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Demography
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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

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

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

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

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

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

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

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

The organization of the remainder of this chapter is the following. Section
1.2 is an overview of components of demography, including the definition of
multiple subpopulations and multiple processes. Section 1.3 presents a pro-
gression of mathematical models more or less corresponding to the components
in section 1.2. Section 1.4 discusses matrix population models (MPMs) and is
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

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

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

1.2 Components of demography

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

$$n_t = \lambda_t n_{t-1} \tag{1.1}$$

where λ_t is the population growth rate, a multiplier which if less than 1 indicates a decline in abundance and if greater than 1 an increase in abundance.

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

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

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

1. Multiple subpopulations of n_t: The population abundance at time t can be partitioned or subdivided into two or more groups or subpopulations.

2. Multiple processes underly λ_t: The mechanisms underlying the population growth rate λ_t include a multitude of processes, including survival and reproduction.

3. Stochasticity: Environmental and demographic variability add uncertainty to projections of population dynamics.

4. Density dependence: The effect of processes can be affected by population size.

5. Competition and predation: The population dynamics of one population can be affected by other populations, of the same species or different species, can be affected in these two ways.

6. Manipulation of the dynamics: Related to the multiple components of λ_t, humans sometimes want to control or manipulate processes and thus affect the population dynamics.

7. Partial observability (Nichols et al., 1995) of n_t: The population abundances cannot be enumerated exactly and at best subsets, or samples, of the population are observed.

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

1.2.1   Multiple subpopulations

Finer characterization of the abundance involve partitioning the total number into numbers in subsets, or subpopulations, where the subsets are distinguished by one or more attributes. Some common distinguishing attributes are listed below.

- sex: female, male, or indeterminate.

- age: 0,1,2,3,..., max age.

- maturity level: young, immature but developing, mature (capable of reproduction), post-reproduction.

- size or size class: distinguished by weight, height, length, etc.

- spatial location: exact location in space (e.g., in two dimensions, latitude and longitude; in three dimensions, depth or height added).

- genotype: hereditary components that can be characterized at a variety of levels, e.g., allele combinations for a single gene or for two or more genes.

- phenotype: external characters that are a consequence of genotype and environment, e.g., color or color pattern (includes some of the above categories such as size class).

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

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

Arbitrariness of partitioning may also occur 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, $10 \leq$ medium < 20kg, and large ≥ 20kg. 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. For example, each animal is unique in its sex, date of birth (age), size, maturity level, number of offspring, location, and so on, and the values of the individual's characteristics throughout its entire existence, at any given point in time, are the most complete description possible. This is often at least conceptually possible (though not necessarily so for large subterranean vegetative populations), but usually not practically possible. A notable exception is the Soay sheep population on St Kilda Archipelago, off the coast of western Scotland, where near complete individual animal identification and labeling is done. As a mathematical exercise, however, the modeling of individuals in a population can be useful for elucidating population level dynamics and this will be discussed in Section 1.6 on IBMs.

1.2.2   Multiple processes

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

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

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

If size is a distinguishing characteristic, defined ordinally (e.g., small, medium, and large) or continuously (e.g., length in cm), then growth is a process affecting dynamics. In particular, the 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} given previous size z_t (as in IPMs, section 1.5).

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

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

1.2.3   Stochasticity

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

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

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

1.2.4   Density dependence

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

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

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

1.2.5   Competition and predation

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

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

1.2.6   Manipulation of dynamics

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

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

For endangered populations, manipulation of dynamics is done by regulating human activities and carrying out actions to increase the quality and quantity of the habitat of the population. In the case of populations harvested by humans, reductions in allowable harvest, including complete harvest bans, are often mandated by regulatory agencies. Such actions translate into effects on survival probabilities for potentially different subpopulations. Habitat alterations can affect survival, reproduction, growth, maturation, and movement. Projections of the effects of such manipulations, and those of factors that are not manipulable, on processes and subsequent population dynamics is central to PVA.

1.2.7 The role of data: Partial observability

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

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

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

1.3 General mathematical features of PDMs

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

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

If $\lambda_t = \lambda$, $n_t = \lambda^t n_0$. As noted previously, if $\lambda > 1$, population will grow exponentially.

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 is

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

The length of the abundance vector over time need not remain fixed. The effects 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 processess

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.

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

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.

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

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 $n_{1,t}$.

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

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

⁴⁴³ *Immigration and emigration.*

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

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

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

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

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

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:

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

Movement.

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

$$M \quad = \quad \begin{bmatrix} t & & t+1 & \\ & \rightarrow A & \rightarrow B & \rightarrow C \\ \hline A & 1 - \mu_{A \rightarrow B} - \mu_{A \rightarrow C} & \mu_{A \rightarrow B} & \mu_{A \rightarrow C} \\ B & \mu_{B \rightarrow A} & 1 - \mu_{B \rightarrow A} - \mu_{B \rightarrow C} & \mu_{B \rightarrow C} \\ C & \mu_{C \rightarrow A} & \mu_{C \rightarrow B} & 1 - \mu_{C \rightarrow A} - \mu_{C \rightarrow B} \end{bmatrix} \tag{1.9}$$

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

Growth.

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

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

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

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).

1.3.3 Stochasticity

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

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

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

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

where [ ] denotes the nearest integer function. An example of a mathematically convenient alternative formulation for environmental stochasticity, which ignores the discrete nature of many populations is the following:

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

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

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

$$\begin{aligned} \lambda_t &\sim \text{Gamma}(\alpha, \beta) \\ n_t|n_{t-1}, \lambda_t &\sim \text{Poisson}(n_{t-1}\lambda_t) \end{aligned} \tag{1.14} \\ \tag{1.15}$$

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

Asymptotic results for environmentally stochastic growth rates.

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

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

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

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

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

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

506 which can be re-expressed as

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

507 The righthand side of eq'n (1.17) is the mean of a sequence of indepen-
508 dent random variables, $\ln(\lambda_i), i = 1, \ldots, t$. 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 $\overline{\ln(\lambda))}$

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

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

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

514 or

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

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,

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

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

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

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.

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

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

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

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.

$$
\begin{aligned}
\text{Survival probability} && logit(\phi_t) &\sim \text{Normal}\left(\beta_\phi, \sigma_\phi^2\right) & (1.23)\\
\text{Survivors} && n_{t'} &\sim \text{Binomial}\left(n_{t-1}, \phi_t\right) & (1.24)\\
\text{Reproductive rate} && \rho_t &\sim \text{Lognormal}\left(\ln(\beta_\rho) - 0.5\sigma_\rho^2, \sigma_\rho^2\right) & (1.25)\\
\text{Reproduction} && n_{c,0,t} &\sim \text{Poisson}\left(\rho_t n_{t'}\right) & (1.26)\\
\text{Emigration probability} && logit(\zeta_t) &\sim \text{Normal}\left(\beta_\zeta, \sigma_\zeta^2\right) & (1.27)\\
\text{Non-emigrants} && n_t &\sim \text{Binomial}\left(n_{t'}, \zeta_t\right) & (1.28)\\
\text{Immigrants} && I &\sim \text{Poisson}\left(\eta\right) & (1.29)
\end{aligned}
$$

₅₄₈ *Movement.*

₅₄₉ Environnmental 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

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

$$
\begin{bmatrix} \ln\left(\frac{\mu_{A \to B}}{1 - \mu_{A \to B} - \mu_{A \to C}}\right) \\ \ln\left(\frac{\mu_{A \to C}}{1 - \mu_{A \to B} - \mu_{A \to C}}\right) \end{bmatrix} \quad \sim \quad \text{MVN}\left(\begin{bmatrix} \beta_{0, \mu_A, B} \\ \beta_{0, \mu_A, C} \end{bmatrix}, \begin{bmatrix} \sigma^2_{A, A \to B} & \sigma_{A, A \to B, A \to C} \\ \sigma_{A, A \to B, A \to C} & \sigma^2_{A, A \to C} \end{bmatrix} \right) \tag{1.30}
$$

$$
n_{A \to B, t}, n_{A \to C, t} \quad \sim \quad \text{Multinomial}\left(n_{A, t-1}, \mu_{A \to B}, \mu_{A \to C}\right) \tag{1.31}
$$

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

Growth.

As for the deterministic case, when growth refers to movement from a categorical size class, a stochastic representation of the advancement is again analogous to the handling of between region movement. In the case of individual entities, assuming that growth is never negative, a stochastic formulation is a Gamma probability density function for the increment in growth:

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

where

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

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

1.3.4   Density dependence

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

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

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

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

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

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

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

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

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.

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

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 survivng offspring, the
590 recruits. The term b is the fecundity of the average adult (with sex being
591 ignored here; if the sex ratio if 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

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

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

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

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

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

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.
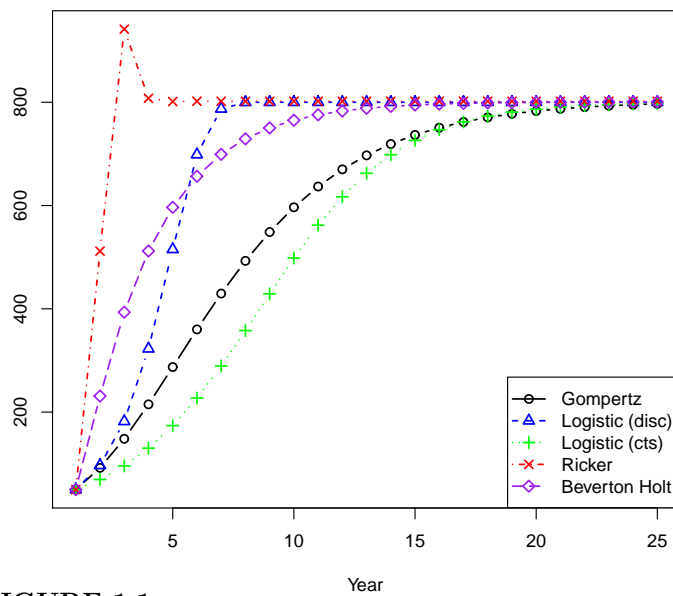
FIGURE 1.1

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:

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

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:

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

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.

$$\left[\begin{array}{c} \beta_{0,\mu_A,B} + \beta_{1,\mu_A,B} \frac{\delta_{A_{t-1}}}{\delta_{B,t-1}} \\ \beta_{0,\mu_A,C} + \beta_{1,\mu_A,C} \frac{\delta_{A_{t-1}}}{\delta_{C,t-1}} \end{array} \right]$$

$_{644}$ 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:

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

$_{653}$ 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 variaty of combined re-
$_{677}$ cruitment rate values, $\phi_j f$, when adult survival, ϕ_a, is zero and the density
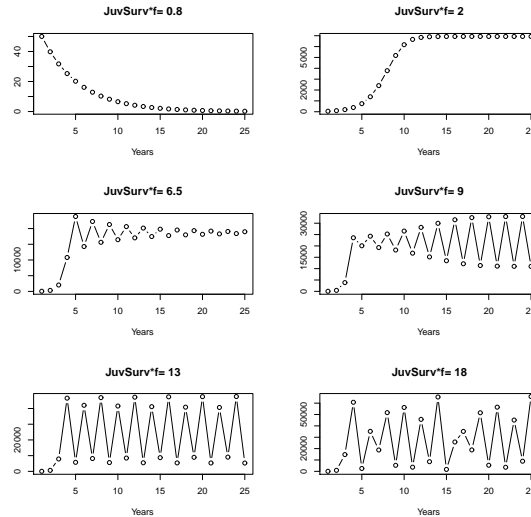
FIGURE 1.2
Population trajectories for the Ricker model for a variety of $\phi_j f$ combinations with ϕ_a=0 and c=0.001.

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

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

1.3.6   Simultaneous versus sequential processes

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

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

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

$$n(t + \Delta) = \exp(-(F + M)\Delta)n(t) \tag{1.38}$$

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

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

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

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

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

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

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

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

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

1.3.7   Remarks: Estimability and Data Collection.

It is relatively 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 fraction, ϕ_t, and reproductive rate, γ_t, in the simple univariate model (1.3). Intuitively given estimates of n_t and n_{t-1} one can just estimate the combination $(1 + \gamma_t)\phi_t$.

One way to disentangle such combinations of parameters, in the case of sequential processes, is to have abundance estimates at time points immediately after the end each process. For example, in the model (1.3) 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 can provide guidance for data collection.

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

1.4 Matrix Projection Models, MPMs

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

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

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

1.4.1 Analysis of MPMs.

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

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

$$
L \quad = \quad \left[\begin{array}{ccc} 0.0 & 1.2 & 1.4 \\ 0.3 & 0.0 & 0.0 \\ 0.0 & 0.5 & 0.9 \end{array} \right]
$$

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
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

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

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

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

And, 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 be determined analytically again using linear algebra, in particular, by carrying out an eigen analysis of L. For a p by p matrix L, the eigen analysis yields p eigenvalues, λ_1, ..., λ_p, and p corresponding right eigenvectors, $\mathbf{v}_1$, ..., $\mathbf{v}_p$. An eigenvalue and its corresponding eigenvector have the relationship, $L\mathbf{v}_i = \lambda_i \mathbf{v}_i$. Denote the largest eigenvalue λ_1 and its corresponding eigenvector $\mathbf{v}_1$. Then λ_1 is equal to limiting population growth rate, in the example 1.13 (more precisely, 1.12938), and dividing each element of $\mathbf{v_1}$ by its total yields the limiting fractions, here (0.54, 0.14, 0.31).

1.4.3   Stochasticity.

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

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

$$N(t) = ||\mathbf{n}_t|| = ||\prod_{i=1}^{t} A_i \mathbf{n}_0|| \qquad (1.46)$$
$$\Rightarrow$$
$$\frac{1}{t} \ln(N(t)) = \frac{1}{t} \ln ||\prod_{i=1}^{t} A_i \mathbf{n}_0|| \qquad (1.47)$$

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

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

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

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

where σ^2 is some constant. Thus, similar to eq'n (1.20), the asymptotic mean 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.

1.4.4   Density dependent MPMs.

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

1.4.5 Building block approach to matrix construction.

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

$$
\begin{aligned}
\left[\begin{array}{c} n_{S,t} \\ n_{L,t} \end{array} \right] &= \left[\begin{array}{cc} 1 & \rho \\ 0 & 1 \end{array} \right] \left[\begin{array}{cc} 1-\pi & 0 \\ \pi & 1 \end{array} \right] \left[\begin{array}{cc} \phi_S & 0 \\ 0 & \phi_L \end{array} \right] \left[\begin{array}{c} n_{S,t-1} \\ n_{L,t-1} \end{array} \right] \\
&= \left[\begin{array}{cc} (1-\pi+\rho\pi)\phi_S & \rho\phi_L \\ \pi\phi_L & \phi_L \end{array} \right] \left[\begin{array}{c} n_{S,t-1} \\ n_{L,t-1} \end{array} \right]
\end{aligned} \tag{1.50}
$$

The matrix in eq'n (1.50) 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.

1.4.6 Estimating the elements of projection matrices.

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

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

1.5 Integral Projection Models, IPMs

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

1.5.1 Kernel structure of IPMs.

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

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

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

The population growth process is the result of other processes, such as 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:

$$K(z_{t+1}^{'}|z_t) = P(z_{t+1}^{'}|z_t) + F(z_{t+1}^{'}|z_t) \tag{1.52}$$

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, is 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 $z^{'}$, $g(z_{t+1}^{'}|z_t)$:

$$P(z_{t+1}^{'}|z_t) = \phi(z_t)g(z_{t+1}^{'}|z_t) \tag{1.53}$$

In principle, though this may be rarely appropiate, a joint density for survival and growth could be used; e.g., movement to a much larger size class could be accompanied by 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, $\phi(z_t) = \phi_{1,z_t}\phi_{2,z_t}$.

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

$$F(z_{t+1}^{'}|z_t) = f(E|z_t)p_E p_h h(z^{'}) \tag{1.54}$$

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 eq'n (1.53) and $(f(E|z_t)p_E p_h)$ in eq'n (1.54), and a *size redistribution component*, e.g., $g(z_{t+1}^{'}|z_t)$ in eq'n (1.53) and $h(z^{'})$ in eq'n (1.54).

1.5.2 Implementation of an IPM.

Equation (1.51) 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 $t+1$ is $\mathbf{n}_{t+1} = L\mathbf{n}_t$, where the ith entry in $\mathbf{n}_{t+1}$ denoted $n_{i,t+1}$ is the following summation:

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

where L has p columns. Each $L_{i,j}$ in the summation is analogous to a kernel 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 ith size class, also known as mesh points (Rees et al., 2014),
956 where

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

957 The integral (1.51) can be approximated by

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

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,

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.

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 the growth transitions between different plant sizes, e.g., stem diameter, and including of processes like flowering strategies. The scope of applications has 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).

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

In addition to population dynamics analysis the scope of 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.

1.6 Individual Based Models, IBMs

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

reflecting competition for resources and density dependence, or individuals of different species, e.g., reflecting predator-prey dynamics or more broadly ecological community interactions. The other central feature is the simulation of interactions of individuals with their abiotic environment, e.g., air temperature and precipitation, and their biotic environment excluding like individuals, e.g., vegetative browse and zooplankton.

IBMs are by design forward simulation based approaches to modeling demographics and, as such, the opportunity to insert complexity into dynamic processes is relatively unlimited, constrained in principle by the available computer storage and processing speed. Population level properties can be examined at arbitrary points in time in the simulation process by aggregating the states of individuals in arbitrary ways. For example, the simulation may start with a vector of 1000 individuals where each individual has an associated vector of initial conditions such as age, weight, sex, spatial location, maturity, and whatever attributes are used to distinguish individuals, i.e., attributes that could serve as potential subpopulation categories in an arbitrarily structured MPM. Processes like survival, growth, movement, reproduction are then applied to each individual and at an arbitrary time point t_1, numbers of individuals in a set of spatial regions further distinguished by sex and age class, say, are tallied to yield abundances of multiple subpopulations. Continuing the simulation to a later time point, t_2 ($> t_1$), the aggregation is done again. Repeating the simulation and aggregation K times yields a multivariate time series of subpopulation abundances, $\mathbf{n_{t_1}}, \mathbf{n_{t_2}}, \ldots, \mathbf{n}_{t_K}$. Analysis of population level dynamics can then be conducted, studying such things as the effects of region-specific harvest regulations on a population of deer, for example. If the effects of changes to or states of environmental and anthropogenic factors on the population dynamics cannot be readily solved in any analytic sense, IBM output can provide some experiential, albeit simulated, insight.

1.6.1   Statistical designs for and analysis of IBMs

The simulation nature of IBMs with multiple attributes and multiple levels to attributes lends itself to using methods from the statistical design of experiments, such as factorial experiments, to construct a set of forward simulations with an arbitrary number of replications, and an arbitrary longitudinal time series length. For example, if three attributes are of particular interest, say sex, spatial location, and age class with corresponding levels of (female, male), (I, II, III, IV) regions, and ages (0,1,2,3+), then a factorial design with $2 \times 4 \times 4 = 32$ "treatment" combinations can be conducted with r replications of each combination. Statistical methods for analyzing data from factorial experiments such as analysis of variance or response surface modeling can then be applied. Aggregated data could also used to construct simple MPMs, like year-specific Leslie matrices, and methods for assessing MPMs, such as calculating annual finite population growth rates for multiple years could be 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 $2\times4\times4$ 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 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".

1.6.3   Applications of IBMs

Some of the earliest applications of IBMs in ecology were 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 such as volume and crown biomass are sometimes functions of diameter. The emergence, growth, and eventual death of a tree is a function of interactions with neighboring trees, their size and proximity and the degree to which their presence led to competition for resources for light and water, for example, and a function of interactions with the abiotic environment, e.g., soil type and chemistry, precipitation, temperature, and light. IBMs have been used for both management purposes, to predict growth and yield of commercially harvested species, and to "explore ecological mechanisms and patterns of structure and functional dynamics in natural forest ecosystem" (Liu and Ashton, 1995).

Applications of IBMs to fish populations have been common as well, where IBMs "track the attributes of individual fish through time and aggregate them to generate insights into population function" (Van Winkle et al., 1993). IBMs simulate how fish of different phenotypes interact with their biotic and abiotic environment. Differences in phenotype can refer to differences in length, weight, sex, and age, the biotic environment can include prey items, such as zooplankton or vegetation, and the abiotic environment can include water temperature, salinity, water clarity. An IBM application to Delta Smelt (*Hypomesus transpacificus, Rose et al., 2013)* also included bioenergetics considerations, namely the transformation of consumed prey into fish growth.

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

1.6.4   Data needs and structure

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

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

The other need is for information about how the individuals interact with each other and with their environment in terms of processes of relevance to the model purpose. 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?

To verify that IBM output, and apparent emergent population level properties, e.g., collective survival, reproduction, and movement rates, are reasonable, field-based observations are needed.

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

1.6.5 Relationship with IPMs

IBMs overlap somewhat with IPMs in that measurements on individuals made over time, i.e., longitudinal data, are central. IPMs use such data to model the relationship between the value of an attribute measured at time t and its value at time $t + 1$, say, the probability of transitions from one value to another are then calculated based on the collective pairings of values from multiple individuals. IBMs at times start a sample of n_0 individuals with randomly chosen initial attribute values, say $x_{0,1}$, $x_{0,2}$, ..., and $x_{0,n}$, and with the relationship between $x_{t,i}$ and $x_{t+1,i}$ for arbitrary individual i, typically a stochastic relationship, and then projects the longitudinal trajectory of each of the n individuals forward in time via stochastic simulation or deterministic projection. IBMs can be used to generate data that are then used to evaluate fitting procedures for IPMs and the subsequent performance of IPMs can be evaluated by comparing IPM predictions to the "true" values generated by 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 $\mathbf{n}_t$, $t=0, 1, 2, \ldots, T$, and the observation time series is $\mathbf{y}_t$ with $t=1,2,\ldots, T$. 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, $\ldots$, 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.

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

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

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

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

1.7.2   Non-normal, nonlinear SSMs

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

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

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

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

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

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

Computer intensive Monte Carlo methods such as Markov chain Monte Carlo (MCMC, Gilks et al., 1996) and Sequential Monte Carlo (SMC Doucet and Gordon, 2001) offer the ultimate flexibility for fitting nonlinear, non-normal SSMs. With the MC procedures applied to such SSMs, Bayesian inference has been the dominant approach, but not always (see De Valpine, 2003; Ionides et al., 2006, for exceptions). One of the first ecological applications using MC methods was by Meyer and Millar (1999), who used the program 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 than abundance, where biomass (B_t) was divided by carrying capacity, K, thus $0 < p_t \leq 1$), and the observation was a biased measure of scaled biomass, an index (y_t):

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

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

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

$$
\begin{aligned}
\text{Prior distribution} &: \quad \pi(\eta, \omega) & (1.57) \\
\text{Stochastic variation in parameter} &: \quad h(\Theta_t, \eta) & (1.58) \\
\text{State process model} &: \quad g_t(\mathbf{n}_t | \mathbf{n}_{t-1}, \Theta_t) & (1.59) \\
\text{Observation model} &: \quad f_t(\mathbf{y}_t | \mathbf{n}_t, \Omega) & (1.60)
\end{aligned}
$$

Newman and Lindley (2006) used Sequential Monte Carlo to fit a Bayesian HSSM to salmon data which included both environmental and demographic stochasticity. The environmental stochasticity was modeled as above with separate distributions for year-specific survival and maturation probabilities. Demographic stochasticity was incorporated in the state process equations using multinomial distributions to reflect between individual variation in survival and maturation (although given the population size, the influence of demographic 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.

1.8 Concluding Remarks

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 Brow-
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.

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.

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

For IBMS, Grimm and Railsback (2013) provide a book length treatment, while DeAngelis and Grimm (2013) is a more recent and considerably briefer 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 a book length and extremely thorough treatment of SSMs about two thirds of the book covering linear SSMs, including classical treatment with the Kalman algorithms and extensions, and the remainder of the book on nonlinear, non-normal SSMs including coverage of special cases as well as 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

Future developments in biological demography can be placed in three categories: data, model formulations, and model fitting.

Data.

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

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

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 some of these options for making inferences for dynamic hierarchical demographic models, like SSMs, with both a state process model and an observation model.

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

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

Computer intensive Monte Carlo (MC) procedures, e.g., MCMC and sequential Monte Carlo, carry out the integration by simulation. In the Bayesian framework, "optimization" per se is not done, as the entire posterior distribution for states and parameters is generated. In the likelihood framework, MC methods can produce estimates of the likelihood function and optimization is then done with that estimate (De Valpine, 2003). Commonly used MCMC software for fitting Bayesian SSMs includes WinBUGS (Lunn et al., 2000) and JAGS (Plummer et al., 2003).

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

fitting state-space models, with including "sequential Monte Carlo, iterated filtering, particle Markov chain Monte Carlo, approximate Bayesian computation, maximum synthetic likelihood estimation, nonlinear forecasting, and trajectory matching" (King et al., 2016).

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