VII UNDERSTANDING, PREDICTING, AND MANAGING REGIME SHIFTS IN LAKES

Introduction

The longer we study ecosystems, the more we see. Regime shifts are one of the remarkable phenomena that come into focus as we analyze longer-term data from more spatially-extensive ecosystems. These patterns offer fascinating scientific opportunity for ecologists. What are the forces and feedbacks that cause regime shifts to occur? Why are there changes in the tempo of regime shifts, over time and among ecosystems? Are there variables that can be manipulated to alter the frequency or intensity of regime shifts? This Excellence in Ecology book suggests several promising research avenues, including (1) experimental study of regime shifts in modular ecosystems such as lakes, islands and watersheds; (2) analysis of multiple models, ranging from the empirical to the mechanistic, to understand regime shifts in long-term data; (3) synthesis of evidence from theory, experiments, comparisons and long-term observations. Basic research on ecological regime shifts has been insightful for more than three decades (Holling 1973), and seems likely to be productive for a long time to come.

History shows that ecosystem management and regime shifts interact (Gunderson et al. 1995). Management changes the susceptibility of ecosystems to regime shifts, and creates regime shifts either deliberately or accidentally. Management agencies, programs and careers are built and broken over regime shifts. The case study of Lake Mendota (Chapter I) suggests an increasing frequency of regime shifts under intensifying human intervention. In lakes, we understand the factors that affect the risk of certain kinds of regime shifts, because we have seen these regime shifts many times before in many lake ecosystems. Despite this experience, it is difficult to predict the timing of a particular regime shift, such as a shift to self-sustaining eutrophication or the depensatory decline of a predator population. Other regime shifts are entirely novel (something we have never seen before) and these are by definition unpredictable. Perversely, statistical models fitted to historical data tend to underestimate the prospect of regime shifts. Such models should not be used to conclude that the probability of irreversible change is negligible, or that reversal of unwanted change will be easy. Instead, managers should expect a wide range of possible ecological regimes in the future. Successful management of ecosystems depends on flexible capabilities to adapt to novel and unexpected events (Gunderson and Holling 2002).

This final chapter of my Excellence in Ecology book returns to the overarching questions outline in Chapter I and summarizes the answers that have emerged. First, what are the implications of the book for basic scientific understanding of ecological regime shifts? Then, I consider the possibility of anticipating regime shifts, and the implications for ecological forecasting. Finally, I summarize the implications of regime shifts for management, and the prospects for learning about regime shifts through the process of ecosystem management.

Synopsis of Previous Chapters

In ecology, a regime shift is a rapid change, with long-term consequences, in ecosystem organization and feedbacks (Chapter I). Regime shifts include exogenously-forced changes, as well as changes that involve endogenous feedbacks. The latter include alternate stable states (Holling 1973, Carpenter 2001) as well as more complex types of dynamics (Levin 1999, Scheffer et al. 2001a, Gunderson and Holling 2002). These complex dynamics may involve many more than two attractors, including cycles or more complicated kinds of attractors (Guckenheimer and Holmes 1983, Kuznetsov 1995). Alternate stable states are a specific type of regime shift that involves switches between two domains of attraction. Such models appear to apply to some ecological changes, and are a useful metaphor for ecological transitions that may be difficult or impossible to reverse. However, many changes in ecosystems are more complicated than alternate stable states. Thus the concept of alternate stable states is too restrictive. "Regime shift" is a broader term for a class of ecological changes that occur relatively rapidly, may be irreversible, and may involve multiple attractors of diverse types, not just alternate stable states.

This Excellence in Ecology book presents case studies and mechanisms for three kinds of regime shifts in lakes: eutrophication, depensation, and trophic cascades (Chapter II). All three phenomena involve internal ecosystem feedbacks as well as external drivers. Understanding of these regime shifts derives from multiple approaches including long time series, comparisons of many ecosystems, and ecosystem experiments. Time series data, the stock-in-trade of long-term ecological research, are a natural place to look for regime shifts. It is difficult, however, to characterize regime shifts from time-series data alone. In part, this is because regime shifts are relatively infrequent events, so it takes a long time to accumulate enough data to characterize regime shifts. Therefore, research on regime shifts employs other approaches in addition to time series data. These other approaches include comparisons of many ecosystems to expand the spatial scope of a study, ecosystem experiments to increase the frequency of regime shifts, and inferences from a diverse set of models. Chapter III shows how a combination of long-term and comparative data gave a clearer picture of the regime shift of eutrophication. Ecosystem experiments are another important tool for characterizing regime shifts. Chapter IV explores experimental data using two contrasting styles of ecosystem modeling to describe regime shifts associated with trophic cascades. Synthesis of long-term, comparative and experimental studies using models is the key to understanding regime shifts.

Ecosystem management often involves the avoidance of unwanted regime shifts (such as eutrophication or the collapse of a fishery) or the creation of desired regime shifts (such as restoration of clear water in a lake, or re-establishment of a fish population). To manipulate or avoid regime shifts, it would be helpful to be able to predict them. Chapter V shows that it is extremely difficult to learn to predict a regime shift without causing a regime shift. In a particular individual ecosystem, such experiments may be disastrous. In such situations, it may be possible to devise precautionary management rules that decrease the risk of regime shifts.

For modular ecosystems like lakes, it is possible to characterize regime shifts using comparative data from a diverse set of lakes. Ecosystem experiments are an even more powerful way of analyzing regime shifts for modular ecosystems. The risks of experimentation may be worth taking if a small number of experimental ecosystems can provide crucial information for management of a larger group of ecosystems. Chapter VI shows that management is substantially more reliable when it is guided by ecosystem experiments. However, even with excellent data, the uncertainties are greatest when ecosystems are on the threshold of regime shift, the very situation when clarity is most needed. Hence the best management strategy is a precautionary one that stays away from situations that could cause a regime shift. For modular ecosystems, then, the best management style is an actively experimental one to learn the approximate location of thresholds using a few ecosystems, combined with precaution to avoid regime shifts in the majority of ecosystems.

Understanding Regime Shifts

Many kinds of changes, including regime shifts, occur in ecosystems. The multiple causes of ecosystem change complicate the analysis of regime shifts.

One of the central challenges is to evaluate the role of external drivers versus endogenous feedbacks. Endogenous feedbacks can cause multiple attractors. Hysteresis is perhaps the best indicator of multiple attractors (Scheffer and Carpenter 2003). In hysteresis, the level of a driver that causes a particular regime shift is different from the level of the driver that causes the reverse regime shift. The difference in thresholds derives from endogenous ecosystem processes (see Fig. 2). In eutrophication, for example, sediments are a slowly-changing reservoir that can recycle substantial amounts of P to overlying water (Chapter II). Massive recycling can be triggered by a period of high P inputs. To reverse eutrophication and restore the clear water state, cutbacks to very low P inputs may be required. The difference between the high P input rates that create eutrophication and the low P input rates that restore clear water demonstrates hysteresis. Hysteresis is most pronounced in lakes with large sediment reservoirs of phosphorus, slow flushing, and relatively warm hypolimnions.

Of course, the distinction between exogenous and endogenous processes follows from decisions about ecosystem definition, boundaries, and scale of analysis. These decisions are part of the process of choosing models for a particular study. Although the decisions may seem arbitrary, some boundaries, models and scales are more useful than others. Many interesting regime shifts, such as the phenomena studied in this book, involve cross-scale feedbacks. If the ecosystem is defined to include these feedbacks, then the appropriate models may exhibit multiple attractors, moving thresholds, hysteresis, and perhaps irreversibility.

Analysis of regime shifts is one of the more complex problems of ecology. It is essentially a problem of synthesis. Multiple types of evidence are usually helpful for sorting out the potential causes of regime shifts (Carpenter 2001, Scheffer and Carpenter 2003). The following section catalogs some of the useful types of evidence.

Field Marks of Regime Shifts

Ecologists use various field marks to recognize species while sampling ecosystems. In a given ecosystem, some species are easy to recognize. If muskellunge *Esox masquinongy* is the only species of Esocidae in a lake, a relatively crude field mark will do – "big and toothy", for example. Other species may be more difficult to recognize and require a more complex set of field marks. If six species of darters (*Etheostoma* spp.) are present in a lake, one might need many different kinds of field marks, for example completeness of the lateral line, number and position of spines, or presence of scales on the opercula and cheeks.

We need multiple field marks to search for regime shifts, just as if we were searching for a particular species in a diverse community (Table 8). All of these characteristics could be considered to evaluate the evidence for regime shifts in any particular situation (Scheffer and Carpenter 2003).

Long-term data exhibit at least two distinctive patterns: In the simplest case, there is a shift in the mean of some indicator. For example, eutrophication of lakes is associated with a shift in the mean of the logarithm of primary producer biomass, while many other indicators (including the variance of the logarithm of primary producer biomass) stay constant. Most shifts in long-term data are more complex. For example, in trophic cascades both the mean and variance of zooplankton biomass change (Chapter IV). In addition to changes in means or variances, there may be changes in autocorrelations or cycles of long-term change. There are numerous examples of relatively complex alterations of dynamic patterns in ecosystems undergoing regime shifts (for examples see Scheffer 1997, Jeppesen et al. 1998, Gunderson and Holling 2002).

Comparative data exhibit at least two distinctive configurations: Modular ecosystems, like lakes and islands, offer a large number of “replicates” for comparative study (Cole et al. 1991, Levin 1999). Comparative studies of modular ecosystems may reveal multiple configurations. For lakes, some examples are shallow lakes dominated by higher plants versus phytoplankton (Scheffer 1997), oligotrophic versus eutrophic lakes (Carpenter et al. 1999b), or lakes with high versus low levels of planktivorous fishes (Carpenter et al. 2001b).

Certain feedbacks act to maintain each regime: Regimes suggested by long-term or comparative data could simply be forced by changes in external drivers. To meet the definition of distinctive regimes, the regimes should be stabilized by particular feedbacks. For example, oligotrophy in lakes is maintained by biogeochemical processes that decrease phosphorus recycling, whereas eutrophy is maintained by biogeochemical processes that increase phosphorus recycling (Chapter II).

Other feedbacks or external drivers cause shifts among regimes: While the regimes are stabilized by certain feedbacks, there are other feedbacks or external drivers that cause shifts among regimes. The processes that cause the regime shifts often have slower rates of change, or act at larger spatial scales, than the processes that stabilize a regime. For example, buildup of phosphorus in soils of the watershed leads to increases in phosphorus input that can shift a lake from the oligotrophic to eutrophic state (Chapter II). This is an example of a regime shift driven from outside the lake ecosystem. The cycle of recruitment of top piscivores in lakes is an example of an internal feedback that drives regime shifts (Chapter II). During piscivore dominance, planktivory is suppressed by predation and recruitment is suppressed by competition and cannibalism. This leads to a regime of high, variable zooplankton biomass and generally low phytoplankton biomass. During recruitment episodes, the situation is reversed. Planktivory is high, zooplankton biomass is low, and phytoplankton biomass is high and variable.

Regime shifts can be produced experimentally: The acid test for understanding of regime shifts is the capacity to cause them by experimental manipulation of whole ecosystems. In the case of lakes, such experiments have been performed for several types of regime shifts (Schindler 1977, Hansson et al. 1998, Jeppesen et al. 1998, Carpenter and Kitchell 1993, Carpenter et al. 2001b).

There is at least one explanation consistent with all the evidence: In evaluating the evidence for regime shifts, the absence of a consistent explanation indicates that more research, or more synthetic thinking, needs to be done. A consistent explanation is one that explains all the available evidence. Synthesis of this sort is essential for understanding regime shifts. There must be at least one consistent explanation for the long-term and comparative data, measurements of feedbacks, and ecosystem experiments relevant to a particular regime shift.

For example, there is an explanation for lake eutrophication that is consistent with all available long-term data, comparative data, ecosystem experiments, and management experiences (Carpenter et al. 1999b). In essence, the explanation involves an ecosystem with two different attractors (caused by different biogeochemical feedbacks in the P cycle) subject to exogenous forcing (by P inputs). Within the framework of this general explanation, a number of more specific and detailed models can be devised. Different models are appropriate for different particular applications. The models of Carpenter et al. (1999b) and Ludwig et al. (2003) are useful for analyzing the ecological economics, whereas different models are useful for understanding the sources of soil phosphorus in the watershed (Bennett et al. 1999), the spatial origin of phosphorus inputs (Soranno et al. 1996), the consequences of particular phosphorus loading strategies (Lathrop et al. 1998), frequencies of cyanobacterial blooms (Stow et al. 1997), or the social dynamics of different groups of lake users (Carpenter et al. 1999b). The multiple models add richness to a more general explanation of eutrophication.

How should these diverse types of evidence be brought together? To my knowledge, there is no simple protocol that applies to all studies of regime shifts. Instead, a few general guidelines can be suggested. These are discussed below.

Basic Research on Regime Shifts

Complex phenomena, such as regime shifts, require polythetic research approaches. Multiple data sets and multiple models are necessary. There is no simple sequence of steps for analyzing or understanding ecological regime shifts, but there are a few guidelines that emerge from the literature as well as analyses presented in this book (Table 9).

There is no single null hypothesis: Because there is no single model for regime shifts, there is no single test for the presence or absence of regime shifts. Instead, multiple types of evidence need to be examined, multiple models need to be fitted, and synthetic explanations need to be discovered and examined for consistency. This is a problem in pattern recognition rather than a problem in null hypothesis testing (Pickett et al. 1994). An approach based on fitting multiple models and integrating multiple kinds of data seems more likely to create new insight. This Excellence in Ecology book has demonstrated some approaches toward the necessary synthesis.

Expect multiple causes: Regime shifts are not turned on and off by simple toggle switches. The examples discussed in this book involve multiple processes. Three or more time scales are involved. Eutrophication involves rapid cycling of phosphorus in water, slow phosphorus dynamics in soil, and recycling from sediments at intermediate turnover times. Depensation emerges from the interaction of long-lived adults, rapidly-growing juveniles, and prey species with intermediate turnover times. Trophic cascades involve three or four trophic levels in lakes, each with a characteristic turnover time. Although this book has emphasized cross-scale interactions in time, cross-scale interactions in space also create rich possibilities for regime shifts (Levin 1999, Gunderson and Holling 2002).

The multiplicity of causes suggest that research on regime shifts must focus on the feedbacks across time and space scales that could potentially cause regime shifts. Three guidelines pertain to research approaches for cross-scale interactions.

Emphasize long-term and spatially-extensive data: Context is essential for understanding regime shifts. Eutrophication depends on long-term changes in soil and sediment phosphorus over entire watersheds, regions or even continents (Bennett et al. 2001). Depensation depends on changes in habitats and food webs that may be gradual or subtle. Trophic cascades depend on long-term dynamics of slowly-growing top predators, or regional dynamics of anglers. These processes are not one-way forcing from larger scales to smaller ones. Instead, they involve feedbacks between slowly and rapidly-changing variables. Analyses that omit such feedbacks are incomplete and potentially misleading.

Consequently, long-term and spatially-extensive data are essential for the study of regime shifts. It is crucial to measure the rapidly-changing features of ecosystems as well as the slowly-changing variables that can stabilize regimes or promote shifts. Many useful guidelines for temporally- and spatially-extensive ecological studies are found in Likens (1989), Cole et al. (1991), Pace and Groffman (1998), Sala et al. (2000) and Turner et al. (2001).

Use multiple contrasting models: There is no single model for regime shifts. Even a set of models is unlikely to contain a single model that is useful under all circumstances. However, a set of models is more likely to be able to represent all the patterns seen in the data. As illustrated by Chapter IV, the residuals of the models may be as useful as the model predictions.

Experiment at the appropriate scales: The only way to learn about a regime shift is to observe one, and the fastest way to observe one is to cause it to occur. Because regime shifts depend on cross-scale feedbacks, it is essential that the experiments be scaled appropriately, in space and time, to observe these feedbacks. While experiments at this scale are challenging, ecologists have conducted insightful experiments at large scales in an impressive diversity of ecosystems (Likens 1985, Carpenter et al. 1995, Carpenter 1998).

Experiments are most likely to be safe on modular ecosystems where the impacts can be contained and reversed. Lakes, islands and small watersheds are examples of ecosystems where experimentation on regime shifts is likely to be insightful. When management is focused on a single ecosystem subject to regime shifts, the most informative experiments may be too dangerous to perform.

The points listed in Table 9 make it clear that synthesis of diverse kinds of information is central to the study of regime shifts. Synthesis begins with a conceptual framework that embraces the time and space scales at which important regime shifts may occur. Models and statistical tools for integrating diverse sources of data are a key element of this synthesis. This book has attempted to demonstrate, by example, some synthetic approaches that expand understanding of regime shifts. Other authors discuss how ecologists can best create useful syntheses (Pickett et al. 1994, Ford 2000).

Predicting Regime Shifts

Ecological understanding may or may not improve our ability to predict (Pickett et al. 1994, Carpenter 2002). The quality of a prediction is related to its information content, which is inversely related to the variance of the prediction, and to its accuracy (Clark et al. 2001). Often, as we learn more about an ecosystem, we learn that reasonably informative predictions are possible for some spatial extents and time horizons, but not for others. Also, it usually turns out that the information content of an ecological prediction depends heavily on what is assumed to be “inside” versus “outside” the system we are trying to predict. This issue of system definition is particularly critical for predictions of regime shifts.

A traditional approach to ecological prediction uses driver variables and a model to calculate the probability distribution for an ecological output (Fig. 48). The drivers are forcing factors (possibly time series) that are assumed to be fixed for the purposes of the analysis. The drivers could be random variables with fixed probability distributions. All ecological processes and feedbacks which are thought to be relevant are built into the model. The model also includes the relevant parameters, possibly including their probability distributions. The output is a probability distribution for some ecological output of interest. An example is the familiar phosphorus-chlorophyll predictions of limnology (Rigler and Peters 1995) in which phosphorus input rate is the driver, and the model is a linear regression of the logarithm of chlorophyll on the logarithm of phosphorus input rate. Given a phosphorus input rate (and its variance in the stochastic case) as well as the regression parameters and their covariance matrix, the probability distribution of chlorophyll concentration can be calculated (Carpenter 2002). The ecological output could be multivariate (Fig. 48 shows only one dimension for the sake of simplicity).

When the traditional approach to ecological prediction is elaborated to account for regime shifts, the probability distribution of the ecological output is viewed as a function of other variables which play key roles in the dynamics of the regime shift (Fig. 49). The probability distribution of the outcomes may be quite complex, reflecting the possibility that the system may end up in one of several regimes. The ecological system could involve more than two variables. Only two are shown in Fig. 49 for the sake of simplicity. This book has presented two examples of predictions similar to Fig. 49: the lake phosphorus system of Chapter V (in which the sediment phosphorus is the second ecological variable) and the fish-habitat system of Chapter VI (in which the habitat is the second ecological variable). Ludwig et al. (2003) present a rigorous analysis of decision-making for a system similar to Fig. 49.

Models for ecological prediction make simplifying assumptions about time scales. To predict over a certain time horizon, drivers and parameters of the model are assumed to be fixed. Over longer periods of time, drivers and parameters may change (Fig. 50). In other words, on longer time scales the drivers and parameters become variables, subject to ecological feedbacks with slower rates than the ones built into the model. These are the “parameters that aren’t” of Walters (1986). One way to deal with this problem is to update the drivers and parameters using data obtained by monitoring the ecosystem. This approach is illustrated in Chapter V, where regular observations of P input and concentration in the water are used to update the probability distribution of the driver (P input) and the parameters of the model for predicting P concentration. The updating approach has the advantage of retaining a simple model, and the disadvantage of delayed response. At best, the updates lag one time step behind the dynamics of the ecosystem, and because of noisy data the lag may be considerably longer than one time step. Of course, the delay matters most when the system is on the threshold of regime shift, exactly the time when better foresight is needed!

The second way to deal with the problem of dynamic drivers and parameters is to completely rebuild the model. In the new model, the dynamic drivers and parameters are converted to variables, and the new model contains the slower ecological feedbacks of Fig. 50. The goal of the new model is to convert the situation of Fig. 50 to the situation of Fig. 49. Generally the output of the new model will have more dimensions than the output of the old model. Also, the new model will contain slowly-changing processes that must be observed for a long time to be quantified. The high dimensionality and interplay of slow and fast processes cause the new model to be harder to calibrate, analyze, understand, and explain to other people. Also, the new model will be harder to upgrade when its deficiencies become unacceptable. For this reason, many ecosystem modelers prefer simpler models (Yorque et al. 2002, Carpenter 2003). The optimal complexity for a model will depend on the goals of the project and the data available for fitting and criticizing the model.

Social-economic feedbacks may also cause drivers and parameters of the model to change (Fig. 51). Now the solution to the problem lies outside the traditional disciplinary boundary of ecology. In general, the possible solutions are the same as the previous case. One can use monitoring data to update the drivers and parameters, or rebuild the model to include the missing feedbacks and convert the changing drivers and parameters into variables. The second option involves building an integrated social-economic-ecological model. The same virtues of simplicity apply to models of social-economic-ecological systems (Yorque et al. 2002).

Integrated social-economic-ecological models exhibit new kinds of complexity that are not seen in most ecosystem models (Anderies 1998, Janssen and de Vries 1998, Janssen and Carpenter 1999, Carpenter et al. 1999a, 2002, Janssen et al. 2000, Carpenter and Gunderson 2001, Peterson et al. 2003). In the natural sciences, causality is assumed to act from the past to the present; dynamics are understood by examining past changes and, in retrospect, fitting models to them (Yorque et al. 2002). People, in contrast, are forward-looking; they can anticipate future events and act in ways that change the course of future events (Westley et al. 2002, Yorque et al. 2002). For example, in the model of Chapter VI, harvest decisions affect the expected future harvest of fishes and this expectation is built into the calculation of the optimal harvest schedule. More sophisticated models of human behavior than those of Chapter VI yield far more complex dynamics (Carpenter et al. 1999a, Janssen et al. 2000). We are barely beginning to understand such systems using simple models. Credible prediction is not on the horizon.

In view of the difficulty of predicting social-economic-ecological systems, how should we address the future of ecosystems which are strongly affected by human action? Outside of simplified experimental systems for purely ecological research, it is impossible to make ecological predictions without considering social-economic context. In many cases, there is no way to estimate an informative probability distribution for these predictions. We may not even know the dimensionality of the appropriate probability distribution or the units of the axes, so it is impossible to calculate a non-informative prior distribution. Systems of this type are beyond the scope of the traditional kinds of decision analyses illustrated in Chapter VI (Funtowicz et al. 1999, Cooman and Walley 2000, Ludwig 2001). For researchers, these highly complex systems are subjects of research in imprecise probabilities (Cooman and Walley 2000) or dynamics of integrated social-economic-ecological systems (Gunderson and Holling 2002). For managers, they demand completely new approaches for confronting uncertainty and imagining the future (Funtowicz et al. 1999, Ludwig 2001).

Managing Regime Shifts

The literature, data and models presented in this book suggest a number of management steps for preventing particular regime shifts in lakes. Most of these involve precautionary action to avoid unwanted regime shifts. In the case of eutrophication, phosphorus inputs must be held at low levels to prevent buildup of phosphorus in lake sediments. Where phosphorus input is due to nonpoint pollution (Carpenter et al. 1998a), it is critical to reduce fertilizer usage to prevent buildup of phosphorus in soils (Bennett et al. 2001). To prevent depensatory collapse of predator populations, it is critical to maintain habitat for all life stages of the predator while reducing harvest to low levels. Fishing is a powerful force in lake ecosystems (Kitchell and Carpenter 1993) and many lake fisheries are overfished (Post et al. 2002). High populations of piscivorous fishes in lakes suppress nuisance phytoplankton through trophic cascades. Unwanted food web changes in lakes can be triggered by species invasions. Once an unwanted species has invaded a lake, control is extremely difficult (Lodge et al. 2000, Kolar and Lodge 2000). Thus, prevention may be the only effective way to deal with the problem (Kolar and Lodge 2000).

There is no operating manual for ecosystems subject to regime shifts. Nevertheless, it is possible to distill a few general management suggestions from this book (Table 10).

Monitor the slowly-changing variables: Regime shifts occur when slowly-changing variables move the ecosystem so close to thresholds that stochastic shocks are likely to trigger ecosystem change (Scheffer et al. 2001a). Thus slowly-changing variables can be “leading indicators” of regime shifts. Examples are soil and sediment phosphorus in eutrophication, age structure of top predators in trophic cascades, or habitat change and exploitation rate for fish stocks subject to depensation. Other examples of feedbacks between slow and fast ecological variables are presented by a set of papers in *Ecosystems* (Volume 3, Issue 6, pages 495-573; Carpenter and Turner 2000).

Use several contrasting models to assess the data: All models are wrong, but some are useful (Box 1980). The difficulty is that we may not know which models are useful until after a costly regime shift has occurred. Thus it is best to keep several contrasting models in play, and continually evaluate their projections and residuals. A model that seems unlikely based on historical data may turn out to provide valuable signals of impending regime shifts.

Experiment at the appropriate scales: Experimentation is a powerful way to learn about potential regime shifts and to calibrate models (Walters 1986). In situations where ecosystems are numerous and modular, experimentation should be used to explore options and improve understanding of ecosystem behavior. It is irresponsible to do otherwise. The information to be gained from experiments on a few ecosystems is crucially important for avoiding regime shifts in the great majority of ecosystems. In this situation, the manager who is not experimenting on a few ecosystems is putting all the ecosystems at risk.

In the case of a single ecosystem subject to regime shifts, experimentation can be dangerous (as explored in Chapter V). It may be possible to identify some safe experiments that are likely to provide useful information. For example, in the case of Chapter V, experiments that reduce P loading are safe and provide some information about the recycling parameter. Alternatively, it may be possible to conduct ecosystem-scale measurements that reduce the uncertainty about certain key parameters. For example, direct estimates of recycling in Lake Mendota helped narrow the scope of possible recycling rates for that lake (Soranno et al. 1997).

Experiments at the wrong scales can be highly misleading. Experiments in small containers are frequently used in ecology because they can be done quickly and have high statistical power, but many cross-scale processes are excluded and the results may be highly dependent on the size of the container (Carpenter 1996, Schindler 1998, Frost et al. 2001, Pace 2001). Experiments that fail to include key cross-scale feedbacks are likely to misrepresent regime shifts. While such highly simplified experiments may reveal something about plausible mechanisms, they are insufficient for ecosystem management.

Expect surprise: Planning for the possibility of surprise is a centerpiece of adaptive ecosystem management (Holling 1978, Walters 1986, Gunderson et al. 1995, Gunderson and Holling 2002), and regime shifts are classic causes of ecological surprise. Regime shifts are infrequent phenomena that are unpredictable even in the best-understood ecosystems. This Excellence in Ecology book demonstrates substantial uncertainty about phosphorus recycling rates and the threshold for eutrophication in Lake Mendota, one of the most intensively-studied ecosystems in the world. In an earlier review of whole-lake experiments on trophic cascades, Jim Kitchell and I concluded that half our predictions were wrong, even though these predictions emerged from state-of-the-art models, were consistent with the then-current wisdom of aquatic ecology, and passed rigorous peer review by the US National Science Foundation (Carpenter and Kitchell 1993). These and many other case studies show that forecasts of regime shifts are highly unreliable. In view of the current rate of transformation of the biosphere (Vitousek et al. 1997b), the prospect of completely novel regime shifts must be kept in mind.

Pay attention to long-term and spatially-extensive ecological research: A substantial subculture of academic ecology is devoted to the understanding of long-term and large-scale change in ecosystems (Pace and Groffman 1998, Turner et al. 2001, Hobbie et al. 2003). This research is gradually building understanding of regime shifts and other important phenomena at the scale of management. The specific future products of this research are no more predictable than the current dynamics of social-ecological systems. It is certain, however, that basic science insights useful for future ecosystem management will emerge from this branch of academic science.

Successful approaches for managing ecosystems subject to regime shifts seem to combine learning with precaution. Herein lies a paradox, because precaution and learning are often incompatible. In ecosystem management, learning should attempt to identify the types of regime shifts that are possible, and the approximate location of thresholds. Precaution implies avoidance of conditions that are likely to produce costly or damaging regime shifts. The paradox is resolved by scale differences. As a rule,

Learning and precaution are compatible when the learning can occur at scales different from the ones where precaution is necessary.

The clearest opportunities for combining learning and precaution arise with modular ecosystems such as lakes. In these cases, learning at the scale of a few ecosystems can be applied to manage a large number of ecosystems.

Many potential regime shifts occur in ecosystems where safe experimentation is not feasible, information content of predictions is low, and costs of an unwanted regime shift are high. The global climate system, for example, is subject to abrupt changes, and future changes could be caused by human action (Alley et al. 2003). Global warming could alter the North Atlantic thermohaline circulation in ways that cause catastrophic cooling in Europe (Broecker 1987, Rahmstorf 1997; see Chapter V). However, experimentation is not an option. Not only is there no reference ecosystem, but the costs of catastrophic cooling in Europe are unacceptably high. Precaution is necessary but it is difficult to decide how much precaution is enough, or evaluate the tradeoffs among different options (Harremoës et al. 2001, Heal and Kriström 2002). Measurements of key ecosystem process rates or monitoring of key slow variables may provide some useful information (Deutsch et al. 2002). Historic or paleoecological information may provide insight from past regime shifts (Taylor 1999). It seems likely, however, that many risks will remain shrouded in uncertainty, many precautionary arguments will not prevail, and some big unwanted changes will occur. Once this happens, management institutions are faced with challenges of learning, innovating and adapting (Berkes et al. 2002, Gunderson and Holling 2002).

Regime shifts have always occurred in ecosystems. The growing impact of humanity appears to be increasing the frequency of regime shifts as well as inducing new kinds of regime shifts (Scheffer et al. 2001a, Folke et al. 2002a,b). Emerging, novel changes are best managed by institutions that are good at inventing new solutions and flexible enough to adopt them (Berkes et al. 2002, Gunderson and Holling

2002). An institution is a set of rules used by people in addressing some collective problem (Berkes et al. 2002). Creation of institutions that are good at learning and adapting may be the best way to manage regime shifts. How can such institutions be created? A merger of ecology with social sciences such as political science and economics is needed to address this challenge.

Summary

Strategies for research on regime shifts, or management of ecosystems subject to regime shift, depend on whether the regime shift in question is known or entirely novel, and whether the ecosystem in question is modular or singular (Table 11). When ecosystems are modular, a large number of similar ecosystems exists (Levin 1999). Modular ecosystems offer the possibility of comparative analysis or ecosystem experimentation. Lakes, islands and small watersheds are examples of modular ecosystems. Singular ecosystems are truly unique. For singular systems, experiments may be difficult or risky, and observations are hard to interpret because too many variables change at the same time. The biosphere is the most obvious example of a singular ecosystem. Many large-scale ecosystems, for example the Amazon basin or the North Pacific Tropical Gyre, are also singular.

This book has focused on known regime shifts – eutrophication, piscivore collapse, and trophic cascades – in lakes, a modular type of ecosystem. Regime shifts are also known from singular systems (Scheffer et al. 2001a). For example, the thermohaline circulation of the North Atlantic Ocean exists in two regimes (Broecker 1987, Rahmstorf 1997; Chapter V). In one regime, the Gulf Stream extends far to the north and transports heat to Europe. This regime has prevailed for the past few thousand years. In the other regime, the Gulf Stream is subducted far to the south, and Europe cools. Paleoclimate reconstructions based on ice and sediment cores show that shifts between these regimes have occurred many times in the past (Taylor 1999). The regime shifts take less than a decade to occur, and the cold regime lasts for hundreds of years (Taylor 1999). This is an example of a regime shift that occurs in a singular system and is known from historical and modeling studies. Other regime shifts are not known to have occurred before, and are entirely novel when they first occur.

Strategies for ecological research include long-term studies, assessments of local stabilizing mechanisms, comparative studies, and ecosystem experiments (Table 11). By “assessment of local stabilizing mechanisms”, I mean research directed at understanding processes that maintain the ecosystem in its current regime. Often such assessments focus on ecosystem process rates combined with ecosystem models. All approaches are possible for modular ecosystems. For singular ecosystems, long-term studies and assessments of local stabilizing mechanisms are available. In some cases, ecosystem experiments may be possible, insightful and safe. It is difficult, however, to meet all three of these criteria at once.

Thresholds can be estimated with moderate precision in modular ecosystems, if appropriate studies are performed and the thresholds change very slowly. This book has shown that comparative studies and ecosystem experiments are especially useful for improving the precision of threshold estimates. However, even in modular systems where replicated ecosystem experiments are possible, errors in threshold estimates will be considerable. In singular systems, precision of threshold estimates will be low. A large number of regime shifts must be observed to improve the precision of threshold measurements, and such observations will be impossible except in rare cases. In the case of novel regime shifts, the precision of threshold estimates is zero, and the variance is infinite.

Strategies for avoiding unwanted regime shifts are to build ecological resilience, stay far away from the threshold, monitor and experiment (Table 11). Resilience is built by increasing the range of conditions that maintain the desired regime (Chapter I; Carpenter et al. 2001a). For example, resilience of the clear water regime in lakes is increased if phosphorus content of soil is low (Bennett et al. 2001). To stay away from thresholds, managers hold key variables in ranges that reduce the risk of crossing thresholds. In lake eutrophication, for example, riparian vegetation is used to reduce the risk of eutrophication by intercepting phosphorus inputs from upland soils (Carpenter et al. 1998a). Monitoring may provide advance warning of regime shifts and promote adaptive responses.

Experimentation is the most powerful method for learning the location of thresholds and the amplitude of ecosystem response to intervention (Walters 1986, Carpenter et al. 1999a). However, experimentation may be inconsistent with precautionary management which attempts to stay away from thresholds. Experimentation and precaution are compatible when the experiments can occur at scales different from the ones at which precaution is needed.

Strategies for sustaining ecosystems and people are similar for modular and singular ecosystems, and for known and novel regime shifts (Table 11). Ecological resilience creates buffers that maintain desirable states of ecosystems in spite of exogenous trends and shocks. Diverse components of ecosystems, including diversity of species, types of ecosystems, or elements of landscapes, often contribute to ecological resilience (Folke et al. 2002a,b). Social memory and creativity appear to be key factors for the persistence of societies that depend on ecosystems subject to regime shifts (Berkes et al. 2002, Gunderson and Holling 2002). Institutions (sets of rules through which people address a collective problem) that adjust rapidly are essential if societies are to change successfully to manage ecosystems subject to regime shifts (Berkes et al. 2002, Gunderson and Holling 2002). Such features of institutions are outside the disciplinary boundary of ecology. The approaches of social scientists to problems of sustainability are unfamiliar to most ecologists today, but must become more familiar as we develop interdisciplinary collaborations aimed at understanding important social issues related to regime shift and resilience of the ecosystems on which life depends.

Tables

Table 7.1. Characteristics of regime shifts in ecosystems.

Long-term observations of an ecosystem exhibit two or more distinctive patterns of dynamics (corresponding to regimes).

Comparisons of many ecosystems of a given type (such as lakes) exhibit two or more distinctive configurations of ecosystem state (corresponding to regimes).

Certain feedbacks act to maintain each of the regimes, and these feedbacks differ in measurable ways among the different regimes.

Other feedbacks, or external drivers, cause shifts among the regimes.

Regime shifts can be produced experimentally, at the appropriate scales.

There is at least one consistent explanation for the patterns in long-term observations, configurations of diverse ecosystems, feedbacks that maintain the regimes, and forces that cause shifts among the regimes.

Table 7.2. Major lessons of this book for basic research to understand regime shifts.

There is no single null hypothesis.

Expect multiple causes.

Look for cross-scale interactions in time and space:

> Emphasize long-term and spatially-extensive data.
>
> Use multiple contrasting models, and examine their residuals as well as their predictions.
>
> Experiment at the appropriate scales.

Synthesis is central.

Table 7.3. Major lessons of this book for management of ecosystems subject to regime shifts.

Monitor the slowly-changing variables that control regimes.

Use several contrasting models to assess the data.

Experiment at the appropriate scales.

  For modular ecosystems, responsible management requires experimentation.

  For unique ecosystems, seek safe experiments.

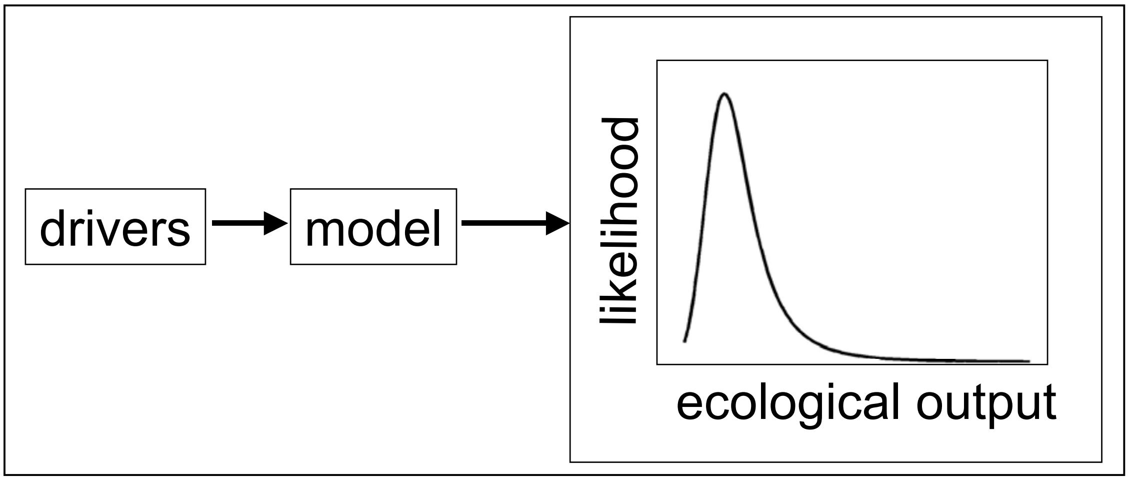
Expect surprise.

Pay attention to long-term and spatially-extensive ecological research.

Table 7.4. Summary of the implications for research and management of two classes of regime shifts (known and novel) in two types of ecosystems (modular and singular).

	Known Regime Shift		Novel Regime Shift	
	Modular	**Singular**	**Modular**	**Singular**
Examples	Eutrophication Piscivore collapse Trophic cascades	Atlantic thermohaline circulation	Any surprise before it has ever been observed	
Strategies for ecological learning	Long-term studies Assessment of local stabilizing mechanisms Comparative studies Ecosystem experiments	Long-term studies Assessment of local stabilizing mechanisms Ecosystem experiments (maybe)	Long-term studies Assessment of local stabilizing mechanisms Comparative studies Ecosystem experiments	Long-term studies Assessment of local stabilizing mechanisms Ecosystem experiments (maybe)
Precision of threshold estimate	Moderate	Low	Negligible	
Strategies for avoiding regime shift	Build ecological resilience Stay away from threshold Monitor Experiment	Build ecological resilience Stay far away from threshold Monitor	Build ecological resilience Monitor Experiment	Build ecological resilience Monitor
Strategies for sustaining ecosystems and people	Build ecological resilience Conserve ecosystem components (species, ecosystem types, landscape elements) Nurture social memory and creativity Build institutions that learn and adapt rapidly			

Figure 48. Traditional approach to ecological prediction. Drivers are input to a model, which yields a predicted probability distribution for an ecological output. (Original)



Figures

Figure 49. The traditional approach to ecological prediction can be elaborated to address regime shifts. In this case, the probability distribution of the ecological output is viewed as a function of a second ecological variable which plays a key role in feedbacks that lead to regime shifts. (Original)

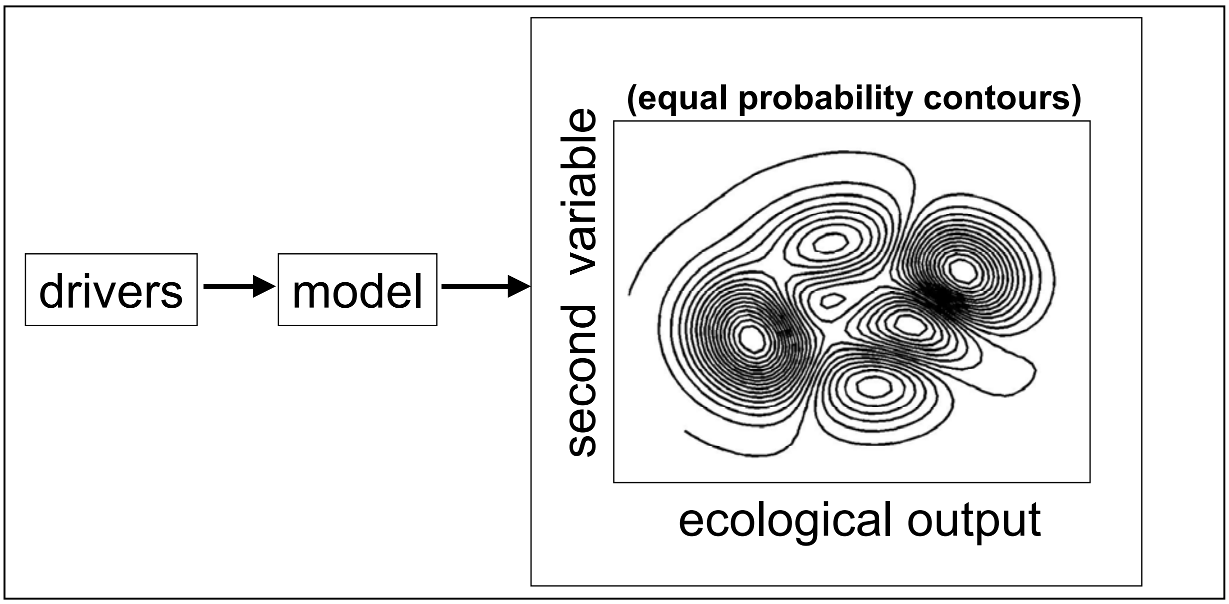


Figure 50. Ecological prediction for regime shifts when slower ecological feedbacks cause the drivers and model parameters to change. (Original)

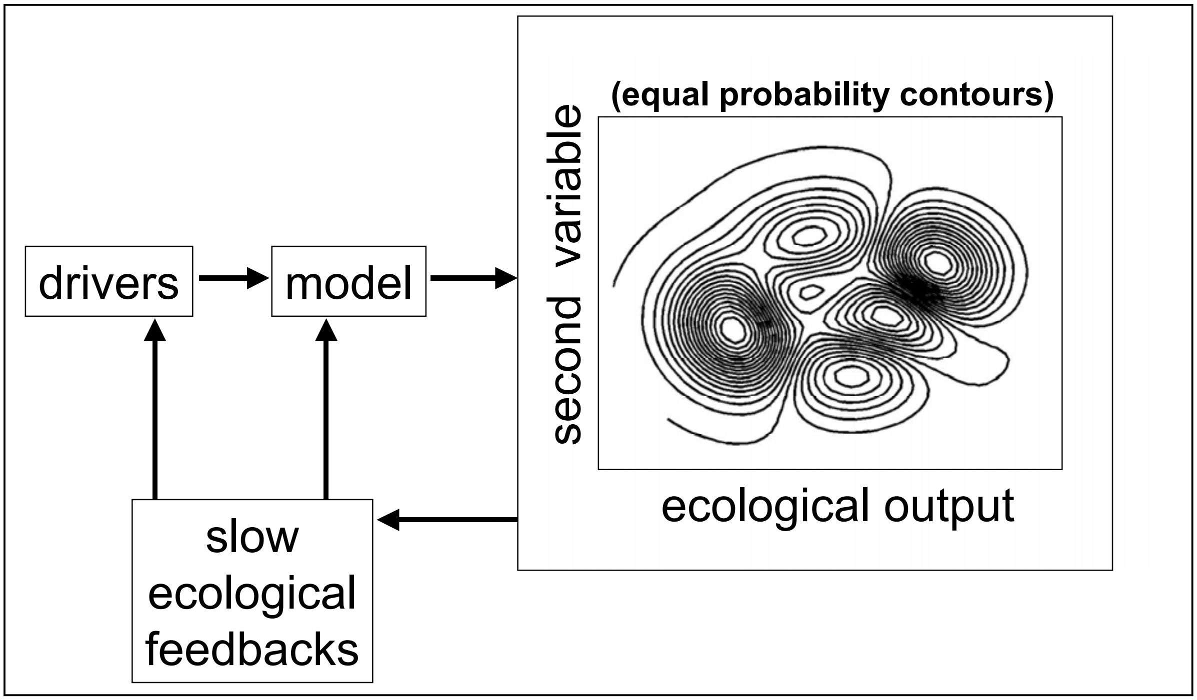


Figure 51. Ecological prediction for regime shifts when slower ecological feedbacks and social-economic feedbacks cause the drivers and model parameters to change. (Original)