

# An Introduction to the Practice of Ecological Modeling

BY LELAND J. JACKSON, ANETT S. TREBITZ, AND KATHRYN L. COTTINGHAM

**M**odeling has become an important tool in the study of ecological systems, as a scan of the table of contents of any major ecological journal makes abundantly clear. A number of books have recently been published that provide excellent advice on model construction, building, and use (e.g., Gotelli 1995, Gurney and Nisbet 1998, Roughgarden 1998) and add to the classic literature on modeling ecological systems and their dynamics (e.g., Maynard Smith 1974, Nisbet and Gurney 1982). Unfortunately, however, little—if any—of this growing literature on ecological modeling addresses the motivation to model and the initial stages of the modeling process, information that beginning students would find useful.

Fast computers and graphical software packages have removed much of the drudgery of creating models with a programming language and opened new avenues of model construction, use, and even misuse. There are many reasons why a student might want to consider modeling as a component of his or her education. Models provide an opportunity to explore ideas regarding ecological systems that it may not be possible to field-test for logistical, political, or financial reasons. Often, learning occurs from apparently strange results and unexpected surprises. The process of formulating an ecological model is extremely helpful for organizing one's thinking, bringing hidden assumptions to light, and identifying data needs. More and more, students want to "do something" with modeling but are not sure how to get started.

The goals of this article are to outline issues concerning the value of ecological models and some possible motivations for modeling, and to provide an entry point to the established modeling literature so that those who are beginning to think about using models in their research can integrate modeling usefully. We therefore envision the typical reader to be an advanced undergraduate, a beginning graduate student, or a new modeler. We first consider some of the values of models and the motivation for modeling. We then discuss the steps involved in developing a model from an initial idea to something that is implemented on a computer, outlining some of the decisions that must be made along the way. Many excellent texts and journal articles deal with the technical details of models and model construction; we do not attempt to replace this literature, but rather try to make the reader aware of the issues that must be considered and point to some of the sources we have found particularly useful.

We begin with the assumption that the reader has decided that he or she would like to "do something" with modeling as part of his or her research (Figure 1). It is important to recognize the difference between models and the modeling process. A *model* is a representation of a particular thing, idea, or condition. Models can be as simple as a verbal statement about a subject or two boxes connected by an arrow to represent some relationship. Alternatively, models can be extremely complex and detailed, such as a mathematical description of the pathways of nitrogen transformations within ecosystems. The *modeling process* is the series of steps taken to convert an idea first into a conceptual model and then into a quantitative model. Because part of what ecologists do is revise hypotheses and collect new data, the model and the view of nature that it represents often undergo many changes from the initial conception to what is deemed the final product.

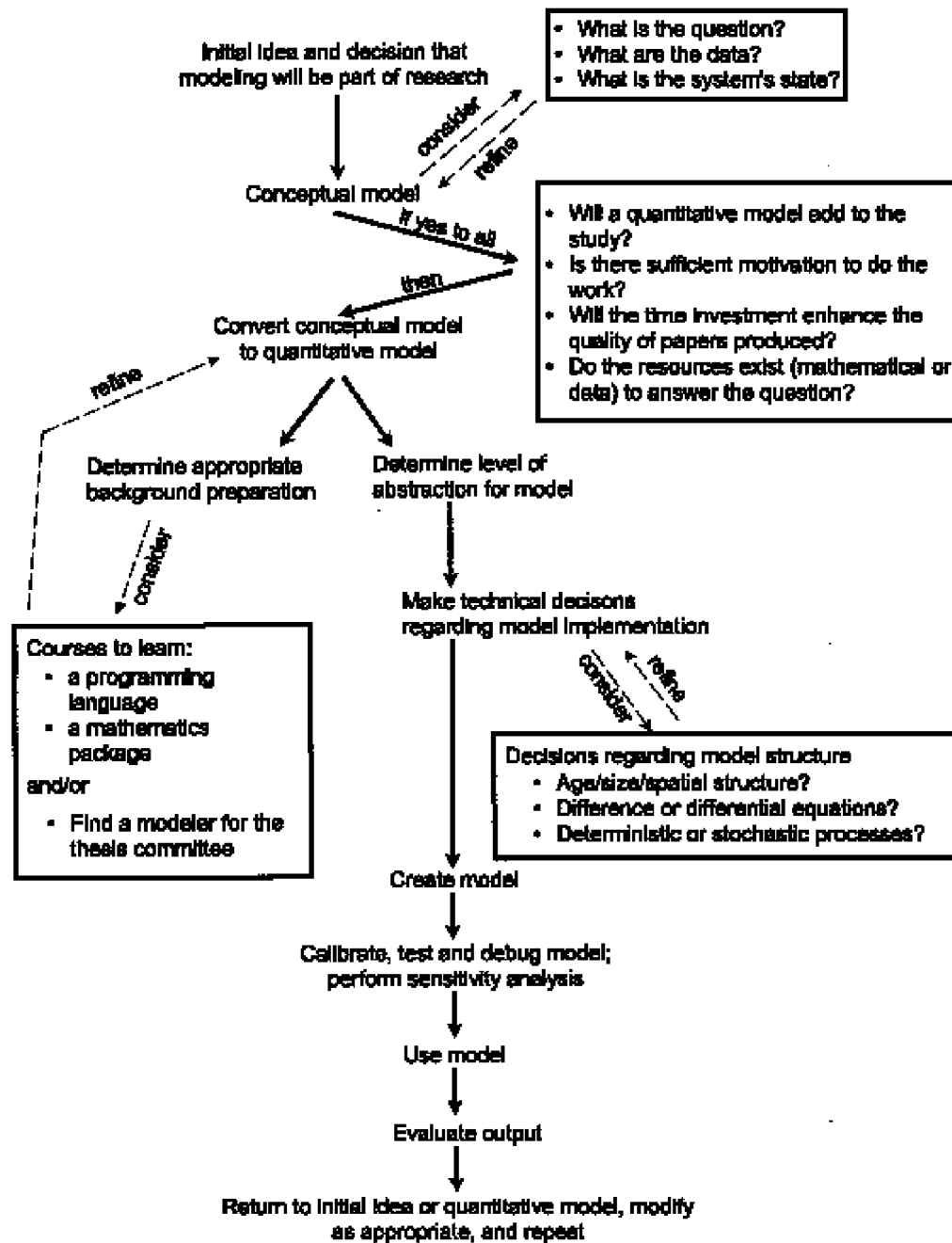
The discussion that follows is organized to consider issues in a sequence similar to what a new modeler would encounter. Because individuals' backgrounds differ, the sequence is not fixed. We map one possible route through the sorts of decisions that will most likely need to be considered; this course is derived from our individual experiences plus the collective knowledge of our reviewers. We begin with conceptual models because many people, even self-labeled nonmodelers, formulate conceptual models.

## *The conceptual model*

The development of a conceptual model can be an integral part of designing and carrying out any research project. Conceptual models are generally written as diagrams with

---

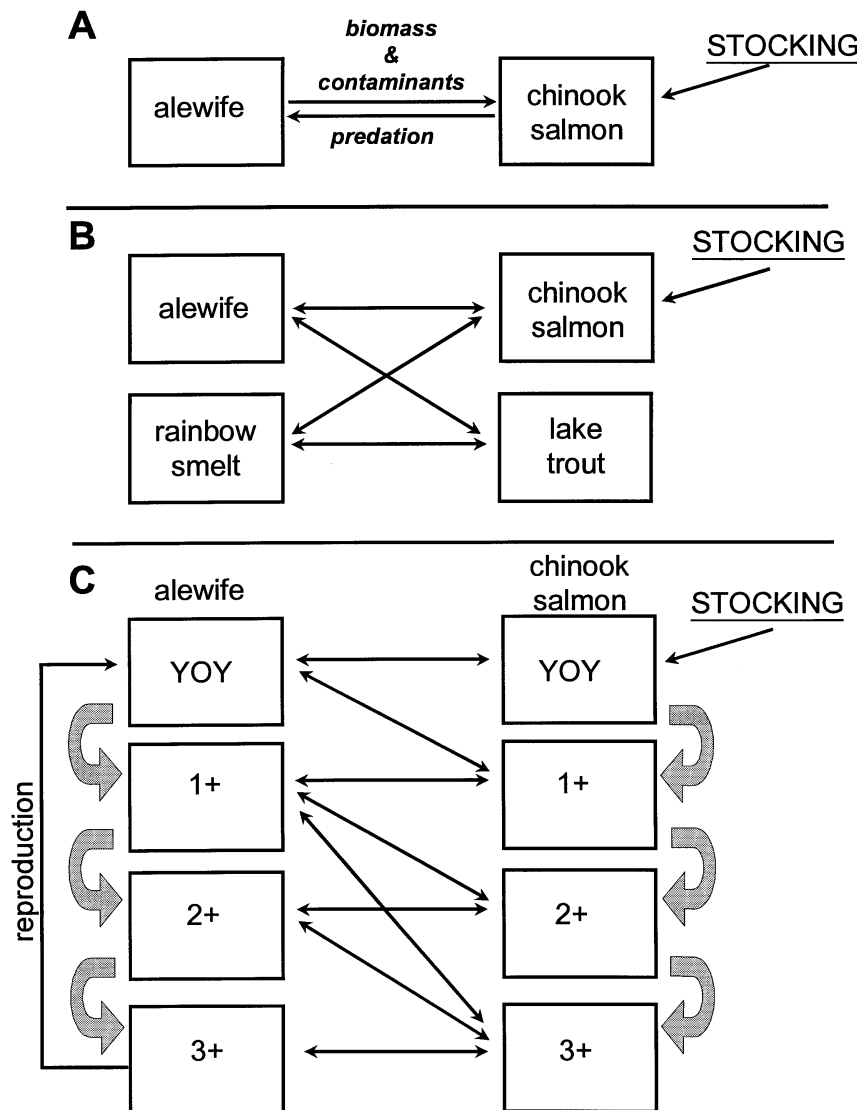
Leland J. Jackson is an assistant professor of community–ecosystem ecology in the Department of Biological Sciences, University of Calgary, Calgary, Alberta, Canada T2N 1N4. His interests are in food web structure, ecosystem stability, and contaminant cycling. Anett S. Trebitz is a research ecologist for the US Environmental Protection Agency, Mid-Continent Ecology Division, Duluth, MN 55804. Her interests are in life history strategies and species–habitat interactions. Kathryn L. Cottingham is an assistant professor in the Department of Biological Sciences, Dartmouth College, Hanover, NH 03755. She is interested in the temporal variability of ecological communities, particularly in response to anthropogenic perturbations. © 2000 American Institute of Biological Sciences.



**Figure 1.** Flow chart summarizing the process of creating an ecological simulation model. The model building process distills current knowledge into a conceptual framework, which forms the scaffolding for the model's construction. A number of steps involve iterations or refinements that follow from consulting data, experienced modelers, or other ecologists. Once there is output from the model, the original idea or state of knowledge may be modified and additional model refinements, data collection or experiments might be planned. Benefits of the modeling process include eliminating alternatives, identifying gaps in knowledge, identifying testable hypotheses, and indicating avenues for additional experimentation and data collection.

boxes and arrows, thereby providing a compact, visual statement of a research problem that helps determine the questions to ask and the part of the system to study. The boxes represent *state variables*, which describe the state or condition of the ecosystem components. The arrows

illustrate relationships among state variables, such as the movement of materials and energy (called *flows*) or ecological interactions (e.g., competition). Shoemaker (1977) provides an excellent discussion about how to develop conceptual models.



**Figure 2.** Example of the iterative nature of building a conceptual model from an initial idea. The first iteration (a) describes a simple relationship between one predator and prey. One arrow identifies biomass and contaminants as the material flowing from alewife to chinook salmon, and the other arrow identifies predation as an important ecological process structuring the alewife population. In this example, interest is in how the rate at which salmon are stocked affects the relationship between salmon and alewife. Additional information at the second iteration might indicate that the dynamics of the salmon and alewife (a) are also affected by rainbow smelt and lake trout, which are subsequently incorporated into the conceptual model (b). Finally, information on contaminant concentrations as a function of body size and more detail on predator preference of prey might indicate that age or size structure should be included (c). Depending on the goal of the modeling exercise, detailed age structure might be examined for the original two species of interest. In b and c, the double-headed arrows indicate state variables that directly interact. In c, the wide gray arrows represent the movement of fish to older age classes. Box labels represent the age of fish; YOY are young-of-year. Two quantitative models might be constructed: one for conceptual model b and one for conceptual model c.

The development of a conceptual model is an iterative process. The skeleton of a conceptual model begins to take shape when a general research question is formulated. For example, suppose the goal of a research project is to determine the relationship between different strategies for stocking exotic salmon in the Great Lakes and the concentrations of potentially toxic contaminants in the salmon and their alewife prey. The initial conceptual model might consist of two linked boxes labeled "alewife" and "chinook salmon," with an additional arrow labeled "stocking" pointing to the salmon's box (Figure 2a). We have chosen to place two-way arrows between the boxes to reflect the flow of biomass and contaminants from alewife to salmon and the effect of salmon on the alewife; an alternative model might have used only one arrow, since the flow of material between boxes is the result of predation by salmon on alewife. Details would then be added to the conceptual model based on the answers to questions such as, Are there other important species besides alewife and chinook salmon? What mechanistic processes should be included? What environmental factors influence each species? What currency should be used to describe compartment interactions (e.g., elements, biomass, individuals, energy)?

After making refinements driven by such questions, the conceptual model might have alewife, chinook salmon, rainbow smelt, and lake trout (Figure 2b), although the research interest might still be with the original two species. The next round of refinements to the conceptual model might be based on available data or consultation with ecologists who have studied the interactions of the four species shown in Figure 2b. For example, if contaminant concentrations are a function of prey body size, and if predators seek certain size classes of prey, then size structure might be added to the model to more accurately reflect these ecological features and to better simulate contaminant intake by predators (Figure 2c). Depending on the nature of the research question, the addition of size structure might be made for just the alewife and chinook salmon. This simple example assumes that there are changes only in the state variables, but there could also be changes in the relationships among the state variables.

In general, a parsimonious approach is best for creating an appropriate conceptual model. The model should strike a balance between incorporating enough detail to capture the necessary ecological structure and processes and being simple enough to be useful in generating hypotheses and organizing one's thoughts. Creating a good conceptual model forces an ecologist to formulate hypotheses, determine what data are available and what data are needed, and assess the degree of understanding about key components of the system. Because outside viewpoints and questions often force clarification of biases and assumptions, discussing the evolving conceptual model with colleagues can be helpful. Group construction of a conceptual model can also be a useful consensus-building tool in collaborative research (Walters 1986, Carpenter 1992). Conceptual models should therefore be included in dissertation and grant proposals, especially in the early stages of project development. Revisions of the initial conceptual model then become focal points for discussion in subsequent meetings of the dissertation committee or research planning group.

### ***The role of quantitative models in ecological research***

A *quantitative model* is a set of mathematical expressions for which coefficients and data have been attached to the boxes and arrows of conceptual models; with those coefficients and data in place, predictions can be made for the value of state variables under particular circumstances. Ecologists use quantitative models for various purposes, including explaining existing data, formulating predictions, and guiding research. Simple quantitative models can be solved with pencil and paper (see mathematical ecology textbooks such as Pielou 1977, Hallam and Levin 1986, and Edelstein-Keshet 1988), but most ecological models are now implemented on a computer.

Quantitative ecological models can guide research in a number of ways. Constructing a quantitative model and running simulations may help in the design of experiments (Carpenter 1989, Hilborn and Mangel 1997), for example, to evaluate experimental power for different hypothesized effect sizes. Sensitivity analysis of a quantitative model can reveal which processes and coefficients have the most influence on observed results and therefore suggest how to prioritize sampling efforts. Quantitative models can even be used to generate "surrogate" data on which to test potential environmental indicators or evaluate potential sampling schemes. Most important, quantitative models translate ecological hypotheses into predictions that can be evaluated in light of existing or new data.

The equations used to convert a process or relationship from a conceptual model to a quantitative model can be thought of as specific expressions of a general hypothesis (Hilborn and Mangel 1997). Suppose, for example, that an ecologist wants to evaluate how predator consumption (the dependent variable) varies as a function of prey avail-

ability (the independent variable) using data on predator consumption across a range of prey availabilities. At least three equations (hypotheses) could be used to relate consumption to availability:

$$(1) C = aP$$

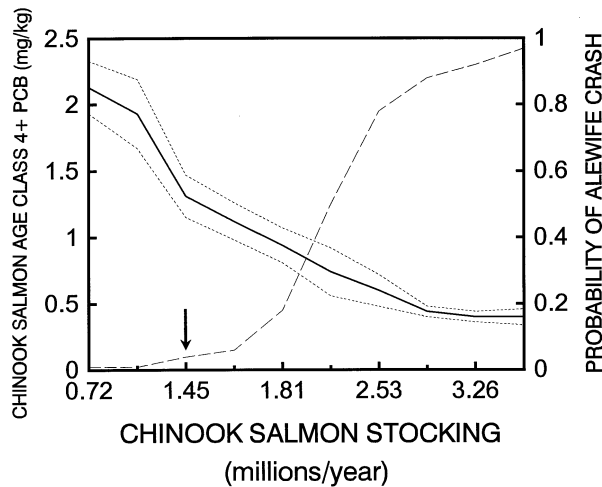
$$(2) C = bP$$

$$(3) C = \frac{1 + cP}{dPe^{-fP}}$$

where  $C$  is the predator's consumption rate;  $P$  is the measure of prey availability;  $a$ ,  $b$ ,  $c$ ,  $d$ , and  $f$  are coefficients determined from data; and  $e$  is the base of the natural logarithms. Equation 1 states that consumption rises as a linear function of prey availability. Equation 2 states that consumption rises at low prey availability and saturates at high prey availability. Equation 3 states that consumption rises at low prey availability but decreases at high prey availability. Equations 1–3 and their parameters can be thought of as specific formulations of the general hypothesis that a predator's consumption is a function of its prey availability. After supplying these models with appropriate initial conditions, each can be tested to determine which (if any) produces patterns that best fit the existing data for  $C$  and  $P$  and to identify plausible values for the coefficients (parameters). Once the most likely form of the model is known, a biological interpretation can be advanced. Hilborn and Mangel (1997) refer to this process as "ecological detection."

Ecologists often use quantitative models to formulate predictions about the systems they study. Some predictive models are empirical, meaning that they represent relationships determined strictly by data. Because empirical models are not based on a knowledge of underlying mechanisms, they are most useful within the bounds of the data with which they are developed (Weiner 1995). A well-known empirical model from aquatic ecology predicts the level of summer chlorophyll from spring total phosphorus (Dillon and Rigler 1974). Other predictive models are more mechanistic, based on hypotheses about the particular ecological processes that cause an observed pattern. The incorporation of key ecological features, such as size-selective predation and increasing contaminant concentrations with increasing prey body size (to use an example similar to that in Figure 2), leads to the prediction of a tradeoff between decreasing concentrations of PCBs in salmon and the probability of survival of salmon prey (Figure 3; Jackson 1997). In the absence of these mechanistic ecological details, lower contaminant concentrations are predicted in predators (Jackson 1996a, 1996b).

Predictive models can become quite complex, especially when their forecasts are used as the basis for resource management and policy decisions. Examples include global climate models, fisheries management models for setting catch and harvest quotas, watershed management models for nutrient control strategies, and risk assessment models for environmental engineering. Often, these complex predictive models are used to generate predictions for



**Figure 3.** PCB concentrations (solid line) of age class 4+ chinook salmon and the probability of an alewife population crash (dashed line) for chinook salmon stocking rates and a Shepherd stock-recruitment relationship. PCB concentrations are the result of 200 model runs to year 2015, at each stocking rate, based on bootstrapped estimates of the Shepherd stock-recruitment relationship from 14 years of data for Lake Ontario. The arrow indicates 1994 stocking rates. The dotted line around the chinook salmon PCB concentrations represents  $\pm 2$  SE.

scenarios for which actual tests are difficult or impossible to run for ecological, social, or economic reasons.

Like a conceptual model, a quantitative model is rarely an end in itself. Often learning results from considering a changing suite of several quantitative models, or several formulations of processes within a particular model (Pascual et al. 1997). The assessment of different models and processes allows an evaluation of the assumptions specific to those formulations and processes. In this context, it is useful to remember that models are only tools and not reality, and there is no “correct” model.

### **When should a quantitative model be developed?**

Models should follow from specific research questions rather than questions following from models. Thus, the decision to build a quantitative model from a conceptual model should occur only after a clear, focused research question has been distilled from initial ideas. A full-scale quantitative model should be created only when each of the following questions can be answered with a yes:

- Will a quantitative model add to the scientific content of the study?
- Is there sufficient motivation to devote the necessary time to develop a quantitative model?
- Will the investment in modeling enhance the quality of knowledge produced?

There are clear advantages to the incorporation of quantitative modeling in a research program. We have already touched on some of these benefits, such as formulating predictions and identifying data needs or knowledge gaps. Models are also useful for organizing one's thinking about a problem. Once a conceptual model is converted to a quantitative model and used, new questions may arise as a result of interesting and unexpected results. However, the time it takes to build a useful quantitative model should not be underestimated. Model building becomes easier with practice, but modelers should expect to spend several weeks or months constructing, parameterizing, testing, and running a modestly complex model. (The time spent depends to some degree on the software used, which is discussed more below.)

### **Building quantitative ecological models**

Once an ecologist has decided to build a quantitative model, how should he or she choose the type of model to build? Some general classes of models used in ecology include energy and mass balance models (e.g., Hewett 1989), population genetics models (e.g., Roughgarden 1979), optimization and game theory models (e.g., Mangel and Clark 1988), individual-based population models (e.g., DeAngelis and Gross 1992), size- or age-structured population models (e.g., Caswell 1989), community and ecosystem models (e.g., Scavia and Robertson 1980), and landscape models (e.g., Baker 1989). Because the degree of detail varies widely within these broad categorizations (Table 1), we recommend reading papers that discuss the merits of various modeling approaches (e.g., Levins 1966, DeAngelis and Waterhouse 1987, DeAngelis 1988). An overview of model types and formulations can also be obtained from a survey course in mathematical modeling, and we strongly recommend taking such a course as soon as the idea to “do something” with models arises. The specific types of models being considered may suggest further course work. For example, differential equations are used in many models, matrix algebra underlies size- and age-structured models, and geographical information systems (GIS) are needed to work with many spatial and metapopulation models.

The choice of model type and detail will depend on the system studied, the questions asked, and the data available. Quantitative models can quickly become complex and clear problem definition is essential to keeping the model focused. A good conceptual model is invaluable for deciding what ecological detail to include and what to ignore. For example, suppose an ecologist is studying two forest stands: One stand is intact, whereas a presumed important seed disperser has been removed from the other. Has the removal of the seed-dispersing animal caused any changes in the population of a particular tree species in the experimental stand? There are several ways in which quantitative modeling can be used to address this question. A simple age-structured model (e.g., Caswell 1989) of

## Common pitfalls and potential solutions

This troubleshooting box outlines some common mistakes made during model construction. It is not an exhaustive list. We hope that the novice modeler will profit from our experience in solving these problems, which arise largely from writing one's own code in a programming language.

Pay careful attention to units, scaling, and conversions. For example, translating prey eaten by one trophic level (units of mass) to a mortality rate for another (numbers) requires a conversion and change of units. We go through our equations and write the dimensions and units to ensure that we are making appropriate conversions. Units and dimensions for empirically derived relationships tend to be built into regression parameters (e.g., ungulate biomass [kg] derived from grass productivity [ $\text{g} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$  of carbon]). Problems often arise when different state variables operate on different spatial scales, which is sometimes less obvious than when the variables operate on different time scales. Fish, for example, occupy a volume ( $\text{g} \cdot \text{m}^{-3}$ ) but may eat benthic invertebrates that occupy a surface ( $\text{g} \cdot \text{m}^{-2}$ ), requiring rescaling when computing trophic transfers. Apparent conversion problems can also be caused by failure to properly share variables among subroutines.

Be careful with time steps and model stability, especially for models with differential equations. The modeler typically must choose a single step size (e.g., hourly, daily, monthly, yearly) over which to have the algorithm solve the equations, even though the time step appropriate for evaluating one

process (e.g., hourly nutrient uptake by phytoplankton) may not be appropriate for evaluating another (e.g., annual growth of fishes). Equations whose dynamics suffer when independent variables change on widely disparate time scales are known as "stiff" equations. Problems often occur because small roundoff or truncation errors in one variable lead to enormously inflated errors in another; such problems can be diagnosed by evaluating output variables at a variety of step sizes. An alternative approach to manually manipulating step size is to use an algorithm with an adaptive step size (Press et al. 1992), which gives smoother dynamics but takes more work to program. One can also explicitly divide the model into "fast" and "slow" components and then update the fast components much more frequently than the slow components.

Pay attention to setting and resetting values. Arrays and matrices are a common source of computer bugs, thus warranting extra attention to their dimensioning, initializing, and indexing. We assign values to parameters before they are used rather than relying on the software to initialize them. We also check that parameters and initial conditions obtained from an input file are properly read and assigned. After the lapse of important time periods, we check that variables have been zeroed or renewed as appropriate. For example, in a model in which seed germination for a plant proceeds only when certain environmental conditions are met, the value for seedlings should be set to zero each

time germination fails rather than (unintentionally) taking the value from the previous year. Similarly, when all individuals in a particular size or age class die or are eaten, the variables tracking their characteristics must be properly reset to prevent carryover effects when a new cohort arrives. Populations modeled with real numbers will approach but not equal zero when subjected to a constant mortality rate, and should be set to zero after some minimum population size is attained. Inspecting graphs of state variables will elucidate what is happening.

Test random number generators before using them. Random number generators vary in quality and should be tested before use. A statistics package can be used to analyze the results of 10,000 or so sequential random numbers to ensure that the mean, standard deviation, and distribution are as specified and the shape is as expected. If qualitatively different results occur when initializing the random number generator at the beginning of the program versus the beginning of each replicate, we look for another random number generator. We recommend reading Press et al.'s (1992) discussion of random-number generating algorithms. One way to keep random numbers the same from run to run, which is useful when developing or debugging a model, is to start each simulation with the same "seed" (the initial number from which the random numbers are generated). When the time comes to use different seeds, the computer's clock can be used for the seed value.

the tree population may be useful if the ecologist wants to look for changes in age structure. Alternatively, a spatially explicit model might be needed if the ecologist wants to explore differences in spatial pattern. If the ultimate goal is to test the findings from the quantitative model in the field, then the model that is developed will dictate the types of data that will need to be collected from the two forest stands.

Once the general type of quantitative model has been chosen, the ecologist must determine the appropriate level of abstraction for the model. Consulting papers on the value of simple (Fagerström 1987, Scheffer and Beets 1993) versus complex (Logan 1994) models may help guide this decision. Good models never include all possible compartments and interactions (Fagerström 1987, Starfield 1997), and the complexity of a model depends

very much on the purpose and question addressed by the model. There are tradeoffs between the generality of a model and its practical utility for a particular situation (Levins 1966). A highly abstract model with few parameters may be best to test general ecological hypotheses. However, for specific questions, such as whether changes in fire frequency have affected the spatial pattern of a species, a detailed spatial model coupled to GIS data may be required. Thus, a model's structure should be consistent with both the question(s) asked and the measurements made (Costanza and Sklar 1985, Ludwig and Walters 1985, DeAngelis et al. 1990). Data for many populations are collected by size or developmental stage or at fixed time intervals, leading naturally to models with size or stage structure and certain time steps (see the box on page 700 for more on time steps). With too little detail in the model, the mechanisms driving the response of interest may not be captured. On the other hand, too much detail makes a model difficult to parameterize (determine coefficients for equations) and to validate (Beck 1983, Ludwig and Walters 1985, DeAngelis et al. 1990). An active area of research therefore considers how to reduce model complexity while retaining essential system behavior (Rastetter et al. 1992, Cale 1995).

### ***Nuts and bolts of assembling a quantitative ecological model***

Once the decision to build a quantitative model has been made, and issues of model complexity and structure have been dealt with, it is necessary to develop algebraic formulations (equations) for model processes, to establish means for solving them, and to choose parameters for each equation before implementing the model on a computer. Thinking about these issues in advance may save a modeler from having to go back and redevelop portions of the model.

**The importance of keeping good notes.** The litmus test for a model description is that a relatively experienced modeler must be able to reproduce the model and its output, just as experiments should be capable of being replicated. Therefore, it is important to document decisions about equation forms, parameter values, and computational details, as well as any sources of information used to make these decisions. Good notes taken during model building will save hours combing the literature to rediscover the source of assumptions or parameter values.

**Choosing equations.** One of the initial steps in converting a conceptual model to a quantitative model involves quantifying the arrows between the state variables. This process actually involves two steps: choosing appropriate equations and determining the parameters for those equations. Equations represent mathematically the interactions among or transfers of energy or materials between state variables in a model. For example, equations 1, 2, and 3 represented different (hypothesized) ways to describe the process of predator consumption. Parameters

are constants in the equations that make the algebraic expressions correspond to actual data.

Equations appropriate to a particular situation may be available in the literature. Certain constructs (e.g., feeding relationships, energetic equations) are common to many ecological models, although they may need to be reparameterized for different systems. Many relationships can be found in modeling textbooks, including *Models in Ecology* (Maynard Smith 1974), *Ecological Implications of Body Size* (Peters 1983), *Handbook of Ecological Parameters and Ecotoxicology* (Jorgensen et al. 1991), *Dynamics of Nutrient Cycling and Food Webs* (DeAngelis 1992), *A Primer of Ecology* (Gotelli 1995), and *Primer of Ecological Theory* (Roughgarden 1998). First principles (i.e., physical laws) can also provide useful relationships. Mathematically important differences among alternative formulations may or may not be important for a particular situation. If the particular form of an equation is of concern, the effects of each formulation on model results can be explored as part of the modeling exercise.

### ***Computational issues associated with equations.***

Two important computational issues concern the type of equations (difference or differential) used to determine changes in state variables and the algorithm used to solve these equations through time. Difference equations separate time into discrete intervals (for example, a day or a year) and in the context of a scalar variable  $x$  have the general form

$$(4) x_{t+1} = F(x_t)$$

where  $x_t$  and  $x_{t+1}$  represent the value of the state variable at the beginning of two successive time intervals, and  $F$  is the function describing the change. State variables that fall naturally into this type of analysis include populations with discrete life stages (e.g., insect larvae instars) or that have nonoverlapping generations (in which the adults die and are replaced by their offspring at fixed intervals). In contrast, differential equations describe processes that occur continuously and for a scalar variable  $x$  have the general form

$$(5) \frac{dx}{dt} = G(x)$$

where  $dx/dt$  is the rate of change of the state variable and  $G$  is the function describing the processes that contribute to the rate of change. One reason for using differential equations is that continuous processes might be difficult to approximate with a difference equation formulation. For example, a differential equation approach is required to accurately describe dynamics such as limit cycles that come about from predator-prey interactions. A difference equation, even with very small time steps, is likely to predict the extinction of one or both species because of inaccuracies at small population values.

Difference equations are simply solved by recursion; that is, later predictions depend on earlier predictions. Differential equations describe continuous processes, but must nevertheless be solved in discrete time steps on a

### Decisions about model implementation

Issues concerning how numbers are stored and updated, how calculations are sequenced, and how inputs and outputs are made may seem unimportant to the novice modeler, but our experience is that computational details merit attention early in the modeling process because they can have substantial implications for model use and behavior.

The nature of inputs and outputs determines how easily a model is used and analyzed. If inputs are part of the model code, the model must be recompiled (translated from text into instructions the computer executes) each time the inputs are changed. If inputs are read in as a separate file (which takes more work to program), the model can be run many times with different inputs without recompiling. It is worth formatting output with the planned analysis in mind—select formats amenable to processing with statistical or graphics software. Excessive output slows the simulation time, but representative subsets of intermediate calculations should be inspected to ensure that everything is reasonable.

The sequence in which events proceed can affect results. Events that happen simultaneously in nature must occur in sequence in computer

models. For example, if the organism or size class that is first in numerical order in a vector of state variables is always the first for which foraging is evaluated, it may unintentionally be the one that gets the most food!

Separating old from new values allows sequential calculations of simultaneous events to proceed correctly. Newly calculated values should be assigned to temporary variables so that subsequent calculations are not based on a mixture of old and new state variables. The value of the state variables should be updated with the values in the temporary variables only after all calculations have been completed for that time step.

Decide whether to model populations as whole or real numbers. Neither choice is perfect. Using real numbers gives fractions of individuals, whereas using integers presents stochasticity and rounding problems. For example, if the number of survivors is calculated by multiplying the survival rate by the number of starting individuals and then rounding to the nearest integer, then a single individual with a survival rate of 0.8 will live forever! It would be better to use 0.8 as a probability and then do the equivalent of flipping a coin—that is, draw a

random number.

Decide how many stability checks and assurances to build into a model. The inherent mathematical and architectural constraints of computers can lead to unexpected model behavior (Acton 1996). It is important to anticipate both mathematically illegal operations (e.g., division by zero) that would cause the simulation to crash and circumstances that would cause the simulation to become invalid. For example, it might be appropriate to stop the simulation if one species in a multispecies model goes extinct, to build in a means for its reestablishment if it goes extinct, or to build in a refuge or alternate food supply so that extinction is prevented. These types of stability guarantees should be used prudently. Excessive stabilizing components can hide programming errors or even dominate model dynamics; on the other hand, if used sparingly, they can prevent the frustration of having a long simulation rendered useless by a circumstance for which a stability check could easily have been programmed.

computer. The two principal methods used to solve differential equations are the Euler and the Runge-Kutta methods. The Euler method steps through the differential equation as if it were a difference equation by using information at the beginning of each time interval to calculate values at the next time interval. The Euler method can be unstable when the interval between solutions (the step size) is small, because rapid accumulation of errors prevents convergence on the real solution. The Euler method may also be unstable at large step sizes because small changes in rates and local maxima and minima in the solution may be missed, which can be particularly problematic if the differential equations are nonlinear (Press et al. 1992). Runge-Kutta algorithms also start with the information at the beginning of a time interval but then sample the solution at several points between the beginning and end of the interval. For most differential equation models, the Runge-Kutta is more accurate than

the Euler method, and fourth-order Runge-Kutta is particularly recommended (Press et al. 1992). Graphical and algebraic explanations of the Euler and Runge-Kutta algorithms appear in Press et al. (1992) and in textbooks on numeric methods in computing (e.g., Atkinson 1989). Variable step-size methods can be used to find the optimum balance between accuracy and computational speed by using small step sizes when variables are rapidly changing and long step sizes when variables are changing slowly.

### *Deterministic or stochastic?*

A deterministic model has no random components; for the same initial conditions and time period projected, it always gives the same result. In contrast, a stochastic model incorporates at least one random factor, and thus the results are different every time the model is run. One type of stochastic model assumes that the values of some or all parameters vary through time or across individuals and



**Table 1. Ecological models for representing populations.<sup>a</sup>**

Model type	Basic features	Single-species models	Common applications		Spatially explicit landscape models
			Multispecies models	Ecosystem models	
Compartment or aggregate <sup>b</sup>	Population represented by a single model compartment. Future numbers or biomass can be made functions of density, food supply, or environment.	Theoretical models (e.g., logistic growth), simple management models (e.g., stock-recruit fisheries models) <sup>c</sup>	Theoretical models (e.g., predator-prey models), as building blocks for community models <sup>d</sup>	As building blocks for ecosystem models <sup>e</sup>	Diffusion models <sup>f</sup> , metapopulation models <sup>g</sup>
Structured <sup>h</sup>	Population divided into size, age, or life-stage classes. Each class at a minimum described by rate of survival, reproduction, and transition to next class. Rates can be made functions of density, food supply, environment, etc.	Demographic and life history analyses <sup>i</sup> , population management models <sup>j</sup>	Two interacting populations or some subset of species in a multispecies models may be structured <sup>k</sup>	Key populations may be structured as needed to capture allometry or changing ecological roles <sup>l</sup>	Structured populations not commonly modeled on landscapes.
Individual-based (IBM) <sup>m</sup>	Simulate many individuals and aggregate to obtain population characteristics. Individual traits such as size, age, location, and history are commonly tracked. Degree of detail in projecting these traits is highly variable	Demographics, life history analyses analysis of variability <sup>n</sup>	Vegetation models are commonly IBMs, key species in other models may be represented individually <sup>o</sup>	Bioaccumulation models <sup>p</sup> , vegetation models <sup>q</sup>	Movement or distribution of plants, animals, and diseases <sup>r</sup>

<sup>a</sup>References provide entry points to relevant modeling literature. We cite textbooks, edited volumes, and review articles where possible. Individual modeling studies cited are from the aquatic literature but many other examples can be found throughout the ecological literature.

<sup>b</sup>Pileou (1977), Chapra and Reckhow (1983), Hallam and Levin (1986), Vandermeer (1990), Jorgensen (1994)

<sup>c</sup>DeAngelis et al. (1990), Hilborn and Walters (1992), Gotelli (1995)

<sup>d</sup>Swartzman and Bentley (1979), O'Neill and Giddings (1980), Dale et al. (1985), Bartell et al. (1988)

<sup>e</sup>Scavia and Robertson (1980), Jones et al. (1993), Cottingham and Carpenter (1994), Hakanson (1994)

<sup>f</sup>DeAngelis and Waterhouse (1987), Anderson and May (1991)

<sup>g</sup>Gibbs (1993), Dunning et al. (1995), McCullough (1996), Grenfell and Harwood (1997)

<sup>h</sup>Pileou (1977), Hallam and Levin (1986), Caswell (1989), Vandermeer (1990)

<sup>i</sup>DeRoos et al. (1992)

<sup>j</sup>Marschall and Crowder (1996)

<sup>k</sup>Post and Rudstam (1992), Trebitz et al. (1997)

<sup>l</sup>He et al. (1993), Jackson (1997)

<sup>m</sup>DeAngelis and Gross (1992), Tyler and Rose (1994)

<sup>n</sup>DeAngelis and Gross (1992), Huston et al. (1988)

<sup>o</sup>Dale et al. (1985), DeAngelis and Gross (1992), Liu and Ashton (1995), Clark and Rose (1997)

<sup>p</sup>Madenjian and Carpenter (1993), Stow and Carpenter (1994)

<sup>q</sup>DeAngelis and Gross (1992)

<sup>r</sup>DeAngelis and Waterhouse (1987), Baker (1989), Jager et al. (1993), Turner et al. (1995), Tyler and Rose (1994), Grenfell and Harwood (1997)

are therefore described by probability distributions. Each time the model is run, the parameter values are drawn from their specified probability distributions. Other stochastic models add random errors following each calculation to simulate the effects of environmental variability. One reason to add stochasticity is to produce realistic variability in the trajectories of the state variables through time, either because the variance as well as the average value is of interest or because the effect of variability in one

state variable on another state variable is of interest. Model results might be cast in terms of probabilities—for example, as the percentage of simulations in which a certain outcome (such as a catastrophic population crash) was attained. A stochastic model is not necessarily more “correct” than a deterministic model, and it is more work to create. It does provide additional information, but whether this information is of value depends on the purpose of the model. We recommend Nisbet and Gurney

(1982) as the starting point for an introduction to deterministic and stochastic models.

**Selecting modeling software.** Implementation of a quantitative model on a computer requires the modeler (or the computer program) to keep track of many details. Some of these details, while necessary for the model to run, are irrelevant to the model predictions (e.g., allocating computer memory for arrays and matrices, creating a user interface, and writing output). Other details, such as how variables are initialized, how random numbers are generated, the order in which equations are solved, and the algorithm (computer instructions) used for solving them, do affect the predictions. We discuss some of these details further in the boxes on pages 697 and 699.

The computer software selected should be determined by the degree to which the modeler wishes to control these details. At one extreme are general programming languages (e.g., C, Basic, Fortran, Pascal) that allow the modeler complete control over the model construction but also require the modeler to handle all of the sometimes tedious details. Model building gets easier with practice and by reusing bits of previously generated code, but it can still be quite time-consuming even for relatively experienced programmers. Prewritten routines for random numbers, matrix algebra, and other algorithms are available for most programming languages, reducing the need to reinvent some wheels (e.g., Numerical Recipes; Press et al. 1992). If this option is chosen, coursework in at least one programming language might be helpful; general programming concepts and skills translate across languages.

At the other extreme are graphical programs (e.g., STELLA, SimuLink, ModelMaker) that allow the user to create the computer program (the model) by choosing icons from a menu while the software handles the details. Models can be constructed quickly, but there are limits on what can be built and the implementation details are often hidden from the user. This final point is a significant weakness of graphical modeling packages, and we therefore tend to create our own models using programming languages. However, intelligent use of modeling packages can permit incorporation of modeling into a study with far less effort than building a model from scratch.

Between these two extremes are programming packages that include functions to handle many of the details but still leave some control to the modeler (e.g., Matlab; see Roughgarden 1998) and spreadsheets (e.g., Excel; see Welton 1999). This intermediate approach may appeal to those who want to know how equations are being solved without becoming mired in the syntax of a programming language.

#### **Parameter estimation and model calibration.**

Parameter estimation is the process of finding parameter values for each equation in the quantitative model. The source of parameter values depends on how the model is going to be used. If the model is being developed to explore the consequences of different parameter values,

then the model will be run for a wide range of different parameters without reference to particular ecological systems. However, if a model is being developed to predict behavior in a particular system, then usually a single (mean) value will be chosen for each parameter. In this case, parameter values are estimated by fitting equations to the data from the system, or perhaps from data available in the literature. Sometimes data are not available, in which case a modeler might estimate parameters by an iterative process of matching model output to observed system behavior. This latter practice is referred to as tuning (calibration) by direct search, and the parameters are altered until the model produces a reasonable fit with observations of the state variables. Tuning can be done systematically or by trial and error. Either way, keeping good notes is essential. Parameters determined by direct search are best viewed as hypotheses to be tested as data become available.

When parameters are estimated from observed data, the modeler seeks the parameters that lead to the best fit between an equation and the observed data (e.g., Hilborn and Mangel 1997). The least-squares criterion and maximum likelihood estimation are the two most commonly employed methods for this kind of parameter estimation. Least-squares estimates of parameters minimize the value of the squared deviations between the simulated and observed data; these estimates can be used for just about any deterministic component of a model for which distributions are near normal and variance is constant throughout the range of an independent variable (Brown and Rothery 1993). However, for models that are nonlinear in the parameters, least squares may produce biased parameter estimates; for these models, maximum likelihood may yield better parameter estimates. Maximum likelihood algorithms determine the parameter values that maximize the probability that the observations would have occurred if the parameters were correct (Hilborn and Walters 1992). Unlike least squares, maximum likelihood does not require that error terms be normally distributed (Hilborn and Mangel 1997). It is beyond the scope of this article to review parameter estimation techniques, but useful information on that subject can be found in Draper and Smith (1981), Hilborn and Walters (1992), and Hilborn and Mangel (1997).

#### **Debugging, sensitivity analysis, and validation.**

Once a quantitative model is assembled, it must be tested to ensure that it is functioning properly; that process is called "debugging." We recommend that the equations be calculated by hand to ensure that the code is performing as it should—that is, arrays and matrices are properly indexed, equations are properly calculated, and so forth. Each module or subroutine of a model developed with a programming language should be tested separately before the completed model is run. Output should be tabulated, state variables graphed, and intermediate parameter and rate values monitored to ensure that they are realistic during

simulations. One also should check that the model behaves as expected in situations for which the analytical solution is known.

Sensitivity analysis explores whether the conclusions would change if the parameters, initial values, or equations were different. Consequently, sensitivity analyses can be used to guide further research (for example, to identify those parameters that would be worth the investment of additional field measurements or experiments), to corroborate the model, and to improve parameter estimates. There are three basic approaches to sensitivity analysis: varying parameter values one at a time, systematic sampling, and random sampling (Hamby 1994). Swartzman and Kaluzny (1987) provide an excellent discussion of the advantages and disadvantages of each of these approaches. The simplest sensitivity analysis examines the effect of each parameter on model dynamics individually (Bartell et al. 1986). The model is typically deemed sensitive to a particular parameter if changing that parameter's value by 10% leads to more than a 10% change in the output from the baseline scenario. Because analysis of one parameter at a time will not identify sensitive interactions among parameters, it may also be worthwhile to explore the effects of variation in two or more parameters at the same time using either systematic or random sampling (Swartzman and Kaluzny 1987). When many parameters may interact, random sampling may be the best approach. Random sampling is most often done with Monte Carlo techniques (e.g., Swartzman and Kaluzny 1987, Bartell et al. 1988), whereby, during each of perhaps 1000 model runs, a value for each parameter is "sampled" from a range or probability distribution. Model runs then undergo partial correlation analyses, which yield estimates of the contribution of each parameter to the overall variance in the output. Parameters with high partial correlations have the most influence on results.

In addition to doing a sensitivity analysis on parameter values, the model should be checked for sensitivity to initial conditions and equations. For example, the model can be initialized with different species ratios or size structures to find out whether output is driven by these choices. Model sensitivity to alternative equations for relationships among state variables can also be checked by rerunning the model with different equations and seeing whether the conclusions change.

Once a model works, the modeler may need to ask whether it sufficiently resembles reality, but whether that question can be answered at all is a matter of considerable philosophical debate (Mankin et al. 1975, Oreskes et al. 1994, Rastetter 1996, Rykiel 1996). Nevertheless, at some point the researcher must decide that the model is good enough and no more tinkering is necessary. For many system-specific ecological models, this decision is made based on comparisons of simulated data with field or experimental data. If the simulated data are sufficiently similar to the observed data, then the model is judged to

be validated or corroborated, and simulations with the model proceed. If the simulated data do not match the observed data, then further work is necessary. Objective criteria for model validation include the standard error of model predictions and the proportion of variance explained by the model (Caswell 1976, Power 1993). It is preferable to have independent data for model corroboration and calibration, although in practice independent data are often hard to find, particularly for whole ecosystems.

### *A way forward*

Modeling offers exciting possibilities for the exploration of ideas that are not easily pursued through field experimentation or laboratory studies. Ecologists, for example, use models to simulate the systems they study and to investigate general theories of the way those systems operate. Moreover, simulation of systems with models helps identify data needs and knowledge gaps.

Many research programs can benefit from the integration and development of conceptual and quantitative models. The process of creating a conceptual model begins with a question; from there, the researcher formulates hypotheses, evaluates available and needed data, and assesses the degree of understanding of the system under consideration. Then the conceptual model is converted to a quantitative model; that process is iterative, evolving as new data and ideas are discovered.

We cannot possibly cover every aspect of ecological modeling—which is both a skill and a process—in one short article. We do hope, however, that we have successfully raised the issues that a beginning modeler must consider, provided an entry point to the modeling literature, and discussed the role of modeling in ecological research.

### *Acknowledgments*

We thank Steve Carpenter for numerous suggestions during the writing of the manuscript. We are grateful to many people at the Center for Limnology, University of Wisconsin–Madison, for support during our model building years there (especially David Christensen, Xi He, Daniel Schindler, Craig Stow, and Rusty Wright). We thank Steve Carpenter, George Gertner, Lloyd Goldwasser, Bruce Kendall, Russell Kreis, Bill Nelson, John Nichols, Daniel Schindler, and, in particular, Rebecca Chasan, Wayne Getz, and an anonymous reviewer for their thoughtful reviews of the manuscript. L. J. J.'s research with simulation models was funded by the Natural Sciences and Engineering Research Council of Canada and by the Wisconsin Sea Grant Institute under grants from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, US Department of Commerce, and from the State of Wisconsin (Federal grant NA90AA-D-SG469, project R/MW-41). K. L. C.'s initial research with simulation models was funded by a predoctoral fellowship from the National Science Foundation. K. L. C. also thanks the

National Center for Ecological Analysis and Synthesis, which is funded by NSF (DEB94-21535); the University of California at Santa Barbara; and the State of California for financial and logistical support while preparing this paper for publication.

## References cited

- Acton FS. 1996. *Real Computing Made Real: Preventing Errors in Scientific and Engineering Calculations*. Princeton (NJ): Princeton University Press.
- Anderson RM, May RM. 1991. *Infectious Diseases of Humans: Dynamics and Control*. London: Oxford University Press.
- Atkinson KE. 1989. *An Introduction to Numerical Analysis*. 2nd ed. New York: John Wiley & Sons.
- Baker WL. 1989. A review of models of landscape change. *Landscape Ecology* 2: 111–133.
- Bartell SM, Breck JE, Gardner RH, Brenkert AL. 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 160–168.
- Bartell SM, Brenkert AL, O'Neill RV, Gardner RH. 1988. Temporal variation in regulation of production in a pelagic food web model. Pages 101–108 in Carpenter SR, ed. *Complex Interactions in Lake Communities*. New York: Springer-Verlag.
- Beck MB. 1983. Uncertainty, system, identification, and the prediction of water quality. Pages 3–68 in Beck MB, van Straten G, eds. *Uncertainty and Forecasting of Water Quality*. New York: Springer-Verlag.
- Brown D, Rothery P. 1993. *Models in Biology: Mathematics, Statistics and Computing*. Toronto: John Wiley & Sons.
- Cale WG. 1995. Model aggregation: ecological perspectives. Pages 230–241 in Patten BC, Jorgensen SE, eds. *Complex Ecology: The Part-Whole Relation in Ecosystems*. Englewood Cliffs (NJ): Prentice Hall.
- Carpenter SR. 1989. Replication and treatment strength in whole-lake experiments. *Ecology* 70: 453–463.
- \_\_\_\_\_. 1992. Modeling in the Lake Mendota program: An overview. Pages 377–380 in Kitchell JF, ed. *Food Web Management: A Case Study of Lake Mendota*. New York: Springer-Verlag.
- Caswell H. 1976. The validation problem. Pages 313–325 in BC Patten, ed. *Systems Analysis and Simulation in Ecology, Vol. IV*. New York: Academic Press.
- \_\_\_\_\_. 1989. *Matrix Population Models: Construction, Analysis, and Interpretation*. Sunderland (MA): Sinauer Associates.
- Chapra SC, Reckow KH. 1983. *Engineering Approaches for Lake Management*, Vols. 1 and 2. Boston: Butterworth Publishers.
- Clark ME, Rose KA. 1997. Factors affecting competitive dominance of rainbow over brook trout in southeastern Appalachian streams: Implications of an individual-based model. *Transactions of the American Fisheries Society* 126: 1–20.
- Costanza R, Sklar FH. 1985. Articulation, accuracy and effectiveness of ecological models: a review of freshwater wetland applications. *Ecological Modelling* 27: 45–69.
- Cottingham KL, Carpenter SR. 1994. Predictive indices of ecosystem resilience in models of north temperate lakes. *Ecology* 75: 2127–2138.
- Dale VH, Doyle TW, Shugart HH. 1985. A comparison of tree growth models. *Ecological Modelling* 29: 145–169.
- DeAngelis DL. 1988. Strategies and difficulties of applying models to aquatic populations and food webs. *Ecological Modelling* 43: 57–73.
- \_\_\_\_\_. 1992. *Dynamics of Nutrient Cycling and Food Webs*. New York: Chapman & Hall.
- DeAngelis DL, Gross LJ. 1992. *Individual-based Models and Approaches in Ecology: Populations, Communities, and Ecosystems*. New York: Chapman & Hall.
- DeAngelis DL, Waterhouse JC. 1987. Equilibrium and nonequilibrium concepts in ecological models. *Ecological Monographs* 57: 1–21.
- DeAngelis DL, Barnhouse LW, Van Winkle W, Otto RG. 1990. A critical appraisal of population approaches in assessing fish community health. *Journal of Great Lakes Research* 16: 576–590.
- DeRoos AM, Diekmann O, Metz JAJ. 1992. Studying dynamics of structured population models: A versatile technique and its application to *Daphnia*. *American Naturalist* 139: 123–147.
- Dillon PJ, Rigler FH. 1974. The phosphorus–chlorophyll relationship in lakes. *Limnology and Oceanography* 19: 767–773.
- Draper N, Smith H. 1981. *Applied Regression Analysis*. 2nd ed. New York: John Wiley & Sons.
- Dunning JB, Stewart DJ, Danielson BJ, Noon BR, Root TL, Lamberson RH, Stevens EE. 1995. Spatially explicit population models: Current forms and future uses. *Ecological Applications* 5: 3–11.
- Edelstein-Keshet L. 1988. *Mathematical Models in Biology*. New York: Random House.
- Fagerström T. 1987. On theory, data and mathematics in ecology. *Oikos* 50: 258–261.
- Gibbs JP. 1993. Importance of small wetlands for the persistence of local population of wetland-associated animals. *Wetlands* 13: 25–31.
- Gotelli NJ. 1995. *A Primer of Ecology*. Sunderland (MA): Sinauer Associates.
- Grenfell B, Harwood J. 1997. (Meta)population dynamics of infectious diseases. *Trends in Ecology and Evolution* 12: 395–399.
- Gurney WSC, Nisbet WR. 1998. *Ecological Dynamics*. New York: Oxford University Press.
- Hakanson L. 1994. A review of effect-dose-sensitivity models for aquatic ecosystems. *Internationale Revue der Gesamten Hydrobiologia* 79: 621–667.
- Hallam TG, Levin SA. 1986. *Mathematical Ecology: An Introduction*. Berlin: Springer-Verlag.
- Hamby DM. 1994. A review of techniques for parameter sensitivity analysis of environmental studies. *Environmental Monitoring and Assessment* 32: 135–154.
- He X, Kitchell JF, Carpenter SR, Hodgson JR, Schindler DE, Cottingham KL. 1993. Food web structure and long-term phosphorus recycling: A simulation model evaluation. *Transactions of the American Fisheries Society* 122: 773–783.
- Hewett SW. 1989. Ecological applications of bioenergetics models. *American Fisheries Society Symposium* 6: 113–120.
- Hilborn R, Mangel M. 1997. *The Ecological Detective: Confronting Models with Data*. Princeton (NJ): Princeton University Press.
- Hilborn R, Walters CJ. 1992. *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*. New York: Chapman & Hall.
- Huston M, DeAngelis DL, Post W. 1988. New computer models unify ecological theory. *BioScience* 38: 682–691.
- Jackson LJ. 1996a. A simulation model of PCB dynamics in the Lake Ontario pelagic food web. *Ecological Modelling* 93: 43–56.
- \_\_\_\_\_. 1996b. How will decreased alewife growth rates and salmonid stocking affect sport fish PCB concentrations in Lake Ontario? *Environmental Science & Technology* 30: 701–705.
- \_\_\_\_\_. 1997. Piscivores, predation, and PCBs in Lake Ontario's pelagic food web. *Ecological Applications* 7: 991–1001.
- Jager HI, DeAngelis DL, Sale MJ, VanWinkle W, Schmoyer DD, Sabo MJ, Orth DJ, Lukas JA. 1993. An individual based model for smallmouth bass reproduction and young-of-year dynamics in streams. *Rivers* 4: 91–113.
- Jones ML, Koonce JE, O'Gorman R. 1993. Sustainability of hatchery-dependent salmonine fisheries in Lake Ontario: The conflict between predator demand and prey supply. *Transactions of the American Fisheries Society* 122: 1002–1018.
- Jorgensen SE. 1994. *Fundamentals of Ecological Modelling*. Amsterdam: Elsevier.
- Jorgensen SE, Nielsen SN, Jorgensen LA. 1991. *Handbook of Ecological Parameters and Ecotoxicology*. Amsterdam: Elsevier.
- Levins R. 1966. The strategy of model building in population biology. *American Scientist* 54: 421–431.
- Liu J, Ashton PS. 1995. Individual-based simulation models for forest succession and management. *Forest Ecology and Management* 73: 157–175.
- Logan JA. 1994. In defense of big ugly models. *American Entomologist* 40: 202–207.

- Ludwig D, Walters CJ. 1985. Are age-structured models appropriate for catch-effort data? *Canadian Journal of Fisheries Aquatic Sciences* 42: 1066–1072.
- Madenjian CP, Carpenter SR. 1993. Simulation of the effects of time and size at stocking on PCB accumulation in lake trout. *Transactions of the American Fisheries Society* 122: 492–499.
- Mangel M, Clark CW. 1988. *Dynamic Modelling in Behavioral Ecology*. Princeton (NJ): Princeton University Press.
- Mankin JB, O'Neill RV, Shugart HH, Rust BW. 1975. The importance of validation in ecosystem analysis. Pages 63–71 in Innis GS, ed. *New Directions in the Analysis of Ecological Systems*. LaJolla (CA): Society for Computer Simulation.
- Marschall EA, Crowder LB. 1996. Assessing population responses to multiple anthropogenic effects: A case study with brook trout. *Ecological Applications* 6: 152–167.
- Maynard Smith J. 1974. *Models in Ecology*. London: Cambridge University Press.
- McCullough DR, ed. 1996. *Metapopulations and Wildlife Conservation*. Washington (DC): Island Press.
- Nisbet RM, Gurney WSC. 1982. *Modelling Fluctuating Populations*. New York: John Wiley & Sons.
- O'Neill RV, Giddings JM. 1980. Population interactions and ecosystem function: Phytoplankton competition and community production. Pages 103–123 in Innis GS, O'Neill RV, eds. *Systems Analysis of Ecosystems*. Fairland (MD): International Cooperative Publishing House.
- Oreskes N, Shrader-Frechette K, Belitz K. 1994. Verification, validation, and confirmation of numerical models in the earth sciences. *Science* 263: 641–646.
- Pascual MA, Karieva P, Hilborn R. 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. *Conservation Biology* 11: 966–976.
- Peters RH. 1983. *The Ecological Implications of Body Size*. New York: Cambridge University Press.
- Pielou EC. 1977. *Mathematical Ecology*. New York: Wiley-Interscience.
- Post JR, Rudstam LG. 1992. Fisheries management and the interactive dynamics of walleye and perch populations. Pages 381–406 in Kitchell JF, ed. *Food Web Management: A Case Study of Lake Mendota*. New York: Springer-Verlag.
- Power M. 1993. The predictive validation of ecological and environmental models. *Ecological Modelling* 68: 33–50.
- Press WH, Teukolsky SA, Vetterling WV, Flannery BP. 1992. *Numerical Recipes in C: The Art of Scientific Computing*. 2nd ed. New York: Cambridge University Press.
- Rastetter EB. 1996. Validating models of ecosystem response to global change. *BioScience* 46: 190–198.
- Rastetter EB, King AW, Cosby BJ, Hornberger CM, O'Neill RV, Hobbie JE. 1992. Aggregating fine-scale geological knowledge to model coarser-scale attributes of ecosystems. *Ecological Applications* 2: 55–70.
- Roughgarden J. 1979. *Theory of Population Genetics and Evolutionary Ecology: An Introduction*. New York: Macmillan.
- \_\_\_\_\_. 1998. *Primer of Ecological Theory*. Upper Saddle River (NJ): Prentice Hall.
- Rykiel EJ. 1996. Testing ecological models: The meaning of validation. *Ecological Modelling* 90: 229–244.
- Scavia D, Robertson A. 1980. *Perspectives on Lake Ecosystem Modeling*. Ann Arbor (MI): Ann Arbor Science.
- Scheffer M, Beets J. 1993. Ecological models and the pitfalls of causality. *Hydrobiologia* 275/276: 115–124.
- Shoemaker CA. 1977. Mathematical construction of ecological models. Pages 76–114 in Hall CAS, ed. *Ecosystem Modeling in Theory and Practice: An Introduction with Case Histories*. New York: John Wiley & Sons.
- Shugart HH, West DC. 1980. Forest succession models. *BioScience* 30: 308–313.
- Starfield AM. 1997. A pragmatic approach to modeling for wildlife management. *Journal of Wildlife Management* 61: 261–270.
- Stow CA, Carpenter SR. 1994. PCB accumulation in Lake Michigan coho and chinook salmon: Individual-based models using allometric relationships. *Environmental Science and Technology* 28: 1543–1549.
- Swartzman GL, Bentley R. 1979. A review and comparison of plankton simulation models. *International Society Ecological Modelling Journal* 1: 30–81.
- Swartzman GL, Kaluzny P. 1987. *Ecological Simulation Primer*. New York: Macmillan.
- Trebitz AS, et al. 1997. A model of bluegill–largemouth bass interactions in relation to aquatic vegetation and its management. *Ecological Modelling*, 94: 139–156.
- Turner MG, Arthaud GJ, Engstrom RT, Hejl SJ, Liu J, Loeb S, McKelvey K. 1995. Usefulness of spatially explicit population models in land management. *Ecological Applications* 5: 12–16.
- Tyler JA, Rose KA. 1994. Individual variability and spatial heterogeneity in fish population models. *Reviews in Fish Biology and Fisheries* 4: 91–123.
- Vandermeer JH. 1990. *Elementary Mathematical Ecology*. New York: John Wiley & Sons.
- Walters C. 1986. *Adaptive Management of Renewable Resources*. New York: Macmillan.
- Weiner J. 1995. On the practice of ecology. *Journal of Ecology* 83: 153–158.
- Weldon C. 1999. Using spreadsheets to teach ecological modeling. *Ecological Society of America Bulletin* 80: 64–67.