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### Citation for published version:

Newman, K 2019, Population Demography in Ecology. in *Handbook of Environmental and Ecological Statistics*. 1 edn, CRC Handbooks of Modern Statistical Methods, Chapman and Hall/CRC.

### Link:

[Link to publication record in Edinburgh Research Explorer](#)

### Document Version:

Version created as part of publication process; publisher's layout; not normally made publicly available

### Published In:

Handbook of Environmental and Ecological Statistics

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# 1

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## *Population Demography for Ecology* *Ken Newman*

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### CONTENTS

1.1	Introduction .....	3
1.2	Components of demography .....	5
1.2.1	Multiple subpopulations .....	6
1.2.2	Multiple processes .....	7
1.2.3	Stochasticity .....	7
1.2.4	Density dependence .....	7
1.2.5	Competitors, predators, and prey .....	8
1.2.6	Human manipulation of dynamics .....	8
1.2.7	Uncertainty in abundances .....	8
1.3	General mathematical features of PDMs .....	9
1.3.1	Multiple subpopulations .....	9
1.3.2	Multiple processes .....	9
1.3.3	Stochasticity .....	11
1.3.4	Density dependence .....	13
1.3.5	Inclusion of covariates .....	14
1.3.6	Remarks: Estimability and Data Collection. ....	14
1.4	Matrix Projection Models, MPMs .....	15
1.4.1	Analysis of MPMs .....	15
1.4.2	Limiting behavior of density independent, time invariant MPMs .....	16
1.4.3	Stochasticity .....	17
1.4.4	Building block approach to matrix construction .....	18
1.4.5	Determining the elements of projection matrices .....	19
1.4.6	Density dependent MPMs .....	19
1.5	Integral Projection Models, IPMs .....	20
1.5.1	Kernel structure of IPMs. ....	20
1.5.2	Implementation of an IPM .....	21
1.5.3	Estimation of kernel components .....	22
1.5.4	Application, use and analysis of IPMs .....	23
1.6	Individual Based Models, IBMs .....	23
1.6.1	Statistical designs for and analysis of IBMs .....	24
1.6.2	Comparison with population models .....	24

2 *Preprint: Chapter in Handbook of Environmental & Ecological Statistics*

1.6.3	Applications of IBMs .....	25
1.6.4	Data needs and structure .....	26
1.6.5	Relationship with IPMs .....	27
1.7	State-Space Models, SSMs .....	27
1.7.1	Normal dynamic linear models .....	27
1.7.2	Non-normal, nonlinear SSMS .....	28
1.7.3	Hierarchical and continuous time SSMS .....	29
1.8	Concluding Remarks .....	30
1.8.1	Omissions and sparse coverage .....	30
1.8.2	Recommended literature .....	30
1.8.3	Speculations on future developments .....	31

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## 1.1 Introduction

The word “Demography” is a combination of the ancient Greek words *demo*, meaning “the people”, and “graphy”, which refers to the “the writing or recording or study of”. One definition of demography is “the science of vital and social statistics, as of births, deaths, diseases, marriages, etc, of populations” (McGraw-Hill, 2005). Our focus here is on ecology and ecological populations, and demography will be defined as the scientific study and characterization of biological populations’ structure and dynamics. The simplest structure is total abundance at arbitrary points in time, while more complex structure includes abundances for multiple partitions of a population, e.g., numbers by sex, age, and spatial location. Dynamics refers to changes in structure and abundances over time as well as processes, sometimes called vital rates, which include reproduction, growth, maturity, movement, and mortality, that cause these changes.

People are interested in demography for a variety of reasons. One is inherent curiosity about abundances and dynamics. Why do the numbers of wolves (*Canis lupus*) on Isle Royale (in Lake Superior) fluctuate the way that they do? What effect will decreased snowpack levels have on the geographic range of American pika (*Ochotona princeps*) in Yosemite National Park? Answers to such questions require not only estimates of abundances of the species but also understanding of the factors that affect the abundances and dynamics.

For species harvested commercially, for sport, or for subsistence, e.g., salmon (*Oncorhynchus spp.*), red deer (*Cervus elaphus*), morel mushrooms (*Morchella spp.*), and black duck (*Anas rubripes*), people want to know how harvest affects population abundances and dynamics. Comparison of alternative harvest regulations is facilitated by predictions of the magnitude and sustainability of harvest levels. Predicting the effects of setting harvest regulations, e.g., a bag limit of 10 black ducks for a one month hunting season, requires some understanding of how this mortality might interact with other sources of mortality and other processes, like reproduction or movement. Estimates of the degree to which harvest mortality will be compensatory (removes individuals that would have died anyway from other factors) and additive (the number of animals that will be removed over and above those that would have died from other factors) are useful.

For species declared threatened or endangered by a government agency there are legal mandates for actions to be taken, or avoided, by managers of land or water resources inhabited by the species. Those actions can pertain directly to the population, such as to not take actions that could kill, harm, or harass the species, or indirectly to the species’s habitat. To recover the population, interest is in identifying actions to increase the species abundance, e.g., by restoring habitat, and predicting the effects of actions. For example, the United States Fish and Wildlife Service (USFWS) has a mandate to de-

43 velop “Conservation Management Plans” for species listed as threatened or  
44 endangered under the US Endangered Species Act. Such plans must include  
45 (a) specification of management actions to conserve the species, (b) measur-  
46 able criteria which would lead to a determination that the species can be  
47 “delisted”, no longer declared threatened, and (c) estimates of the time and  
48 cost to carry out such actions. Demographic models are central to identifying  
49 such actions, to predicting the effects of actions, and to prioritizing multiple  
50 actions.

51 Questions about demographics split into questions about *abundances* and  
52 about *processes*. *How many* individuals, or what volume or mass, are there,  
53 and were there previously, in the entire population and in subpopulations dis-  
54 tinguished by sex, location, age, or genotype? Answering this question is often  
55 quite challenging depending on the magnitude of the abundances, geographic  
56 location and range, physical size, mobility, degree of elusiveness, and ability  
57 to detect individuals. A variety of statistical sampling methods, e.g., mark-  
58 recapture, and technological tools and devices, e.g., radio tracking, have been  
59 developed to help provide answers to the *how many* question. A variety of  
60 methods of estimating population abundances are discussed in Williams et al.  
61 (2002), Borchers et al. (2002), Buckland et al. (2001) and Elzinga et al. (2009),  
62 with the latter focused on plant populations.

63 Even if population abundances were known with certainty, questions about  
64 population processes remain. Why were the numbers what they were last  
65 year and why are they what they are now? What are the relative effects  
66 of each process on abundances at specific points in time? For example, how  
67 do adult female fecundity rates of salmon, egg hatching success rates, and  
68 larval to juvenile survival combine to affect the abundance of juveniles? How  
69 do environmental conditions, both natural and anthropogenic, affect these  
70 processes?

71 The focus of this chapter is on mathematical and statistical approaches  
72 to answering such *process* questions. Answering these questions involves a  
73 population dynamics model (PDM), a quantification of the relationship be-  
74 tween past abundance and current abundances. PDMs can characterize how  
75 changes in environmental and anthropogenic factors influence population pro-  
76 cesses, and how changes in these processes translate into changes in popula-  
77 tion abundances. Measures of the degree of uncertainty as to the consequences  
78 are critical as well. For endangered species, PDMs are central to population  
79 viability analysis (PVA, Morris et al., 2002). PVAs use PDMs to make predic-  
80 tions about population trajectories, typically via computer simulation. PDMs  
81 are used to estimate extinction probabilities as a function of environmental  
82 conditions and anthropogenic factors, including accidents, like oil spills, and  
83 deliberate actions, like habitat restoration.

84 Answers to these initial what, why, and how questions often lead to further  
85 what, why, and how questions. Answers at the end of sequence of questions  
86 can lead to ideas about management actions to take and implementation of  
87 a particular action may then be justified by reversing the direction to yield a

88 so-called results chain (Margoluis et al., 2013). For example, a proposed man-  
89 agement action is to plant riparian vegetation along a stream where juvenile  
90 salmon rear. The results chain is the vegetation grows and provides increas-  
91 ing shade along the stream, the shade reduces water temperatures, lowered  
92 temperatures increases juvenile survival, and population abundance increases.  
93 This conceptual understanding guides data collection and long term biological  
94 monitoring programs (Reynolds et al., 2016), and further model development.  
95 To assess the effects of planting riparian vegetation, a monitoring program  
96 collects a time series of measurements of vegetation biomass, hours of shade,  
97 stream temperatures, juvenile abundances before and after the month of May  
98 (to estimate survival) at both treatment sites and control sites where no plant-  
99 ing is done (Before-After-Control-Impact BACI designs, Smith, 2002).

100 The organization of the remainder of this chapter is the following. Section  
101 1.2 is an overview of components of demography, including subpopulations and  
102 processes, while Section 1.3 is a progression of mathematical models more or  
103 less corresponding to these components. The next four sections discuss differ-  
104 ent approaches to modeling population dynamics. Section 1.4 discusses matrix  
105 population models (MPMs) which project the abundances of a finite and dis-  
106 crete set of sub-populations forward at discrete points in times. Section 1.5 is  
107 on integral projection models (IPMs), which can be viewed as extensions of  
108 MPMs where a continuous valued covariate, e.g., length, can be used to char-  
109 acterize sub-populations without arbitrary discretization of the covariate into  
110 disjoint intervals. Individual based models (IBMs), discussed in Section 1.6,  
111 are the ultimate partitioning of a population into multiple sub-populations  
112 where the life history of each individual member of the population is modeled  
113 separately. Section 1.7 is on state-space models (SSMs) which are statistical  
114 time series models that separate stochastic variation in processes from sta-  
115 tistical sampling error in estimates of population components, and can, in  
116 principle, contain MPMs, IPMs, and IBMs. Section 1.8 concludes the chapter  
117 with pointers to further literature on MPMs, IPMs, IBMs, and SSMs, com-  
118 ments on topics of demography that were minimally or not at all discussed,  
119 and thoughts about the future of biological demography.

120 For convenience some of the more frequently used acronyms are shown in  
121 Table 1.1.

---

## 122 1.2 Components of demography

123 The basic components of demography are abundances and processes. Total  
124 abundances at evenly spaced points in time are denoted  $n_t$ ,  $t=1,2,\dots,T$ . The  
125 simplest process is the change in abundance from one time point to the next.  
126 Such changes can be expressed either in an absolute sense,  $n_t - n_{t-1}$ , or a

**TABLE 1.1**

Listing of frequently used acronyms and their meaning.

Acronym	Meaning
PDM	Population Dynamics Model
MPM	Matrix Projection Model
IPM	Integral Projection Model
IBM	Individual-Based Model
SSM	State-Space Model
PVA	Population Viability Analysis

127 relative sense,  $n_t/n_{t-1}$ , and in both cases we refer to the change as population  
 128 growth.

129 If population abundance can be enumerated, then a succinct and com-  
 130 pletely accurate characterization of the population and its dynamics is trivial.  
 131 For example, the numbers of fish in an aquarium on July 1, 2011, July 1, 2012,  
 132 and July 1, 2013 were  $n_{2011} = 70$ ,  $n_{2012} = 61$ , and  $n_{2013} = 82$ , respectively.  
 133 The additive abundance changes were -9 and 21, and the relative changes were  
 134 0.87 and 1.34.

135 Exact enumeration is relatively rare and uninteresting in isolation. Com-  
 136 plexity in demographic modeling arises in several ways: (1) multiple subpop-  
 137 ulations, (2) multiple processes, (3) environmental and demographic stochas-  
 138 ticity, (4) density dependence, (5) competition and predation, (6) human ma-  
 139 nipulation of process dynamics, (7) uncertainty in abundances.

### 140 1.2.1 Multiple subpopulations

141 Multiple subpopulations are subsets of a populations that are distinguished by  
 142 attributes, including sex, age, sexual maturity level, spatial location, genotype,  
 143 and phenotype. Such partitioned populations are sometimes called structured  
 144 population, e.g., age-structured or stage-structured populations, and, in the  
 145 case of spatially distinct populations, metapopulations (Levins, 1969).

146 Partitioning can be subjective and arbitrary, and depends on the available  
 147 data. Arbitrariness occurs when the distinguishing attributes are continuous  
 148 variables, such as measures of individual size like weight, height, length. For  
 149 example, if the variable is weight, the number of partitions can vary as can  
 150 the labeling of the partitions; e.g., small =  $< 10$  kg,  $10 \leq$  medium  $< 20$ kg,  
 151 and large  $\geq 20$ kg. The partitioning of continuous attributes is an important  
 152 distinction between MPMs (Section 1.4) and IPMs (Section 1.5).

153 The finest partitioning of a population is at the individual entity level as  
 154 the values of each individual's characteristics throughout its entire existence  
 155 are the most complete description possible. This may be conceptually possi-

156 ble, but usually not practically possible. As a mathematical exercise, however,  
157 the modeling of individuals in a population can be useful for elucidating pop-  
158 ulation level dynamics and will be discussed in Section 1.6 on IBMs.

### 159 **1.2.2 Multiple processes**

160 The process of population growth can be partitioned into multiple processes  
161 that include at least survival and reproduction, but can also include move-  
162 ment, individual growth, and maturation. Partitioning a population into mul-  
163 tiple subpopulations can lead to additional process partitioning, e.g., age class  
164 specific survival probabilities. Partitioning by sex and size affects handling  
165 of reproduction, while spatial partitioning requires a movement process and  
166 location-specific movement probabilities.

167 Conversely, the temporal nature of processes, sequential, overlapping, or  
168 simultaneous, can lead to population partitioning. For example, a sequence of  
169 life cycle processes for salmon is egg fertilization in freshwater, egg hatching  
170 and larval emergence, survival to fry stage, smoltification, migration to the  
171 ocean, survival in the ocean, migration back to the freshwater, spawning, and  
172 death. Subpopulations of a cohort are then distinguished by life stage.

173 If size is a distinguishing characteristic, defined ordinally (e.g., small,  
174 medium, and large) or continuously (e.g., length in cm), then individual  
175 growth is a process affecting dynamics. Individual growth dynamics are quan-  
176 tified in terms of the probability of moving from one size class to another (as  
177 in MPMs, section 1.4) or by a conditional probability density function for size  
178  $z'_{t+1}$  given previous size  $z_t$  (as in IPMs, section 1.5).

### 179 **1.2.3 Stochasticity**

180 Population dynamics are complicated by environmental and demographic  
181 stochasticity. Environmental stochasticity is between year (or any time period)  
182 variation in underlying vital rates, such as survival or reproduction, that is  
183 typically due to variation in environmental conditions such as air temperature  
184 or precipitation. Demographic stochasticity is between-individual variability  
185 conditional on a specific vital rate; e.g., if the survival probability for 100 fish is  
186 0.7, the number surviving will not be exactly 70 and variation in that number  
187 is due to demographic stochasticity. Unless population numbers are relatively  
188 low, as for a severely endangered species, demographic stochasticity has lit-  
189 tle effect on population dynamics compared to environmental stochasticity.  
190 A rule of thumb when doing PVA, (Morris et al., 2002) is that demographic  
191 variation can be ignored in the case of a single population with at least 100  
192 individuals, and in the case of multiple subpopulations, or life stages, there  
193 are at least 20 individuals in the most important subpopulations.



194 **1.2.4 Density dependence**

195 As any population increases in abundance, resource limits necessarily reduce  
 196 population growth; e.g., values of  $n_t/n_{t-1} > 1$  cannot be sustained. Resource  
 197 limits directly affect survival and reproduction, and influence growth and  
 198 movement processes, as well, in other words, these vital rates are abundance  
 199 or density dependent. While decreasing abundance or density typically leads  
 200 to increases in survival and reproduction, there are situations where decreases  
 201 in abundance beyond a threshold lower vital rates; e.g., individuals have dif-  
 202 ficulty finding mates and cannot reproduce, what is known as an Allee effect,  
 203 a problem for critically endangered species.

204 **1.2.5 Competitors, predators, and prey**

205 Vital rate processes for a given species, say species A, can be affected by the  
 206 abundance of other species in several ways. If another species, species B, uses  
 207 the same resources, e.g., consumes the same prey items, the the species are  
 208 in competition, and the increased abundance of the competitor B lowers the  
 209 survival and reproduction of species A. If a third species, species C, preys upon  
 210 species A, then the abundance of the predator C obviously affects survival  
 211 of A. If a fourth species, species D, is a prey item, then its abundance can  
 212 also affect the vital rates of A. An important consideration in mathematical  
 213 modeling is whether abundances of competitors, predators, or prey are treated  
 214 as covariates, i.e., input variables for vital rates of a given species, or the  
 215 abundances of these other species are modeled simultaneously in a multi-  
 216 species PDM.

217 **1.2.6 Human manipulation of dynamics**

218 Human activities affecting population dynamics include harvest and species  
 219 protection. Survival probabilities in PDMs need to be modified by harvest, and re-  
 220 production and movement can also be affected. PDMs can be used to evaluate  
 221 alternative harvest regulations including cases of selective harvest of subpop-  
 222 ulations; e.g., only mature male red deer can be harvested during a summer  
 223 time period. For endangered populations, dynamics are manipulated by reg-  
 224 ulating human activities and carrying out actions to increase and improve  
 225 habitat. Projections of the effects of such regulations and actions on popula-  
 226 tion dynamics are central to PVA.

227 **1.2.7 Uncertainty in abundances**

228 Uncertainties about abundance, or vital rates, introduce uncertainty in PDMs  
 229 over and above the environmental and demographic stochasticity, what  
 230 (Nichols et al., 1995) label “partial observability”. The time at which samples  
 231 are taken can also affect the ability to estimate various process parameters,

232 and can affect mathematical model formulation. Rees et al. (2014) give an ex-  
 233 ample of a sequence of processes: reproduction, followed by mortality, and then  
 234 growth. If abundance estimates are made just before reproduction, abundance  
 235 change includes a term for the probability of the previous year's reproduction  
 236 (recruits) living an entire year. If abundance estimates are made just after  
 237 reproduction, the annual abundance change does not reflect the survival of  
 238 this year's reproduction as the estimates were made before subsequent mor-  
 239 tality, and the survival of the previous year's reproduction is entangled with  
 240 the survival of the previous year's abundance of old entities (non-recruits).  
 241 Inserting additional sampling or estimation points in the year is one means of  
 242 disentangling the effects of multiple processes.

---

### 243 1.3 General mathematical features of PDMs

244 Here we present various mathematical and probabilistic formulations of demo-  
 245 graphic models paralleling some of the features of Section 1.2. The simplest  
 246 demographic model is for a single population with a single deterministic and  
 247 density independent process. Such a model can be expressed in terms of abso-  
 248 lute or relative changes in abundance. Absolute changes,  $n_t - n_{t-1}$ , translate  
 249 into additive models,

$$n_t = n_{t-1} + \Delta_t, \quad (1.1)$$

250 with  $\Delta_t < 0$  and  $\Delta_t > 0$  indicating decline and growth, respectively, while  
 251 relative changes,  $n_t/n_{t-1}$ , translate into multiplicative models,

$$n_t = \lambda_t n_{t-1}, \quad (1.2)$$

252 with  $0 \leq \lambda_t < 1$  or  $\lambda_t > 1$  for decline or growth.

#### 253 1.3.1 Multiple subpopulations

254 Partitioning a single population into two or more populations extends the  
 255 scalar  $n_t$  to a vector  $\mathbf{n}_t$ . For example, if a population of deer is distinguished  
 256 by three life stages, young, immature, and mature, then the abundance vector  
 257 at time  $t$  is

$$\mathbf{n}_t = \begin{bmatrix} n_{y,t} \\ n_{i,t} \\ n_{m,t} \end{bmatrix}$$

258 The length of the abundance vector over time need not remain fixed. The ef-  
 259 fects of a sequence of processes may cause the vector to expand, e.g., following  
 260 reproduction, or to shrink, following an aggregation of age classes (Buckland  
 261 et al., 2007).

### 1.3.2 Multiple processes

*Survival and reproduction.*

With the additive single population model (1.1),  $\Delta_t$  can be partitioned into survival and reproduction components,

$$n_t = n_{t-1} + R_t - M_t \quad (1.3)$$

where  $R_t$  is the number of (surviving) young produced between  $t-1$  and  $t$  and  $M_t$  is the number of mortalities from the  $n_{t-1}$ .  $R_t$  and  $M_t$  may or may not be functions of  $n_{t-1}$ . In contrast, multiplicative models make explicit the dependence of change on previous abundance. Assume that in the interval  $(t-1, t)$  mortality occurs first (the fraction surviving begin  $\phi_t$ ), followed by reproduction (with rate  $\rho_t$ ), and there is no additional mortality before time  $t$ . Then the growth rate,  $\lambda_t$  (1.2), is simply the product of survival and reproduction:

$$n_t = (1 + \rho_t)\phi_t n_{t-1}. \quad (1.4)$$

The order of processes, mortality and reproduction, relative to the time of measurement ( $t$ ) does not affect  $\lambda_t$  in this case but the following cases demonstrate when order does matter.

A more complex model with subpopulations of young and mature individuals has different survival fractions for just born young and the mature individuals,  $\phi_{y,t}$  and  $\phi_{m,t}$ , and the time  $t$  at which abundances are counted relative to the reproductive process affects model formulation. For one scenario,  $t$  occurs immediately after reproduction, the young subpopulation are those just born (denoted  $n_{0,t}$  in Scenario 1 below). Under a second scenario,  $t$  occurs just before reproduction, and, assuming the time interval is one year, the young will be nearly age 1 at the time of counting (denoted  $n_{1,t}$  in Scenario 2).

Scenario 1: $t$ just after reproduction	$\begin{bmatrix} n_{m,t} = \phi_{m,t}n_{t-1} + \phi_{y,t}n_{0,t-1} \\ n_{0,t} = \rho_t(\phi_{m,t}n_{t-1} + \phi_{y,t}n_{0,t-1}) \end{bmatrix}$
Scenario 2: $t$ just before reproduction	$\begin{bmatrix} n_{m,t} = \phi_{m,t}n_{t-1} \\ n_{1,t} = \phi_{y,t}\rho_t n_{t-1} \end{bmatrix}$

*Immigration and emigration.*

The scalar additive model with reproduction and survival (1.3) can be extended to include immigration and emigration,

$$n_t = n_{t-1} + R_t - M_t + I_t - E_t$$

where  $I_t$  is the number immigrating into the population and  $E_t$  is the number emigrating from the population. The scalar multiplicative model (1.4) can be extended but does not necessarily remain multiplicative. The ordering of

291 processes is again important. Assuming that immigrants arrive, and emigrants  
292 leave after mortality occurs, but prior to reproduction, the model is

$$n_t = (1 + \rho_t)(\zeta_t \phi_t n_{t-1} + I_t)$$

293 where  $\zeta_t$  is the fraction of the survivors from  $n_{t-1}$  that stay and  $I_t$  is again the  
294 number of immigrants. If the order of processes change, the model changes. For  
295 example, suppose that immigrants arrive and emigrants leave after mortality  
296 and reproduction, then

$$n_t = \zeta_t \rho_t \phi_t n_{t-1} + I_t.$$

297 *Movement.*

298 For spatially-defined subpopulations, the process of movement is relevant.  
299 Immigration and emigration is of course a movement process but where the  
300 individuals are coming from or going to are not distinguished. A multiplicative  
301 formulation is more natural than an additive model, and a movement tran-  
302 sition matrix can be inserted into the dynamics equation, say  $\mathbf{n}_t = M_t \mathbf{n}_{t-1}$   
303 where survival and reproduction are ignored. For example with three regions  
304 labeled A, B, and C, a time invariant transition matrix has the following  
305 structure.

$$M = \begin{bmatrix} \mu_{A \rightarrow A} & \mu_{A \rightarrow B} & \mu_{A \rightarrow C} \\ \mu_{B \rightarrow A} & \mu_{B \rightarrow B} & \mu_{B \rightarrow C} \\ \mu_{C \rightarrow A} & \mu_{C \rightarrow B} & \mu_{C \rightarrow C} \end{bmatrix}$$

306 where  $\mu_{i \rightarrow j}$  is the probability of moving from area  $i$  to area  $j$  in one time step,  
307 and the rows sum to 1.

308 *Individual animal growth.*

309 For subpopulations distinguished by size classes, transition between classes can  
310 be modeled as the fractions moving from one class to another. The process  
311 is analogous to that for movement between spatial regions. For populations  
312 partitioned to the individual entity level, growth from the size, e.g., length or  
313 weight, at time  $t$ ,  $z_t$ , to another size at time  $t + 1$ ,  $z_{t+1}$ , can be modeled by  
314 the addition of an individual growth increment,  $x_{t+1}$ ,

$$z_{t+1}|z_t = z_t + x_{t+1}$$

315  $x_{t+1}$  could be a function of the size at time  $t$ ,  $z_t$ . Such fine scale handling of  
316 growth is central to IPMs (Section 1.5) and can be a part of IBMs (Section  
317 1.6).

### 318 1.3.3 Stochasticity

319 The mathematical distinction between demographic and environmental  
320 stochasticity is demonstrated using the scalar multiplicative model (1.2). De-

321 mographic stochasticity arises when, for a given year  $t$ , there is constant un-  
 322 derlying annual population growth rate, denoted  $\lambda$ , but there is between-  
 323 individual variation in the growth rate contribution. Environmental stochas-  
 324 ticity reflects between year variation in that underlying rate  $\lambda_t$ . Environmental  
 325 and demographic variation typically coincide, and a hierarchical model makes  
 326 clear the relationships:

$$\begin{array}{ll} \text{Environmental stochasticity} & \lambda_t \sim \text{Gamma}(\alpha, \beta) \\ \text{Demographic stochasticity} & n_t | n_{t-1}, \lambda_t \sim \text{Poisson}(n_{t-1} \lambda_t) \end{array}$$

327 *Asymptotic results for environmentally stochastic growth rates.*

328 The long term, or asymptotic, behavior of a single population trajectory with  
 329 environmentally stochastic annual growth rates is tractable and has similar-  
 330 ities with deterministic exponential growth models. Consider the following  
 331 single population model with environmental stochasticity only (ignoring the  
 332 issue of abundances necessarily being discrete values):

$$n_t = \lambda_t n_{t-1}, \text{ where } \lambda_t \stackrel{iid}{\sim} \text{Distribution}(\mu, \sigma^2) \quad (1.5)$$

333 where  $E[\lambda_t]=\mu$  and  $V[\lambda_t]=\sigma^2$ . Given an initial abundance  $n_0 > 0$ ,  $n_t$  can be  
 334 rewritten as

$$n_t = n_0 \prod_{i=1}^t \lambda_i$$

335 Taking the natural logarithm of both sides of the equation,

$$\ln(n_t) = \ln(n_0) + \sum_{i=1}^t \ln(\lambda_i),$$

336 which can be re-expressed as

$$\frac{\ln(n_t) - \ln(n_0)}{t} = \frac{1}{t} \sum_{i=1}^t \ln(\lambda_i) \quad (1.6)$$

337 The righthand side of (1.6) is the mean of a sequence of independent random  
 338 variables,  $\ln(\lambda_i)$ ,  $i = 1, \dots, t$ . Adding the assumption that the  $E(\ln(\lambda_t)^2) < \infty$ ,  
 339 the strong law of large numbers says that the average converges to  $E[\ln(\lambda)]$ .  
 340 Further, by the Central Limit Theorem, the asymptotic distribution the mean  
 341 of the log of the “annual” growth rates is normal. Denoting the sample average  
 342 log growth rate by  $\overline{\ln(\lambda)}$

$$\overline{\ln(\lambda)} = \frac{1}{t} \sum_{i=1}^t \ln(\lambda_i) \sim \text{Asymptotic Normal}(E[\ln(\lambda)], V(\ln(\lambda)))$$

343 Another way to express this result, using the lefthand side of (1.6),

$$\ln(n_t) \sim \text{Asymptotic Normal}(\ln(n_0) + tE[\ln(\lambda)], tV(\ln(\lambda)))$$

344 OR

$$n_t \sim \text{Asymptotic Lognormal}(n_0 \exp(tE[\ln(\lambda)]), tV(\ln(\lambda))) \quad (1.7)$$

345 Thus, the median population abundance at  $t$  is identical to a deterministic  
346 exponential growth model.

347 *Stochasticity in individual processes.*

348 Survival, reproduction, movement, individual animal growth, and other pro-  
349 cesses can be made stochastic. An example is a survival process for a scalar  
350 population with a logit-normal model for environmental stochasticity and a bi-  
351 nomial distribution for demographic stochasticity. Letting  $\phi_{c,t}$  be the survival  
352 probability for subpopulation  $c$  at time  $t$ ,

$$\begin{aligned} \text{logit}(\phi_{c,t}) &\sim \text{Normal}(\beta_{0,\phi,c}, \sigma_{\phi,c}^2) \\ n_{c,t} &\sim \text{Binomial}(n_{c,t-1}, \phi_c) \end{aligned}$$

353 where  $\text{logit}(x) = \ln(x/(1-x))$ .

### 354 1.3.4 Density dependence

355 In the ecological literature, there are several well-known single population,  
356 deterministic and discrete time-indexed models with density dependent pop-  
357 ulation growth rates including the Gompertz (Dennis et al., 2006), Ricker,  
358 Beverton-Holt, and logistic models (Gurney and Nisbet, 1998). Here we just  
359 present a deterministic Ricker model formulation (taken from Gurney and  
360 Nisbet, 1998). The Ricker model originated with fish populations, but is now  
361 applied many other kinds of populations.

$$\text{Ricker model} : n_t = (\phi_a + \phi_y b \exp(-cn_{t-1}))n_{t-1}, \quad b > 0, c > 0, \quad (1.8)$$

362 where  $n_t$  can be viewed as the sum of surviving adults from the previous year  
363 ( $\phi_a n_{t-1}$ ) and surviving progeny, with  $\phi_y$  the survival fraction for offspring  
364 produced at rate  $b \exp(-cn_{t-1})$ . The parameter  $b$  is the maximum number of  
365 offspring per adult, theoretically possible in the absence of any resource limita-  
366 tions, while  $\exp(-cn_{t-1})$  is a density dependent dampening of that maximum.

367 In the case of multiple subpopulations, if the vital rates and abundances  
368 for one subpopulation do not affect another subpopulation, then the above  
369 univariate density dependent models can be applied on a per subpopulation  
370 basis. If subpopulations occupy the same geographic area and compete for  
371 resources, then density dependent formulations will include the abundances of  
372 other subpopulations. Density dependent dynamics also arise for populations

373 of different species that are either in predator-prey relationships or competing  
 374 for an in-common resource.

375 In the case of multiple processes, e.g., survival, reproduction, movement,  
 376 and individual animal growth, process-specific density dependence relation-  
 377 ships can arise. In the Ricker model, for example, reproduction is density  
 378 dependent while survival is density independent. Density dependence in move-  
 379 ment processes for spatially distinct subpopulations (metapopulations) is  
 380 likely as the probability of movement from one region to another could be  
 381 a function of the relative densities of individuals in each region, e.g., the prob-  
 382 ability of moving from a high density region to a low density region increases  
 383 as the difference in densities increases. Of course, stochasticity can be incor-  
 384 porated into density dependent formulations for different processes.

385 Density dependence both within a single population and for populations  
 386 of two or more different species, e.g., predator and prey populations, can lead  
 387 to relatively complex population dynamics. The Lotka-Volterra predator-prey  
 388 model (Gurney and Nisbet, 1998) can with certain parameter combinations  
 389 lead to periodic oscillations in the abundances of each population. Within a  
 390 single population, discrete time single population models like the Ricker and  
 391 discrete logistic model can lead to damped or expanding oscillations, different  
 392 periodicities, or chaos (no periodicity and apparently random fluctuations;  
 393 (see, for example, Figure 2.6 in Gurney and Nisbet, 1998).

### 394 **1.3.5 Inclusion of covariates**

395 Mathematical formulations of population processes often include covariates,  
 396 one of the earliest examples being the modeling of survival as a function of  
 397 weather data (North and Morgan, 1979). The effects of deliberate human ma-  
 398 nipulations or incidental anthropogenic consequences, e.g., the erection of a  
 399 wind turbine and subsequent bird mortality, can be translated into covari-  
 400 ates for process models. Abundances of predators, competitors, or prey can  
 401 also be used as covariates in models for survival and reproduction of a single  
 402 species population dynamics model in contrast to jointly modeling the popu-  
 403 lation dynamics of several species. The legitimacy of such handling of these  
 404 other populations may depend upon the degree to which other populations  
 405 are affected by the abundance of the population of interest.

### 406 **1.3.6 Remarks: Estimability and Data Collection.**

407 It is easy to formulate a population dynamics model where the parameters  
 408 cannot be estimated given the available data. For example, annual surveys  
 409 alone do not allow separate estimation of the survival probability,  $\phi_t$ , and  
 410 reproductive rate,  $\gamma_t$ , in the simple univariate model (1.4). Intuitively given  
 411 estimates of  $n_t$  and  $n_{t-1}$  one can just estimate the combination  $(1 + \gamma_t)\phi_t$ .

412 One way to disentangle such combinations of parameters, in the case of se-  
 413 quential processes, is to have abundance estimates at time points immediately

414 after the end each process. For example, in the model (1.4) abundance should  
 415 be measured twice a year, once immediately following the survival process, and  
 416 once after reproduction. The reality of the processes is typically more com-  
 417 plicated, with such sharp demarcations unlikely, but formulating such models  
 418 can provide guidance for data collection.

---

## 419 1.4 Matrix Projection Models, MPMs

420 One of the oldest and most popular types of population dynamics models are  
 421 matrix projection models (MPMs). Lewis (1942) and Leslie (1945) independ-  
 422 ently proposed MPMs as a means of modeling the population dynamics of  
 423 age-structured populations (age-specific subpopulations). Let  $n_{0,t}$  denote the  
 424 number of young at time  $t$  and  $n_{a,t}$  be the abundance for ages 1 to  $A - 1$ ,  
 425 and  $n_{A+,t}$  be the abundance of age  $A$  and older individuals. A deterministic  
 426 formulation for the dynamics can be written as

$$\begin{bmatrix} n_{0,t} \\ n_{1,t} \\ n_{2,t} \\ \vdots \\ n_{A,t} \\ n_{A+,t} \end{bmatrix} = \begin{bmatrix} \gamma_0 & \gamma_1 & \gamma_2 & \dots & \gamma_{A-1} & \gamma_A \\ \phi_1 & 0 & 0 & \dots & 0 & 0 \\ 0 & \phi_2 & 0 & \dots & 0 & 0 \\ \vdots & 0 & 0 & \dots & \phi_A & \phi_{A+} \end{bmatrix} \begin{bmatrix} n_{0,t-1} \\ n_{1,t-1} \\ n_{2,t-1} \\ \vdots \\ n_{A,t-1} \\ n_{A+,t-1} \end{bmatrix} \quad (1.9)$$

427 or more compactly as  $\mathbf{n}_t = \mathbf{L}\mathbf{n}_{t-1}$ , where  $\mathbf{L}$  is referred to as a Leslie matrix,  
 428 and is analogous to the scalar multiplicative model (1.2). Lefkovich (1965)  
 429 proposed MPMs where subpopulations are distinguished by life stage, e.g.,  
 430 young, immature, and mature, thus a stage-structured model in contrast to an  
 431 age-structured model. Of course, partitioning by gender, genotype, and many  
 432 other subpopulation identifiers is possible. This simple structure,  $\mathbf{n}_t = \mathbf{L}\mathbf{n}_{t-1}$ ,  
 433 has been extended in many ways including time varying  $\mathbf{L}$ , the use of covariates  
 434 to model the components of  $\mathbf{L}$ , adding stochasticity and density dependence.

### 435 1.4.1 Analysis of MPMs

436 Apparently simple MPMs, such as (1.9), can yield complex dynamics depend-  
 437 ing upon the components of  $\mathbf{L}$ , and the many extensions of MPMs have added  
 438 to this complexity. To gain deeper understanding of the dynamics of MPMS,  
 439 Caswell (2001, p. 18) developed four sets of questions, which have been para-  
 440 phrased below.

- 441 1. *What is the asymptotic behavior of the MPM?* As time increases,  
 442 does the total population grow or decline exponentially? Do the rel-  
 443 ative proportions of each subpopulation become constant? Does the



444 population approach an upper bound (carrying capacity)? Do the  
 445 total population and individual subpopulation abundances oscillate  
 446 (in a damped or undamped manner)? Do the abundances display  
 447 periodicity? Do the abundances become chaotic?

- 448 2. *Is the MPM ergodic?* In other words, are the asymptotic dynamics  
 449 independent of the initial conditions, e.g., independent of the actual  
 450 values of  $\mathbf{n}_0$ ?
- 451 3. *What are the transient dynamics?* What are the dynamics like in  
 452 the short term as opposed to the asymptotic or limiting results?
- 453 4. *How sensitive are the results to the values of the elements of  $\mathbf{L}$ ?*  
 454 The survival probabilities and fecundity rates, for example, are es-  
 455 timates, and will have some degree of estimation error. How much  
 456 would the population dynamics, including asymptotic and tran-  
 457 sient dynamics, change if some elements of the matrix were changed  
 458 “slightly”?

459 We will not address all these questions further here and refer the inter-  
 460 ested reader to Caswell (2001). However we will briefly discuss one type of  
 461 asymptotic behavior, for both deterministic and stochastic MPMs, which is  
 462 analogous to single population exponential growth models.

#### 463 1.4.2 Limiting behavior of density independent, time invari- 464 ate MPMs

465 Results from matrix algebra can be used to describe the asymptotic behavior  
 466 of a time invariant projection matrix (see Caswell, 2001, chap 4.5). If the  
 467 matrix is (a) nonnegative (all elements are  $\geq 0$ ), (b) irreducible (e.g., every  
 468 age class can contribute to every other age class at some point in time), (c)  
 469 primitive (there is some positive integer  $k$  such that every element in the  
 470 matrix raised to the power  $k$ ,  $\mathbf{L}^k$ , is a positive number), then in the limit  
 471 the population dynamics are either exponential growth or decay, i.e.,  $A^T \mathbf{n}_t =$   
 472  $\lambda \mathbf{n}_t$ , where  $\lambda$  is a scalar value that is multiplied against each component of  
 473 the vector  $\mathbf{n}_t$ . Further, the relative proportions of each component of  $\mathbf{n}_t$  will  
 474 remain constant.

475 For example, consider an MPM with three age classes (Young, Adult,  
 476 Adult) and an initial abundance  $\mathbf{n}'_0 = (100, 50, 10)$  and the following Leslie  
 477 matrix

$$478 \mathbf{L} = \begin{bmatrix} \gamma_{Young} & \gamma_{Adult} & \gamma_{Old} \\ \phi_{Young} & 0 & 0 \\ 0 & \phi_{Adult} & \phi_{Old} \end{bmatrix} = \begin{bmatrix} 0.0 & 1.2 & 1.4 \\ 0.3 & 0.0 & 0.0 \\ 0.0 & 0.5 & 0.9 \end{bmatrix} \quad (1.10)$$

478 The population abundances over 9 iterations are:

---

Stage	1	2	3	4	5	6	7	8	9	10
Young	100	74	84	90	103	116	131	148	167	189
Adult	50	30	22	25	27	31	35	39	44	50
Old	10	34	46	52	59	67	76	86	97	109

---

479

480 The population growth rates, per stage, over time:

---

Stage	2	3	4	5	6	7	8	9	10
Young	0.74	1.13	1.08	1.14	1.12	1.13	1.13	1.13	1.13
Adult	0.60	0.74	1.13	1.08	1.14	1.12	1.13	1.13	1.13
Old	3.40	1.34	1.14	1.14	1.13	1.13	1.13	1.13	1.13

---

481

482 Thus after six generations the annual growth rate reaches 13% and stays there.

483 The fraction of the population in each stage class stabilizes as well:

---

Stage	1	2	3	4	5	6	7	8	9	10
Young	0.62	0.54	0.55	0.54	0.54	0.54	0.54	0.54	0.54	0.54
Adult	0.31	0.22	0.15	0.15	0.14	0.14	0.14	0.14	0.14	0.14
Old	0.06	0.25	0.30	0.31	0.31	0.31	0.31	0.31	0.31	0.31

---

484

485 Thus, after six generations the fractions in the Young, Adult, and Old stages  
486 remain 0.54, 0.14, and 0.31.

487 The limiting population growth rate and proportions of each category can  
488 be determined analytically using matrix algebra, in particular, by carrying  
489 out an eigen analysis of  $\mathbf{L}$ . For a  $p$  by  $p$  matrix  $\mathbf{L}$ , the eigen analysis yields  
490  $p$  eigenvalues,  $\lambda_1, \dots, \lambda_p$ , and  $p$  corresponding right eigenvectors,  $\mathbf{v}_1, \dots, \mathbf{v}_p$ .  
491 An eigenvalue and its corresponding eigenvector have the relationship,  $\mathbf{L}\mathbf{v}_i$   
492  $= \lambda_i\mathbf{v}_i$ . Denote the largest eigenvalue  $\lambda_1$  and its corresponding eigenvector  
493  $\mathbf{v}_1$ . Then  $\lambda_1$  is equal to limiting population growth rate, in the example 1.13  
494 (more precisely, 1.12938), and dividing each element of  $\mathbf{v}_1$  by its total yields  
495 the limiting fractions, here (0.54, 0.14, 0.31).

### 496 1.4.3 Stochasticity

497 One way to add stochasticity to MPMs is to randomly draw elements of the  
498 matrix from probability distributions, e.g., randomly draw survival probabili-  
499 ties for age  $a$  individuals, thereby introducing environmental stochasticity.  
500 Under some conditions, in the absence of density dependence for example,  
501 the introduction of environmental, or demographic, stochasticity will not ap-  
502 precibly alter the asymptotic dynamics from that of a deterministic MPM.  
503 In other words, the above eigen analysis results more or less hold: in the  
504 limit there is an average growth rate and stable population structure. Caswell  
505 (2001, Chap. 14) provides details of these results (with some of earliest work

506 from Cohen, 1976; Tuljapurkar and Orzack, 1980). Below we closely follow  
 507 (Caswell, 2001, p. 393) and somewhat mimic the derivation of the asymp-  
 508 totic distribution of the stochastic univariate model shown in (1.5 - 1.7). We  
 509 start with a stochastic process of matrices,  $\mathbf{L}_1, \mathbf{L}_2, \dots$ , which satisfy certain  
 510 regularity conditions, including being stationary (the joint distribution for  
 511  $(\mathbf{L}_{t_1}, \mathbf{L}_{t_2}, \dots, \mathbf{L}_{t_n})$  is the same as that for  $(\mathbf{L}_{t_1+h}, \mathbf{L}_{t_2+h}, \dots, \mathbf{L}_{t_n+h})$  for any fi-  
 512 nite  $n > 0, t_1, t_2, \dots, t_n$ , and  $h > 0$ ), and ergodic (roughly put, the initial value  
 513 of  $\mathbf{L}_1$  does not affect the eventual behavior of the sequence). Further assume  
 514 an upper bound on the magnitude of the initial matrix,  $E(\ln^+ \|\mathbf{L}\|_1) < \infty$ ,  
 515 where  $\|\mathbf{L}\| = \sup_{\mathbf{n} \neq 0} \frac{\|\mathbf{L}\mathbf{n}\|}{\|\mathbf{n}\|}$  and  $\ln^+(x) = \max(0, \ln(x))$ . The total population  
 516 size at time  $t$ , denoted  $N(t)$ , is the vector norm of  $\mathbf{n}_t$  ( $\|\mathbf{n}_t\| = \sum_i |n_{t,i}|$ ). Given  
 517 an initial vector  $\mathbf{n}_0$ :

$$N(t) = \|\mathbf{n}_t\| = \left\| \prod_{i=1}^t \mathbf{L}_i \mathbf{n}_0 \right\| \quad (1.11)$$

$$\Rightarrow \frac{1}{t} \ln(N(t)) = \frac{1}{t} \ln \left\| \prod_{i=1}^t \mathbf{L}_i \mathbf{n}_0 \right\|. \quad (1.12)$$

518 Furstenberg and Kesten (1960) proved that, with probability 1, the limit of  
 519 (1.12) exists:

$$\lim_{t \rightarrow \infty} \frac{1}{t} \ln(N(t)) = \lim_{t \rightarrow \infty} \frac{1}{t} \ln \left\| \prod_{i=1}^t \mathbf{L}_i \mathbf{n}_0 \right\| = \ln(\lambda_s), \quad (1.13)$$

520 where  $\lambda_s$  is called the stochastic growth rate. Lower and upper bounds on  $\lambda_s$   
 521 can be calculated from the average minimum row sums and average maximum  
 522 row sums of the matrices, namely,

$$\sum_i \pi_i R_{\min}^{(i)} \leq \ln(\lambda_s) \leq \sum_i \pi_i R_{\max}^{(i)} \quad (1.14)$$

523 where  $\pi_i$  is the asymptotic probability of environment  $i$  occurring (correspond-  
 524 ing to matrix  $\mathbf{L}_i$ ) and  $R_{\min}^{(i)}$  and  $R_{\max}^{(i)}$  are the minimum and maximum row  
 525 sums of  $\mathbf{L}_i$  (Caswell, 2001, p. 395).

526 With further conditions on the matrices,  $\mathbf{L}_i$ , including nonnegativity, the  
 527 asymptotic distribution of the population total is lognormal:

$$N(t) \sim \text{Asymptotic Lognormal}(\exp(t \ln(\lambda_s)), t\sigma^2) \quad (1.15)$$

528 where  $\sigma^2$  is some constant. Thus, similar to (1.7), the asymptotic median of the  
 529 population total is the same as for a univariate exponential population growth  
 530 model, and  $\lambda_s$  is analogous to the largest eigenvalue,  $\lambda_1$ , of a deterministic  
 531 MPM.

#### 532 1.4.4 Building block approach to matrix construction

533 Deterministic skeletons for relatively complex MPMs can be constructed using  
 534 a building block approach (Buckland et al. (2007); Newman et al. (2014)).  
 535 A crucial assumption is the approach is that there is a particular sequence  
 536 to processes which operate on a vector of population abundances, such as  
 537 survival, then movement, then reproduction. An example from Newman et al.  
 538 (2014, eq. 2.11, p. 18) has two size-class subpopulations, small and large, and  
 539 a sequence of three processes: survival, followed by growth (from small to  
 540 large), and then reproduction. The survival probabilities are size specific ( $\phi_S$   
 541 and  $\phi_L$ ), the probability that a small individual becomes large is  $\pi$ , and only  
 542 large individuals can reproduce and they do so with rate  $\rho$ .

$$\begin{aligned} \begin{bmatrix} n_{S,t} \\ n_{L,t} \end{bmatrix} &= \begin{bmatrix} 1 & \rho \\ 0 & 1 \end{bmatrix} \begin{bmatrix} 1 - \pi & 0 \\ \pi & 1 \end{bmatrix} \begin{bmatrix} \phi_S & 0 \\ 0 & \phi_L \end{bmatrix} \begin{bmatrix} n_{S,t-1} \\ n_{L,t-1} \end{bmatrix} \\ &= \begin{bmatrix} (1 - \pi + \rho\pi)\phi_S & \rho\phi_L \\ \pi\phi_L & \phi_L \end{bmatrix} \begin{bmatrix} n_{S,t-1} \\ n_{L,t-1} \end{bmatrix} = \mathbf{L}\mathbf{n}_{t-1} \end{aligned} \quad (1.16)$$

543 The matrix in (1.16) is an example of a Lefkovich matrix which is arguably  
 544 more simply constructed by using such a building block approach than by  
 545 trying to construct the final matrix in a single operation.

#### 546 1.4.5 Determining the elements of projection matrices

547 The most common way to use MPMs has been to plug in estimates of ma-  
 548 trix components from various, and often independent, studies, and then make  
 549 population projections using those point estimates. Caswell (2001, p. 22), for  
 550 example, states that, to fill the elements of the matrix, life tables are used.  
 551 Life tables contain mortality probabilities, the probability that an individual  
 552 of age  $a$  will die before reaching age  $a + 1$ , and maternity functions, the ex-  
 553 pected number of offspring that an age  $a$  individual will produce in the next  
 554 year, from which survival probabilities  $\phi$  and reproductive rates  $\gamma$  (1.9) can  
 555 be calculated. However, how mortality probabilities and maternity functions  
 556 are constructed in the first place may be no trivial task. With wildlife pop-  
 557 ulations, mark-recapture studies where animals are aged at time of marking  
 558 can provide estimates of age-specific survival, and, in some situations, esti-  
 559 mates of reproductive success. Of course, the addition of more subpopulations  
 560 and processes increases the “data requirements and mathematical complex-  
 561 ities [which] can quickly overwhelm an investigation of these parameter-rich  
 562 models” (Williams et al., 2002, p161).

563 An alternative to the above approach of estimating matrix elements sep-  
 564 arately from inference about population abundances is to combine stochas-  
 565 tic population dynamics with statistical sampling error, or estimation uncer-  
 566 tainty, in matrix elements and population abundances. The SSM framework  
 567 provides a structure for doing this and is discussed in Section 1.7.

568 **1.4.6 Density dependent MPMs**

569 Density dependence can be introduced into MPMs by simply making some  
 570 of the elements of the projection matrix density dependent. For example,  
 571 referring to (1.10), the fecundity of the old group could be expressed as  
 572 a function of the total abundance of adult and old individuals,  $\gamma_{Old,t} =$   
 573  $(n_{Adult,t} + n_{Old,t}) \exp(-c(n_{Adult,t} + n_{Old,t}))$ , a variant of the Ricker model.  
 574 The linearity aspect of the MPM is subsequently altered and the analyses  
 575 carried out for density independent MPMs do not directly apply, e.g., the  
 576 eigen analysis is no longer directly applicable. See Caswell (2001, Chap. 16)  
 577 for detailed discussion of a variety of density dependent models, subsequent  
 578 dynamics, and analytical approaches.

---

 579 **1.5 Integral Projection Models, IPMs**

580 The partitioning of a population into discrete subpopulations, namely for-  
 581 mulating a structured population, may be arbitrary when natural divisions  
 582 are lacking. For example, suppose individual weight (in kg) is the feature  
 583 used to subdivide the population for an MPM. The specified weight classes,  
 584 small, medium, and large, necessarily have arbitrary boundaries, say, (0,5),  
 585 [5,10), [10+]. An animal weighing 4.99 kg is labeled small and one weighing  
 586 5.0 kg is medium. Those two individuals will be treated differently in terms  
 587 of population processes, e.g., the survival probability is 0.5 for small individ-  
 588 uals and 0.8 for medium individuals, while the actual survival probabilities  
 589 for both individuals may be much more similar. Integral Projection Models  
 590 (IPMs; Easterling et al., 2000), sometimes called integrodifference equation  
 591 models (see Caswell, 2001, for historical references), are a modeling approach  
 592 that maintains the continuous nature of a factor that distinguishes population  
 593 members, while (generally) maintaining the discrete time step characteristic  
 594 of MPMs.

595 **1.5.1 Kernel structure of IPMs.**

596 The core of an IPM is the *kernel*, denoted  $K(z'_{t+1}|z_t)$ , which is analogous to  
 597 an element in the transition matrix of an MPM. The kernel can be viewed  
 598 as a conditional probability density function for the “probability” that an  
 599 animal of size  $z$  at time  $t$ , denoted  $z_t$ , is size  $z'$  at time  $t + 1$ , denoted  $z'_{t+1}$ .  
 600 The word probability is put in quotation marks as this is a density not a  
 601 probability. More accurately  $K(z'_{t+1}|z_t)\Delta$  is an approximate probability for  
 602 such a movement from size  $z_t$  to a size in an interval of width  $\Delta$  containing  
 603  $z'_{t+1}$ , e.g.,  $z'_{t+1} \pm 0.5\Delta$ . The number of individuals in a given size class at  
 604 time  $t + 1$  is then the sum of all individuals of *any* size class at time  $t$ ,  $n(z_t^*)$ ,

605 that survive, grow, and/or contribute to individuals of size class  $z_{t+1}$  at time  
606  $t + 1$  where  $z_t^* \in \Omega$  and  $\Omega$  is a suitably large range of sizes, so

$$n(z_{t+1}) = \int_{z_t \in \Omega} K(z_{t+1}|z_t)n(z_t)dz_t \quad (1.17)$$

607 A simpler version of the kernel is time invariant,  $F(z'|z)$ , where the conditional  
608 density for the contribution to size class  $z'$  at time  $t + 1$  from size class  $z_t$  is  
609 the same for all times  $t$ .

610 The population growth process is the result of multiple processes, including  
611 survival and reproduction. So the kernel  $K$  can be decomposed into survival  
612 of the current population and reproduction entering the population. Here,  
613 however, individual size is also a factor and survival and reproduction is into  
614 a specific size class,  $z_{t+1}$ . Thus growth from size class  $z_t$  to  $z_{t+1}$  is a third  
615 process to account for. The resulting partitioning of the kernel is

$$K(z_{t+1}|z_t) = P(z_{t+1}|z_t) + F(z_{t+1}|z_t) \quad (1.18)$$

616 where  $P$  is the survival/growth kernel, the combined conditional density for  
617 surviving to time  $t + 1$  and changing to size class  $z_{t+1}$ , and  $F$  is the fecundity  
618 kernel, the conditional density for recruits at time  $t + 1$  of size  $z_{t+1}$  (Merow  
619 et al., 2014).

620 There are a wide variety of formulations for the survival/growth kernel.  
621 One formulation is to treat the two processes as independent, the result be-  
622 ing the product of the conditional probability of surviving,  $\phi(z_t)$ , and the  
623 conditional density of moving to size class  $z'$ ,  $g(z'_{t+1}|z_t)$ :

$$P(z'_{t+1}|z_t) = \phi(z_t)g(z'_{t+1}|z_t) \quad (1.19)$$

624 In principle, a joint density for survival and growth could be used; e.g., move-  
625 ment to a much larger size class is linked with lowered survival probability.  
626 The survival probability could be a more complicated function of competing or  
627 sequential mortality factors; e.g., there are two mortality processes occurring  
628 in sequence,  $\phi(z_t) = \phi_{1,z_t}\phi_{2,z_t}$ .

629 The fecundity kernel can be made complex as well. For example, it could be  
630 a function of four processes: a size dependent probability distribution for the  
631 number of eggs produced,  $f(E|z_t)$ , a probability that the eggs are fertilized,  
632  $p_E$ , a probability that the fertilized eggs will hatch,  $p_h$ , and a density function  
633 for the size of hatched larvae,  $h(z')$ . Then

$$F(z'_{t+1}|z_t) = f(E|z_t)p_Ep_hh(z') \quad (1.20)$$

634 Merow et al. (2014) note that a common feature of the survival/growth  
635 and fecundity kernel formulations is an *individual component*, e.g.,  $\phi(z_t)$  in  
636 (1.19) and  $(f(E|z_t)p_Ep_h)$  in (1.20), and a *size redistribution component*, e.g.,  
637  $g(z'_{t+1}|z_t)$  in (1.19) and  $h(z')$  in (1.20).

638 **1.5.2 Implementation of an IPM**

639 Equation (1.17) is analogous to the generation of a single component in the  
 640 state vector of an MPM. With an MPM, the entire state vector at time  $t + 1$   
 641 is  $\mathbf{n}_{t+1} = L\mathbf{n}_t$ , where the  $i$ th entry in  $\mathbf{n}_{t+1}$ , denoted  $n_{i,t+1}$ , is the following  
 642 sum:

$$n_{i,t+1} = \sum_{j=1}^p L_{i,j} n_{j,t} \quad (1.21)$$

643 where  $L$  has  $p$  columns. Each  $L_{i,j}$  in the summation is akin to a kernel function  
 644 as it is the per individual contribution from “size” class  $i$  at time  $t$  to “size”  
 645 class  $j$  from time  $t + 1$ . If the vector  $\mathbf{n}_t$  is further partitioned into a relative  
 646 large number of size classes, the summation operation in (1.21) approaches an  
 647 integration operation.

648 Implementation of an IPM is in practice the reverse operation. Referring  
 649 to the integral in (1.17), the interval  $\Omega$ , which contains the range of size classes  
 650 that can contribute to size class  $z_t$ , is partitioned into  $m$  size classes. A finite  
 651 sum approximation to integration, e.g., the midpoint rule, the trapezoid rule,  
 652 or Simpson’s rule, is used calculate the number of individuals in size class  
 653  $z_t$ . An example of the midpoint rule: suppose  $\Omega$  is an interval  $[L, U]$  which  
 654 is partitioned into  $m$  intervals of equal length  $(U - L)/h$ , and let  $z_i$  be the  
 655 midpoint of the  $i$ th size class, also known as mesh points (Rees et al., 2014),  
 656 where

$$z_i = L + (i - 0.5) * h, \quad i = 1, 2, \dots, m$$

657 The integral (1.17) can be approximated by

$$n(z_{t+1}) \approx \sum_{i=1}^m K(z_t|z_i) h n(z_i, t) \quad (1.22)$$

658 **1.5.3 Estimation of kernel components**

659 The problem of specifying kernel components parallels the problem of de-  
 660 termining components of the transition matrices in MPMs. Assuming that  
 661 relevant data on size, survival, reproduction success, etc, are available, there  
 662 are many standard statistical model fitting procedures, linear regression, non-  
 663 linear regression, generalized linear models including logistic regression, and  
 664 generalized additive models, that can be used to construct the components of  
 665  $K(z_{t+1}|z_t)$ . Likewise, many of the associated model fit diagnostic procedures  
 666 could, and should be, used to assess the quality of the estimated components  
 667 of the kernel (Rees et al., 2014).

668 A number of probability and density functions are needed to calculate the  
 669 transition densities of the survival/growth kernel (e.g., (1.19), and the fecun-  
 670 dity kernel (e.g., (1.20)). For individual components that are probabilities,

671 e.g., the conditional probability of survival, sample data on size conditional  
672 outcomes can be used to calculate estimates. For example, a mark-recovery  
673 study of banded ducks could provide size-specific annual survival probabilities  
674 based on a smooth fitted survival function, e.g.,  $\log(\phi/(1-\phi))|z = \beta_0 + \beta_1 z$ .  
675 Whether or not time-specific functions could be fit may depend upon the num-  
676 ber of years of data available. Survival probabilities can be a function of size  
677 and environmental covariates, e.g., winter temperatures. For size redistribu-  
678 tion components, such as the conditional density for moving from size class  $z$   
679 to  $z^*$  in (1.19), size measurements made over time on multiple individuals are  
680 required.

681 Inference methods for IPMs are continually developing. For example,  
682 Ghosh et al. (2012) use Bayesian hierarchical models where the size distribu-  
683 tion is a point pattern on some interval and carry out an integrated analysis  
684 that combines the parameter estimation/model fitting stage and the projec-  
685 tion stage.

#### 686 1.5.4 Application, use and analysis of IPMs

687 Plant species were the most common organisms in early applications of IPMs,  
688 e.g., Northern Monkhood (Easterling et al., 2000), with growth transitions  
689 between different plant sizes, e.g., stem diameter, and processes like flower-  
690 ing strategies. The scope of applications has since expanded to include birds  
691 (Great tits, Childs et al., 2016), arachnids (soil mites, Brooks et al., 2015),  
692 mammals (Soay sheep), diseases (hosts and parasites, Metcalf et al., 2016).

693 The questions asked of MPMs in Section 1.4.1 can be asked of IPMs.  
694 Is there a limiting population growth rate, a dominant eigenvalue  $\lambda_1$  and  
695 corresponding stable “size” class distribution? Ellner and Rees (2006) gives  
696 examples of sensitivity analyses of IPMs. Software for IPMs includes the R  
697 package `IPMpack`.

698 In addition to analysis of population dynamics, ecological inference us-  
699 ing IPMs includes analysis of evolutionary strategies (Ellner and Rees, 2006).  
700 Brooks et al. (2015) separated out the effects of individual body size on devel-  
701 opmental rates from the effects of environmental conditions on reproductive  
702 rates. Metcalf et al. (2016) examined the feedback between host and parasite  
703 in an epidemiological analysis.

---

## 704 1.6 Individual Based Models, IBMs

705 Individual based models in ecology (IBMs; DeAngelis and Grimm, 2013) are  
706 computer simulation procedures that can track the entire life history of mul-  
707 tiple individuals simultaneously. Variables tracked include emergence into the  
708 population (date of birth, germination, hatch date), size at birth, sex, size



709 over time, time and duration of sexual maturity and reproduction, spatial  
710 location and movement, senescence, and death. A central feature is the mod-  
711 eling of interactions of individuals with each other, including individuals of  
712 the same species, e.g., reflecting competition for resources and density de-  
713 pendence, and individuals of different species, e.g., reflecting predator-prey  
714 dynamics or, more broadly, ecological community interactions. Another key  
715 feature is the simulation of interactions of individuals with their abiotic envi-  
716 ronment, e.g., air temperature and precipitation, and their biotic environment  
717 excluding like individuals, e.g., vegetative browse and zooplankton.

718 The opportunity to insert complexity into dynamic processes underlying  
719 demographics is relatively unlimited, constrained primarily by computer stor-  
720 age and processing speed. Population level properties can be examined at  
721 any time in the simulation process by aggregating the states of individuals  
722 in arbitrary ways. For example, a simulation starts at time  $t_0$  with a vector  
723 of 1000 individuals where each individual has an associated vector of initial  
724 conditions such as age, weight, sex, spatial location, and maturity. Survival,  
725 growth, movement, and reproduction processes are then applied to each in-  
726 dividual and, at time  $t_1$ , numbers of individuals in different spatial regions  
727 further distinguished by sex and age class, say, are tallied to yield abundances  
728 of multiple subpopulations. Repeating the simulation and aggregation  $K$  times  
729 yields a multivariate time series of subpopulation abundances,  $\mathbf{n}_{t_1}, \mathbf{n}_{t_2}, \dots,$   
730  $\mathbf{n}_{t_K}$ . Analysis of population level dynamics can then be conducted, studying  
731 such things as the effects of region-specific harvest regulations on different  
732 sub-populations of deer, for example. If the effects of environmental and an-  
733 thropogenic factors on the population dynamics cannot be readily examined  
734 analytically, IBM output can provide some experiential, albeit simulated, in-  
735 sight.

### 736 1.6.1 Statistical designs for and analysis of IBMs

737 The simulation nature of IBMs with multiple attributes and multiple levels  
738 to attributes lends itself to using methods from the statistical design of ex-  
739 periments to construct a time series of any length with an arbitrary number  
740 of sub-populations. For example, if the attributes of interest are sex, spatial  
741 location, and age class with corresponding levels of (female, male), (I, II, III,  
742 IV) regions, and ages (0,1,2,3+), then a factorial design with  $2 \times 4 \times 4 = 32$   
743 “treatment” combinations can be conducted with  $r$  replications of each com-  
744 bination. Statistical methods such as analysis of variance or response surface  
745 modeling can then be used to examine the effects of the factors and treat-  
746 ment combinations. Aggregated data can be used to construct simple MPMs,  
747 like year-specific Leslie matrices, and methods for assessing MPMs, such as  
748 calculating annual finite population growth rates for multiple years can be  
749 employed (for such an example, see Rose et al., 2013).

750 The computational burden of IBMs can grow in a number of ways. First,  
751 as the number of attributes of interest and the levels of each attribute in-

752 creases, the number of treatment combinations can grow rapidly. Second, as  
753 the level of environmental stochasticity (or demographic) increases, the num-  
754 ber of replicates required to provide a desired level of precision for estimates  
755 of average population level responses increases as well. Third, questions about  
756 the effects of the distribution of initial attribute values at time  $t_0$  as well as  
757 questions about the nature of the processes, e.g., density dependent or density  
758 independent recruitment success or the chosen value, or distribution of values,  
759 for juvenile survival probabilities, can lead to extensive sensitivity analyses.

### 760 1.6.2 Comparison with population models

761 In contrast to population models, such as the Ricker model (1.8), for which  
762 long term population dynamics such as exponential growth, an asymptotic  
763 upper bound, or periodicity can sometimes be determined analytically or by  
764 elementary computer simulation, population-level behavior for IBMs is an  
765 *emergent* property. The dynamics are the result of potentially complex in-  
766 teractions of individuals with each other and with their abiotic environment  
767 (DeAngelis and Grimm, 2013), and can demonstrate “the importance of local  
768 interactions between individuals in ecological systems” (Judson, 1994).

769 A succinct way to contrast population-level models and IBMs is top-down  
770 versus bottom-up. Population-level models are *top-down* in that they predict  
771 what happens to individuals as function of population level characteristics,  
772 e.g., fecundity of the individual decreases as the total population abundance  
773 increases (density dependence exists). Conversely, IBMs are *bottom-up* in that  
774 modeling begins with the characteristics of multiple individuals and mani-  
775 fests characteristics of the population as a whole. An interesting example of  
776 the latter is with *Anolis* lizards in the Caribbean (discussed in Roughgarden,  
777 2012) where an IBM simulated energy gained per unit time after a lizard con-  
778 sumed a prey item as a function of distance from the prey and the optimal  
779 foraging distance could then be determined. From that model for the “energy  
780 capture” the daily growth rate of the lizard was predicted, with distinction  
781 made between growth prior to reproductive stage and during the reproductive  
782 stage. Using these results an optimal growth rate, as a function of age, was  
783 calculated, which was then used with information on survival probabilities  
784 and maternity rates to determine that optimal female body size was 45mm.  
785 As Roughgarden (2012) said “[t]his example illustrates a complete and suc-  
786 cessful modeling protocol that begins with the properties of an individual and  
787 culminates in the an evolutionary prediction of the adult body size for lizards  
788 on an island in the absence of congeneric competitors”.

### 789 1.6.3 Applications of IBMs

790 The earliest applications of IBMs in ecology were mostly in forestry, and such  
791 applications remain common. In the IBM JABOWA (Botkin et al., 1972),  
792 individual trees were the fundamental entities and the central measure on each

793 tree was its stem diameter (at some height on the tree). Other tree measures  
794 such as volume and crown biomass can be functions of diameter. Emergence,  
795 growth, and death of a tree are functions of interactions with neighboring trees,  
796 their size and proximity and the degree to which they compete for resources  
797 like light and water, for example, and functions of interactions with the abiotic  
798 environment, e.g., soil type and chemistry, precipitation, temperature, and  
799 light. Forestry IBMs have been used for management purposes, e.g., to predict  
800 growth and yield of commercially harvested species, as well as purely scientific  
801 reasons, i.e., to “explore ecological mechanisms and patterns of structure and  
802 functional dynamics in natural forest ecosystem” (Liu and Ashton, 1995).

803 Applications to fish populations are common as well, where IBMs “track  
804 the attributes of individual fish through time and aggregate them to generate  
805 insights into population function” (Van Winkle et al., 1993). IBMs simulate  
806 how fish of different phenotypes interact with their biotic and abiotic environ-  
807 ment. Differences in phenotype can refer to differences in length, weight, sex,  
808 and age, the biotic environment can include prey items, such as zooplankton or  
809 vegetation, and the abiotic environment can include water temperature, salin-  
810 ity, water clarity. An IBM for a small estuarine fish, delta smelt (*Hypomesus*  
811 *transpacificus*, Rose et al., 2013) also included bioenergetics considerations,  
812 namely the transformation of consumed prey into fish growth.

813 IBMs in ecology can be broadly divided into applications for (individual)  
814 populations, communities and ecosystems. Single population-level IBMs have  
815 been mentioned above, e.g., *Anolis* lizards and Delta Smelt, but IBMs have  
816 used to model predator-prey dynamics (Cuddington and Yodzis, 2002). A  
817 community-level application by Weiss et al. (2014) used an IBM to simulate  
818 how the dynamics of a community assembly of 90 hypothetical plant types  
819 were affected by soil attributes and grazing intensities. The results were then  
820 compared to field-based observations of species richness and diversity. Least  
821 common are ecosystems level applications; a hypothetical food web system  
822 used an IBM to model interactions between three trophic levels, plant, herbi-  
823 vore and carnivore (Schmitz and Booth, 1997).

#### 824 1.6.4 Data needs and structure

825 IBMs have at least three levels of data needs. One is an initial individual  
826 attribute vector (Van Winkle et al., 1993), and initial values for components  
827 of the biotic and abiotic environment. When proximity to other individuals  
828 is a factor in the dynamics, an initial spatial distribution is needed and loca-  
829 tions might be randomly placed as in a Poisson process, systematically placed,  
830 clustered, or placed with probabilities proportional to particular habitat con-  
831 ditions. Other individual attributes, e.g., size, sex, age, need to be assigned. To  
832 achieve greater realism, the actual multivariate distribution of such attributes  
833 should be mimicked. Initial biotic attributes can include type, abundance, and  
834 spatial location of competitors, predators, and food items. Initial abiotic fea-

835 tures may be relatively static, e.g., soil types, water sources, or dynamic, e.g.,  
836 air temperature and precipitation.

837 A second data need is for information about how the individuals interact  
838 with each other and with their environment. For example, how is the prob-  
839 ability of survival affected by the availability and proximity to food items?  
840 How is movement affected by population density, biotic and abiotic features?

841 A third data need is field-based observations to verify that IBM output,  
842 and apparent emergent population level properties, e.g., collective survival,  
843 reproduction, and movement rates, are reasonable.

844 Given these data needs, IBMs, particularly those designed for specific ap-  
845 plied problems have been criticized as being too “data hungry” (Grimm and  
846 Railsback, 2013). Available data may thus constrain and guide IBM formu-  
847 lation, affecting things like the time step resolution, spatial scope, number of  
848 attributes followed, and number of interactive processes simulated.

### 849 1.6.5 Relationship with IPMs

850 Longitudinal data on individuals are central to both IPMs and IBMs. IPMs  
851 *use* such data to model population, or sub-population, level probabilities of  
852 transitions from one attribute value to another. In contrast, IBMs, starting  
853 at time  $t = 0$  with a vector of  $n_0$  individuals each with an associated at-  
854 tribute vector, *generate* longitudinal data per individual. Such data generated  
855 by IBMs can be used to evaluate fitting procedures for IPMs and the subse-  
856 quent performance of IPMs can be evaluated by comparing IPM predictions  
857 to the “true” values generated by simulated IBM output (Rees et al., 2014).

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## 858 1.7 State-Space Models, SSMs

859 State-space models (SSMs) are models for two parallel time series, a state pro-  
860 cess and an observation time series. The state process time series describes the  
861 temporal evolution of the true, but generally unknown, state of nature; it is  
862 here denoted  $\mathbf{n}_t$ ,  $t=0, 1, 2, \dots, T$ , where  $\mathbf{n}_t$  can be a vector of varying length.  
863 The state  $\mathbf{n}_0$  is referred to as the initial state. The observation time series,  
864 denoted  $\mathbf{y}_t$  with  $t=1, 2, \dots, T$ , is a sequence of imperfect or inexact measure-  
865 ments of the state process time series. The integer valued subscripting of both  
866 time series is used here,  $t_1, t_2, \dots, t_T$ , but arbitrary time points are possible.  
867 The time series indexing for both time series do not necessarily coincide, e.g.,  
868 there could be half the observations if the state is only observed every other  
869 time point, although statistical estimation limitations might occur. Also, the  
870 dimensions of  $\mathbf{n}_t$  and  $\mathbf{y}_t$  need not be the same, although situations where the  
871 dimensions differ can affect estimability. For an ecological example:  $\mathbf{n}_t$  is a

872 vector of true abundances of subpopulations at time  $t$  and the components of  
873  $\mathbf{y}_t$  are estimates of one or more components of  $\mathbf{n}_t$ .

874 The probabilistic structure of a SSM is a paired sequence of probability  
875 distributions (probability mass functions for integer valued components or  
876 probability density functions for continuous valued components) that charac-  
877 terize the evolution of  $\mathbf{n}_t$  and the relationship between  $\mathbf{y}_t$  and  $\mathbf{n}_t$ . The  
878 probability distribution for  $\mathbf{n}_t$  is typically first order Markov, i.e.,  $\mathbf{n}_t$  given  
879  $\mathbf{n}_{t-1}$  is conditionally independent of all other states, and  $\mathbf{y}_t$  given  $\mathbf{n}_t$  is inde-  
880 pendent of all other state vectors and all other observation vectors.

### 881 1.7.1 Normal dynamic linear models

882 A classic SSM, originating from Kalman (1960), is the normal dynamic linear  
883 model (NDLM); for example,

$$\begin{aligned} \mathbf{n}_0 &\sim D(\theta) \\ \mathbf{n}_t|\mathbf{n}_{t-1} &\sim \text{MVN}(\mathbf{L}\mathbf{n}_{t-1}, \Sigma), \quad t = 1, 2, \dots, T \\ \mathbf{y}_t|\mathbf{n}_t &\sim \text{MVN}(\mathbf{B}\mathbf{n}_t, \Omega), \quad t = 1, 2, \dots, T \end{aligned}$$

884 where  $D(\theta)$  denotes an arbitrary probability distribution with parameter  $\theta$   
885 which may be degenerate, i.e.,  $\mathbf{n}_0$  is a fixed value,  $MVN$  is multivariate normal,  
886  $L$  and  $B$  are matrices, and  $\Sigma$  and  $\Omega$  are variance-covariance matrices.  
887 As denoted here all the matrices are time invariant, but that is not necessary.  
888 Given  $\mathbf{y}_t$ ,  $t=1, 2, \dots, T$ , and the values of  $\mathbf{n}_0$ ,  $\mathbf{L}$ ,  $\mathbf{B}$ ,  $\Sigma$ , and  $\Omega$ , the conditional  
889 distribution of  $\mathbf{n}_t$ , which is multivariate normal, can be determined using an  
890 algorithm known as the Kalman filter. The Kalman filter also yields the calcu-  
891 lated value of the likelihood (the joint marginal distribution of  $\mathbf{y}_t$ ,  $t=1, 2, \dots, T$ ),  
892 which can then, in principle, be used to estimate unknown parameters of the  
893 transition and variance-covariance matrices. However, in practice there are  
894 considerable restrictions on the estimability of the parameters, and poten-  
895 tially high correlations between estimates of  $\Sigma$  and  $\Omega$  (Dennis et al., 2006).  
896 The notation  $\mathbf{L}$  for the state transition matrix was selected to suggest the no-  
897 tion of a Leslie matrix (1.9) as SSM extensions of MPMs are not uncommon  
898 (Sullivan (1992); Newman (1998), and see the gray whale example in section  
899 6.4.2.2 of Newman et al. (2014)).

### 900 1.7.2 Non-normal, nonlinear SSMs

901 The NDLM structure is often too constricting and unrealistic for popula-  
902 tion dynamics modeling. More realistic state-space models can on occasion be  
903 “shoe-horned” into the NDLM framework by a mathematical transformation  
904 of states or observations, e.g., a log transformation, and thus allow usage of the  
905 Kalman filter. For example, Dennis et al. (2006) used a stochastic Gompertz  
906 model for the state process distribution.

$$n_t|n_{t-1} = \lambda n_{t-1}^{1+\alpha} \exp \epsilon_t$$

907 where  $\alpha \leq 0$  and  $\epsilon_t \sim \text{Normal}(0, \sigma_\epsilon^2)$ . A natural log transform yields a linear  
 908 normal state distribution.

$$\ln(n_t) | \ln(n_{t-1}) \sim \text{Normal}(\ln(\lambda) + (1 + \alpha) \ln(n_{t-1}), \sigma_\epsilon^2)$$

909 Another way to modify an otherwise non-normal, and perhaps nonlinear SSM,  
 910 into a NDLM approximation is to work with just the first two moments of the  
 911 state process distribution and then use the mean and covariance structure as  
 912 the normal mean vector and covariance matrix. Newman (1998) and Newman  
 913 et al. (2014) give examples of such substitutions. A simplistic univariate ex-  
 914 ample is to suppose that a scalar valued state  $n_t$  is Binomial( $n_{t-1}, \phi_t$ ), where  
 915  $\phi_t$  is the survival probability, perhaps a function of covariates. The conditional  
 916 expected value of  $n_t$  is of course  $\phi_t n_{t-1} \equiv L_t n_{t-1}$ , and the conditional variance  
 917 is  $n_{t-1} \phi_t (1 - \phi_t) \equiv Q_t$ . Other, perhaps somewhat slight, departures from the  
 918 NDLM formulation can be accommodated by Taylor series transformations  
 919 of the process, using the Extended Kalman Filter (EKF; Einicke and White,  
 920 1999). A more recent alternative to the EKF, which has been shown to have at  
 921 least equal and often far superior performance (Durbin and Koopman, 2012,  
 922 p. 236) is the Unscented Kalman Filter (Julier and Uhlmann, 2004).

923 Computer intensive Monte Carlo methods such as Markov chain Monte  
 924 Carlo (MCMC, Gilks et al., 1996) and Sequential Monte Carlo (SMC Doucet  
 925 and Gordon, 2001) offer the ultimate flexibility for fitting nonlinear, non-  
 926 normal SSMs. With the MC procedures applied to such SSMs, Bayesian infer-  
 927 ence has been the dominant approach, but not always (see De Valpine, 2003;  
 928 Ionides et al., 2006, for exceptions). One of the first ecological applications  
 929 using MC methods was by Meyer and Millar (1999), who used the program  
 930 BUGS (Bayesian inference Using Gibbs Sampling) to fit an SSM with scalar  
 931 states and observations. The state was scaled biomass ( $p_t = B_t/K$ ), rather  
 932 than abundance, where biomass ( $B_t$ ) was divided by carrying capacity,  $K$ ,  
 933 thus  $0 < p_t \leq 1$ ), and the observation was a biased measure of scaled biomass,  
 934 an index ( $y_t$ ):

$$p_t | p_{t-1} \sim \text{Lognormal} \left( \ln \left( p_{t-1} + r p_{t-1} (1 - p_t) - \frac{c_{t-1}}{K} \right), \sigma_p^2 \right)$$

$$y_t | p_t \sim \text{Lognormal} (\ln(qKp_t), \sigma_o^2)$$

935 Thus the SSM was intrinsically nonlinear (no transformation of the state would  
 936 linearize the mean structure) and non-normal.

937 **1.7.3 Hierarchical and continuous time SSMs**

938 An extension of SSMs is a hierarchical state-space model (HSSM). A general  
939 formulation for an HSSM in a Bayesian framework is the following

$$\text{Prior distribution} : \pi(\eta, \omega) \quad (1.23)$$

$$\text{Stochastic variation in parameter} : h(\Theta_t, \eta) \quad (1.24)$$

$$\text{State process model} : g_t(\mathbf{n}_t | \mathbf{n}_{t-1}, \Theta_t) \quad (1.25)$$

$$\text{Observation model} : f_t(\mathbf{y}_t | \mathbf{n}_t, \Omega) \quad (1.26)$$

940 where  $\pi$ ,  $h$ ,  $g_t$ , and  $f_t$  denote probability distribution functions. Newman and  
941 Lindley (2006) used Sequential Monte Carlo to fit a Bayesian HSSM to salmon  
942 data which included both environmental and demographic stochasticity. The  
943 environmental stochasticity was modeled as above with separate distributions  
944 for year-specific survival and maturation probabilities. Demographic stochas-  
945 ticity was incorporated in the state process equations using multinomial dis-  
946 tributions to reflect between individual variation in survival and maturation  
947 (although given the population size, the influence of demographic stochasticity  
948 on the results was likely minimal).

949 Durbin and Koopman (2012) discuss continuous time SSMs for a couple  
950 cases including what is called a continuous time local level SSM. Here  $n(t)$   
951  $= n(0) + \sigma_\epsilon \omega(t)$ , where  $\omega_t$  arises from a Brownian motion process, which  
952 means  $\omega(0)=0$ ,  $\omega(t) \sim \text{Normal}(0,t)$  for  $0 < t < \infty$ , and “jumps” or increments  
953 without common endpoints are independent, e.g.,  $\omega(2) - \omega(1)$  is independent of  
954  $\omega(4) - \omega(3)$ . For an ecological application of continuous time SSMs see Johnson  
955 et al. (2008) who model the location of marine mammals using telemetry data.

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956 **1.8 Concluding Remarks**

957 **1.8.1 Omissions and sparse coverage**

958 Continuous time demographic models have been largely ignored here, except-  
959 ing the Lotka-Volterra predator-prey model. Williams et al. (2002) provides an  
960 introduction to continuous Markov processes, including birth and death pro-  
961 cesses, and Brownian motion in the context of models for animal populations.  
962 Differences in the ecological dynamics of discrete time and continuous time  
963 models are examined by Gurney and Nisbet (1998). Durbin and Koopman  
964 (2012) and Johnson et al. (2008) are references for continuous time SSMs.

965 Some aspects of ecological theory which have demographic implications  
966 that were omitted include fitness, adaptation, and mutation. Effective popu-  
967 lation size,  $N_e$ , of an existing population, here defined as the minimum num-  
968 ber of individuals necessary in a hypothetical population that would represent  
969 existing populations ability to retain the genetic diversity present, is an im-

970 portant concept for endangered species, and methods for calculating  $N_e$  were  
971 not addressed. Coverage of the demography of multiple populations, commu-  
972 nities, and ecosystems was scanty, and measures of community structure such  
973 as species richness and models for changes in such measures were not men-  
974 tioned at all. Demographic modeling of ecosystems has been popular in fish-  
975 eries (Christensen and Pauly, 1992; Walters et al., 1997, 1999) with *Ecopath*  
976 with *Ecosim* and *Ecospace* the leading software.

### 977 1.8.2 Recommended literature

978 For MPMs, Caswell (2001) remains an outstanding reference with near ency-  
979 clopedic coverage of material to 2001. For stochastic MPMs, the Tuljapurkar  
980 (1990) book is a classic.

981 For IPMs, there are two “How To” papers, Rees et al. (2014) and Merow  
982 et al. (2014) which provide the basic components of IPMs, ways of estimating  
983 the kernel components, and ways of making the projections (using numerical  
984 integration methods). The original paper (Easterling et al., 2000) includes  
985 detailed discussion of the advantages of IPMs over MPMs, while Ellner and  
986 Rees (2006) include detailed examples of stable population analyses often done  
987 with MPMs. More sophisticated and integrated IPM fitting and projection  
988 approaches are described by Ghosh et al. (2012).

989 For IBMs, Grimm and Railsback (2013) provide a book length treatment,  
990 with DeAngelis and Grimm (2013) a more recent overview paper. Roughgar-  
991 den (2012) gives an alternative perspective on the definition of and uses of  
992 IBMs, viewing agent-based models as a special case, for example.

993 For SSMs, Durbin and Koopman (2012) is an extremely thorough book  
994 length treatment of SSMs. Two thirds of the book covers linear SSMs, in-  
995 cluding classical treatment with the Kalman algorithms and extensions. The  
996 remainder discusses nonlinear, non-normal SSMs including special cases and  
997 quite general formulations that are typically fit by Monte Carlo procedures.  
998 Specific focus on the use of SSMs for population dynamics modeling is given  
999 by Newman et al. (2014).

### 1000 1.8.3 Speculations on future developments

1001 *Data.*

1002 The volume and complexity of data on individual organisms continues to grow  
1003 as the life spans of biological monitoring programs extend, as new monitoring  
1004 programs are established, and as data collection technology advances. Elec-  
1005 tronic monitoring devices, e.g., radio tag collars, acoustic tags, tags that record  
1006 the diving depths of marine animals, provide increasingly fine temporal and  
1007 spatial resolution information on individual animal movement. Chemical anal-  
1008 yses of organisms yield more information about individual life histories, e.g.,  
1009 chemical analyses of bony structures in fish, such as otoliths, can pinpoint



1010 birth place and migration paths (Secor et al., 1995). Environmental DNA  
 1011 (eDNA) is an emerging tool for indirectly detecting species presence (Thom-  
 1012 sen and Willerslev, 2015). Remote sensing is adding increasingly detailed data  
 1013 abiotic environments. In short, “attribute vectors” (Van Winkle et al., 1993)  
 1014 for individuals, populations, and abiotic and biotic environments are getting  
 1015 longer and longer.

1016 *Model formulations.*

1017 Appreciation of the need to separately model process variation (environmental  
 1018 and demographic stochasticity) and observation noise (e.g., sampling errors)  
 1019 will increase. Consequently, formulation of SSMs, and, more generally, hierar-  
 1020 chical models (Kery and Royle, 2016; King et al., 2009), for demographic data  
 1021 will increase. Extensions of MPMs, IPMs, and IBMs that explicitly distinguish  
 1022 both types of variation will likely become more common, too.

1023 Hierarchical extensions of MPMs within the normal dynamic linear model  
 1024 framework of SSMs date back to the 1990s, e.g., Sullivan (1992) and Newman  
 1025 (1998). More recently, Newman et al. (2014), in an application to the Eastern  
 1026 North Pacific gray whales (*Eschrichtius robustus*) population, contrasted an  
 1027 MPM with observation error only with a NDLM extension. Differences in some  
 1028 of the parameter estimates were considerable, e.g., juvenile survival probabili-  
 1029 ty was estimated to be 0.9999 (upper bound) for the observation error only  
 1030 model and 0.8281 for the SSM. Advances in model fitting procedures lessen the  
 1031 need to restrict process models to linear formulations, implicit to MPMs, with  
 1032 additive normal (or multiplicative lognormal) distributions. More biologically  
 1033 realistic nonlinear, and non-Gaussian formulations may make applications in  
 1034 the MPM framework less common. However, the MPM structure will remain  
 1035 valuable for formulating approximate deterministic skeletons underlying more  
 1036 realistic models (Buckland et al., 2007).

1037 For IPMs and IBMs, process and observation uncertainty can be readily  
 1038 partitioned and accounted for by computer simulation. With IPMs, bootstrap-  
 1039 ping the kernel density components yields measures of parameter estimate un-  
 1040 certainty as well as between animal variation. For example, uncertainty about  
 1041 parameters of the growth density model,  $g(z_{t+1}|z_t)$ , in the survival/growth  
 1042 kernel (1.19), can be assessed by resampling the longitudinal data on sizes to  
 1043 generate a bootstrapped distribution of growth densities. For a given fitted  
 1044 growth density model, simulated variation of individual sizes around the ex-  
 1045 pected size at time  $t + 1$  reflects demographic variation. For IBMs, computer  
 1046 simulation of between individual variation and parameter uncertainty can be  
 1047 carried out within a designed experiment structure to (a) determine the rela-  
 1048 tive import of specific factors on the model predictions and (b) quantify the  
 1049 degree of uncertainty in model predictions.

1050 *Model fitting.*

1051 Extended attribute vectors for increasingly large numbers of individuals, along  
1052 with increasingly complex demographic model formulations, necessitate in-  
1053 creasingly complex model fitting procedures. The pace of development for  
1054 fitting such models is rapid and the variety of model fitting options avail-  
1055 able is increasing. Here we focus on options for fitting dynamic hierarchical  
1056 demographic models.

1057 Mathematical integration and numerical optimization are at the heart of  
1058 hierarchical model fitting procedures, with the integration being over the un-  
1059 observed state process. In special cases, algorithms exist for analytic evalu-  
1060 ation of the integrals, e.g., NDLMs and the Kalman filter. As discussed in  
1061 section 1.7.2, numerical approximations to nonlinear, but Gaussian, popula-  
1062 tion dynamics models yield models amenable to such analytic solutions. For  
1063 general hierarchical dynamic models approximate analytic solutions to the in-  
1064 tegration problems include the Laplace approximation (Tierney and Kadane,  
1065 1986) and the Integrated Nested Laplace Approximation (INLA, Rue et al.,  
1066 2009). The software packages, AD Model Builder (ADMB, Fournier et al.,  
1067 2012) and Template Model Builder (<https://github.com/kaskr/adcomp/>),  
1068 use Laplace approximations to integrate over the state process to yield the  
1069 likelihood and then automatic differentiation for calculating maximum likeli-  
1070 hood estimates of the parameters. Widely used and well established software  
1071 for carrying out the integration using Monte Carlo procedures such as MCMC  
1072 and sequential Monte Carlo (section 1.7.2 includes WinBUGS (Lunn et al.,  
1073 2000) and JAGS (Plummer et al., 2003). Two recent software additions are  
1074 NIMBLE (de Valpine et al., 2015) and the R package `pomp`, both of which allow  
1075 users to choose from a variety of computer intensive model fitting procedures.  
1076 NIMBLE extends the BUGS software and allows estimation within Bayesian  
1077 or likelihood frameworks. The R package `pomp`, for “partially observed Markov  
1078 processes” , contains a variety of procedures for fitting state-space models,  
1079 with including “sequential Monte Carlo, iterated filtering, particle Markov  
1080 chain Monte Carlo, approximate Bayesian computation, maximum synthetic  
1081 likelihood estimation, nonlinear forecasting, and trajectory matching” (King  
1082 et al., 2016).



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