

Application of a Multistate Model to Estimate Culvert Effects on Movement of Small Fishes

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Abstract.—While it is widely acknowledged that culverted road–stream crossings may impede fish passage, effects of culverts on movement of nongame and small-bodied fishes have not been extensively studied and studies generally have not accounted for spatial variation in capture probabilities. We estimated probabilities for upstream and downstream movement of small (30–120 mm standard length) benthic and water column fishes across stream reaches with and without culverts at four road–stream crossings over a 4–6-week period. Movement and reach-specific capture probabilities were estimated using multistate capture–recapture models. Although none of the culverts were complete barriers to passage, only a bottomless-box culvert appeared to permit unrestricted upstream and downstream movements by benthic fishes based on model estimates of movement probabilities. At two box culverts that were perched above the water surface at base flow, observed movements were limited to water column fishes and to intervals when runoff from storm events raised water levels above the perched level. Only a single fish was observed to move through a partially embedded pipe culvert. Estimates for probabilities of movement over distances equal to at least the length of one culvert were low (e.g., generally ≤ 0.03 , estimated for 1–2-week intervals) and had wide 95% confidence intervals as a consequence of few observed movements to nonadjacent reaches. Estimates of capture probabilities varied among reaches by a factor of 2 to over 10, illustrating the importance of accounting for spatially variable capture rates when estimating movement probabilities with capture–recapture data. Longer-term studies are needed to evaluate temporal variability in stream fish passage at culverts (e.g., in relation to streamflow variability) and to thereby better quantify the degree of population fragmentation caused by road–stream crossings with culverts.

Roadways have a significant presence on landscapes across the globe, with more than 6.4 million km of roads occurring in the United States alone (NRC 2005). Roads can have large effects on stream biota by altering watershed hydrology and sediment transport (Forman and Alexander 1998), stream channel geomorphology and habitat (Wang et al. 2001; Forman et al. 2003; Wheeler et al. 2005), water quality (Trombulak and Frissell 2000; NRC 2005; Wheeler et al. 2005), and organism migration and dispersal. Although effects of runoff generated by roads conceivably could be managed by practices applied on the landscape (e.g., stormwater detention and infiltration technologies), effects of roads on movements by aquatic fauna typically must be managed at stream crossings. Mounting evidence shows that structures at road–

stream crossings, especially pipe and box culverts, can limit passage or dispersal of freshwater mussels (Voelz et al. 1998), aquatic insects (Blakely et al. 2006), shrimps (Resh 2005), crayfishes (Light 2003; Kerby et al. 2005), and fishes (Belford and Gould 1989; Warren and Pardew 1998; Schaefer et al. 2003). Given the large potential for biological consequences (e.g., Fausch and Young 1995; Schlosser and Angermeier 1995; Wofford et al. 2005), accurately understanding the effects of culverts on fish passage is necessary for making informed regulatory and planning decisions regarding new and replacement structures at road crossings on streams.

Several field studies have evaluated the effects of road–stream crossings on the movement of small stream fishes. Warren and Pardew (1998) reported that bidirectional fish movement through crossings was an order of magnitude lower through pipe culverts than through slab, open-box, and ford crossings or natural reaches, while open-box and ford crossings showed

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little difference from natural reaches in terms of overall fish movement. Using live-resighting data from snorkel and scuba surveys, Schaefer et al. (2003) found that upstream movement of the federally threatened leopard darter *Percina pantherina* appeared to be inhibited by a low-water pipe culvert crossing in a southeastern Oklahoma river. More recently, Benton et al. (2008) recorded significantly reduced movement by small fishes through box and pipe culverts compared with reaches with clear-span bridges and reaches with no obstructions in six streams belonging to the Etowah River system in northwest Georgia.

While these studies have demonstrated effects of road–stream crossings on the movement of small fishes, none have accounted for varying capture probability in their estimates of fish movement. Estimates of movement probability between areas will be biased if spatial variability in capture probability is not taken into account. For example, consider an estimate of movement rates from one stream reach (reach A) to a second reach (reach B) based on the proportion of recaptured individuals (originally marked and released in reach A) observed in reaches A and B. If a fish are recaptured in reach A and b fish are recaptured in reach B, then a commonly used estimate of proportional movement from reach A to reach B is $b/(a + b)$. However, for a fish to be recaptured in reach A or B, it must (1) survive and remain in the study area with probability S , (2) either move to reach B (with probability Ψ) or remain in reach A (with probability $1 - \Psi$), and (3) be recaptured (with probability p_a in reach A or probability p_b in reach B). Proportional movement can be thus expressed as:

$$\begin{aligned} b/(a + b) &= S\psi p_b / [S(1 - \psi)p_a + S\psi p_b] \\ &= \psi p_b / [(1 - \psi)p_a + \psi p_b]. \end{aligned}$$

The observed proportional movement is an unbiased estimate of movement probability Ψ if and only if $p_a = p_b$. However, capture probabilities may be expected to vary spatially in streams in relation to differences in habitat structure (Peterson et al. 2004), which is an effect that could be pronounced in the vicinity of road crossings, where runoff and crossing structures alter stream geomorphology.

Estimating capture probabilities for stream fishes can present logistical challenges requiring, for example, population censuses (often using destructive sampling that may not be possible or desirable) or use of closed population and mark–recapture techniques. Where resource constraints or other factors (e.g., land owner concerns, public interference) limit the ability to leave block nets in place for sufficient periods for mark–recapture studies (e.g., 24–48 h; Peterson et al. 2004), a

multistate modeling approach (e.g., Williams et al. 2002; Schwarz 2005) may be applied to capture–recapture data, allowing for simultaneous estimation of reach-specific capture probability and probability of fish movement between reaches.

Our objective was to estimate the effects of culverts on short-term movements by stream fishes, identified as either primarily benthic or water column foragers, using open population capture–recapture data in multistate models that incorporate capture probability estimates. In particular, we asked whether a culvert positioned above the streambed (perched culvert) presented a greater barrier to fish movement than did culverts that were embedded below the streambed or bottomless, as has been suggested in previous studies. We hypothesized that benthic species would show less frequent movement through perched culverts than water column species, which would be important information for managing road crossings to conserve imperiled fishes.

Methods

Study site.—Study sites were located within the Etowah River system, Georgia. The Etowah River catchment (4,823 km²) lies on the northern edge of the Atlanta metropolitan area and has been the focus of habitat conservation planning for nine imperiled fish species (see www.etowahhcp.org). The Etowah River basin has relatively high fish species diversity and endemism, harboring 76 extant native species, including four endemic fishes and multiple imperiled taxa (Burkhead et al. 1997); many of these taxa are small-bodied fishes with limited ranges that could be detrimentally affected by blocked fish passage at road–stream crossings. In particular, the Cherokee darter *Etheostoma scotti* is federally protected as a threatened species, primarily occurs in tributary streams, and is present only in the Etowah River basin (Bauer et al. 1995).

We selected four study sites where streams were crossed by roads using culverts and met additional criteria: (1) stream size sufficient to support relatively high fish abundances, (2) comparable stream habitat extending upstream and downstream from the crossing with no nearby tributaries or additional potential barriers to fish passage, and (3) no impediments to setting block nets during repeat sampling visits. Study sites were located on Canton and Bluff creeks in Cherokee County, Champion Creek in Pickens County, and Nimblewill Creek in Lumpkin County. The sites were all coolwater streams (temperature during the study, <22.2°C) with gravel-dominated streambeds, watershed sizes ranging from 4.09 to 28.06 km², and mean stream widths ranging from 2.7 to 5.93 m. The

TABLE 1.—Culvert characteristics for study sites in the Etowah River system, Georgia. Length measurements include the length of the concrete apron downstream from the culvert, where applicable. Height of the culvert outlet above the water surface is for estimated base flow conditions (i.e., stable low-water condition in late summer during a normal water year) at the beginning of the study, as measured at lowest and highest points across the barrels. Observed stage changes are the range of values for sampling intervals ($n = 3$ or 4) at each site and include the maximum stage reached between sampling intervals.

Creek	Description	Barrel width \times height or diameter (m)	Length (m)	Culvert placement relative to streambed
Canton	Three-barrel pipe culvert, corrugated metal	3.18	18.6	Pipes embedded to 1.2 m
Bluff	Three-barrel box culvert, concrete with headwalls	3.25 \times 3.75	19.6	Bottomless middle barrel
Champion	Four-barrel box culvert, concrete with headwalls and downstream apron	3 \times 1.85	18.2	Boxes above streambed
Nimblewill	Four-barrel box culvert, concrete with headwalls and downstream apron	3.5 \times 3	18.6	Boxes above streambed

culverts at Canton and Bluff creeks were embedded below the streambed or had a bottomless section, respectively, in contrast to the culverts at Champion and Nimblewill creeks, which were perched above the streambed and water surface (Table 1).

Open population mark-recapture study.—We conducted open population mark-recapture studies at each of the four sites during August and September 2006 to estimate fish movement rates between culvert-free reaches and through culverts and to compare non-perched culvert effects on fish movement with the effects of perched culverts. Upstream and downstream fish movement was assessed over 4 weeks at Canton, Bluff, and Champion creeks and over 6 weeks at Nimblewill Creek. Sampling intervals were weekly at Canton, Bluff, and Champion creeks, except that Canton Creek was sampled five times, with the first mark and mark-recapture occasion at Canton Creek conducted over 24 h as an initial trial to ensure that we could capture and recapture an adequate number of fishes for analysis. Because of rain events, actual times between sampling occasions at Nimblewill Creek were 14, 11, and 9 d.

To increase the opportunities for observing movements comparable in distance to movements through the culverts, we divided each site into 10 reaches, with five reaches upstream and five downstream from the culvert. Moving upstream and downstream from the culvert, we designated three 25-m (± 3 m) reaches that were separated by two “false-culvert” reaches (Figure 1). The false-culvert reaches were approximately equal to the length of the culvert at each site (range, 17.6–21 m). Three weeks before the first sampling occasion, we measured and flagged the individual reaches at each site; length and position of block nets for each reach remained constant throughout the study.

Fish sampling started in the most downstream reach and proceeded upstream on each visit. Before sampling fish, all five downstream reaches and the culvert inlet

and outlet were blocked off using nets (3.2-mm mesh, 2.0–2.4 m deep \times 6–20 m long). Once we completed sampling in the downstream reaches, all block nets were removed downstream from the culvert and set in place at the ends of the upstream reaches before sampling resumed. When installing block nets, we walked along the stream banks so as to cause minimal disturbance within the reach before sampling. In each reach, we sampled fish in a single pass using a Smith-Root Model 12-B POW backpack electrofisher and a 2.4- \times 2.0-m seine (3.2-mm mesh).

All captured fish were held in buckets containing aerated, frequently refreshed stream water until they could be processed. In batches of 20–50 individuals, fish were transferred to a basket within a cooler containing stream water with a 30-mg/L dilution of AQUI-S (AQUI-S New Zealand, Ltd.; used under Investigational New Animal Drug Permit 10–541), which was used to anesthetize the fish. The cooler was modified by the addition of a copper coil through which we pumped stream water to regulate water temperature within the cooler. While briefly anesthetized (typically for <12 min), individuals of at least 30 mm standard length (SL) and no larger than 120 mm SL were measured, identified to species, and injected with a survey- and reach-specific mark using visible implant elastomer (VIE) tags (Northwest Marine Technology, Inc.). The VIE tags were administered to indicate sampling occasion (identified by color: yellow, orange, pink, or blue) and the reach where the fish was located when it was captured (identified by the body position of the mark). The VIE tags have no apparent significant effect on the growth or survival rates of fishes (Olsen and Vollestad 2001; Roberts and Angermeier 2004), although tag retention and the ability to correctly identify tags can vary depending upon the species, marking position on the body, and color combinations used (Walsh and Winkelmann 2004; Hartman and Janney 2006). We avoided using

TABLE 1.—Extended.

Creek	Height, culvert outlet above water surface (range, cm)	Height, lip on concrete apron (cm)	Observed stage changes (cm)
Canton	Not perched	No apron	0.00–7.5
Bluff Champion	Not perched 4–39	No apron 9	4.1–40 5.6–21.2
Nimblewill	23–60	11	16.0–51.3

combinations of colors that have been reported as difficult to separately identify (Curtis 2006).

We found that VIE tags were not easily identifiable at some body positions and with some colors on the largescale stoneroller *Camptostoma oligolepis* and the Alabama hog sucker *Hypentelium etowanum*, so fish of these species were given unique partial fin clips on the caudal, pectoral, and dorsal fins to indicate sampling occasion and position in the stream at time of marking. Because of the lack of unique fin clip combinations, we were only able to distinguish between those captured either upstream or downstream from the culvert on each sampling occasion. Caudal and pectoral fin clips have been used in previous mark–recapture studies without significant bias (Hohausova 2000; Dietrich and Cunjak 2006) and appear to have no significant effect on fish swimming performance (Webb 1973; Parsons et al. 2003).

We held fish in aerated stream water until they had completely recovered from the anesthesia. We added a standard dilution (0.1 mg/L) of kanamycin sulfate powder (National Fish Pharmaceuticals) to the recovery container to help prevent infection at the VIE injection site. Individuals were released in the middle of the reach from which they were captured on each sampling occasion. Once released, they were free to move among reaches and through the culvert until the reaches were blocked at the start of the next sampling occasion.

Modeling fish movement and culvert effects on transition probabilities.—We used the Arnason–Schwarz multistate model (Arnason 1973; Schwarz et al. 1993) as implemented in Program MARK (White and Burnham 1999) to estimate transition probabilities (i.e., ψ) for fish movement among stream reaches as well as through culverts. The Arnason–Schwarz multistate model, an extension of Cormack–Jolly–Seber single-state models used to model survival and capture probabilities, permits stochastic transitions

among states (Williams et al. 2002; Schwarz 2005), which in our case were movements by fishes among stream reaches. Multistate and single-state population models both use maximum likelihood methods to estimate survival and recapture probabilities. In multistate models, survival probabilities incorporate the probabilities of transition among states (i.e., reaches) with capture probabilities that are reach specific. Survival estimates combine losses from mortality, permanent emigration from the study area, and complete loss of the tag. Under the assumption that survival from time i to time $i + 1$ does not depend on the location at time $i + 1$, survival probabilities and transition probabilities can be separately estimated (Williams et al. 2002).

Conceivably, survival, transition, and capture probabilities could be estimated for each reach and sampling occasion, including all transition probabilities for all possible movements among reaches. However, sparse recapture data prevented estimation of all possible parameters (e.g., 660 and 880 parameters in our fully saturated, 10-state models with four or five capture dates). Therefore, we compared a series of reduced, time-independent (i.e., survival, capture, and transition probabilities held constant across all sampling dates) candidate models chosen a priori to represent a set of biologically reasonable assumptions about fish movement among reaches and through culverts. First, data were modeled as site specific, allowing estimation of movement separately for benthic and water column species, and as a function of fish SL. Secondly, data from all sites were combined to evaluate evidence of an effect of culvert characteristics on movement probabilities. Reach-dependent capture probabilities were included in all candidate models and upstream and downstream movement probabilities were separately estimated in all models.

For the site-specific models, parameters were estimated separately for benthic and water column

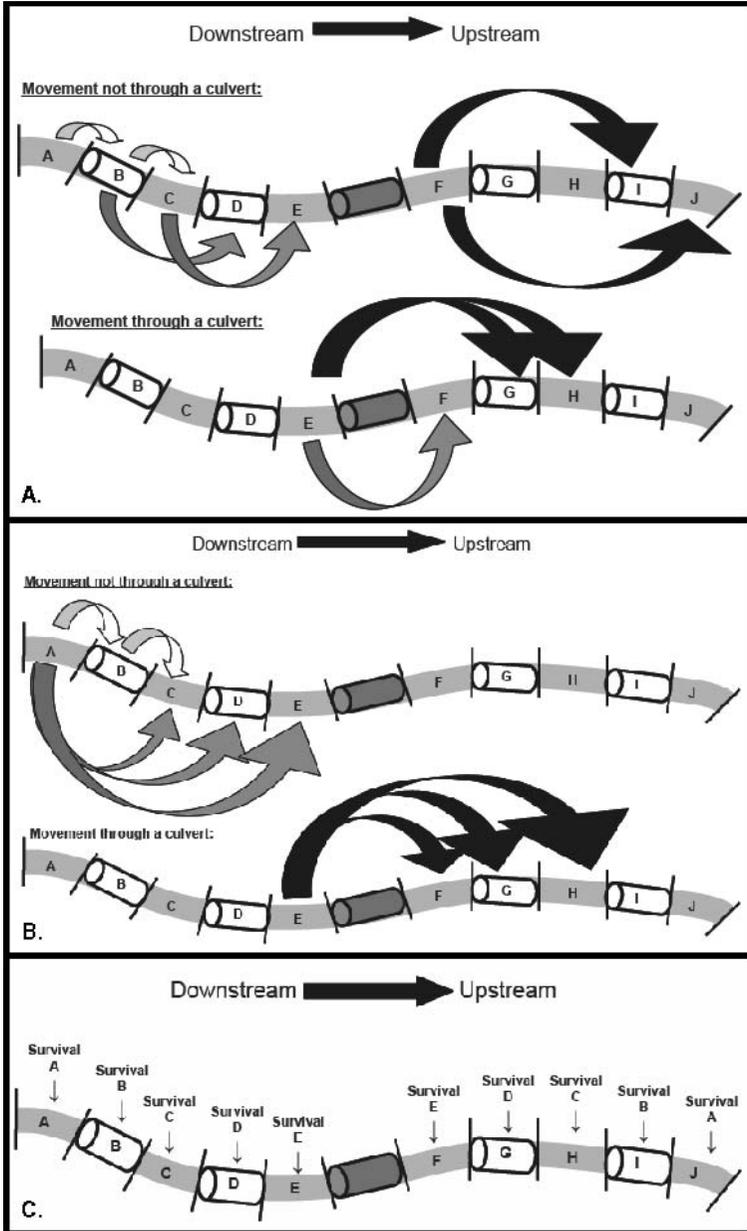


FIGURE 1.—Upstream transition and reach-paired survival probabilities estimated in the full movement (FM) and reduced movement (RM) models. The road–stream crossing is the shaded cylinder; reaches designated as “false culverts” are shown as lettered cylinders. Arrows illustrate examples of each movement type; corresponding downstream transition probabilities are not shown but were also estimated. (A) The FM transition probabilities for movements not through the culvert (upper diagram; between adjacent reaches: e.g., A to B or B to C; across an intervening reach: e.g., B to D or C to E; across multiple reaches: e.g., F to I or F to J) and movements through the culvert (lower diagram; short: e.g., E to F; long: e.g., E to G, H, I, or J) are illustrated. (B) The RM transition probabilities for movements not through the culvert (upper diagram; between adjacent reaches: e.g., A to B or B to C; across at least one intervening reach: e.g., A to C, A to D, or A to E) and movements through the culvert (lower diagram: e.g., E to F, G, H, I, or J) are illustrated. (C) Reach pairs for estimating survival (including emigration) are shown.

species (based on the foraging behavior most characteristic of the species). Candidate models differed in the number of movement–distance categories and in assumptions about survival. Our most general site-specific model, termed the full movement (FM) model (Figure 1A), combined transition probabilities for culvert-free movement into three distance groupings: movement to adjacent reaches, movement approximately equal to one culvert length, and movement greater than one culvert length. Transition probabilities for movement through the culvert were combined into two distance groupings: movement through the culvert between the immediately adjacent reaches, and movement through the culvert and additional reaches. The FM model represented the hypotheses that (1) adjacent moves were more likely than short moves, which were in turn more likely than long moves, and (2) culvert-free moves were more likely than moves through a culvert.

The competing reduced movement (RM) model (Figure 1B) combined transition probabilities for culvert-free movement into two distance groupings: movement to adjacent reaches and movement greater than or equal to one culvert length. A single distance grouping was used for movement through the culvert. The RM model represented the hypotheses that (1) adjacent moves were more likely than longer moves, but short and long moves had similar probabilities of occurrence, and (2) culvert-free moves were more likely than moves through a culvert.

We hypothesized that fish closer to the edges of the study site would be more likely to emigrate from the site; therefore, survival estimates in the FM and RM models were paired by upstream and downstream reaches that were equidistant from the ends of our study sites (Figure 1C). Alternatively, full movement with constant survival (FMCS) and reduced movement with constant survival (RMCS) models treated survival and emigration as constant across all reaches.

Movements of largescale stonerollers and Alabama hog suckers were modeled according to the same process described previously, except there were only two candidate models, a FM model and a FMCS model. Largescale stoneroller and Alabama hog sucker models consisted of two states (i.e., upstream and downstream from the culvert) as opposed to 10 states, and survival probabilities for the upstream and downstream reaches were estimated separately in the FM model and as one parameter in the FMCS model.

To evaluate model goodness of fit, we used the program MSSURVIV (Hines 1994) to estimate Pearson chi-square values based on the observed recaptures and frequencies expected from the multinomial probabilities generated by the FM model. The FM model

was our most general model but was not fully time-dependent as is generally required for goodness-of-fit testing in multistate models (Pradel et al. 2003). The chi-square test and output provided by MSSURVIV allowed us to examine capture data for separate cohorts (i.e., groups of individuals released in a given reach on a given date) for systematic deviation from model assumptions.

We assessed relative model support by pairwise comparisons of model parsimony using Akaike's information criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002; see Cooch and White 2006 for implementation in Program MARK). The best-supported model has the lowest AIC_c value; we report the model weight or relative support for each model pair (Burnham and Anderson 2002). The best-supported (highest weighted) FM or RM model for each site was compared with the corresponding constant survival model (FMCS or RMCS). The best supported of those general models was then compared with a similar model that included individual fish SL as a covariate on probability of movement.

The combined-site models were structured in the same way as the site-specific models except that fish characteristics (benthic or water column, body length) were ignored. Instead, data were grouped by site to evaluate an effect of culvert elevation relative to the water level on fish movement. We used the same pairwise model selection process as for the site-specific models, with the best-supported general model in the final step compared with a similar model that included culvert characteristics as covariates on movement probability. The minimum height that the culvert was perched above the water surface (culvert height in Table 1) was used as a covariate on probability of movement upstream through a culvert. The height of the apron lip (apron height in Table 1) above the culvert bottom was used as a covariate on probability of movement downstream through a culvert. The most general constrained model contained both covariates, while the reduced competing model contained only the minimum perched height covariate.

Multistate models with more than two states are prone to converging to a local, rather than global, maximum, which can lead to faulty parameter estimates (Lebreton and Pradel 2002; Schwarz 2005). Because there is no known simple diagnostic procedure for potential global optimization problems a priori, we used the alternative global optimization process, termed simulated annealing (Goffe et al. 1994), as implemented in Program MARK. The simulated annealing algorithm periodically makes a random jump to a new parameter value, facilitating convergence on a global maximum.

TABLE 2.—Summary of fish movements by site in the Etowah River system, Georgia. The number of fish that moved and the percentage of total moves are shown for each of the five movement categories: (1) to an adjacent reach, (2) across an intervening reach equal to one culvert length (=1 CL), and (3) across multiple reaches (>1 CL), but not through the culvert; (4) through the culvert to the adjacent upstream or downstream reach (through culvert, adj.), and (5) through the culvert and additional reaches (through culvert, >1 CL). Upstream (US), Downstream (DS), or both upstream and downstream movements (US–DS) are indicated. Benthic and water column species are listed for through-culvert moves.

Creek (culvert type)	Distance movement category	Number of fish	Percent of total moves	Species that moved through the culvert
Canton (embedded pipe)	Adjacent	77	87	Benthic: Mobile logperch <i>Percina kathae</i>
	=1 CL	8	9	
	>1 CL	3	3	
	Through culvert, adj.	0		
	Through culvert, >1 CL	1 (US)	1	
Bluff (bottomless box)	Adjacent	52	63	Water column: Coosa shiner <i>Notropis xaenocephalus</i> , yellowfin shiner <i>Notropis lutipinnis</i> , Alabama shiner <i>Cyprinella callistia</i> , bluehead chub <i>Nocomis leptocephalus</i> , creek chub <i>Semotilus atromaculatus</i> Benthic: Cherokee darter, Mobile logperch, largescale stoneroller, Alabama hog sucker ^a
	=1 CL	12	15	
	>1 CL	1	1	
	Through culvert, adj.	5 (US–DS)	6	
	Through culvert, >1 CL	12 (US–DS)	15	
Champion (perched box)	Adjacent	61	70	Water column: Coosa shiner, Alabama shiner
	=1 CL	12	14	
	>1 CL	7	8	
	Through culvert, adj.	3 (US)	3	
	Through culvert, >1 CL	4 (US)	5	
Nimblewill (perched box)	Adjacent	79	71	Water column: yellowfin shiner
	=1 CL	21	19	
	>1 CL	7	6	
	Through culvert, adj.	0		
	Through culvert, >1 CL	5 (DS)	4	

^a Species evaluated in two-state (upstream–downstream) models; movements (total = 4) are not included in totals.

We used transition probabilities from the best-supported model at each site to calculate the effect size of the culvert on movement of benthic and water column fishes at each site. Effect size was calculated by taking the arithmetic difference between the parameter estimates for culvert-free movement and movement through a culvert. Corresponding estimated 95% confidence intervals (CIs) were also calculated for each effect size value as:

$$SE = [\text{var}(\psi_{\text{culvert-free move}}) + \text{var}(\psi_{\text{move through culvert}}) - 2 \text{cov}(\psi_{\text{culvert-free move}}, \psi_{\text{move through culvert}})]^{1/2}$$

and

$$95\% \text{ CI} = (\text{effect size} \pm 2SE),$$

where ψ = transition probability, var = variance, and cov = covariance (Cooch and White 2006). We only calculated effect size where transition probabilities could be estimated for both culvert-free movement and movement through a culvert in the same direction (upstream or downstream) and over the same distance grouping.

Maximum stage height and stage at time of sampling.—We installed maximum stage recorders constructed of 7.6-cm-diameter polyvinyl chloride pipe packed with finely ground cork and coffee grinds (Gordon et al. 2004) at each site. On each visit, we recorded the maximum stage that occurred between sampling occasions and the stage height at the time of the survey. We calculated the maximum change in stage height and the effective minimum perched height (the difference between the minimum height of the culvert above the water surface and the maximum change in stage height) for the time interval between each sampling occasion. Because we were not able to estimate fully time-dependent parameters, we could not explicitly model the effects of stage and effective minimum perched height on recapture or transition probabilities, but we could tabulate observed movements in relation to whether the culvert was submerged during the preceding time interval.

Results

A total of 5,805 individual fish representing 30 species were marked at the four sites (8–21 species/

TABLE 3.—Estimates for survival (S) and reach-specific capture probabilities (p) for benthic and water column fishes from the best-supported model for each site in the Etowah River system, Georgia. Constant S across reaches was best supported, except at Nimblewill Creek, for which a range of S estimates is given.

Parameter	Canton Creek		Bluff Creek		Champion Creek		Nimblewill Creek	
	Benthic	Water column	Benthic	Water column	Benthic	Water column	Benthic	Water column
S	0.82	0.82	0.84	0.81	0.81	0.94	0.64–0.93	0.55–0.84
p	0.11–0.40	0.08–0.33	0.05–0.37	0.05–0.36	0.18–0.39	0.03–0.47	0.14–0.35	0.11–0.47

site). Recapture rates (number of recaptures from a single sampling event divided by the total number of individuals marked before the sampling event) ranged between 0.18 and 0.36 across all sites, with a mean of 0.24 across sites and sampling events. Recaptures mostly occurred in the same reaches where individuals were initially marked; only 6% to 11% of recaptured individuals moved among reaches, and more fish were observed to move upstream than downstream at all four sites (210 total upstream moves and 160 total downstream moves). The majority (63% to 87%) of observed movements were to adjacent reaches (Table 2). At each site, we observed at least one fish that moved through the culvert; overall, such fish represented four benthic species and five water column species (Table 2).

The chi-square goodness-of-fit tests indicated a significant lack of fit for the general FM model to recapture data from three of our four sites (we did not test the Canton Creek data, which had an additional sampling date). However, the tests were based on relatively sparse recaptures, and examination of data for individual cohorts did not reveal strong evidence for systematic departures of observed frequencies from expected frequencies. Additionally, none of the ranking orders for models in our candidate model sets were strongly sensitive to incremental adjustments in the variance inflation factor (Anderson et al. 1998), indicating that our conclusions with respect to

alternative hypotheses would not be affected by underestimating variances.

The best supported site-specific models were the FM models (AIC_c model weight range, 0.854–0.992), except for Canton Creek, where the RMCS model was best supported (AIC_c weight = 0.581). Adding SL as a covariate reduced model support (AIC_c weight range, 0.004–0.097 at three sites; model for Bluff Creek failed to converge). Models with constant survival across reaches were best supported at all sites except Nimblewill Creek. Estimated survival was generally high (>0.8) and similar for benthic and water column groups (Table 3). Capture probability (p) estimates had similar ranges for benthic and water column fishes but varied among reaches by a factor of 2 to over 10 (Table 3).

Transition probabilities were generally small ($0.005 < \psi < 0.16$) with wide 95% CIs. Transition probabilities were highest for movement between adjacent culvert-free reaches, except at Bluff Creek, where the highest probability of movement for benthic fishes was downstream through the culvert (Tables 4, 5). No benthic fish movements were observed through either of the perched box culverts even though estimated upstream movement probabilities through culvert-free reaches were 5–6% at these sites (Table 5). In contrast, benthic fishes moved upstream and downstream through the bottomless culvert (Bluff Creek) more frequently than across culvert-free reaches (Table 5). In most cases, we could not calculate a

TABLE 4.—Transition probabilities (ψ) from reduced movement with constant survival models for benthic and water column fishes at Canton Creek, Georgia (embedded pipe culvert); 95% confidence intervals are shown in parentheses for Ψ estimates. Culvert effect was only estimated for upstream movements by benthic fishes because no other through-culvert movements were observed.

Direction and distance of move	ψ_{benthic}	$\psi_{\text{water column}}$
Upstream to adjacent reach	0.063 (0.015, 0.23)	0.160 (0.12, 0.21)
Upstream across at least one intervening reach	0.007 (0.000, 0.36)	0.012 (0.004, 0.03)
Upstream through the culvert	0.005 (0.000, 0.04)	None observed
Culvert effect, upstream movement	0.002 (–0.032, 0.04)	
Downstream to adjacent reach	0.068 (0.025, 0.17)	0.091 (0.063, 0.13)
Downstream across at least one reach	None observed	0.006 (0.002, 0.02)
Downstream through the culvert	None observed	None observed
Culvert effect, downstream movement		

TABLE 5.—Transition probabilities (ψ) for benthic and water column fishes at Georgia study sites where the full movement model was best supported; 95% confidence intervals are shown in parentheses for ψ estimates. Culvert effects were only estimated for sites and groups where across-reach and through-culvert movements were observed for equivalent distance categories ($=1$ or >1 culvert length [CL]). Culvert type is given next to each site name.

Direction and distance of move	Bluff Creek (bottomless box)		Champion Creek (perched box)	
	Benthic	Water column	Benthic	Water column
Upstream to adjacent reach	0.056 (0.017, 0.17)	0.130 (0.087, 0.19)	0.083 (0.046, 0.15)	0.092 (0.062, 0.13)
Upstream across one reach ($=1$ CL)	0.022 (0.003, 0.17)	0.026 (0.010, 0.07)	0.056 (0.023, 0.13)	0.007 (0.002, 0.03)
Upstream through culvert ($=1$ CL)	None observed	0.110 (0.037, 0.27)	None observed	0.051 (0.017, 0.14)
Culvert effect, short upstream movement		No effect		No effect
Upstream across >1 reach (>1 CL)	None observed	0.010 (0.003, 0.04)	0.010 (0.00, 0.18)	0.008 (0.003, 0.02)
Upstream through culvert, >1 CL	0.011 (0.003, 0.04)	0.007 (0.002, 0.02)	None observed	0.002 (0.00, 0.01)
Culvert effect, long upstream movement		0.003 (-0.012 , 0.02)		0.006 (-0.003 , 0.02)
Downstream to adjacent reach	0.070 (0.026, 0.18)	0.140 (0.091, 0.21)	0.026 (0.010, 0.06)	0.140 (0.099, 0.19)
Downstream across one reach ($=1$ CL)	0.026 (0.004, 0.17)	0.026 (0.008, 0.08)	0.006 (0.00, 0.050)	0.015 (0.005, 0.04)
Downstream through culvert ($=1$ CL)	0.095 (0.012, 0.47)	None observed	None observed	None observed
Culvert effect, short downstream movement		No effect		
Downstream across >1 reach (>1 CL)	None observed	None observed	None observed	0.005 (0.00, 0.04)
Downstream through culvert, >1 CL	None observed	0.011 (0.0052, 0.02)	None observed	None observed
Culvert effect, long downstream movement				

culvert effect due to lack of observed movements, particularly through culverts. When there was a culvert effect, its size was either small or negative with a 95% CI that included no effect (0; Tables 4, 5).

Stage height increased during the time intervals between each sampling occasion at all sites (except for the initial 24-h interval at Canton Creek; Table 1). All observed movements through the perched culverts (Champion and Nimblewill creeks) were by water column fishes and occurred after runoff events that raised the water level over the perched level (by 17 cm [Champion Creek] to 28 cm [Nimblewill Creek]). In contrast, movement through the bottomless culvert at Bluff Creek was observed between each sampling event.

For the combined-site models (in which sites were treated as groups), the FM model and the FM model constrained by minimum perched height had equivalent support (AIC_c weight = 0.370). Both FM models produced identical estimates of transition probabilities, which were intermediate to estimates from the site-specific models. Adding apron height as a covariate reduced model support (AIC_c weight = 0.132). The FM model with increasing survival toward the center of the site (AIC_c weight = 0.370) was almost three times better supported than the FMCS model (AIC_c weight = 0.128). The RM model had essentially no support (AIC_c weight = 0.000).

For the two species evaluated with two-state (upstream–downstream) models (largescale stoneroller and Alabama hog sucker), we only observed movement at the bottomless culvert site (Table 2). Only one

individual largescale stoneroller was observed to move through the culvert. Because the recapture rate was low (11 of 81 marked individuals at Bluff Creek), we were unable to estimate survival, capture, and transition probabilities reliably for largescale stonerollers. We had more opportunities to observe movements by Alabama hog suckers, with recaptures of 135 marked individuals at Bluff Creek and estimated upstream and downstream capture probabilities of 0.45 and 0.34, respectively. Only three Alabama hog suckers were recorded moving either upstream ($n = 1$) or downstream ($n = 2$) through the culvert. Transition probabilities through the culvert were 0.01 for upstream movement and 0.02 for downstream movement. Survival probability estimates were 0.75 upstream and 0.74 downstream for Alabama hog suckers.

Discussion

Fish Movement

In this study, we observed fish movement through a culvert at each of four study sites, but only the bottomless box culvert at Bluff Creek appeared to allow unrestricted movement for both benthic and water column fishes. Moves through the culvert comprised 24% of the total moves observed at Bluff Creek, compared with 1% to 8% at the other study sites. Bluff Creek was the only site where we observed upstream and downstream movements through the culvert by benthic and water column fishes between each sampling occasion.

Only water column fishes were observed to move through the two perched culverts following periods of

TABLE 5.—Extended.

Direction and distance of move	Nimblewill Creek (perched box)	
	Benthic	Water column
Upstream to adjacent reach	0.097 (0.058, 0.16)	0.081 (0.056, 0.11)
Upstream across one reach (=1 CL)	0.049 (0.021, 0.11)	0.015 (0.006, 0.04)
Upstream through culvert (=1 CL)	None observed	None observed
Culvert effect, short upstream movement		
Upstream across >1 reach (>1 CL)	None observed	0.009 (0.003, 0.03)
Upstream through culvert, >1 CL	None observed	None observed
Culvert effect, long upstream movement		
Downstream to adjacent reach	0.016 (0.0052, 0.05)	0.067 (0.047, 0.10)
Downstream across one reach (=1 CL)	None observed	0.019 (0.010, 0.04)
Downstream through culvert (=1 CL)	None observed	None observed
Culvert effect, short downstream movement		
Downstream across >1 reach (>1 CL)	None observed	0.007 (0.002, 0.02)
Downstream through culvert, >1 CL	None observed	0.008 (0.003, 0.02)
Culvert effect, long downstream movement		No effect

runoff when water levels exceeded the perched level. Only one individual, a Mobile logperch, was observed to have moved through the embedded pipe culvert. Our findings were similar to those of Warren and Pardew (1998), who reported that movement of fishes through pipe culverts on small streams was an order of magnitude less than movement through box culverts, fords, or natural reaches. Benton et al. (2008) also observed significantly reduced fish movement through box and pipe culverts.

Recaptured fishes were found in the reach of initial capture or in an adjacent reach 96% to 99% of the time at all four sites. This result is similar to the findings of other studies on movements of small stream fishes (e.g., Hill and Grossman 1987; Johnston 2000; Schaefer et al. 2003). Since 63% to 71% of marked individuals were never recaptured, we can make only limited assumptions about their movement. We did not sample to detect long-distance movement (Albanese et al. 2003); however, in some cases, models assuming lower survival near the boundaries of our study area were better supported than models assuming constant survival across all reaches, possibly due to higher emigration from the study reach near reach boundaries (see later discussion).

Application of Multistate Models

Using multistate models allowed simultaneous estimation of capture probability with survival and transition probabilities. Estimated capture probabilities varied substantially among reaches, potentially as a result of differences in habitat structure (Peterson et al.

2004), and failure to account for these effects would bias transition probability estimates. Even with group-specific (benthic versus water column fishes) and reach-specific capture probabilities included, the transition probability estimates had wide 95% CIs as a result of the low number of observed fish moves at our study sites. We also included covariates on transition probabilities (i.e., fish body size and perched height of the culvert); although the covariates did not improve model fit here, the ability to include them is a benefit of the multistate modeling approach.

Relative sparseness in the number of fish that were recaptured from any given reach and on any given date limited our ability to model time-varying effects on transition probabilities. Our observations, however, suggested that the ability of fish to pass through culverts probably varied with changes in stage height, a source of temporal variation. We designed the study to maximize the potential for observing individual movement among culvert-free reaches (i.e., by sampling 10 reaches at each site) for comparison with movement through the culvert. Lack of fit for our model with time-averaged parameter estimates was, thus, not unreasonable. Spatial variation among reaches in the probability that fish would remain over the next time interval and nonindependence among individuals (e.g., in schooling cyprinids) could also have contributed to lack of model fit. In general, we see the multistate modeling approach used as providing a promising framework for understanding the extent to which road-stream crossings actually fragment populations because fish movement can be modeled as a

function of constant (e.g., culvert characteristics) and time-varying (e.g., stage height, effective culvert height, storm flow velocities, geomorphic features, and fish behavior related to movement during spawning season) covariates hypothesized to influence fish passage.

Use of multistate models allowed us to account for a bias toward detecting short-distance movements (distance-weighted bias). A distance-weighted bias can occur in open-population mark-recapture studies when the study area is small relative to animal movement and animals leave the study area. Albanese et al. (2003) showed that increasing length of the recapture section to account for fish movement outside the study area can help reduce the effects of distance weighting on observed movement distance distributions. For this study, increasing survey reach lengths was not feasible; however, the incorporation of survival estimates that assumed lower survival near site boundaries accounted for the bias because survival estimates include site losses from permanent emigration. Thus, multistate models may provide an alternative to the increased sampling effort required to account for a distance-weighted bias in all types of movement studies.

Implications

Our study provides further insight into the effects of culverts on the movement of small-bodied stream fishes while demonstrating possibilities in the application of multistate models in fish movement studies. Our results indicate that multiple-barrel box culverts with bottomless main barrels can allow fish passage comparable with that of natural stream reaches. Movement of fishes through multiple-barrel embedded pipe and perched box culverts was restricted during this study, but the culverts were not complete barriers. This implies that there may be a range of flow levels that allow some passage through culverts, including those structures that are situated on top of the bed sediments or perched above stream water level. Because resources for construction and replacement of culverts are usually limited, it may be useful to evaluate trade-offs among the expense of construction options, position of the crossing within the stream drainage network, and species likely to be affected. Improved understanding of the extent to which culvert conditions impede fish movements will better inform that evaluation.

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