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Demography

Ken Newman

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1.1 Introduction

Demography is often thought of in terms of human populations. The word's origin is a combination of the ancient Greek words *demos*, 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” (Companies, 2005). The focus here is on ecology and ecological populations, and demography will be defined similarly but without the human social science component, e.g., the notion of marriage is not relevant. In particular demography will be defined as the scientific study and characterization of biological populations' structure and dynamics. In the case of a single population, structure can include total abundance at arbitrary points in time. Structure can also refer to how the population might be partitioned into different categories such as sex, age, or spatial location. Dynamics refers both the changes in structure and abundances over time as well as the collection of processes that cause these changes. These processes, sometimes referred to as “vital rates” include reproduction, growth, maturity, movement, and mortality.

Demography is of central importance to scientists and natural resource managers (not that these are mutually exclusive groups) for a variety of reasons. There is of course inherent curiosity, pure scientific interest, about the abundances and dynamics of many species. 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 that are 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*), there is interest in

30 the effect of harvest on the population abundances and dynamics. Comparison
31 of alternative harvest regulations is facilitated by predictions of the magni-
32 tude and sustainability of harvest levels. To have some idea as to the effects of
33 setting harvest regulations, e.g., a bag limit of 10 black ducks for a one month
34 hunting season, requires some understanding of how this mortality might inter-
35 act with other sources of mortality and other processes, like reproduction
36 or movement. Estimates of the degree to which harvest mortality will be com-
37 pensatory (removes individuals that will die anyway from other factors during
38 that time period) and additive (the number of animals that will be removed
39 over and above those that would have died from other factors) can be useful.

40 In the case of species declared threatened or endangered by a government
41 agency there is often a legal mandate for actions to be taken, or avoided, by the
42 owners or managers of land or water regions inhabited by the species. Those
43 actions can pertain directly to the population, such as to not take actions that
44 could kill, harm, or harass the species, or pertain to actions which could harm
45 or reduce the species' habitat. More positively, managers wanting to recover
46 the population would like to identify actions that could increase the species
47 abundance by making habitat restoration efforts or eliminating habitat loss.
48 For example, the United States Fish and Wildlife Service (USFWS) has a
49 mandate to develop "Conservation Management Plans" for species listed as
50 threatened or endangered under the US Endangered Species Act. Such plans
51 must include (a) specification of management actions to conserve the species,
52 (b) measurable criteria which would lead to a determination that the species
53 can be "delisted", no longer declared threatened, and (c) estimates of the
54 time and cost to carry out such actions. Demographics models are central to
55 identifying such actions, to predicting the effects of actions, and to prioritizing
56 multiple actions.

57 Questions about demographics can be coarsely divided into questions
58 about *abundances* and about *processes*. *How many* individuals, or what volume
59 or mass, have there been in the past and how many are there currently? As
60 noted previously questions about population abundances over time can be fur-
61 ther refined by partitioning the population into subgroups or subpopulations,
62 e.g., sex, location, age, genotype, etc. Answering the *how many* question alone
63 can be a challenging problem depending on the magnitude of the abundances,
64 geographic location and range, physical size, mobility, degree of elusiveness,
65 and/or ability to see or to detect individuals. A variety of statistical sampling
66 methods, e.g., mark-recapture, and technological tools and devices, e.g., radio
67 tracking, have been developed to help provide answers to the *how many* ques-
68 tion. Answering the *how many* question is the primary focus of other chapters
69 in this volume, and further discussion here is limited.

70 Even if population abundances, however partitioned, were known with cer-
71 tainty, questions about population processes remain. Why were the numbers
72 what they were last year and why are they what they are now? What are the
73 relative effects of each process on abundances at specific points in time? For
74 example, how do adult female fecundity rates of salmon, egg hatching success

75 rates, and larval to juvenile survival combine to affect the abundance of ju-
76 veniles? How do environmental conditions, both natural and anthropogenic,
77 affect these processes?

78 The primary focus of this chapter is on mathematical and statistical ap-
79 proaches to answering such *process* questions. Answering these questions in-
80 volves a quantification of the relationship between past abundance and current
81 abundances. In other words, a population dynamics model (PDM) is needed.
82 The more complete and accurate the PDM, the better the understanding of
83 how changes in environmental and anthropogenic factors influence population
84 processes, and how changes in these processes translate into changes in popula-
85 tion abundances. Measures of the degree of uncertainty as to the consequences
86 are critical as well. For threatened or endangered species, in particular, PDMs
87 are also central to population viability analysis (PVA, Morris et al., 2002).
88 PVAs use PDMs to make predictions about population trajectories, typically
89 via computer simulation. They are a means of estimating the probability of
90 the species surviving, or not, as a function of environmental conditions and an-
91 thropogenic factors, including accidental actions, like oil spills, and deliberate
92 actions, like habitat restoration.

93 While attention here will be centered largely on general notions about fac-
94 tors influencing population dynamics and some popular quantitative models,
95 it is worth pointing out how answers to initial what, why, and how questions
96 typically lead to deeper investigation and potentially a chain of subsequent
97 what, why, and how questions. Answers at the end of the chain can lead to
98 ideas about management actions to take, assuming some actions are desired,
99 and implementation of a particular action may then be justified by reversing
100 the direction to yield a so-called results chain (Margoluis et al., 2013). For
101 example, a proposed management action is to plant riparian vegetation along
102 a stream where juvenile salmon rear. The results chain is the vegetation grows
103 and provides increasing shade along the stream, the shade causes reductions in
104 water temperatures, which leads to an increase in juvenile survival during the
105 month of May, resulting in an increase in the population abundance. Having
106 such a conceptual understanding in place can then both guide data collection,
107 such as long term biological monitoring programs (Reynolds et al., view), and
108 guide further model development. For example, to assess the effects of planting
109 riparian vegetation, one might collect a time series of measurements of veg-
110 etation biomass, hours of shade, stream temperatures, juvenile abundances
111 before and after the month of May (to estimate survival) at both treatment
112 sites and control sites where no planting is done (Before-After-Control-Impact
113 BACI designs, Smith, 2002).

114 The organization of the remainder of this chapter is the following. Section
115 1.2 is an overview of components of demography, including the definition of
116 multiple subpopulations and multiple processes. Section 1.3 presents a pro-
117 gression of mathematical models more or less corresponding to the components
118 in section 1.2. Section 1.4 discusses matrix population models (MPMs) and is
119 followed by Section 1.5 on integral projection models (IPMs). Individual based

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

120 models (IBMs) are discussed in Section 1.6 and are contrasted with popula-
 121 tion based models. Section 1.7 is on state-space models (SSMs). Section 1.8
 122 concludes the chapter with pointers to further literature on MPMs, IPMs,
 123 IBMs, and SSMs, comments on topics of demography that were minimally or
 124 not at all discussed, and thoughts about the future of biological demography.

125 There are a number of acronyms used repeatedly and for convenience some
 126 of the more frequently used ones are shown in Table 1.1.

127 1.2 Components of demography

128 At a very simple level, demography can be understood as a time series of
 129 the abundance of individuals in the population. To reduce notation the time
 130 series indexing is a sequence of integers at discrete evenly spaced points in
 131 time, $t=1,2,\dots,T$. Abundances are denoted n_1, n_2, \dots, n_T . A correspondingly
 132 simple mathematical model for the population dynamics relates abundance at
 133 time t to abundance at time $t-1$ is the following

$$n_t = \lambda_t n_{t-1} \quad (1.1)$$

134 where λ_t is the population growth rate, a multiplier which if less than 1 indi-
 135 cates a decline in abundance and if greater than 1 an increase in abundance.

136 If the population abundance is small enough and easy enough to enumerate
 137 without error, not elusive or secretive or difficult to detect, then a succinct
 138 and completely accurate characterization of the population and its dynamics
 139 is trivial. For example, on July 1, over the period 2011-2015, in a 500 liter tank
 140 aquarium populated by angelfish (*Pterophyllum spp*), which did not receive
 141 any introduced fish, there were $n_{2011} = 70$, $n_{2012} = 61$, $n_{2013} = 82$, $n_{2014} =$
 142 53 , and $n_{2015} = 63$ fish. The annual population growth rates were $\lambda_{2012} =$

143 0.87 (61/70), $\lambda_{2013} = 1.34$ (82/61), $\lambda_{2014} = 0.65$ (53/82), and $\lambda_{2015} = 1.19$
144 (63/53).

145 Such instances of exact enumeration are relatively rare or uninteresting in
146 isolation. Complexity and more interesting aspects of demographic studies or
147 population dynamics arise in several general ways:

- 148 1. Multiple subpopulations of n_t : The population abundance at time t can
149 be partitioned or subdivided into two or more groups or subpopulations.
- 150 2. Multiple processes underly λ_t : The mechanisms underlying the population
151 growth rate λ_t include a multitude of processes, including survival and
152 reproduction.
- 153 3. Stochasticity: Environmental and demographic variability add uncertainty
154 to projections of population dynamics.
- 155 4. Density dependence: The effect of processes can be affected by population
156 size.
- 157 5. Competition and predation: The population dynamics of one population
158 can be affected by other populations, of the same species or different
159 species, can be affected in these two ways.
- 160 6. Manipulation of the dynamics: Related to the multiple components of λ_t ,
161 humans sometimes want to control or manipulate processes and thus affect
162 the population dynamics.
- 163 7. Partial observability (Nichols et al., 1995) of n_t : The population abun-
164 dances cannot be enumerated exactly and at best subsets, or samples, of
165 the population are observed.

166 Each of these complications are addressed individually below in Sections 1.2.1
167 - 1.2.7.

168 **1.2.1 Multiple subpopulations**

169 Finer characterization of the abundance involve partitioning the total num-
170 ber into numbers in subsets, or subpopulations, where the subsets are distin-
171 guished by one or more attributes. Some common distinguishing attributes
172 are listed below.

- 173 • sex: female, male, or indeterminate.
- 174 • age: 0,1,2,3,..., max age.
- 175 • maturity level: young, immature but developing, mature (capable of re-
176 production), post-reproduction.
- 177 • size or size class: distinguished by weight, height, length, etc.

- 178 • spatial location: exact location in space (e.g., in two dimensions, latitude
179 and longitude; in three dimensions, depth or height added).
- 180 • genotype: hereditary components that can be characterized at a variety of
181 levels, e.g., allele combinations for a single gene or for two or more genes.
- 182 • phenotype: external characters that are a consequence of genotype and
183 environment, e.g., color or color pattern (includes some of the above cat-
184 egories such as size class).

185 The general term structured population, or in specific cases age-structured or
186 stage-structured populations, is commonly used in ecological literature. When
187 the partitioning is in terms of some other factors, like sex or spatial location,
188 however, the term structured population is less common. Spatially distinction
189 populations are sometimes labeled metapopulations (Levins, 1969). Here the
190 term multiple subpopulations will be used to include any partitioning of a
191 population.

192 The degree and nature of the partitioning of a population may be a subjective
193 determination, as it depends on who is studying the population and the
194 objectives of analysis. For plentiful non-commercial species, the population
195 partitioning might be coarse for all but scientists studying a particular aspect
196 of the population. The partitioning might be fine for harvested populations
197 distinguished by sex, age, and spatial locations, as well as for closely studied
198 rare populations. Limitations on the available data about the population can
199 limit the degree of partitioning, and restrict the type of population dynamics
200 modeling that can be done.

201 Arbitrariness of partitioning may also occur when the distinguishing at-
202 tributes are continuous variables, such as measures of individual size like
203 weight, height, length. For example, if the variable is weight, the number of
204 partitions can vary as can the labeling of the partitions; e.g., small = < 10
205 kg, $10 \leq$ medium < 20kg, and large \geq 20kg. The partitioning of continuous
206 attributes is an important distinction between MPMs (Section 1.4) and IPMs
207 (Section 1.5).

208 The finest partitioning of a population is at the individual entity level. For
209 example, each animal is unique in its sex, date of birth (age), size, maturity
210 level, number of offspring, location, and so on, and the values of the individ-
211 ual's characteristics throughout its entire existence, at any given point in time,
212 are the most complete description possible. This is often at least conceptually
213 possible (though not necessarily so for large subterranean vegetative popula-
214 tions), but usually not practically possible. A notable exception is the Soay
215 sheep population on St Kilda Archipelago, off the coast of western Scotland,
216 where near complete individual animal identification and labeling is done. As
217 a mathematical exercise, however, the modeling of individuals in a popula-
218 tion can be useful for elucidating population level dynamics and this will be
219 discussed in Section 1.6 on IBMs.

220 1.2.2 Multiple processes

221 The population growth rate λ_t in eq'n (1.1) can be a function on multiple
 222 processes, including survival, reproduction, immigration, emigration, growth,
 223 maturation, and movement between regions. If the population is defined for a
 224 specific geographic area, and other individuals located outside that area can
 225 move into the area, then immigration is a factor, and conversely, if individuals
 226 can move outside the area, then emigration is a factor.

227 The partitioning of the population affects the complexity of λ_t with each
 228 additional partition adding at least one additional demographic parameter.
 229 For example, if the population is partitioned into 3 age classes, ages 0, 1, and
 230 2+, where 2+ is age 2 and older, there could be three age-specific survival
 231 probabilities, contributions to reproduction, and different propensities to emi-
 232 grate and immigrate. The reproduction process could be further distinguished
 233 on the basis of sex, or maturation class, or size. For some species, the num-
 234 ber of females are more critical to reproductive success than the number of
 235 males, when a single male can mate with multiple females (are polygynous),
 236 e.g., elk (*Cervus elaphus*), and reproductive output might be viewed entirely
 237 as a function of female abundances. Maturation classifications can distinguish
 238 sexually immature and sexually mature individuals. Size of the animal can
 239 affect reproductive contribution; e.g., larger female fish will have more eggs
 240 than smaller fish.

241 Spatial partitioning of the population into metapopulations leads to the
 242 addition of a movement process. The probabilities of moving from one region
 243 to another region within the overall defined population boundaries can be
 244 affected by other categorizations of the population, e.g., age or sex or maturity
 245 level.

246 If size is a distinguishing characteristic, defined ordinally (e.g., small,
 247 medium, and large) or continuously (e.g., length in cm), then growth is a
 248 process affecting dynamics. In particular, the individual growth dynamics are
 249 quantified in terms of the probability of moving from one size class to another
 250 (as in MPMS, section 1.4) or by a conditional probability density function for
 251 size z'_{t+1} given previous size z_t (as in IPMS, section 1.5).

252 Whether or not processes occur sequentially, partially overlap, or are si-
 253 multaneous affects the modeling of processes and the temporal partitioning
 254 of abundances. In the simplest case where processes occur sequentially and
 255 do not overlap, abundances for points in time immediately following the oc-
 256 currence of a process need to be considered. For example, the life history of
 257 coho salmon starts with egg fertilization in freshwater, egg hatching and larval
 258 emergence, fry and then smolt stages while rearing in freshwater, migration to
 259 the ocean, and a period of time in the ocean followed by migration back to the
 260 freshwater, spawning, and death. Within for a single cohort, and letting t be
 261 the time of egg fertilization, abundances that could be acknowledged include
 262 the number of eggs fertilized, n_{t_1} , the number of smolts two months later, n_{t_2} ,
 263 the number of immature adults in the ocean just prior to return migration,

264 n_{t_3} , and the number of adults surviving to spawn, n_{t_4} . The life cycle of the
265 species is thus guiding the temporal indexing of the abundance vector. When
266 multiple cohorts overlap in time, the abundance vector becomes even more
267 complicated as multiple cohorts will be at different life stages at a single point
268 in time.

269 1.2.3 Stochasticity

270 Population dynamics are complicated by two types of stochasticity, environ-
271 mental and demographic. Environmental stochasticity refers to between year
272 (or any time period) variation in underlying vital rates, such as survival, repro-
273 duction, or the overall population growth rate. Such between year variation
274 is typically due to variation in environmental conditions, e.g., precipitation
275 and air temperature. For example, the underlying average probability that a
276 juvenile salmon in a given stream will survive from 1 May to 1 June is 0.7 in
277 one year, and 0.6 in the following year.

278 Demographic stochasticity, on the other hand, reflects inherent between-
279 individual variability conditional on a specific vital rate. For example, in 2016,
280 the underlying average May to June survival probability for the juvenile Chi-
281 nook salmon is 0.7 and there are 1000 salmon present on 1 May. While the
282 expected number surviving to 1 June is 700, assuming independence between
283 the fish which means the number surviving is a binomial random variable,
284 the observed number surviving will with high probability (0.972) not equal
285 700, with 95% probability the observed numbers will lie between 671 and 728.
286 That variation around 700 reflects demographic stochasticity.

287 Unless population numbers are relatively low, as for a severely endangered
288 species, the influence of demographic stochasticity on population dynamics
289 will be minor relative to the influence of environmental stochasticity. As pop-
290 ulation size increases, the deviation of the observed value from the expected
291 value will be relatively small. For a survival probability of 0.7, if $n=50$, the
292 95% interval is (28,41) a relative range of 37%, $(41-28)/35$, but with $n=10,000$,
293 the 95% interval is (6910, 7090) with a relative range of 2.6%. The inherent
294 survival probability for a group of animals is unlikely to be the same, however,
295 even within a year. Kendall and Fox (2002) examined the effect of between
296 individual variation in the survival probability *within* a year and showed that
297 a binomial distribution based measure of demographic stochasticity can be
298 an overestimate of true demographic stochasticity. A rule of thumb regarding
299 whether or not to account demographic variation when doing PVA, provided
300 by Morris et al. (2002), is that demographic variation can be ignored when
301 just a single population is of interest and there are at least 100 individuals,
302 and for PVA with multiple subpopulations, or life stages, there are at least 20
303 individuals in the most important subpopulations.

304 1.2.4 Density dependence

305 Consider a simple univariate population model similar to eq'n (1.1) but where
306 a constant value of λ is substituted for the λ_t s. If $\lambda > 1$, the population will
307 grow exponentially, and if $\lambda < 1$ the population will go extinct. While expo-
308 nential decline is possible, exponential growth cannot continue indefinitely as
309 resources available for survival and reproduction, e.g., food, water, and space,
310 are finite. For example, a population of plants introduced to a burned over
311 acre of land may initially grow at a near exponential rate. As there is a limited
312 amount of space for the plant to take root and grow, the population size will
313 eventually reach an upper bound, and this bound is sometimes referred to a
314 carrying capacity.

315 Limits on population growth can be viewed as limits on population pro-
316 cesses like survival, reproduction, growth, and movement with these vital rates
317 generally decreasing as population abundance increases. In other words these
318 vital rates are abundance dependent; equivalently, scaling abundance by the
319 available area or volume, the vital rates are density dependent.

320 Conversely as population abundance decreases, survival and reproduction
321 rates typically increase, due to less competition for finite resources. However,
322 there are situations where decreases beyond a certain lower bound can lead
323 to decreases in vital rates. For example, if the numbers of animal population
324 get so low that individuals have difficulty finding mates, reproductive rate will
325 decline. This is known as an Allee effect, and can be a concern for critically
326 endangered species.

327 1.2.5 Competition and predation

328 Denote a population and species of primary interest as species A, and popula-
329 tions of two different species as species B and C. If species B uses some of the
330 same finite resources as species A, i.e., it is a *competitor* for those resources,
331 and, similar to intra-specific density dependence, increases in the population
332 size of species B can reduce survival, reproduction, growth, etc, of species A.

333 If individuals in the population of species C consumes members of species
334 A, i.e., A is *prey* for C, then the abundance of species C affects the vital rates
335 of species B, most obviously survival. Conversely, if individuals of species C
336 are consumed by species A, namely A is a *predator* of C, and species C is
337 a primary food source for A, a decline in the abundance of C can lead to
338 decreases in vital rates of A.

339 1.2.6 Manipulation of dynamics

340 There are various motivations for manipulating the dynamics of a population.
341 One is that the population is being used by humans. For example, portions
342 of the population are being removed by fishing, hunting, or otherwise har-
343 vesting. In managed populations there are questions about the number that

344 can be removed from the population without causing irreparable damage, i.e.,
345 a sustainable harvest, or the harvest rate that yields the maximum sustain-
346 able harvest. The harvesting of a population can be quite selective and based
347 on particular attributes, i.e., subpopulations. For example, only mature male
348 moose (*Alces alces*) can be harvested during a summer time period, or only
349 white sturgeon (*Acipenser transmontanus*) between 100 and 150cm in length
350 can be caught and kept, or morels (*Morchella esculenta*) can only be harvested
351 in a designated area of a state park. In terms of characterizing population dy-
352 namics such removals are in effect components of the survival process for a
353 specific subpopulation.

354 For endangered populations, manipulation of dynamics is done by regu-
355 lating human activities and carrying out actions to increase the quality and
356 quantity of the habitat of the population. In the case of populations harvested
357 by humans, reductions in allowable harvest, including complete harvest bans,
358 are often mandated by regulatory agencies. Such actions translate into effects
359 on survival probabilities for potentially different subpopulations. Habitat al-
360 terations can affect survival, reproduction, growth, maturation, and move-
361 ment. Projections of the effects of such manipulations, and those of factors
362 that are not manipulable, on processes and subsequent population dynamics
363 is central to PVA.

364 1.2.7 The role of data: Partial observability

365 In most cases abundances of a population or subpopulations are unknown.
366 Some sort of sampling is required and many methods have been developed
367 since the early 1900s to produce estimates of abundance, as well as estimates
368 of process related parameters like survival, reproductive success, and move-
369 ment. For abundance estimation, the simplest methods are based on classic
370 sample survey designs and related estimators (Thompson, 2012). These can
371 be used when the area occupied by the population can be subdivided into a
372 set of sampling units, thus constructing a sample frame. Largely non-mobile
373 populations, such as plants, are more amenable to such methods; e.g., the
374 population of interest is an invasive non-native grass on a wildlife refuge and
375 the refuge can be subdivided into 100,000 square meter plots, a simple random
376 sample of 50 plots is drawn, and appropriate measures of grass biomass, say,
377 are made on the selected plots. For more mobile populations, abundances can
378 be estimated using mark-recapture methods (Williams et al., 2002), line tran-
379 sect and point transect (Buckland et al., 2001) and presence/absence sampling
380 (occupancy modeling, MacKenzie et al., 2005). See Chapters X, Y, and Z for
381 further discussion of abundance estimation procedures.

382 The fact that only estimates of abundance are available has two effects on
383 the modeling of population dynamics. One obvious effect is that additional
384 uncertainties about abundances and processes are introduced. Suppose abun-
385 dances are estimated annually at the same time of the year. Population growth
386 rate, λ_t , can be estimated by $\hat{\lambda}_t = \hat{n}_t / \hat{n}_{t-1}$, and uncertainty in the estimate

387 is a function of uncertainty in the abundance estimates. A second, and less
 388 obvious, effect is that mathematical model formulation can be affected by the
 389 time at which the estimates are made. Rees et al. (2014) give an example of a
 390 sequence of processes, beginning with reproduction, then mortality, and then
 391 growth. If abundance estimates are made just before reproduction, λ_t includes
 392 a term for the probability of the previous year's reproduction (recruits) living
 393 an entire year. If abundance estimates are made just after reproduction, the λ_t
 394 does not reflect the survival of this year's reproduction as the estimates were
 395 made before subsequent mortality, and the survival of the previous year's re-
 396 production is entangled with the survival of the previous year's abundance of
 397 old entities (non-recruits). Inserting additional sampling or estimation points
 398 in the year, say, is one means of disentangling the effects of multiple processes,
 399 but partial observability remains a factor.

400 1.3 General mathematical features of PDMs

401 Demographic models can be classified by the factors given in Section 1.2 such
 402 as the number and types of subpopulations, the number and types of pro-
 403 cesses, type of stochasticity, and degree of density dependence. In this section
 404 we present various mathematical and probabilistic formulations of such de-
 405 mographic models. We begin with the simplest demographic models, a single
 406 population, a single process, deterministic, and density independent. Viewing
 407 the growth rate parameter in eq'n (1.1) as deterministic means that λ_t is by
 408 definition n_t/n_{t-1} . For convenience this model is shown again.

$$n_t = \lambda_t n_{t-1}$$

409 If $\lambda_t = \lambda$, $n_t = \lambda^t n_0$. As noted previously, if $\lambda > 1$, population will grow expo-
 410 nentially.

411 1.3.1 Multiple subpopulations

412 Partitioning a single population into two or more populations extends the
 413 scalar n_t to a vector \mathbf{n}_t . For example, if a population of deer is distinguished
 414 by three life stages, young, immature, and mature, then the abundance vector
 415 is

$$\begin{bmatrix} n_{y,t} \\ n_{i,t} \\ n_{m,t} \end{bmatrix}$$

416 The length of the abundance vector over time need not remain fixed. The ef-
 417 fects of a sequence of processes may cause the vector to expand, e.g., following

418 reproduction, or to shrink, following an aggregation of age classes (Buckland
419 et al., 2007).

420 1.3.2 Multiple processes

421 *Survival and reproduction.*

422 Simple single population growth models can be modified by partitioning the
423 population growth rate into survival and reproduction processes. One way of
424 doing so is a balance equation with additions and subtractions.

$$n_t = n_{t-1} + R_t - M_t \quad (1.2)$$

425 where R_t is the number of (surviving) young produced between $t - 1$ and t
426 and M_t is the number of mortalities from the number n_{t-1} . Such additive
427 formulations do not make clear the relationship between the previous abun-
428 dance, n_{t-1} , and reproduction and mortality, however. The effect of previous
429 abundance on reproduction and mortality can be made clearer with a multi-
430 plicative model which extends eq'n (1.1). Assume that the survival, a fraction
431 ϕ_t , precedes reproduction rate, ρ_t , and there is no mortality of the young
432 between the time of reproduction and time t .

$$n_t = (1 + \rho_t)\phi_t n_{t-1} \quad (1.3)$$

433 Implicit to this formulation is that the survival rates for the young and adult
434 components which made up n_{t-1} was the same, ϕ_t . Given this assumption
435 about survival, the model remains the same even if the abundance denotes
436 the number just prior to reproduction.

437 A more realistic model has different survival fractions for just born young
438 and the older individuals, $\phi_{y,t}$ and $\phi_{a,t}$, and the model should have subpopu-
439 lations for young and adult. The subpopulations for young will be those just
440 born if the time period is just after reproduction, denoted $n_{0,t}$, while, if the
441 time period is just before reproduction, the young will be nearly age 1 (if the
442 time interval is one year), denoted $n_{1,t}$.

$$t \text{ just after reproduction} \quad \left[\begin{array}{l} n_{a,t} = \phi_{a,t}n_{t-1} + \phi_{y,t}n_{0,t-1} \\ n_{0,t} = \rho_t(\phi_{a,t}n_{t-1} + \phi_{y,t}n_{0,t-1}) \end{array} \right] \quad (1.4)$$

$$t \text{ just before reproduction} \quad \left[\begin{array}{l} n_{a,t} = \phi_{a,t}n_{t-1} \\ n_{1,t} = \phi_{y,t}\rho_t n_{t-1} \end{array} \right] \quad (1.5)$$

443 *Immigration and emigration.*

444 Immigration and emigration can be included in the dynamics. Extending the
445 balance equation model,

$$n_t = n_{t-1} + R_t - M_t + I_t - E_t \quad (1.6)$$

446 where I_t is the number immigrating into the population and E_t is the number
447 emigrating from the population. The multiplicative model can be extended

448 but does not necessarily remain multiplicative. The ordering of processes is
 449 again important. Assuming that immigrants arrive, and emigrants leave after
 450 mortality occurs, but prior to reproduction, the model is

$$n_t = (1 + \rho_t)(\zeta_t \phi_t n_{t-1} + I_t) \quad (1.7)$$

451 where ζ_t is the fraction of the survivors from n_{t-1} that stay and I_t is again the
 452 number of immigrants. If the order of processes change, the model changes. For
 453 example, suppose that immigrants arrive and emigrants leave after mortality
 454 and reproduction:

$$n_t = \zeta_t \rho_t \phi_t n_{t-1} + I_t \quad (1.8)$$

455 *Movement.*

456 When components of the population are distinguished by spatial location,
 457 sometimes called metapopulations, the process of movement becomes relevant.
 458 Immigration and emigration is of course a movement process but where the
 459 individuals are coming from (immigrants) or going to (emigrants) are not
 460 distinguished. With multiple locations there is often a movement transition
 461 matrix which may or may not be time invariant. For example with three
 462 regions labeled A, B, and C, a time invariant transition matrix, M , has the
 463 following structure.

$$M = \left[\begin{array}{c|ccc} t & & & \\ \hline A & 1 - \mu_{A \rightarrow B} - \mu_{A \rightarrow C} & \mu_{A \rightarrow B} & \mu_{A \rightarrow C} \\ B & \mu_{B \rightarrow A} & 1 - \mu_{B \rightarrow A} - \mu_{B \rightarrow C} & \mu_{B \rightarrow C} \\ C & \mu_{C \rightarrow A} & \mu_{C \rightarrow B} & 1 - \mu_{C \rightarrow A} - \mu_{C \rightarrow B} \end{array} \right] \quad (1.9)$$

464 where the $\mu \in [0,1]$ and the columns sum to 1.

465 *Growth.*

466 When subpopulations are defined in terms of size categories, movement be-
 467 tween size classes could be defined in terms of the fractions of a given size
 468 category moving from one category to another. The process is analogous to
 469 that for movement between spatial regions.

470 In the case of finest scale partitioning of populations to the individual
 471 entity level, growth from one size at time t , z_t , to another size at time $t + 1$,
 472 z_{t+1} , could be modeled by the addition of an individual growth increment,
 473 x_{t+1} ,

$$z_{t+1}|z_t = z_t + x_{t+1} \quad (1.10)$$

474 x_{t+1} could be a function of the size at time t , z_t . Such fine scale handling of
 475 growth is central to IPMs (Section 1.5) and can be a part of IBMs (Section
 476 1.6).

477 **1.3.3 Stochasticity**

478 As discussed previously, environmental stochasticity is often more important
 479 to account for than demographic stochasticity so long as the population is not
 480 too small. An example of the mathematical distinction between the two forms
 481 is presented by modifying the simple population model in equation (1.1).
 482 Assume that the underlying annual population growth rate does not vary
 483 between years, namely, does not have environmental stochasticity, and denote
 484 that rate λ . However, there is between-individual variation in the growth rate
 485 contribution. A demographic stochasticity extension to eq'n (1.1) is

$$n_t | n_{t-1} \sim \text{Poisson}(n_{t-1}\lambda) \quad (1.11)$$

486 Environmental stochasticity alone is reflected by population growth rates that
 487 vary between years but the per individual contribution to the growth rate is
 488 the same for all individuals. An example model is

$$\begin{aligned} \lambda_t &\sim [\text{Gamma}(\alpha, \beta)], \\ n_t | n_{t-1} &= \lambda_t n_{t-1} \end{aligned} \quad (1.12)$$

489 where $[\]$ denotes the nearest integer function. An example of a mathemati-
 490 cally convenient alternative formulation for environmental stochasticity, which
 491 ignores the discrete nature of many populations is the following:

$$n_t | n_{t-1} \sim \text{Lognormal}(\log(n_{t-1}\lambda) - 0.5\sigma_\epsilon^2, \sigma_\epsilon^2) \quad (1.13)$$

492 The term $0.5\sigma_\epsilon^2$ is a bias correction which ensures that the expected abun-
 493 dance, $E[n_t | n_{t-1}]$, is $n_{t-1}\lambda$.

494 Environmental and demographic variation typically coincide. One way to
 495 demonstrate this is with a hierarchical model:

$$\lambda_t \sim \text{Gamma}(\alpha, \beta) \quad (1.14)$$

$$n_t | n_{t-1}, \lambda_t \sim \text{Poisson}(n_{t-1}\lambda_t) \quad (1.15)$$

496 Specific ways of introducing demographic and environmental stochasticity
 497 to other processes, e.g., survival, are described later.

498 *Asymptotic results for environmentally stochastic growth rates.*

499 The long term, or asymptotic, behavior of a single population trajectory
 500 with environmentally stochastic annual growth rates, such as in eq'n (1.12) is
 501 tractable and has similarities with deterministic exponential growth models.
 502 Consider the following general single population model:

$$n_t = \lambda_t n_{t-1}, \text{ where } \lambda_t \stackrel{iid}{\sim} \text{Distribution}(\mu, \sigma^2) \quad (1.16)$$

503 where $E[\lambda_t] = \mu$ and $V[\lambda_t] = \sigma^2$. Given an initial abundance n_0 , n_t can be rewrit-
 504 ten as

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

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

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

506 which can be re-expressed as

$$\frac{\ln(n_t) - \ln(n_0)}{t} = \frac{1}{t} \sum_{i=1}^t \ln(\lambda_i) \quad (1.17)$$

507 The righthand side of eq'n (1.17) is the mean of a sequence of indepen-
 508 dent random variables, $\ln(\lambda_i), i = 1, \dots, t$. Adding the assumption that the
 509 $E(\ln(\lambda_t)^2) < \infty$, the strong law of large numbers says that the average con-
 510 verges to $E[\ln(\lambda)]$. Further, by the Central Limit Theorem, the asymptotic
 511 distribution the mean of the log of the "annual" growth rates is normal. De-
 512 noting the sample average log growth rate by $\overline{\ln(\lambda)}$

$$\overline{\ln(\lambda)} = \frac{1}{t} \sum_{i=1}^t \ln(\lambda_i) \sim \text{Asymptotic Normal}(E[\ln(\lambda)], V(\ln(\lambda))) \quad (1.18)$$

513 Another way to express this result, using the lefthand side of eq'n (1.17),

$$\ln(n_t) \sim \text{Asymptotic Normal}(\ln(n_0) + tE[\ln(\lambda)], tV(\ln(\lambda))) \quad (1.19)$$

514 OR

$$n_t \sim \text{Asymptotic Lognormal}(n_0 \exp(tE[\ln(\lambda)]), tV(\ln(\lambda))) \quad (1.20)$$

515 Thus, the average population abundance at t is identical to a deterministic
 516 exponential growth model.

517 *Survival.*

518 Environmental and demographic variation in the survival fractions can be
 519 modeled with the same hierarchical structure used for population growth
 520 (eq'ns 1.14 and 1.15). One such combination is a logit-normal model for envi-
 521 ronmental stochasticity and a binomial distribution for demographic stochas-
 522 ticity. Letting $\phi_{c,t}$ be the survival probability for subpopulation c at time
 523 t ,

$$\begin{aligned} \text{logit}(\phi_{c,t}) &\sim \text{Normal}(\beta_{0,\phi,c}, \sigma_{\phi,c}^2) \\ n_{c,t} &\sim \text{Binomial}(n_{c,t-1}, \phi_c) \end{aligned} \quad (1.21)$$

524 where $\text{logit}(x) = \ln(x/(1-x))$. Beta distributions for the $\phi_{c,t}$ are alternative
 525 for environmental stochasticity,

$$\phi_{c,t} \sim \text{Beta}(\alpha_{\phi,c}, \beta_{\phi,c})$$

526 but this distribution may be more awkward when it comes to including co-
 527 variates.

528 *Reproduction.*

529 One way to characterize reproduction is in terms of the number of progeny
 530 produced by a given individual in the population, perhaps only mature and
 531 female individuals. Letting $\rho_{c,t}$ be the expected progeny multiplier for sub-
 532 population c at time t , a hierarchical model for both levels of stochasticity is
 533 a Lognormal and Poisson combination.

$$\begin{aligned}\rho_{c,t} &\sim \text{Lognormal}(\ln(\mu_c) - 0.5\sigma_{\mu,c}^2, \sigma_{\mu,c}^2) & (1.22) \\ n_{c,0,t} &\sim \text{Poisson}(\rho_{c,t}n_{c,t})\end{aligned}$$

534 where $n_{c,0,t}$ is the number of progeny produced. An alternative distribution
 535 for $\rho_{c,t}$ is the Gamma,

$$\rho_{c,t} \sim \text{Gamma}(\alpha_\rho, \beta_\rho)$$

536 but again the inclusion of covariates may be more awkward than for the log-
 537 normal.

538 *Immigration and Emigration.*

539 Only the case of multiplicative survival, reproduction, and emigration pro-
 540 cesses with additive immigration is considered and the only partitioning of
 541 the population is of adults and young. Immigrants are generated from an ar-
 542 bitrary non-negative integer valued distribution, here a Poisson will be used.
 543 The hierarchical structure for survival and reproduction used previously (1.21
 544 and 1.22) is used again and the emigration probability is dealt with the same
 545 as the survival probability. The order of processes is survival, reproduction,
 546 emigration, and immigration where just born individuals do not emigrate. The
 547 notation t' denotes time just after survival but before emigration.

$$\text{Survival probability} \quad \textit{logit}(\phi_t) \sim \text{Normal}(\beta_\phi, \sigma_\phi^2) \quad (1.23)$$

$$\text{Survivors} \quad n_{t'} \sim \text{Binomial}(n_{t-1}, \phi_t) \quad (1.24)$$

$$\text{Reproductive rate} \quad \rho_t \sim \text{Lognormal}(\ln(\beta_\rho) - 0.5\sigma_\rho^2, \sigma_\rho^2) \quad (1.25)$$

$$\text{Reproduction} \quad n_{c,0,t} \sim \text{Poisson}(\rho_t n_{t'}) \quad (1.26)$$

$$\text{Emigration probability} \quad \textit{logit}(\zeta_t) \sim \text{Normal}(\beta_\zeta, \sigma_\zeta^2) \quad (1.27)$$

$$\text{Non-emigrants} \quad n_t \sim \text{Binomial}(n_{t'}, \zeta_t) \quad (1.28)$$

$$\text{Immigrants} \quad I \sim \text{Poisson}(\eta) \quad (1.29)$$

548 *Movement.*

549 Environmental stochasticity can be introduced by randomly drawing a vector
 550 of movement probabilities for each row of the movement matrix, eq'n (1.9),
 551 and then conditional on these probabilities the numbers moving to each lo-
 552 cation are drawn at random. One hierarchical formulation is a multi-vector

553 extended logit-multivariate normal (Newman and Brandes, 2010) and multi-
 554 nomial combination. Just one vector of the formulation, the case of being in
 555 location A at time t , is shown here, and subscripting notation for parameters
 556 indicating time are omitted.

$$\begin{aligned} \begin{bmatrix} \ln \left(\frac{\mu_{A \rightarrow B}}{1 - \mu_{A \rightarrow B} - \mu_{A \rightarrow C}} \right) \\ \ln \left(\frac{\mu_{A \rightarrow C}}{1 - \mu_{A \rightarrow B} - \mu_{A \rightarrow C}} \right) \end{bmatrix} &\sim \text{MVN} \left(\begin{bmatrix} \beta_{0, \mu_{A, B}} \\ \beta_{0, \mu_{A, C}} \end{bmatrix}, \begin{bmatrix} \sigma_{A, A \rightarrow B}^2 & \sigma_{A, A \rightarrow B, A \rightarrow C} \\ \sigma_{A, A \rightarrow B, A \rightarrow C} & \sigma_{A, A \rightarrow C}^2 \end{bmatrix} \right) \\ n_{A \rightarrow B, t}, n_{A \rightarrow C, t} &\sim \text{Multinomial}(n_{A, t-1}, \mu_{A \rightarrow B}, \mu_{A \rightarrow C}) \end{aligned} \quad (1.31)$$

557 An alternative distribution for environmental stochasticity for the μ 's is a
 558 Dirichlet distribution but it does not necessarily lend itself as easily to the
 559 inclusion of covariates as the extended logit-MVN.

560 *Growth.*

561 As for the deterministic case, when growth refers to movement from a cate-
 562 gorical size class, a stochastic representation of the advancement is again anal-
 563 ogous to the handling of between region movement. In the case of individual
 564 entities, assuming that growth is never negative, a stochastic formulation is a
 565 Gamma probability density function for the increment in growth:

$$z_t | z_{t-1} = z_{t-1} + x_t$$

566 where

$$x_t \sim \text{Gamma}(\alpha, \beta)$$

567 with parametric formulation being $E[x_t]$ being $\alpha\beta$. The parameters α and β
 568 could be individual specific, say functions of other covariates, or draws from
 569 another probability distribution, thus introducing additional stochasticity.

570 1.3.4 Density dependence

571 A variety of univariate models with density dependent population growth
 572 rates, $\lambda(n_t)$, are commonly used. We begin with some well known determi-
 573 nistic, and mostly discrete time, models. These univariate models are readily
 574 applied to individual subpopulations of a structured population, but appli-
 575 cations where the subpopulations interact, as in predator-prey situations or
 576 spatially partitioned partitions, are more involved.

577 A slight variation on the exponential growth model is the Gompertz model,
 578 where the following formulation is taken from Dennis et al. (2006).

$$\text{Gompertz model} : n_t = \lambda n_{t-1}^{1+\alpha} \quad (1.32)$$

579 where $\alpha < 0$ is the parameter inducing density dependence. Substituting n
 580 for n_t and n_{t-1} the equilibrium abundance for the Gompertz distribution is

$$n_{\text{Gompertz}, e} = \lambda^{\frac{-1}{\alpha}}$$

581 Another well known model is the logistic model, which has discrete and
582 continuous time forms:

$$\text{Logistic (discrete) model} : n_t = n_t + \lambda n_t \left(1 - \frac{n_t}{K}\right) \quad (1.33)$$

$$\text{Logistic (continuous) model} : n(t) = \frac{K}{1 + \frac{K-n(0)}{n(0)}\lambda t} \quad (1.34)$$

583 In both cases K is the upper bound on the population abundance, i.e., the
584 carrying capacity.

585 A well-known model that originated with fish populations, but is now
586 applied many other kinds of populations, is the Ricker model.

$$\text{Ricker model} : n_t = (\phi_a + \phi_y b \exp(-cn_{t-1}))n_{t-1} \quad (1.35)$$

587 The Ricker model formulation citep[taken from][gurney1998ecological can be
588 viewed as a balance equation where the product $\phi_a n_{t-1}$ is the number of sur-
589 viving adults and $\phi_y f \exp(-cn_{t-1})$ is the number of surviving offspring, the
590 recruits. The term b is the fecundity of the average adult (with sex being
591 ignored here; if the sex ratio is 50:50, b could equal half the average female fe-
592 cundity), $\exp(-cn_{t-1})$ is a density dependent reproductive success rate which
593 decreases as abundance increases and reproductive success is the number alive
594 at some point in time prior to time t , and ϕ_y is the survival probability from
595 that time point to t . Combining the product f and ϕ_y into a single term has no
596 effect on the model dynamics. Substituting n for n_t and n_{t-1} the equilibrium
597 abundance for the Ricker model is

$$n_{Ricker,e} = \frac{-1}{c} \ln \left(\frac{1 - \phi_a}{\phi_y b} \right)$$

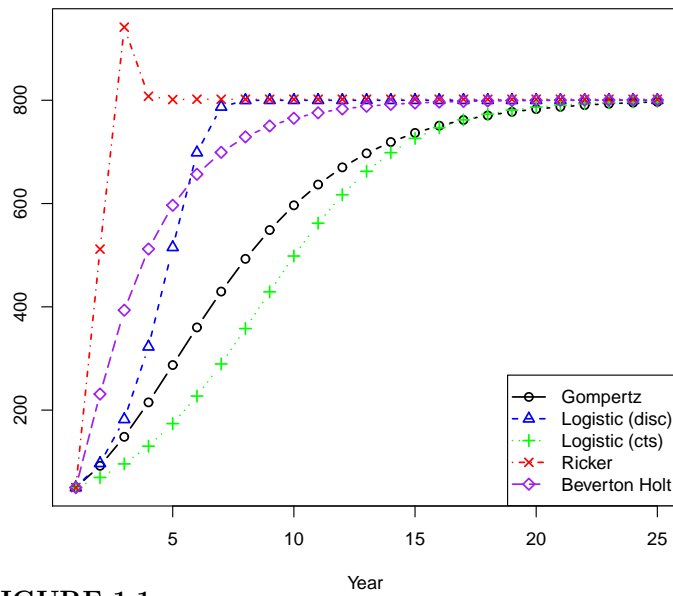
598 Another well known model from fisheries science is the Beverton Holt
599 model, again taking the formulation from citepgurney1998ecological.

$$\text{Beverton Holt} : n_t = \left(\phi_a + \frac{\phi_y b}{1 + cn_{t-1}} \right) n_{t-1} \quad (1.36)$$

600 The parameters ϕ_a , ϕ_y , and b have the same interpretation as for the Ricker
601 model, and the parameter c is again the density dependent parameter. The
602 equilibrium abundance is

$$n_{BevertonHolt,e} = \frac{\phi_y b(1 - \phi_a)}{(1 - \phi_a)c}$$

603 Figure 1.1 shows population growth trajectories for these five models such that
604 the equilibrium abundances are nearly identical (around 800) and ϕ_a is 0.7 and
605 ϕ_y is 0.2 for both the Ricker and Beverton Holt models. The Ricker model
606 can overshoot the equilibrium abundance while the other models converge
607 monotonically.

**FIGURE 1.1**

Population trajectories with initial abundance=50 for Gompertz, Ricker, and Beverton Holt growth models. Equilibrium abundances are around 800 for all three models and ϕ_a is 0.7 and ϕ_y is 0.2 for both the Ricker and Beverton Holt models.

608 The density dependent formulations for population growth λ_t in the Ricker
 609 and Beverton Holt models can be seen to be simply density dependent repro-
 610 duction rates as opposed to density dependent survival rates by simply re-
 611 moving the number of adults and the adult survival term ϕ_a from the model.
 612 Then the reproductive rate multipliers are:

$$\begin{aligned} \text{Ricker reproduction rate} & : (\phi_y b) \exp(-cn_{t-1}) \\ \text{Beverton Holt reproduction rate} & : (\phi_y b) \frac{1}{1 + cn_{t-1}} \end{aligned}$$

613 The difference in the density dependent effects for the two models can be
 614 seen in the terms following $(\phi_y b)$. Density dependence in the Gompertz model
 615 cannot be disentangled into effects on reproduction and survival as λ is not
 616 being adjusted. Instead the per capita contribution of each individual to the
 617 population growth rate is being diminished abundance increases.

618 *Density dependence at a subprocess level.*

619 Density dependence can be introduced for other vital rates such as survival,
 620 movement, and individual animal growth rates. An example formulation of
 621 density dependence and environmental stochasticity is a logit-normal distri-
 622 bution with population abundance as a covariate:

$$\text{logit}(\phi_t) \sim \text{Normal}(\beta_{0,\phi} + \beta_{1,\phi} n_{t-1}, \sigma_\phi^2)$$

623 where $\beta_{1,\phi}$ is constrained to be negative. Similar adjustments can be made for
 624 movement probabilities between spatially distinct subpopulations, an example
 625 is given shortly.

626 *Density dependence for multiple (sub)populations.*

627 If the vital rates for one subpopulation do not affect another subpopulation,
 628 then the above univariate density dependent models can be applied on a per
 629 subpopulation basis for subpopulation specific vital rates. More realistically,
 630 subpopulation abundances will impact vital rates for other subpopulations, if
 631 the subpopulations occupy the same geographic area this is likely obvious as
 632 it is the total resource consumption or usage that matters.

633 Even when subpopulations are defined by spatially distinct locations, the
 634 density in one spatial subpopulation can affect another spatial subpopulation,
 635 e.g., one region is becoming crowded and individuals leave to seek less densely
 636 populated regions, thus movement probabilities are affected by density de-
 637 pendence. Referring to stochastic movement example given previously, eq'n
 638 (1.30), adjustments could be made to the mean parameters in the multivari-
 639 ate normal model. Movement from one location to another is made a function
 640 of the relative densities in the originating region and the destination region. In
 641 the following formulation, assuming that the slopes (β_1 's) are positive valued,
 642 the probability of moving from A to either B or C increases as the density in

643 A relative to the density in B or C increases.

$$\begin{bmatrix} \beta_{0,\mu_A,B} + \beta_{1,\mu_A,B} \frac{\delta_{A,t-1}}{\delta_{B,t-1}} \\ \beta_{0,\mu_A,C} + \beta_{1,\mu_A,C} \frac{\delta_{A,t-1}}{\delta_{C,t-1}} \end{bmatrix}$$

644 where $\delta_x = n_x/\|x\|$ and $\|x\|$ is the area of x .

645 *Density dependence, predation and competition*

646 The dynamics of predator-prey interactions and between species competition
647 are implicitly density dependent. For example, as the abundance (density) of a
648 predator increases survival probabilities for the prey population decrease. One
649 of the best known, and simpler, mathematical models for predator-prey dy-
650 namics is the Lotka-Volterra model which is a continuous time model defined
651 in terms of differential equations for the instantaneous population growth rate
652 citep[[p. 155]gurney1998ecological:

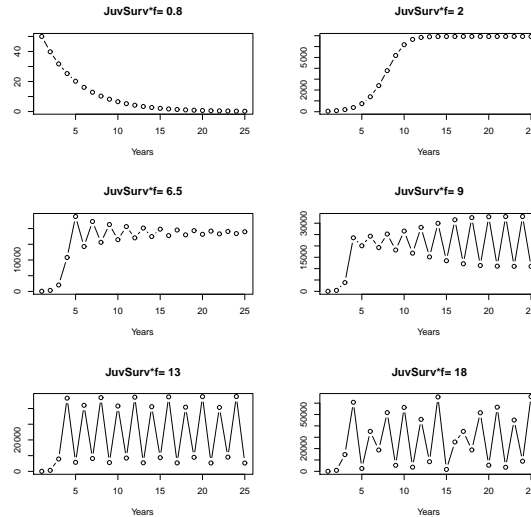
$$\frac{dPrey}{dt} = (r - \alpha Predator(t))Prey(t) \quad \frac{dPredator}{dt} = (\epsilon\alpha Prey(t) - \delta)Predator(t)$$

653 Following convention, the indexing for continuous time models is in parenthe-
654 ses $n(t)$ in contrast to discrete time indexing with subscripts n_t .

655 Referring to the prey equation, in the absence of predators, the instan-
656 taneous growth rate of the prey population is r and the population trajec-
657 tory is exponential growth, $Prey(t) = \exp(r)Prey(t-1)$. The addition of
658 predators to the population is causing mortality at rate $\alpha Predator(t)$, where
659 α is the per capita consumption rate of prey by predators. For predator
660 dynamics, the mortality rate is a constant independent of predator abun-
661 dance; in the absence of prey, the population trajectory is exponential de-
662 cline, $Predator(t) = \exp(-\delta)Predator(t-1)$. Predator growth is entirely
663 dependent on the presence of prey with instantaneous growth rate $\epsilon\alpha Prey(t)$,
664 where ϵ is the per prey item predator offspring rate. If $Prey(t)$ was a con-
665 stant, $Prey^*$, the resulting dynamics would be exponential, $Predator(t) =$
666 $\exp(\epsilon\alpha Prey^* - \delta)Predator(t-1)$. The Lotka-Volterra model is considered a
667 relative simple, and unrealistic model (Gurney and Nisbet, 1998, p. 159), but
668 the resulting dynamics can be relatively complex with oscillating population
669 trajectories. See Gurney and Nisbet (1998) for examples of the trajectories and
670 dynamics as well as extensions, such as a prey model where prey abundance
671 also affects the population growth rate (self-limiting prey).

672 *Periodicity and chaos.*

673 The periodicity observed in the Lotka-Volterra model, and much more com-
674 plex dynamics, can occur with discrete time single population models like the
675 Ricker and discrete logistic model. Figure 1.3.4 Gurney and Nisbet (based
676 on Figure 2.6 in 1998) shows what can happen for a variety of combined re-
677 cruitment rate values, $\phi_j f$, when adult survival, ϕ_a , is zero and the density

**FIGURE 1.2**

Population trajectories for the Ricker model for a variety of $\phi_j f$ combinations with $\phi_a=0$ and $c=0.001$.

678 dependent parameter $c=0.001$. With too little recruitment (a), the population
 679 goes extinct, (b) shows a stable equilibrium, (c) and (d) show damped and
 680 expanding oscillations, respectively, (e) and (f) have two and four year period-
 681 icities, respectively, and (g) is chaotic (no periodicity and apparently random
 682 fluctuations).

683 1.3.5 Inclusion of covariates

684 Similar to density dependent models where abundance was used as a covari-
 685 ate to modify vital rates, environmental and anthropogenic covariates can be
 686 included; e.g., bird survival modeled as a function of weather data (North and
 687 Morgan, 1979).

688 Covariates can also be used as a means of assessing the effects of predators,
 689 competitors, or prey abundance when the populations' dynamics of predators,
 690 competitors, or prey are *not* modeled. Instead the abundances of these groups
 691 are simply treated as fixed input values that affect the vital rates for the pop-
 692 ulation of interest. The legitimacy of such handling of these other populations
 693 assumes that these other populations are not receiving any feedback from the
 694 population of interest. If the primary population's abundance has relatively
 695 little effect on the abundances of the other populations, for example, the pri-
 696 mary population is a minor food item for predators, then treating these other

697 population abundances as covariates may not adequate. Otherwise the more
 698 complex models for the joint dynamics, as in the Lotka-Volterra model, would
 699 be more appropriate.

700 1.3.6 Simultaneous versus sequential processes

701 The modeling of multiple processes in previous examples, e.g., eq'ns (1.23-
 702 1.29), assumed that the processes occur in a specific sequence. Such a tidy
 703 partitioning of processes may be a poor approximation to reality for some
 704 populations. In the case of harvested populations, for example, harvest-related
 705 mortality is co-occurring with other sources of mortality. One of the simpler
 706 treatments of such simultaneous mortality is frequently used in fisheries science.
 707 The underlying differential equation in the simplest case of two sources
 708 of mortality, say fishing and natural mortality, is the following:

$$\frac{dn(t)}{dt} = -(F + M)n(t) \quad (1.37)$$

709 where F and M are instantaneous fishing and natural mortality rates. The
 710 solution to the differential equation is

$$n(t + \Delta) = \exp(-(F + M)\Delta)n(t) \quad (1.38)$$

711 where $\exp(-(F + M)\Delta)$ is the survival fraction over a time interval of length
 712 Δ . The number that die in total and from each source is then

$$\text{Total Mortality} = (1 - \exp(-(F + M)\Delta))n(t) \quad (1.39)$$

$$\text{Fishing Mortality} = \frac{F}{F + M}(1 - \exp(-(F + M)\Delta))n(t) \quad (1.40)$$

$$\text{Natural Mortality} = \frac{M}{F + M}(1 - \exp(-(F + M)\Delta))n(t) \quad (1.41)$$

713 Formulations and simultaneous and competing sources of mortality can be
 714 translated into discrete time population dynamics models in various ways.
 715 For example, a hierarchical model for survival which includes environmental
 716 and demographic stochasticity and covariates can be constructed.

$$\ln(F_t) \sim \text{Normal}(\beta_{0,F} + \beta_{1,F}x_{1,t}, \sigma_F^2) \quad (1.42)$$

$$\ln(M_t) \sim \text{Normal}(\beta_{0,M} + \beta_{1,M}x_{2,t}, \sigma_M^2) \quad (1.43)$$

$$n_t \sim \text{Binomial}(n_{t-1}, \exp[-(F_t + M_t)]) \quad (1.44)$$

717 The mortality due to each source between time t and $t + 1$ can be predicted
 718 using eq'ns (1.40) and (1.41) with $\Delta=1$.

719 1.3.7 Remarks: Estimability and Data Collection.

720 It is relatively easy to formulate a population dynamics model where the
 721 parameters cannot be estimated given the available data. For example, annual

722 surveys alone do not allow separate estimation of the survival fraction, ϕ_t , and
 723 reproductive rate, γ_t , in the simple univariate model (1.3). Intuitively given
 724 estimates of n_t and n_{t-1} one can just estimate the combination $(1 + \gamma_t)\phi_t$.

725 One way to disentangle such combinations of parameters, in the case of se-
 726 quential processes, is to have abundance estimates at time points immediately
 727 after the end each process. For example, in the model (1.3) abundance should
 728 be measured twice a year, once immediately following the survival process, and
 729 once after reproduction. The reality of the processes is typically more com-
 730 plicated with such sharp demarcations unlikely, but formulating such models
 731 can provide guidance for data collection.

732 Detailed discussion of issues of estimability, or parameter redundancy, for
 733 population dynamics-related models can be found in Catchpole and Morgan
 734 (1997, 2001); Cole and Morgan (2010); Cole et al. (2012).

735 1.4 Matrix Projection Models, MPMs

736 Lewis (1942) and Leslie (1945) independently proposed matrix projection
 737 models as a means of modeling the population dynamics of populations with
 738 age-specific subpopulations, more commonly referred to as age-structured
 739 models. Let $n_{0,t}$ denote the number of young at time t and $n_{a,t}$ be the abun-
 740 dance for ages 1 to $A - 1$, and $n_{A+,t}$ be the abundance of age A and older
 741 individuals. A deterministic formulation for the dynamics can be written as

$$\begin{bmatrix} n_{0,t} \\ n_{1,t} \\ n_{2,t} \\ \vdots \\ n_{A,t} \\ n_{A+,t} \end{bmatrix} = \begin{bmatrix} \gamma_0 & \gamma_1 & \gamma_2 & \cdots & \gamma_{A-1} & \gamma_A \\ \phi_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & \phi_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & 0 & \cdots & \phi_A & \phi_{A+} \end{bmatrix} \begin{bmatrix} n_{0,t-1} \\ n_{1,t-1} \\ n_{2,t-1} \\ \vdots \\ n_{A,t-1} \\ n_{A+,t-1} \end{bmatrix} \quad (1.45)$$

742 or more compactly as $\mathbf{n}_t = \mathbf{L}\mathbf{n}_{t-1}$. Lefkovich (1965) proposed an MPM where
 743 the subpopulations were distinguished by life stage rather than age class,
 744 e.g., young, immature, and mature, thus a stage-structured model. Of course,
 745 partitioning by gender, genotype, and many other subpopulation identifiers is
 746 possible.

747 1.4.1 Analysis of MPMs.

748 Caswell (2001, p. 18) refers to four sets of general questions which can be
 749 asked about MPMs for which the answers can elucidate deeper understanding
 750 of the dynamics. His questions (paraphrased and italicized) are shown below.

751 1. *What is the asymptotic behavior of the MPM?* As time increases, does the

- 752 total population grow or decline exponentially? Do the relative propor-
 753 tions of each subpopulation become constant? Does the population ap-
 754 proach an upper bound (carrying capacity)? Do the total population and
 755 individual subpopulation abundances oscillate (in a damped or undamped
 756 manner)? Do the abundances display periodicity? Do the abundances be-
 757 come chaotic?
- 758 2. *Is the MPM ergodic?* In other words, are the asymptotic dynamics inde-
 759 pendent of the initial conditions, e.g., independent of the actual values of
 760 \mathbf{n}_0 ?
- 761 3. *What are the transient dynamics?* What are the dynamics like in the short
 762 term as opposed to the asymptotic or limiting results?
- 763 4. *How sensitive are the results to the values of the elements of the matrix?*
 764 The survival probabilities and fecundity rates, for example, are estimates,
 765 and will have some degree of estimation error. How much would the pop-
 766 ulation dynamics, including asymptotic and transient dynamics, change if
 767 some elements of the matrix were changed “slightly”?

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

772 1.4.2 Limiting behavior of density independent, time invari- 773 ate MPMs.

774 Results from linear algebra can be used to describe the asymptotic behavior
 775 of a time invariant projection matrix, if the matrix has certain mathematical
 776 properties. Three properties are (a) non-negativity (all elements are ≥ 0), (b)
 777 irreducible (e.g., every age class can contribute to every other age class at
 778 some point in time), (c) primitive (there is some positive integer k such that
 779 every element in the matrix raised to the power k , L^k , is a positive number).
 780 If these conditions are met, in the limit the population dynamics are either
 781 exponential growth or decay, i.e., $A^T \mathbf{n}_t = \lambda \mathbf{n}_t$, where λ is a scalar value that
 782 is multiplied against each component of the vector \mathbf{n}_t . Further, the relative
 783 proportions of each component of \mathbf{n}_t will remain constant.

784 For example, a MPM with three age classes has the following Leslie matrix

$$L = \begin{bmatrix} 0.0 & 1.2 & 1.4 \\ 0.3 & 0.0 & 0.0 \\ 0.0 & 0.5 & 0.9 \end{bmatrix}$$

785 The initial abundance vector is $\mathbf{n}'_0 = (100, 50, 10)$. The population over 9 iter-
 786 ations is:

	Stage	1	2	3	4	5	6	7	8	9	10
787	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

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

	Stage	2	3	4	5	6	7	8	9	10
789	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

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

791 The fraction of the population in each stage class:

	Stage	1	2	3	4	5	6	7	8	9	10
792	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

793 And, after six generations the fractions in the Young, Adult, and Old stages
794 remain 0.54, 0.14, and 0.31.

795 The limiting population growth rate and proportions of each category can
796 be determined analytically again using linear algebra, in particular, by carry-
797 ing out an eigen analysis of L . For a p by p matrix L , the eigen analysis yields
798 p eigenvalues, $\lambda_1, \dots, \lambda_p$, and p corresponding right eigenvectors, $\mathbf{v}_1, \dots, \mathbf{v}_p$.
799 An eigenvalue and its corresponding eigenvector have the relationship, $L\mathbf{v}_i$
800 $= \lambda_i\mathbf{v}_i$. Denote the largest eigenvalue λ_1 and its corresponding eigenvector
801 \mathbf{v}_1 . Then λ_1 is equal to limiting population growth rate, in the example 1.13
802 (more precisely, 1.12938), and dividing each element of \mathbf{v}_1 by its total yields
803 the limiting fractions, here (0.54, 0.14, 0.31).

804 1.4.3 Stochasticity.

805 There are various ways to add stochasticity to MPMs, one of which is to
806 randomly draw elements of the matrix from probability distributions, e.g.,
807 randomly draw survival probabilities for age a individuals. This has the effect
808 of introducing environmental stochasticity. Under some conditions, in the ab-
809 sence of density dependence for example, the introduction of environmental, or
810 demographic, stochasticity will not appreciably alter the asymptotic dynamics
811 from that of a deterministic MPM, namely that the above eigen analysis re-
812 sults more or less hold, in the limit there is an average growth rate and stable
813 population structure. Caswell (2001, Chap. 14) provides details of these results
814 (with some of earliest work from Cohen, 1976; Tuljapurkar and Orzack, 1980).

815 Below we closely follow (Caswell, 2001) and somewhat mimic the derivation of
 816 the asymptotic distribution of the stochastic univariate model shown in eq'ns
 817 (1.16 - 1.20). Let A_1, A_2, \dots , be a "stationary, metrically transitive stochastic
 818 process with $E(\ln^+ \|A\|_1) < \infty$, where $\ln(x+) = \max(0, \ln(x))$. Suppose that
 819 the matrices A_t are drawn from an ergodic set of matrices," (Caswell, 2001,
 820 p. 393) . The total population size at time t , denoted $N(t)$, is the vector norm
 821 of \mathbf{n}_t ($\sum_i |n_{t,i}|$). Given an initial vector \mathbf{n}_0 :

$$N(t) = \|\mathbf{n}_t\| = \left\| \prod_{i=1}^t A_i \mathbf{n}_0 \right\| \quad (1.46)$$

$$\Rightarrow \frac{1}{t} \ln(N(t)) = \frac{1}{t} \ln \left\| \prod_{i=1}^t A_i \mathbf{n}_0 \right\| \quad (1.47)$$

822 Furstenberg and Kesten (1960) proved that the limit of (1.47) existed (with
 823 probability 1). That limiting value, denoted $\ln(\lambda_s)$, is called the stochastic
 824 growth rate.

$$\lim_{t \rightarrow \infty} \frac{1}{t} \ln(N(t)) = \lim_{t \rightarrow \infty} \frac{1}{t} \ln \left\| \prod_{i=1}^t A_i \mathbf{n}_0 \right\| = \ln(\lambda_s) \quad (1.48)$$

825 With further conditions on the matrices, A_i , including nonnegativity, the
 826 asymptotic distribution of the population total is lognormal:

$$N(t) \sim \text{Asymptotic Lognormal}(\exp(t \ln(\lambda_s)), t\sigma^2) \quad (1.49)$$

827 where σ^2 is some constant. Thus, similar to eq'n (1.20), the asymptotic mean
 828 of the population total is the same as for a univariate exponential popula-
 829 tion growth model, and λ_s is analogous to the largest eigenvalue, λ_1 , of a
 830 deterministic MPM.

831 1.4.4 Density dependent MPMs.

832 Density dependence can be introduced into MPMs by simply making some of
 833 the elements of the projection matrix density dependent. Consider the exam-
 834 ple given previously with three age classes, young, adult, and old, and suppose
 835 that the fecundity of the old group was a function of the total abundance of
 836 adult and old individuals. Then the (1,3) element in the transition matrix is
 837 simply written as such a function. The linearity aspect of the MPM is subse-
 838 quently altered and the analyses carried out for density independent MPMs
 839 do not directly apply, e.g., the eigen analysis is no longer directly applicable.
 840 Caswell (2001, Chap. 16) provides considerable details on the construction
 841 and analysis of density dependent MPMs.

842 1.4.5 Building block approach to matrix construction.

843 Buckland et al. (2007) present a building block approach to formulating the
 844 MPMs and further examples are given in Newman et al. (2014). The essential
 845 idea assumes a particular sequence to processes which operate on a vector of
 846 population abundances, such as survival, then movement, then reproduction.
 847 An example from Newman et al. (2014, eq. 2.11, p. 18) is based on two sub-
 848 populations distinguished by size class (small and large) with three processes,
 849 survival, then size class changes (only from small to large), and reproduction.
 850 The survival probabilities are size specific (ϕ_L and ϕ_S), the probability that a
 851 small individual becomes large is π , and only large individuals can reproduce
 852 and they do so with rate ρ .

$$\begin{aligned} \begin{bmatrix} n_{S,t} \\ n_{L,t} \end{bmatrix} &= \begin{bmatrix} 1 & \rho \\ 0 & 1 \end{bmatrix} \begin{bmatrix} 1 - \pi & 0 \\ \pi & 1 \end{bmatrix} \begin{bmatrix} \phi_S & 0 \\ 0 & \phi_L \end{bmatrix} \begin{bmatrix} n_{S,t-1} \\ n_{L,t-1} \end{bmatrix} \\ &= \begin{bmatrix} (1 - \pi + \rho\pi)\phi_S & \rho\phi_L \\ \pi\phi_L & \phi_L \end{bmatrix} \begin{bmatrix} n_{S,t-1} \\ n_{L,t-1} \end{bmatrix} \end{aligned} \quad (1.50)$$

853 The matrix in eq'n (1.50) is an example of a Lefkovitch matrix which is ar-
 854 guably more simply constructed by using such a building block approach than
 855 by trying to construct the final matrix in a single operation.

856 1.4.6 Estimating the elements of projection matrices.

857 Caswell (2001, p. 22) states that, to fill the elements of the matrix, life tables
 858 are used. Life tables contain mortality probabilities, the probability that an
 859 individual of age a will die before reaching age $a + 1$, and maternity functions,
 860 the expected number of offspring that an age a individual will produce in the
 861 next year. How the life tables and maternity functions are constructed in the
 862 first place may be no trivial task, and is beyond the scope of this section.
 863 However, we do note that with wildlife populations, mark-recapture studies
 864 where the animals are aged at time of marking, can provide estimates of age-
 865 specific survival. For example, a population of ducks were banded, aged at
 866 time of banding, and later recovered. Mark-recapture methods are used to
 867 calculate $\hat{\phi}_a$, the estimated probability that an age a animal lives to age $a + 1$.
 868 Similarly, the average number of young produced by age a females is used as
 869 an estimate of the fecundity parameter for age a females, or when the total
 870 population is modeled and a 50:50 sex ratio is assumed, the estimated average
 871 fecundity is $0.5\hat{f}_a$.

872 An alternative approach is to integrate inference about vital rates with
 873 inference about the entire population dynamics model where stochasticity in
 874 the population dynamics is accounted for simultaneously with sampling error
 875 in the estimation of vital rate parameters. The SSM framework provides a
 876 structure for doing this and is discussed in Section 1.7.

877 1.5 Integral Projection Models, IPMs

878 The partitioning of a population into discrete subpopulations, namely formu-
 879 lating a structured population, may be arbitrary when natural divisions are
 880 lacking. For example, suppose the population cannot be readily aged nor sub-
 881 divided into distinct life stages and individual size, say weight, is the feature
 882 used to subdivide the population. The selection of size classes, small, medium,
 883 and large, will necessarily have arbitrary boundaries. The weight classes for the
 884 three size classes are (0,10), [10,20), [20+], an animal weighing 9.99 pounds is
 885 labeled small and one weighing 10.0 pounds is medium. Those two individuals
 886 will be treated differently in terms of population processes, e.g., the survival
 887 probability is 0.5 for small individuals and 0.8 for medium individuals, while
 888 in reality the survival probabilities for both individuals may be much more
 889 similar. Integral Projection Models (IPMs; Easterling et al., 2000), sometimes
 890 called integrodifference equation models (see Caswell, 2001, for historical refer-
 891 ences), are a modeling approach that maintains the continuous nature of a
 892 factor that distinguishes population members, while (generally) maintaining
 893 the discrete time step characteristic of MPMs.

894 1.5.1 Kernel structure of IPMs.

895 The core of an IPM, which is analogous to an element in the transition matrix
 896 of an MPM, is the *kernel* denoted $K(z'_{t+1}|z_t)$. The kernel can be viewed as a
 897 conditional probability density function for the “probability” that an animal
 898 of size z at time t , denoted z_t , is size z' at time $t + 1$, denoted z'_{t+1} . The word
 899 probability is put in quotation marks as this is a density not a probability.
 900 More accurately $K(z'_{t+1}|z_t)\Delta$ is an approximate probability for such a move-
 901 ment from size z_t to a size in an interval of width Δ containing z'_{t+1} , e.g.,
 902 $z'_{t+1} \pm 0.5\Delta$. The number of individuals in a given size class at time $t + 1$ is
 903 then the sum of all individuals, of *any* size class at time t , say $n(z_t^*)$ where
 904 $z_t^* \in \Omega$ and Ω is a suitably large range of sizes, that survive, growth, and/or
 905 contribute to individuals of size class z_{t+1} at time $t + 1$:

$$n(z'_{t+1}) = \int_{z_t \in \Omega} K(z'_{t+1}|z_t)n(z_t)dz_t \quad (1.51)$$

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

909 The population growth process is the result of other processes, such as
 910 survival and reproduction. So the kernel K can be decomposed into survival
 911 of the current population and reproduction entering the population. Here,
 912 however, individual size is also a factor and survival and reproduction is into
 913 a specific size class, z_{t+1} , thus growth from size class z_t to z_{t+1} is a third

914 process to account for. The resulting partitioning of the kernel:

$$K(z'_{t+1}|z_t) = P(z'_{t+1}|z_t) + F(z'_{t+1}|z_t) \quad (1.52)$$

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

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

$$P(z'_{t+1}|z_t) = \phi(z_t)g(z'_{t+1}|z_t) \quad (1.53)$$

923 In principle, though this may be rarely appropriate, a joint density for survival
 924 and growth could be used; e.g., movement to a much larger size class could be
 925 accompanied by lowered survival probability. The survival probability could
 926 be a more complicated function of competing or sequential mortality factors;
 927 e.g., there are two mortality processes occurring in sequence, $\phi(z_t) = \phi_{1,z_t}\phi_{2,z_t}$.

928 There are also a wide variety of formulations for the fecundity kernel. For
 929 example, a female fish has a probability distribution for the number of eggs
 930 produced, $f(E|z_t)$, there is a probability that the eggs will be fertilized, p_E ,
 931 a probability that the fertilized eggs will hatch, p_h , and then there is density
 932 function that hatched larvae will be a particular size, $h(z')$, where the last
 933 three processes are independent of z_t . Then

$$F(z'_{t+1}|z_t) = f(E|z_t)p_Ep_hh(z') \quad (1.54)$$

934 Merow et al. (2014) note that a common feature of the survival/growth and
 935 fecundity kernel formulations is an *individual component*, e.g., $\phi(z_t)$ in eq'n
 936 (1.53) and $(f(E|z_t)p_Ep_h)$ in eq'n (1.54), and a *size redistribution component*,
 937 e.g., $g(z'_{t+1}|z_t)$ in eq'n (1.53) and $h(z')$ in eq'n (1.54).

938 1.5.2 Implementation of an IPM.

939 Equation (1.51) is analogous to the generation of a single component in the
 940 state vector of an MPM. With an MPM, the entire state vector at time $t + 1$
 941 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
 942 summation:

$$n_{i,t+1} = \sum_{j=1}^p L_{i,j}n_{j,t} \quad (1.55)$$

943 where L has p columns. Each $L_{i,j}$ in the summation is analogous to a kernel
 944 function as it is the per individual contribution from “size” class i at time t

945 to “size” class j from time $t + 1$. If the vector \mathbf{n}_t is further partitioned into a
 946 relative large number of size classes, the summation operation in eq’n (1.55)
 947 approaches an integration operation.

948 Implementation of an IPM is in practice the reverse operation. Referring
 949 to the integral in eq’n 1.51, the interval Ω , which contains the range of size
 950 classes that can contribute to size class z' , is partitioned into m size classes. A
 951 finite sum approximation to integration, e.g., the midpoint rule, the trapezoid
 952 rule, or Simpson’s rule, is used calculate the number of individuals in size class
 953 z' . An example of the midpoint rule: suppose Ω is an interval $[L, U]$ which
 954 is partitioned into m intervals of equal length $(U - L)/h$, and let z_i be the
 955 midpoint of the i th size class, also known as mesh points (Rees et al., 2014),
 956 where

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

957 The integral (1.51) can be approximated by

$$n(z'_{t+1}) \approx \sum_{i=1}^m K(z'_{t+1} | z_i) h n(z_{i,t}) \quad (1.56)$$

958 1.5.3 Estimation of kernel components.

959 Assuming that relevant data on size, survival, reproduction success, etc, are
 960 available, there are many standard statistical model fitting procedures, linear
 961 regressions, nonlinear regression, generalized linear models including logistic
 962 regression, and generalized additive models, that can be utilized to construct
 963 the components of the transition kernel, $K(z'_{t+1} | z_t)$. Likewise, many of the
 964 associated model fit diagnostic procedures could, and should be, used to assess
 965 the quality of the estimated components of the kernel (Rees et al., 2014).

966 Referring to the example survival/growth kernel in eq’n (1.53) and the
 967 example fecundity kernel in eq’n (1.54), a number of probability and den-
 968 sity functions are needed to calculate the transition densities. For individual
 969 components that are probabilities, e.g., the conditional probability of sur-
 970 vival, sample data on size conditional outcomes can be used to calculate es-
 971 timates. For example, a mark-recovery study of banded ducks could provide
 972 size-specific annual survival probabilities where a smooth fitted survival func-
 973 tion, such as a logit model, $\log(\phi/(1 - \phi)) | z = \beta_0 + \beta_1 z$. Whether or not
 974 time-specific functions could be fit may depend upon the number of years of
 975 data available. Survival probabilities can be a function of size and environmen-
 976 tal covariates, e.g., winter temperatures. For size redistribution components,
 977 e.g., the conditional density for moving from size class z to z^* in eq’n (1.53),
 978 longitudinal data is required. Size measurements made over time on multiple
 979 individuals are required.

980 Inference methods for IPMs are continually developing. For example,

981 Ghosh et al. (2012) use Bayesian hierarchical models where the size distribu-
982 tion is a point pattern on some interval and carry out an integrated analysis
983 that combines the parameter estimation/model fitting stage and the projec-
984 tion stage.

985 1.5.4 Application, use and analysis of IPMs

986 Plant species were the most common organisms in early applications of IPMs,
987 e.g., Northern Monkhood (Easterling et al., 2000), with the growth transitions
988 between different plant sizes, e.g., stem diameter, and including of processes
989 like flowering strategies. The scope of applications has expanded to include
990 birds (Great tits, Childs et al., 2016), arachnids (soil mites, Brooks et al.,
991 2015), mammals (Soay sheep), diseases (hosts and parasites, Metcalf et al.,
992 2016).

993 The set of questions asked of MPMs in Section 1.4.1 can be asked of IPMs.
994 For example the asymptotic behavior of IPMs can be examined. Is there a
995 limiting population growth rate, a dominant eigenvalue λ_1 and corresponding
996 stable “size” class distribution? Sensitivity analyses are also possible. See Ell-
997 ner and Rees (2006) for examples of such analyses. Available software includes
998 the R package `IPMpack` which does the following: “Construction and analysis
999 of integral projection models and associated measures of population growth,
1000 structure, perturbations (sensitivities and elasticities), overall population dy-
1001 namics, age-specific metrics, etc”.

1002 In addition to population dynamics analysis the scope of ecological infer-
1003 ence using IPMs includes analysis of evolutionary strategies (Ellner and Rees,
1004 2006). Brooks et al. (2015) separated out the effects of individual body size
1005 on developmental rates from the effects of environmental conditions on repro-
1006 ductive rates. Metcalf et al. (2016) examined the feedback between host and
1007 parasite in an epidemiological analysis.

1008 1.6 Individual Based Models, IBMs

1009 Individual based models (IBMs; DeAngelis and Grimm, 2013), sometimes re-
1010 ferred to as agent-based models (but see Roughgarden, 2012, for a definition of
1011 agents narrower than individuals), in ecology are computer simulation proce-
1012 dures that, in their most complete form, track the entire life history of multiple
1013 individuals simultaneously. Variables that are tracked include emergence into
1014 the population (date of birth, germination, hatch date), size at birth, sex,
1015 size over time, maturation process including time of sexually mature and re-
1016 production, spatial location and movement over time, senescence, and death.
1017 One central feature of many ecological IBMs is the modeling of interactions
1018 of individuals with each other, including individuals of the same species, e.g.,

1019 reflecting competition for resources and density dependence, or individuals of
1020 different species, e.g., reflecting predator-prey dynamics or more broadly eco-
1021 logical community interactions. The other central feature is the simulation of
1022 interactions of individuals with their abiotic environment, e.g., air tempera-
1023 ture and precipitation, and their biotic environment excluding like individuals,
1024 e.g., vegetative browse and zooplankton.

1025 IBMs are by design forward simulation based approaches to modeling de-
1026 mographics and, as such, the opportunity to insert complexity into dynamic
1027 processes is relatively unlimited, constrained in principle by the available com-
1028 puter storage and processing speed. Population level properties can be exam-
1029 ined at arbitrary points in time in the simulation process by aggregating the
1030 states of individuals in arbitrary ways. For example, the simulation may start
1031 with a vector of 1000 individuals where each individual has an associated vec-
1032 tor of initial conditions such as age, weight, sex, spatial location, maturity,
1033 and whatever attributes are used to distinguish individuals, i.e., attributes
1034 that could serve as potential subpopulation categories in an arbitrarily struc-
1035 tured MPM. Processes like survival, growth, movement, reproduction are then
1036 applied to each individual and at an arbitrary time point t_1 , numbers of indi-
1037 viduals in a set of spatial regions further distinguished by sex and age class,
1038 say, are tallied to yield abundances of multiple subpopulations. Continuing
1039 the simulation to a later time point, $t_2 (> t_1)$, the aggregation is done again.
1040 Repeating the simulation and aggregation K times yields a multivariate time
1041 series of subpopulation abundances, $\mathbf{n}_{t_1}, \mathbf{n}_{t_2}, \dots, \mathbf{n}_{t_K}$. Analysis of population
1042 level dynamics can then be conducted, studying such things as the effects of
1043 region-specific harvest regulations on a population of deer, for example. If the
1044 effects of changes to or states of environmental and anthropogenic factors on
1045 the population dynamics cannot be readily solved in any analytic sense, IBM
1046 output can provide some experiential, albeit simulated, insight.

1047 1.6.1 Statistical designs for and analysis of IBMs

1048 The simulation nature of IBMs with multiple attributes and multiple lev-
1049 els to attributes lends itself to using methods from the statistical design of
1050 experiments, such as factorial experiments, to construct a set of forward simu-
1051 lations with an arbitrary number of replications, and an arbitrary longitudinal
1052 time series length. For example, if three attributes are of particular interest,
1053 say sex, spatial location, and age class with corresponding levels of (female,
1054 male), (I, II, III, IV) regions, and ages (0,1,2,3+), then a factorial design with
1055 $2 \times 4 \times 4 = 32$ “treatment” combinations can be conducted with r replications
1056 of each combination. Statistical methods for analyzing data from factorial
1057 experiments such as analysis of variance or response surface modeling can
1058 then be applied. Aggregated data could also used to construct simple MPMs,
1059 like year-specific Leslie matrices, and methods for assessing MPMs, such as
1060 calculating annual finite population growth rates for multiple years could be
1061 employed (for such an example, see Rose et al., 2013).

1062 The computational burden of IBMs can grow in a number of ways. First,
1063 as might have been apparent from the previous $2 \times 4 \times 4$ factorial above, as the
1064 number of attributes of interest and the levels of each attribute increases, the
1065 number of treatment combinations can grow rapidly. Second, as the level of
1066 environmental stochasticity (or demographic) increases, the number of repli-
1067 cates required to provide a desired level of precision for estimates of average
1068 population level responses along with the associated stochastic variation in-
1069 creases as well. Third, questions about the effects of the distribution of initial
1070 attribute values at time t_0 as well as questions about the nature of the pro-
1071 cesses, e.g., density dependent or density independent recruitment success or
1072 the chosen value, or distribution of values, for juvenile survival probabilities,
1073 can lead to a considerable number of sensitivity analyses.

1074 1.6.2 Comparison with population models

1075 In contrast to population models, such as the Ricker model (eq'n 1.35), for
1076 which long term population-level behavior such as exponential growth, an
1077 asymptotic upper bound, or periodicity can sometimes be determined ana-
1078 lytically or by elementary computer simulation, population-level behavior for
1079 IBMs is an *emergent* property that might only be apparent from simulation.
1080 The resulting behavior is the result of potentially complex interactions of in-
1081 dividuals with each other and with their abiotic environment (DeAngelis and
1082 Grimm, 2013), and can demonstrate “the importance of local interactions
1083 between individuals in ecological systems” (Judson, 1994).

1084 A succinct way to contrast population-level models and IBMs is top-down
1085 versus bottom-up. Population-level models are *top-down* in that they predict
1086 what happens to individuals as function of population level characteristics,
1087 e.g., fecundity of the individual decreases as the total population abundance
1088 increases (density dependence exists). Conversely, IBMS are *bottom-up*
1089 in that modeling begins with the characteristics of multiple individuals and
1090 manifests characteristics of the population as a whole. An interesting example
1091 of the latter is with *Anolis* lizards in the Caribbean (discussed in Roughgar-
1092 den, 2012) where an IBM simulated energy gained per unit time after a lizard
1093 consumed a prey item as a function of distance from the prey and the optimal
1094 foraging distance could then be determined. From that model for the “energy
1095 capture” the daily growth rate of the lizard was predicted, with distinction
1096 made between growth prior to reproductive stage and during the reproductive
1097 stage. Using these results an optimal growth rate, as a function of age, was
1098 calculated, which was then used with information on survival probabilities
1099 and maternity rates to determine that optimal female body size was 45mm.
1100 As Roughgarden (2012) said “[t]his example illustrates a complete and suc-
1101 cessful modeling protocol that begins with the properties of an individual and
1102 culminates in the an evolutionary prediction of the adult body size for lizards
1103 on an island in the absence of congeneric competitors”.

1104 1.6.3 Applications of IBMs

1105 Some of the earliest applications of IBMs in ecology were in forestry, and such
1106 applications remain common. In the IBM JABOWA (Botkin et al., 1972),
1107 individual trees were the fundamental entities and the central measure on each
1108 tree was its stem diameter (at some height on the tree). Other tree measures
1109 such as volume and crown biomass are sometimes functions of diameter. The
1110 emergence, growth, and eventual death of a tree is a function of interactions
1111 with neighboring trees, their size and proximity and the degree to which their
1112 presence led to competition for resources for light and water, for example,
1113 and a function of interactions with the abiotic environment, e.g., soil type and
1114 chemistry, precipitation, temperature, and light. IBMs have been used for both
1115 management purposes, to predict growth and yield of commercially harvested
1116 species, and to “explore ecological mechanisms and patterns of structure and
1117 functional dynamics in natural forest ecosystem” (Liu and Ashton, 1995).

1118 Applications of IBMs to fish populations have been common as well, where
1119 IBMs “track the attributes of individual fish through time and aggregate them
1120 to generate insights into population function” (Van Winkle et al., 1993). IBMs
1121 simulate how fish of different phenotypes interact with their biotic and abi-
1122 otic environment. Differences in phenotype can refer to differences in length,
1123 weight, sex, and age, the biotic environment can include prey items, such
1124 as zooplankton or vegetation, and the abiotic environment can include wa-
1125 ter temperature, salinity, water clarity. An IBM application to Delta Smelt
1126 (*Hypomesus transpacificus*, Rose et al., 2013) also included bioenergetics con-
1127 siderations, namely the transformation of consumed prey into fish growth.

1128 More generally, the use of IBMs in ecology can be broadly divided into
1129 applications for (individual) populations, communities and ecosystems. Sin-
1130 gle population-level IBMs have been mentioned above, e.g., *Anolis* lizards and
1131 Delta Smelt, but IBMs have used to model predator-prey dynamics (Cudding-
1132 ton and Yodzis, 2002). A community-level application by Weiss et al. (2014)
1133 used an IBM to simulate how the dynamics of a community assembly of 90 hy-
1134 pothetical plant types were affected by soil attributes and grazing intensities.
1135 The results were then compared to field-based observations of species richness
1136 and diversity. Least common are ecosystems level applications; a hypothetical
1137 food web system used an IBM to model interactions between three trophic
1138 levels, plant, herbivore and carnivore (Schmitz and Booth, 1997).

1139 1.6.4 Data needs and structure

1140 There are at least three levels of data or information needs for IBMs. One is
1141 the information on the initial attributes to be assigned to the individuals, an
1142 attribute vector (Van Winkle et al., 1993), and the biotic and abiotic environ-
1143 ment. Due to general case where proximity to other individuals is a factor in
1144 the dynamics, information is needed at least about spatial location, thus an
1145 initial spatial distribution is needed: should locations be randomly placed as in

1146 a Poisson process, systematically placed, clustered, placed with probabilities
1147 proportional to particular habitat conditions? In addition to spatial location
1148 other individual attributes, e.g., size, sex, age, need to be assigned. To achieve
1149 greater realism, the actual multivariate distribution of such attributes should
1150 be mimicked. Attributes of the environment that the individuals populate
1151 are also needed, included spatial location. For example, if the population of
1152 interest is an herbivore, then the types of plants, abundance and spatial dis-
1153 tribution must be specified. Similarly, abiotic features, e.g., soil types, water
1154 sources, etc, need to be determined.

1155 The other need is for information about how the individuals interact with
1156 each other and with their environment in terms of processes of relevance to
1157 the model purpose. For example, how is the probability of survival affected
1158 by the availability and proximity to food items? How is movement affected by
1159 population density, biotic and abiotic features?

1160 To verify that IBM output, and apparent emergent population level prop-
1161 erties, e.g., collective survival, reproduction, and movement rates, are reason-
1162 able, field-based observations are needed.

1163 Given these data needs, “IBMs have therefore been criticized as being too
1164 ‘data hungry’-especially IBMs designed for specific, applied problems (Grimm
1165 and Railsback, 2013). The available data may thus constrain and guide the
1166 formulation on an IBM, affecting things like the time step resolution, spatial
1167 scope, number of attributes followed, and number of interactive processes
1168 simulated.

1169 1.6.5 Relationship with IPMs

1170 IBMs overlap somewhat with IPMs in that measurements on individuals made
1171 over time, i.e., longitudinal data, are central. IPMs use such data to model
1172 the relationship between the value of an attribute measured at time t and
1173 its value at time $t + 1$, say, the probability of transitions from one value to
1174 another are then calculated based on the collective pairings of values from
1175 multiple individuals. IBMs at times start a sample of n_0 individuals with
1176 randomly chosen initial attribute values, say $x_{0,1}, x_{0,2}, \dots$, and $x_{0,n}$, and with
1177 the relationship between $x_{t,i}$ and $x_{t+1,i}$ for arbitrary individual i , typically a
1178 stochastic relationship, and then projects the longitudinal trajectory of each
1179 of the n individuals forward in time via stochastic simulation or deterministic
1180 projection. IBMs can be used to generate data that are then used to evaluate
1181 fitting procedures for IPMs and the subsequent performance of IPMs can be
1182 evaluated by comparing IPM predictions to the “true” values generated by
1183 simulated IBM output (Rees et al., 2014).

1.7 State-Space Models, SSMs

State-space models (SSMs) are models for two time series running in parallel. One time series, here referred to as the state process time series, describes the evolution of the true, but generally unknown, state of nature over time. The other time series, here called the observation time series, is a sequence of imperfect or inexact measurements of the state process time series. The state process time series will be denoted \mathbf{n}_t , $t=0, 1, 2, \dots, T$, and the observation time series is \mathbf{y}_t with $t=1, 2, \dots, T$. The state \mathbf{n}_0 is referred to as the initial state. The discrete integer valued subscripting of the two time series is used here primarily to reduce notation as somewhat arbitrary time points could be used, t_1, t_2, \dots, t_T . The time series indexing for both time series do not necessarily need to coincide, e.g., there could be half the observations if the state is only observed every other time point, although statistical estimation limitations might occur. Also, the dimensions of \mathbf{n}_t and \mathbf{y}_t need not be the same, although situations where the dimensions differ, in particular the dimension of \mathbf{n}_t is greater than the dimension of \mathbf{y}_t statistical inference limitations or problems may result. For an ecological application, \mathbf{n}_t could be viewed as a vector of true abundances of subpopulations at time t and \mathbf{y}_t as estimates of individual components or combinations of components of \mathbf{n}_t .

Given these two time series, the structure of a SSM is a paired sequence of probability distributions (probability mass functions for integer valued components or probability density functions for continuous valued components) that characterize the evolution of the state process and the relationship between the observation vector and the state vector. The the probability distribution for the state process is typically first order Markov, i.e., the state at time t given the state at time $t - 1$ is conditionally independent of all other states. This conditional distribution is sometimes called the state transition “equation”. The observation vector at time t , given the state vector at time t , is conditionally independent all other state vectors and all other observation vectors.

1.7.1 Normal dynamic linear models

A classic SSM, originating from Kalman (1960), is the normal dynamic linear model (NDLM). A specific example of an NDLM is the following. form.

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

where $D(\theta)$ denotes an arbitrary probability distribution with parameter θ which may be degenerate, i.e., \mathbf{n}_0 is a fixed value, MVN is multivariate normal, L and B are matrices (most simply square matrices), and Σ and Ω are

1220 variance-covariance matrices. As denoted here all the matrices are time invari-
 1221 ant, but that does not need to be the case. Given the observation time series,
 1222 \mathbf{y}_t , $t=1,2,\dots,T$, and the values of \mathbf{n}_0 , L_t , B_t , Σ_t , and Ω_t , an algorithm known
 1223 as the Kalman filter can be used to calculate the conditional distribution of \mathbf{n}_t ,
 1224 which is multivariate normal, given $\mathbf{y}_1, \dots, \mathbf{y}_t$. The Kalman filter also yields
 1225 the calculated value of the likelihood (the joint marginal distribution of \mathbf{y}_t ,
 1226 $t=1,2,\dots,T$), which can in principle then be used to estimate unknown pa-
 1227 rameters of the transition and variance-covariance matrices. In practice there
 1228 are considerable restrictions on the estimability of the parameters, and cor-
 1229 relations between estimates of the parameters of the state process covariance
 1230 matrix and parameters of the observation covariance matrix (Dennis et al.,
 1231 2006).

1232 The notation L for the state transition matrix was selected to suggest the
 1233 notion of a Leslie matrix as for an age-structured MPM, a SSM extensions
 1234 of MPMs are not uncommon (Sullivan (1992); Newman (1998), and see the
 1235 gray whale example in section 6.4.2.2 of Newman et al. (2014)). Thus the
 1236 components of L can include fecundity and survival, for example, or can be
 1237 considerably more complex, as suggested in the building block approach to
 1238 MPM formulation discussed previously.

1239 1.7.2 Non-normal, nonlinear SSMs

1240 The NDLM structure, while it has the advantage of the Kalman algorithm
 1241 machinery, may often be considered too constricting and unrealistic for popu-
 1242 lation dynamics modeling. More realistic state-space models can on occasion
 1243 be “shoe-horned” into the NDLM framework. Log transformations to linearize
 1244 multiplicative relationships can sometimes work depending upon the formu-
 1245 lation of the state (and observation) models. For example, Dennis et al. (2006)
 1246 used a stochastic Gompertz model for the state process distribution.

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

1247 where $\alpha \leq 0$ and $\epsilon_t \sim \text{Normal}(0, \sigma_\epsilon^2)$. A natural log transform yields a linear
 1248 normal state distribution.

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

1249 Another way to modify an otherwise non-normal, and perhaps nonlinear SSM,
 1250 into a NDLM approximation is to work with just the first two moments of the
 1251 state process distribution and then use the mean and covariance structure as
 1252 the normal mean vector and covariance matrix. Newman (1998) and Newman
 1253 et al. (2014) give examples of such substitutions. A simplistic univariate ex-
 1254 ample is to suppose that a scalar valued state n_t is $\text{Binomial}(n_{t-1}, \phi_t)$, where
 1255 ϕ_t is the survival probability, perhaps a function of covariates. The conditional
 1256 expected value of n_t is of course $\phi_t n_{t-1} \equiv L_t n_{t-1}$, and the conditional variance
 1257 is $n_{t-1} \phi_t (1 - \phi_t) \equiv Q_t$. Other, perhaps somewhat slight, departures from the

1258 NDLM formulation can be accommodated by Taylor series transformations
 1259 of the process, using the Extended Kalman Filter (EKF; Einicke and White,
 1260 1999). A more recent alternative to the EKF, which has been shown to have at
 1261 least equal and often far superior performance (Durbin and Koopman, 2012,
 1262 p. 236) is the Unscented Kalman Filter (Julier and Uhlmann, 2004).

1263 Computer intensive Monte Carlo methods such as Markov chain Monte
 1264 Carlo (MCMC, Gilks et al., 1996) and Sequential Monte Carlo (SMC Doucet
 1265 and Gordon, 2001) offer the ultimate flexibility for fitting nonlinear, non-
 1266 normal SSMs. With the MC procedures applied to such SSMs, Bayesian infer-
 1267 ence has been the dominant approach, but not always (see De Valpine, 2003;
 1268 Ionides et al., 2006, for exceptions). One of the first ecological applications
 1269 using MC methods was by Meyer and Millar (1999), who used the program
 1270 BUGS (Bayesian inference Using Gibbs Sampling) to fit an SSM with scalar
 1271 states and observations. The state was scaled biomass ($p_t = B_t/K$), rather
 1272 than abundance, where biomass (B_t) was divided by carrying capacity, K ,
 1273 thus $0 < p_t \leq 1$), and the observation was a biased measure of scaled biomass,
 1274 an index (y_t):

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

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

1275 Thus the SSM was intrinsically nonlinear (no transformation of the state would
 1276 linearize the mean structure) and non-normal. Environmental stochasticity
 1277 was implicit to the Millar and Meyer model in the lognormal variation around
 1278 the median response.

1279 1.7.3 Hierarchical and continuous time SSMs

1280 An extension of SSMs is a hierarchical state-space model (HSSM). A general
 1281 formulation for an HSSM in a Bayesian framework is the following

$$\text{Prior distribution} : \pi(\eta, \omega) \quad (1.57)$$

$$\text{Stochastic variation in parameter} : h(\Theta_t, \eta) \quad (1.58)$$

$$\text{State process model} : g_t(\mathbf{n}_t | \mathbf{n}_{t-1}, \Theta_t) \quad (1.59)$$

$$\text{Observation model} : f_t(\mathbf{y}_t | \mathbf{n}_t, \Omega) \quad (1.60)$$

1282 Newman and Lindley (2006) used Sequential Monte Carlo to fit a Bayesian
 1283 HSSM to salmon data which included both environmental and demographic
 1284 stochasticity. The environmental stochasticity was modeled as above with sep-
 1285 arate distributions for year-specific survival and maturation probabilities. De-
 1286 mographic stochasticity was incorporated in the state process equations using
 1287 multinomial distributions to reflect between individual variation in survival
 1288 and maturation (although given the population size, the influence of demo-
 1289 graphic stochasticity on the results was likely minimal).

1290 Durbin and Koopman (2012) discuss continuous time SSMs for a couple
1291 cases including what is called a continuous time local level SSM. Here $n(t)$
1292 $= n(0) + \sigma_\epsilon \omega(t)$, where ω_t arises from a Brownian motion process, which
1293 means $\omega(0)=0$, $\omega(t) \sim \text{Normal}(0,t)$ for $0 < t < \infty$, and “jumps” or increments
1294 without common endpoints are independent, e.g., $\omega(2) - \omega(1)$ is independent of
1295 $\omega(4) - \omega(3)$. For an ecological application of continuous time SSMs see Johnson
1296 et al. (2008) who model the location of marine mammals using telemetry data.

1297 1.8 Concluding Remarks

1298 1.8.1 Omissions and sparse coverage

1299 Demography is vast topic with considerable depth and breadth, as book length
1300 treatments of MPMs and IBMs alone indicate. Continuous time demographic
1301 models, including models based on deterministic or stochastic differential
1302 equations, have been largely ignored here (the Lotka-Volterra predator-prey
1303 model being one exception). Williams et al. (2002) provides an introduction to
1304 continuous Markov processes, including birth and death processes, and Brown-
1305 nian motion in the context of models for animal populations. Gurney and
1306 Nisbet (1998) present several topics in modeling ecological dynamics where
1307 discrete time and continuous time models are compared and contrasted. For
1308 continuous time SSMs, Durbin and Koopman (2012) is a reference.

1309 Key principles or aspects of ecological theory which have demographic im-
1310 plications that were not mentioned include fitness (of which there are multiple
1311 interpretations, with reproductive success an approximate measure), adapta-
1312 tion, mutation. Effective population size, N_e , of an existing population, here
1313 defined as the minimum number of individuals necessary in a hypothetical
1314 population that would represent existing populations ability to retain the ge-
1315 netic diversity present, is an important concept for endangered species, and
1316 methods for calculating N_e were not addressed. Coverage of the demogra-
1317 phy of multiple populations, communities, and ecosystems was scanty, with
1318 some mention made using IBMs, but measures of community structure such as
1319 species richness and models for changes in such measures were not mentioned.
1320 Demographic modeling of ecosystems has been particularly popular in fish-
1321 eries (Christensen and Pauly, 1992; Walters et al., 1997, 1999) with *Ecopath*
1322 with *Ecosim* and *Ecospace* being the best known software.

1323 1.8.2 Recommended literature

1324 For MPMs, the Caswell (2001) book remains an outstanding reference with
1325 near encyclopedic coverage of material to 2001. For stochastic MPMs, the
1326 Tuljapurkar (1990) book is a classic.

1327 For IPMs, there are two “How To” papers, Rees et al. (2014) and Merow
1328 et al. (2014) which provide the basic components of IBMs, ways of estimating
1329 the kernel components, and ways of making the projections (using numerical
1330 integration methods). The original paper (Easterling et al., 2000) includes
1331 detailed discussion of the advantages of IPMs over MPMs, while Ellner and
1332 Rees (2006) include detailed examples of stable population analyses often done
1333 with MPMs. More sophisticated and integrated IPM fitting and projection
1334 approaches are described by Ghosh et al. (2012).

1335 For IBMs, Grimm and Railsback (2013) provide a book length treatment,
1336 while DeAngelis and Grimm (2013) is a more recent and considerably briefer
1337 overview paper. (Roughgarden, 2012) gives an alternative perspective on the
1338 definition of and uses of IBMs, viewing agent-based models as a special case,
1339 for example.

1340 For SSMS, Durbin and Koopman (2012) is a book length and extremely
1341 thorough treatment of SSMS about two thirds of the book covering linear
1342 SSMS, including classical treatment with the Kalman algorithms and exten-
1343 sions, and the remainder of the book on nonlinear, non-normal SSMS including
1344 coverage of special cases as well as quite general formulations that are typ-
1345 ically fit by Monte Carlo procedures. Specific focus on the use of SSMS for
1346 population dynamics modeling is given by Newman et al. (2014).

1347 **1.8.3 Speculations on future developments**

1348 Future developments in biological demography can be placed in three cate-
1349 gories: data, model formulations, and model fitting.

1350 *Data.*

1351 The volume and complexity of data on individual organisms will continue
1352 to grow as the life spans of biological monitoring programs extend, as new
1353 monitoring programs are established, and as technology for collecting data
1354 advances. Electronic monitoring devices, e.g., radio tag collars, acoustic tags,
1355 tags that record the diving depths of marine animals, are providing increas-
1356 ingly fine temporal and spatial resolution information on individual animal
1357 movement. Chemical analyses of organisms are providing more information
1358 about some aspects of individual life histories, e.g., chemical analyses of bony
1359 structures in fish, such as otoliths, can provide information about where the
1360 fish were born and migration paths (Secor et al., 1995). Environmental DNA
1361 (eDNA) is an emerging tool for indirectly detecting the presence of various
1362 species (Thomsen and Willerslev, 2015). Remote sensing data provides in-
1363 creasingly abundant and detailed information about the abiotic environment
1364 inhabited by organisms. In short, the “attribute vectors” (Van Winkle et al.,
1365 1993) for individuals, for populations, and abiotic and biotic environments
1366 will grow in length.

1367 *Model formulations.*

1368 Of the four general formulations for demographic modeling, SSMs are unique
 1369 in making explicit the distinction between process variation (environmental
 1370 and demographic stochasticity), and observation noise (e.g., sampling errors).
 1371 Inclusion of both sources of uncertainty in demographic models will be more
 1372 common. Bolker (2008) has a nice discussion of differences in methods for
 1373 fitting models with process variation alone, observation noise alone, and both
 1374 process and observation variation, and argues for the latter. In brief, *hierarchi-*
 1375 *cal* modeling (Kery and Royle, 2016; King et al., 2009), whether in a Bayesian
 1376 framework (eq'ns 1.57-1.60), or non-Bayesian framework (eq'ns 1.58-1.60) will
 1377 become more commonplace.

1378 Hierarchical extensions of MPMs which separate process and observation
 1379 variation within the normal dynamic linear model framework of SSMs date
 1380 back to the 1990s, e.g., Sullivan (1992) and Newman (1998). Separate account-
 1381 ing of process and observation variation in MPMs (as well as other frame-
 1382 works) can lead to substantive differences in inferences; An example given by
 1383 Newman et al. (2014) for modeling the population dynamics of Eastern North
 1384 Pacific gray whales (*Eschrichtius robustus* contrasted an MPM with observa-
 1385 tion error only with a SSM extension. Differences in some of the parameter
 1386 estimates were considerable, e.g., juvenile survival probability was estimated
 1387 to be 0.9999 (upper bound) for the observation error only model and 0.8281
 1388 for the SSM. NDLM formulations have been used primarily for computational
 1389 convenience as the Kalman filter provides an efficient means of calculating the
 1390 likelihood. Given advances in model fitting procedures there is less need to re-
 1391 strict process models to linear formulations, implicit to MPMs, with additive
 1392 normal (or multiplicative lognormal) distributions. More biologically realistic
 1393 nonlinear, and non-Gaussian formulations may make applications in the MPM
 1394 framework less common. However, the MPM structure will remain valuable
 1395 for formulating approximate deterministic skeletons underlying more realistic
 1396 models (Buckland et al., 2007).

1397 For IPMs and IBMs, computer simulations can explicitly partition and ac-
 1398 count for process and observation uncertainty. With IPMs, bootstrapping the
 1399 process model fitting procedure, namely the estimation of the kernel density
 1400 components, would provide measures of parameter estimate uncertainty as
 1401 well as between animal variation. For example, when estimating the growth
 1402 density, $g(z'_{t+1}|z_t)$, in the survival/growth kernel (eq'n 1.53), the longitudinal
 1403 data on sizes would be resampled and a bootstrapped distribution of growth
 1404 densities would provide a measure of parameter uncertainty. For a given fitted
 1405 growth density model, the simulated variation of individual sizes around the
 1406 expected size at time $t + 1$ would provide a measure of demographic variation.

1407 For IBMs, computer simulation of between individual variation and param-
 1408 eter uncertainty can be carried out within a designed experiment structure,
 1409 e.g., factorial designs, to (a) determine the relative import of specific factors

1410 on the model predictions and (b) quantify the degree of uncertainty in model
1411 predictions.

1412 *Model fitting.*

1413 Extended attribute vectors for increasingly large numbers of individuals, along
1414 with increasingly complex demographic model formulations, necessitate in-
1415 creasingly complex model fitting procedures. The pace of development for
1416 fitting such models is rapid and the variety of model fitting options available
1417 is increasing. Here we focus on some of these options for making inferences
1418 for dynamic hierarchical demographic models, like SSMs, with both a state
1419 process model and an observation model.

1420 At the heart of the fitting procedures for hierarchical models is mathe-
1421 matical integration and numerical optimization. For some of these models,
1422 exact, closed form solutions to the integration and optimization problems do
1423 exist. The NDLM is a notable case where the Kalman filter in effect does the
1424 integration to yield the conditional distribution for states and the likelihood,
1425 which then facilitates maximum likelihood estimation. Numerical approxima-
1426 tions to nonlinear, but Gaussian, population dynamics models yield models
1427 amenable to such analytic solutions, e.g., the extended Kalman filter with its
1428 first order Taylor series approximation to the state process and observation
1429 models.

1430 Inference for more general hierarchical dynamic models requires approx-
1431 imate techniques for integrating over the unobserved state process to yield
1432 the likelihood, or the conditional distribution for the states given the observa-
1433 tions. Approximate analytic solutions to the integration problems include the
1434 Laplace approximation (Tierney and Kadane, 1986) and the Integrated Nested
1435 Laplace Approximation (INLA, Rue et al., 2009). The software package, AD
1436 Model Builder (ADMB, Fournier et al., 2012), uses Laplace approximations
1437 to integrate over the state process distributions to yield the likelihood and
1438 then automatic differentiation for calculating maximum likelihood estimates
1439 of the parameters.

1440 Computer intensive Monte Carlo (MC) procedures, e.g., MCMC and se-
1441 quential Monte Carlo, carry out the integration by simulation. In the Bayesian
1442 framework, “optimization” per se is not done, as the entire posterior distribu-
1443 tion for states and parameters is generated. In the likelihood framework, MC
1444 methods can produce estimates of the likelihood function and optimization
1445 is then done with that estimate (De Valpine, 2003). Commonly used MCMC
1446 software for fitting Bayesian SSMs includes WinBUGS (Lunn et al., 2000) and
1447 JAGS (Plummer et al., 2003).

1448 Two recent software programs, NIMBLE and the R package `pomp`, allow
1449 users to choose from a variety of computer intensive model fitting procedures.
1450 NIMBLE (de Valpine et al., 2015) extends the BUGS software and allows es-
1451 timation within Bayesian or likelihood frameworks. The R package `pomp`, for
1452 “partially observed Markov processes”, contains a variety of procedures for

1453 fitting state-space models, with including “sequential Monte Carlo, iterated
1454 filtering, particle Markov chain Monte Carlo, approximate Bayesian compu-
1455 tation, maximum synthetic likelihood estimation, nonlinear forecasting, and
1456 trajectory matching” (King et al., 2016).



Bibliography

- 1457 Bolker, B. M. (2008). *Ecological models and data in R*. Princeton University
1458 Press.
- 1459 Botkin, D. B., Janak, J. F., and Wallis, J. R. (1972). Some ecological con-
1460 sequences of a computer model of forest growth. *The Journal of Ecology*,
1461 pages 849–872.
- 1462 Brooks, M. E., Mugabo, M., Rodgers, G. M., Benton, T. G., and Ozgul, A.
1463 (2015). How well can body size represent effects of the environment on
1464 demographic rates? disentangling correlated explanatory variables. *Journal*
1465 *of Animal Ecology*.
- 1466 Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers,
1467 D., and Thomas, L. (2001). *Introduction to distance sampling estimating*
1468 *abundance of biological populations*. Oxford University Press.
- 1469 Buckland, S. T., Newman, K. B., Fernández, C., Thomas, L., and Harwood,
1470 J. (2007). Embedding population dynamics models in inference. *Statistical*
1471 *Science*, pages 44–58.
- 1472 Caswell, H. (2001). *Matrix population models*. Wiley Online Library.
- 1473 Catchpole, E. and Morgan, B. (2001). Deficiency of parameter-redundant
1474 models. *Biometrika*, pages 593–598.
- 1475 Catchpole, E. A. and Morgan, B. J. (1997). Detecting parameter redundancy.
1476 *Biometrika*, 84(1):187–196.
- 1477 Childs, D. Z., Sheldon, B. C., and Rees, M. (2016). The evolution of labile
1478 traits in sex-and age-structured populations. *Journal of Animal Ecology*,
1479 85(2):329–342.
- 1480 Christensen, V. and Pauly, D. (1992). Ecopath iia software for balancing
1481 steady-state ecosystem models and calculating network characteristics. *Eco-*
1482 *logical modelling*, 61(3):169–185.
- 1483 Cohen, J. E. (1976). Ergodicity of age structure in populations with marko-
1484 vian vital rates, i: countable states. *Journal of the American Statistical*
1485 *Association*, 71(354):335–339.

- 1486 Cole, D. J. and Morgan, B. J. (2010). Parameter redundancy with covariates.
1487 *Biometrika*, page asq041.
- 1488 Cole, D. J., Morgan, B. J., Catchpole, E. A., and Hubbard, B. A. (2012).
1489 Parameter redundancy in mark-recovery models. *Biometrical Journal*,
1490 54(4):507–523.
- 1491 Companies, M.-H. (2005). *Random House Webster’s college dictionary*. Ran-
1492 dom House Incorporated.
- 1493 Cuddington, K. and Yodzis, P. (2002). Predator-prey dynamics and movement
1494 in fractal environments. *The American Naturalist*, 160(1):119–134.
- 1495 De Valpine, P. (2003). Better inferences from population-dynamics ex-
1496 periments using monte carlo state-space likelihood methods. *Ecology*,
1497 84(11):3064–3077.
- 1498 de Valpine, P., Turek, D., Paciorek, C. J., Anderson-Bergman, C., Lang,
1499 D. T., and Bodik, R. (2015). Programming with models: writing statisti-
1500 cal algorithms for general model structures with nimble. *arXiv preprint*
1501 *arXiv:1505.05093*.
- 1502 DeAngelis, D. L. and Grimm, V. (2013). Individual-based models in ecology
1503 after four decades. *F1000prime reports*, 6:39–39.
- 1504 Dennis, B., Ponciano, J. M., Lele, S. R., Taper, M. L., and Staples, D. F.
1505 (2006). Estimating density dependence, process noise, and observation er-
1506 ror. *Ecological Monographs*, 76(3):323–341.
- 1507 Doucet, A. d. F. and Gordon, N. (2001). *Sequential Monte Carlo methods in*
1508 *practice*. Springer-Verlag.
- 1509 Durbin, J. and Koopman, S. J. (2012). *Time series analysis by state space*
1510 *methods*. Number 38 in Oxford Statistical Science Series. Oxford University
1511 Press.
- 1512 Easterling, M. R., Ellner, S. P., and Dixon, P. M. (2000). Size-specific sensitiv-
1513 ity: applying a new structured population model. *Ecology*, 81(3):694–708.
- 1514 Einicke, G. A. and White, L. B. (1999). Robust extended kalman filtering.
1515 *IEEE Transactions on Signal Processing*, 47(9):2596–2599.
- 1516 Ellner, S. P. and Rees, M. (2006). Integral projection models for species with
1517 complex demography. *The American Naturalist*, 167(3):410–428.
- 1518 Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maun-
1519 der, M. N., Nielsen, A., and Sibert, J. (2012). Ad model builder: using
1520 automatic differentiation for statistical inference of highly parameterized
1521 complex nonlinear models. *Optimization Methods and Software*, 27(2):233–
1522 249.

- 1523 Furstenberg, H. and Kesten, H. (1960). Products of random matrices. *The*
1524 *Annals of Mathematical Statistics*, 31(2):457–469.
- 1525 Ghosh, S., Gelfand, A. E., and Clark, J. S. (2012). Inference for size demog-
1526 raphy from point pattern data using integral projection models. *Journal of*
1527 *agricultural, biological, and environmental statistics*, 17(4):641–677.
- 1528 Gilks, W., Richardson, S., and Spiegelhalter, D. (1996). *Markov chain Monte*
1529 *Carlo in practice*. Chapman & Hall Nueva York.
- 1530 Grimm, V. and Railsback, S. F. (2013). *Individual-based modeling and ecology*.
1531 Princeton university press.
- 1532 Gurney, W. and Nisbet, R. M. (1998). *Ecological dynamics*. Oxford University
1533 Press.
- 1534 Ionides, E., Bretó, C., and King, A. (2006). Inference for nonlinear dynamical
1535 systems. *Proceedings of the National Academy of Sciences*, 103(49):18438–
1536 18443.
- 1537 Johnson, D. S., London, J. M., Lea, M.-A., and Durban, J. W. (2008).
1538 Continuous-time correlated random walk model for animal telemetry data.
1539 *Ecology*, 89(5):1208–1215.
- 1540 Judson, O. P. (1994). The rise of the individual-based model in ecology. *Trends*
1541 *in Ecology & Evolution*, 9(1):9–14.
- 1542 Julier, S. J. and Uhlmann, J. K. (2004). Unscented filtering and nonlinear
1543 estimation. *Proceedings of the IEEE*, 92(3):401–422.
- 1544 Kalman, R. E. (1960). A new approach to linear filtering and prediction
1545 problems. *Journal of basic Engineering*, 82(1):35–45.
- 1546 Kendall, B. E. and Fox, G. A. (2002). Variation among individuals and reduced
1547 demographic stochasticity. *Conservation Biology*, 16(1):109–116.
- 1548 Kery, M. and Royle, J. (2016). *Applied Hierarchical Modeling in Ecology:*
1549 *Analysis of distribution, abundance and species richness in R and BUGS,*
1550 *Vol. 1*. Academic Press.
- 1551 King, A., Nguyen, D., and Ionides, E. (2016). Statistical inference for partially
1552 observed markov processes via the r package pomp. *Journal of Statistical*
1553 *Software*.
- 1554 King, R., Morgan, B., Gimenez, O., and Brooks, S. (2009). *Bayesian analysis*
1555 *for population ecology*. CRC Press.
- 1556 Lefkovich, L. (1965). The study of population growth in organisms grouped
1557 by stages. *Biometrics*, pages 1–18.

- 1558 Leslie, P. H. (1945). On the use of matrices in certain population mathematics.
1559 *Biometrika*, 33(3):183–212.
- 1560 Levins, R. (1969). Some demographic and genetic consequences of environ-
1561 mental heterogeneity for biological control. *Bulletin of the Entomological*
1562 *society of America*, 15(3):237–240.
- 1563 Lewis, E. (1942). On the generation and growth of a population. *Sankhya*,
1564 pages 93–96.
- 1565 Liu, J. and Ashton, P. S. (1995). Individual-based simulation models for forest
1566 succession and management. *Forest Ecology and Management*, 73(1):157–
1567 175.
- 1568 Lunn, D. J., Thomas, A., Best, N., and Spiegelhalter, D. (2000). Winbugs-a
1569 bayesian modelling framework: concepts, structure, and extensibility. *Statist-*
1570 *ics and computing*, 10(4):325–337.
- 1571 MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L., and
1572 Hines, J. E. (2005). *Occupancy Estimation and Modeling: Inferring Patterns*
1573 *and Dynamics of Species Occurrence*. Academic Press.
- 1574 Margoluis, R., Stem, C., Swaminathan, V., Brown, M., Johnson, A., Placci, G.,
1575 Salafsky, N., and Tilders, I. (2013). Results chains: a tool for conservation
1576 action design, management, and evaluation. *Ecology and Society*, 18(3):22.
- 1577 Merow, C., Dahlgren, J. P., Metcalf, C. J. E., Childs, D. Z., Evans, M. E.,
1578 Jongejans, E., Record, S., Rees, M., Salguero-Gómez, R., and McMahan,
1579 S. M. (2014). Advancing population ecology with integral projection models:
1580 a practical guide. *Methods in Ecology and Evolution*, 5(2):99–110.
- 1581 Metcalf, C., Graham, A., Martinex-Bakker, M., and Childs, D. (2016). Op-
1582 portunities and challenges of integral projection models for modelling host-
1583 parasite dynamics. *Journal of Animal Ecology*, 85:343–355.
- 1584 Meyer, R. and Millar, R. B. (1999). Bugs in bayesian stock assessments.
1585 *Canadian Journal of Fisheries and Aquatic Sciences*, 56(6):1078–1087.
- 1586 Morris, W. F., Doak, D. F., et al. (2002). Quantitative conservation biology.
1587 *Sinauer, Sunderland, Massachusetts, USA*.
- 1588 Newman, K., Buckland, S., Morgan, B., King, R., Borchers, D., Cole, D. J.,
1589 Besbeas, P., Gimenez, O., and Thomas, L. (2014). *Modelling population dy-*
1590 *namics: Model formulation, fitting and assessment using state-space meth-*
1591 *ods*. Springer.
- 1592 Newman, K. B. (1998). State-space modeling of animal movement and mor-
1593 tality with application to salmon. *Biometrics*, pages 1290–1314.

- 1594 Newman, K. B. and Brandes, P. L. (2010). Hierarchical modeling of juvenile
1595 chinook salmon survival as a function of sacramento–san joaquin delta water
1596 exports. *North American Journal of Fisheries Management*, 30(1):157–169.
- 1597 Newman, K. B. and Lindley, S. T. (2006). Accounting for demographic and
1598 environmental stochasticity, observation error, and parameter uncertainty
1599 in fish population dynamics models. *North American Journal of Fisheries
1600 Management*, 26(3):685–701.
- 1601 Nichols, J. D., Johnson, F. A., and Williams, B. K. (1995). Managing north
1602 american waterfowl in the face of uncertainty. *Annual review of ecology and
1603 systematics*, pages 177–199.
- 1604 North, P. M. and Morgan, B. J. (1979). Modelling heron survival using weather
1605 data. *Biometrics*, pages 667–681.
- 1606 Plummer, M. et al. (2003). Jags: A program for analysis of bayesian graphical
1607 models using gibbs sampling. In *Proceedings of the 3rd international work-
1608 shop on distributed statistical computing*, volume 124, page 125. Technische
1609 Universit at Wien Wien, Austria.
- 1610 Rees, M., Childs, D. Z., and Ellner, S. P. (2014). Building integral projection
1611 models: a user’s guide. *Journal of Animal Ecology*, 83(3):528–545.
- 1612 Reynolds, J., Knutson, M., Newman, K., Silverman, E., and Thompson, W. (in
1613 review). A road map for designing and implementing a biological monitoring
1614 program. description and baseline results. *Transactions of the American
1615 Fisheries Society*.
- 1616 Rose, K. A., Kimmerer, W. J., Edwards, K. P., and Bennett, W. A. (2013).
1617 Individual-based modeling of delta smelt population dynamics in the upper
1618 san francisco estuary: I. model description and baseline results. *Transactions
1619 of the American Fisheries Society*, 142(5):1238–1259.
- 1620 Roughgarden, J. (2012). Individual based models in ecology: An evaluation,
1621 or how not to ruin a good thing. In *Philosophy of Science Assoc. 23rd
1622 Biennial Mtg (San Diego, CA); PSA 2012 Symposia*.
- 1623 Rue, H., Martino, S., and Chopin, N. (2009). Approximate bayesian inference
1624 for latent gaussian models by using integrated nested laplace approxima-
1625 tions. *Journal of the royal statistical society: Series b (statistical methodol-
1626 ogy)*, 71(2):319–392.
- 1627 Schmitz, O. J. and Booth, G. (1997). Modelling food web complexity: the
1628 consequences of individual-based, spatially explicit behavioural ecology on
1629 trophic interactions. *Evolutionary Ecology*, 11(4):379–398.
- 1630 Secor, D. H., Henderson-Arzapalo, A., and Piccoli, P. (1995). Can otolith
1631 microchemistry chart patterns of migration and habitat utilization in

- 1632 anadromous fishes? *Journal of experimental marine Biology and Ecology*,
1633 192(1):15–33.
- 1634 Smith, E. P. (2002). Baci design. *Encyclopedia of environmetrics*.
- 1635 Sullivan, P. J. (1992). A kalman filter approach to catch-at-length analysis.
1636 *Biometrics*, pages 237–257.
- 1637 Thompson, S. K. (2012). *Sampling*. Wiley.
- 1638 Thomsen, P. F. and Willerslev, E. (2015). Environmental dna—an emerging
1639 tool in conservation for monitoring past and present biodiversity. *Biological*
1640 *Conservation*, 183:4–18.
- 1641 Tierney, L. and Kadane, J. B. (1986). Accurate approximations for poste-
1642 rior moments and marginal densities. *Journal of the american statistical*
1643 *association*, 81(393):82–86.
- 1644 Tuljapurkar, S. (1990). *Population dynamics in variable environments*.
1645 Springer-Verlag.
- 1646 Tuljapurkar, S. and Orzack, S. H. (1980). Population dynamics in variable en-
1647 vironments i. long-run growth rates and extinction. *Theoretical Population*
1648 *Biology*, 18(3):314–342.
- 1649 Van Winkle, W., Rose, K. A., and Chambers, R. C. (1993). Individual-based
1650 approach to fish population dynamics: an overview. *Transactions of the*
1651 *American Fisheries Society*, 122(3):397–403.
- 1652 Walters, C., Christensen, V., and Pauly, D. (1997). Structuring dynamic mod-
1653 els of exploited ecosystems from trophic mass-balance assessments. *Reviews*
1654 *in fish biology and fisheries*, 7(2):139–172.
- 1655 Walters, C., Pauly, D., and Christensen, V. (1999). Ecospace: prediction
1656 of mesoscale spatial patterns in trophic relationships of exploited ecosys-
1657 tems, with emphasis on the impacts of marine protected areas. *Ecosystems*,
1658 2(6):539–554.
- 1659 Weiss, L., Pfestorf, H., May, F., Körner, K., Boch, S., Fischer, M., Müller, J.,
1660 Prati, D., Socher, S. A., and Jeltsch, F. (2014). Grazing response patterns
1661 indicate isolation of semi-natural european grasslands. *Oikos*, 123(5):599–
1662 612.
- 1663 Williams, B. K., Nichols, J. D., and Conroy, M. J. (2002). *Analysis and*
1664 *management of animal populations*. Academic Press.