Population Demography for Ecology Ken Newman

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1 1.1 Introduction

The word "Demography" 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" (McGraw-Hill, 2005). Our focus here is on ecology and ecological populations, and demography will be defined as the scientific study and characterization of biological populations' structure and dynamics. The simplest structure is total abundance at arbitrary points in time, while more complex structure includes abundances for multiple partitions of a population, 10 e.g., numbers by sex, age, and spatial location. Dynamics refers to changes in 11 structure and abundances over time as well as processes, sometimes called vital 12 rates, which include reproduction, growth, maturity, movement, and mortal-13 ity, that cause these changes. 14

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

For species harvested commercially, for sport, or for subsistence, e.g., 22 salmon (Oncorhynchus spp.), red deer (Cervus elaphus), morel mushrooms 23 (Morchella spp.), and black duck (Anas rubripes), people want to know how 24 harvest affects population abundances and dynamics. Comparison of alter-25 native harvest regulations is facilitated by predictions of the magnitude and 26 sustainability of harvest levels. Predicting the effects of setting harvest reg-27 ulations, e.g., a bag limit of 10 black ducks for a one month hunting season, 28 requires some understanding of how this mortality might interact with other 29 sources of mortality and other processes, like reproduction or movement. Esti-30 mates of the degree to which harvest mortality will be compensatory (removes 31 individuals that would have died anyway from other factors) and additive (the 32 33 number of animals that will be removed over and above those that would have died from other factors) are useful. 34

For species declared threatened or endangered by a government agency 35 there are legal mandates for actions to be taken, or avoided, by managers of 36 land or water resources inhabited by the species. Those actions can pertain 37 directly to the population, such as to not take actions that could kill, harm, or 38 harass the species, or indirectly to the species's habitat. To recover the pop-39 ulation, interest is in identifying actions to increase the species abundance, 40 e.g., by restoring habitat, and predicting the effects of actions. For example, 41 the United States Fish and Wildlife Service (USFWS) has a mandate to de-42

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

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

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

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

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

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

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

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

122 1.2 Components of demography

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

TABLE 1.1

Listing of frequently used acronyms and their meaning.

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

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

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

Exact enumeration is relatively rare and uninteresting in isolation. Complexity in demographic modeling arises in several ways: (1) multiple subpopulations, (2) multiple processes, (3) environmental and demographic stochasticity, (4) density dependence, (5) competition and predation, (6) human manipulation of process dynamics, (7) uncertainty in abundances.

¹⁴⁰ 1.2.1 Multiple subpopulations

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

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

The finest partitioning of a population is at the individual entity level as the values of each individual's characteristics throughout its entire existence are the most complete description possible. This may be conceptually possi¹⁵⁶ ble, but usually not practically possible. As a mathematical exercise, however,
¹⁵⁷ the modeling of individuals in a population can be useful for elucidating pop¹⁵⁸ ulation level dynamics and will be discussed in Section 1.6 on IBMs.

159 **1.2.2** Multiple processes

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

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

If size is a distinguishing characteristic, defined ordinally (e.g., small, medium, and large) or continuously (e.g., length in cm), then individual growth is a process affecting dynamics. Individual growth dynamics are quantified in terms of the probability of moving from one size class to another (as in MPMs, section 1.4) or by a conditional probability density function for size z_{t+1}^{τ} given previous size z_t (as in IPMs, section 1.5).

179 1.2.3 Stochasticity

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

¹⁹⁴ 1.2.4 Density dependence

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

²⁰⁴ 1.2.5 Competitors, predators, and prey

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

²¹⁷ 1.2.6 Human manipulation of dynamics

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

²²⁷ 1.2.7 Uncertainty in abundances

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

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

²⁴³ 1.3 General mathematical features of PDMs

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

$$n_t = n_{t-1} + \Delta_t, \tag{1.1}$$

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

$$n_t = \lambda_t n_{t-1}, \tag{1.2}$$

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

²⁵³ 1.3.1 Multiple subpopulations

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

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

²⁵⁸ The length of the abundance vector over time need not remain fixed. The ef-

²⁵⁹ fects of a sequence of processes may cause the vector to expand, e.g., following

²⁶⁰ reproduction, or to shrink, following an aggregation of age classes (Buckland

²⁶¹ et al., 2007).

²⁶² 1.3.2 Multiple processes

²⁶³ Survival and reproduction.

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

$$n_t = n_{t-1} + R_t - M_t \tag{1.3}$$

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

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

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

A more complex model with subpopulations of young and mature indi-276 viduals has different survival fractions for just born young and the mature 277 individuals, $\phi_{y,t}$ and $\phi_{m,t}$, and the time t at which abundances are counted 278 relative to the reproductive process affects model formulation. For one sce-279 nario, t occurs immediately after reproduction, the young subpopulation are 280 those just born (denoted $n_{0,t}$ in Scenario 1 below). Under a second scenario, t 281 occurs just before reproduction, and, assuming the time interval is one year, 282 the young will be nearly age 1 at the time of counting (denoted $n_{1,t}$ in Scenario 283 2).284

Scenario 1: t just after reproduction	$\left[\begin{array}{c} n_{m,t} = \phi_{m,t} n_{t-1} + \phi_{y,t} n_{0,t-1} \\ n_{0,t} = \rho_t (\phi_{m,t} n_{t-1} + \phi_{y,t} n_{0,t-1}) \end{array} \right]$
Scenario 2: t just before reproduction	$\left[\begin{array}{c}n_{m,t} = \phi_{m,t}n_{t-1}\\n_{1,t} = \phi_{y,t}\rho_t n_{t-1}\end{array}\right]$

²⁸⁵ Immigration and emigration.

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

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

where I_t is the number immigrating into the population and E_t is the number emigrating from the population. The scalar multiplicative model (1.4) can be extended but does not necessarily remain multiplicative. The ordering of processes is again important. Assuming that immigrants arrive, and emigrants
 leave after mortality occurs, but prior to reproduction, the model is

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

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

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

297 Movement.

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

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

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

308 Individual animal growth.

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

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

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

318 1.3.3 Stochasticity

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

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

Environmental stochasticity	$\lambda_t \sim \text{Gamma}(\alpha, \beta)$
Demographic stochasticity	$n_t n_{t-1}, \lambda_t \sim \text{Poisson}(n_{t-1}\lambda_t)$

327 Asymptotic results for environmentally stochastic growth rates.

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

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

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

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

Taking the natural logarithm of both sides of the equation,

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

336 which can be re-expressed as

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

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

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

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

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

344 Or

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

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

347 Stochasticity in individual processes.

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

$$\begin{array}{rcl} logit(\phi_{c,t}) & \sim & \mathrm{Normal}\left(\beta_{0,\phi,c}, \sigma_{\phi,c}^2\right) \\ & n_{c,t} & \sim & \mathrm{Binomial}\left(n_{c,t-1}, \phi_c\right) \end{array}$$

353 where logit(x) = ln(x/(1-x)).

1.3.4 Density dependence

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

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

where n_t can be viewed as the sum of surviving adults from the previous year 362 $(\phi_a n_{t-1})$ and surviving progeny, with ϕ_y the survival fraction for offspring 363 produced at rate $b \exp(-cn_{t-1})$. The parameter b is the maximum number of 364 offspring per adult, theoretically possible in the absence of any resource limita-365 tions, while $\exp(-cn_{t-1})$ is a density dependent dampening of that maximum. 366 In the case of multiple subpopulations, if the vital rates and abundances 367 368 for one subpopulation do not affect another subpopulation, then the above univariate density dependent models can be applied on a per subpopulation 369 basis. If subpopulations occupy the same geographic area and compete for 370 resources, then density dependent formulations will include the abundances of 371 other subpopulations. Density dependent dynamics also arise for populations 372

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

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

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

³⁹⁴ 1.3.5 Inclusion of covariates

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

⁴⁰⁶ 1.3.6 Remarks: Estimability and Data Collection.

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

⁴¹² One way to disentangle such combinations of parameters, in the case of se-⁴¹³ quential processes, is to have abundance estimates at time points immediately after the end each process. For example, in the model (1.4) abundance should
be measured twice a year, once immediately following the survival process, and
once after reproduction. The reality of the processes is typically more complicated, with such sharp demarcations unlikely, but formulating such models

⁴¹⁸ can provide guidance for data collection.

⁴¹⁹ 1.4 Matrix Projection Models, MPMs

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

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

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

435 1.4.1 Analysis of MPMs

Apparently simple MPMs, such as (1.9), can yield complex dynamics depending upon the components of L, and the many extensions of MPMs have added to this complexity. To gain deeper understanding of the dynamics of MPMS, Caswell (2001, p. 18) developed four sets of questions, which have been para-phrased below.

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

444 445 446 447		population approach an upper bound (carrying capacity)? Do the total population and individual subpopulation abundances oscillate (in a damped or undamped manner)? Do the abundances display periodicity? Do the abundances become chaotic?
448 449 450	2.	Is the MPM ergodic? In other words, are the asymptotic dynamics independent of the initial conditions, e.g., independent of the actual values of \mathbf{n}_0 ?
451 452	3.	What are the transient dynamics? What are the dynamics like in the short term as opposed to the asymptotic or limiting results?
453 454 455 456 457 458	4.	How sensitive are the results to the values of the elements of L ? The survival probabilities and fecundity rates, for example, are estimates, and will have some degree of estimation error. How much would the population dynamics, including asymptotic and transient dynamics, change if some elements of the matrix were changed "slightly"?

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

Limiting behavior of density independent, time invari ate MPMs

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

For example, consider an MPM with three age classes (Young, Adult, Adult) and an initial abundance $\mathbf{n}_{0}^{'} = (100,50,10)$ and the following Leslie matrix

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

⁴⁷⁸ The population abundances over 9 iterations are:

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

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

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

⁴⁸² Thus after six generations the annual growth rate reaches 13% and stays there.
⁴⁸³ The fraction of the population in each stage class stabilizes as well:

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

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

The limiting population growth rate and proportions of each category can 487 be determined analytically using matrix algebra, in particular, by carrying 488 out an eigen analysis of **L**. For a p by p matrix **L**, the eigen analysis yields 489 p eigenvalues, $\lambda_1, \ldots, \lambda_p$, and p corresponding right eigenvectors, $\mathbf{v}_1, \ldots, \mathbf{v}_p$. 490 An eigenvalue and its corresponding eigenvector have the relationship, $\mathbf{L}\mathbf{v}_i$ 491 $= \lambda_i \mathbf{v}_i$. Denote the largest eigenvalue λ_1 and its corresponding eigenvector 492 \mathbf{v}_1 . Then λ_1 is equal to limiting population growth rate, in the example 1.13 493 (more precisely, 1.12938), and dividing each element of $\mathbf{v_1}$ by its total yields 494 the limiting fractions, here (0.54, 0.14, 0.31). 495

496 1.4.3 Stochasticity

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

from Cohen, 1976; Tuljapurkar and Orzack, 1980). Below we closely follow 506 (Caswell, 2001, p. 393) and somewhat mimic the derivation of the asymp-507 totic distribution of the stochastic univariate model shown in (1.5 - 1.7). We 508 start with a stochastic process of matrices, L_1, L_2, \ldots , which satisfy certain 509 regularity conditions, including being stationary (the joint distribution for 510 $(\mathbf{L}_{t_1}, \mathbf{L}_{t_2}, \dots, \mathbf{L}_{t_n})$ is the same as that for $(\mathbf{L}_{t_1+h}, \mathbf{L}_{t_2+h}, \dots, \mathbf{L}_{t_n+h})$ for any fi-511 nite $n > 0, t_1, t_2, \ldots, t_n$, and h > 0), and ergodic (roughly put, the initial value 512 of L_1 does not affect the eventual behavior of the sequence). Further assume 513 an upper bound on the magnitude of the initial matrix, $E(ln^+||\mathbf{L}||_1) < \infty$, 514 where $||\mathbf{L}|| = \sup_{\mathbf{n}\neq 0} \frac{||\mathbf{L}\mathbf{n}||}{||\mathbf{n}||}$ and $\ln^+(x) = \max(0, \ln(x))$. The total population size at time t, denoted N(t), is the vector norm of \mathbf{n}_t ($||\mathbf{n}_t|| = \sum_i |n_{t,i}|$). Given 515 516 an initial vector \mathbf{n}_0 : 517

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

$$\frac{1}{t}\ln\left(N(t)\right) = \frac{1}{t}\ln\left\|\prod_{i=1}^{t}\mathbf{L}_{i}\mathbf{n}_{0}\right\|.$$
(1.12)

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

$$\lim_{t \to \infty} \frac{1}{t} \ln \left(N(t) \right) = \lim_{t \to \infty} \frac{1}{t} \ln \left\| \prod_{i=1}^{t} \mathbf{L}_{i} \mathbf{n}_{0} \right\| = \ln(\lambda_{s}), \quad (1.13)$$

where λ_s is called the stochastic growth rate. Lower and upper bounds on λ_s can be calculated from the average minimum row sums and average maximum row sums of the matrices, namely,

$$\sum_{i} \pi_{i} R_{\min}^{(i)} \leq \ln(\lambda_{s}) \leq \sum_{i} \pi_{i} R_{\max}^{(i)}$$
(1.14)

where π_i is the asymptotic probability of environment *i* occurring (corresponding to matrix \mathbf{L}_i) and $R_{\min}^{(i)}$ and $R_{\max}^{(i)}$ are the minimum and maximum row sums of \mathbf{L}_i (Caswell, 2001, p. 395).

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

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

where σ^2 is some constant. Thus, similar to (1.7), the asymptotic median of the population total is the same as for a univariate exponential population growth model, and λ_s is analogous to the largest eigenvalue, λ_1 , of a deterministic MPM.

⁵³² 1.4.4 Building block approach to matrix construction

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

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

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

⁵⁴⁶ 1.4.5 Determining the elements of projection matrices

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

An alternative to the above approach of estimating matrix elements separately from inference about population abundances is to combine stochastic population dynamics with statistical sampling error, or estimation uncertainty, in matrix elements and population abundances. The SSM framework provides a structure for doing this and is discussed in Section 1.7.

⁵⁶⁸ 1.4.6 Density dependent MPMs

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

⁵⁷⁹ 1.5 Integral Projection Models, IPMs

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

⁵⁹⁵ 1.5.1 Kernel structure of IPMs.

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

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

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

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

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

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

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

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

$$P(z_{t+1}|z_t) = \phi(z_t)g(z_{t+1}|z_t)$$
(1.19)

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

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

$$F(z_{t+1}|z_t) = f(E|z_t)p_E p_h h(z_t)$$
(1.20)

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

⁶³⁸ 1.5.2 Implementation of an IPM

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

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

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

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

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

 $_{657}$ The integral (1.17) can be approximated by

$$n(z\prime_{t+1}) \approx \sum_{i=1}^{m} K(z\prime|z_i) hn(z_{i,t})$$
(1.22)

658 1.5.3 Estimation of kernel components

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

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

e.g., the conditional probability of survival, sample data on size conditional 671 outcomes can be used to calculate estimates. For example, a mark-recovery 672 study of banded ducks could provide size-specific annual survival probabilities 673 based on a smooth fitted survival function, e.g., $\log(\phi/(1-\phi))|z = \beta_0 + \beta_1 z$. 674 Whether or not time-specific functions could be fit may depend upon the num-675 ber of years of data available. Survival probabilities can be a function of size 676 and environmental covariates, e.g., winter temperatures. For size redistribu-677 tion components, such as the conditional density for moving from size class z678 to z^* in (1.19), size measurements made over time on multiple individuals are 679 required. 680

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

⁶⁸⁶ 1.5.4 Application, use and analysis of IPMs

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

⁶⁹³ The questions asked of MPMs in Section 1.4.1 can be asked of IPMs. ⁶⁹⁴ Is there a limiting population growth rate, a dominant eigenvalue λ_1 and ⁶⁹⁵ corresponding stable "size" class distribution? Ellner and Rees (2006) gives ⁶⁹⁶ examples of sensitivity analyses of IPMs. Software for IPMs includes the R ⁶⁹⁷ package IPMpack.

In addition to analysis of population dynamics, ecological inference using IPMs includes analysis of evolutionary strategies (Ellner and Rees, 2006). Brooks et al. (2015) separated out the effects of individual body size on developmental rates from the effects of environmental conditions on reproductive rates. Metcalf et al. (2016) examined the feedback between host and parasite in an epidemiological analysis.

⁷⁰⁴ 1.6 Individual Based Models, IBMs

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

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

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

⁷³⁶ 1.6.1 Statistical designs for and analysis of IBMs

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

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

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

⁷⁶⁰ 1.6.2 Comparison with population models

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

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

789 1.6.3 Applications of IBMs

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

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

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

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

⁸²⁴ 1.6.4 Data needs and structure

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

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

A second data need is for information about how the individuals interact
with each other and with their environment. For example, how is the probability of survival affected by the availability and proximity to food items?
How is movement affected by population density, biotic and abiotic features?
A third data need is field-based observations to verify that IBM output,
and apparent emergent population level properties, e.g., collective survival,
reproduction, and movement rates, are reasonable.

Given these data needs, IBMs, particularly those designed for specific applied problems have been criticized as being too "data hungry" (Grimm and Railsback, 2013). Available data may thus constrain and guide IBM formulation, affecting things like the time step resolution, spatial scope, number of attributes followed, and number of interactive processes simulated.

⁸⁴⁹ 1.6.5 Relationship with IPMs

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

⁸⁵⁸ 1.7 State-Space Models, SSMs

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

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

The probabilistic 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 \mathbf{n}_t and the relationship between \mathbf{y}_t and \mathbf{n}_t . The the probability distribution for \mathbf{n}_t is typically first order Markov, i.e., \mathbf{n}_t given \mathbf{n}_{t-1} is conditionally independent of all other states, and \mathbf{y}_t given \mathbf{n}_t is independent of all other state vectors and all other observation vectors.

⁸⁸¹ 1.7.1 Normal dynamic linear models

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

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

884 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 nor-885 mal, L and B are matrices, and Σ and Ω are variance-covariance matrices. 886 As denoted here all the matrices are time invariant, but that is not necessary. 887 Given \mathbf{y}_t , $t=1,2,\ldots,T$, and the values of \mathbf{n}_0 , \mathbf{L} , \mathbf{B} , Σ , and Ω , the conditional 888 distribution of \mathbf{n}_t , which is multivariate normal, can be determined using an 889 algorithm known as the Kalman filter. The Kalman filter also yields the calcu-890 lated value of the likelihood (the joint marginal distribution of $\mathbf{y}_t, t=1,2,\ldots,T$), 891 which can then, in principle, be used to estimate unknown parameters of the 892 transition and variance-covariance matrices. However, in practice there are 893 considerable restrictions on the estimability of the parameters, and poten-894 tially high correlations between estimates of Σ and Ω (Dennis et al., 2006). 895 The notation L for the state transition matrix was selected to suggest the no-896 tion of a Leslie matrix (1.9) as SSM extensions of MPMs are not uncommon 897 (Sullivan (1992); Newman (1998), and see the gray whale example in section 898 6.4.2.2 of Newman et al. (2014)). 899

⁹⁰⁰ 1.7.2 Non-normal, nonlinear SSMs

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

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

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

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

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

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

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

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

⁹³⁷ 1.7.3 Hierarchical and continuous time SSMs

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

Prior distribution :
$$\pi(\eta, \omega)$$
 (1.23)

Stochastic variation in parameter :
$$h(\Theta_t, \eta)$$
 (1.24)

- State process model : $g_t(\mathbf{n}_t | \mathbf{n}_{t-1}, \Theta_t)$ (1.25)
 - Observation model : $f_t(\mathbf{y}_t | \mathbf{n}_t, \Omega)$ (1.26)

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

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

956 1.8 Concluding Remarks

⁹⁵⁷ 1.8.1 Omissions and sparse coverage

⁹⁵⁸ Continuous time demographic models have been largely ignored here, except⁹⁵⁹ ing the Lotka-Volterra predator-prey model. Williams et al. (2002) provides an
⁹⁶⁰ introduction to continuous Markov processes, including birth and death pro⁹⁶¹ cesses, and Brownian motion in the context of models for animal populations.
⁹⁶² Differences in the ecological dynamics of discrete time and continuous time
⁹⁶³ models are examined by Gurney and Nisbet (1998). Durbin and Koopman
⁹⁶⁴ (2012) and Johnson et al. (2008) are references for continuous time SSMs.

Some aspects of ecological theory which have demographic implications that were omitted include fitness, adaptation, and mutation. Effective population size, N_e , of an existing population, here defined as the minimum number of individuals necessary in a hypothetical population that would represent existing populations ability to retain the genetic diversity present, is an important concept for endangered species, and methods for calculating N_e were not addressed. Coverage of the demography of multiple populations, communities, and ecosystems was scanty, and measures of community structure such as species richness and models for changes in such measures were not mentioned at all. Demographic modeling of ecosystems has been popular in fisheries (Christensen and Pauly, 1992; Walters et al., 1997, 1999) with Ecopath with Ecosim and Ecospace the leading software.

977 1.8.2 Recommended literature

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

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

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

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

1.8.3 Speculations on future developments

1001 Data.

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

birth place and migration paths (Secor et al., 1995). Environmental DNA
(eDNA) is an emerging tool for indirectly detecting species presence (Thomsen and Willerslev, 2015). Remote sensing is adding increasingly detailed data
abiotic environments. In short, "attribute vectors" (Van Winkle et al., 1993)
for individuals, populations, and abiotic and biotic environments are getting
longer and longer.

1016 Model formulations.

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

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

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

1050 Model fitting.

Extended attribute vectors for increasingly large numbers of individuals, along with increasingly complex demographic model formulations, necessitate increasingly complex model fitting procedures. The pace of development for fitting such models is rapid and the variety of model fitting options available is increasing. Here we focus on options for fitting dynamic hierarchical demographic models.

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

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