

# Philosophical approach to population modeling

Over the past century, population models have evolved from being simply clever ways of plotting a reasonable curve of abundance versus time to being a tool both to improve understanding of population dynamics and to make predictions for the purpose of management. That understanding has been gained by examining how the mechanisms embodied in the equations lead to the particular pattern of abundance over time and space. This focus on the connection between the model structure (the form of the equations) and emergent population properties contained in the model solutions (what kind of population dynamics do the equations produce?) has allowed broader and more useful employment of population models, in both the scientific endeavor of understanding population dynamics and in the application of population dynamics to practical problems. This chapter describes how the approach to population modeling has evolved over the past several decades and the nature of its current state (see Box 1.1 for a vocabulary of conceptual terms that we will use throughout the book).

We begin our description of modeling philosophy in this chapter with a somewhat historical digression to give the reader a sense of the way that ecologists began to approach population modeling in the mid twentieth century, and how that approach has evolved (Section 1.1). One remnant of that meandering has endured as a useful concept: the difference between *strategic* and *tactical* population models.

Next we describe the formal logic underlying both the scientific and the practical use of models (Section 1.2). This logic provides useful ways of structuring how one uses results from population models in the context of one's goals and available data. This section also serves as a reminder that using models to achieve greater scientific understanding and using them for predictions in practical application are actually based on different logical foundations. The principal outcome of this section is the fact that for both scientific progress and practical applications, we need models that provide the opportunity to compare explicitly the structure of the model to the real world, either empirically or, at least, conceptually. We refer to that characteristic as *realism*, and it connotes a quality of testability or observability in models. This characteristic guides the organization of model descriptions throughout the book.

Next we turn to the basic research on system theory during the 1970s for a formal definition of the *state* of a system to provide us with that realism (Section 1.3). While this topic may sound a bit esoteric, it provides the key rationale for development of models to achieve scientific understanding and effective management. The basic idea underpinning this book is that a description of the state of a system at any time instant needs to include all of the information necessary to project uniquely the state of that system at the next

time instant. This concept forms the basis for understanding the different roles of models with age structure, size structure, stage structure, and spatial structure, the backbone of this book.

The next section (Section 1.4) explores the limitations in our ability to detect the actual structure and state of an ecological system in the real world. These limitations are cast in terms of the different kinds of uncertainty we encounter. Although we do not include estimation of population parameters in this book, our development of population models, our analysis of them, and our examples of applications, are heavily influenced by the relative uncertainty in various components. Basically, we seek ways to formulate models that allow our conclusions to depend as closely as possible on the parameters and concepts we can know well, and we identify the important aspects we would like to know better, i.e. the most critical remaining uncertainties. The role of uncertainties, of stochastic versus deterministic approaches, will be another important theme of this book.

Next we turn to a description of how the analysis and study of populations is related to other disciplines that focus on different *levels of integration* in biology (Section 1.5). Different disciplines focus on different levels of integration. Research at the different levels of integration employs different approaches, and they lead to different emergent properties, with each level tending to explain the next higher level. For example, population dynamics depends on the survival and reproductive rates of individual organisms. Also, lower levels of integration are usually more sensitive to smaller temporal and spatial scales of environmental variability. These differences are important because population models can serve to scale-up individual-level observations to the population scale.

We end this chapter with a synthesis of current thinking on these topics as reflected in recent publications, as of 2019. These illustrate how the conversation in the ecological literature regarding how best to formulate and use population models continues to be active.

## 1.1 Simplicity versus complexity, and four characteristics of models

An obvious question addressed in any modeling activity is how complex should the model be? Simpler models are preferred because they are easier to analyze and to understand. On the other hand, simple models are not useful if they omit key aspects that are essential to the dynamics. The brute force method of making sure to avoid this error of omission is to develop a model of sufficient complexity to completely replicate the actual system being modeled. However, this elusive goal is not necessarily desirable, especially when the operation of some mechanisms or components included are poorly understood.

Two different approaches for reaching a model of the appropriate complexity are possible. One could start with the simplest possible model, such as deterministic exponential growth, and add features to the model that would allow better understanding. Alternatively, one could start with a complex description that includes all features one could envision, and then make simplifying assumptions. Each approach has its advantages and disadvantages, as will emerge later.

The topic of model complexity for ecological models is currently an area of active discussion in population science and management. For example, national and international panels (e.g. the Pew Oceans Commission (Pew Oceans Commission, 2003) and the US Commission on Ocean Policy (US Commission on Ocean Policy, 2004)) have recommended that resource management transition from using single-species population models to models that include all components of the ecosystem, including food web interactions, the variable physical environment, and socioeconomic factors (i.e. ecosystem

based management, EBM; Pikitch et al., 2004). However, these additional factors are often poorly understood. A challenging question, therefore, is whether it is better to add poorly understood structure to the management model; i.e. will it actually improve management (Botsford et al., 1997)? This remains a vexing problem that influences how population dynamics will be described in these models (Collie et al., 2014).

An important step in the history of population modeling was mathematical ecologist Richard Levins' (1966) analysis of the question of simplicity versus complexity. He pointed out the problems with models of high complexity: (a) there are too many parameters to estimate; (b) the equations are not solvable analytically and would exceed the capacity of the fastest computers (in 1966), and (c) the resulting expressions are so complex as to be meaningless. These problems are still present forty years later, except that computational limitations continue to shrink with time.

Levins (1966) declared that it was “of course desirable to work with manageable models which maximized *generality*, *realism*, and *precision* toward the overlapping but not identical goals of understanding, predicting, and modifying nature” [emphasis ours]. He further proposed that we could not achieve all three qualities in a single model, but rather that only two out of three could be achieved in any specific case. We do not quibble with why these three characteristics should be the ones chosen, nor with the basis for the statement that one can achieve two, but not three. However, Levins did not define the three characteristics. We will. The simplest definition of *generality* is the characteristic of applying to all possible examples. *Realism* is open to several different definitions, but it is reasonably clear that what Levins meant is the characteristic introduced in the introduction to this chapter, that of allowing for direct comparison to the real world. For example, a model that included the mortality rates and reproductive rates of individuals at all ages would be considered realistic, but a model that included a (presumed) simple summary of their effects, such as population carrying capacity, would be less realistic. We can observe the amount of reproduction and the rates of death of individuals, but carrying capacity is an emergent property of a model solution and would require longer-term observations to determine. Note that this definition of realism includes no relationship to truth, as the more common, everyday definition of realism implies. In the context of the truth, Levins' definition of realism can be interpreted as meaning that an element's truth in the real world is testable, not that the element is a true depiction of reality. Levins' definition of *precision* is the standard statistical definition, though he probably actually meant accuracy, i.e. not just consistently similar answers, but consistently the correct answer (see Box 1.1).

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### **Box 1.1** DEFINITIONS RELATED TO MODELING PHILOSOPHY

Generality—strictly speaking, the quality of a statement applying to all cases.

Realism—having the same structural form as a real object.

Precision—the quality of a statistical estimate having a narrow distribution of error about a point, but not necessarily about the true value.

Accuracy—the quality of a statistical estimate having a narrow distribution of error about the true value.

Holism—including all of the relevant factors

Strategic models—models devised to answer very general questions about population behavior, with little attention to accurately portraying a specific situation.

Tactical models—models devised to answer specific questions about real situations for the purpose of making projections on which management will be based.

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According to Levins' two-out-of-three rule, some models sacrifice generality for the sake of achieving realism and precision. Levins offered the models used in fisheries management as an example. Those models include individual growth rates, reproductive rates, and mortality rates, which are comparable to the real world, and values of catch can be projected precisely, but the modelers do not intend for a single model to describe all fished populations.

Levins offered Volterra's (1926) predator-prey system as an example of the second category: models that sacrifice realism for generality and precision. This model omits the time lags often involved in predator-prey cycles and the effects of a species' population density on its birth and death rates. Instead, the model uses phenomenological model parameters such as carrying capacity. Although this model parameter cannot be directly linked to an observable ecological interaction in the field (hence the lack of realism), the model nonetheless represents the essential characteristics of general predatory-prey dynamics, and the results can be stated very precisely.

The remaining class of models in the two-out-of-three scheme sacrifices precision for the sake of realism and generality. Levins' example for this case was the set of simple biogeographical models describing broad latitudinal patterns. For example, Bergmann's rule states that animal body size will be larger in colder climates (Bergmann, 1847; Meiri and Dayan, 2003). These models are general in that they apply to many species, and they possess the quality of realism since they can easily be compared to observations, but they do not yield precise values, rather they are merely qualitative predictions in the form of inequalities.

The value of Levins' contribution was that he acknowledged that models can be quite different in function, and that different kinds of models may be best for different uses. This topic has continued to evolve up to the present.

The noted systems ecologist C. S. ("Buzz") Holling (Holling, 1968) assessed Levins' (1966) view and added a fourth characteristic of models: *holism*, the quality of including all relevant factors. As noted in the second paragraph of this section, requiring that all relevant factors be included in a model is a questionable step when there is only a poor understanding of the dynamic behavior of the proposed additions. The modern advice in favor of including all species of an ecosystem in ecosystem models is an example of the quest for greater holism. However, as noted previously, there is not a clear advantage to adding a prey species to a model when the consumption rates and the consequences of consumption are not well known (Collie et al., 2014), and a predator that consumes many different prey species can be represented just as well by a model without prey explicitly included (Murdoch et al., 2002).

An assessment of Levin's (1966) views by Robert May (May, 1973), a physicist-turned-mathematical ecologist, concluded that most ecological models were neither general, realistic, nor precise, and that the central issue did not involve those three qualities, but rather should focus on the relative advantages of simple, general models versus complex, specific models. May held that both simple and complex models had their place, with the former being useful for descriptions of the general trends in large complex systems, while the latter were useful in dealing with specific aspects of parts of such a system, as would occur in a management situation. Additional factors that would influence model complexity include the amount of data available: in data-poor situations there is less justification for complex models (as well as a need for more data, to permit the use of more complex models). These two notions were similar to what Holling (1973) had referred to as *strategic* and *tactical* approaches to modeling, respectively. These two terms are now commonly used to differentiate between these two different kinds of modeling activities (Box 1.1).

An illustrative example of the difference between strategic and tactical approaches is the development of population models to design marine reserves, following their increase in popularity as a management tool in the 1990s. As the idea of managing marine resources by creating areas of no fishing (i.e. marine reserves) began to gain prominence in the 1990s (Botsford et al., 1997; Murray et al., 1999), it became necessary to develop population models to evaluate how marine metapopulations would persist when distributed over heterogeneous habitats with fishing permitted in some locations but not in others. A marine metapopulation is a number of separate subpopulations distributed over space, linked by a dispersing larval stage (Roughgarden et al., 1988; Botsford et al., 1994; Kritzer and Sale, 2004; Chapter 9). Initially, ecologists used simplified, strategic models to understand the effects of marine reserves on fish populations. They addressed broad questions such as how does management with reserves compare to conventional management in terms of fishery yield (e.g. Holland and Brazee, 1996; Mangel, 1998; Hastings and Botsford, 1999; Hart, 2006; White and Kendall, 2007)? The answers all indicated the dual nature of conventional management and management by reserves: a certain catch was possible, and it could be achieved by a range of pairs of values of fishing mortality rates and fractions of the coastline in reserves. Another important question was which spatial configurations of reserves connected by a dispersing larval stage would support persistent fish populations (e.g. Botsford et al., 2001; Gaines et al., 2003; Kaplan, 2006, White et al., 2010a)? The general answers were that (a) single reserves would support persistent populations of species with dispersal distances shorter than the width of the reserve, and (b) combinations of many reserves that covered a certain fraction of the coastline could support species with a range of dispersal distances. These strategic models typically described populations along idealized, linear coastlines with logistic dynamics or simple age structure. They provided early guidance when decisions were needed to be made in the face of limited data and knowledge, and they also later provided a check on whether the eventual, more detailed tactical models made sense.

When management agencies actually began to implement marine reserves early in the twenty-first century, the decision-making process required the ability to compare the costs and benefits to specific fish species of specific proposed MPAs at specific locations, hence tactical modeling was required. The models became much more realistic, including age structured models with density-dependent recruitment, linked to life history data from several species, and using data on habitat distribution and ocean currents along real coastlines. These models projected the relative amounts of biomass and fishery catch expected at specific locations after reserve implementations (e.g. Kaplan et al., 2006; Pelletier et al., 2008; Kaplan et al., 2009; White et al., 2010c, 2013b; Hopf et al., 2015; reviewed by Pelletier and Mahevas, 2005; White et al., 2011).

Fortunately, the results of simulations of these realistic, tactical models turned out to be consistent with the characteristics predicted by the earlier strategic models. For example, when the fishing rate already managed a species at the maximum sustained yield, adding a reserve would only cause the yield to decline, a characteristic of the dual nature of reserve and conventional fishery management identified earlier in the strategic modeling. Moreover, the strategic modeling often provided valuable interpretations of the results of tactical modeling, that may not have been appreciated otherwise. The characteristics of persistence and yield in reserves mentioned here are developed more thoroughly in Chapters 9 and 11.

What useful information can we take from these early musings by Levins, Holling, and May? Ideally we would want all three of Levins' characteristics, but realism seems most important. For scientific progress and useful practical applications, we need to be

able to connect our results to the real world, hence we need to use model components that can be observed and measured. It will be advantageous to be general, but we need not always be; sometimes our interest will be focused on specific situations. In some situations we will need to be precise, e.g. when making projections of the consequences of proposed management, but in other situations a comparative description of results (e.g. this parameter value leads to greater population stability than a lower value) will still be valuable.

Obviously we will sometimes be concerned with a broad range of instances and issues, and will be following a strategic approach, while in others we will be concerned with specific cases, and will be following a tactical approach. An essential question concerns the true degree of generality involved in strategic models. Models that yield more general results by applying to a greater number of specific instances often do so because they apply less well to any specific instance. This tradeoff is illustrated by the old joke about the drunk seen looking for his lost ring outside of Sam's Bar. When asked what he is looking for, he replies that he is looking for the ring he lost while coming out of Joe's Bar. When it is pointed out that Joe's Bar is several blocks down the street, the drunk replies, "I know, but the light is better here near Sam's Bar."

The key to making good use of both strategic and tactical approaches is to choose simple strategic models that possess enough realism in their critical aspects that their general results are apparent in the specific results of tactical model implementations. The results described above for strategic and tactical models of reserves are an example (discussed further in Chapter 11).

## 1.2 Logical basis for population modeling

We can also gain insights into the appropriate use of population models from a formal description of the logical bases for their use. In this book the planned uses of models can be viewed as twofold: (1) *scientific* use to improve understanding of the mechanisms of population dynamics, and (2) *practical* use to provide projections for management. These depend on different logical bases. We review those here with the caveat that these are only sketches of the basic ideas; adequate to discern the nature of the type of model needed for a particular usage, but not necessarily expert views of the current status of the philosophy of science. Also note that these two uses of population models do not cover all of their uses. For example, another use of models is simply as a *pedagogical tool* to illustrate the behavior of populations without great concern for actual mechanisms. We will not be concerned with such use of models in this book, although some of the models in Chapter 2 are often used in that way.

### 1.2.1 *Deductive reasoning and the scientific uses of modeling*

We characterize the scientific use of models in terms of how we might answer specific questions regarding the causes of observed population phenomena. For example, there is often concern over why certain populations have declined over time, or have increased to dramatically high abundance, or have exhibited cyclic behavior. In almost all instances, there are multiple proposed causes for the observed behavior. Taking cyclic behavior as an example, hypothetical factors potentially responsible for the observed cycles would include (a) an over-compensatory stock-recruitment relationship (i.e. a case where recruitment actually decreases as stock increases, for large enough stock levels), (b) a cyclic

environmental variable, (c) a predator/prey relationship, and so forth. We refer to these as hypotheses, and describe a program for using population models to evaluate these hypotheses as causes of the observed cycling, decline, or increase.

The basic deductive approach to testing hypotheses in population modeling is to incorporate each hypothesis in a population model of the species of interest, and run a simulation or solve the model to see whether its output (e.g. the pattern of abundance over time) produces the observed behavior. We then evaluate the model and its derived consequences as a conditional argument from deductive logic (Box 1.2).

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### Box 1.2 CONDITIONAL ARGUMENTS

Conditional arguments from deductive logic are arguments of the following form, with two premises (P1 and P2) and a conclusion (C):

P1: If  $a$  then  $b$

P2:  $a$  true (or  $b$  true, or  $a$  false, or  $b$  false)

C:  $b$  true (or  $a$  true, or  $b$  false, or  $a$  false, respectively).

Here " $a$ " is called the *antecedent* and " $b$ " is called the *consequent*. Of the four possible outcomes of P2 and C, two are valid arguments and two are invalid. The valid arguments are (1):

P2:  $a$  true

C:  $b$  true,

which is called confirming the antecedent, and (2):

P2:  $b$  not true

C:  $a$  not true,

which is called denying the consequent.

The logically invalid arguments are (1):

P2:  $b$  true

C:  $a$  true,

which is called confirming the consequent, and (2):

P2:  $a$  not true

C:  $b$  not true,

which is called denying the antecedent. Note that the arguments are named after the statement in P2, which contains the information available on which we can base the conclusion.

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In using models and these conditional arguments from deductive logic, we obviously want to make use of the valid arguments and avoid using the invalid arguments (Box 1.2). We will describe this approach formally using the terminology in Box 1.2, and then show an example of its application to cyclic population dynamics in Dungeness crabs. The basic argument begins with the initial premise P1,

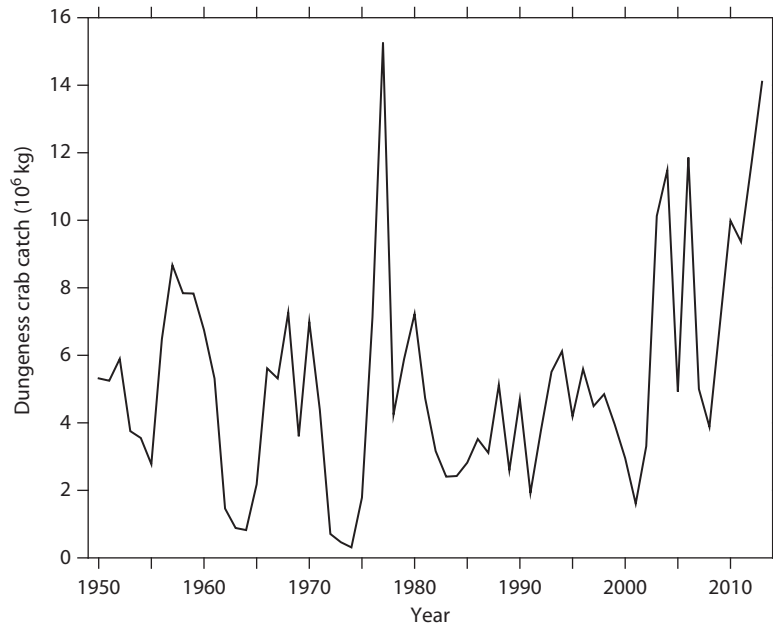
If [MODEL] then [MODEL OUTPUT],

where the MODEL contains one of the hypothetical explanations of the observed phenomenon whose cause is in question; it is "true" if it is the correct explanation. MODEL OUTPUT is the pattern of population dynamics produced by the model; it is "true" if it matches the observed natural phenomenon. If the model output does not match the behavior in question, then the second premise P2 will be "[MODEL OUTPUT] not true"

(which corresponds to “P2:  $b$  not true” in Box 1.2), whereas if the model output does match the behavior in question, the second premise will be “[MODEL OUTPUT] true” (which corresponds to “P2:  $b$  true”). We can see from Box 1.2 that if  $b$  is not true (i.e. the model output does not match the observed population behavior), we can draw the conclusion (C) that  $a$  is not true by applying the valid argument of denying the consequent. This would mean that MODEL is not true, which we take to mean that the hypothesized mechanism in that model is not the cause of the observed behavior (presuming the other assumptions of the model are true). If, on the other hand,  $b$  is true, the corresponding argument would be confirming the consequent, an invalid argument. If  $b$  is true, we do not have a valid argument available, hence we cannot draw a conclusion about the truth of the MODEL.

These results from deductive logic have been used to formulate a program for research that depends on strong results that reject hypotheses, while avoiding weak results that confirm hypotheses (Popper, 1959; Platt, 1964). It consists of sequentially testing all proposed hypothetical causes. If the hypothesis is rejected (i.e. model output does not match the empirical population observation), the next step is to test the sub-hypotheses, i.e. the assumptions of the model other than the hypothesis being tested. This step is taken (and repeated) because of the importance of the step of rejecting a hypothesis. If, on the other hand the hypothesis is not rejected, the program simply moves on to the next hypothetical cause of the phenomenon at issue.

Research that used age-structured models to study the cause of the cycles in Dungeness crab populations in northern California in the late 1970s (Fig. 1.1) provide an example of the use of this approach in interpretation of population models. At that time, research on whether the cycles could be caused by over-compensatory density-dependent recruitment



**Fig. 1.1** The catch of Dungeness crab in California since 1950. This pattern of cyclic variability was analyzed in the late 1970s to determine its cause. Catch is a reasonably close approximation to male abundance in this species because it is a male-only fishery with high levels of harvest of males greater than a minimum size limit. Data from the NOAA Fisheries Information System <https://www.fisheries.noaa.gov/national/commercial-fishing/fisheries-information-system-program>



focused on two hypothetical mechanisms: (a) cannibalism of older crabs on new recruits to the benthic habitat, which had been shown to occur; and (b) density dependence in fecundity, which was proposed to exist but had not been documented. Two research groups concerned with determining the cause of the cycles both showed that in age-structured models with density-dependent recruitment, cycles could occur with period roughly twice the mean age of adult crabs. Based on that result, Botsford and Wickham (1978) noted that cannibalism of older crabs on young crabs could cause cycles, but that their period would be less than the period of the observed cycles (i.e. 10 y). However, McKelvey et al. (1980) interpreted the same result from a similar, age-structured model as evidence to reject cannibalism as the cause, and declared density-dependent fecundity to be the cause, because a model with density-dependent fecundity produced cycles of the observed period.

The differences in the two approaches lay in their conclusions and recommended next steps. Both groups rejected cannibalism as modeled, but Botsford and Wickham (1978) recommended further testing of the sub-hypotheses (essentially the assumptions of their model that cannibalism rate would be proportional to individual metabolic demand), before rejecting cannibalism as a possible mechanism. McKelvey et al. (1980), on the other hand, rejected cannibalism as a possible cause, and accepted fecundity as the cause (thus confirming the consequent). They recommended a program of study to show that density dependence of fecundity existed. Botsford and Wickham (1978) focused on the potential for a strong result, i.e. possibly being able to reject the cannibalism hypothesis by further study of the actual age dependence of cannibalism. McKelvey et al. (1980), on the other hand, rejected cannibalism and focused on further study of a different hypothesis based on the deductively invalid argument of confirming the consequent. Their recommended first step would be to show that fecundity was density dependent. The question of the cause of the cycles went beyond scientific curiosity since the practical implication of the different hypotheses for fishery management differed. If the females were responsible for the cycles, fishing would not be affecting the cyclic behavior. However, if males were involved in the density dependence, as in cannibalism, truncation of the age structure of males by fishing would have a destabilizing effect on the population (more on this in Chapter 7).

As we shall see in Section 1.2.2, the logic followed by McKelvey, et al. (1980), while invalid in deductive logic (confirming the consequent), is not unlike that followed in an acceptable inductive argument. In essence their conclusions were based on choosing the model that currently provided the best fit, a common approach in applied ecology.

### 1.2.2 *Inductive reasoning and practical applications of modeling*

Inductive arguments consist of conclusions drawn from a number of observations. The basic form of an inductive argument is that out of  $n$  trials a certain proposition has been observed to be true  $Z$  percent of the time, therefore we can conclude that it is true  $Z$  percent of the time. This is referred to as an argument by enumeration (Salmon, 1973). Inductive arguments are not described as being “valid” or “invalid,” rather they are referred to as being relatively “stronger” or “weaker.” An argument by enumeration is stronger for greater  $n$ , and conversely weaker for lower  $n$ .

In representing population dynamics, we make use of a specific form of an argument by enumeration, referred to as an argument by analogy. The form of that argument is: if an object,  $A$ , is the same as another object,  $B$ , in characteristic 1, in characteristic 2, in characteristic 3, and so on, up to characteristic  $n$ , then one can conclude that  $A$  and  $B$  will

be the same in terms of a new characteristic not yet compared. This argument becomes stronger as the number of comparisons increases. In the case of population dynamics, the argument could be that a population model is similar to the population in terms of the pattern of survival versus age, fecundity versus age, individual growth versus age, and past abundance versus time; therefore one can conclude that the model will be similar to model behavior predicted for the future. Again, this argument by analogy also becomes stronger as the number of comparisons increases. Doing this formally with statistical approaches and information criteria requires stochastic models (but often less formal approaches are useful and appropriate).

Stock assessments made for the purpose of managing fisheries are a good example of turning to arguments by induction for the purposes of management. Examples of these can be seen at websites for the regional federal fishery management councils in the USA (e.g. the Pacific Fishery Management Council (PFMC) for the west coast of the contiguous USA), and other similar sites elsewhere around the world. These are typically based on a model fit to several types of data at once: data on age structure of the catch, a fishery independent survey of abundance, and existing information on growth versus age fit previously to size-at-age data.

### 1.2.3 *Consequences of deductive and inductive logic for population dynamics*

The question of why we need two different kinds of logic (inductive and deductive), with two different sets of seemingly conflicting rules, may have occurred to the reader, just as we imagine it did to the early Greek students of logic several millennia ago. Deductive logic is very conservative, leading us only to a number of potential causes of phenomena that have been tested and found not to be actual causes; it withholds judgement on phenomena that have not been rejected, and never confirms that a particular cause is correct (this would be confirming the consequent). This does not provide the information needed for practical applications to management. To manage populations in the future, we need to know what the actual causes of the dynamic behavior are, and that requires the approach of inductive logic.

The separate uses of inductive and deductive logic have a long history in ecology in general (e.g. Dayton, 1973). Also, Caswell et al. (1972) long ago separated models into those developed for the purposes of better understanding and those developed for prediction. He was addressing the “problem of validation,” which has to do with what one can conclude from positive outcomes of model predictions. As stated previously, these outcomes mean something in inductive logic, but much less in deductive logic.

Much more could be said about inductive and deductive logic, but here we describe them only briefly, solely to assess their requirements of models (see Salmon, 1973 and Chapter 7 of Ford, 2000 for more information). We simply conclude for our purposes here that whether you are employing deductive logic in a scientific use of models or inductive logic in a practical application of models, you will be more effective if the models explicitly contain the actual observable mechanisms in the populations. This would be satisfied by the models having a high degree of what is called “realism” in the trichotomy of Levins (1966). In the use of deductive logic, one ultimately needs specific hypothetical mechanisms that can be tested. In the use of inductive logic, the arguments improve as the number of comparisons increases, and realism is by definition comparability with reality.

### 1.3 The state of a system

A formal approach to deciding how to construct population models can be found in the early developments of system science (Caswell et al., 1972; Zadeh, 1973; Caswell 2001). In the 1960s, scientists were beginning to grapple with complex systems through mathematical models and computer solutions for those models in an effort called system science. A system was “a collection of objects, each behaving in such a way as to maintain behavioral consistency with its environment” (Caswell et al., 1972). System science required a formal, consistent method for constructing models, which was achieved by carefully defining the *state* of a system. The basic idea was that the behavior of a system would depend not just on the current stimulus from the environment, but also on its history, i.e. how it had responded to past environments. System scientists represented the effect of the past completely by expressing the current state of the system. In order to describe how a system would respond to an external stimulus from the environment, the state and the stimulus–response–state relationship had to satisfy several conditions. The most illuminating condition for our purposes was that the combination of the state variable, the current stimulus from the environment, and the stimulus–response relationship had to *uniquely* determine the response of the system (i.e. the state of the system at the next time instant; see Caswell (2001) for a more extensive discussion). The idea that the state of the system at one time point should completely determine the state of the system at the next time point is analogous to the *Markovian* property of certain stochastic models (Box 1.3).

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#### Box 1.3 MARKOVIAN PROCESSES

One important property of a properly defined state variable is that adding information about the past state of the system provides no more information about the future than the knowledge of the current state. This is the same property shared by an important class of stochastic models called Markov processes. One common example of a Markov process is a Markov chain, which is a random sequence of events (such as the position of a particle in a fluid exhibiting Brownian motion) in which the position at any point in time depends only on the position at the previous time. That is, predictions of the future state of the system based on the current state are not changed by adding information about past states. Markov chains are commonly encountered in statistics, and in Chapter 8 we discuss their use in stochastic population models. Most of the models we discuss in this book are not stochastic, but the state variables nonetheless happen to share this same property of being Markovian, and of containing all of the information at time  $t$  needed to predict the state of the system at time  $t + 1$ .

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This simple concept of state may sound obvious and trivial, but it is very powerful. In a sense it determines the organization of the rest of this book. Glancing at the table of contents, you will see that we begin in Chapter 2 with simple models that represent a population in terms of the total number of individuals (i.e. abundance,  $N$ ), then we move quickly to adding age structure, and representing the population in terms of the number

at each age. The reason for doing so is that we show that representing a population by its current abundance  $N$  is not sufficient for us to predict, uniquely, how many there will be next year. That depends (at least) on the age structure of the population, i.e. how many of the  $N$  were younger than age of maturity, and how many were older and hence reproductive.

While we develop a fairly comprehensive view of population dynamics using age-structured models, we ultimately decided that we had to move on to models that add representation of population state in terms of size structure, i.e. the number of individuals at each age and size. This is because for many taxa, reproductive maturity depends on size, not on age. If all individuals grew along the same plot of size versus age, we would not need a model with both age and size, but could use either an age-structured or a size-structured model. However, many taxa exhibit plastic growth, whereby the growth at any time could depend on population density or the environment (e.g. temperature or food). Also, for many species, individuals at a certain age do not all have the same size.

### 1.3.1 *Models of i-states and p-states*

The concept of state can apply to either an individual or a population (Metz and Diekmann, 1986). From an individual perspective, the *i*-state variables are the things you need to know about an individual to be able to uniquely predict what its state will be in the next time instant and its response in terms of reproduction and mortality. The so-called *i*-states could include the individual's age, size, reproductive status, level of energy reserves, and so forth.

From a population perspective, one of the ways of formulating a *p*-state, i.e. a description of the state of a population, is to describe the *p*-state as the number of individuals at each *i*-state in the population. The stimulus–response function is then a law of mass action that describes the “flow” of individuals through the space defined by the *i*-state variables. The number at each *i*-state at time  $t$  is determined by the number there previously that died, the number reproduced to that state, and the numbers that “grew” or “traveled” to and from that state. One of the conditions necessary for this *i*-state distribution to be a sufficient description of the *p*-state is that individuals with the same *i*-state respond identically to the environment and each other. A second necessary condition is that the population output, the production of new individuals and their *i*-states, can be calculated from the distribution over the *i*-state. Together, these two conditions are sufficient to satisfy the definition of state (Metz and Diekmann, 1986). One might notice that they are also an example of the Markovian property we introduced earlier (Box 1.3).

These definitions were envisioned in a deterministic context. The unique prediction of the future would obviously not be possible if outcomes were stochastic. When populations become locally small, they become inherently stochastic because of demographic stochasticity (see next paragraph). This means that the approach of using the distribution over *i*-states as the state variable will only work if the population abundance remains high enough at all points in the *i*-state. High enough here means such that the outcomes of mortality and/or behavioral interactions do not have to be expressed in terms of discrete numbers of individuals.

This condition can be understood by explaining demographic stochasticity as an example, a phenomenon we will refer to in Chapter 8 on random variability in populations, but which we introduce here to understand the consequences of populations being *locally small*. Suppose we have a population in which, on average, ninety percent of the individuals survive each year. There are two different ways that we could represent that

in a model. One would be simply to multiply the number at the beginning of the year by 0.9 to obtain the number at the end of the year. To see how that would work, assume we start with fifteen individuals, as an example. Multiplying that by 0.9 gives us 13.5, which is problematic, since the real population will not have fractions of individuals. We can get around this departure from reality by following a different procedure to obtain the number surviving: for each individual in the population, each year we conceptually flip a coin that comes up heads ninety percent of the time and tails ten percent of the time. Heads means that the individual survives, tails means they die. The result of this will be an integer each year, thus getting around the problem of ending up with fractions of individuals. However, now of course the outcome will not be the same for every sequence of fifteen coin flips. Thus we have introduced a kind of randomness that is actually present in a population. Fortunately this kind of randomness is well studied, and the distribution of outcomes is a binomial distribution (Box 1.4).

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#### **Box 1.4** THE BINOMIAL DISTRIBUTION

The binomial distribution is useful in understanding demographic stochasticity and in deciding how many simulation runs to make when trying to compute a probability of an outcome such as extinction.

The binomial distribution describes the outcome of a number of Bernoulli trials. A Bernoulli trial is the process of conducting a random experiment that has one of two possible outcomes. The most common examples are flipping a coin, or drawing a marble out of a bag that contains red and white marbles. In the latter case, the probability of drawing a red marble could range between 0 and 1, depending on the ratio of red to white marbles in the bag. We will use coin flipping as our example, but imagine a coin does not necessarily have a probability of 0.5 of being heads and 0.5 of being tails, but rather has a probability  $p$  of being heads (like the bag of marbles,  $p$  could be any value between 0 and 1) and probability  $1 - p$  of being tails.

Imagine you flip the coin several times in a row. The probability of obtaining  $k$  heads in  $n$  flips of the coin is  $p(k) = \binom{n}{k} p^k (1 - p)^{(n-k)}$ , where  $\binom{n}{k}$  is the binomial coefficient, which is the number of ways that a sequence of  $n$  flips with  $k$  heads can occur:  $\binom{n}{k} = n! / [k! (n - k)!]$ . The important characteristics for our purposes are the mean and variance of this distribution. The mean, or what is called *expected value* in statistics, of this distribution is  $np$ , which makes intuitive sense (the number of flips times the probability of getting heads on each flip), and the variance is  $np(1 - p)$ . In both of the examples for which we will use this, we will be interested in the relative amount of variability, the standard deviation divided by the mean, which is called the coefficient of variation (CV).

This means that the amount of demographic stochasticity (i.e. variability in the outcome of the Bernoulli trials) declines in proportion to the square root of the number of individuals in the population. This simple result is also useful in other ways; for example, when estimating a probability of extinction by repeated random simulations, the relative standard error of that estimate also declines in proportion to the square root of the number of simulations (Harris et al., 1987).

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Using the formulas described in Box 1.4, we can see that the relative amount of variability due to this binomial process (survival) declines with the square root of  $n$ . Thus, as long as we start with a high enough number, the error incurred by simply multiplying the

number of individuals by 0.9 is small. For example, with fifteen individuals the coefficient of variation would be 0.0775, while if we had 150 individuals it would be 0.0245, and with 1500 individuals it would be merely 0.0077.

Demographic stochasticity is an important source of variability in population dynamics. The example we just used is demographic stochasticity in survival, but it is not difficult to imagine that this kind of randomness can arise in processes other than survival, such as the sex ratio of a mother's offspring, or specific kinds of behavioral interactions between individuals. Demographic stochasticity is the key reason why the  $p$ -state description in terms of the distribution of abundance at each  $i$ -state breaks down when population numbers at any  $i$ -state are small. It is important to emphasize, for example, that in a population with very large total numbers, but small numbers of reproducing individuals, stochasticity will be important even though total numbers are large.

### 1.3.2 *Individual based models (IBM)*

In the late 1980s and early 1990s, mathematical ecologists began to develop an alternative to forming a representation of a  $p$ -state as a distribution over  $i$ -states. They began to realize that distribution-based  $p$ -states were not consistent with two of the basic tenets of population biology: (1) that individuals are inherently heterogeneous, and are inherently different in more ways than can be described with a few  $i$ -state variables, and (2) that in some of the most important population situations, one of the causes of problems is that populations become locally small. One example of the latter is low spatial density, but others were less obvious, e.g. behavioral interactions among individuals. Characteristics (1) and (2) are of course not independent, being two ways of stating the same thing: adding more dimensions to a multi-dimensional space makes individual densities per unit space lower, by definition. In other words, adding more  $i$ -states in order to improve realism will necessarily reduce the number of individuals in each  $i$ -state category, and thus reduce the precision of  $p$ -state representations of  $i$ -state distributions.

Some mathematical ecologists decided to avoid formulating a distribution-based  $p$ -state model, and instead to write computer programs that just kept track of the  $i$ -states of all individuals within a population directly (Huston et al., 1988; DeAngelis and Gross, 1992; Judson, 1994; Grimm and Railsback, 2005; Railsback and Grimm, 2011). This meant that instead of analyzing how a distribution over  $i$ -states changed with time, instead they numerically computed how the  $i$ -state of each individual changed, then added them up to present results. These models were termed *individual-based models (IBM)*, which is a bit of a misnomer since the  $p$ -state distribution models were also ultimately individual based. These are now also called *agent-based models* (Railsback and Grimm, 2011). We do not discuss IBMs further in this book because they tend to depend on brute force computations rather than requiring mathematical descriptions of population dynamics. The fact that computers continue to become faster and IBMs require little background in matrix algebra or partial differential equations has made them popular, and other books address them directly (Grimm and Railsback, 2005; Railsback and Grimm, 2011).

Population viability analyses (PVA) of the red-cockaded woodpecker (*Picoides borealis*) provides a good example of using IBMs in order to accurately represent population dynamics at low abundance. In the 1990s, initial PVA analyses for this species were accomplished with deterministic and stochastic stage-structured models (Heppell et al., 1994; Maguire et al., 1995). However, these models could not adequately represent the breeding behavior of red cockaded woodpeckers. Some red cockaded woodpeckers disperse to acquire breeding positions, but others remain on their natal territory as non-breeding

helpers (Walters et al., 1988). These helpers constitute a pool of replacement breeders who can replace breeders that die. This has a buffering effect on breeder mortality that reduces the variability in reproduction in a way that required an IBM to represent. Subsequent analyses showed that while probabilities of extinction increased with a reduction in breeding colonies, greater clumping of territories ameliorated that by maintaining larger potential replacement pools of helpers (Letcher et al., 1998; Walters et al., 2002).

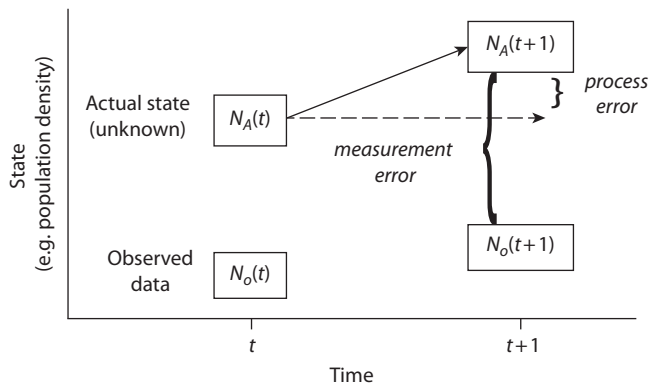
The fact that IBMs or agent-based models are primarily simulation based limits the easy application of analytical solutions, and the potential easy or elegant interpretation of those solutions. It also limits opportunities to make use of various mathematical methods such as stability analysis and optimization. However, simulation approaches can be a useful check on the formulation of analytic models—if the behavior of the analytic model and the simulation approach are similar over a range of parameters, then one has much greater confidence in using the simpler analytic model. Additionally, Metz and Diekmann (1986) emphasized that their approach based on *i*-states and *p*-states was essentially an analytic description of an IBM approach. However, the *i*-state, *p*-state approach is not a panacea as models based on this approach can quickly become complex. Yet, the approach has been shown to be powerful for understanding structured populations (de Roos and Persson, 2013; and the examples we give in the rest of this book).

## 1.4 Uncertainty and population models

In this book we do not include the topic of estimating population parameters or population states from data, hence we do not directly address aspects of randomness associated with estimation. Nonetheless we will need to refer to the different kinds of variability or uncertainty in population modeling. The three categories of uncertainty in population models are: (1) process error, (2) measurement (or observation) error, and (3) structural error. The first, process error, is variability that we decide not to account for with explicit causal mechanisms in a population model; rather, we simply treat it as noise in the population dynamics. The dramatic variability in recruitment to most fish populations is a good example. We could conceivably describe the multiple interacting physical and biological processes that lead to that variability, e.g. Caselle et al. (2010), but the increase in explanatory power would likely not be worth the huge effort, so we simply treat it as “noise.”

Measurement error (or alternatively “observation error”) results from the inherent imprecision in the methods we use to estimate population rates or cumulative states such as abundance or biomass. Most observations of populations include a combination of measurement and process error (Fig. 1.2), and a major challenge is to separate them (de Valpine and Hastings, 2002). We try to separate them because process error will affect dynamics, whereas measurement error does not. For example, population variability (e.g. year-to-year changes in the mortality rate) influences the level of risk of extinction, but observation error (e.g. slightly overestimating the number of animals one year and underestimating the next) does not (directly). Therefore, one would not want to use the total variability in an abundance time series to calculate risk, because that would overestimate the process error.

Structural error refers to the effects of using the wrong model formulation. The sequence of chapters in this book from Chapter 3 to Chapter 9 shows efforts to determine the *i*-states that lead to a valid definition of the state of a population, hence they are efforts to reduce structural errors. Another familiar effort to reduce structural errors would be



**Fig. 1.2** A schematic illustration of process error and measurement error. At time  $t$ , the observed data,  $N_O(t)$ , differs from the actual state,  $N_A(t)$ , because of measurement error. The actual state is expected to move along the dashed line but does not, rather it moves to a higher value because it has been perturbed by process error (e.g. environmental noise). Again, at  $t + 1$ , the actual state differs from the observed state by the measurement error (which has a different value at  $t + 1$  than at  $t$ ).

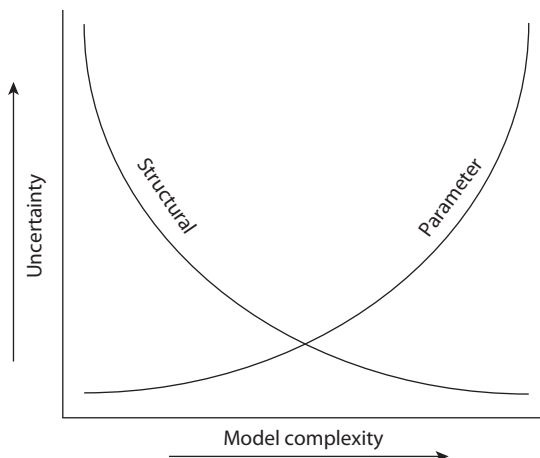
the call to model whole ecosystems instead of individual populations (ecosystem-based management; Pickett et al., 2004; Fulton, 2010).

Of the three types of uncertainty, this book will deal with how process error and structural error affect population dynamics. With regard to process error, we have mentioned previously how the presence of demographic stochasticity influences the conceptual foundation for our choice of  $i$ -state variables. We will also account for a second source of process error: the large amount of environmental variability in population vital rates, especially in younger stages. For example, marine fish populations exhibit order-of-magnitude variability in recruitment. Near the end of the book we will see that age structure of populations causes them to be more sensitive to certain frequencies of variability in environmental drivers (such as temperature or rainfall) than others. Since the frequency content of environmental variability has changed in the past (e.g. Cobb et al., 2003), and will likely change with a changing climate in the future (e.g. Timmermann et al., 1999), we will be interested in how populations respond to such changes.

While we will not deal with population estimation in this book, observation error will influence our efforts. For example, we will see in Chapters 4, 10, and 11 that one of the critical parameters for population persistence is one that is highly uncertain and extremely difficult to estimate. As a consequence, we are forced to pursue modeling avenues that seek to minimize dependence on knowing that parameter.

As previously noted, structural error plays a fundamental role in this book, at least conceptually. It guides our choices among the different age, size, and spatial models throughout the book, together with consideration of measurement uncertainty. The essential tension between these two types of uncertainty as model complexity varies is illustrated in Fig. 1.3. Simple models (Chapter 2), for example, do not possess the age structure necessary to represent the behavior of most populations faithfully, so would be on the left side of that figure. In this book, we generally increase model complexity, thus reducing structural error. However, as this figure indicates, in so doing, we accumulate a greater number of parameters whose values need to be determined, thus nominally increasing measurement uncertainty. This effect becomes increasingly important as one goes from describing population behavior to attempting to describe the behavior of





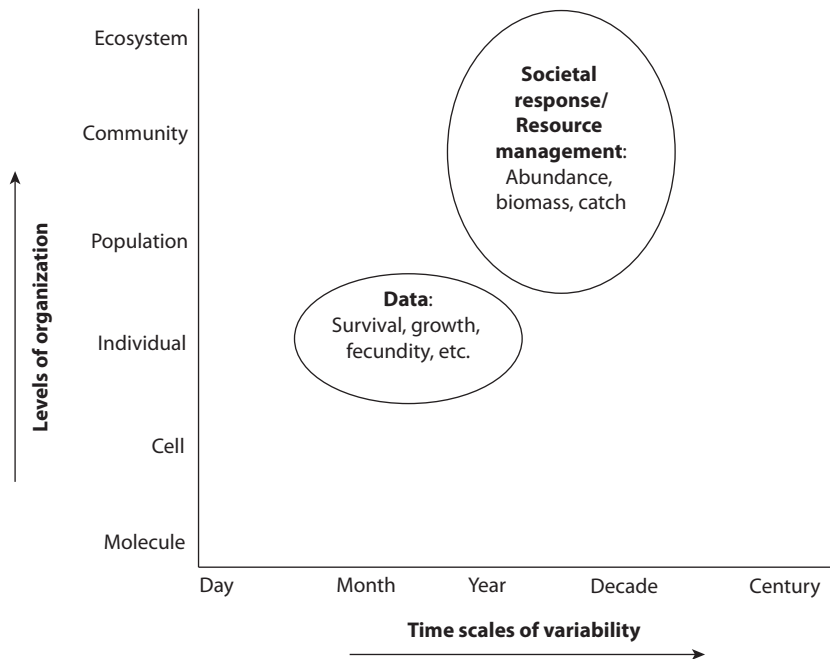
**Fig. 1.3** A schematic view of the relative amounts of structural and parameter (measurement) uncertainty as model complexity increases from left to right.

whole communities or ecosystems (Plagányi et al., 2014; Collie et al., 2014). Note that community modelers have evaluated the effects of lumping components in communities (referred to as aggregation error, Gardner et al., 1982), but we know of no similar attempts in population dynamics.

## 1.5 Levels of integration in ecology

Most readers will have been introduced to the different levels of ecological integration, perhaps even as early as in their secondary education (Fig. 1.4). In this book we will obviously be focused on the population level, and in this chapter we have spent considerable time describing some relationships between the population and the individual levels. Those relationships are a consequence of the more general characteristic of the levels of ecological integration: the explanation of behavior at one level will be found in the rates at the next lower level. That is, population dynamics are determined by the combination of individual reproductive, mortality, growth, and movement rates. By the same token, ecosystem dynamics will be determined by the growth rates of populations and their interactions.

A second important characteristic of the levels of integration in Fig. 1.4 is that both temporal and spatial scales of variability generally increase with increasing levels of integration. This means, for example, that we will generally be better able to study individuals over sufficient time and space to understand their processes, than we are able to study populations or ecosystems. Recent developments in ocean acidification illustrate this idea. Since the 1990s, when it began to be obvious that increasing  $\text{CO}_2$  levels in the atmosphere would change the bicarbonate chemistry in the ocean, thereby decreasing pH, there have been many studies of changes in individual survival and growth rates brought about by lower pH (see Kroeker et al. (2010) for a review), but very few studies of the effects of pH on marine populations or communities. The studies at the individual level provide little direction for management, so there is a growing appreciation of the need for modeling studies to “scale up” effects at the individual level to their consequences at the population and ecosystem levels, e.g. Le Quesne and Pinnegar (2012).



**Fig. 1.4** The different scales of ecological integration, showing the differences in time scales of variability. A similar plot could be made for spatial scales. Because individual-level processes occur on shorter temporal and spatial time scales, we can observe them more easily, but there is a need for models that can scale them up to the population, community, or ecosystem level, where decisions are made.

## 1.6 State of the field

In this chapter, using a historical account of how ecologists have approached population (and other) models, we have distilled a number of desirable features of population models. From Levins' trichotomy and a review of how population models can be used in deductive and inductive models, we concluded that realism was a desirable characteristic of models, i.e. that we wanted models whose components could be compared to the real world in as many ways as possible. From May's and Holling's assessments we realized that there could be two useful categories of model: early, more general, strategic models and later, more specific, tactical models, but that simple, general models often achieved generality by saying less about a broader range of situations. Therefore, we decided that to achieve realism in our models, we should seek models with appropriate definitions of the state of a system. From a description of the three different types of uncertainty, we realized that our use of appropriate definitions of state to achieve realism was an effort to minimize structural uncertainty. We also concluded that even though we are not concerned with estimation in this book, we needed to identify and characterize both process error and observation error. From a review of the concept of ecological levels of integration, we noted that our focus on population dynamics here was, in a sense, translating information at the individual level to its consequences at the population level, and that these two levels operated at different temporal and spatial scales.

We now ask the question, what are others currently thinking about these issues? We review this ongoing conversation as seen in recent publications as of 2017.

Evans and associates (Evans et al., 2013b) asked the question as to whether simple models lead to generality in ecology. They first noted that simplicity can be defined in three different ways: number of model components, brevity of equations, and level of difficulty in analysis. They then noted, as we have previously, that the term general may not mean simply “applies to all or many,” but may mean “applies less well to more.” They recommended a pathway to generality that involves individually testing components of complex simulation models.

Loneragan (2014) pointed out that Evans et al. (2013b) had neglected the effects on models of the amount of data available. Specifically, he noted that increasing complexity with limited data could lead to overfitting. The response by Evans et al. (2014) was that they had addressed that concern in another publication (Evans et al., 2013a). Evans et al. (2013a) proposed an approach to “predictive systems ecology” to “understand and predict the properties and behavior of ecological systems.” They proposed that the best available tools are process-based models, i.e. models that capture the important underlying biological mechanisms driving the behavior of systems. They then described key considerations for systems approaches: uncertainty, complexity, and constraining models with data. In that context, they described several examples in which systems ecology is already being practiced. One example is models that produce robust predictions of community structure in forest ecosystems over time from a combination of ecophysiology, individual-based modeling, and data from long-term forest inventory surveys. A second example is the models of ocean ecosystems with physical, chemical, and biological components, including ECOPATH models based on physiological energetics, and models with universal size structures of many species. These models are also discussed in publications in which some of us participated (Fogarty et al., 2013; Collie et al., 2014). The former is a survey of models recently used to scale up behavior at the individual level to their consequences at the ecosystem level. The latter is a synthesis of what is required of models formulated for the purpose of ecosystem based modeling in fisheries. The third example, given by Evans et al. (2013a) is models enabling the dynamics of ecological systems to emerge at global scales, based on fundamental birth and death, interactions and dispersal of modeled individuals (Purves et al., 2013). The fourth category is models that include both humans and ecosystems. Evans et al. (2013a) listed two major challenges ahead for predictive systems ecology: modeling at the appropriate scale and accounting for evolution.

Cuddington et al. (2013) addressed the use of models to connect data to management systems. They evaluated four classes of possible models: expert opinion, statistical extrapolation, process-based models, and detailed simulation models, and selected process-based models as the most promising. The reasons given for that choice were the transparency of explicit assumptions regarding causality, and the ability to account for uncertainty. For the chosen type of model, they evaluate issues such as whether tactical or strategic models should be used, choice of appropriate scale, whether the system is in flux due to global change, the impact of legacy effects, the potential for threshold dynamics, and including socio-economic impacts in process models.

Marquet et al. (2014) addressed a related, but nonetheless different, question: how ecological theory can best drive scientific progress and address environmental challenges. They describe theories, that: (1) are grounded in first principles, (2) are usually expressed mathematically, (3) are efficient (i.e. generate a large number of predictions per free parameter), (4) are approximate, and (5) provide well-understood standards for comparison with empirical data. Thus efficient theories have some of the characteristics of models favored

by us and others, but seem to favor simpler models by including the characteristic of providing a large number of predictions per free parameter, and allowing the theory to be approximate. And indeed most theories in ecology (listed in Marquet, et al., 2014) are not the basis on which one would make management decisions.

In the spirit of providing a broad range of views: related recent comments by scientists concerned more with ecosystem policy than population dynamics (Schindler and Hilborn, 2015) suggest that we accept the fact that ecosystems may never be as understandable as we had hoped, and that we account for the consequent extant uncertainty by formulating robust policies that will work across a broad range of the actual unknown states of nature. They diminish the role of models (particularly complex ecosystem models) to “heuristic tools for communication,” with little hope of reliable forecasts. This stems from their belief that “the best forecast models are typically mechanism-free, relying on emergent statistical properties of data to make short-term predictions,” and “verification and validation of ecosystem models (i.e. fitting models to data) likely produce overly optimistic impressions of the reliability of forecasts.”

From these publications we can at least conclude that the issues described in this chapter are still very much part of the conversation in ecology, and that there continues to be a concern for getting the methodology right. Also, there seems to be a gradual maturation process that leaves us currently less likely to depend on simple models for general answers. Throughout this book, we will describe the historical evolution of different approaches to population modeling while also addressing ongoing challenges. As we will see, some of these current challenges include the role of stochasticity, the role of non-autonomous systems in which there are underlying parameter changes through time, the role of analytical versus computational or simulation approaches, and how complex models should be.