Modeling structured population dynamics using data from unmarked individuals

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Abstract. The study of population dynamics requires unbiased, precise estimates of abundance and vital rates that account for the demographic structure inherent in all wildlife and plant populations. Traditionally, these estimates have only been available through approaches that rely on intensive mark–recapture data. We extended recently developed *N*-mixture models to demonstrate how demographic parameters and abundance can be estimated for structured populations using only stage-structured count data. Our modeling framework can be used to make reliable inferences on abundance as well as recruitment, immigration, stage-specific survival, and detection rates during sampling. We present a range of simulations to illustrate the data requirements, including the number of years and locations necessary for accurate and precise parameter estimates. We apply our modeling framework to a population of northern dusky salamanders (*Desmognathus fuscus*) in the mid-Atlantic region (USA) and find that the population is unexpectedly declining. Our approach represents a valuable advance in the estimation of population dynamics using multistate data from unmarked individuals and should additionally be useful in the development of integrated models that combine data from intensive (e.g., mark–recapture) and extensive (e.g., counts) data sources.

Key words: Desmognathus fuscus; detection probability; N-mixture model; northern dusky salamander; stage-structured models; state-space models.

Introduction

Accurate knowledge of population abundance, survivorship, reproduction, and movement is necessary for testing ecological theory and predicting the impacts of environmental change on population viability (Beissinger and McCullough 2002). Yet, inference about these demographic processes typically requires intensive data collection efforts that track individual animals over time, such as mark–recapture methods (Williams et al. 2002, Royle et al. 2013). While these detailed data can produce high-quality information on the demography of populations, the costs of implementing mark–recapture studies at large spatial and temporal scales can be prohibitive, and thus, methods that can provide similar inference for unmarked populations (e.g., populations where individuals cannot be distinguished) are needed.

Recently developed *N*-mixture models allow for the estimation of abundance and spatial variation in abundance from count data alone for both closed (Royle 2004) and open (Dail and Madsen 2011) populations. *N*-mixture models are a class of state-space models in which the true state of the system (abundance) is observed imperfectly. Unlike classical state-space models used in ecology (e.g., de Valpine and Hastings 2002, Staples et al. 2004), *N*-mixture models do not make unrealistic assumptions about Gaussian process and sampling error and instead assume abundance is a discrete random variable (but see Buckland et al. 2004). Similarly, *N*-mixture models attribute observation error to a specific phenomenon: the inability to detect all individuals that are available during sampling (i.e., false negatives), referred to as imperfect detection. The open *N*-mixture model (Dail and Madsen 2011) provides a framework for estimating demographic parameters such as survival and population growth (via reproduction and immigration) using count data from multiple years and locations (Chandler and King 2011).

While the open *N*-mixture model (hereafter the Dail-Madsen model) presents an important advancement in the use of count data for estimating population

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abundance, it lacks realism by assuming that survivorship, fecundity, and movement are constant for all individuals at a particular location. Heterogeneity in survival and reproduction rates among individuals is ubiquitous and has important ecological and evolutionary implications. When demographic heterogeneity is attributable to age, sex, size, or other discrete stages, a robust body of theory and models are available to predict population dynamics and viability (Caswell 2001); however, the stage-specific parameters must typically be estimated using multistate mark–recapture models (Nichols et al. 1992, Lebreton et al. 2009). To our knowledge, no analogous methods are available for making similar inferences from data collected on unmarked populations.

We extend the Dail-Madsen model to allow state-specific estimation of demographic rates from stage-structured populations using associated count data, analogous to the estimation of state-specific parameters in multistate mark–recapture models (Schwarz et al. 1993). We present our analysis for populations that are structured by life stage (e.g., juveniles and adults), but our framework could be used for any classification for which data are available (i.e., age, sex, size). We demonstrate the approach using simulations and explore the data requirements (e.g., number of survey locations, years, and replicate sampling events) for accurate and precise estimates of parameters. We show the utility of our modeling framework by applying the approach to a population of northern dusky salamanders (*Desmognathus fuscus*) in headwater streams in the mid-Atlantic region.

Review of the Closed and Open N-mixture Models for Count Data

N-mixture models are concerned with inference about N_j, population abundance at location j, where the $j = 1, 2, \ldots, J$ locations are spatially distinct sites. In a closed population (i.e., one in which there are no births, deaths, or migrations between $k = 1, 2, \ldots, K$ sampling events), the observed number of individuals, $n_{j,k}$, at location j during sampling replicate k are modeled as $n_{j,k} \sim \text{Bin}(N_j, p)$, where p is the detection probability of individuals, independent of the detection of other animals. Royle (2004) suggested modeling N_j as a random effect using an appropriate discrete distribution, such as the Poisson or negative binomial with expected value, $E(N_j) = \lambda_j$. Covariates can then be added to the model using link functions to incorporate environmental characteristics (or other factors) that may influence expected abundance, λ_j, and/or detection probability of individuals, p_j, at different j locations.

The Dail-Madsen model extends this model to open populations by allowing local abundances, $N_{j,t}$, to vary over time, t, through births, deaths, and dispersal. Abundance at location j in the first time interval is described using a discrete distribution with expected value λ_j, similar to a closed population. However, for

subsequent years, the model assumes that local population abundances in time t are random variables such that $N_{j,t}$ is dependent only on $N_{j,t-1}$ according to a Markovian process. Although any population growth model (e.g., exponential, logistic, theta-logistic, and so on) could be used to describe temporal variation in abundance, Dail and Madsen (2011) considered a more mechanistic model in which $N_{j,t}$ is decomposed into two independent quantities: $S_{j,t}$, the number of individuals at location j that survive from time $t - 1$ to t and remain at j, and $G_{j,t}$, the number of individuals that were gained, either by recruitment or immigration, at location j between time $t - 1$ to t. Dail and Madsen (2011) modeled these quantities as

$$S_{j,t} \sim \text{Bin}(N_{j,t-1}, \omega)$$

$$G_{j,t} \sim \text{Pois}(\gamma N_{j,t-1})$$

where ω is the apparent survival probability of individuals, and γ is the arrival rate of individuals, dependent on the population's local abundance. Here $G_{j,t}$ is specified as a function of $N_{j,t-1}$, but the number of individuals gained at a location could also be independent of abundance in the previous time step if such an assumption more accurately described the population of interest. We focus on the Poisson distribution for $G_{j,t}$, but other distributions, such as the negative binomial, could be used. The total population abundance at a location in time t is $N_{j,t} = S_{j,t} + G_{j,t}$. Note that, in this model, it is not possible to distinguish between reproduction and immigration or death and emigration. As in the closed population N-mixture model, the Dail-Madsen model requires data on the total number of observed individuals, $n_{j,k,t}$ at each location j, during survey replicate k at time interval t. These observed counts are modeled using a binomial distribution, $n_{j,k,t} \sim \text{Bin}(N_{j,t}, p)$, where p is the detection probability of individuals at each survey event k and could also be indexed by space or time, if data are available.

State-structured Models

We extend the open N-mixture model (Dail and Madsen 2011) to accommodate stage-structured population dynamics. We assume that stage-specific count data (e.g., observed numbers of juveniles and adults) are available at a given location and year and that locations are independent of one another. Let $n_{i,j,k,t}$ be the observed count of individuals in stage i recorded at each location j during survey replicate k and time interval t where $n_{i,j,k,t} \sim \text{Bin}(N_{i,j,t}, p_i)$ and p_i is the stage-specific detection probability. Our interest lies in modeling $N_{i,j,t}$, the true abundance of each stage i in location j at time t, where stage-specific abundances are linked by the organism's specific life history traits. In the simplest case, we assume that changes in abundance occur annually through births and deaths only (e.g., no immigration and emigration) and that the population can be divided into two stages: juveniles and adults.

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Surviving juveniles have an annual probability of transitioning to adults and adults can survive for multiple years. As in the Dail-Madsen model, the population abundance for juveniles ($i = 1$) and adults ($i = 2$) in the first year of sampling is modeled using a discrete distribution appropriate for count data. We assume $N_{i,j,1} \sim \text{Pois}(\lambda_i)$ for all of the j sampled locations (but other distributions such as the negative binomial could also be used). Subsequent years ($t \geq 2$) are modeled by allowing transitions between stages according to the life cycle of the population and by again considering the number of individuals that survive (S) and are gained (G) in the population (in this case, through recruitment). We define an additional category, $T_{i,j,t}$, to account for the stochastic stage transitions as follows:

$$S_{1,j,t} \sim \text{Bin}(N_{1,j,t-1}, \omega_1)$$

$$S_{2,j,t} \sim \text{Bin}(N_{2,j,t-1}, \omega_2)$$

$$T_{1,j,t} \sim \text{Bin}(S_{1,j,t}, \varphi)$$

$$G_{1,j,t} \sim \text{Pois}(\gamma N_{2,j,t-1})$$

where ω_1 and ω_2 are the stage specific survival parameters, γ is the reproduction rate (i.e., the number of new juveniles produced annually per adult), and φ is the probability that a surviving juvenile transitions to adulthood. Note that if $\varphi < 1$, there is some probability that a juvenile remains at that stage for multiple years, and that if $\varphi = 1$, all juveniles mature in exactly one year. The stage-specific and total population abundances at a given location j is then determined by

$$N_{1,j,t} = G_{1,j,t} + S_{1,j,t} - T_{1,j,t}$$

$$N_{2,j,t} = S_{2,j,t} + T_{1,j,t}$$

where total population abundance is the sum of both stages. Additional life history features can easily be incorporated provided that there is sufficient data, making this modeling approach flexible and broadly applicable. Here we assume that the transition from juveniles to adults occurs annually with a fixed probability, but transitions among stages could occur for a variety of reasons. For example, adults could transition between breeding and nonbreeding stages or individuals could move among stages nonsequentially if the population were structured by size. The model can be specified more generally in these cases using a transition matrix **T** where transitions are allowed to and from all states in the population (such as in a multistate mark–resight transition matrix). The model can also be modified to include immigration or emigration at one or both life stages, with these rates dependent (or independent) on local population abundance, survivorship, and/or reproduction. Similarly, covariates can be added to the transition parameters

to account for relevant habitat characteristics on survival, recruitment, movement, and/or detection probabilities during the sampling process.

We use a Bayesian approach to estimate model parameters, which provides a computationally tractable method to integrate across unobserved states and quantify the uncertainty in our estimates. Bayesian analysis requires specification of prior distributions for parameters. We assume vague priors in all analyses presented in this paper, but note that prior information on parameter values could be incorporated if it were available. We implemented our analyses using Markov chain Monte Carlo (MCMC) to sample from posterior distributions for each of the parameters with the programs R and JAGS (Plummer 2003).

Simulation study

We developed a simulation study to explore the ability of our stage structured model to estimate demographic rates and annual abundances. We used the model outlined in the previous section, which assumes that the recruitment, survivorship, and stage transition probabilities are time invariant and independent of habitat and sampling covariates. We set juvenile survivorship ($\omega_1 = 0.5$) lower than that of adult survivorship ($\omega_2 = 0.75$), and annual maturity rate to either $\varphi = 0.75$ (stochastic transitions) or $\varphi = 1.0$ (deterministic transitions). We then selected per capita recruitment rates (γ) and expected initial abundance for juveniles (λ_1) and adults (λ_2) such that the population had an equilibrium abundance of 30 adults per site (Fig. 1). We simulated 10 years of dynamics at 20 locations prior to the data collection period such that site stage structure had plausible deviations away from equilibrium values. To simulate data collection, we assumed that individuals in each stage were observed with a stage-specific detection probability (p_i) at the 20 locations every year during the five-year sampling period. We explored how high and low detection probabilities influenced model performance given that juvenile detection was always half that of adults (i.e., $p_1 = 0.5p_2$ and $p_2 = 0.8$ or 0.4). Surveys are typically designed so that the total number of replicates (K) exceeds one during a time period where the population is closed; this allows for explicit estimation of the detection probability of individuals during sampling events. However, obtaining replicate samples during a closed time period can be logistically challenging for a spatially broad study. It is possible to estimate parameters of open N-mixture models with only one sampling replicate at various locations by tabulating between-year variance as a function of year and extrapolating to the case of within-year variance, where this within-year variance is then used to estimate p (Dail and Madsen 2011). We thus explored how repeated sampling affected the ability of our model to recover parameters by assuming that sampling occurred on either one or three replicate occasions within each year over a time frame in which
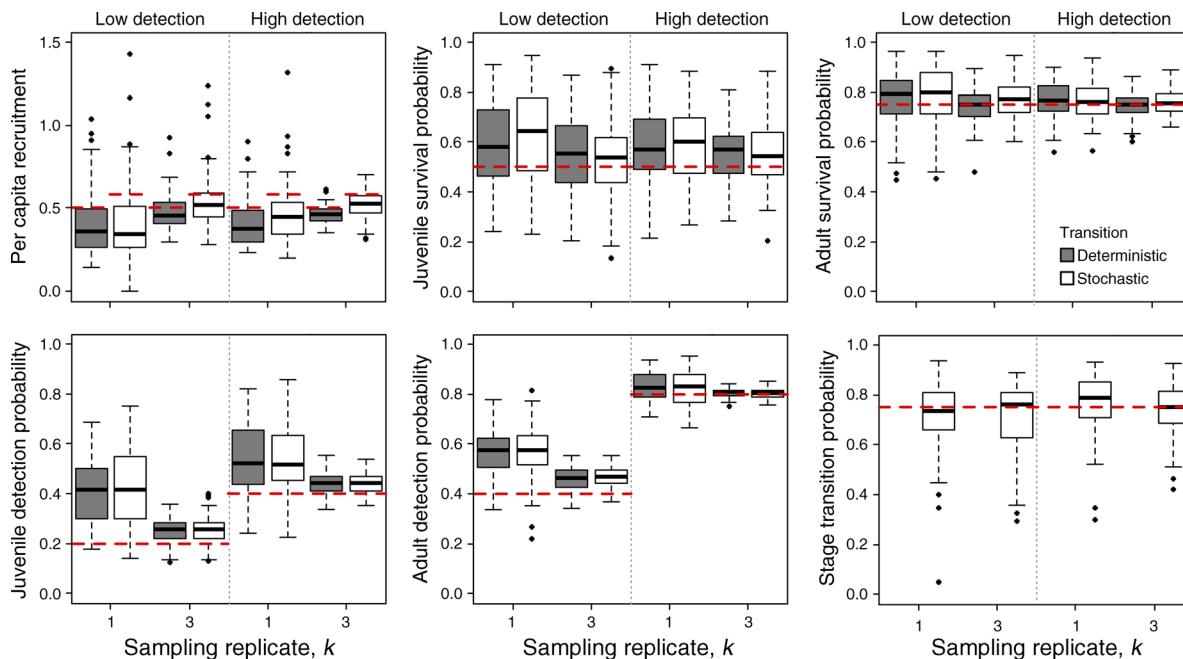
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Fig. 1. Simulation results showing the true parameter values (dashed red lines) and a summary of the estimated median values from 100 simulated data sets assuming populations with deterministic (gray) and stochastic (white) stage transitions for high and low detection probabilities with one sampling replicate ($k = 1$) and three sampling replicates ($k = 3$) per time period. Recruitment is the number of new juveniles produced annually per adult, while the other parameters are probabilities ranging from 0 to 1. The dark black line in the middle of the box shows the median value (of the 100 median points estimated from the simulated data sets), while the outer lines show the interquartile range. The whiskers show the highest/lowest values within ± 1.5 times the interquartile range. Outliers are points beyond that range.

site populations were closed $k = 1$ *or* 3). We then simulated 100 replicate data sets for each scenario. We estimated seven parameters for each model: expected initial abundance for juveniles (λ_1) and adults (λ_2), survival for juveniles (ω_1) and adults (ω_2), detection probabilities for juveniles (p_1) and adults (p_2), and recruitment rate (γ). For the stochastic transition model, we also estimated the transition probability φ from juvenile to adults; φ was fixed to one in the deterministic model. The JAGS model code for the simulation study as well as details on the MCMC implementation can be found in Appendix A.

Our simulation results show that the ability of our model to recover parameters is dependent on the complexity of the system and the amount of available data (Fig. 1). For example, estimates of per capita recruitment were nearly twice as precise when the transition from juvenile to adult was deterministic as compared to stochastic (and thus requires an additional parameter to be estimated). With low detection probabilities ($p_1 = 0.2$ and $p_2 = 0.4$), both juvenile and adult detection was overestimated for the stochastic and deterministic stage transition models. Replicate survey events reduced the overestimation, but did not remove it completely. Detection estimates were fairly accurate when detection was high ($p_1 = 0.4$ and $p_2 = 0.8$) and locations were visited three times annually. The overestimation of detection probabilities may be linked to an

overestimation of juvenile survivorship, which was fairly imprecise, especially with only one sampling replicate. Estimates of adult survivorship were accurate and fairly precise for all model run scenarios.

To gain a better understanding of the data requirements for unbiased parameter estimation (in the frequentist sense: posterior point summaries, e.g., the median, evaluated with respect to repeated realizations of the data), we ran several additional simulations of the deterministic model (with $p_1 = 0.4$ and $p_2 = 0.8$) for various combinations of sampling locations and years assuming both one and three survey replicates (Appendix B): (1) 50 locations with 2 years, (2) 5 locations with 20 years, (3) 20 locations and 10 years, and (4) 100 locations and 2 years. Note that scenarios 1 and 2 produce the same amount of overall data as our original simulation, and that scenario 3 and 4 help us to determine if the model provides accurate and precise parameter estimates with additional data.

In all scenarios, adult detection and survivorship probabilities were generally accurate and reasonably precise, especially when three replicate surveys were available annually. With only two years of data (scenarios 1 and 4), estimates of recruitment were underestimated, juvenile detection was overestimated, and to a lesser extent, juvenile survivorship was also overestimated (Appendix B). Although the bias was reduced when locations were sampled three times

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(compared to once), our simulation results suggest that parameter accuracy requires many more than 100 sampling locations when the objective is to estimate demographic rates with only two years of data. Increasing the length of the data time series led to much more accurate and precise estimates for all parameters, especially when three survey replicates were available. Although estimates of juvenile survivorship were still somewhat imprecise, all parameters had a high degree of accuracy (and precision) for scenarios 2 and 3. This is a particularly interesting result, as scenario 2 had only five sampling locations (with 20 years of collection), suggesting that the addition of more time steps combined with sufficient repeated measures at survey locations (in this case three) improves the quality of demographic estimates to a much greater extent than adding survey locations (Appendix B). Similar simulation results have been obtained for dynamic occupancy models in terms of tradeoffs in sampling design (e.g., Popescu et al. 2012). We note that the inclusion of habitat and/or environmental covariates necessarily requires additional sampling locations and that estimates of abundance in the first year of sampling are increasingly less precise as the number of sampled locations is decreased. Similarly, greater sampling intensity will be required for parameter identifiability if data do not strictly conform to parametric assumptions. Further simulations could explore the data requirements for more complicated model structures such as the condition where initial abundance and/or recruitment parameters were derived from over-dispersed distributions (e.g., negative binomial).

Application: Northern Dusky Salamander Model

Despite worldwide observations of amphibian population declines, stream salamander populations are assumed to be stable, with significantly smaller annual variation in population abundance than terrestrial or pond-breeding amphibians (Green 2003). Because of concern for amphibians and a desire to detect changes in populations within managed lands, the U.S. National Park Service chose amphibians as one of the "Vital Signs" for monitoring the status of park resources in the National Capital Region. As part of the program, northern dusky salamanders (*Desmognathus fuscus*; Fig. 2A) were sampled within headwater streams annually in June and July from 2005 to 2012 in two parks (seven streams within the Chesapeake and Ohio National Historic Park in Maryland, USA, and five streams within the Rock Creek Park in the District of Columbia, USA). Most streams were sampled at two locations separated by at least 100 m along the stream reach for a total of 21 survey locations (11 upstream sites, near headwaters, and 10 in sites further downstream). At each location, an observer walked two 15-m transects along the channel and turned cover objects <6 cm in the water and on the bank within 2 m of the stream. Observers recorded

all individuals found, as well their snout-to-vent lengths. We assumed that the population abundance could change between years, but that local populations were closed between the June and July sampling events, a reasonable assumption because reproduction does not occur during this time frame and studies of other northern dusky populations in the Shenandoah mountains (E. H. C. Grant, *unpublished data*) and the western Piedmont of North Carolina (Price et al. 2012) indicate that survivorship is high and movement rates are low over this time frame.

While it is not possible to accurately age individuals without sacrifice, juveniles can be discriminated from adults by snout-to-vent lengths <35 mm (Orser and Shure 1975). We specified a stage-based model for the northern dusky salamander comprised of three stages (Fig. 2B): first-year juveniles ($i = 1$), second-year juveniles ($i = 2$), and adults ($i = 3$). We distinguished two classes of juveniles to account for a reproductive lag because individuals do not start reproducing until their third year of life (Danstedt 1979); the two juvenile classes were otherwise given identical parameterizations. Both juveniles and adults are capable of migrating in and out of sampling locations between years, and we assumed that an individual's probability of survivorship and movement was likely to vary between juveniles and adults (Grant et al. 2010). We modeled the first year of sampling ($t = 1$) by assuming that $N_{i,j,1} \sim \mathrm{Pois}(\lambda_i)$ where λ_i is the mean local abundances for stage i, in the first year of sampling across all locations. For $t \geq 2$, we defined ω_1 and ω_2 as the apparent annual survival (the probability that an individual survived and remained at the same location) for juveniles and adults, respectively such that

$$S_{1,j,t} \sim \mathrm{Bin}(N_{1,j,t-1}, \omega_1)$$

$$S_{2,j,t} \sim \mathrm{Bin}(N_{2,j,t-1}, \omega_1)$$

$$S_{3,j,t} \sim \mathrm{Bin}(N_{3,j,t-1}, \omega_2).$$

Note that we did not estimate stage transition probabilities because all transitions in this model are deterministic. We used our knowledge of the northern dusky life cycle to parameterize reproduction and movement as (Fig. 2B):

$$G_{1,j,t} \sim \mathrm{Pois}(\gamma_1 N_{3,j,t-1} + \gamma_2)$$

$$G_{2,j,t} \sim \mathrm{Pois}(\gamma_2)$$

$$G_{3,j,t} \sim \mathrm{Pois}(\gamma_3)$$

where γ_1 is the reproductive rate (e.g., per capita recruitment of adults), γ_2 is the number of immigrating juveniles, and γ_3 is the number of immigrating adults. By setting the immigration rate constant across age-1 and age-2 juveniles (such that the expected number of individuals that immigrate to both N_1 and N_2 is γ_2), we are able to parse out immigration from reproduction
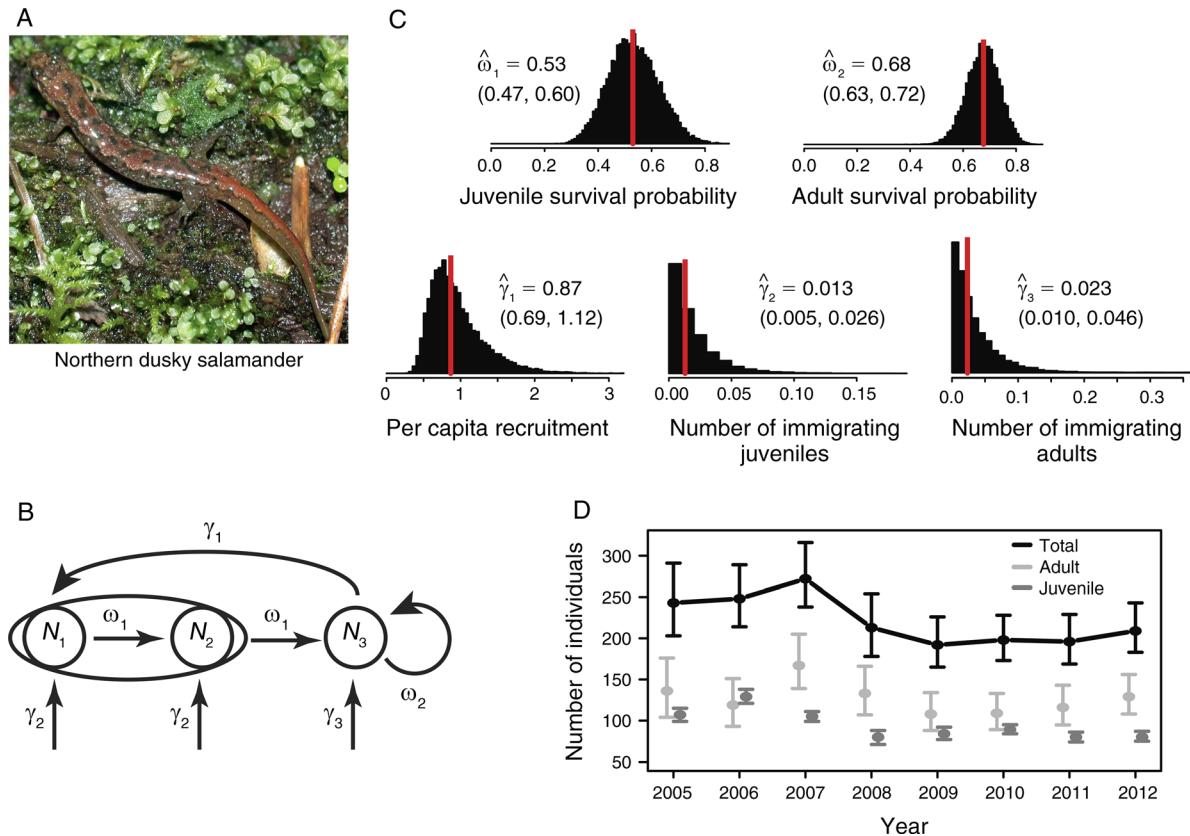
FIG. 2. (A) Northern dusky salamander (*Desmognathus fuscus*). (B) Life cycle diagram for the northern dusky salamander. The N nodes indicate the three life stages, where N_1 is age-1 juveniles, N_2 is age-2 juveniles, and N_3 is adults. The parameters ω_1 and ω_2 are the apparent annual survival probabilities for juveniles and adults. Reproduction and movement are shown with the γ parameters, where γ_1 is per capita recruitment (of adults, the only breeding stage), γ_2 is the number of immigrating juveniles, and γ_3 is the number of immigrating adults. (C) Parameter estimates (denoted by variables with hats) including full posterior distributions, median values (red lines), and 25th–75th posterior intervals (50% posterior intervals [PI]) for the demographic transition rates. (D) Annual total abundance estimates (median values and 50% PIs) at the 21 sampled locations of all individuals combined (black), adults (light gray), and juveniles (dark gray) from 2005 to 2012.

by assuming that the balance of individuals gained to N_1 are the offspring of adults from the previous year. The total population abundance in year $t \geq 2$ can be described as the sum of growth (reproduction and immigration) and survival, where

$$N_{1,j,t} = G_{1,j,t}$$

$$N_{2,j,t} = S_{1,j,t} + G_{2,j,t}$$

$$N_{3,j,t} = S_{2,j,t} + S_{3,j,t} + G_{3,j,t}.$$

In our specification of the model, $N_{i,j,t}$ represents the number of individuals in stage i at a given location after the demographic processes (reproduction, movement, and survivorship) have occurred within the year t (e.g., a post-breeding census). The data, n, are only distinguishable to the level of juveniles and adults (i.e., it is not possible to separate $i = 1$ and $i = 2$ individuals). We incorporated errors from the sampling process by allowing detection to differ for juveniles (n_{juv}) and adults (n_{ad}) such that:

$$n_{juv,j,k,t} \sim \text{Bin}(N_{1,j,t} + N_{2,j,t}, p_1)$$

$$n_{ad,j,k,t} \sim \text{Bin}(N_{3,j,t}, p_2)$$

where p_1 is the detection probabilities of juveniles (stage 1 and 2 individuals), and p_2 is the detection probability of adults (stage 3) at each location j, during survey replicate k at time interval t. Complete model details on the MCMC implementation along with the JAGS code used for this analysis can be found in Appendix C.

The parameter estimates generated by our analysis demonstrate that our stage-structured model can produce precise estimates of recruitment, survivorship, and dispersal for this population of northern dusky salamanders (Fig. 2C). As expected, survivorship was higher for adults than juveniles (Grant et al. 2010, Price et al. 2012). Recruitment accounted for the majority of individuals gained at locations (median annual per capita recruitment = 0.87), while immigration rates were very low, with a median estimate of 0.05 immigrating individuals (juveniles and adults) per sampling location

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annually (Fig. 2C). Detection probabilities were significantly higher for adults (median = 0.38, 95% posterior interval [PI] = 0.310–0.455) than juveniles (median = 0.16, 95% PI = 0.091–0.259), suggesting that not accounting for heterogeneity in detection could lead to misleading estimates of demographic rates and abundance. The low estimates for detection could be caused by temporary immigration among individuals between the June and July sampling events. Total abundance was highly variable among years (Fig. 2D), and median abundance estimates declined over the time frame of our study. Ignoring the small amount of migration in the system allowed us to calculate the growth rate for this population using a Lefkovitch (stage-based) matrix model with the estimated demographic rates (Caswell 2001). The growth rate for this northern dusky salamander population is less than one (median = 0.95, 95% PI = 0.908–0.996), suggesting that local abundance will decline in the absence of immigration. A simulation of the population indicates that the small amount of immigration in the system is not enough to prevent abundances from declining. Using the posterior distributions of the parameter estimates, we projected that total abundance at the 21 sampled locations could be reduced by one-third (median value = 134, 95% PI = 51–315) in the 10th year after sampling (2022) if survivorship, recruitment, and immigration stay constant.

The decline in this northern dusky population is surprising, as small stream Plethodontid salamanders are expected to have more stable populations than other amphibian species (Green 2003). However, our results are consistent with Price et al. (2012), who found reduced survival and abundance in populations of *D. fuscus* at urbanized and urbanizing sites, similar to our study area, relative to undisturbed stream sites. Additionally, our study occurred during years with below-average precipitation, which resulted in reduced base-flows in these headwater stream habitats, possibly leading to lower survival and recruitment of juveniles.

DISCUSSION

We demonstrated how stage-specific abundance, including associated estimates of survivorship, movement, and recruitment can be obtained using only stage-specific count data. Our model represents a multistate extension of the Dail-Madsen model (comparable to multistate mark–recapture models) and can result in high-quality estimates of population dynamics because it incorporates a realistic representation of a species' life cycle. The model requires only stage-specific count data, which is collected in many monitoring programs where the life stage of individuals can be observed visually or through other methods. Stage-specific survivorship and recruitment estimates have previously only been available from mark–recapture data, which, although preferable in terms of the information content, are costly and time intensive to collect.

The accuracy and precision of stage-specific estimates are dependent on the amount and quality of available count data (Fig. 1; Appendix B). Although it is theoretically possible to obtain parameter estimates with only one survey replicate per time period, our simulations suggest that these values could be imprecise even for relatively large sampling efforts. As such, we caution against the use of a single sampling event unless prior information on detection probabilities is available (Link et al. 2003). We presented the median parameter values of 100 simulated data sets for several levels of data collection intensity. Although the accuracy of the median parameter values were variable in some cases, the 90% posterior intervals for the demographic parameters (Fig. 2; Appendix B) contained the true values in 77–97% of the model runs with five or more years of data when three sampling replicates were available. This suggests that the full posterior distributions of parameter estimates (which will be wider with small amounts of data) can provide a good representation of a population's dynamics while also capturing uncertainty in parameter values, as we showed with our northern dusky salamander example in estimating that population's decline. Our simulation results demonstrate that increasing the time series of data leads to accurate and precise estimates of demographic rates, even with a relatively small number of sampling locations. However, survey data rarely conform to all model assumptions, and we suggest that researchers aim to survey as many locations as is feasible, especially if interest lies in understanding the effects of habitat and environmental covariates on population abundance or demographic rates.

Mark–recapture approaches are useful because they can provide detailed information on a population that may only be available using methods that track individuals over time. However, data collection for these analyses is necessarily costly and time consuming. Our stage-structured model provides another framework for estimating stage-specific vital rates and abundances. Integrated models (e.g., Brooks et al. 2004) that combine our stage-structured approach for count data with mark–recapture techniques can lead to efficient uses of resources and offer exciting alternatives to obtain comprehensive inferences on population dynamics over broad spatial and temporal scales.

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Supplemental Material

Appendix A

Model implementation details and JAGS code for the simulation study (*Ecological Archives* E095-003-A1).

Appendix B

Extended results from the simulation study (*Ecological Archives* E095-003-A2).

Appendix C

Model implementation details and JAGS code for the northern dusky salamander model (*Ecological Archives* E095-003-A3).

Reports