IV ASSESSING REGIME SHIFTS IN ECOSYSTEM EXPERIMENTS

Introduction

It is easier to test for multiple regimes in long-term data if the ecosystems are manipulated experimentally (Chapter III). We have also seen, however, that field data pose a number of complications that were bypassed in the minimal model employed in Chapter III. What can a whole-ecosystem experiment tell us about regime shifts? This chapter explores that question, using time series data from manipulated lakes.

Regime shifts are a diverse group of ecological phenomena, with no single mathematical model and no simple statistical test. Different situations call for different models and different statistical approaches. In any given situation, it is not easy to choose which model to use (Scheffer and Beets 1994).

Because no single mathematical model or statistical approach is optimal for study of ecological regime shifts, it is helpful to examine time series data through the lens of more than one model. By examining the consistency or inconsistency of the evidence using multiple models, one obtains a broader understanding of the conditions under which the regime shift may occur. To gain a broader perspective on regime shifts, this chapter uses two distinctly different types of models to assess regime shifts.

Although a wide variety of models could be chosen to explore regime shifts in time series data, some models are more interesting than others. Two classes of models used widely in ecology are linear statistical models and nonlinear process-based (or partly-mechanistic) ones. Linear statistical models are easily fitted to data using well-known statistical methods (Burnham and Anderson 1998). Such models are linear in the parameters, but may not be linear in the predictor variables. Multivariate autoregressive models (Ives et al. 2003) are a particularly useful kind of linear statistical model for ecology. Although the fitting and analysis of linear statistical models is straightforward, the parameters may not represent any particular ecological process. Often, the models are not intended to represent any specific ecological mechanism.

Models that are nonlinear in the parameters can represent alternate stable states or other processes for regime shifts. Often, these nonlinear models are partly mechanistic, because they contain at least some terms which are thought to represent processes of ecosystem change. Such models can be more difficult to fit to data because the optimal parameter estimates are not analytically calculated, but rather require a numerical estimation, and the fitting may require additional data beyond the time series observations (Hilborn and Mangel 1997). On the other hand, the mechanistic formulation of the model may make it possible to combine many sources of data. In the Lake Mendota example of Chapter III, for example, a nonlinear partly-mechanistic model was fit using two independent data sets.

Time series models, whether linear or nonlinear, may provide information about regime shifts in at least two ways. The mechanism for the regime shift could be built into the structure of the model itself. By fitting the model to data and exploring the stability properties of the model predictions, one can investigate whether the ecosystem behavior is consistent with regime shifts. This approach has been used to test for alternate states of lake metabolism related to dissolved organic carbon inputs, for example (Carpenter and Pace 1997). Alternatively, systematic patterns in the residuals may indicate regime shifts (Brock et al. 1996). Slowly-changing variables that are not included in the model may explain patterns in the residuals (Walters 1986, Rastetter 2003). The presence of patterns consistent with slowly-changing, but missing variables may suggest new hypotheses for regime shifts.

In this chapter, data from an ecosystem experiment, to be described below, are analyzed using two different models. The purpose of the analysis is to assess the evidence about regime shifts using predictions of the models themselves, and the deviations of the data from the predictions. The information about regime shifts is first examined for each model separately, and then the results of the two models are compared.

The two models are a linear one and a nonlinear, partly-mechanistic one. The linear model uses regression to select a "best" equation for predicting the ecosystem dynamics from a set of candidate predictor variables. The set of candidate predictors is chosen on the basis of ecological knowledge, but the model involves no special

ecological assumptions. It is a linear autoregression that uses several predictors and a standard statistical form for the relationships among variables (Ives et al. 2003). Under this model, the ecosystem is expected to have a single steady state. A regime shift could occur, if driven by changes in the level of one or more of the predictor variables. The appearance of the regime shift in the output of the model depends on the nature of the shift in predictors and the statistical effects built into the regression itself. It is possible that a regime shift is evident in the data, but not well-represented by the equations of the model. In this case the residuals (differences between observations and predictions) should show a systematic pattern indicative of the regime shift.

The nonlinear model includes some standard ecological mechanisms for interactions of the ecosystem components. The parameters for these nonlinear relationships are estimated by fitting the model to data. In the nonlinear model, regime shifts could emerge from the nonlinear equations themselves, as well as from changes in the level of input variables. The appearance of the regime shift in the output of the model depends on the shift of inputs and the nonlinear dynamics of the mechanisms built into the model. As in the linear model, a regime shift could occur through mechanisms that are not built into the nonlinear model, and in this case the residuals (differences between observations and predictions) should show a systematic pattern indicative of the regime shift.

The chapter will proceed as follows. First the ecological hypothesis that motivated the ecosystem experiment is described, along with the data set for

phytoplankton and zooplankton dynamics that was gathered to address the hypothesis. Then the linear model is introduced and fitted to the data. This analysis suggests that predictions break down at a certain level of planktivory which separates two regimes, one with highly variable zooplankton biomass and low phytoplankton biomass, the other with low zooplankton biomass and highly variable phytoplankton biomass. Then the nonlinear model is introduced and fitted to data. The predictions of this model suggest multiple regimes including cycles and multiple stable points. A nonlinear dynamic regression is used to study the dynamics of parameter estimates. The outcome suggests that regime shifts in planktivory by fishes are not adequately represented in the nonlinear model. Overall, the analysis suggests that at least two regimes of plankton behavior are present in the data, and that shifts between regimes can result from gradual changes in planktivory by fishes. The chapter closes with a comparison of the results from the linear and nonlinear models.

Description of the Ecosystem Experiments

The trophic cascades explained in Chapter II suggest that lake food webs with piscivores should respond differently to nutrient input than lakes without piscivores (Fig. 21). At any particular level of nutrient input, a lake without piscivores should have higher biomass of phytoplankton than a lake with piscivores. This response is expected because biomass of zooplankton and grazing mortality of phytoplankton should be larger in the lake with piscivores. Furthermore, the increase of phytoplankton biomass per unit nutrient input should be greater in a lake without piscivores than in a lake with

piscivores. This response is expected because the large-bodied zooplankton found in lakes with piscivores should be able to control phytoplankton biomass over a wide range of nutrient input rates, unlike the smaller-bodied zooplankton found in lakes that lack piscivores but support planktivorous fishes.

These hypotheses were tested by whole-lake experiments in Paul, Peter, and West Long lakes (USA) from 1991 to 1997 (Carpenter et al. 2001b). Paul Lake was not manipulated and served as a reference ecosystem throughout the experiment. Both Peter and West Long lakes were enriched with inorganic phosphorus and nitrogen from 1993-1997. Food webs of Paul and West Long lakes were dominated by piscivorous bass throughout the experiment. These lakes had low biomass of planktivorous fishes and the zooplankton tended to be large-bodied and abundant. Peter Lake lacked piscivores, except for a few weeks in 1991 and 1996. Its food web was dominated by planktivorous minnows. Zooplankton tended to be small-bodied.

The general patterns shown in Fig. 21 were consistent with results of the whole-lake experiments (Carpenter et al. 2001b). The purpose of this chapter is not to re-examine these hypotheses. Instead, the same data will be used to test for evidence of regime shifts, such as those that occur in the model of trophic cascades by Scheffer et al. (1997). That model was described in Chapter II (Fig. 13).

The analysis presented in this book uses only a subset of the extensive data set described by Carpenter et al. (2001b). Models will be constructed to describe dynamics

of chlorophyll (an index of phytoplankton biomass) and biomass of crustacean zooplankton. Extrinsic drivers considered in the models are phosphorus input rate and an index of planktivory. In these whole-lake experiments, crustacean body size appears to be driven by planktivory not resource supply (Pace 1984, Carpenter and Kitchell 1993, Carpenter et al. 2001b). Therefore, crustacean size was used to calculate an index of planktivory for use in this modeling exercise. Planktivory was assumed proportional to the planktivory index $(L_{max} - L_t) / L_{max}$ where L_t is the mean crustacean length observed in the sample from a lake on date t, and L_{max} is the largest possible value of mean crustacean length. The planktivory index ranges from nearly zero (when zooplankton body size is as large as possible, and planktivory is minimal) to nearly one (when zooplankton body size is nearly zero, and planktivory is intense). I assumed L_{max} = 1.5 mm, larger than any value observed in the course of this study.

Model fits described here assumed that observation error was negligible. This assumption is justified for phosphorus load, chlorophyll, and zooplankton body length. Phosphorus input was controlled by the investigators, except for a small amount of natural input which was estimated independently (Houser et al. 2000, Carpenter et al. 2001b). Chlorophyll observation errors in these studies are only a few percent of the mean, and much smaller than the observed fluctuations in chlorophyll. Errors in estimating mean zooplankton body length are negligible because of the large numbers of animals counted. Coefficients of variation for measurements of zooplankton biomass, however, are in the neighborhood of 25 to 50%. Neglect of this observation error could cause grazer impacts on chlorophyll to be underestimated (Carpenter et al.

1994). It can also influence parameter estimates for all of the other predictor variables in the regression, depending on the co-linearity of the predictor variable set. Even though observation errors could prevent us from seeing some of the ecosystem responses, it turns out that many interesting patterns are discernable.

Linear Model of Plankton Dynamics

This section presents a model of plankton dynamics that is linear in the parameters. This model has a single stable point, but patterns in the residuals of the model could suggest regime shifts. Within the framework of this linear model, such regime shifts could be explained by external forcing or some nonlinear process that was omitted from the model.

Linear Modeling Approach

Linear autoregressive models were fit to weekly data for all lakes using standard statistical methods (Draper and Smith 1981, Burnham and Anderson 1998). Response variates were net chlorophyll growth rate = $\log(chl_{t+1} / chl_t)/\Delta t$ and net zooplankton biomass growth rate = $\log(ZB_{t+1} / ZB_t)/\Delta t$. The candidate predictors for the autoregressions were all measured at time t. For regressions to predict net chlorophyll growth rate, the candidate predictors were phosphorus input rate, chlorophyll, chlorophyll squared, chlorophyll per unit phosphorus load, zooplankton biomass, and net zooplankton biomass growth rate. For regressions to predict net zooplankton

growth rate, the candidate predictors were chlorophyll, zooplankton biomass, zooplankton biomass squared, the planktivory index, and zooplankton biomass times the planktivory index. For each autoregression, all possible regressions were examined and the model with the minimum value of Akaike's information criterion (AIC) was selected (Burham and Anderson 1998).

Linear Model Results

Predictions of chlorophyll from the linear model were significantly correlated with observations (Fig. 22A). For predicting net chlorophyll growth rate, the model with lowest AIC included parameters for intercept (-0.239, s.e. 0.200), chlorophyll (-0.00341, s.e. 0.00085), chlorophyll per unit P load (-0.00635, s.e. 0.00156), net zooplankton growth rate (-0.0788, s.e. 0.0182), and planktivory index (0.867, s.e. 0.323). This model suggests significant density dependent limitation (negative effects of chlorophyll and chlorophyll per unit P input), negative effects of grazing (negative effect of zooplankton growth), and additional food web effects not captured by the linear relationship with zooplankton growth (positive effect of planktivory index). These additional food web effects could be attributed to nutrient cycling (Vanni and Layne 1997) or indirect effects not represented in the model structure (Ives et al. 1999, 2003).

Predictions of zooplankton biomass from the linear model were significantly correlated with observations (Fig. 22B). When predicting net growth rate of zooplankton biomass, the model with lowest AIC included intercept (-1.96, s.e. 0.27), zooplankton

biomass in the previous time step (0.527, s.e. 0.041), planktivory index (2.91, s.e. 0.363), and zooplankton biomass X planktivory index (-0.833, s.e. 0.059). There is no evidence of density-dependent limitation. The strongly negative effect of zooplankton biomass X planktivory index is analogous to a type 1 or Lotka-Volterra functional response. However, there is also a significant positive effect of the planktivory index. When the planktivory index is high, zooplankton body size is low and this is associated with faster growth rates, as would be expected from allometry (Peters 1983).

Implications of the Linear Model

Steady-state values were computed to examine the implications of the linear model for long-run levels of chlorophyll and zooplankton. To calculate the steady-state for chlorophyll, model predictions for rate of change in chlorophyll were set to zero and the resulting equation was solved for chlorophyll. The same process was used to find the steady state for zooplankton biomass. In both cases, model error was set to zero, the expected value. If the error distribution was included in the calculations, the result would be a stable probability distribution instead of a point value (Ives et al. 2003). For the purposes of this chapter, the point values are sufficient.

The linear models for net chlorophyll and zooplankton growth lead to asymptotically stable steady-state values across the range of the extrinsic drivers. For chlorophyll, the steady state values are consistent with intuition (Fig. 23). Chlorophyll is predicted to approach stable steady state values which are within the scope of the data.

Steady-state chlorophyll declines linearly with zooplankton growth rate, increases

linearly with planktivory index, and increases hyperbolically with P load.

For zooplankton biomass, steady-state values are more complex (Fig. 24).

Steady-state zooplankton biomass is roughly independent of planktivory index over

most of the range (Fig. 24A), but there is a discontinuity at planktivory index ~ 0.64.

The lack of trend in zooplankton biomass is consistent with previous observations which

show that zooplankton body size, but not biomass, responds to planktivory (Carpenter

and Kitchell 1993). The discontinuity suggests two different regimes of plankton

dynamics. Perhaps these are related to the shift in chlorophyll response to planktivory

index (Fig. 24B). Below planktivory index values of ~0.64, chlorophyll values fall in a

limited range, but above ~0.64 the range of chlorophyll values is much larger.

Observed zooplankton biomass trends downward across the range of 0.45 to 0.85 in

the planktivory index (Fig. 24C). These patterns suggest that outbreaks of high

chlorophyll begin to occur when zooplankton biomass and/or body size becomes

sufficiently small. Beisner et al. (2003a) reached a similar conclusion using a different

model.

Both the parameter estimates and the steady-state analyses of the linear model

are consistent with the trophic cascade hypothesis (Carpenter et al. 1985). As

expected, chlorophyll responded positively to phosphorus input, inversely to

zooplankton biomass, and positively to planktivory. The rate of change of zooplankton

biomass was inversely related to planktivory X zooplankton biomass, consistent with a

predation effect. Steady-state zooplankton biomass appeared to relate discontinuously to planktivory, as corroborated by the analysis by Beisner et al. (2003a). Two regimes are suggested, one with low planktivory and low chlorophyll, and one with high planktivory and high and variable chlorophyll.

A Nonlinear Model for Plankton Dynamics

This section turns to the nonlinear model of plankton dynamics of Scheffer et al. (1997), which was discussed in Chapter II. Here, the model is fitted to data and the implications for regime shifts in the experimental lakes are explored.

Nonlinear Model

The model of Scheffer et al. (1997, 2000b, 2001b) includes several mechanistic features of plankton dynamics, including density dependent limitation of phytoplankton (e.g. through self-shading), a saturating (hyperbolic or Type 2) functional response for grazing, and a switching (sigmoid or type 3) functional response for a planktivorous fish that eats zooplankton when they are sufficiently abundant (Table 1). In addition, the model includes colonization of the water column by phytoplankton from littoral or benthic refugia (Hansson 1996).

A rich variety of dynamics is possible in this model (Scheffer 1997; Chapter II). Phytoplankton dynamics can switch from a stable point to a limit cycle with nutrient

enrichment (paradox of enrichment, Rosenweig 1971). Extreme cycles can lead to collapse of the zooplankton and the onset of stable algal blooms under some circumstances. Planktivore dynamics create alternate basins of attraction for zooplankton and phytoplankton. This model has been proposed as an integrated explanation for several well-known patterns of plankton dynamics, including clear-water phases, phytoplankton-zooplankton cycles, algal blooms, zooplankton collapses, and alternate states of abundant and sparse zooplankton (Scheffer 1997).

For fitting the model to data, I expressed the model as difference equations presented in Table 1. This form of the model is easier to fit to data than the differential equations analyzed by Scheffer et al. (1997). It has the same equilibria as the differential equations.

Fitting the Nonlinear Model

The nonlinear model was fitted using Bayesian inverse modeling (Appendix). I used an informative prior distribution based on my previous experience building simulation models for these lakes. This prior distribution was combined with the time series data to estimate the parameters as described in the Appendix. Unlike the general case described in the Appendix, here there are two variables to be predicted, chlorophyll and zooplankton biomass. Therefore the method described in the Appendix was modified to include a term for both response variables as well as the prior distribution. Specifically, the parameters were estimated by minimizing the negative log posterior probability

$$-\log(L_P) = -\log(L_0) - \log(L_{1A}) - \log(L_{1Z})$$

where

$$-\log(L_0) = 0.5 \left[(\boldsymbol{\beta} - \mathbf{B}_0)' \, \mathbf{S}_0^{-1} \, (\boldsymbol{\beta} - \mathbf{B}_0) + k \log(2\pi) + \log(|\mathbf{S}_0|) \right]$$

$$-\log(L_{1A}) = 0.5 \left[(\mathbf{E}_A' \, \mathbf{E}_A / s_A^2) + n \log(2\pi s_A^2) \right]$$

$$-\log(L_{1Z}) = 0.5 \left[(\mathbf{E}_Z' \, \mathbf{E}_Z / s_Z^2) + n \log(2\pi s_Z^2) \right]$$

In the above equations, $\boldsymbol{\beta}$ is the vector of parameters to be estimated. The prior estimates of these parameters are $\mathbf{B}_0$ with covariance matrix $\mathbf{S}_0$. $\mathbf{E}_A$ and $\mathbf{E}_Z$ are vectors of errors in predicting the time series of chlorophyll and zooplankton biomass, respectively. The standard deviations of these errors, s_A and s_Z, are additional parameters estimated from the data. All parameters ($\boldsymbol{\beta}$, s_A and s_Z) are estimated simultaneously by minimizing $-\log(L_P)$ over the parameters. Note that the chlorophyll and zooplankton equations share common parameters, so it is necessary to optimize all parameter estimates simultaneously.

The parameters could have been estimated by ordinary least squares or maximum likelihood methods (Hilborn and Mangel 1997). However, there are advantages in bringing in additional information through the informative prior

distribution. The informative prior distribution may help solve the problem of parameter

shrinkage that arises when fitting dynamic pool models such as this one. When fitting

both inputs and outputs to time series for a dynamic pool that exhibits little net change,

rate coefficients for inputs and outputs tend to shrink toward zero. Yet, independent

evidence, such as direct field measurements of production or loss rates, may indicate

that the rates are far from zero and roughly in balance.   The prior distribution can be

used to bring this information into the calculation, and perhaps lead to more realistic

parameter estimates.

The one-week ahead predictions of the nonlinear model were significantly

correlated with observations (Fig. 25). Many of the posterior parameter estimates were

close to prior estimates (Table 2). However, the maximum chlorophyll growth rate, r,

and the maximum grazing rate, g, were both lower than expected. Despite the narrow

prior distribution centered on biologically reasonable values, the small net changes

observed in the weekly data drove the estimates of these parameters to small values.

Although these rates seem inconsistent with phytoplankton production and grazing rates

measured directly in the field, they yield reasonable predictions and therefore were used

in the analyses described below.

Nonlinear Model Stability

Using the fitted parameters, the equilibria of the model were calculated and analyzed for

stability. There was at least one stable point over the full range of planktivory index and

P input rate (Fig. 26). For some of the combinations of planktivory index and P input rate, there were two stable states (Fig. 26). Dual stable points tended to occur at higher levels of P input and lower levels of planktivory. In addition, cyclic attractors were found at many combinations of planktivory index and P input rate (not shown in Fig. 26). Thus, the fits of the nonlinear model suggest that the data are consistent with multiple attractors. Some of these attractors are cycles and others are stable points, as shown by Scheffer et al. (1997) and described in Chapter II (Fig. 13).

In the linear model analysis, a transition between two regimes occurred at a planktivory index value near 0.64. Characteristics of the two regimes were (1) high zooplankton biomass and low chlorophyll and (2) low zooplankton biomass and variable chlorophyll. The nonlinear model provides no evidence of a change in stability properties near the same value of the planktivory index. There are number of possible explanations for the variable chlorophyll dynamics seen at high values of planktivory, including cycles or, at high P input rates, switches between stable points. The simplest explanation is that chlorophyll is highly responsive to variations in nutrient input when planktivory is high, but not when planktivory is low.

Changing Drivers and Ecosystem Dynamics

How might shifts in planktivory or P input affect dynamics of the ecosystem? This question has no simple answer, because the model is capable of very complex

dynamics (Scheffer 1997) and a large number of scenarios are conceivable for changes in planktivory. Some scenarios are shown here to illustrate the range of possibilities.

Fig. 27A shows dynamics of chlorophyll and zooplankton biomass under low P inputs (1 mg m^{-2} d^{-1}) with parameters fixed at the optimal values (Table 2). Zooplankton gradually decline, leading to an increase in chlorophyll.

If P input is increased to 6 mg m^{-2} d^{-1} (Fig. 27B), there are high-amplitude cycles of both chlorophyll and zooplankton biomass. Such cycles can be portrayed as resource-driven or predator-driven, depending on the type of data that are presented (Carpenter and Kitchell 1988). Of course, they are both resource- and predator-driven, but the balance of control changes over the course of the cycle.

In the last scenario, c increased linearly over the range of 0.1 to 50 during the simulation, while P input remained high (6 mg m^{-2} d^{-1}) and constant (Fig. 27C). The gradual increase in c represents a gradual increase in planktivory over the course of the simulation, as might occur during a change in fish community structure. After an initial cycle, zooplankton biomass steadily declines while chlorophyll steadily rises. This simulation shows that gradual, directional change in planktivory could have profound effects on ecosystem dynamics consistent with a trophic cascade. One way to see such effects is to watch ecosystems carefully, for a long time. Paleoecological evidence shows that such changes have occurred in aquatic ecosystems, with substantial impacts on food webs and ecosystem dynamics (Kitchell and Carpenter 1987, Leavitt et

al. 1989, Carpenter and Leavitt 1991, Jackson et al. 2001).   Similar conclusions derive

from long-term ecological observations of lakes (Post et al. 1997, Sanderson 1998,

Sanderson et al. 1999, Beisner et al. 2003b).

Changes in Parameters Over Time: Nonlinear Dynamic Regression

All ecological models are approximations. The parameters are not universal constants.

This is not a failing of ecology. Instead, it is a property of all models, all of which

represent complex abstractions of the world in forms that can be manipulated and

thereby help us understand. Many other sciences, such as physics and chemistry, have

quantities which can be considered constant in some domains, but must be considered

as dynamic variables in other domains. Carl Walters (1986) described such quantities

with the memorable phrase "parameters that aren't".

One way of addressing parameter change, Bayesian dynamic modeling, uses the

concept of pooled information (Appendix). Suppose that we are making repeated

observations of an ecosystem. The observations are noisy; there are stochastic shocks

that create variability over time. We can also predict the next observation, using a

model fitted to past observations. The model may be as simple as "next time, this

variable should have the same value as it did last time", or it may be a sophisticated

dynamic model. Thus, we have two independent sources of information about the state

of the system at any given time: the current observation, with some variance, and a

prediction based on the past, also with variance. From these, we can calculate a

pooled estimate of the current state of the system. We can also re-evaluate our estimates of the parameters of the model. If the new observation is quite different from the model prediction, then we could alter the parameter estimates so that predictions conform more closely to observations. This process can be repeated for every data point in a time series. The evolving fit of the model can be used to assess dynamics in the parameters. The dynamics of parameters can be an important clue to system structure.

Bayesian dynamic regression yields forecasts of the time series as well as time series of parameter estimates (Appendix). Using Bayesian dynamic regression, one can ask if the parameter estimates vary over time in a systematic way, or if the temporal variations appear to be completely random. To address the possibility that the parameters are changing in systematic ways, time series for each lake were analyzed by Bayesian dynamic regression using the procedure described in the Appendix. Results for one lake, West Long Lake, are presented here to illustrate parameter change.

One-step ahead predictions by the dynamic regression were reasonably accurate for both chlorophyll and zooplankton biomass (Fig. 28). This is to be expected, because the estimate is updated each week. This plot confirms that the algorithm is stable and that predictions converge on the observed time series.

Parameter dynamics were calculated for the three parameters that control fluxes between compartments: r (flux from nutrients to chlorophyll), g (flux from chlorophyll to zooplankton), and c (flux from zooplankton to fishes) (Fig. 29). If the parameter is in fact constant for the data set, then the time series of parameter estimates should form a band parallel to the x-axis. Within the band, variation should be patternless.

The time series of r and g appear rather patternless compared to the time series of c (Fig. 29). There may be some nonrandom pattern in g, or even in r, but the plot for c is notably different from the other two plots. The time series of c estimates is stable initially, then increases sharply, stabilizes, declines sharply, then undergoes damped oscillations toward a stable value.

Evidently some sharp changes in c are necessary to fit the data with this model. It is possible that changes in fish biomass, which are not considered in the model, impact the values of c. To consider this possibility, compare time series of piscivores (Fig. 30A) and planktivores (Fig. 30B) to changes in c (Fig. 30C). Piscivore and planktivore biomasses were measured only twice each year, so shifts between years sometimes appear large and abrupt. Even though c is updated at each time step, its dynamics show some "stairstep" changes similar to those seen in the fish data. The fish data were not used in fitting the model, so the corresponding changes in c and the fish data are not an artifact of the statistical procedure.

The first jump in c (Time step 27) corresponds to an increase in planktivory at the beginning of 1993, the first year of nutrient enrichment. The sharp decline in c (Time step 38) corresponds to the beginning of 1994 and a sharp increase in biomass of planktivores. Evidently the impact of these planktivores per unit biomass was different from past planktivore impacts in West Long Lake, leading to a sharp adjustment in the value of c. Subsequently, piscivore biomass increased, planktivore biomass declined, and the value of c gradually declined.

The analysis of parameter dynamics shows that the nonlinear model is not a complete representation of the dynamics of fishes and their impacts on zooplankton. The planktivory coefficient is not a parameter. Instead, it is a variable that reflects changes in fish-zooplankton interactions which are not captured adequately by the model. Fishes are a slowly-changing variable that are not well represented by the simple parameter c. This is not surprising. It does suggest that the model could be improved by explicitly including fish dynamics.

Implications of the Nonlinear Model

Not surprisingly, the nonlinear model suggests that ecosystem dynamics are more complex than the linear model. According to the nonlinear model, multiple stable states occur over a wider range of planktivory as P input increases. Furthermore, some of the fluctuations of chlorophyll may be explainable by cyclic attractors. The dynamics of the nonlinear model are generally consistent with expectations of the trophic cascade

hypothesis. However, the equilibrial patterns are more complicated than the general trends predicted from trophic cascades (Carpenter et al. 1985, Scheffer et al. 1997).

Conclusions from Both Linear and Nonlinear Models

The fits of the linear and nonlinear models are not remarkably different. Based on one-step-ahead predictions, correlations of predictions with observations are similar for the two models. The number of parameters estimated is about the same (11 for the linear model; 9 for the nonlinear model, plus 3 parameters – D, m and q – which were not fitted but instead were fixed at arbitrary and plausible values). While discriminating the models is not the point of this exercise, well-known methods exist for comparing rival models (Hilborn and Mangel 1997, Burnham and Anderson 1998) and these have been used in other studies of trophic cascades (Carpenter et al. 1998b, Strong et al. 1999). In the case of the models studied in this chapter, such comparisons are not straightforward. Instead, my goal is to explore the data using different models and assess the possibility of regime shifts. This was achieved without choosing a single "best" model.

The data reveal different patterns when viewed through the lenses of the linear versus nonlinear models (Fig. 31). The linear model fits the data rather well without incorporating any mechanisms for endogenous regime shifts or multiple attractors. The steady-state predictions of the linear model are consistent with two regimes in the data, one with low planktivory, large-bodied zooplankton, and low chlorophyll, the other with

high planktivory, small-bodied zooplankton and high, variable chlorophyll. The nonlinear model also fits the data rather well. Steady-state analyses suggest multiple dynamic regimes driven by the endogenous dynamics of the plankton. Furthermore, the nonlinear dynamic regression suggested regimes of planktivory that were not represented in the structure of the model (Fig. 30).

Collectively, the two models indicated strong effects of phosphorus input and trophic cascades (Fig. 31). However, the models predict different dynamics from changes in P input or changes in planktivory. The linear model predicts simple trends consistent with expectations from the trophic cascade hypothesis (Carpenter et al. 1985). The dynamics of the nonlinear model are much more complicated, although many general patterns are consistent with the trophic cascade hypothesis. In general, the predictions from the linear model are easier to understand, and therefore the deviations of data from the linear model can be interpreted more easily.

Both models also suggested the existence of distinct dynamic regimes (Fig. 31). However, the implications for regime shifts are different. The linear model suggests two major regimes, as noted above (low planktivory, large-bodied zooplankton and low chlorophyll versus high planktivory, small-bodied zooplankton and high and variable chlorophyll). The nonlinear model suggests multiple attractors involving both stable points and stable cycles.

While both models suggest multiple regimes, it is difficult to determine the extent to which these regimes are endogenously created versus externally forced. It is plausible that the high variability of chlorophyll seen at high levels of planktivory is the result of oscillating attractors, as suggested by the nonlinear model. It is equally plausible that the chlorophyll is much more responsive to variable forcing (e.g. weather variability) when zooplankton are suppressed by high planktivory. It is difficult to draw conclusions about the importance of alternate attractors versus external forcing in the dynamics. It is plausible that both are involved.

This chapter has attempted to understand ecosystem dynamics by analyzing patterns in time series using two contrasting models. If instead the goal was predicting ecosystem dynamics, the approach would be different and the task more difficult. Prediction would require choosing the best model, or at least estimating posterior probabilities for all plausible models (Appendix; see also Fernández et al. 2001). This problem is faced by managers who wish to make decisions guided by predictions of future ecosystem conditions. The two models presented in this chapter make very different predictions about the future, yet both are consistent with past data and with many theoretical expectations about lake dynamics. Some problems of prediction for ecosystems subject to regime shifts will be taken up in the next two chapters.

Summary

It is often useful to consider distinctly different types of models. By representing a broader range of potential ecosystem dynamics, a set of models provides multiple views of the data. Just as an artist might draw a three-dimensional object from several different perspectives to provide a richer two-dimensional representation, multiple models provide a more inclusive understanding of complex data sets. Scientific explanations that embrace multiple models are likely to be more general and more useful.

The two models analyzed in this chapter yield some complementary insights. Patterns in the data can be fit rather well by both models, and both models demonstrate the effects of nutrients and trophic cascades on phytoplankton.

Both models suggest regime shifts in the experimental lakes. The linear model predicts a discontinuity in the zooplankton equilibrium, which is associated with a change in the distribution of chlorophyll concentrations. The plankton exhibit two regimes, one with low zooplanktivory and low phytoplankton biomass, and one with high zooplanktivory and high, variable phytoplankton biomass. The nonlinear model suggests multiple attractors, including stable states and stable cycles in chlorophyll-zooplankton dynamics. Also, in the nonlinear model, there are large shifts in the zooplankton consumption parameter in West Long Lake which suggests qualitatively different regimes of fish control of zooplankton.

This chapter shows that inferences about regime shifts can be drawn from time series data alone, when key ecosystem drivers are manipulated experimentally. The ecosystem experiments analyzed here were designed to yield sharp contrasts, so it may not be surprising that different regimes were discernable in the time series.

It is more difficult to determine the extent to which the different dynamic regimes are due to endogenous processes in the lakes versus external forcing. Apparently the regime shifts were caused by both changes in external drivers and shifts among attractors.

The models compared in this chapter make quite different predictions about future ecosystem change, even though both models fit past data rather well and are consistent in many ways with current theories of lake dynamics. It is difficult, however, to choose between the models for purposes of prediction. This difficulty raises serious challenges for ecosystem management based on forecasting future dynamics.

Tables

Table 1. Equations of the nonlinear model for plankton dynamics. Time step is Δt (7 d in results presented here). Time series, with symbols and units: chlorophyll (A, mg m^{-2}), zooplankton biomass (Z, g dry mass m^{-2}), phosphorus input rate (P, mg m^{-2} d^{-1}), planktivory index (F, dimensionless).   Parameters, with symbols and units: assimilation ratio for zooplankton (a, dimensionless), maximum planktivory rate (c, d^{-1}), eddy diffusion rate of phytoplankton (D, m^2 mg^{-1} d^{-1}), grazing rate (g, m^2 g^{-1} d^{-1}), half-saturation parameter for grazing (h_A, mg m^{-2}), half-saturation parameter for planktivory (h_Z, g m^{-2}), chlorophyll carrying capacity per unit phosphorus load (k, d), maximum chlorophyll growth rate (r, m^2 mg^{-1} d^{-1}), exponent for planktivory functional response (q, dimensionless).

Dynamics of chlorophyll (A):

$A_{t+1} = A_t \exp\{ \Delta t \ [f_1(A_t,P_t,r,k) - f_2(A_t,Z_t,g,h_A) + D(k\,P_t - A_t)]\}$

Dynamics of zooplankton (Z):

$Z_{t+1} = Z_t \exp\{ \Delta t \ [a\,f_2(A_t,Z_t,g,h_A) - m\,Z_t - f_3(Z_t,F_t, ,c,q,h_Z)] \}$

primary production, function f_1:

$f_1(A_t,P_t, r, k) = r\,A_t\,[1 - (A_t / k\,P_t)]$

grazing, function f_2:

$f_2(A_t,Z_t,g,h_A) = g\,Z_t\,A_t / (h_A + A_t)$

planktivory, function f_3:

$f_3(Z_t,F_t,c,q,h_Z) = c\,F_t\,Z_t^{\,q} / (h_Z^{\,q} + Z_t^{\,q})$

Table 2. Results of Bayesian inverse fitting of the nonlinear model to data from all three experimental lakes. Parameters that fixed at arbitrary values and not estimated: $D = 10^{-8}$; $m = 0.01$; $q = 6$.

Parameter	Prior mean	Prior std. dev.	Posterior mean
r	0.4	0.01	0.00025
k	300	30	298
g	0.3	0.1	0.045
h_A	200	5	202
a	0.7	0.05	0.75
c	1	0.5	1.02
h_Z	7	0.3	8.8
s_A	0.5	--	0.56
s_Z	1	--	0.83

Figures

Figure 21. Conceptual diagram showing the response of phytoplankton biomass or production to nutrient input in a lake with a piscivore (lower curve) and a lake with fish planktivores but not piscivores (upper curve). Reproduced from Carpenter et al. 2001b by permission of Ecological Society of America.
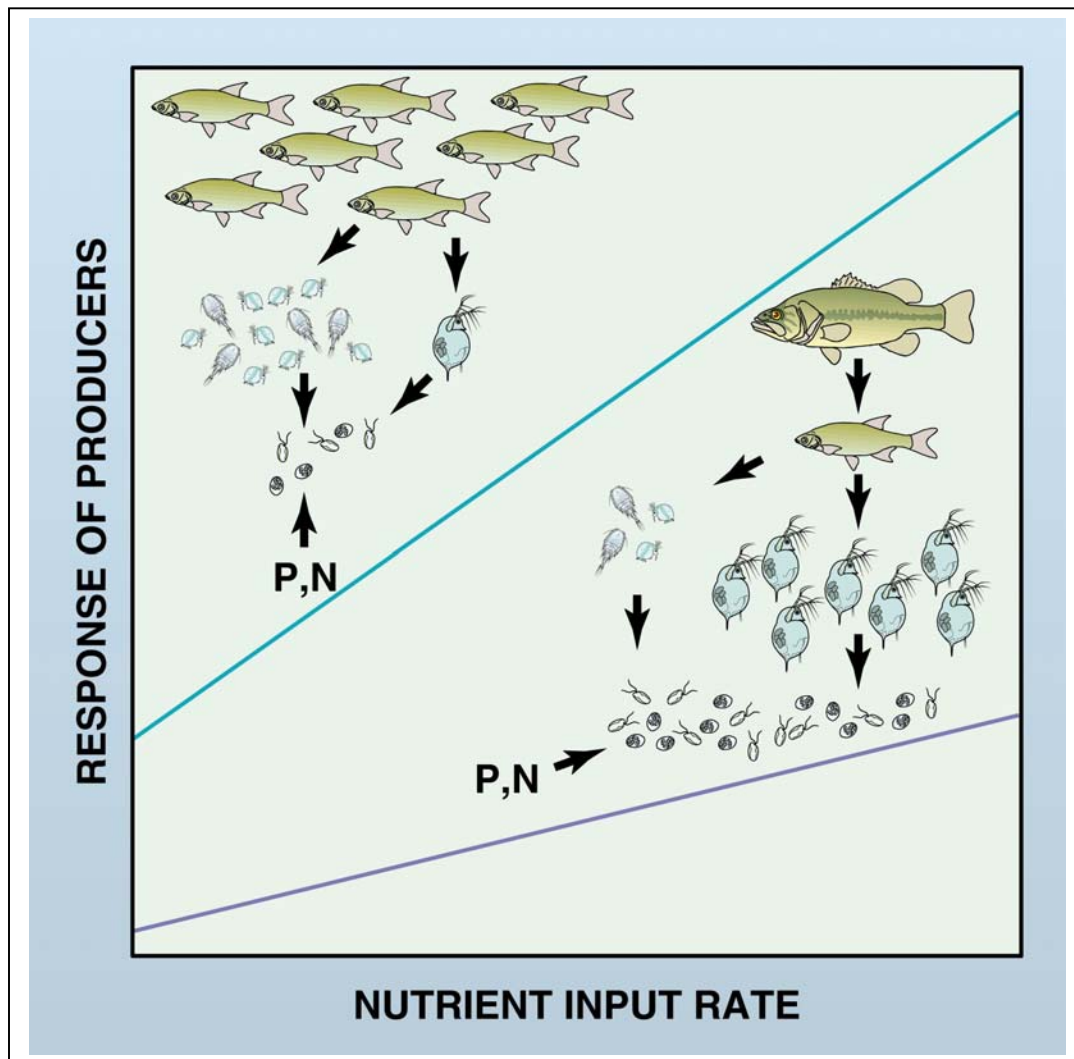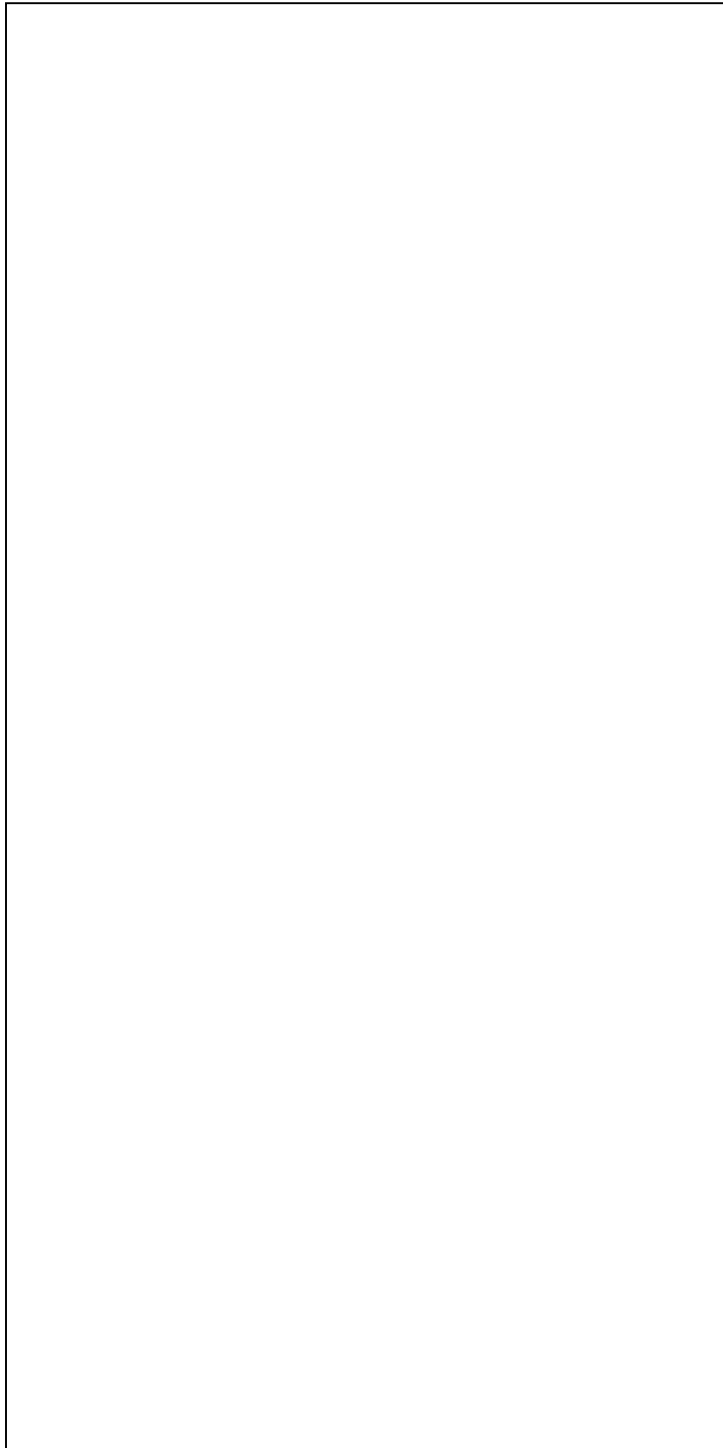
Figure 22. Comparison of predictions and observations for the linear model. Solid lines denote observations identical to predictions. (A) One-step-ahead predictions of chlorophyll. (B) One-step-ahead predictions of zooplankton biomass. (Original)
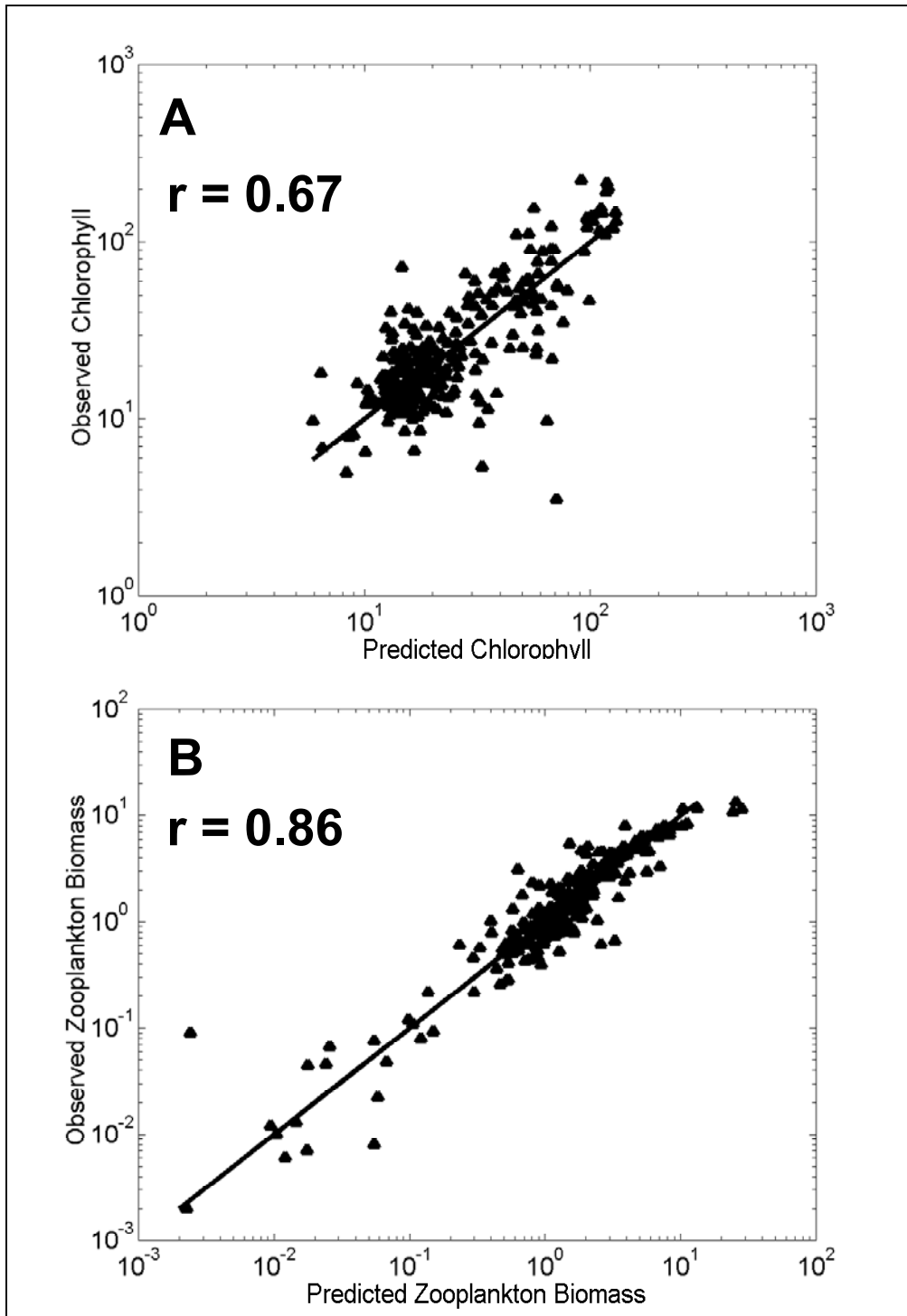
Figure 23. Steady-state values of chlorophyll from the linear model versus (A) rate of change in zooplankton biomass, (B) planktivory index, and (C) phosphorus input rate. (Original)
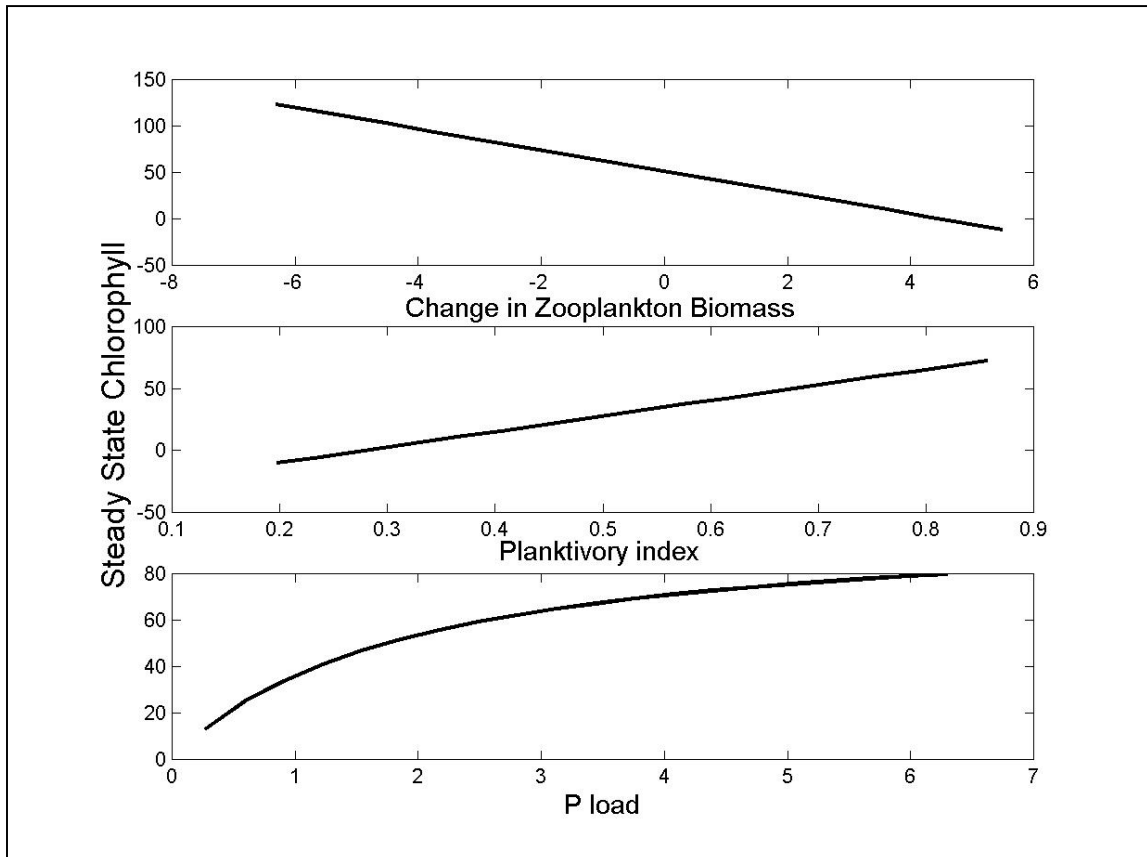
Figure 24. (A) Steady-state values of zooplankton biomass from the linear model versus planktivory index. (B) Observed chlorophyll concentration versus planktivory index (triangles). Solid lines are steady-state values of zooplankton biomass. (C) Zooplankton biomass +/- standard error versus planktivory index. Planktivory index is discretized in bins of width 0.1. (Original)

Figure 25. Comparison of predictions and observations for the nonlinear model. Solid lines denote observations identical to predictions. (A) One-step-ahead predictions of chlorophyll. (B) One-step-ahead predictions of zooplankton biomass. (Original)
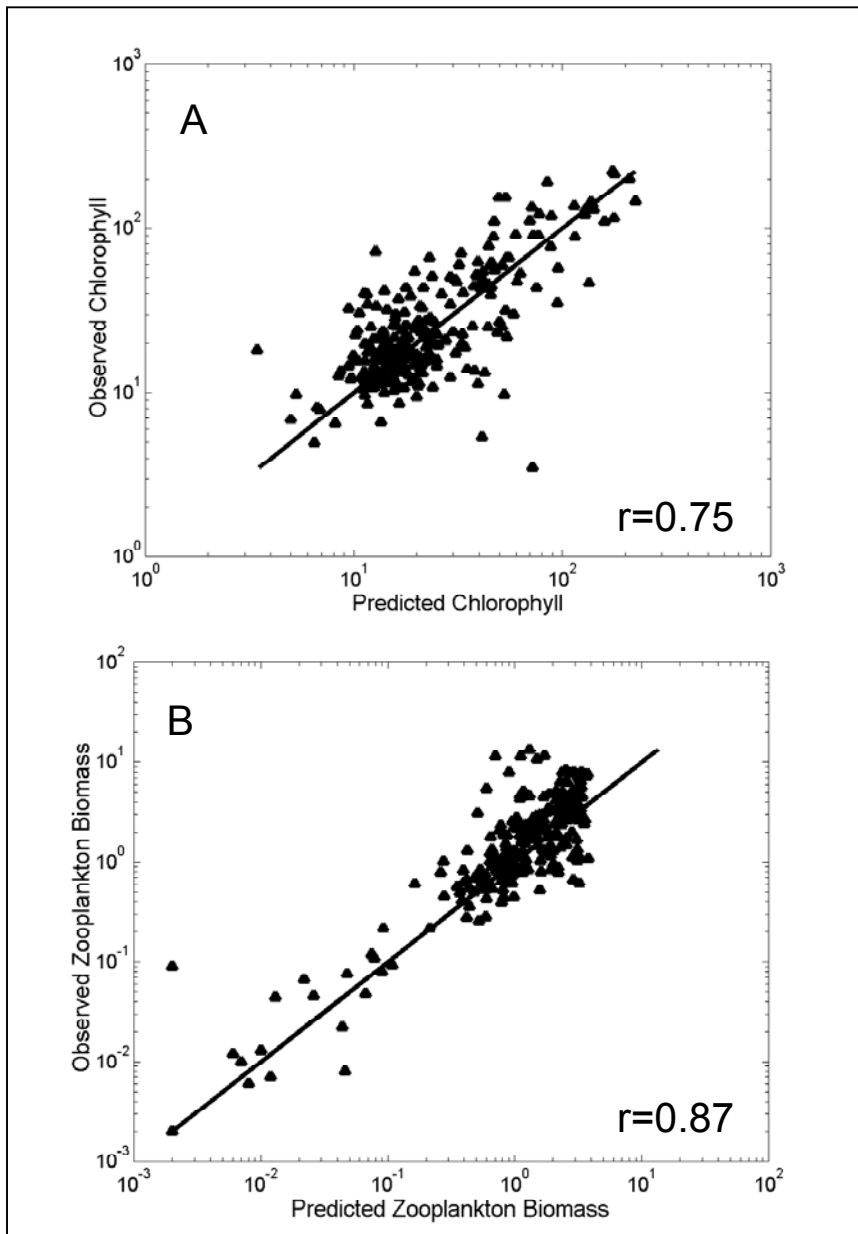
Figure 26. Plot of P input rate versus planktivory index, showing regions with one stable point or multiple stable points. Stable cycles are possible at all combinations of P input rate and planktivory index. (Original)
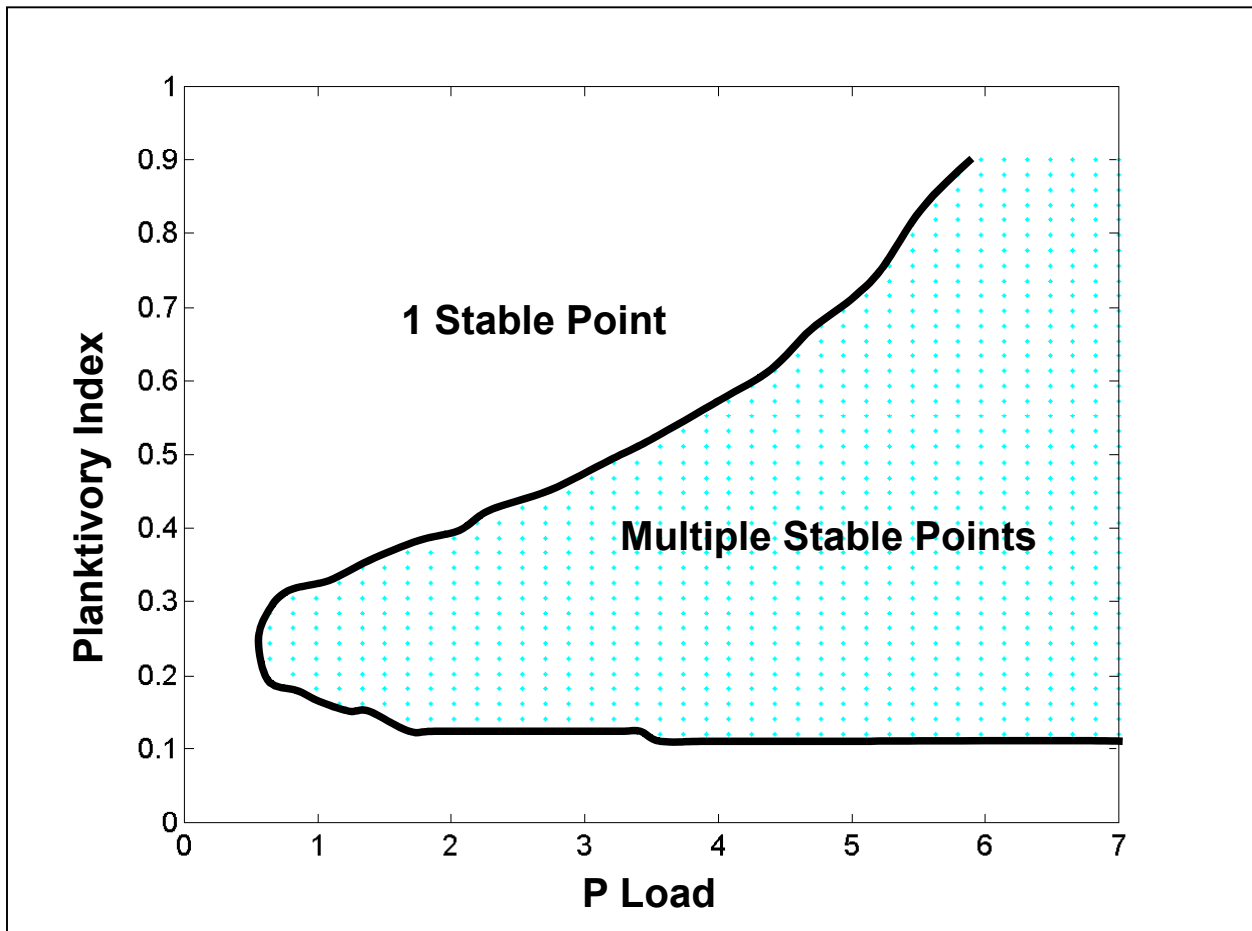
Figure 27. Simulations using the nonlinear model showing chlorophyll (black line) and zooplankton biomass (gray line). (A) Low phosphorus input (1 mg m^{-2} d^{-1}), constant c fixed at nominal value (Table 2). (B) High phosphorus input (6 mg m^{-2} d^{-1}), constant c fixed at nominal value (Table 2). (C) High phosphorus input (6 mg m^{-2} d^{-1}), c ramped from 0.1 to 50 over the course of the simulation. (Original)
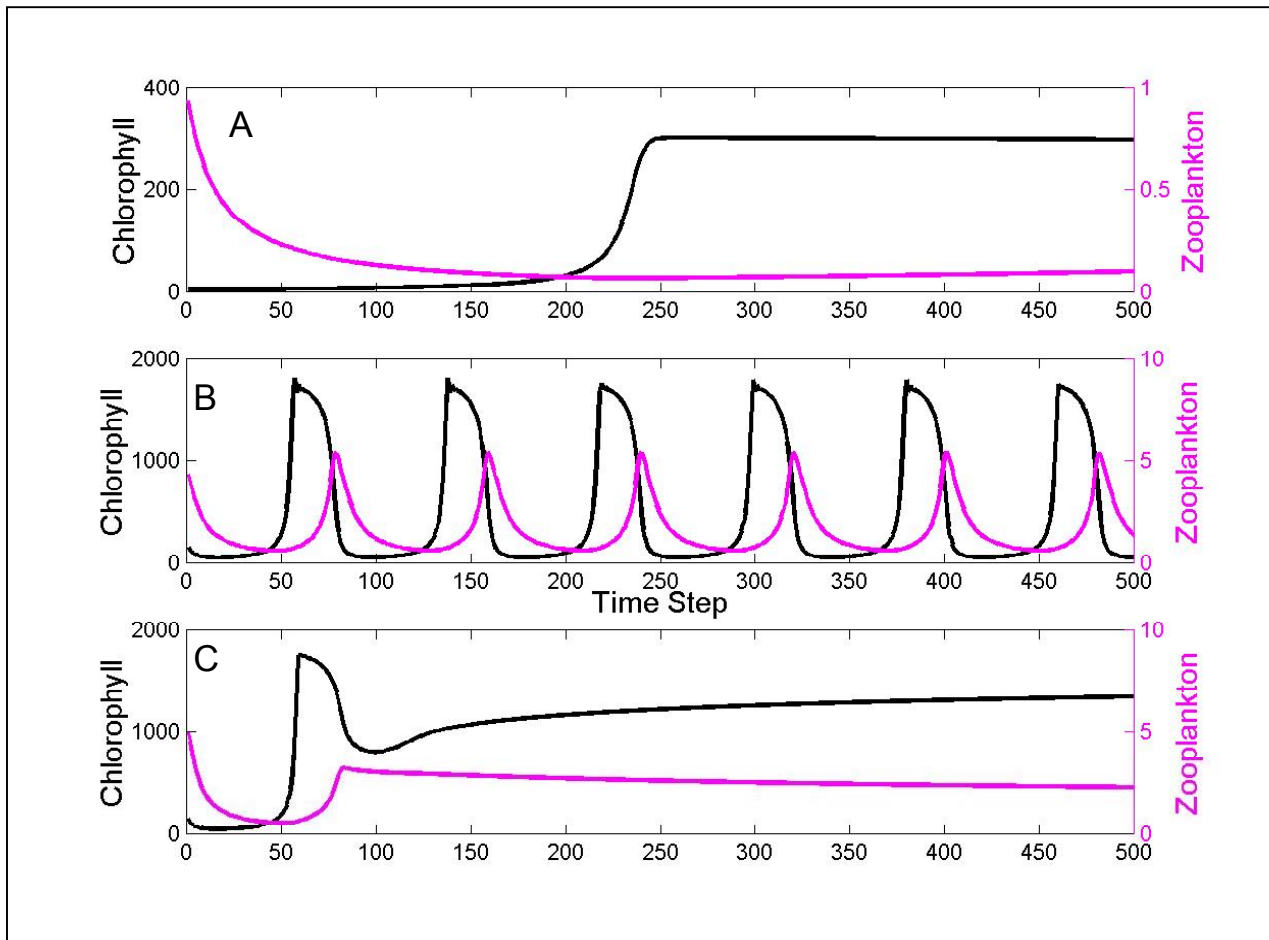
Figure 28. Predictions (solid line) and observations (crosses) from nonlinear dynamic
regression of the nonlinear model for West Long Lake time series. (A) Chlorophyll (B)
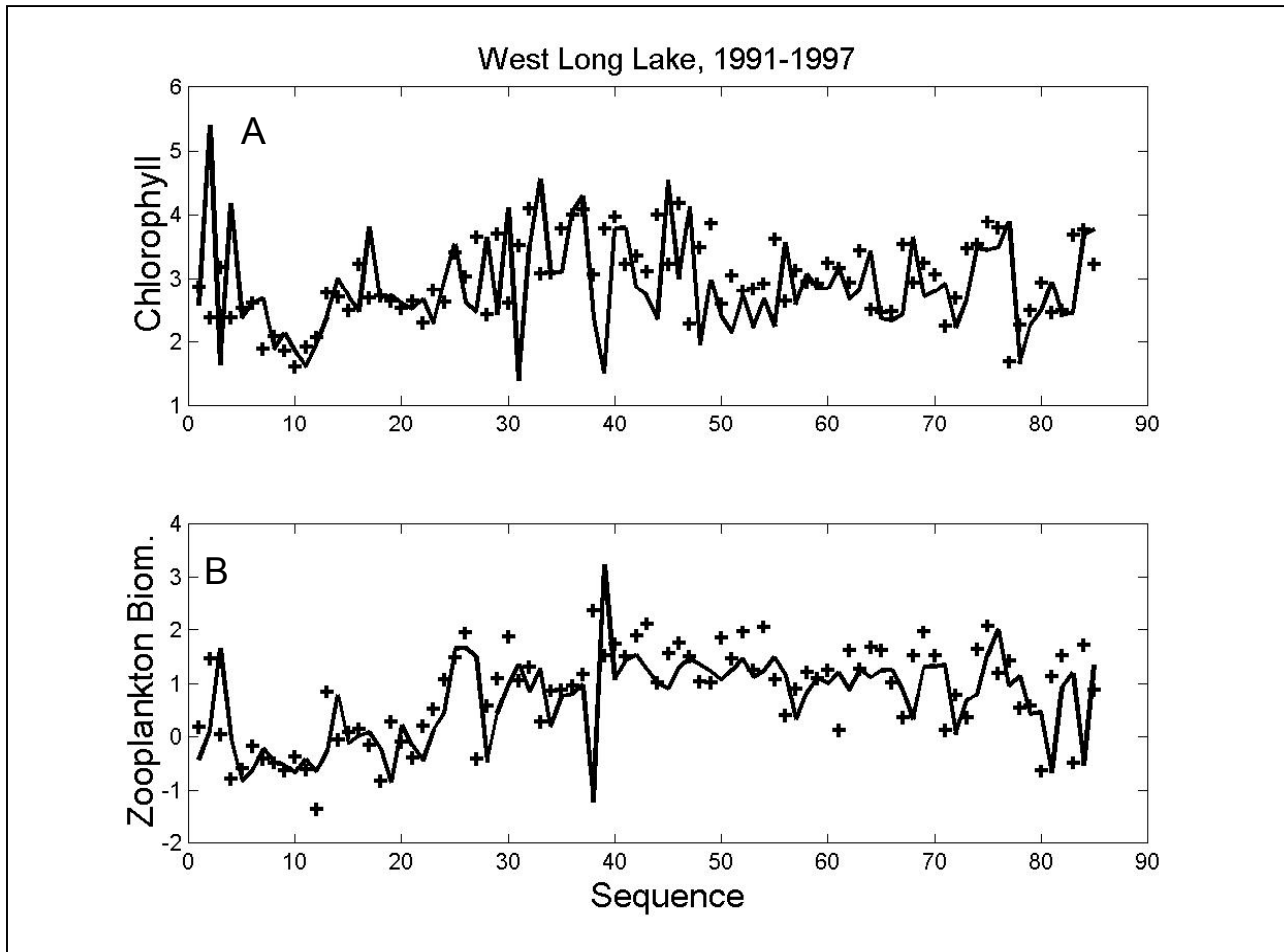Zooplankton biomass. (Original)

Figure 29. Time series of parameters for West Long Lake based on nonlinear dynamic regression. (A) Maximum phytoplankton growth rate, r (B) Maximum grazing rate, g (C) Maximum planktivory rate, c. (Original)
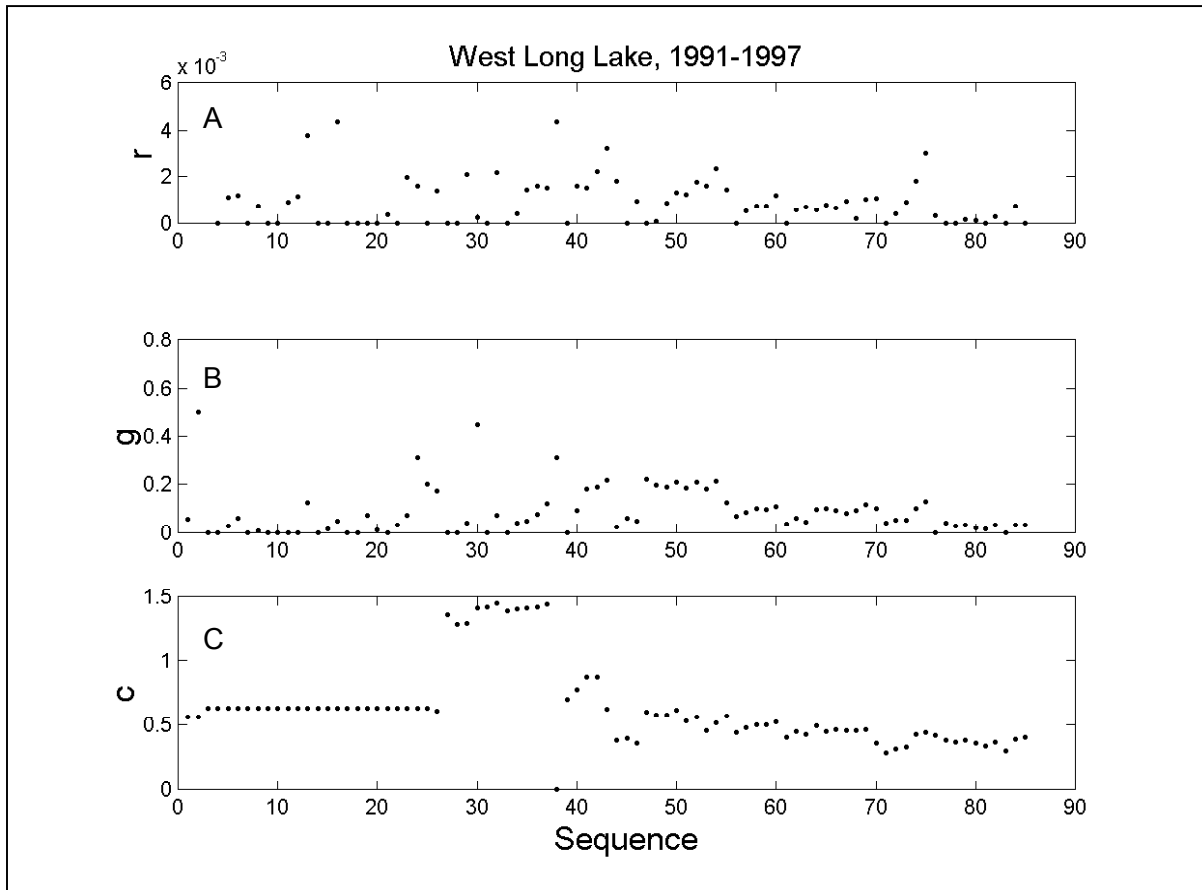
Figure 30. Time series of fish observations and the planktivory parameter for West

Long Lake. (A) Piscivore biomass (kg / ha). (B) Planktivore biomass (kg / ha). (C)

Maximum planktivory rate, c, from nonlinear dynamic regression. Note that fish data

were not used in computing the dynamic linear regression. (Original)
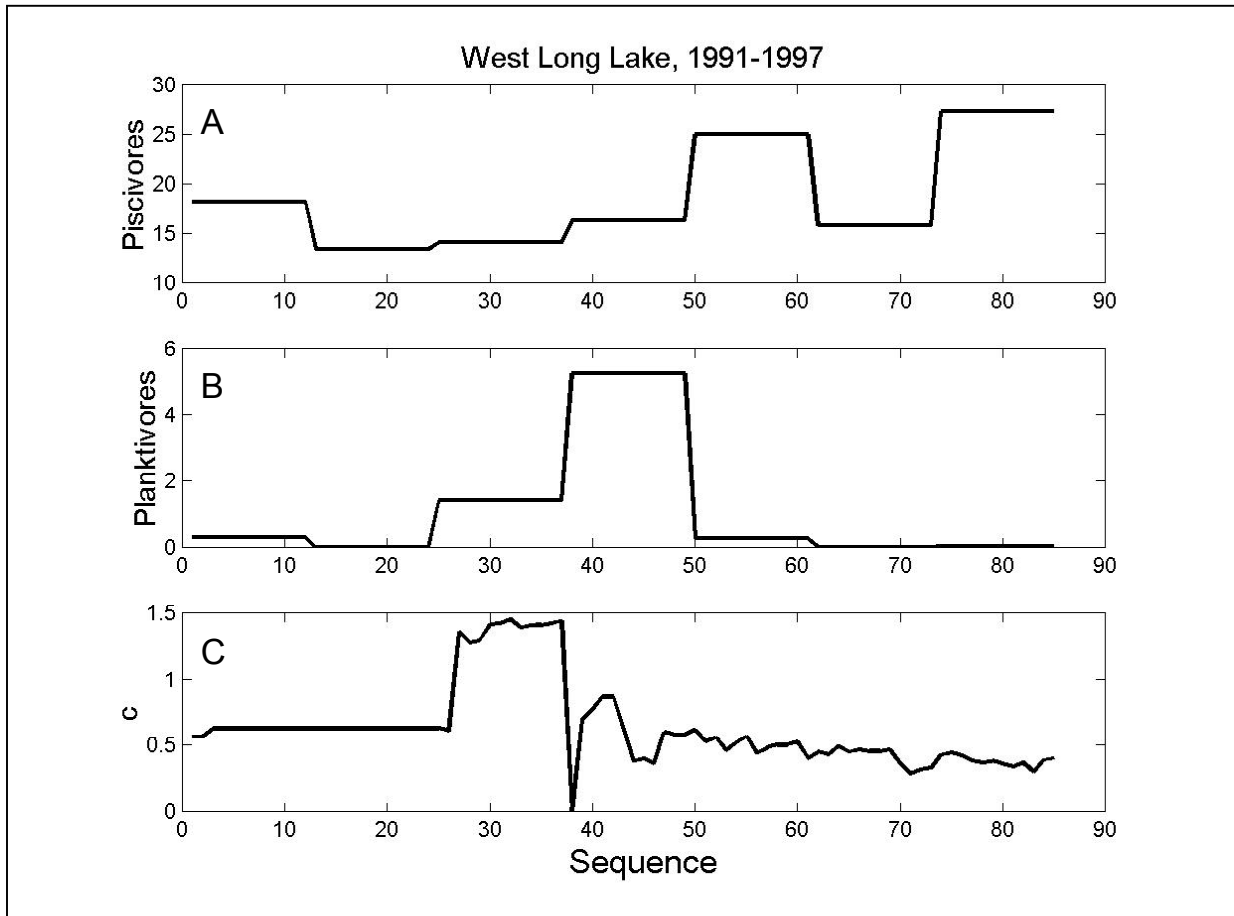

West Long Lake, 1991-1997

Figure 31. Conclusions that emerge from projecting the data through the lens of the linear versus nonlinear model. Conclusions that emerge from both models are in the intersection of the two circles. (Original)