

A spatial capture–recapture model to estimate fish survival and location from linear continuous monitoring arrays

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Abstract: We developed a spatial capture–recapture model to evaluate survival and activity centres (i.e., mean locations) of tagged individuals detected along a linear array. Our spatially explicit version of the Cormack–Jolly–Seber model, analyzed using a Bayesian framework, correlates movement between periods and can incorporate environmental or other covariates. We demonstrate the model using 2010 data for anadromous American shad (*Alosa sapidissima*) tagged with passive integrated transponders (PIT) at a weir near the mouth of a North Carolina river and passively monitored with an upstream array of PIT antennas. The river channel constrained migrations, resulting in linear, one-dimensional encounter histories that included both weir captures and antenna detections. Individual activity centres in a given time period were a function of the individual's previous estimated location and the river conditions (i.e., gage height). Model results indicate high within-river spawning mortality (mean weekly survival = 0.80) and more extensive movements during elevated river conditions. This model is applicable for any linear array (e.g., rivers, shorelines, and corridors), opening new opportunities to study demographic parameters, movement or migration, and habitat use.

Résumé : Nous avons mis au point un modèle spatial de capture–recapture pour évaluer la survie et les centres d'activité (c.-à-d. emplacement moyen) d'individus marqués détectés le long d'un réseau linéaire. Notre version spatialement explicite du modèle de Cormack–Jolly–Seber, analysée selon un cadre bayésien, corrèle les déplacements d'une période à l'autre, et des covariables du milieu ou autres peuvent y être incorporées. Nous faisons une démonstration du modèle à l'aide de données de 2010 sur des aloses savoureuses (*Alosa sapidissima*) anadromes munies de radio-étiquettes passives intégrées (PIT) à une fascine près de l'embouchure d'une rivière de Caroline du Nord, ayant fait l'objet d'une surveillance passive à l'aide d'un réseau d'antennes PIT en amont. Les migrations étaient restreintes par le chenal de la rivière, les distributions des observations, dont des captures dans la fascine et des détections avec les antennes, étant par conséquent linéaires et unidimensionnelles. Les centres d'activité individuels dans une période de temps donnée étaient fonction de l'emplacement estimé précédent de l'individu concerné et des conditions de la rivière (c.-à-d. le niveau d'eau). Les résultats du modèle indiquent une forte mortalité en rivière (taux de survie hebdomadaire moyen = 0,80) et des mouvements plus importantes durant des conditions de niveau d'eau élevé dans la rivière. Ce modèle est applicable à tout réseau linéaire (p. ex. rivières, rives et corridors), offrant ainsi de nouvelles possibilités d'étude des paramètres démographiques, des déplacements ou de la migration et de l'utilisation de l'habitat. [Traduit par la Rédaction]

Introduction

Continued advances in tagging technology allow researchers to collect an expansive amount of data on tagged individuals (Lucas and Baras 2000; Heupel et al. 2006; Rogers and White 2007). Fisheries research examples include telemetry transmitters decreasing in physical dimensions but increasing in battery capacity and signal strength while passive integrated transponders (PIT) are a small, relatively inexpensive, and lifelong (i.e., lack batteries) option (Prentice et al. 1990; Lucas and Baras 2000; Heupel and Webber 2012). Yet, the greatest increase in data collection potential corresponds with the advent of continuous monitoring stations (e.g., acoustic telemetry receivers and PIT antennas) that passively detect tagged individuals (Castro-Santos et al. 1996; Lucas and Baras 2000; Heupel and Webber 2012), creating temporal and spatial individual encounter histories (Zydlewski et al. 2006; Hewitt et al. 2010).

Quantitative methods to analyze fisheries data obtained from continuous monitoring systems are also advancing, but at a

slower pace than tagging and computing technologies (Heupel et al. 2006). Descriptive statistics, plots, and maps are often used to summarize habitat use, distributions, migrations, and fish passage rates (Rogers and White 2007) but lack quantitative rigor. Habitat use and home ranges have been evaluated with geographic information systems and position averaging techniques (Simpfendorfer et al. 2002; Rogers and White 2007). Yet, demographic analyses are typically conducted separately from spatial analyses. Capture–recapture models, in particular the “Jolly–Seber” (JS) and “Cormack–Jolly–Seber” (CJS) models (Cormack 1964; Jolly 1965; Seber 1965), use individual encounter histories to estimate demographic parameters (e.g., survival) while accounting for imperfect detection rates (Pollock et al. 1990; Williams et al. 2002; Pine et al. 2003). Capture–recapture models have successfully been used in fisheries studies with continuous monitoring stations; however, useful information may be lost when data are consolidated into a single observed – not observed binary datum in either temporal (e.g., Hewitt et al. 2010) or spatial (e.g.,

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Skalski et al. 1998) intervals (Gardner et al. 2010). Spatial multi-state models are an extension of capture–recapture models that estimate apparent survival along with transition (migration) probabilities into different geographical states such as river reaches (Lebreton and Pradel 2002; Schwarz 2009). Few multistate fisheries models exist, especially those using continuous monitoring stations (Buchanan and Skalski 2010; Horton et al. 2011), as data requirements often limit them to a few states and time periods (Lebreton and Pradel 2002; Ovaskainen et al. 2008).

Continuous monitoring station studies may benefit from statistical models that use all collected data to estimate both spatial and demographic parameters in one analysis. A review of terrestrial literature shows a variety of two-dimensional spatial capture–recapture models for fixed continuous monitoring stations (e.g., camera traps and hair snares) arranged in a spatial grid (e.g., latitude and longitude) (Karanth et al. 2006; Gardner et al. 2009; Royle et al. 2009; Gardner et al. 2010). Recent models estimate survival, abundance and density, and also individual “activity centres” that represent the mean spatial location in a time period and are conceptually similar to home range centres (Gardner et al. 2009; Royle et al. 2009; Gardner et al. 2010). In spatial capture–recapture models, the individual encounter histories can be binary (observed – not observed) or counts (number of detections) for each individual, at each sampling location, in each time period so all spatial and temporal data can be analyzed. While aquatic studies with an analogous spatial grid of continuous monitoring stations (e.g., estuary, marine protected area, and lake) can use these models, modifications are necessary for studies where continuous monitoring stations are arranged in a one-dimensional linear array (e.g., rivers, shorelines, and migratory paths). Also, previously developed spatial capture–recapture models have not correlated individual movement among primary periods, although newer model developments have incorporated resource selection functions.

We developed a linear spatial capture–recapture model to evaluate both survival and location of migratory fishes. We used the basic framework of the JS open spatial capture–recapture model (Gardner et al. 2010) for terrestrial detector arrays, but made two significant changes. (i) We used a CJS formulation, conditional on first capture, and because the river constrained movement to a linear manner, the continuous monitoring stations were treated in one dimension (i.e., river kilometre, rkm) instead of two dimensions (e.g., latitude and longitude). (ii) We modeled the individual activity centres as a function of the previous estimated location of the tagged fish (i.e., correlated movement). This model is flexible, allowing for a suite of covariates to be included, and applicable to other aquatic and terrestrial studies using linear continuous monitoring stations.

We demonstrate the model with American shad (*Alosa sapidissima*) data collected from a linear array of PIT antennas in a North Carolina river with multiple dam removals. Populations of anadromous American shad, native to the Atlantic coast of North America, are currently at historic low levels and the focus of considerable restoration efforts (Limburg et al. 2003; Limburg and Waldman 2009). Population declines have been attributed to multiple factors including dams restricting access to habitat (Cooke and Leach 2003; St. Pierre 2003). One approach to restoration is increasing connectivity to upstream spawning habitat (Weaver et al. 2003; Burdick and Hightower 2006). However, spawning migrations are energetically expensive and may lead to substantial mortality because minimal feeding occurs in rivers (Chittenden 1976; Leggett and Carscadden 1978; Leonard and McCormick 1999). No previous studies have empirically estimated within-river survival rates. Therefore, a model characterizing mortality and migration would provide a better understanding of how dam removal can contribute to American shad restoration.

Materials and methods

Model development

We maintained standard open capture–recapture model assumptions including that tagging does not influence survival, recapture probability is similar among tagged individuals, and that tags are not lost or missed (Pollock et al. 1990; Williams et al. 2002). We followed the framework of the open spatial capture–recapture model in Gardner et al. (2010) but instead of a JS formulation to estimate density, recruitment, and survival, we used a CJS structured model to estimate survival and location; movement patterns can be inferred from model estimates. The main components of the linear spatial capture–recapture model are an observational model based on the data (e.g., detections), a state model based on whether an individual is alive and in the system or not, and latent activity centres.

In the observational model, encounter histories, $y(i, j, t)$, are the counts of observations for each individual ($i = 1, 2, \dots, n$), at each location ($j = 1, 2, \dots, J$), during each primary sample occasion ($t = 1, 2, \dots, T$). We assigned each sampling location (j) a linear (i.e., rkm) coordinate ($x(j) = (\text{rkm}_j)$). Each tagged individual could be detected at any functioning continuous monitoring station, any number of times, during a particular period.

The observational model is conditional on an individual’s “alive state” (z). For each individual i during each time period t , $z(i, t)$ describes whether an individual is alive and within the study area of the river ($z(i, t) = 1$) or not alive ($z(i, t) = 0$, individuals may also have left the study area). We determined the first period (f_i) to be the period of tagging or first detection (e.g., individuals tagged in a previous year). A tagged individual is known to be alive and in the river in its first period (f_i), so the initial alive state is

$$z(i, f_i) = 1$$

with probability 1. We censored individuals clearly emigrating from the river after their last period (l_i) in the river, while the final study period (T) was the last period for all other individuals. For intervening time periods ($t = f_i + 1 \dots l_i$), the alive state is defined as

$$z(i, t) \sim \text{Bernoulli}[\phi z(i, t - 1)]$$

where the individual survives to time t with probability ϕ when $z(i, t - 1) = 1$. Apparent survival probability (ϕ), survival minus emigration, can be estimated as constant or varying across time periods.

Because individuals could be detected multiple times at any functioning monitoring station during a time period, the encounter histories $y(i, j, t)$, conditional on the alive state $z(i, t)$, follow a Poisson distribution such that

$$y(i, j, t) | z(i, t) \sim \text{Poisson}[\lambda_0 g(i, j, t) z(i, t)]$$

where the parameter λ_0 is a baseline encounter rate, the expected number of observations (e.g., detections) when an individual’s activity centre $s(i, t)$ is located precisely at a sampling location $x(j)$. When $z(i, t) = 1$, an individual i is considered to be in the river and alive in time period t . When $z(i, t) = 0$, an individual i is inferred to either be not alive or not in the river in time period t , and the observations are zero with a probability of 1. The function g is a general distance function commonly used in distance and other sampling approaches (Buckland et al. 2001; Efford 2004; Gardner et al. 2010). We applied a Gaussian kernel, often called the “half-normal” in distance sampling, defining $g(i, j, t) \equiv g(s(i, t), x(j)) = \exp[-d(i, j, t)^2/2\sigma^2]$, where $d(i, j, t) = \|s(i, t) - x(j)\|$ is the distance between an estimated individual activity centre $s(i, t)$ and each sampling location $x(j)$ in a time period t and σ is the scale param-

eter for the distance function (g). The parameter σ determines the rate of decline in detection probability as a function of distance from the activity centre $s(i, t)$ to a sampling location $x(j)$. Royle and Young (2008) suggested that σ could be associated with movement or home range calculations. For example, as σ increases, the decline in the detection function becomes more gradual and a tagged individual is more likely to move farther within a period and thus is more likely to be detected at one or more sampling locations. A small λ_0 (e.g., 0.1) may indicate elusive individuals or detection probability issues (e.g., mechanical failures), whereas a larger λ_0 (e.g., 0.9) implies an individual is more likely to be observed. Parameters σ and λ_0 may be constant, vary with sampling period or location, and also can be modeled with covariates.

Individual activity centres (s) within the overall state-space (S) are unknown and thus must be estimated within the model (Efford 2004; Royle and Young 2008; Gardner et al. 2010). In general, the state-space S encompasses the sampled area plus a buffered region (Royle et al 2009; Gardner et al. 2009). For example, S may contain an entire river or range from the mouth to the first impassible dam, a strict boundary on fish movement. Despite that fish enter the river at $\text{rkm} = 0$, they may migrate extensively within short periods and be captured or detected in more than one location within the first sample occasion. Thus, prior distributions for activity centres in individuals' first time periods (f_i) were assumed to be uniform (Efford 2004; Royle and Young 2008; Gardner et al. 2010):

$$s(i, f_i) \sim \text{Uniform}(S)$$

where S in this case is bounded by the lower and upper river coordinates (x_l, x_u). For subsequent time periods ($t = f_i + 1 \dots l_i$), activity centres were assumed to follow

$$s(i, t) \sim \text{Normal}[s(i, t - 1), \tau] T(x_l, x_u)$$

where activity centres are defined as a random draw from a normal distribution truncated (T), or bound, by the state-space coordinates (x_l, x_u) and the mean is the previous activity centre, $s(i, t - 1)$, with an estimated variance (τ) that can be held constant or allowed to vary with time. This Markovian structure informed the model of an individual's previous location and provided a way to estimate activity centres in time periods when an individual was not observed.

American shad example

Data collection and preparation

The base model described above is flexible, and we made modifications to account for sampling gear and American shad behaviors. A resistance board fish weir was used to capture and tag American shad in the Little River, a fourth order tributary to the Neuse River with the confluence near Goldsboro, North Carolina (Fig. 1). The rivers meet approximately 212 rkm from Pamlico Sound. Three low head (≤ 4 m in height), run-of-river dams were recently removed from the Little River and another dam was partially removed; upstream intact dams still exist (Raabe 2012). Sampling occurred in the springs of 2007 through 2010 (Raabe 2012); we illustrate the model using 2010 data.

The fish weir was installed at the former Cherry Hospital Dam site (rkm 3.7), allowing us to tag immigrating fish prior to upstream migrations, censor emigrating fish, and install an array of upstream PIT antennas (Fig. 1). We inserted a small (3.9 mm \times 31.2 mm, 0.8 g) Texas Instruments PIT tag (RI-TRP-RE2B) into the abdominal cavity of all visibly healthy, immigrating fish via a small incision between the pectoral and pelvic fins; this rapid procedure required no anesthetic. We scanned all captured fish with a handheld PIT reader (Allflex Compact Reader RS200). We

were unable to estimate tagging mortality or tag loss rates, therefore, we only included individuals detected at antennas located at or upstream of rkm 13.4 with at least two observations (e.g., weir and antenna detection). We assumed these fish were healthy and retained their tags because they migrated 10 rkm or more after tagging; delayed tag loss was still a possibility but is typically low with PIT tags (Prentice et al. 1990; Gries and Letcher 2002). Returning American shad (tagged in 2009) clearly retained their tags and were healthy; we included three returning individuals detected at multiple antennas but excluded two returning individuals detected only once. A total of 315 American shad were included.

We installed six PIT antennas as continuous monitoring stations to detect tagged individuals during their migrations (Fig. 1) (Raabe 2012). Our antenna site selection criteria included proximity to dam sites and overall river coverage, but options were limited by permissible access and suitable river channel characteristics for installation. Water gage height data (m), used as a covariate in the model, were recorded hourly immediately downstream of the weir site at a United States Geological Survey monitoring station (0208863200).

To increase temporal and spatial resolutions, observations occurred as both weir captures ($x(1)$: rkm 3.7) and detections at PIT antennas ($x(2-7)$: rkm 7.7, 13.4, 45.3, 56.4, 72.0, and 77.0, respectively) at a total of seven locations ($J = 7$). We used a weekly interval for sampling occasions (t), with a total of 12 weeks ($T = 12$) from 10 March 2010 to 1 June 2010. During this time, the fish weir and all antennas were installed (the antenna at rkm 13.4 was installed on 11 March 2010). We determined the days sampling gear did not function properly, such as flooding at the weir or antennas not detecting stationary PIT tags installed within the antenna detection field and activated once per hour (Raabe 2012).

We constructed individual encounter histories as the capture (1) or noncapture (0) at the weir and the count of detections at each antenna within a weekly time period, resulting in a three-dimensional data set of capture – detection frequencies (individual \times location \times week). Weir observations were limited to a capture and tagging event during upstream immigration and a recapture during downstream emigration. To limit repetitive detections at an antenna (e.g., tagged fish resting near an antenna), we included only the first detection when additional subsequent detections occurred within 30 min; this differs slightly from one count per 30 min bins. A total of 3406 weir and antenna observations were used in analyses. An individual's week of entry into the study (f_i) was either its capture at the weir or first detection at an antenna (individuals tagged in 2009). The last period (l_i) was either the week of emigration for censored individuals or week 12. We censored individuals recaptured emigrating at the fish weir or displaying distinct downstream trajectories in lower portions of the river during periods when the weir did not function properly.

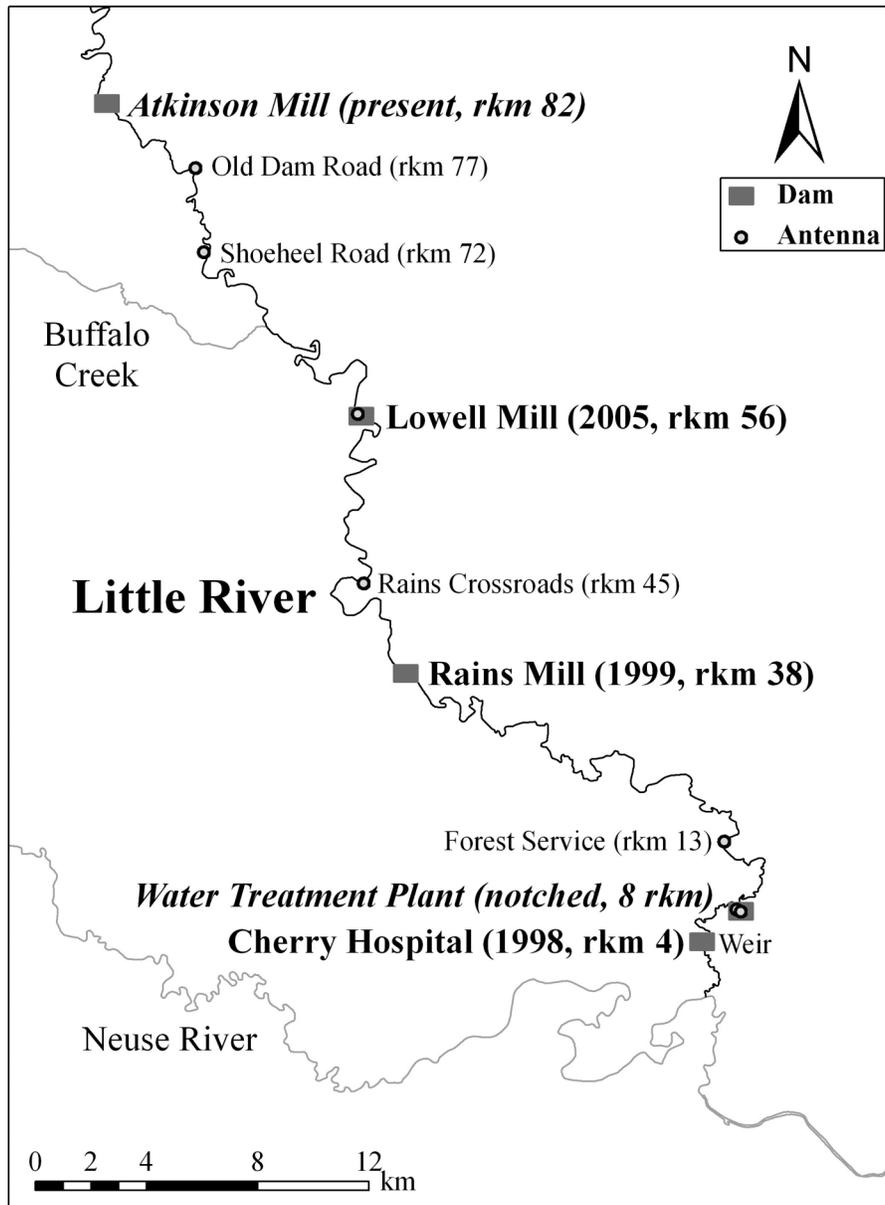
Model specifications and modifications

We considered the Little River state-space S to range from the river mouth (rkm 0) to the most downstream impassible dam, Atkinson Mill Dam (rkm 82), containing all river habitat available to American shad during their spawning migrations. Because weekly weir ($j = 1$) captures were binary (captured or not captured), we modeled those observations as

$$y(i, j, t) | z(i, t) \sim \text{Bernoulli}[p_0 g(i, j, t) z(i, t)]$$

where p_0 is the baseline detection (constrained between 0 and 1). Antenna observations were counts and thus were modeled with the Poisson function described above. We modeled weekly apparent survival probability (ϕ) as a constant across time periods because of relatively sparse encounter histories for certain individuals. Raw data suggested that American shad made longer movements in higher flows and were detected less often in low flows (Raabe

Fig. 1. Map of the Little River, North Carolina, depicting dam locations and status (year removed, notched, and present) and fish sampling (weir and antennas) locations in 2010.



2012). We modeled weekly σ_t as $\log(\sigma_t) = \beta_0 + \beta_1 \text{gage}_t$, where β_0 is the intercept and β_1 is the coefficient for mean weekly gage height (m). To inform the model of gear sampling issues, we included the proportion of days in a week that gear at each sampling location worked properly (e.g., $0.71 = 5$ functioning days/7 total days) as an offset in the encounter rate estimation.

Model inference

We fit the linear spatial capture–recapture model using a Bayesian framework for analysis. We used the open-source software programs JAGS (Plummer 2003, 2012) and R (R Development Core Team 2012) via the R package “rjags” (see online Supplementary Material¹ for R code). A uniform distribution was used to constrain priors for $\phi(0, 1)$, $p_0(0, 1)$, $\tau(0, 40)$, and σ_t coefficients ($\beta_0(-3, 3)$ and $\beta_1(-3, 3)$). We ran three chains with an adaptive phase of 1000

iterations and then evaluated output from an additional 20 000 iterations. We confirmed chain convergence with the potential scale reduction factor ($R_{\text{hat}} < 1.01$) (Gelman and Rubin 1992; Brooks and Gelman 1998). Models required reasonably high computing capabilities (i.e., sufficient random access memory).

We evaluated model fit and examined survival, movement, and habitat use by comparing output with other models, descriptive statistics, and plots using the same data as the model analysis. We compared the linear spatial capture–recapture model weekly survival estimate with a nonspatial CJS model (Raabe 2012). We calculated a weekly population mean location (in rkm) from the posterior mean estimate of all activity centres ($s(i,t)$) for individuals estimated to very likely be alive and in the river (mean z across chains >0.99). For comparison, we computed two weekly population

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2013-0198>.

mean locations (rkm) from the empirical observations: (i) all observations combined (sum of each observation rkm/count of all detections) and (ii) by individuals (sum of mean rkm for each individual/count of detected individuals). To determine if σ_t varied as expected, we compared the estimated posterior means with the mean range in observations (rkm) for all individuals detected at least twice in a week (Raabe 2012). We also calculated the mean number of weekly detections per individual as the total number of detections divided by the number of detected individuals to compare with the baseline antenna encounter rate (λ_{0t}).

Results

The estimated posterior mean of weekly apparent survival (ϕ) was 0.80 (SD = 0.01) in 2010 (Table 1), very similar to the nonspatial CJS model weekly estimate of 0.81 (SD = 0.01) (Raabe 2012). We censored 18 individuals that emigrated prior to week 12; five others were documented emigrating in week 12. Gage height (m) was positively related to σ_t (Table 1; Fig. 2). A similar positive relationship existed between river flow conditions and the weekly mean range in observations of tagged individuals (Fig. 2). The weekly posterior means of the baseline encounter rate (λ_{0t}) followed a similar trend as the mean weekly detections per individual (Fig. 3 and 4). Posterior means for λ_{0t} were highest in week 2 and week 3 when individuals were partially or completely hindered at the notched dam (rkm 7.9), lower in week 4 when higher flows decreased weir and antenna efficiencies and individuals spread throughout the river, and then relatively low during several weeks of declining flow until week 11 when a freshet occurred. The posterior mean for baseline detection at the weir (p_0) was low, likely because of limited recaptures (Table 1). The pattern in the weekly mean of all individual activity centres generally tracked the overall and individual means of the raw observations, with some divergences as the model estimated the location of undetected individuals (Fig. 5).

Examining all estimated individual activity centres $s(i, t)$ depicted the upstream movements of American shad, their use of restored habitat following dam removals, and a gradual decline in the number of individuals over the spawning season (Fig. 6). The model estimated fish located in reaches restored by complete dam removals at rkm 37.7 and rkm 56.4 from week 2 to week 12, including clusters of individuals downstream of the present impassible dam (rkm 82), the upper extent of the model state-space S.

Individual American shad displayed a wide range of survival and migratory patterns, characterized well by model activity centre estimates but with increased uncertainty in periods of few or no detections and when individuals may have died or emigrated (mean $z < 0.5$) (Fig. 7). Activity centre uncertainty (e.g., 95% credible intervals) was much lower when an individual was observed multiple times in a period (e.g., Fig. 7c; week 2: 23 detections) compared with once (e.g., Fig. 7c; week 5) or not at all (e.g., Fig. 7c; week 6). A few American shad remained in downstream reaches throughout the spawning period despite being in the river during freshets (Fig. 7a). A number of American shad were only detected for a short time period at downstream reaches, potentially succumbing to early mortality or using habitat in the long unsampled region between antennas at rkm 13.4 and 45.3 and dying (Fig. 7b). Other individuals migrated into and used habitat in middle reaches and either successfully emigrated (Fig. 7c) or died (Fig. 7d). Movement into upstream reaches was typically rapid during high flow events, with individuals beginning downstream emigration shortly after (Fig. 7e) or weeks later and completing emigration (Fig. 7h), while others died in upper reaches (Fig. 7f) or during emigration (Fig. 7g).

Discussion

Spatial capture–recapture models allow estimation of both spatial and demographic parameters, and our model provides a flex-

Table 1. Summary statistics (2.5% and 97.5% = 95% credible intervals) of the posterior distributions of parameters for the 2010 Little River American shad linear spatial capture–recapture model.

Parameter	Mean	SD	2.5%	Median	97.5%
ϕ	0.80	0.01	0.78	0.80	0.82
τ	27.31	1.23	25.05	27.26	29.88
p_0	0.09	0.02	0.05	0.09	0.14
β_0	0.25	0.02	0.21	0.25	0.29
β_1	2.11	0.02	2.07	2.11	2.16

Note: ϕ , weekly apparent survival rate; τ , normal distribution variance for locations of individual activity centres; and regression parameters β_0 and β_1 , intercept and slope, respectively, for log-linear function relating flow (gage height (m)) to σ_t , the scale parameter.

ible option to estimate survival and location and infer movement from linear continuous monitoring array data. Advances in tagging technology (i.e., low cost PIT tags and continuous monitoring antennas) allowed us to tag hundreds of American shad and passively record thousands of detections. Outside of a 30 min buffer for consecutive detections, the model used all collected data and retained the spatial structure of sampling locations to provide useful estimates of within river survival and weekly locations of American shad. We modeled both binary and count data, varied certain parameters with time, and included gage height as a covariate for a scale parameter that inferred the extent of weekly movements. Additional modifications and improvements are possible depending on the study design, available data, and quantitative capabilities.

In our American shad example, the linear spatial capture–recapture weekly survival estimate was very similar to the nonspatial CJS weekly survival estimate. However, this is likely to not always be the case, particularly if survival varies spatially or when dispersal directly affects survival estimates (Ergon and Gardner, in press). In our example, the state-space is confined by a physical barrier (impassible upstream dam) and biological barrier (emigrated American shad did not return), thus constraining the movement of fish and limiting the potential influence of dispersal or movement outside the state-space.

The σ_t parameter, a scale parameter on the detection function, represented apparent increases in movement during higher flow conditions. Both the model and empirical weekly movement extent metrics (Fig. 2) depicted American shad undergoing extensive movements during high flows in week 4, were relatively stationary during low flow conditions in the middle of the spawning season, and increased movements at the end of the study period during moderate to high flows. The weekly movement means were more variable because the calculation included fewer fish (individuals detected at least twice) and could be influenced by extreme movements (ranges), whereas the σ_t estimates included all fish (any individual i with posterior mean $z_i > 0$) and is a general regulator of weekly movements for the whole population.

The posterior means for the baseline detection rate, λ_{0t} , followed a similar trend as the mean weekly detections per individual (Fig. 3) and were highest in week 2 and week 3 as immigration (weir captures) continued and migrations were partially or completely hindered at the notched dam, resulting in multiple detections at the antenna immediately downstream of the dam (rkm 7.7) and the nearby upstream antenna (rkm 13.4). A noticeable decrease in the estimated baseline encounter rates occurred in week 4; higher flows likely allowed individuals to efficiently pass the notched dam and spread throughout the river, reducing multiple detections at antennas near the notched dam and at upstream antennas that were farther apart and passed rapidly (e.g., one or two detections). In addition, observations were lower in week 4 because of high flows that caused the weir to fail (no captures) and reduced antenna efficiencies. The posterior means

Fig. 2. Weekly sigma (σ_t), a scale parameter related to weekly movements, estimated with a river flow condition covariate (gauge height) followed a similar trend as the mean of individual American shad weekly movement distance (range in observations). Grey vertical lines represent 95% confidence interval for movement range; 95% credible intervals for sigma were narrow and not visible in plot.

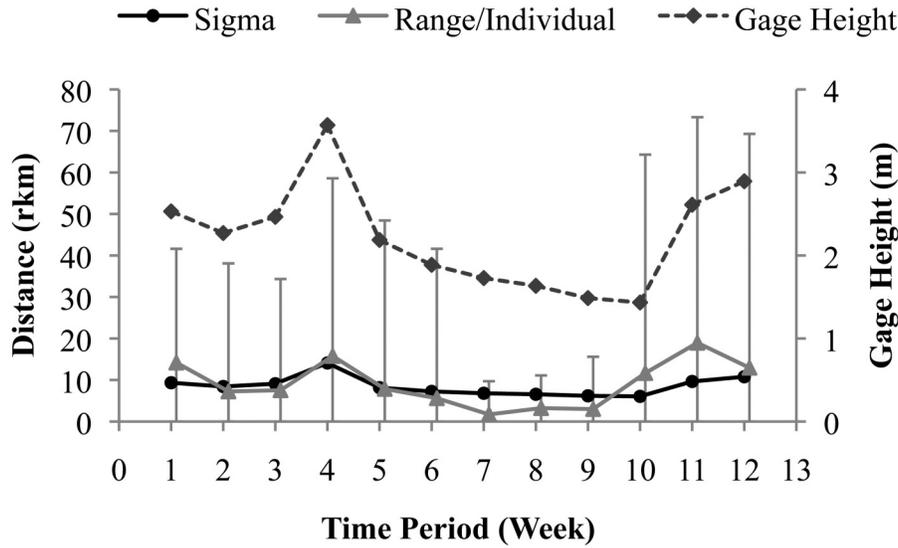
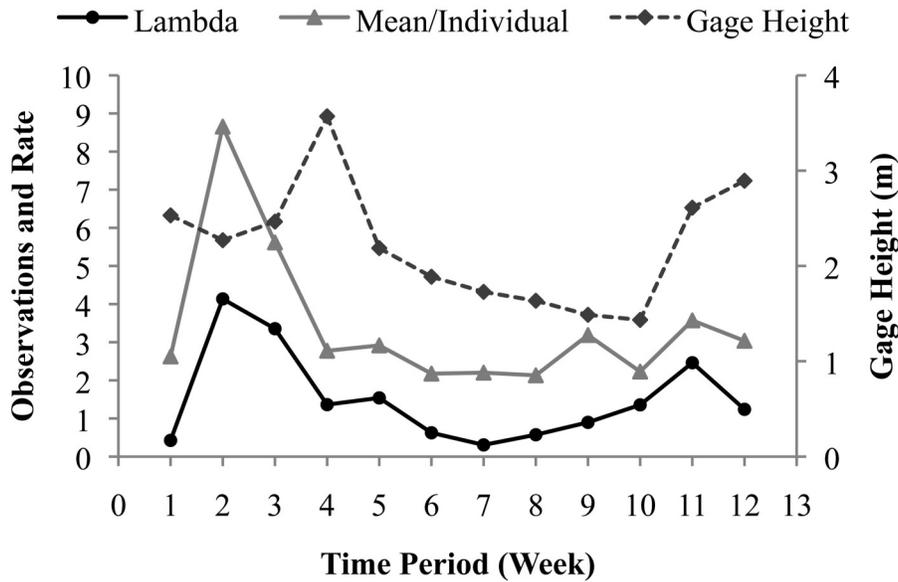


Fig. 3. Baseline encounter rate (λ_0) depicting the expected number of weekly observations when an individual's activity centre ($s(i, t)$) was located at an antenna. The rate closely followed the mean number of weekly observations per individual, with both metrics likely influenced by river conditions such as gage height.



of λ_{0t} remained relatively low in weeks 5 through 10 during low flow but increased in week 11 during freshets.

The means of weekly posterior means of all activity centres were similar to empirical means of observations (Fig. 5). The model mean was near the overall and individual means in week 1, but slightly higher in week 2 and week 3. This divergence is likely due to the model estimating the location of undetected individuals during moderately high flow conditions and when detected fish were expected to be detected more often (high λ_{0t} estimates) and migrate more extensively (higher σ_t estimates). The posterior means of the activity centres were similar to the raw overall, individual, or both means in the remaining periods. One exception was week 9, when two individuals (of 19 detected individuals) detected often (44% of 54 total detections) at rkm 72.0 heavily influenced the overall mean.

Spatially, the individual activity centres visually matched raw observations and were still estimated in periods without observations, but with higher uncertainty as is expected (Fig. 7). Correlating individual activity centres $s(i, t)$ to the previous estimate $s(i, t - 1)$ helped maintain migration patterns by estimating weekly location even when an individual was unobserved and the censored normal distribution contained estimates to the part of the Little River below the impassable Atkinson Mill Dam (rkm 82). For periods with no observations, individual activity centre estimates shifted towards the middle of the state-space (i.e., towards the mean of the prior distribution). The 95% credible intervals accounted for this location uncertainty, whereas in other analyses (e.g., mean location) unobserved individuals were omitted. Uncertainty increased when an individual was not detected for multiple periods.

Fig. 4. Weekly total number of observations (weir captures and antenna detections) for all individuals at each sampling location in the Little River in 2010. Total observations ranged from 1 to 714 detections, and bubble sizes are relative to the highest number of observations (714, week 3, rkm 7.7).

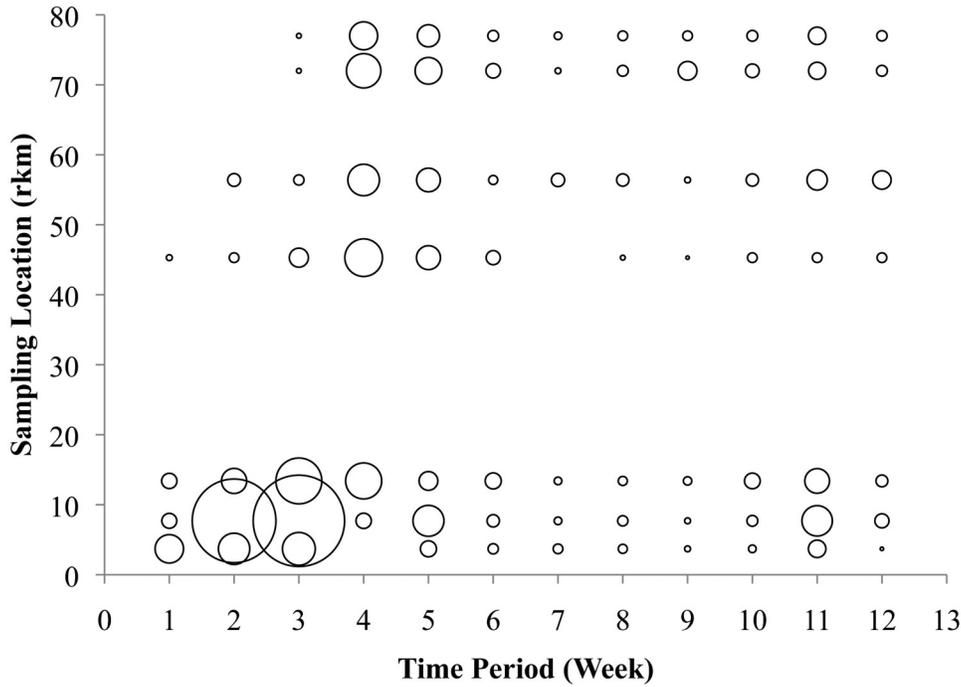
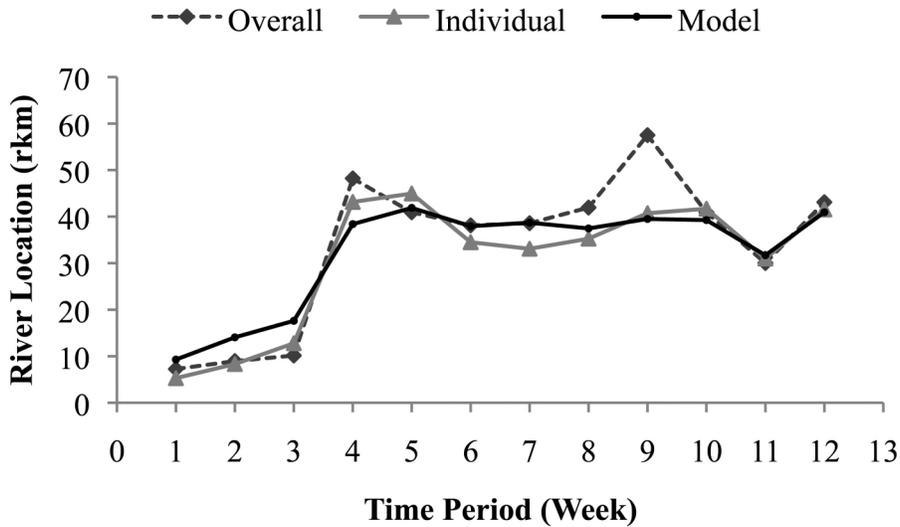


Fig. 5. Estimated weekly mean location of the American shad population in the Little River during the spring of 2010 based on the linear spatial capture–recapture model (mean of posterior distributions of all individual activity centres) and observations (overall = sum of rkm/count of observed individuals; individual = sum of mean rkm/count of observed individuals).

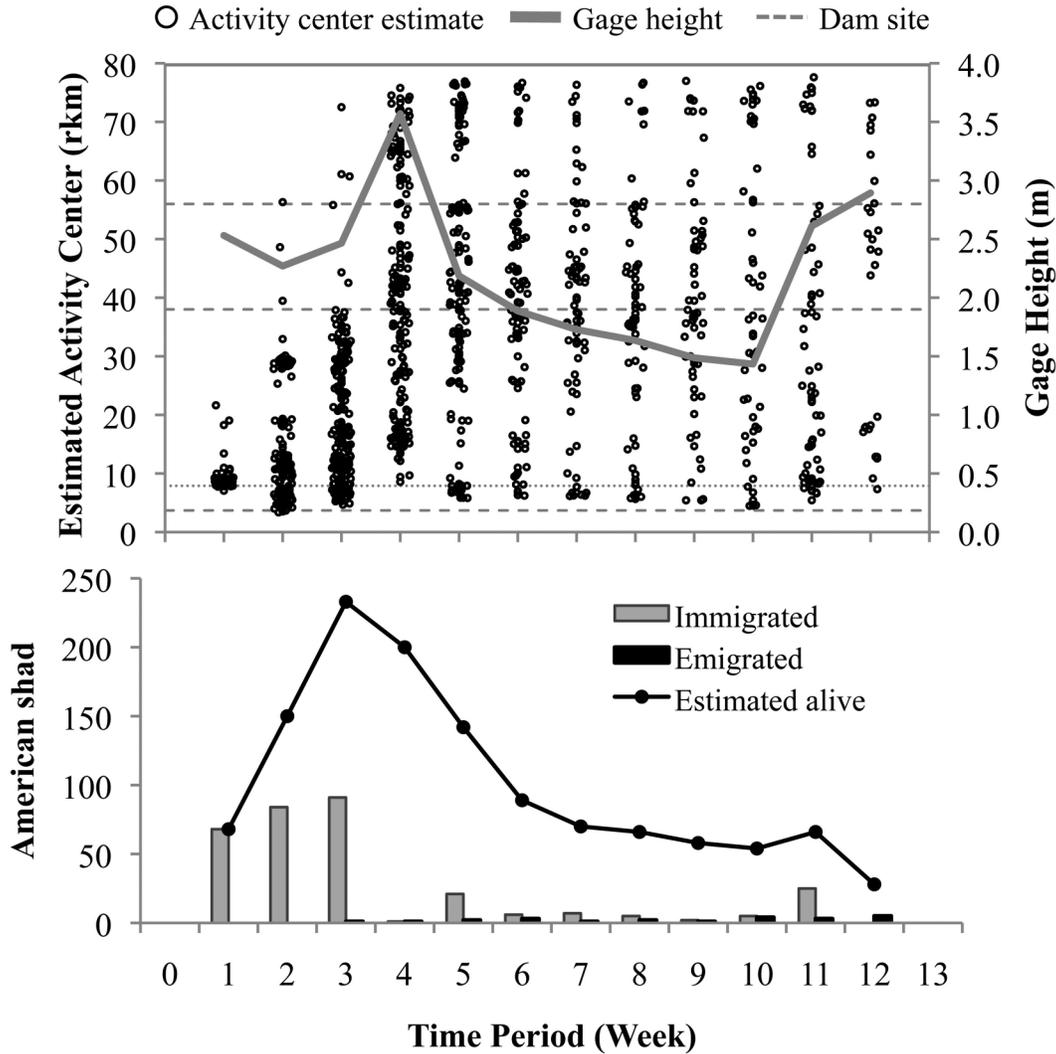


For comparison, we also estimated activity centres correlated with a normal distribution without truncation (effectively allowing individuals to move beyond the lower weir and into the Neuse River and above the impassible dam in the time periods following first capture). This allowed activity centre estimates that can be either biologically unlikely (downstream of functioning fish weir, <3.7 rkm) or impossible (upstream of impassible dam, >82.0 rkm) and may bias model survival, activity centre, and other estimates. For example, survival was estimated to be higher in the normal model compared with the truncated normal model, likely due to estimated activity centres being located in unsampled regions (i.e., <3.7 rkm and >77.0 rkm) where fish could not occur. We note that our system presents a very limited space for individuals to

exist because of the clear boundaries; in many other systems, this is not reasonable and the model and state-space should be specified appropriately for those systems.

The precision of the model estimates and the overall spatial resolution could be improved with additional sampling locations and increased detection capability of continuous monitoring stations. In our example, we had only seven sampling locations covering 82 rkm; the minimum spatial gap between locations was 4 rkm and the maximum nearly 32 rkm. Individuals went unobserved for multiple periods, in part because of minimal movement during low flow periods but also because of these spatial gaps in sampling locations. A number of individuals immigrated into the largest spatial gap (rkm 13.4–35.3) and were never

Fig. 6. (Top panel) Individual activity centre (s) estimates for each American shad in the Little River estimated to be alive and in the river with high certainty (mean z across chains ≥ 0.99) relative to weekly mean water depth and former and current dam sites (dashed line, removed; dotted line, partially removed; and solid line, present). Note: circles randomly offset from time period for visual purposes. (Bottom panel) Weekly number of American shad that immigrated, emigrated, and were estimated to be alive and in the river.



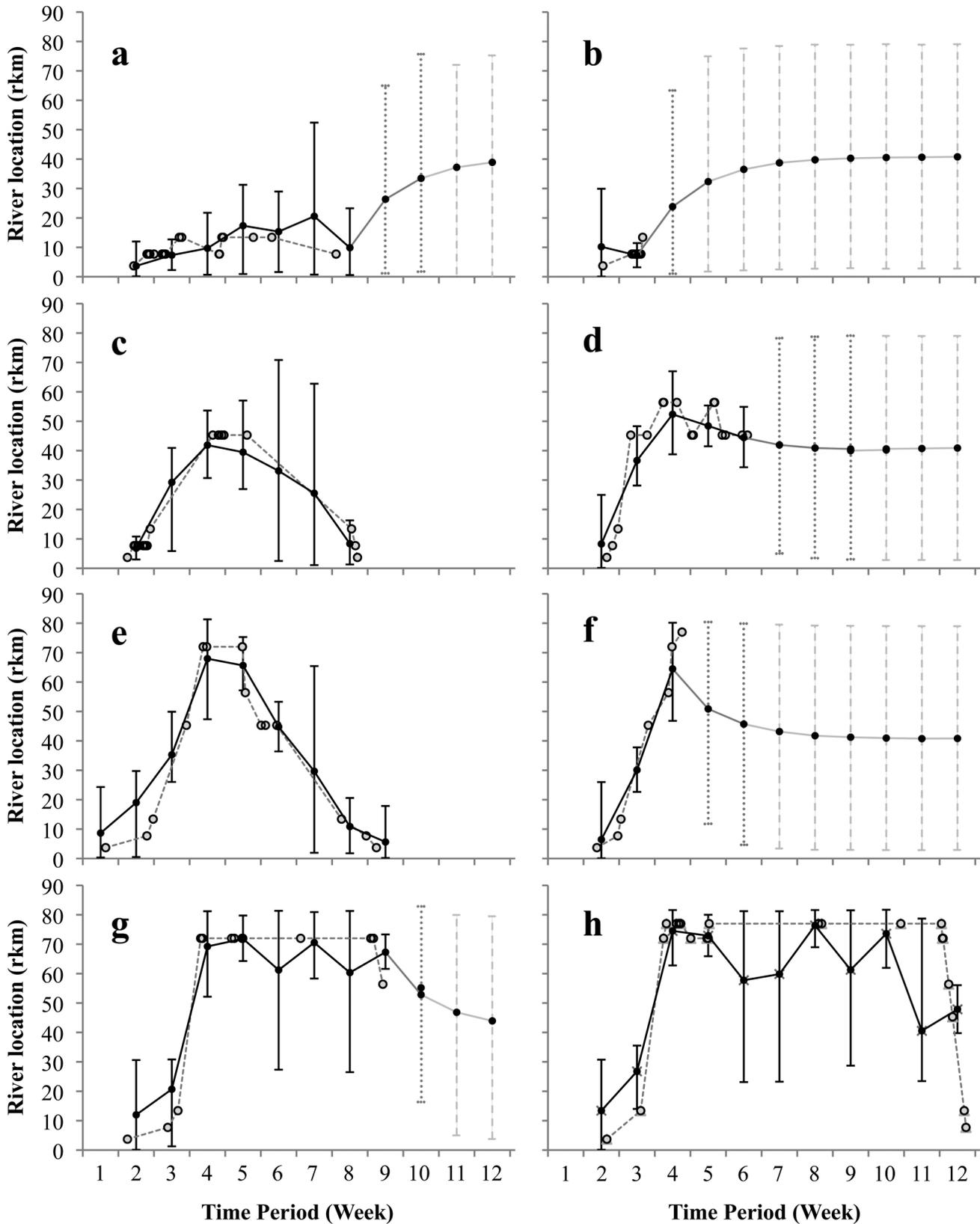
observed again. Adding continuous monitoring stations to fill this and other gaps (e.g., downstream of Atkinson Mill Dam) would likely increase observations and decrease unobserved periods, improving estimates of activity centres (and migration patterns) and survival. Ideally, individuals would be constantly observed. Although unrealistic for PIT antennas that require tagged fish to swim through or within the detection range (~ 1 m) (Raabe 2012), this is a possibility with acoustic telemetry where transmitters can be detected 450 to 600 m from receivers (Simpfendorfer et al. 2008). The main disadvantages of telemetry compared with PIT technology are a lower sample size (transmitter costs) and shorter study periods (transmitter battery life) (Lucas and Baras 2000). A constant monitoring of tagged individuals would produce an enormous data set that would likely need to be consolidated such as the 30 min buffer used in this model (Heupel et al. 2006).

A finer temporal scale (e.g., daily) or indicating the temporal sequence of observations may also improve resolution in location, migratory patterns, and relationships with environmental conditions. For example, mean weekly gage height and the scale parameter (σ_r) may not fully capture a scenario where movements are minimal during 6 days of low flow but extensive during the 7th day when a freshet occurs. Because we aggregated weekly obser-

varations, the model used the number of observations at each sampling location but did not incorporate when an individual was detected at different locations. Informing the linear spatial capture-recapture model of the temporal sequence of observations could aid in estimating subsequent activity centres (or even model directional movement patterns) and the scale parameter as some individuals detected multiple times at multiple antennas in a week was due to upstream and downstream movements rather than consecutive detections. However, finer temporal resolution data may be rather sparse and the consequences should be weighed on a case-by-case basis.

The linear spatial capture-recapture model had sufficient data despite coarse spatial resolution because American shad are a highly mobile species driven to migrate during the spawning season. This mobility presented issues when trying to use a multi-state model (Kéry and Schaub 2012) with three reaches (states) in the Little River. A daily time interval was too coarse to assign states as certain individuals were detected in multiple states during high flow events. This led us to develop the linear spatial capture-recapture model that is not restricted to defining a state and instead uses all spatial data. However, the linear spatial capture-recapture model may not provide as much of an advance

Fig. 7. Examples of American shad migratory and survival patterns in the Little River. Individual activity centres (solid circles, solid line, weekly midpoint, 95% credible intervals (CI)) were predicted from weekly observations (open circles, dashed line, continuous time). Different CI lines represent the probability (mean z across chains) the individual is alive and in the river. Black solid CIs, $z > 0.99$; dark grey dotted CIs, $z = 0.1-0.5$; and light grey dashed CIs, $z < 0.1$. No individuals are in the 0.5–0.99 range because of high mortality and censoring of emigrating individuals.



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for less mobile species unless the spatial resolution is increased (e.g., improved sampling coverage), the temporal scale is longer (e.g., month and year), or active sampling is conducted (e.g., manual tracking and electrofishing).

The simplistic movement model we implemented was well suited for our system and available data, but it is possible to specify more complex movement models. Previously, movement in mark–recapture models focused on modeling individual locations rather than activity centres (Ovaskainen et al. 2008; Patterson et al. 2008; Hooten et al. 2010), but these approaches are directly applicable to spatial capture–recapture models. Recent developments have also extended spatial capture–recapture models to include non-Euclidean distances, estimating dispersal, and directly incorporating resource selection functions (Royle et al. 2013; Ergon and Gardner, in press). Future advances could also include extended spatial capture–recapture models to allow for weighted directional movement and different movement states (Johnson et al. 2008; McClintock et al. 2012).

Based on the results from the linear spatial capture–recapture model, American shad in the Little River used all habitat restored by dam removals, migrated more extensively in higher flow conditions, and experienced high spawning mortality. The estimated posterior mean of weekly survival was 0.80, equating to an apparent survival of only 7% after 12 weeks in the river. While this is an apparent survival estimate, it appears spawning mortality is indeed high as documented emigration events were uncommon in 2010. Mortalities are likely a result of depleted energy reserves (Chittenden 1976; Leggett and Carscadden 1978; Leonard and McCormick 1999), but also could be attributed to predation by invasive flathead catfish whose Little River abundance was higher in 2010 than the previous two years (Raabe 2012). Similar studies and use of the linear spatial capture–recapture model along the Atlantic coast would provide insight into whether differing iteroparity rates are a result of spawning or annual (ocean) survival.

The linear spatial capture–recapture model opens new opportunities to study demographic parameters and patterns in movement or migration and habitat use in both aquatic and terrestrial systems. The base model is flexible; parameters may be constant, vary by time, or be a function of environmental or other covariates. Further developments may include heterogeneity in survival, movement, and baseline encounter rates. If the field design includes closely spaced sampling locations (e.g., antenna and acoustic receivers), the model will provide detailed estimates that could be used to infer habitat use and potentially habitat selection. Temporal and spatial overlap and possible interactions among species could be examined by tagging multiple species. The linear spatial capture–recapture model advances quantitative options to analyze continuous monitoring data in a robust manner. Our approach is intended for a relatively linear river system where hydrologic distances are very similar to Euclidean distances, whereas a complex river network may require different quantitative approaches to account for spatial variability related to flow direction, discharge, and connectivity (e.g., mixed models) (Peterson and Ver Hoef 2010). Modifications to this model and future quantitative developments are necessary to fully take advantage of tagging technologies that are continuously advancing (Heupel and Webber 2012).

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