of total captures), brassy minnow (26%), and green sunfish (*Lepomis cyanellus*; 23%) dominated the samples numerically, followed by northern plains killifish (*Fundulus zebrinus*; 10%), central stoneroller (*Campostoma anomalum*; 10%), creek chub (*Semotilus atromaculatus*; 4%), and orange-throat darter (1%). Black bullhead (*Amerius melas*) and white sucker (*Catostomus commersonii*) were rare, and green sunfish was collected in only two sites during one week at the end of sampling in 2006 and 2007, so these three species were excluded from our analyses.

Habitat and occupancy dynamics

Our joint habitat–occupancy analyses indicated that the probability of a site being wet (i.e., available for spawning) varied randomly from year to year. For all six species, models with $\psi_{t+1}^{[0=1=2]}$ were more parsimonious than models where the probability of suitable habitat in year $t + 1$ depended on the habitat state in year t ($\psi_{t+1}^{[0,1=2]}$; Table 1). Similarly, for five of the six species, the most parsimonious model showed that occupancy dynamics were also independent of the site's previous habitat and occupancy state (i.e., $R_{t+1}^{[0=1=2]}$), indicating little site fidelity. Thus, dry or suitable unoccupied sites were just as likely to contain larvae in the following year ($t + 1$) as sites that supported spawning in year t, provided the site contained suitable (wet) habitat in year $t + 1$. Northern plains killifish was the only species that showed spawning site fidelity, with higher conditional occupancy probabilities for sites that were occupied in the previous year ($R_{t+1}^{[2]} > R_{t+1}^{[1]}$ or $R_{t+1}^{[0]}$). Detectability varied among sampling occasions within a year [δ(OCC)] for most species, probably due to larval growth and increasing mobility (Tables 1 and 2; see also Falke et al. 2010*a*). In contrast, model selection results for fathead minnow indicated that detection probability was either constant across years and occasions [$\delta(.)$] or varied among years [δ(YEAR)].

Climate and groundwater connectivity were important drivers of local extinction and colonization, but the

TABLE 1. Model selection metrics for joint habitat–occupancy dynamic models fit to habitat and larval detection data for six fish species at 59 potential spawning sites in the Arikaree River, Colorado, USA, from 2005 to 2007.

Species and models	K	$-2l$	AIC	ΔAIC	w_i
Central stoneroller					
$\psi_{t+1}^{[0=1=2]}R_{t+1}^{[0=1=2]}\delta(\mathrm{OCC})$	13	572.97	598.97	0	0.3466
$\psi_{t+1}^{[0,1=2]}R_{t+1}^{[0=1=2]}\delta(\mathrm{OCC})$	14	571.88	599.88	0.91	0.2199
$\psi_{t+1}^{[0=1=2]}R_{t+1}^{[0=1,2]}\delta(\mathrm{OCC})$	15	570.97	600.97	2.00	0.1275
$\psi_{t+1}^{[0,1=2]}R_{t+1}^{[0=1,2]}\delta(\mathrm{OCC})$	16	569.80	601.80	2.83	0.0842
Orangethroat darter					
$\psi_{t+1}^{[0=1=2]}R_{t+1}^{[0=1=2]}\delta(\mathrm{OCC})$	13	308.97	332.97	0	0.4706
$\psi_{t+1}^{[0,1=2]}R_{t+1}^{[0=1=2]}\delta(\mathrm{OCC})$	14	307.89	333.89	0.92	0.2971
$\psi_{t+1}^{[0=1=2]}R_{t+1}^{[0=1,2]}\delta(\mathrm{OCC})$	15	308.29	336.29	3.32	0.0895
$\psi_{t+1}^{[0,1=2]}R_{t+1}^{[0=1,2]}\delta(\mathrm{OCC})$	16	307.23	337.23	4.26	0.0559
Brassy minnow					
$\psi_{t+1}^{[0=1=2]}R_{t+1}^{[0=1=2]}\delta(\mathrm{OCC})$	13	576.44	602.44	0	0.2451
$\psi_{t+1}^{[0=1=2]}R_{t+1}^{[0=1,2]}\delta(\mathrm{OCC})$	15	572.84	602.84	0.40	0.2007
$\psi_{t+1}^{[0,1=2]}R_{t+1}^{[0,1,2]}\delta(\mathrm{OCC})$	17	569.32	603.32	0.88	0.1579
$\psi_{t+1}^{[0,1=2]}R_{t+1}^{[0=1=2]}\delta(\mathrm{OCC})$	14	575.36	603.36	0.92	0.1547
$\psi_{t+1}^{[0,1=2]}R_{t+1}^{[0=1,2]}\delta(\mathrm{OCC})$	16	571.66	603.66	1.22	0.1332
$\psi_{t+1}^{[0,1=2]}R_{t+1}^{[0,1,2]}\delta(\mathrm{OCC})$	18	568.08	604.08	1.64	0.1080
Northern plains killifish					
$\psi_{t+1}^{[0=1=2]}R_{t+1}^{[0,1,2]}\delta(\mathrm{OCC})$	16	338.61	370.61	0	0.5062
$\psi_{t+1}^{[0,1=2]}R_{t+1}^{[0,1,2]}\delta(\mathrm{OCC})$	17	336.66	370.66	0.05	0.4937
Fathead minnow					
$\psi_{t+1}^{[0=1=2]}R_{t+1}^{[0=1=2]}\delta(.)$	10	478.34	498.34	0	0.2519
$\psi_{t+1}^{[0=1=2]}R_{t+1}^{[0=1=2]}\delta(\mathrm{YEAR})$	12	475.22	499.22	0.88	0.1622
$\psi_{t+1}^{[0,1=2]}R_{t+1}^{[0=1=2]}\delta(.)$	11	477.26	499.26	0.92	0.1590
$\psi_{t+1}^{[0,1=2]}R_{t+1}^{[0=1=2]}\delta(\mathrm{YEAR})$	13	474.14	500.14	1.80	0.1024
Creek chub					
$\psi_{t+1}^{[0=1=2]}R_{t+1}^{[0=1=2]}\delta(\mathrm{OCC})$	13	336.83	360.83	0	0.4857
$\psi_{t+1}^{[0,1=2]}R_{t+1}^{[0=1=2]}\delta(\mathrm{OCC})$	14	335.43	361.43	0.60	0.3598
$\psi_{t+1}^{[0=1=2]}R_{t+1}^{[0=1,2]}\delta(\mathrm{OCC})$	15	336.75	364.75	3.92	0.0684
$\psi_{t+1}^{[0,1=2]}R_{t+1}^{[0=1,2]}\delta(\mathrm{OCC})$	16	335.35	365.35	4.52	0.0507

Notes: Models with Akaike information criteria (AIC) weights (w_i) > 0.05 are given for each species. Model parameters include: $\psi_{t+1}^{[m]}$, the probability that a site has suitable (wet) habitat in year $t+1$ given that it was in state m in year t, and $R_{t+1}^{[m]}$, the conditional probability that a wet site was occupied in year $t+1$ given that it was in state m in year t. Here, m denotes the true state of the site: dry ($m=0$), wet but unoccupied ($m=1$), and wet and occupied ($m=2$). Species detectability (δ) was modeled as either constant (.), or varying from year to year, but not within years (YEAR), or varying among sampling occasions (OCC). For each model, K is the number of estimated parameters, ΔAIC is the difference in AIC relative to the top model, and $-2l$ is twice the negative log-likelihood.

importance of groundwater differed between periods. Our first set of extinction and colonization probabilities were estimated for the transition between a relatively wet year (2005) and the dry year (2006). During this period, local extinction probabilities, $\hat{\varepsilon}_{2006}$, were greater for all species compared to those between the dry year and subsequent wet year, $\hat{\varepsilon}_{2007}$ (Table 3). Moreover, extinction probabilities were higher for sites not fed by groundwater, although the magnitude of this effect varied among species. For example, local extinction probabilities for orangethroat darter and creek chub were extremely high ($\hat{\varepsilon}_{2006} \geq 0.90$) regardless of groundwater connectivity, whereas $\hat{\varepsilon}_{2006}$ was lower for central stoneroller, northern plains killifish, brassy minnow, and fathead minnow in

TABLE 2. Model-averaged estimates of detectability ($\hat{\delta}$) and their standard errors for larvae of six fish species in the Arikaree River, Colorado, USA, from 2005 to 2007.

Species	Survey occasion				Year		
	1	2	3	4	2005	2006	2007
Central stoneroller	0.252 ± 0.05	0.629 ± 0.06	0.660 ± 0.06	0.562 ± 0.06			
Orangethroat darter	0.820 ± 0.08	0.861 ± 0.07	0.369 ± 0.10				
Northern plains killifish		0.500 ± 0.08	0.955 ± 0.07	0.955 ± 0.10			
Brassy minnow	0.667 ± 0.06	0.781 ± 0.05	0.838 ± 0.04	0.483 ± 0.06			
Fathead minnow					0.818 ± 0.03	0.823 ± 0.04	0.783 ± 0.03
Creek chub	0.998 ± 0.01	0.429 ± 0.07	0.04 ± 0.03				

Notes: Top models for all species included variation in detectability among survey occasions within a year (OCC), except fathead minnow for which detection varied by year, but not among occasions within a year (see Table 1). Empty cells under "Survey occasion" indicate that the species was never detected during that survey week.

groundwater fed sites than those that lacked groundwater (Table 3; Appendix). Colonization probabilities during this period were relatively low for both previously dry ($\hat{\gamma}^{[0]}_{2006}$ range: 0.02–0.38) and previously wet sites ($\hat{\gamma}^{[1]}_{2006}$ range: 0.02–0.43; Table 4).

In contrast, local extinction and colonization probabilities were nearly identical for sites fed and not fed by groundwater during the transition from the dry year (2006) to a wet year (2007). Extinction probabilities were lower than the previous period, primarily because no habitats dried between these years (i.e., $\psi^{[1=2]}_{2007} = 1$). Despite persistence of all wet habitat, local extinction probabilities were substantially greater than zero (Table 3). Colonization probabilities were higher during the second period for previously suitable ($\hat{\gamma}^{[1]}_{2007}$ range: 0.06–0.86) or unsuitable sites ($\hat{\gamma}^{[0]}_{2007}$ range: 0.37–0.79; Table 4). Among species, northern plains killifish, brassy minnow, and fathead minnow were relatively good at colonizing previously dry sites. Interestingly, northern plains killifish was a poor colonist of previously wet, but unoccupied sites ($\hat{\gamma}^{[1]}_{2007} = 0.06$). Conditional occupancy probabilities ($R^{[2]}_{t+1}$) were high and consistent regardless of climatic transitions for northern plains killifish, brassy minnow, and fathead minnow (Fig. 1). In contrast, $R^{[2]}_{t+1}$ were higher during the transition between the dry to wet year (2006–2007) for central stoneroller, orangethroat darter, and creek chub.

DISCUSSION

By simultaneously modeling habitat and species occupancy using a relatively new and innovative approach, we were able to gain deeper insight into factors influencing colonization, extinction, and persistence of highly mobile organisms in a dynamic ecosystem that would not be evident from more traditional analyses (e.g., steady state metapopulation models, traditional occupancy models). Importantly, integrated habitat–occupancy modeling allowed us to separate two components of local extinction probability and estimate colonization probabilities based on a site's previous habitat state, thus quantifying the ability of different species to recolonize previously unsuitable habitats. We found that suitable (wet) habitat was so

TABLE 3. Model averaged components of extinction probabilities ($\hat{\varepsilon}_{t+1}$) and their standard errors for six Great Plains stream fish species among 59 potential spawning habitats (sites) in the Arikaree River, Colorado, USA, from 2005 to 2007.

Species	Habitat dried	Habitat wet but unoccupied		Extinction probability	
	$(1 - \hat{\psi}^{[2]}_{2006})$	$\hat{\psi}^{[2]}_{2006}(1 - \hat{R}^{[2]}_{2006})$	$\hat{\psi}^{[2]}_{2007}(1 - \hat{R}^{[2]}_{2007})$	$\hat{\varepsilon}_{2006}$	$\hat{\varepsilon}_{2007}$
Groundwater fed					
Central stoneroller	0.39 ± 0.10	0.38 ± 0.10	0.25 ± 0.03	0.76 ± 0.02	0.25 ± 0.03
Orangethroat darter	0.39 ± 0.04	0.53 ± 0.10	0.63 ± 0.02	0.92 ± 0.03	0.63 ± 0.02
Northern plains killifish	0.37 ± 0.02	0.21 ± 0.04	0.19 ± 0.02	0.59 ± 0.06	0.19 ± 0.02
Brassy minnow	0.39 ± 0.06	0.13 ± 0.02	0.16 ± 0.09	0.52 ± 0.06	0.16 ± 0.09
Fathead minnow	0.39 ± 0.03	0.18 ± 0.06	0.20 ± 0.10	0.57 ± 0.03	0.20 ± 0.10
Creek chub	0.39 ± 0.10	0.53 ± 0.03	0.28 ± 0.10	0.91 ± 0.06	0.28 ± 0.10
Not groundwater fed					
Central stoneroller	0.83 ± 0.07	0.10 ± 0.05	0.25 ± 0.03	0.94 ± 0.12	0.25 ± 0.03
Orangethroat darter	0.83 ± 0.05	0.15 ± 0.05	0.63 ± 0.02	0.98 ± 0.06	0.63 ± 0.02
Northern plains killifish	0.82 ± 0.05	0.06 ± 0.01	0.19 ± 0.02	0.88 ± 0.07	0.19 ± 0.02
Brassy minnow	0.83 ± 0.01	0.04 ± 0.09	0.16 ± 0.09	0.87 ± 0.04	0.16 ± 0.09
Fathead minnow	0.83 ± 0.09	0.05 ± 0.07	0.20 ± 0.10	0.88 ± 0.06	0.20 ± 0.10
Creek chub	0.83 ± 0.07	0.14 ± 0.02	0.28 ± 0.10	0.98 ± 0.07	0.28 ± 0.10

Notes: Estimates are given for sites within river segments fed by groundwater or not. Extinction probability is the sum of the probabilities that: (1) occupied habitat dried and became unsuitable ($1 - \psi^{[2]}_{t+1}$), and (2) occupied habitat remained suitable (i.e., wet) but was unoccupied in year $t + 1$, $\psi^{[2]}_{t+1}(1 - R^{[2]}_{t+1})$. No occupied habitat became unsuitable in 2007 [i.e.,$(1 - \psi^{[2]}_{2007} = 0)$].

TABLE 4. Model-averaged colonization probability ($\hat{\gamma}_{t+1}^{[m]}$) and standard errors for six Great Plains stream fish species in 59 potential spawning habitats (sites) in the Arikaree River, Colorado, USA, from 2005 to 2007.

Species	Previously dry habitat ($m = 0$)		Wet but unoccupied ($m = 1$)	
	$\hat{\gamma}_{2006}^{[0]}$	$\hat{\gamma}_{2007}^{[0]}$	$\hat{\gamma}_{2006}^{[1]}$	$\hat{\gamma}_{2007}^{[1]}$
Groundwater fed				
Central stoneroller	0.18 ± 0.08	0.66 ± 0.08	0.21 ± 0.09	0.69 ± 0.08
Orangethroat darter	0.08 ± 0.08	0.37 ± 0.07	0.10 ± 0.15	0.38 ± 0.09
Northern plains killifish	0.19 ± 0.03	0.79 ± 0.12	0.06 ± 0.02	0.06 ± 0.07
Brassy minnow	0.28 ± 0.07	0.77 ± 0.06	0.34 ± 0.05	0.86 ± 0.12
Fathead minnow	0.38 ± 0.04	0.77 ± 0.05	0.43 ± 0.02	0.80 ± 0.07
Creek chub	0.08 ± 0.11	0.70 ± 0.01	0.09 ± 0.02	0.73 ± 0.03
Not groundwater fed				
Central stoneroller	0.04 ± 0.05	0.66 ± 0.08	0.06 ± 0.03	0.69 ± 0.08
Orangethroat darter	0.02 ± 0.06	0.37 ± 0.04	0.03 ± 0.04	0.38 ± 0.12
Northern plains killifish	0.04 ± 0.10	0.79 ± 0.05	0.02 ± 0.03	0.06 ± 0.05
Brassy minnow	0.07 ± 0.02	0.77 ± 0.05	0.09 ± 0.05	0.86 ± 0.05
Fathead minnow	0.09 ± 0.03	0.77 ± 0.05	0.12 ± 0.03	0.80 ± 0.04
Creek chub	0.02 ± 0.09	0.70 ± 0.14	0.02 ± 0.04	0.73 ± 0.03

Note: Estimates are given for sites fed by groundwater or not.

variable through time and across space that fish species occupancy was best modeled as a random process. As a result, the likelihood that fish produced larvae in the same sites from year to year (i.e., site fidelity) was low. Across species, local colonization rates were lower, and local extinction rates higher, during the transition from wet to dry, especially in sites not connected to groundwater. In contrast, no sites dried or remained dry during the transition from dry to wet conditions, yielding lower but still substantial extinction probabilities and higher colonization probabilities, with little difference among sites with and without groundwater. Overall, local persistence and occupancy probabilities of the six plains fish species varied with respect to climate and hydrologic conditions, suggesting that individual species respond differentially to these processes.

Although the rate of habitat turnover in the Arikaree River is unprecedented, the random nature of the dynamic process is logical, given the interaction of climate and hydrology that drives disturbances in Great Plains stream ecosystems. Wetting and drying processes are controlled by variation in interannual precipitation,

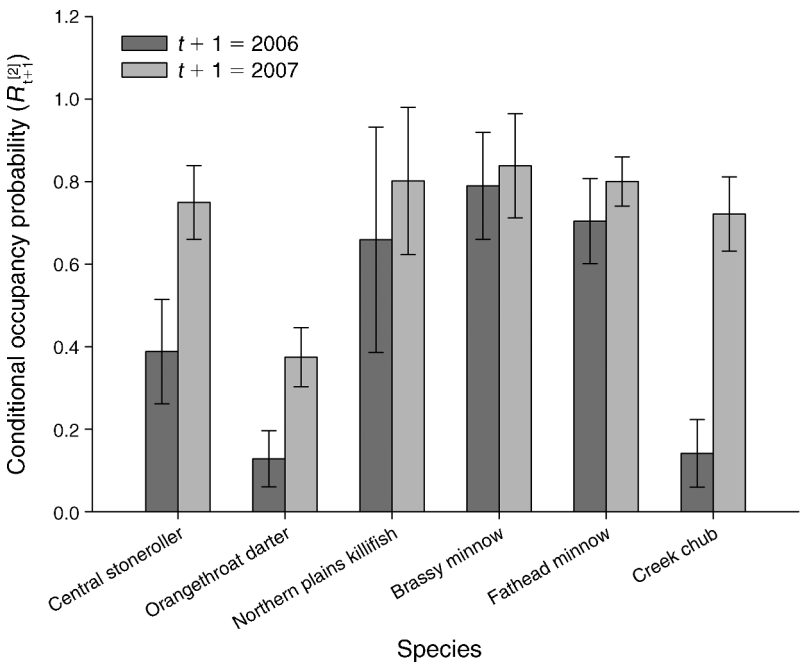

FIG. 1. Model-averaged estimates of occupancy $R_{t+1}^{[2]}$, given suitable habitat, for an assemblage of Great Plains stream fishes in the Arikaree River, Colorado, USA. Estimates are presented for the transition from wet to dry conditions (2005–2006), and from dry to wet conditions (2006–2007). Error bars are unconditional standard errors.

which is a random process in this semiarid ecoregion. The importance of habitat change on species dynamics was clearly illustrated by transitions between a wet and dry year where (1) 43–95% of species extinction probabilities were attributed to habitat drying, i.e.,

$$\frac{(1-\hat{\psi}^{[2]}_{2006})}{\hat{\varepsilon}_{2006}}$$

and (2) the contribution of habitat drying to overall extinction probability was higher for sites not fed by groundwater. Still, habitat dynamics alone were not enough to explain species dynamics. Even when all suitable habitats persisted ($\psi^{[1=2]}_{2007} = 1$), extinction probabilities were substantial across species (0.16–0.63; Table 3), again emphasizing the need to estimate both habitat and occupancy dynamics simultaneously.

The ability of plains fishes to quickly recolonize previously dry habitats is an adaptive response to dynamic habitat availability across both space and time (sensu Wiens 1976), and may result from the high dispersal ability of adult fishes in this assemblage. Colonization probabilities increased dramatically during a dry–wet transition, with dry sites being just as likely to be newly occupied as previously wet sites. Still, some species were better colonizers than others. For example, fathead minnow was among the best Arikaree River colonizers following a dry year, similar to their rapid colonization of intermittent arroyos after floods in a southern Colorado basin (Fausch and Bramblett 1991). We also found that site fidelity was low among potential spawning habitats, even when habitats persisted from year to year, suggesting that these species change spawning locations as habitats become unsuitable owing to drying, or exploit new locations after wetting (Scheurer et al. 2003). As a result, our findings indicate that as long as a habitat is suitable (wet) and accessible, it is equally likely to be used by many of the species we studied.

Extreme habitat dynamics such as those in the Arikaree River are widespread in other riverine ecosystems (Robinson et al. 2002, van der Nat et al. 2002, Larned et al. 2010). For example, frequent wetting and drying processes have a major influence on demographic rates of aquatic organisms found in other dynamic dryland riverscapes (e.g., Cooper Creek, Australia; see Arthington et al. 2005, Balcombe and Arthington 2009). Empirical examples of other systems where species occupancy dynamics track or are influenced by habitat dynamics are rare, but include: birds and invertebrates in coastal or island habitats subject to hurricanes (Covich et al. 1996, Reitsma et al. 2002); reptiles and amphibians in temporary wetlands (Willson et al. 2006, Roe and Georges 2008); and invertebrates, fishes, and amphibians in floodplain wetlands (Jepsen 1997, Tockner et al. 2006). Integrated habitat suitability–occupancy models that allow for unbiased estimates of processes that contribute to local colonization and extinction rates should prove beneficial in understanding such systems, and will be particularly useful for identifying appropriate conservation actions (Wilcox et al. 2006). Moreover, ecologists frequently use presence and absence or relative abundance patterns for multiple species through time to infer important processes driving community assembly (e.g., Diamond 1975, Hubbell 2001, Chase 2003, 2007). Expanding dynamic habitat–occupancy models to include multiple species may help resolve questions regarding community assembly in other systems as well.

An assumption of all occupancy models is that detection and occupancy are independent across sites (MacKenzie et al. 2006). Our sampling design and the nature of our sampled potential spawning habitat support this assumption for these populations of fish larvae. For example, most backwater habitats were off-channel with little flow between them and the river, and the river was often dry between sites. Moreover, larval fish are relatively immobile organisms, and with the exception of orangethroat darter, all detected larvae were preserved, so no detected individual was available for detection at other sites. Still, at some scale, the probability of one sample unit being occupied is likely to be affected by whether a neighboring sample unit is also occupied. However, if the underlying reason for the spatial correlation (or aggregation) among sites is due primarily to a habitat feature that is modeled as a covariate (e.g., groundwater input, as we did in this study), the inclusion of the covariate in the analyses will account for the spatial correlation in occurrence (D. MacKenzie, *personal communication*, *unpublished manuscript*). We are not aware of any method that simultaneously accounts for nondetection (or misclassification) and residual spatial autocorrelation in a linear or dendritic network. Techniques for investigating and incorporating spatial autocorrelation in occupancy models are an active and important area of research (e.g., Hines et al. 2010) and future extensions of occupancy models will likely yield better ways of testing for and incorporating residual spatial autocorrelation.

Based on our data, we were able to model 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 unknown. However, using the estimates provided here, managers could construct models to predict occupancy dynamics under various climate scenarios. Monitoring data could support or refute such predictions and the information could be used to update models in an adaptive management framework (Williams et al. 2002). Additionally, although we found little support for fidelity to individual habitats, understanding the underlying processes that influence the spatial and temporal distribution of wet and dry habitats (e.g., groundwater input) allows for more informed conservation decisions. These might include protection of reaches with high groundwater connectivity or manage-

ment actions to increase aquifer connections. This information will be especially valuable in light of increased human-caused stream drying from over-appropriation of groundwater and surface water resources (Falke et al. 2011), and the impacts of global climate change (Ficke et al. 2007).

Acknowledgments

We thank K. Bentley, N. Cathcart, A. Ficke, R. Fitzpatrick, J. Hammer, M. Hill, A. Klug, W. Pate, C. Saunders, and Z. Underwood for their help in the field and lab. We also thank D. Winkelman, D. Durnford, D. MacKenzie, and J. Hines for their input on study design and analyses. W. Burnidge (The Nature Conservancy) provided valuable logistical support. This research was funded by a grant from the Colorado Division of Wildlife, and we thank T. Nesler and H. Crockett for their administrative support.

Literature Cited

Arthington, A. H., S. R. Balcombe, G. A. Wilson, M. C. Thoms, and J. Marshall. 2005. Spatial and temporal variation in fish-assemblage structure in isolated waterholes during the 2001 dry season of an arid-zone floodplain river, Cooper Creek, Australia. Marine and Freshwater Research 56:25–35.

Balcombe, S. R., and A. H. Arthington. 2009. Temporal changes in fish abundance in response to hydrological variability in a dryland floodplain river. Marine and Freshwater Research 60:146–159.

Bonner, T. H., and G. R. Wilde. 2000. Changes in the Canadian River fish assemblage associated with reservoir construction. Journal of Freshwater Ecology 15:189–198.

Breininger, D. R., J. D. Nichols, B. W. Duncan, E. D. Stolen, G. M. Carter, D. K. Hunt, and J. H. Drese. 2010. Multistate modeling of habitat dynamics: factors affecting Florida scrub transition probabilities. Ecology 91:3354–3364.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Chase, J. M. 2003. Community assembly: when should history matter? Oecologia 136:489–498.

Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. Proceedings of the National Academy of Sciences USA 104:17430–17434.

Clinchy, M., D. T. Haydon, and A. T. Smith. 2002. Pattern does not equal process: What does patch occupancy really tell us about metapopulation dynamics? American Naturalist 159:351–362.

Covich, A. P., T. A. Crowl, S. L. Johnson, and M. Pyron. 1996. Distribution and abundance of tropical freshwater shrimp along a stream corridor: response to disturbance. Biotropica 28:484–492.

Diamond, J. M. 1975. Assembly of species communities. Pages 342–444 *in* M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Belknap, Cambridge, Massachusetts, USA.

Diaz, A. M., M. A. L. Alonso, and M. R. V. Gutiérrez. 2008. Biological traits of stream macroinvertebrates from a semi-arid catchment: patterns along complex environmental gradients. Freshwater Biology 53:1–21.

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.

Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. Ecological Applications 9:642–655.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169–175.

Falke, J. A., K. R. Bestgen, and K. D. Fausch. 2010*a*. Streamflow reductions and habitat drying affect growth, survival, and recruitment of brassy minnow *Hybognathus hankinsoni* 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. Pages 207–233 *in* D. A. Jackson and K. B. Gido, editors. Community ecology of stream fishes: concepts, approaches and techniques. Symposium 73. American Fisheries Society, Bethesda, Maryland, USA.

Falke, J. A., K. D. Fausch, K. R. Bestgen, and L. L. Bailey. 2010*b*. Spawning phenology and habitat use in a Great Plains stream fish assemblage: an occupancy estimation approach. Canadian Journal of Fisheries and Aquatic Sciences 67:1942–1956.

Falke, J. A., K. D. Fausch, R. Magelky, A. Aldred, D. S. Durnford, L. K. Riley, and R. Oad. 2011. The role of groundwater pumping and drought in shaping ecological futures for stream fishes in a dryland river basin of the western Great Plains, USA. Ecohydrology 4:682–697.

Falke, J. A., and K. B. Gido. 2006. Spatial effects of reservoirs on fish assemblages in Great Plains streams in Kansas, USA. River Research and Applications 22:55–68.

Fausch, K. D., and K. R. Bestgen. 1997. Ecology of fishes indigenous to the Central and Southwestern Great Plains. Pages 131–166 *in* F. L. Knopf and F. B. Samson, editors. Ecology and conservation of Great Plains vertebrates. Springer-Verlag, New York, New York, USA.

Fausch, K. D., and R. G. Bramblett. 1991. Disturbance and fish communities in intermittent tributaries of a western Great Plains river. Copeia 1991:659–674.

Ficke, A. D., C. A. Myrick, and L. J. Hansen. 2007. Potential effects of global climate change on freshwater fisheries. Reviews in Fish Biology and Fisheries 17:581–613.

Fisher, S. G., L. J. Gray, N. B. Grimm, and D. E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. Ecological Monographs 52:93–110.

Gido, K. B., W. K. Dodds, and 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.

Gotelli, N. J., and C. M. Taylor. 1999. Testing metapopulation models with stream-fish assemblages. Evolutionary Ecology Research 1:835–845.

Graf, W. L. 2006. Downstream hydrologic and geomorphic effects of large dams on American rivers. Geomorphology 79:336–360.

Hanski, I., and O. E. Gaggiotti. 2004. Ecology, genetics, and evolution of metapopulations. Elsevier, San Diego, California, USA.

Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. Nature 404:755–758.

Harrison, S., and A. D. Taylor. 1997. Empirical evidence for metapopulation dynamics. Pages 27–43 *in* I. Hanski and M. E. Gilpin, editors. Metapopulation biology: ecology genetics and evolution. Academic Press, London, UK.

Hines, J. E., J. D. Nichols, J. A. Royle, D. I. MacKenzie, and A. M. Gopalaswamy. N. Samba Kumar, and K. U. Karanth, editors. 2010. Tigers on trails: occupancy modeling for cluster sampling. Ecological Applications 20:1456–1466.

Hoagstrom, C. W., J. E. Brooks, and S. R. Davenport. 2008. Recent habitat association and the historical decline of *Notropis simus pecosensis*. River Research and Applications 24:789–803.

SRP16748

Hubbell, S. P. 2001. The unified neutral theory of bio-diversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Jepsen, D. B. 1997. Fish species diversity in sand bank habitats of a neotropical river. Ecology of Freshwater Fishes 49:449–460.

Kilgore, K. J. 1994. Design and application of a larval fish trap. Wetlands Research Program Bulletin 4:1–3.

Koizumi, I., and K. Maekawa. 2004. Metapopulation structure of stream-dwelling Dolly Varden charr inferred from patterns of occurrence in the Sorachi River basin, Hokkaido, Japan. Freshwater Biology 49:973–981.

Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. American Naturalist 130:624–635.

Larned, S. T., T. Datry, D. B. Arscott, and K. Tockner. 2010. Emerging concepts in temporary-river ecology. Freshwater Biology 55:717–738.

MacKenzie, D. I., L. L. Bailey, J. E. Hines, and J. D. Nichols. 2011. An integrated model of habitat and species occurrence dynamics. Methods in Ecology and Evolution 2:612–622.

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. Elsevier, San Diego, California, USA.

MacKenzie, D. I., J. D. Nichols, M. E. Seamans, and R. J. Gutierrez. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. Ecology 90:823–835.

Martin, J., S. Chamaillé-Jammes, J. D. Nichols, H. Fritz, J. E. Hines, C. J. Fonnesbeck, D. I. MacKenzie, and L. L. Bailey. 2010. Simultaneous modeling of habitat suitability, occupancy, and relative abundance: African elephants in Zimbabwe. Ecological Applications 20:1173–1182.

Matthews, W. J. 1988. North American prairie streams as systems for ecological study. Journal of the North American Benthological Society 7:387–409.

McPeek, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. American Naturalist 140:1010–1027.

Moilanen, A. 2002. Implications of empirical data quality to metapopulation model parameter estimation and application. Oikos 96:516–530.

Omernik, J. M. 1987. Ecoregions of the conterminous United States. Map Supplement (scale 1:7,500,000). Annals of the American Association of Geographers 77:118–125.

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 evolutionary significant units of anadromous salmonids in the Pacific Northwest. Pages 334–349 *in* J. L. Nielsen and D. A. Powers, editors. Evolution and the aquatic ecosystem: defining unique units in population conservation. Symposium 17. American Fisheries Society, Bethesda, Maryland, USA.

Reitsma, L., P. Hunt, S. L. Burnson, and B. B. Steele. 2002. Site fidelity and ephemeral habitat occupancy: northern waterthrush use of Puerto Rican black mangroves during the nonbreeding season. The Wilson Bulletin 114:99–105.

Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. American Naturalist 158:87–99.

Robinson, C. T., K. Tockner, and J. V. Ward. 2002. The fauna of dynamic riverine landscapes. Freshwater Biology 47:661–677.

Roe, J. H., and A. Georges. 2008. Terrestrial activity, movements and spatial ecology of an Australian freshwater turtle, *Chelodina longicollis*, in a temporally dynamic wetland system. Austral Ecology 33:1045–1056.

Scheurer, J. A., K. D. Fausch, and K. R. Bestgen. 2003. Multiscale processes regulate brassy minnow persistence in a Great Plains river. Transactions of the American Fisheries Society 132:840–855.

Schlosser, I. J. 1995. Critical landscape attributes that influence fish population dynamics in headwater streams. Hydrobiologia 303:71–81.

Scott, J. M., P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and E. B. Samson, editors. 2002. Predicting species occurrences. Island Press, Washington, D.C., USA.

Stelter, C., M. Reich, V. Grimm, and C. Wissel. 1997. Modelling persistence in dynamic landscapes: lessons from a metapopulation of the grasshopper *Bryodema tuberculata*. Journal of Animal Ecology 66:508–518.

Thomas, C. D., and I. Hanski. 2004. Metapopulation dynamics in changing environments: butterfly responses to habitat and climate change. Pages 489–514 *in* I. Hanski and O. E. Gaggiotti, editors. Ecology, genetics, and evolution of metapopulations. Elsevier Academic Press, London, UK.

Tockner, K., I. Klaus, C. Baumgartner, and J. V. Ward. 2006. Amphibian diversity and nestedness in a dynamic floodplain river (Tagliamento, NE-Italy). Hydrobiologia 565:121–133.

van der Nat, D., A. P. Schmidt, K. Tockner, P. J. Edwards, and J. V. Ward. 2002. Innundation dynamics in braided floodplains: Tagliamento River, Northeast Italy. Ecosystems 5:636–647.

Wiens, J. A. 1976. Population response to patchy environments. Annual Review of Ecology and Systematics 7:81–120.

Wilcox, C., B. J. Cairns, and H. P. Possingham. 2006. The role of habitat disturbance and recovery in metapopulation persistence. Ecology 87:855–863.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Elsevier Academic Press, San Diego, California, USA.

Willson, J. D., C. T. Winne, M. E. Dorcas, and J. W. Gibbons. 2006. Post-drought responses of semi-aquatic snakes inhabiting an isolated wetland: insights on different strategies for persistence in a dynamic habitat. Wetlands 26:1071–1078.

Winston, M. R., C. M. Taylor, and J. Pigg. 1991. Upstream extirpation of four minnow species due to damming of a prairie stream. Transactions of the American Fisheries Society 120:98–105.

Supplemental Material

Appendix

Local persistence of larval stream fishes in groundwater and non-groundwater fed river segments (*Ecological Archives* E093-076-A1).