

Chapter 3

State-Space Models

In the previous chapter, a sequence of matrices was used to model the sequence of subprocesses, birth, survival, movement, etc., which characterize population dynamics. We find this building block perspective attractive for at least two reasons: (1) it allows one to mentally “divide and conquer” sometimes complicated population dynamics processes; (2) the resulting product of matrices is a generalization of Leslie and Lefkovich matrices, something familiar to many biologists.

While the building block matrix model is an aid to model formulation and understanding, it may not be as useful for fitting models to data and making population projections. Matrix representations of population dynamics describe at best the expected changes in a population, for example, conditional expected numbers at time t given numbers at time $t - 1$, and often, as noted in Sect. 2.5, are just approximations of these expectations, as in the case of density-dependent birth processes. Consequently, such matrix models fail to describe the variation and uncertainty around these expected outcomes. There are various ways of extending matrix models to incorporate both variability (Quinn and Deriso 1999: Sect. 7.3; Caswell 2001: Chaps. 14 and 15) and nonlinearity (Quinn and Deriso 1999: Sect. 7.4; Caswell 2001: Chap. 16). For example, variability around the expected outcome can be described by randomly selecting elements of a matrix (Caswell 2001: Sect. 14.5.5) or randomly selecting a matrix from a set of matrices (Caswell 2001: Sect. 14.5.3).

However, limitations of stochastic and nonlinear matrix models become apparent when one considers modelling population dynamics that involve a sequence of random and nonlinear sub-processes. Example 1 from the previous chapter, the BAS model, included binomial distributions for survival of two different age classes and a third binomial distribution for births. A Leslie matrix was formulated that accurately characterised the expected states at time t (conditional on \mathbf{n}_{t-1}). For projecting the population forward in time, however, one cannot readily, if at all, formulate a stochastic version of the matrix that accurately captures the variation of these binomials. For example, simply adding a vector of random variables to the

matrix model, i.e. $\mathbf{n}_t = \mathbf{B}\mathbf{A}\mathbf{S}\mathbf{n}_{t-1} + \boldsymbol{\epsilon}_t$, is problematic at best. The distribution for $\boldsymbol{\epsilon}_t$ will be quite complex; e.g. its components cannot be so large that a corresponding component of \mathbf{n}_t is less than 0.

State-space models (SSMs) are a more flexible approach for realistically modelling population dynamics than matrix models. SSMs are the backbone of the methods discussed in this book and this chapter is an introduction to their basic structure. Similar to some of the matrix models discussed in the previous chapter, SSMs have a state model and an observation model, but each is now a *stochastic time series*. The state model is a first-order Markov process, i.e. the distribution for state \mathbf{n}_t is defined conditional on the previous state \mathbf{n}_{t-1} , and the distribution for the observation \mathbf{y}_t is defined conditional on the current state \mathbf{n}_t . The classic SSM is a Normal Dynamic Linear Model (NDLM, West and Harrison 1997), which consists of two normally distributed linear models conditioning on \mathbf{n}_{t-1} and \mathbf{n}_t , respectively. The two equations below are a simplistic example of an NDLM in the context of animal abundance dynamics, where N_t is the true, but unknown, abundance of an animal population at time t and y_t is an index of N_t , i.e. $y_t = \gamma N_t$ where γ is a constant of proportionality.

$$\text{State process model } N_t | N_{t-1} \sim \text{normal}(\lambda N_{t-1}, \sigma_N^2). \quad (3.1)$$

$$\text{Observation model } y_t | N_t \sim \text{normal}(\gamma N_t, \sigma_y^2). \quad (3.2)$$

Here λ is the population growth rate; in a deterministic setting, $\lambda > 1$ leads to exponential growth, and $\lambda < 1$ is exponential decline. We use the terms state process model and state model interchangeably. Variation around the expected value, in this case λN_{t-1} , is sometimes called process noise or variation. In this example, the magnitude of the process variation depends on the size of σ_N^2 . An example of simulated projections of states with $\lambda = 1.02$ (2 % growth rate) and $\sigma_N^2 = 4$, and unbiased observations ($\gamma = 1$) with $\sigma_y^2 = 16$, is shown in Fig. 3.1.

Thus SSMs simultaneously account for two distinct sources of variation, natural or process variation (e.g. environmental or demographic stochasticity) and observation error (e.g. sampling or measurement errors) within a single framework. SSMs are much more general and flexible than matrix models, readily accommodating multiple random nonlinear sub-processes. Given the conditionally-defined state process model, forward stochastic population projection is relatively simple so long as random samples can be generated from the distribution. When the state process is a sequence of stochastic sub-processes, simulation is often easier than evaluation of the pdf; i.e. it is easier to simulate \mathbf{n}_t given \mathbf{n}_{t-1} than it is to calculate $\Pr(\mathbf{n}_t | \mathbf{n}_{t-1})$. The inclusion of a stochastic observation process model for the observations provides a framework for estimating parameters and accounting for uncertainty in the data, in a way which is consistent with the underlying state process model. This is in contrast to standard usage of matrix models where vital rate parameters, or their estimates, are somehow supplied external to the model, and error in such estimates is often not accounted for.

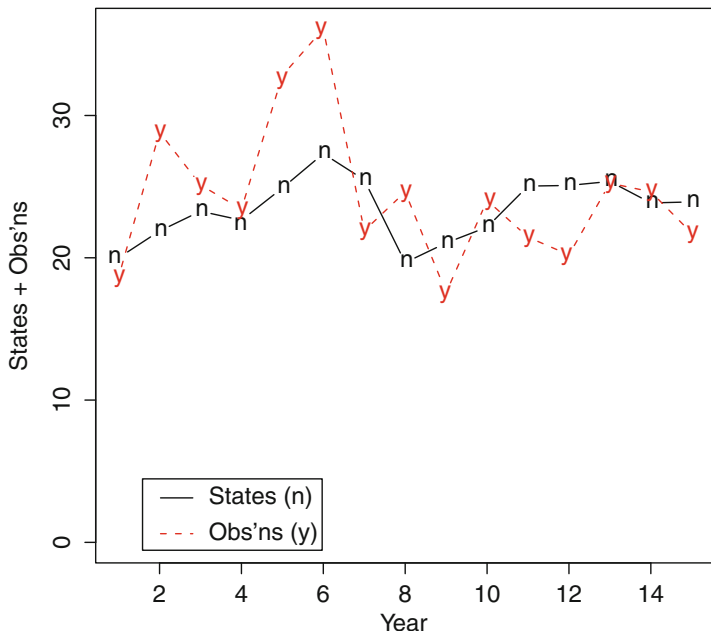


Fig. 3.1 Simulation of NDLM for animal abundance and estimates, where the population dynamics of the states are $N_t \sim \text{normal}(1.02N_{t-1}, 4)$ and estimates are unbiased, $y_t \sim \text{normal}(N_t, 16)$

In addition to the integrative nature of SSMs, there is also opportunity for a convenient division of labour between the modelling of the population dynamics and the modelling of the sampling and measurement of the population. Subject matter specialists such as ecologists can focus their attention on the underlying science through the state process model. The building block matrix models can serve as useful first approximations to the formulation of state process models, e.g. characterizing the deterministic portion of the state process model. Alternative and competing hypotheses about the underlying dynamics can be formalized by alternative state process models. Specialists in sampling, or mark-recapture, or transect sampling, or however the population is monitored, can focus on the formulation of one or more observation models. Different formulations of the observation model might result by working with summarized or derived calculations of sample data, e.g. mark-recapture-based point estimates of abundance, or the raw sample data, e.g. recaptured marks. This potential division of labour, of course, does not preclude a single individual, knowledgeable about the subject matter science and quantification of the observation process, from doing both.

Applications of state-space models to ecological data sets have steadily increased since the late 1980s. Early applications were largely restricted to the special case of NDLMs, because such models could be readily fitted using the Kalman filter (West and Harrison 1997). Several of the first applications were to fisheries data including

Mendelsohn (1988) who fitted an NDLM to Pacific mackerel *Scomber japonicus* catch data categorized by age class to estimate annual abundances and recruitment to the population, and Sullivan (1992) who fitted an NDLM to fisheries catch data categorized by length classes and then estimated parameters such as growth and survival. Advancements in computing power combined with simulation-based estimation procedures, such as Markov chain Monte Carlo (MCMC), extended the class of SSMs that could be fitted to nonlinear and non-normal distributions. Meyer and Millar (1999) gave one of the earliest demonstrations of such models for ecological data, South Atlantic albacore *Thunnus alalunga* biomass, using MCMC to fit an SSM where the state model was a univariate nonlinear, non-normal Schaefer surplus production model and the observation model used catch-per-unit-effort indices.

While many of the first applications of SSMs were to fisheries data, the diversity of species modelled by SSMs has expanded considerably. Animal species modelled by SSMs include red deer *Cervus elaphus* (Trenkel et al. 2000), grey herons *Ardea cinerea* and northern lapwings *Vanellus vanellus* (Besbeas et al. 2002), grey seals *Halichoerus grypus* (Thomas et al. 2005; Harrison et al. 2006), Chinook salmon *Oncorhynchus tshawytscha* (Newman and Lindley 2006), leatherback turtles *Dermochelys coriacea* (Jonsen et al. 2006), black bears *Ursus americanus* (Conn et al. 2008), red grouse *Lagopus lagopus scoticus* (New et al. 2009), hen harriers *Circus cyaneus* (New et al. 2011), desert bighorn sheep *Ovis canadensis mexicana* (Colchero et al. 2009), skate *Leucoraja ocellata* (Swain et al. 2009), Weddell seals *Leptonychotes weddelli* (Rotella et al. 2009), California sea lions *Zalophus californianus* (Ward et al. 2010), octopus *Octopus vulgaris* (Robert et al. 2010) and the Glanville fritillary butterfly *Melitaea cinxia* (Harrison et al. 2011).

State variables other than abundances have been considered as well. Royle and Kéry (2007) let the true state be whether or not a particular site was occupied by animals (and the observations were imperfect estimates of presence or absence). Gimenez et al. (2007) and Royle (2008), considering marked and recaptured or recovered animals, let the true state of marked animals (whether still alive or not) be the state variable. Anderson-Sprecher and Ledolter (1991) modelled the true location of radio-collared mule deer *Odocoileus hemionus*, while Jonsen et al. (2006) did the same for individual tagged leatherback turtles. King (2014) describes how various types of ecological data can be modelled using a state-space formulation.

The biological processes explicitly modelled by the state model include mortality, birth or recruitment, and movement. Models for mortality have distinguished natural mortality for different life history stages (e.g. age 2, 3 and 4 Chinook salmon, Newman and Lindley 2006) and harvest-related mortality (e.g. black bears, Conn et al. 2008). Models for movement have included the movement of single animals (e.g. turtles, Jonsen et al. 2006), movement between areas of members of a single population (e.g. coho salmon, Newman 1998), and movement between metapopulations (e.g. four sets of pupping colonies used by grey seals, Thomas et al. 2005).

The remainder of this chapter includes a general statistical formulation of SSMs and simple examples. General approaches to inference, i.e. the fitting of SSMs to data, are discussed in Chap. 4, while Chap. 5 is a discussion of issues in SSM formulation and diagnostics. The remaining chapters show how to put specific problems, such as survival estimation (Chap. 7), into an SSM framework and include more detailed examples.

3.1 State-Space Models

Here we give a more formal and mathematically general definition of state-space models. State-space models are models for two discrete time processes running in parallel, one called the state process and the other the observation process. The state process is modelled by a conditional probability density function (pdf) or probability mass function (pmf) that describes the change of the state vector from time $t - 1$ to time t , and is denoted by g_t . As will become clear in some of the later examples, g_t can be quite complicated and analytically intractable, reflecting a sequence of stochastic sub-processes. With some abuse of terminology, we will refer to pdf's and pmf's simply as pdf's. Note that we allow only discrete time indices, and to simplify notation, we assume that these are evenly spaced.

The value of the state vector at a given point in time is seldom known with certainty. Additionally, the parameters, such as survival rates and birth rates, are almost never known with certainty. If inferences about the state model are to be possible and defensible, field data must be collected. For example, various components of the state vector might be estimated from mark-recapture or line transect surveys. This leads to the observation process, which is modelled by another conditional pdf, denoted f_t , that describes the relationship between the state vector, \mathbf{n}_t , and a vector of observations, \mathbf{y}_t . As noted previously, point estimates of state vector components are typically quantities derived from sample data. We might instead use the raw sample data as observations. In contrast with the matrix model formulation, the general formulation presented here, which does not require a linear relationship between states and observations, can make modelling the raw observations more feasible.

The combination of the state model and the observation model is a state-space model and can be mathematically described as follows:

$$\text{Initial state pdf : } g_0(\mathbf{n}_0|\boldsymbol{\theta}) \quad (3.3)$$

$$\text{State } t \text{ pdf : } g_t(\mathbf{n}_t|\mathbf{n}_{t-1}, \boldsymbol{\theta}) \quad (3.4)$$

$$\text{Observation } t \text{ pdf : } f_t(\mathbf{y}_t|\mathbf{n}_t, \boldsymbol{\psi}), \quad (3.5)$$

where $\boldsymbol{\theta}$ is a vector of parameters corresponding to the state model, $\boldsymbol{\psi}$ is a vector of parameters corresponding to the observation model, and $t=1, \dots, T$. A sequence of state vectors, $\mathbf{n}_a, \mathbf{n}_{a+1}, \dots, \mathbf{n}_b$, will be denoted $\mathbf{n}_{a:b}$; $\mathbf{y}_{a:b}$ has a similar meaning.

The state process model, Eq. (3.4), is first-order Markov, i.e. the present state only depends on the previous state. Higher order Markov models can be re-written as first order Markov models by extending the dimension of the state vector to include previous states (see, for example, Schnute 1994). However, simply writing a univariate pdf for \mathbf{n}_t as a function of previous states, e.g. $g_t(\mathbf{n}_t | \mathbf{n}_{t-1}, \mathbf{n}_{t-2}, \boldsymbol{\theta})$, does not pose any inference difficulties with modern approaches such as MCMC and sequential Monte Carlo, e.g., sequential importance sampling (see Chap. 4). The general class of such higher order Markov models was termed hidden process models by Newman et al. (2006).

Environmental, or temporal, variation in the state process can be made explicit by adding another level to the SSM for variability in survival, birth and other parameters.

$$\text{Parameter pdf : } h(\boldsymbol{\theta}_t | \boldsymbol{\Gamma}) \quad (3.6)$$

$$\text{Initial state pdf : } g_0(\mathbf{n}_0 | \boldsymbol{\theta}_t) \quad (3.7)$$

$$\text{State } t \text{ pdf : } g_t(\mathbf{n}_t | \mathbf{n}_{t-1}, \boldsymbol{\theta}_t) \quad (3.8)$$

$$\text{Observation } t \text{ pdf : } f_t(\mathbf{y}_t | \mathbf{n}_t, \boldsymbol{\psi}). \quad (3.9)$$

Such a model is an example of a random effects or hierarchical state-space model (see Sect. 2.2.2). The pdf $h(\boldsymbol{\theta}_t | \boldsymbol{\Gamma})$ describes environmental stochasticity in $\boldsymbol{\theta}_t$, where $\boldsymbol{\Gamma}$ is a hyperparameter. Time-varying covariates could be used to model $\boldsymbol{\Gamma}$.

For Bayesian inference, another level is added to the state-space model formulation, namely, the prior pdf for the fixed and unknown parameters. For example, referring to the above hierarchical state-space model, Eqs. (3.6)–(3.9),

$$\text{Prior pdf : } \pi(\boldsymbol{\Gamma}, \boldsymbol{\psi}) \quad (3.10)$$

$$\text{Parameter pdf : } h(\boldsymbol{\theta}_t | \boldsymbol{\Gamma}) \quad (3.11)$$

$$\text{Initial state pdf : } g_0(\mathbf{n}_0 | \boldsymbol{\theta}_t) \quad (3.12)$$

$$\text{State } t \text{ pdf : } g_t(\mathbf{n}_t | \mathbf{n}_{t-1}, \boldsymbol{\theta}_t) \quad (3.13)$$

$$\text{Observation } t \text{ pdf : } f_t(\mathbf{y}_t | \mathbf{n}_t, \boldsymbol{\psi}). \quad (3.14)$$

As will be described in more detail in Chap. 4, the end result of Bayesian inference for a state-space model is the joint posterior distribution for the parameters and the unknown states, i.e. $\pi(\mathbf{n}_{0:T}, \boldsymbol{\Gamma}, \boldsymbol{\psi} | \mathbf{y}_{1:T})$.

Finally, yet another layer of uncertainty is model uncertainty, also known as structural uncertainty (Williams et al. 2001). Alternative formulations for any of the above pdf's are often postulated. Competing theories about the science underlying the population dynamics translate into different state pdf's, g_t , or parameter pdf's, h . Denoting a particular model by \mathcal{M} , the Bayesian hierarchical model of Eqs. (3.10)–(3.14) can be extended as follows.

$$\text{Model prior pdf : } r(\mathcal{M}) \quad (3.15)$$

$$\text{Parameter prior pdf : } \pi(\mathbf{\Gamma}, \boldsymbol{\psi} | \mathcal{M}) \quad (3.16)$$

$$\text{Parameter pdf : } h(\boldsymbol{\theta}_t | \mathbf{\Gamma}, \mathcal{M}) \quad (3.17)$$

$$\text{Initial state pdf : } g_0(\mathbf{n}_0 | \boldsymbol{\theta}_t, \mathcal{M}) \quad (3.18)$$

$$\text{State } t \text{ pdf : } g_t(\mathbf{n}_t | \mathbf{n}_{t-1}, \boldsymbol{\theta}_t, \mathcal{M}) \quad (3.19)$$

$$\text{Observation } t \text{ pdf : } f_t(\mathbf{y}_t | \mathbf{n}_t, \boldsymbol{\psi}, \mathcal{M}). \quad (3.20)$$

The pdf's and associated parameters in Eqs. (3.16)–(3.20) are conditional on the model \mathcal{M} , where parameters and the pdf's can vary between models. Chapter 5 will discuss model selection and model averaging.

3.2 Examples of State-Space Models

Here we give four examples of SSMs with the state pdf g_t and observation pdf f_t fully specified. The first is a nonlinear and non-normal coho salmon SSM with a scalar state and a scalar observation variable. The other examples are stochastic extensions of examples from Chap. 2.

3.2.1 Simplified Salmon Example

In this simplified SSM,¹ the state variable is a scalar N_t , the number of juvenile salmon alive in year t (at some point in time in that year) in a particular river. The dynamics of N_t are modelled as a Poisson distribution version of a Ricker stock-recruitment model (Quinn and Deriso 1999).

$$N_t | N_{t-1} \sim \text{Poisson}(\alpha N_{t-1} e^{-\beta N_{t-1}}), \quad \alpha > 0, \beta > 0. \quad (3.21)$$

Implicitly, the parameter α includes survival between time $t-1$ and t , the proportion that are female, fecundity (number of eggs produced), and survival between egg deposition and juvenile life stage. For the deterministic version of the model at least, to avoid chaotic behaviour, the value of α needs to be less than 2.69, and to avoid cycling, α must be less than 2. The parameter β is a measure of density dependence: as β increases, density dependence increases. The equilibrium value is $\ln(\alpha)/\beta$.

¹The state process in this salmon SSM is a considerable oversimplification of the population dynamics for most, maybe all, species of salmon. Typically juvenile salmon production in a given year is the result of spawning from two or more age classes (different cohorts) and those age classes were juveniles two or more years previously, so that N_{t-2} , N_{t-3} , ... contribute to N_t .

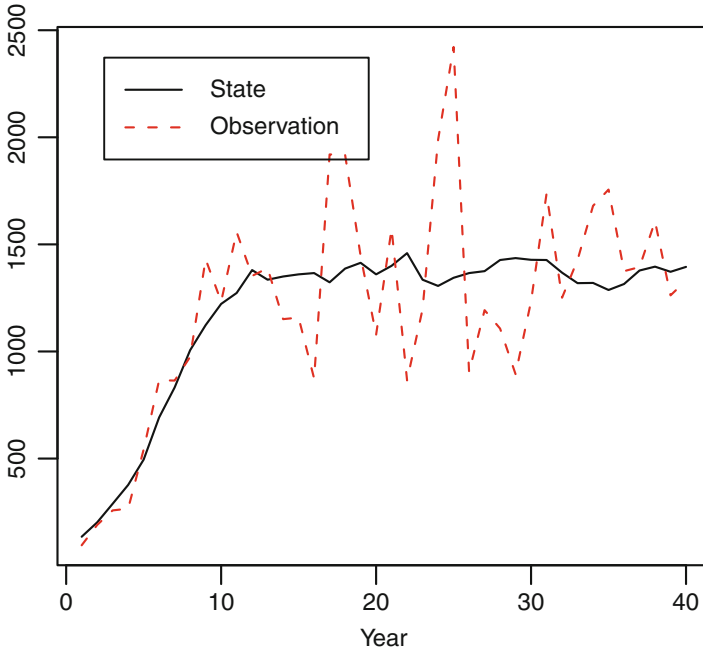


Fig. 3.2 Elementary salmon SSM with Ricker population dynamics with Poisson variation and lognormal observations. Ricker parameters are $\alpha = 1.5$ and $\beta = 0.0003$. Lognormal observations are bias-corrected with a coefficient of variation of 30%

The observations are estimates of juvenile abundance, e.g. based upon samples take from in-river traps. A convenient probability distribution for non-negative valued observations is the lognormal distribution, although for counts of animals, continuous random variables are clearly an approximation:

$$y_t | N_t \sim \text{lognormal} \left(\log(N_t) - \sigma_y^2/2, \sigma_y^2 \right). \quad (3.22)$$

This model is a bias-corrected lognormal, i.e. $E[y_t | N_t] = N_t$.

Forty years of simulated population dynamics and estimates are shown in Fig. 3.2. The estimates have a coefficient of variation of 30%. (The code that generates this plot is given on the book website, see Sect. 1.2.)

3.2.2 BRS Model

For a more complex example, we return to the BRS formulation, an example of two states (e.g. immature and mature animals), summarized in Sect. 2.3. The sequence of sub-processes was survival (S), growth (R) and birth (B). Now we define stochastic processes for each of these sub-processes. The pdf g_t is difficult to

evaluate analytically because it is a function of three different pdf's, but it is easy to describe symbolically and easy to simulate from. Symbolically, we write g_t as the following composite function (with the parameter vector θ omitted to reduce notation):

$$g_t(\mathbf{n}_t | \mathbf{n}_{t-1}) = g_{3,t}(g_{2,t}(g_{1,t}(\mathbf{n}_{t-1}))). \quad (3.23)$$

The three pdf's, $g_{1,t}$, $g_{2,t}$, and $g_{3,t}$, represent the processes of survival, growth and birth. Statistically, this is a more useful formulation of the BRS model than is Eq. (2.11), because the latter tells us only the expected values of the states in \mathbf{n}_t , conditional on \mathbf{n}_{t-1} , whereas Eq. (3.23) represents the full joint distribution of the states in \mathbf{n}_t , conditional on \mathbf{n}_{t-1} .

The pdf $g_{1,t}(\mathbf{u}_{1,t} | \mathbf{n}_{t-1})$ corresponding to survival is the result of two binomial processes [Eq. (2.2)]:

$$\begin{pmatrix} u_{1(s),1,t} \sim \text{binomial}(n_{1,t-1}, \phi_1) \\ u_{1(s),2,t} \sim \text{binomial}(n_{2,t-1}, \phi_2) \end{pmatrix}. \quad (3.24)$$

Growth from immature to mature is another binomial process, so that $g_{2,t}(\mathbf{u}_{2,t} | \mathbf{u}_{1,t})$ is determined from Eq. (2.5):

$$\begin{pmatrix} u_{2(r),1,t} \sim \text{binomial}(u_{1(s),1,t}, 1 - \pi) \\ u_{2(r),2,t} = u_{1(s),2,t} + (u_{1(s),1,t} - u_{2(r),1,t}) \end{pmatrix}. \quad (3.25)$$

If each adult can have at most one young, birth can be modelled as a third binomial process, so that $g_{3,t}(\mathbf{n}_t | \mathbf{u}_{2,t})$ is determined from a slight reformulation of Eq. (2.6):

$$\begin{pmatrix} n_{1,t} \equiv u_{3(b),1,t} = u_{2(r),1,t} + b_t \\ \text{where } b_t \sim \text{binomial}(u_{2(r),2,t}, \rho) \\ n_{2,t} \equiv u_{3(b),2,t} = u_{2(r),2,t} \end{pmatrix}. \quad (3.26)$$

In contrast to evaluation of the state pdf \mathbf{g}_t , simulation from the distribution is easy: one simply simulates from g_1 , that output is then input to simulate from g_2 , and that output is then input to simulate from g_3 . Suppose $\phi_1 = 0.50$, $\phi_2 = 0.71$, $\pi = 0.60$, and $\rho = 0.80$ and let the initial numbers, \mathbf{n}_0 , be (50,70). A simulation of the population dynamics for the two size classes for 30 years is shown in Fig. 3.3. The eventual population growth in this example is exponential and density dependence is needed in survival or birth processes to stabilize the population. The observations $y_{I,t}$ (estimated number of immature animals) and $y_{M,t}$ (estimated number of mature animals) were taken to be lognormally distributed, unbiased, with a coefficient of variation of 30 %, i.e.

$$\begin{aligned} y_{I,t} &\sim \text{lognormal}\left(\ln(n_{1,t}) - \sigma_y^2/2, \sigma_y^2\right) \\ y_{M,t} &\sim \text{lognormal}\left(\ln(n_{2,t}) - \sigma_y^2/2, \sigma_y^2\right) \end{aligned}$$

where $\sigma_y^2 = \ln(0.3^2 + 1)$.

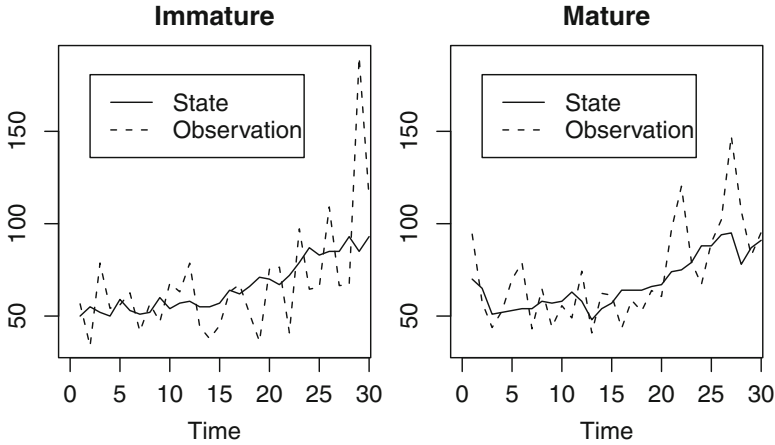


Fig. 3.3 Simulation of state process with two states, immature (I) and mature (M) animals, for $T = 30$ years, with three sub-processes, survival, growth and birth. Lognormally distributed estimates (the observations), with a coefficient of variation of 30%, are also plotted

3.2.3 Coho Salmon

The processes survival, movement and harvest, that characterize the spatially partitioned coho salmon recoveries model described in Sect. 2.7.1, could be modelled using binomial (for survival and harvest) and multinomial (for movement) distributions. Here we describe a normal dynamic linear model (NDLM) approximation to those processes (Newman 1998):

$$\mathbf{n}_t | \mathbf{n}_{t-1} \sim \text{multivariate normal}(\mathbf{M}_t \mathbf{S}_{t-1} \mathbf{n}_{t-1}, \boldsymbol{\Sigma}_{n_t}), \quad t = 1, \dots, 16 \quad (3.27)$$

$$\mathbf{y}_t | \mathbf{n}_t \sim \text{multivariate normal}(\mathbf{H}_t \mathbf{n}_t, \boldsymbol{\Sigma}_{y_t}), \quad t = 1, \dots, 16. \quad (3.28)$$

The expected values are identical to the deterministic matrix models of Eqs. (2.18) and (2.22). The covariance matrix for the observations, $\boldsymbol{\Sigma}_{y,t}$, is a diagonal matrix with components $\sigma_{y,a,t}^2$, where

$$\sigma_{y,a,t}^2 = n_{a,t} h_{a,t} (1 - h_{a,t}), \quad (3.29)$$

which is the variance for a binomial($n_{a,t}$, $h_{a,t}$) random variable. The components of the covariance matrix for the states, $\boldsymbol{\Sigma}_{n_t}$, can be constructed similarly using the variances and covariances of binomial random variables (for survival) and multinomial random variables (for movement); Newman (1998) gives a detailed example of the construction. Sullivan (1992) used a similar approach to constructing the covariance matrix in an NDLM approximation to binomial state processes.

3.2.4 Deer Metapopulation

The deer metapopulation model (Sect. 2.7.2) had five sub-processes characterizing the dynamics of the two deer population abundances. For convenience the expected state vector model is shown again below.

$$E[\mathbf{n}_t | \mathbf{n}_{t-1}] = \mathbf{CBAM}_t \mathbf{S}_{t-1} \mathbf{n}_{t-1}$$

Letting \mathbf{n}' denote the transpose of the column vector \mathbf{n} ,

$$\mathbf{n}'_t = [n_{A,f,1,t}, n_{A,m,1,t}, n_{A,f,2,t}, n_{A,f,3+,t}, n_{A,m,2+,t}, n_{B,f,1,t}, n_{B,m,1,t}, \\ n_{B,f,2,t}, n_{B,f,t}, n_{B,m,t}],$$

abundances distinguished by population (A or B), sex (f or m), and age class (1, 2 or 3+ for females, and 1 or 2+ for males). The matrices correspond to the processes of survival (\mathbf{S}_{t-1}), movement between populations A and B (\mathbf{M}_t), age incrementation (\mathbf{A}), births (\mathbf{B}), and assignment of sex (\mathbf{C}). Age incrementation is treated as a deterministic process, but the remaining processes can be modelled stochastically. Similar to the *BRS* model above, sub-process pdfs are specified, say g_S, g_M, g_A (a deterministic function), g_B and g_C . Consequently, the pdf $g_t(\mathbf{n}_t | \mathbf{n}_{t-1})$ is a composite function, analytically intractable, but potentially easy to simulate from using the individual component pdf's. Relatedly, and of relevance to issues of model fitting addressed in Chap. 4, analytic evaluation of probabilities of states is only tractable by separately evaluating the pdf's for intermediate or "latent" states, the " u 's".

Here we describe one construction of $g_t(\mathbf{n}_t | \mathbf{n}_{t-1})$. Beginning with survival, survivors for each of the ten components of \mathbf{n}_t are independent binomial random variables with various survival probabilities [e.g. Eq. (2.29)]. Given the c th component of \mathbf{n}_{t-1} , the survivors $u_{1(s),c,t}$ have the following distribution:

$$u_{1(s),c,t} | n_{c,t-1} \sim \text{binomial}(n_{c,t-1}, \phi_{c,t-1}). \quad (3.30)$$

The survivors in each component then move from their current population to the other population with probabilities specified previously; e.g. $\mu_{A \rightarrow B,t}$ specifies the probability that an animal moves from population A to population B , Eq. (2.30). The number moving is modelled as a binomial random variable; e.g. the movement of first year females from A to B ,

$$u_{2(m),A \rightarrow B,f,1,t} | u_{1(s),A,f,1,t} \sim \text{binomial}(u_{1(s),A,f,1,t}, \mu_{A \rightarrow B,t}). \quad (3.31)$$

The new number in a given population (of sex s and age class a) is the sum of two independent binomial random variables, the "stayers" and the "movers", e.g. the first year females in B are those staying in B and those moving from A to B ,

$$u_{2(m),B,f,1,t} = u_{2(m),A \rightarrow B,f,1,t} + u_{2(m),B \rightarrow B,f,1,t}. \quad (3.32)$$

As explained in Sect. 2.7.2, within each population, age incrementation shifts surviving first-year females to the second-year females group, surviving second-year and older females are combined (and labelled older females), and all surviving first-year and older males are combined (as older males). The fourth sub-process, birth, is modelled as a binomial process, with different success probabilities for second-year females and for older females, Eq. (2.32); e.g. the total births, males and females (total denoted \cdot) in population A , are the sum of births from the two sets of fecund females,

$$u_{4(b),A,\cdot,1,t} = u_{4(b),A,\cdot,1(2),t} + u_{4(b),A,\cdot,1(3+),t} \quad (3.33)$$

where

$$u_{4(b),A,\cdot,1(2),t} | u_{3(a),A,f,2,t} \sim \text{binomial} (u_{3(a),A,f,2,t}, \rho_1) \quad (3.34)$$

$$u_{4(b),A,\cdot,1(3+),t} | u_{3(a),A,f,3+,t} \sim \text{binomial} (u_{3(a),A,f,3+,t}, \rho_2). \quad (3.35)$$

The final sub-process, sex assignment, is treated as another binary (Bernoulli) process, where the number of females in the newly born animals is binomial; e.g. the number of first-year females in population A ,

$$n_{A,f,1,t} | u_{4(b),A,\cdot,1,t} \sim \text{binomial} (u_{4(b),A,\cdot,1,t}, \alpha). \quad (3.36)$$

The observations were defined in Sect. 2.7.2 to be estimates of the total number of deer in each of the two populations, with no distinction between sex and age. Again lognormal distributions (with bias correction) are used; assuming independence between the population estimates,

$$y_{A,t} | \mathbf{n}_{A,\cdot,\cdot,t} \sim \text{lognormal} \left(\ln(\mathbf{n}_{A,\cdot,\cdot,t}) - \sigma_y^2/2, \sigma_y^2 \right) \quad (3.37)$$

$$y_{B,t} | \mathbf{n}_{B,\cdot,\cdot,t} \sim \text{lognormal} \left(\ln(\mathbf{n}_{B,\cdot,\cdot,t}) - \sigma_y^2/2, \sigma_y^2 \right) \quad (3.38)$$

where $\mathbf{n}_{A,\cdot,\cdot,t} = n_{A,f,1,t} + n_{A,m,1,t} + n_{A,f,2,t} + n_{A,f,3+,t} + n_{A,m,2+,t}$, and likewise for $\mathbf{n}_{B,\cdot,\cdot,t}$.