

Evaluating the impacts of small impoundments on stream salamanders

JEFFERY KIRCHBERG^a, KRISTEN K. CECALA^{a,*}, STEVEN J. PRICE^b, EMILY M. WHITE^c and DAVID G. HASKELL^a

^a*Department of Biology, University of the South, TN, USA*

^b*Department of Forestry, University of Kentucky, Lexington, KY, USA*

^c*Department of Chemistry, University of the South, USA*

ABSTRACT

1. Large dams have been repeatedly implicated in declines of riverine species, but the impacts of small dams are largely understudied. The placement of small dams (< 5 m high) on headwater streams, their density, and lack of regulation suggests that these dams may also have significant adverse impacts on headwater biota.

2. The objective of this study was to determine whether small impoundments affect downstream salamander abundance and water quality. Salamanders were identified and counted from 10 paired catchments draining either a small impoundment (< 0.8 ha) or a free-flowing stream. A binomial mixture model was used to estimate abundance after accounting for incomplete detection.

3. Estimated abundance of larval *Desmognathus conanti*, *Eurycea wilderae*, and *Pseudotriton ruber* was 3.9, 19.6, and 9.8 times greater downstream of small impoundments than in unaltered streams. Iron concentrations and pH had positive effects on salamander abundance while conductivity was negatively associated with salamander abundance.

4. Increases in abundance may be due to increased hydrologic stability below dams, different geomorphology, and altered water quality. Despite their small size, small impoundments can have localized, downstream effects on water chemistry and species abundance and may create high quality habitat for some stream species in a heterogeneous landscape.

Copyright © 2016 John Wiley & Sons, Ltd.

Received 15 June 2015; Revised 12 December 2015; Accepted 26 March 2016

KEY WORDS: Amphibians; habitat management; impoundment; landscape; pollution; stream; water quality

INTRODUCTION

Despite the benefits of dams to surrounding human communities, human impacts on natural river flow regimes are one of the primary mechanisms responsible for biodiversity loss in fresh waters

(Nilsson *et al.*, 2005; Dudgeon *et al.*, 2006). Dams physically prevent connectivity of upstream and downstream populations, and downstream habitats undergo significant alterations of physical, chemical, and biological characteristics (Poff *et al.*, 1997; Bunn and Arthington, 2002). Specifically,

*Correspondence to: K. K. Cecala, 735 University Avenue, Sewanee, TN 37383, USA. Email: kkecala@sewanee.edu

downstream habitats experience altered flow regimes including asynchronous floods, altered thermal regimes, and limited sediment transport creating scoured and incised channels (Ligon *et al.*, 1995; Poff *et al.*, 1997; Freeman *et al.*, 2001). Reduced downstream transport of organic matter and alterations to the chemical composition of released water can also alter the food webs of downstream communities (Hall *et al.*, 2000; Arthington *et al.*, 2009). These conditions cause downstream declines in biodiversity of multiple taxa ranging from plants (Auble *et al.*, 1994; Zhang *et al.*, 2013) to invertebrates (Richter *et al.*, 1997; Martinez *et al.*, 2013) and vertebrates including fish (Lytle and Poff, 2004; Nilsson *et al.*, 2005) and herpetofauna (Eskew *et al.*, 2012; Hunt *et al.*, 2013).

Amphibian responses to river regulation are poorly understood, yet amphibians represent a significant component of freshwater biodiversity and may drive important ecological processes (Covich *et al.*, 2004; Davic and Welsh, 2004; Best and Welsh, 2014). Amphibian occupancy tends to increase with downstream distance from large dams suggesting that river regulation adversely affects habitat suitability (Eskew *et al.*, 2012). Eskew *et al.* (2012) suggested that reduced magnitude floods that do not create floodplain wetlands may be one mechanism responsible for this pattern, but reduced magnitude floods may improve amphibian persistence below dams by allowing larval stages and eggs to remain in suitable aquatic habitat (Lind *et al.*, 1996; Kupferberg *et al.*, 2011). Conversely, aseasonal floods resulting from water releases may cause downstream displacement of multiple amphibian life stages (Lind *et al.*, 1996).

Although the impacts of large dams (> 50 m high) are well known, the role of pervasive, small impoundments (< 5 m high) located on fishless headwater streams is poorly understood (Graf, 2005; Csiki and Rhodes, 2010). Small impoundments, which are common in rural and residential regions of the south-eastern United States, are not regulated and typically lack flow release management (Poff and Hart, 2002; Graf, 2005). Small impoundments are thought to have greater cumulative downstream effects than large dams because of their frequency (Kibler and

Tullos, 2013). When these small dams are created out of earthen material, seepage through the dam will occur (Craft *et al.*, 2008), and it is not well understood how discharge from earthen dams may differ from large impoundments. Because water seepage through earthen dams must travel through the clay used to construct the dam, water quality and sediment transport may differ below earthen dams compared with large concrete dams.

In the study area on the southern Cumberland Plateau USA, small impoundments are common (1.3 impoundments km⁻²). Streams of the southern Cumberland Plateau are often ephemeral and flow from late autumn or early winter until early to mid-summer. Earthen dams were constructed in the study area during the 1950s and 1960s as a method for providing permanent water (Knoll *et al.*, 2015). Dams were constructed with clay-rich soils from local borrow pits, and impoundments fill from seeps and rainfall. Water can flow downstream by either seeping through the dam or via overflow channels (Knoll *et al.*, 2015). Because dams in this study were made of clay, they can affect water quality through interaction between negatively charged clay particles and aquatic cations that alter conductivity and pH (Chapin *et al.*, 2002). Impoundments on the Cumberland Plateau cause leaching of iron from underlying sandstone layers (Barnden, 2005; Arnwine *et al.*, 2006). When iron seeps through earthen dams, iron oxidizing bacteria cause iron deposition and form a deep orange-brown flocculant (Barnden, 2005; Arnwine *et al.*, 2006). A previous survey found that sites downstream of dams had impaired macroinvertebrate communities, iron concentrations that exceeded criteria recommended by EPA for aquatic life (1 mg L⁻¹), elevated manganese concentrations, and greater variation in pH relative to unimpounded streams (Arnwine *et al.*, 2006). Earlier studies suggest that high concentrations of iron (20 mg L⁻¹) can be lethal to anurans (Porter and Hakanson, 1976) and more acidic pH increases the damaging effects of metals on amphibians (Freda, 1991; Green and Pelloquin, 2008; Schorr *et al.*, 2013). Iron concentrations have been used to assess the adverse impacts of small impoundments on the Cumberland Plateau (Arnwine *et al.*, 2006; Knoll *et al.*, 2015), but impacts of environmentally relevant

iron concentrations on amphibian populations have not yet been determined.

The southern highlands of the eastern United States are recognized as a region of globally significant salamander diversity, but the primary focus of research has been on salamanders in the Appalachian mountains, leaving much of their ecology on the Cumberland Plateau unknown. The stream-dwelling salamander community of the southern Cumberland Plateau is composed primarily of *Desmognathus conanti* (spotted dusky salamander), *Eurycea wilderae* (Blue Ridge two-lined salamander), and *Pseudotriton ruber* (red salamander). *Desmognathus conanti* is a medium-sized, robust salamander with a short larval period (9 months, Petranka, 1998). *Eurycea wilderae* is a slender salamander with a 1–2 year larval period (Petranka, 1998). They are often found in heavily disturbed streams and may occupy warm, slow-moving water owing to their vascularized gills (Petranka, 1998). Eggs of *D. conanti* and *E. wilderae* are often laid under rocks and wood in the stream channel (Petranka, 1998). *Pseudotriton ruber* is a large and robust salamander with a 1.5–3.5 year larval period (Petranka, 1998; Cecala *et al.*, 2009). Their larvae are often found in slow-moving water with dense leaf packs, but all life stages of this species can be found in subsurface stream reaches (Petranka, 1998). By studying these three species, it was possible to evaluate if species with different life histories responded differently to dams.

The present study investigated whether small impoundments adversely affect salamander abundance downstream, and whether changing abundance was linked to changes in water quality. Salamander abundance and water quality parameters were compared in streams with and without flow regulation. We hypothesized that salamander density would be: (1) lower downstream of dams compared with free-flowing control streams; and (2) negatively correlated with impaired water quality as measured by pH, conductivity, and dissolved iron concentrations. We also predicted that the least difference between control and dammed streams would be observed in *E. wilderae* because of their tolerance to disturbance and high rates of occupancy in other disturbed habitats.

METHODS

Salamander data collection

First-order streams, defined using Strahler's stream classification system, were selected such that all sample locations had shallow slopes and were located upstream of the landscape transition into steeply inclined coves. Ten pairs of catchments (N = 20 catchments) were selected on the southern Cumberland Plateau surrounding Sewanee, Tennessee in Franklin County (Table S1, Supplementary material). A paired approach investigating adjacent catchments with downstream confluences was used to reduce the likelihood of identifying erroneous treatment effects caused by the potential influence of spatial autocorrelation. All impounded catchments on the 54 km² campuses of the University of the South and adjacent St. Andrew's Sewanee School were selected for which appropriate unaltered paired catchments could be found. For each paired catchment, one catchment drained into a stream with a dam and the other catchment had an unaltered stream. At each dammed stream, two 20 m transects were designated: one immediately downstream of the dam and a second 50 m downstream of the upstream transect (Figure 1). For each undammed stream, transects at the control (free-flowing) stream were positioned within 10 m of the elevations of experimental streams (below dam). To detect salamanders, 20 min active searches of each transect were conducted and included searches of all areas of the stream and 0.5 m of the bank on both sides. Active surveys involved flipping cover objects and using both hands and nets to capture salamanders. Searches were distributed to ensure coverage of the entire transect. During each sampling event, the number of captures for each species and life stage was recorded. Surveys were repeated between three and six times per site from April to October, 2013. Although sampling events were irregularly spaced throughout the study period, all transects from both streams within a pair were sampled on the same day.

Water quality data collection

Conductivity and pH were measured in the field at the upstream edge of salamander transects using a

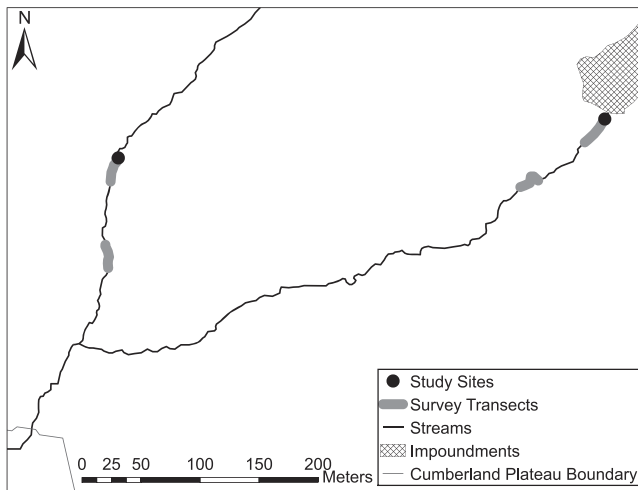


Figure 1. Study design depicting two paired catchments: one with an impoundment and one without. Survey transects were 20 m long spaced 50 m apart from one another. At the site with an impoundment, the upstream transect was located immediately downstream of the dam. At the free-flowing site, the upstream transect was located at approximately the same elevation as the upstream transect in the impounded catchment.

calibrated, handheld Oakton 35-Series Multiparameter PCS Tester. Water samples were collected at the same location during each survey and stored in 10% nitric acid-washed 50 mL plastic centrifuge tubes. Water samples were acidified (by adding 1 mL of concentrated nitric acid to 50 mL of sample), filtered through a 0.45 μm nylon syringe filter, and stored at 4 °C. The ferrozine method (Stookey, 1970) was used to evaluate total dissolved iron from filtered water samples. After allowing 5 min for colour development, absorbance was measured at 562 nm with a Hach DR/2500 spectrophotometer. Standards (ranging from 0.05 to 3.1 mg L⁻¹) were prepared by dilution of a 1000 mg L⁻¹ certified iron reference solution (Thermo Fisher Scientific Inc.) and used to generate a calibration curve.

Data analysis

To evaluate how dams alter water quality while providing additional information about streams on the Cumberland Plateau, water quality variation was assessed between paired catchments and by treatment. The mean of all water samples taken from a site was used to avoid pseudoreplication (Hurlbert, 1984). Specifically, three ANOVAs were performed evaluating the effect of dam and catchment pair on

mean values of total dissolved iron, conductivity, and pH.

Because salamanders are cryptic animals that spend much of their lives underground and their capture probabilities are often low (Petranka, 1998; Mazerolle *et al.*, 2007; Cecala *et al.*, 2013), abundance was analysed using a model that takes into account imperfect detection (Cecala *et al.*, 2013). Specifically, a binomial mixture model (Royle, 2004) was used to estimate abundance from repeated counts of unmarked individuals at specific geographic locations with unknown population sizes (Royle and Nichols, 2003; Royle and Dorazio, 2008; Kéry and Schaub, 2012; Price *et al.*, 2012). For this model, captures from 20 sites during the first three sampling occasions were used to maintain similar sampling effort among sites and to meet closure assumptions of the model (Kéry and Schaub, 2012). The first three samples at a site generally occurred within 2 weeks, which was assumed to meet the closure assumption. Counts were combined from upstream and downstream transects to represent counts for each stream. Furthermore, detections of adults were not included because they were infrequent. Capture probability models included a random intercept for treatment and covariates for day of sampling. Models for estimated abundance included treatment, and z-scored values for the three water quality parameters (total dissolved iron concentration, conductivity, and pH).

Abundance and capture parameters were evaluated for each species using Bayesian inference via Markov-chain Monte Carlo methods (MCMC) in WinBUGS Version 1.4 (Spiegelhalter *et al.*, 2003) with data handling in R (R Development Core Team 2013; add-in library R2WinBUGS). Convergence of the posterior distribution was reached after 60 000 samples, which were discarded as the burn-in period (Kéry, 2008). Thereafter, 600 000 iterations thinned by a factor of three to reduce autocorrelation between iterations were used for inferences. Non-informative prior distributions were used for all the parameters ($\beta_x \sim N(0, 10^2)$, $\alpha_x \sim N(0, 1.6^2)$; Royle and Dorazio, 2008; Kéry and Schaub, 2012). Means, standard deviations, and the 95% Bayesian credible intervals of the marginal posterior distribution were used to evaluate the effect of dams on capture

Table 1. Water quality parameters (standard error) between unaltered and dammed streams on the Cumberland Plateau

	Control		Dam	
	Mean	Range	Mean	Range
Total dissolved iron (mg L ⁻¹)	0.16 (0.06)	0–0.48	6.10 (2.73)	0.46–23.00
pH	6.63 (0.17)	5.76–7.37	6.29 (0.29)	5.06–7.55
Conductivity (µS cm ⁻¹)	222.83 (16)	19–187	73 (20)	16–193

probability and the effect of dams and water quality on abundance. An effect was considered to be biologically relevant if 75% or more of its distribution fell above or below zero.

RESULTS

Six different species were found represented by 766 captures including *E. wilderae* (N = 557; 72% downstream of impoundments), *P. ruber* (N = 150, 44% downstream of impoundments), and *D. conanti* (N = 39, 81% downstream of impoundments). Other species captured included *Plethodon glutinosus* (N = 1), *Plethodon dorsalis* (N = 5), and *Notophthalmus viridescens* (N = 14). Conductivity and pH were not significantly different between dam sites and control sites ($F_{df=1,17} = 0.218$, $P = 0.647$, $F_{df=1,17} = 0.539$, $P = 0.243$, respectively; Table 1); however, they did vary by paired catchment ($F_{df=1,17} = 6.773$, $P = 0.020$, $F_{df=1,17} = 7.772$, $P = 0.013$). Total dissolved iron concentrations were higher below dams ($F_{df=1,17} = 7.083$, $P = 0.017$; Table 1) and varied among paired catchments ($F_{df=1,17} = 5.497$, $P = 0.032$).

Capture probabilities for all three focal salamander species were consistently lower below dams (Table 2). Capture probabilities were lowest

for *D. conanti* below dams and highest for *E. wilderae* in control streams (Table 2). Dams were positively correlated with the abundance of all three study species (Table 3). Specifically, *D. conanti*, *E. wilderae*, and *P. ruber* had abundances 3.9, 19.6, and 9.8 times higher, respectively, below dams than in free-flowing streams (Figure 2). Water quality parameters generally influenced salamander abundance (Table 3). pH was positively associated with salamander abundance for all three species (Table 3). *Desmognathus conanti* abundance was not influenced by total dissolved iron or conductivity, but *E. wilderae* and *P. ruber* abundances were negatively associated with conductivity and positively associated with total dissolved iron (Table 3). Dam presence had 1.43–4.68 times greater influence on abundance than water quality.

DISCUSSION

Contrary to our hypothesis based on the findings of studies at large dams (Dudgeon *et al.*, 2006), stream salamander abundance was not adversely affected by small dams; dams positively affected abundance of each of the three study species. Likewise, water quality parameters were associated with salamander abundance, but they had smaller effects on salamander abundance than the presence of a dam. Generally, salamanders were positively associated with more neutral pH, and *E. wilderae* and *P. ruber* were found at higher abundances in catchments with lower conductivity and higher total dissolved iron.

Small impoundments alter stream habitats in a variety of ways that may increase salamander abundance. First, dams may create a more stable hydrologic regime (Poff *et al.*, 1997). Seepage and spillway flow from earthen dams contribute a high

Table 2. Capture probabilities of focal species (with 95% credible intervals) showing consistency between unaltered and dammed streams on the Cumberland Plateau

Species	Capture probability in unaltered streams	95% Credible interval	Capture probability below dams	95% Credible interval
<i>Desmognathus conanti</i>	0.134	(0.048, 0.354)	0.001	(<0.001, 0.167)
<i>Eurycea wilderae</i>	0.663	(0.291, 0.792)	0.087	(0.008, 0.676)
<i>Pseudotriton ruber</i>	0.228	(0.222, 0.379)	0.126	(0.011, 0.395)

Table 3. Estimates of the posterior means for parameters with 95% credible intervals (in parentheses) for the effect of dam, total dissolved iron, conductivity, and pH on abundance of the three focal species on the Cumberland Plateau. Significant effects (in bold) were interpreted as those with 95% credible intervals that have at least 75% of their distribution in the positive or negative range

Species	Dam	Total dissolved Iron	Conductivity	pH
<i>Desmognathus conanti</i>	2.10 (0.96, 7.73)	-0.13 (-4.78, 3.60)	-0.14 (-1.36, 0.89)	1.39 (-0.57, 3.90)
<i>Eurycea wilderae</i>	3.41 (2.24, 5.68)	1.08 (0.72, 1.54)	-0.74 (-1.30, 0.73)	1.34 (0.90, 1.92)
<i>Pseudotriton ruber</i>	1.32 (0.35, 3.30)	0.62 (0.21, 1.00)	-0.92 (-1.69, -0.31)	0.85 (0.35, 1.33)

degree of water permanence and maintained base flow (Poff *et al.*, 1997). Providing consistent aquatic habitat less prone to seasonal droughts may create more reliable habitat for salamanders on the Cumberland Plateau (Arnwine *et al.*, 2006). Dampening of flood pulses creates a more stable hydrologic system and reduces risks of downstream displacement (Barrett *et al.*, 2010). Second, changes to the hydrologic regime and to seepage patterns from earthen dams will alter the fluvial geomorphology creating a wider, shallower channel (Brant, 2000). Because these channels are in canopy gaps formed by the dam and its impoundment, they may experience increased solar

radiation and stream temperatures, which may ultimately increase salamander production and growth (Pough, 1980; Caissie, 2006; Sanuy *et al.*, 2008). Increased light penetration to the stream may also increase autotrophic production stimulating production of salamander prey (Thorp and Delong, 2002; Lessard and Hayes, 2003; Cross *et al.*, 2006; Julian *et al.*, 2011), but preliminary data suggest that salamanders from below dams are of similar body condition to individuals from perennial streams (Colyar, unpublished data; Figure S1). Lastly, stream organisms including salamanders and some macroinvertebrates exhibit persistent, upstream movement biases (Lowe, 2003; Macneale *et al.* 2005; Cecala *et al.*, 2009). As individuals move upstream, the dam impedes their movement forcing individuals to accumulate below dams (Spence and Hynes, 1971). At present, which of these mechanisms may be the cause of the patterns observed is unknown and may vary for different taxa.

The presence of small dams had species-specific influences that are probably a result of unique physiologies and life histories (Petranka, 1998). Increased water permanence, that is otherwise infrequent on top of the Cumberland Plateau could explain increased abundance of species with long larval stages that require water continuously for months or years, such as *E. wilderae*, which had the strongest response to dam presence (Petranka, 1998). *Pseudotriton ruber* is also known to have a multi-year larval period (Bruce, 1972; Semlitsch, 1983), yet this species was the least responsive to the presence of dams. *Pseudotriton ruber* also uses subterranean habitats for all life stages and therefore may be less reliant on surface

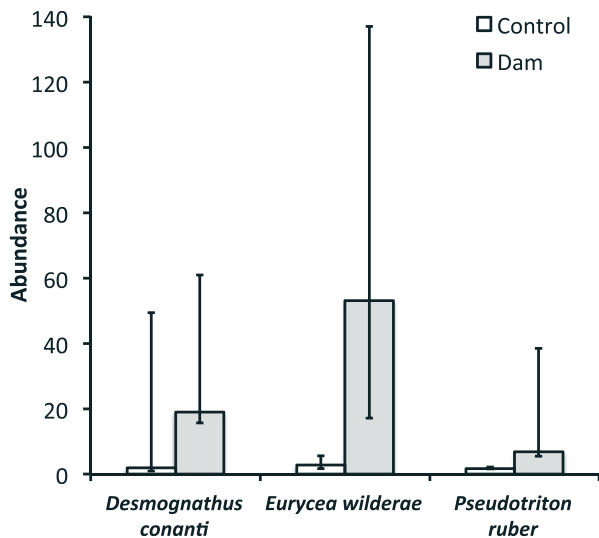


Figure 2. Abundance estimates (per 40 m) including 95% credible intervals for three salamander species on the Cumberland Plateau obtained from the binomial mixture model for salamanders located below a dam or in control, free-flowing streams. *Desmognathus conanti*, *Eurycea wilderae*, and *Pseudotriton ruber* have abundances 3.9, 19.6, and 9.8 times higher below dams than in free-flowing streams (Table 3).

water, particularly in a region well known for subterranean habitat (Miller *et al.*, 2008; Niemiller *et al.*, 2013). Conversely, *D. conanti* has a relatively short aquatic larval phase that suggests it may be capable of inhabiting more ephemeral streams, yet its abundance increased below dams (Juterbock, 1990; Petranka, 1998). We hypothesize that this pattern may best be explained by adult behaviour, as adult *D. conanti* prefer to occupy permanent stream edges where foraging opportunities may be more frequent relative to ephemeral stream channels with more variable microclimates (Hairston, 1987; Petranka, 1998; Bruce, 2007; Peterman *et al.*, 2008). Adult distributions are unlikely to fully explain larval *E. wilderae* and *P. ruber* distributions because adults of these species are terrestrial for most of the year (Bruce, 1978; Petranka, 1998). Lastly, *Eurycea wilderae* exhibited the largest response to the presence of dams. Like *P. ruber*, *E. wilderae* have vascularized gills that assist them in extracting oxygen from low oxygen environments such as warm habitats below dams (Petranka, 1998). This physiological adaptation and lack of subterranean use may best explain the strong, positive response to dams by *E. wilderae*.

On the southern Cumberland Plateau, small impoundments have positive effects on stream salamander populations, but the mechanisms behind this pattern are unclear. It is recommended that future research examines the causes behind this pattern and determines whether it applies generally among taxa and geographical locations. Small dams on the Cumberland Plateau often occur in headwaters as opposed to impoundments in the middle reaches that may induce habitat and population fragmentation in other regions. Overall, natural and altered streams on the Cumberland Plateau harbour stream salamander densities 5–14 times lower than those observed in other ecoregions (Means and Travis, 2007; Milanovich, 2010; Cecala *et al.*, 2013). Therefore, these data suggest that small impoundments may play an important role in maintenance of stream salamander populations in an ecoregion characterized by ephemeral streams. This supports conclusions by others that habitat protection for salamanders is complex and requires attention to important habitats that are infrequently located and represent a small proportion of available habitat (Romano *et al.*, 2008; Diaz *et al.*, 2015).

This study joins a growing body of literature indicating that small dams may play ecologically important roles for downstream communities (Jackson and Pringle, 2010; Gangloff, 2013). Although small dams may still impede the dispersal of migratory species (Watters, 1996; Hitt *et al.*, 2012), they appear to support more diverse and healthier populations of mussels (Gangloff *et al.*, 2011; Singer and Gangloff, 2011) and salamanders (present study) in downstream habitat compared with populations in unmanaged river or stream habitats. As ancillary benefits, small dams also inhibit the movement of aquatic invasive species and serve as a sink for environmental contaminants and toxins (Lemly *et al.*, 1993; Jackson *et al.*, 2005). As Gangloff (2013) recommends, a more nuanced view towards the environmental impacts of dams appears to be necessary. In some contexts, maintenance of small dams may in fact maintain biological diversity and success in riverine networks relative to intervention strategies such as dam removal (Sethi *et al.*, 2004; Gangloff *et al.*, 2011). For example, the small dams observed in this study were located above the seeps for these streams. In these instances, riverine migratory patterns remain uninterrupted, and the small dams may be considered to enhance habitat quality for salamanders via hydrologic stability that allows some species to occupy a broader range of habitats than would otherwise be available to them. Although large and small dams can cause environmental problems and conservation groups regularly support their removal, we encourage careful considerations of dam removal within the context of dam size, network position, and presence or absence of rare, migratory, or invasive species.

ACKNOWLEDGEMENTS

Chris Van de Ven facilitated site selection. John Palisano and two anonymous reviewers provided comments that improved this manuscript. Brock Colyar supplied supplementary data on salamander body condition. Funding for this project was provided by the Biology and Chemistry Departments at The University of the South, and a Yeatman Summer Fellowship to J.K.

REFERENCES

- Arnwine DH, Sparks KJ, James RR. 2006. Probabilistic monitoring of streams below small impoundments in Tennessee. Tennessee Department of Environment and Conservation, Division of Water Pollution Control, Nashville, TN.
- Arthington AH, Naiman RJ, McClain ME, Nilsson C. 2009. Preserving the biodiversity and ecological services of rivers: new challenges and research opportunities. *Freshwater Biology* **55**: 1–16.
- Auble GT, Friedman JM, Scott ML. 1994. Relating riparian vegetation to present and future streamflows. *Ecological Applications* **4**: 544–554.
- Barnden AR. 2005. *Ecology of streams affected by iron precipitates and iron flocculants*, MS thesis, University of Canterbury, Christchurch, NZ.
- Barrett K, Helms BS, Guyer C, Schoonover JE. 2010. Linking process to pattern: causes of stream-breeding amphibian decline in urbanized watersheds. *Biological Conservation* **143**: 1998–2005.
- Best ML, Welsh HH. 2014. The trophic role of a forest salamander: impacts on invertebrates, leaf litter retention, and the humification process. *Ecosphere* **5**: article 16.
- Brant SA. 2000. Classification of geomorphological effects downstream of dams. *Catena* **40**: 375–401.
- Bruce RC. 1972. The larval life of the red salamander, *Pseudotriton ruber*. *Journal of Herpetology* **6**: 43–51.
- Bruce RC. 1978. Reproductive biology of the salamander *Pseudotriton ruber* in the southern Blue Ridge mountains. *Copeia* **978**: 417–423.
- Bruce RC. 2007. Out of the frying pan into the fire: an ecological perspective on evolutionary reversal in life history in plethodontid salamanders (Amphibia: Plethodontidae). *Evolutionary Ecology* **21**: 703–726.
- Bunn SE, Arthington AH. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* **30**: 492–507.
- Caissie D. 2006. The thermal regime of rivers. *Freshwater Biology* **51**: 1389–1406.
- Cecala KK, Price SJ, Dorcas ME. 2009. Evaluating existing movement hypotheses in linear systems using larval stream salamanders. *Canadian Journal of Zoology* **87**: 292–298.
- Cecala KK, Price SJ, Dorcas ME. 2013. Modeling the effects of life-history traits on estimation of population parameters for a cryptic stream species. *Freshwater Science* **32**: 116–125.
- Chapin FS, Matson PA, Mooney HA. 2002. *Principles of Terrestrial Ecosystem Ecology*, Springer-Verlag: New York.
- Covich AP, Austen MC, Barlocher F, Chauvet E, Cardinale BJ, Biles CL, Inchausti P, Dangles O, Solan M, Gessner MO, et al. 2004. The role of biodiversity in the functioning of freshwater and marine benthic ecosystems. *Bioscience* **54**: 767–775.
- Craft CD, Pearson RM, Hurcomb D. 2008. Mineral dissolution and dam seepage chemistry. *Reclamation: Managing Water in the West US* Department of the Interior. Bureau of Reclamation, Washington DC.
- Cross WF, Wallace JB, Rosemond AD, Eggert SL. 2006. Whole-system nutrient enrichment increases secondary production in a detritus-based ecosystem. *Ecology* **87**: 1556–1565.
- Csiki S, Rhodes BL. 2010. Hydraulic and geomorphological effects of run-of-river dams. *Progress in Physical Geography* **34**: 755–780.
- Davic RD, Welsh HH. 2004. On the ecological roles of salamanders. *Annual Review of Ecology, Evolution, and Systematics* **35**: 405–434.
- Diaz PH, Fries JN, Bonner TH, Alexander ML, Nowlin WH. 2015. Mesohabitat associations of the threatened San Marcos salamander (*Eurycea nana*) across its geographic range. *Aquatic Conservation: Marine and Freshwater Ecosystems* **25**: 307–321.
- Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Leveque C, Naiman RJ, Prieur-Richard AH, Soto D, Stiassny MLJ, Sullivan CA. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Review* **2006**: 163–182.
- Eskew EA, Price SJ, Dorcas ME. 2012. Effects of river-flow regulation on anuran occupancy and abundance in riparian zones. *Conservation Biology* **26**: 504–512.
- Freda J. 1991. The effects of aluminum and other metals on amphibians. *Environmental Pollution* **71**: 305–328.
- Freeman MC, Bowen ZH, Bovee KD, Irwin ER. 2001. Flow and habitat effects on juvenile fish abundance in natural and altered flow regimes. *Ecological Applications* **11**: 179–190.
- Gangloff MM. 2013. Taxonomic and ecological tradeoffs associated with small dam removals. *Aquatic Conservation: Marine and Freshwater Ecosystems* **23**: 475–480.
- Gangloff MM, Hartfield EE, Werneke DC, Feminella JW. 2011. Associations between small dams and mollusk assemblages in Alabama streams. *Journal of the North American Benthological Society* **30**: 1107–1116.
- Graf W. 2005. Geomorphology and American dams: the scientific, social, and economic context. *Geomorphology* **71**: 3–26.
- Green LE, Peloquin JE. 2008. Acute toxicity of acidity in larvae and adults of four stream salamander species (*Plethodontidae*). *Environmental Toxicology and Chemistry* **27**: 2361–2367.
- Hairston NG. 1987. *Community Ecology and Salamander Guilds*, Cambridge University Press: New York.
- Hall RO, Wallace JB, Eggert SL. 2000. Organic matter flow in stream food webs with reduced detrital resource base. *Ecology* **81**: 3445–3463.
- Hitt NP, Eyler S, Wofford JEB. 2012. Dam removal increases American eel abundance in distant headwater streams. *Transactions of the American Fisheries Society* **141**: 1171–1179.
- Hunt SD, Guzy JC, Price SJ, Halstead BJ, Eskew EA, Dorcas ME. 2013. Responses of riparian reptile communities to damming and urbanization. *Biological Conservation* **157**: 277–284.
- Hurlbert SH. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**: 187–211.
- Jackson CR, Pringle CM. 2010. Ecological benefits of reduced hydrologic connectivity in intensively developed landscapes. *Bioscience* **60**: 37–46.
- Jackson CR, Martin JK, Leigh DS, West LT. 2005. A southeastern piedmont watershed sediment budget: evidence for a multi-millennial agricultural legacy. *Journal of Soil and Water Conservation* **60**: 298–310.
- Julian JP, Seegert SZ, Powers SM, Stanley EH, Doyle MW. 2011. Light as a first-order control on ecosystem structure in a temperate stream. *Ecohydrology* **4**: 422–432.
- Juterbock JE. 1990. Variation in larval growth and metamorphosis in the salamander *Desmognathus fuscus*. *Herpetologica* **46**: 291–303.

- Kéry M. 2008. Estimating abundance from bird counts: binomial mixture models uncover complex covariate relationships. *The Auk* **125**: 336–345.
- Kéry M, Schaub M. 2012. *Bayesian Population Analysis Using WinBUGS*, Academic Press: New York.
- Kibler KM, Tullos DD. 2013. Cumulative biophysical impact of small and large hydropower development in Nu River, China. *Water Resources Research* **49**: 3104–3118.
- Knoll MA, Potter DB, Van de Ven C. 2015. Geology, hydrology, and water use history atop the Cumberland Plateau in the Sewanee and Tracy City, Tennessee area. *The Geological Society of America Field Guide* **39**: 1–22.
- Kupferberg SJ, Lind AJ, Thill V, Yarnell SM. 2011. Water velocity tolerance in tadpoles of the foothill yellow-legged frog (*Rana boylei*): swimming performance, growth, and survival. *Copeia* **2011**: 141–152.
- Lemly AD, Finger SE, Nelson MK. 1993. Ecological implications of subsurface irrigation drainage. *Journal of Arid Environments* **28**: 85–94.
- Lessard JL, Hayes DB. 2003. Effects of elevated temperature on fish and macroinvertebrate communities below small dams. *River Research and Applications* **19**: 721–732.
- Ligon FK, Dietrich WE, Trush WJ. 1995. Downstream ecological effects of dams. *Bioscience* **45**: 183–192.
- Lind AJ, Welsh HH, Wilson RA. 1996. The effects of a dam on breeding habitat and egg survival of the foothill yellow-legged frog (*Rana boylei*) in northwestern California. *Herpetological Review* **27**: 62–7.
- Lowe WH. 2003. Linking dispersal to local population dynamics: a case study using a headwater salamander system. *Ecology* **84**: 2145–2154.
- Lytle DA, Poff NL. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution* **19**: 94–100.
- Macneale KH, Peckarsky BL, Likens GE. 2005. Stable isotopes identify dispersal patterns of stonefly populations living along stream corridors. *Freshwater Biology* **50**: 1117–1130.
- Martinez A, Larranga A, Basaguren A, Perez J, Mendoza-Lera C, Pozo J. 2013. Stream regulation by small dams affects benthic macroinvertebrate communities: from structural changes to functional implications. *Hydrobiologia* **711**: 31–42.
- Mazerolle MJ, Bailey LL, Kendall WL, Royle JA, Converse SJ, Nichols JD. 2007. Making great leaps forward: accounting for detectability in herpetological field studies. *Journal of Herpetology* **41**: 672–689.
- Means DB, Travis J. 2007. Declines in ravine-inhabiting Dusky salamanders of the southeastern US Coastal Plain. *Southeastern Naturalist* **6**: 83–96.
- Milanovich JR. 2010. Modeling the current and future roles of stream salamanders in headwater streams. PhD thesis, University of Georgia, GA.
- Miller BT, Niemiller ML, Reynolds RG. 2008. Observations on egg-laying behavior and interactions among attending female red salamanders (*Pseudotriton ruber*) with comments on the use of caves by this species. *Herpetological Conservation and Biology* **3**: 203–210.
- Nilsson C, Reidy CA, Dynesius M, Revenga C. 2005. Fragmentation and flow regulation of the world's large river systems. *Science* **308**: 405–408.
- Niemiller ML, Zigler KS, Fenolio DB. 2013. *Cave Life of TAG: A Guide to the Commonly Encountered Species in Tennessee, Alabama, and Georgia*. Biological Section of the National Speleological Society.
- Peterman WE, Crawford JA, Semlitsch RD. 2008. Productivity and significance of headwater streams: population structure and biomass of the black-bellied salamander (*Desmognathus quadramaculatus*). *Freshwater Biology* **53**: 347–357.
- Petranka JW. 1998. *Salamanders of the United States and Canada*, Smithsonian Institution Press: Washington DC.
- Poff NL, Hart DD. 2002. How dams vary and why it matters for the emerging science of dam removal. *Bioscience* **52**: 660–668.
- Poff NL, Allan JD, Bain MB, Karr JR, Prestegard KL, Richter BD, Sparks RE, Stromberg JC. 1997. The natural flow regime. *Bioscience* **47**: 769–784.
- Porter KR, Hakanson DE. 1976. Toxicity of mine drainage to embryonic mortality and larval boreal toads. *Copeia* **1976**: 237–331.
- Pough FH. 1980. The advantages of ectothermy for tetrapods. *American Naturalist* **115**: 92–112.
- Price SJ, Browne RA, Dorcas ME. 2012. Evaluating the effects of urbanization on salamander abundances using a before-after control-impact design. *Freshwater Biology* **57**: 193–203.
- R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Richter BD, Braun DP, Mendelson MA, Master LL. 1997. Threats to imperilled freshwater fauna. *Conservation Biology* **11**: 1081–1093.
- Romano A, Forcina G, Barbanera F. 2008. Breeding site selection by olfactory cues in the threatened northern spectacled salamander *Salamandrina perspicillata* (Savi, 1821). *Aquatic Conservation: Marine and Freshwater Ecosystems* **18**: 799–805.
- Royle JA. 2004. N-mixture models for estimating population size from spatially replicated counts. *Biometrics* **60**: 108–115.
- Royle JA, Dorazio RM. 2008. *Hierarchical Modeling and Inference in Ecology: The Analysis of Data from Populations, Metapopulations and Communities*, Academic Press: New York.
- Royle JA, Nichols JD. 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology* **84**: 777–790.
- Sanuy D, Oromi N, Galofre A. 2008. Effects of temperatures on embryonic and larval development and growth in the natterjack toad (*Bufo calamita*) in a semi-arid zone. *Animal Biodiversity and Conservation* **31**: 41–46.
- Schorr MS, Dyson MC, Nelson CH, Van Horn GS, Collins DE, Richards SM. 2013. Effects of stream acidification on lotic salamander assemblages in a coal-mined watershed in the Cumberland Plateau. *Journal of Freshwater Ecology* **28**: 339–353.
- Semlitsch RD. 1983. Growth and metamorphosis of larval red salamanders (*Pseudotriton ruber*) on the Coastal Plain of South Carolina. *Herpetologica* **39**: 48–52.
- Sethi SA, Selle AR, Doyle MW, Stanley EH, Kitchel HE. 2004. Response of unionid mussels to dam removal in Koshkonong Creek, Wisconsin (USA). *Hydrobiologia* **525**: 157–165.
- Singer EE, Gangloff MM. 2011. Effects of a small dam on freshwater mussel growth in an Alabama (USA) stream. *Freshwater Biology* **56**: 1904–1915.
- Spence JA, Hynes HBN. 1971. Differences in benthos upstream and downstream of an impoundment. *Journal of Fisheries Research Board of Canada* **28**: 35–43.

- Spiegelhalter DJ, Thomas A, Best NG, Lunn D. 2003. *WinBUGS Version 1.4 Users Manual*, MRC Biostatistics Unit: Cambridge.
- Stookey L. 1970. Ferrozine - a new spectrophotometric reagent for iron. *Analytical Chemistry* **42**: 779–781.
- Thorp JH, DeLong MD. 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. *Oikos* **96**: 543–550.
- Watters GT. 1996. Small dams as barriers to freshwater mussels (Bivalvia, Unionoidea) and their hosts. *Biological Conservation* **75**: 79–85.
- Zhang ZY, Wan CY, Zheng ZW, Hu L, Feng K, Chang JB, Xie P. 2013. Plant community characteristics and their

responses to environmental factors in the water level fluctuation zone of the three gorges reservoir in China. *Environmental Science and Pollution Research* **20**: 7080–7091.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web site.