PREFACE

Ecosystems can be predictable, or they can change in surprising ways. Ecological research may appear to make rapid progress when it focuses on scales at which ecosystems seem predictable. The art of experimentation is to simplify systems so that they behave in transparent, interpretable, and ultimately predictable ways. The same could be said of modeling. But too much emphasis of predictable scales may cause us to neglect big, surprising changes. Long-term ecological research and landscape ecology show that big changes sometimes occur. The most important of these garner public attention. Yet the massive changes are infrequent, so it is difficult to study them in repeatable, statistically significant ways. Consequently, prediction of big changes remains difficult or impossible. This book is about ecological phenomena that are often at the edge of statistical significance, yet are at the forefront of significance to ecologists and the public.

If big changes were readily reversible, they would be easier to study and less problematic for ecosystem managers. But often the big changes are not reversible, or can be reversed only slowly, with long time delays. The big changes punctuate longer periods of modest variability, called regimes. While regimes are probably not truly stable, they are persistent. The processes that cause regimes to persist, and those that cause them to break down, pose challenges for ecological research and management.
Better understanding of regime shifts requires sustained, long-term ecological research at multiple spatial scales. Comparative studies of similar ecosystems, such as lakes, islands and watersheds, also broaden our knowledge of ecosystem regimes. Experimentation on whole ecosystems is perhaps the most powerful and rapid method for understanding regime shifts. However, where people depend on ecosystems for their livelihoods, such experiments may be risky. Ironically, these are the ecosystems for which we most need information about regime shifts. In these situations, there are creative possibilities for ecosystem studies and safe experiments that can build our understanding of regime shifts.

Ecologists frequently point out the value of species, ecosystem, and landscape diversity. The discipline of ecology has an analogous need for diverse models. Providing these models is the job of ecological theory. Ecology seems to oscillate between the demand for new models of unexplained phenomena and the deductive processes that winnow models. Both theory and experiments limit our understanding of regime shifts. We sorely need new empirical work to address important models that have been neglected, or in some cases rejected prematurely, due to inadequate data. We also need better theory, framed in terms of observables and parameters that can be identified using ecological field data. I have attempted to provide some bridges between theory and field observations in this Excellence in Ecology book.

I am grateful to many friends and institutions for their role in the creation of this work.
The Ecology Institute of Oldendorf/Luhe awarded me a prize for Excellence in Ecology that led to this book. To Otto Kinne and his colleagues I am deeply grateful. Funding for a leave of absence to write the book was provided by a Kellett Mid-Career Award from the Graduate School of the University of Wisconsin-Madison.

The U.S. National Science Foundation and the Andrew W. Mellon Foundation have generously supported my research. NSF support for various ecosystem experiments and the North Temperate Lakes Long-Term Ecological Research site has provided a solid foundation for my field programs. Sustained, rigorous field data are crucial for research on regime shifts, and NSF has made it possible to gather such data. The Mellon Foundation has provided unusually flexible support that allowed novel explorations of models and time series data. Bill Robertson at the Mellon Foundation has been willing to support my intuitive guesses over the years, some of which were rather vague in their initial expressions. Some of those guesses paid off in the form of insights reflected in this volume.

The Center for Limnology, University of Wisconsin-Madison, is a superb place to do science. This book could have been written nowhere else. John Magnuson, and now Jim Kitchell, manages a magnificent institution dedicated to creative ecological research. The operating definition of limnology at CFL extends beyond fresh waters to embrace landscape ecology, theoretical ecology, ecological economics and applications of ecology to societal issues. The resulting environment encourages broad thinking.
I have had the good fortune to be affiliated with three outstanding field stations. Trout Lake Station provided a haven for much field work, but more importantly it was home to the intellectual contributions of Tom Frost and Tim Kratz. I deeply miss the insight of Tom Frost, who died in a tragic accident before we were able to discuss the work reported here. The University of Notre Dame Environmental Research Center (UNDERC) has provided a venue for my research since 1979. UNDERC’s capacities for whole-lake experiments are unparalleled in the United States, and were crucial for the data analyzed in Chapter IV. The Laboratory of Limnology in Madison, Wisconsin is the base station for work on Lake Mendota and other nearby lakes. In Madison I am fortunate to work with Dick Lathrop, an energetic and productive collaborator who knows more about Lake Mendota than anyone ever has, or likely ever will.

Whole-lake experiments on trophic cascades first prompted my interest in hysteresis and regime shifts. I am grateful to Jim Kitchell for more than 20 years of collaboration on theories, models and field experiments addressing trophic cascades. Mike Pace and Jon Cole joined us in this work over a decade ago. They have taught me a lot. Jim Hodgson has anchored the fish work for the whole-lake experiments from the beginning. The Cascade Collaboration brings together creative people from several disciplines to learn from whole-lake experiments and collaborative models. It is remarkably productive, and fun. Long may it run.
The Resilience Alliance (sometimes known as the “island-hopping crazy herd of nerds”) developed ecological theory that has infiltrated this book in many ways. My focus on regime shifts owes a great intellectual debt to C.S. (Buzz) Holling, founder of the R.A. Much of what I know about models for regime shifts was learned through collaborations with R.A. friends, especially W.A. (Buz) Brock, Don Ludwig, Garry Peterson, and Marten Scheffer.

I’m grateful to Bill Feeny for drawing figures 21 and 32.

Many colleagues provided helpful reviews of the book draft. Craig Stow read the whole draft, and provided perceptive advice throughout. Several people wrote useful reviews of one or more chapters. For this valuable service I thank Darren Bade, Elena Bennett, Jeff Cardille, Paul Hanson, Buzz Holling, Pieter Johnson, Genkai Motomi-Kato, Garry Peterson, Greg Sass, Emily Stanley and Jake Vander Zanden. Liz Levitt helped with all aspects of the manuscript.

To Susan, thanks for everything.

Stephen R. Carpenter
Madison, Wisconsin
January 2003
I PREVALENCE AND IMPORTANCE OF REGIME SHIFTS

A Tale of a Lake

More than 15,000 years ago, glaciers advancing from the northeast gouged a basin of more than 200 km$^2$ near what is now Madison, Wisconsin, USA. The ice was more than 300 m thick. A considerable amount of water flowed over the land as the glaciers melted, about 12,000 years ago. This water filled much of the basin, which became the watershed of what is now the Madison Lakes (Fig. 1). Wooly mammoths roamed the shoreline, and giant beavers were active in the extensive shallows and wetlands surrounding the lake. Gradually the water receded until the five lakes of the present day were distinguishable. By about 10,000 years ago, Lake Mendota, the largest of the Madison lakes, was identifiable, although it stood more than 2 m above the present-day lake level and was perhaps two or three times larger in area than in 2002. Extensive wetlands spread northward from the lake. Other plant species migrated into the area as the glaciers receded northward. Eventually forests of maple, red oak and basswood cloaked the southern shores of Lake Mendota, while oak savannas and prairies were found in the uplands of the lake’s watershed.

The first people arrived thousands of years ago. The abundant game, waterfowl and fish of Lake Mendota and its watershed were an important resource for these people. They built large ceremonial mounds in the shapes of animals. These effigy mounds were made of lakeshore sediment. In some cases the sediment was carried hundreds of meters from the lake to build the effigies.
The first written descriptions of Lake Mendota date to about 200 years ago. Travelers record a brilliantly clear lake of crystalline blue waters. The white rocky bottom was visible even in deep water. The southern shores of the lake were fringed with deep woods of large, old trees.

Madison was settled in 1836 and grew rapidly as the seat of Wisconsin’s state government and site of the University of Wisconsin. Sanitation was primitive, and a considerable amount of untreated sewage found its way into the lake. The deep loess soils of Lake Mendota’s watershed proved to be some of the richest farmland in the world. By 1870, most of the watershed was put to the plow, with the exception of woodlots on steep slopes and wetlands yet to be drained. The bottom of the lake turned black as it was covered by soil eroded from the newly-plowed lands of the watershed. When America’s first limnologist, E.A. Birge, arrived in Madison in 1875, Lake Mendota’s waters were turbid and green. By the 1880s, Madison’s newspapers regularly reported choking blooms of algae, foul odors, and fish kills in the lake. It was no longer possible to see the white rocky bottom.

Lake Mendota has always been important to the people of the region, who attempted to modify the lake in various ways to meet their changing needs during the 20th century. Some modifications succeeded, others failed, and some produced unexpected effects. A lock system was built to regulate lake levels. Various chemical treatments were used to control algae or higher aquatic plants, with limited successes. Carp were introduced about 1880, as a game and food fish. Unfortunately, these
bottom-feeding fishes stirred up sediments and further diminished water clarity. During the 1930s, freshwater drum and lake sturgeon were introduced to Lake Mendota. A number of fish species were extirpated from the lake during the first half of the 1900s, including burbot and 11 species of small-bodied fishes, such as fantail darter, banded killifish and emerald shiner. Causes of the extirpations are unclear, but probably include predation by larger fishes, and loss of higher aquatic plants which were uprooted by carp or shaded out by algae blooms. After about 1950, brook silversides increased in population, as did four other species of small-bodied fishes that were introduced to the lake (spotfin shiner, spottail shiner, Iowa darter, and logperch). Fish species turnover rates during the 20th century averaged about 1.8 species added and 2.4 species lost per decade.

Although sanitation systems improved during the first half of the 20th century, the number of people around the lake was growing. Nutrients added to the lake from sanitary sewage fostered heavy blooms of toxic algae. After the Second World War, there was an increase in the manufacturing of nitrate and ammonia fertilizers. Phosphorus was added to this fertilizer, which was distributed on croplands at increasing rates. Some of the remaining wetlands were drained. Ultimately three-quarters of the original wetlands were drained for agriculture or development.

Algae blooms in Lake Mendota were exceptionally thick by the 1950s. A diverse coalition of concerned citizens, including famed limnologist Arthur Hasler, pushed for reductions in nutrient inputs. During more than two decades of political turbulence,
sewage inputs were gradually diverted from Lake Mendota to a sewage treatment plant downstream. Diversion was completed in 1971.

Improvements in the lake were slow. By the early 1980s, it was clear that diversion of sewage was not enough to improve water quality. Blooms of toxic cyanobacteria were common. Eurasian milfoil, a conspicuous and noxious aquatic plant, had invaded during the late 1960s and spread throughout the lake. Eurasian milfoil interfered with boating, swimming and fishing. When it died and decayed, it created serious odor problems. Mounting public concern led to Wisconsin's first nonpoint pollution control program, which was intended to reduce nutrient runoff from farms and towns in the Pheasant Branch subwatershed of Lake Mendota. Unfortunately, this program failed due to lack of participation by farmers and municipalities.

The late 1970s brought a remarkable ecological event to Lake Mendota. Cisco (*Coregonus artedii*), a native midwater planktivore thought to be extinct in the lake, returned in spectacular numbers during 1977 and 1978. The resurgence of this sensitive species was thought to be a sign that the lake was getting better. Cisco were remarkably effective in reducing populations of *Daphnia pulicaria*, the most important grazer among Lake Mendota's zooplankton. Despite rising hopes for restoration of the lake, loss of *Daphnia pulicaria* led to more algae in the water and even poorer water quality.
Starting in 1986, state managers and University of Wisconsin scientists worked together to change the food web of Lake Mendota. Populations of piscivorous walleye and northern pike were increased by massive stocking and restrictive harvest regulations. The goal was to decrease populations of planktivorous fishes through predation. If planktivorous fish populations could be reduced, predation on *Daphnia pulicaria* would decrease, leading to higher populations of *Daphnia pulicaria*, increased grazing of phytoplankton and greater water clarity. In August 1987, an unexpected die-off of cisco accelerated the food web manipulation. By 1988, water clarity in Lake Mendota had improved. *Daphnia pulicaria* and clearer water have persisted to 2002, with considerable variability associated with weather and runoff events.

While it is better than it was in the 1950s, water quality still does not meet the needs of the users of Lake Mendota. Blooms of toxic cyanobacteria are common. Burgeoning suburban development of the watershed, in concert with intensive agriculture, have kept nutrient inputs high, despite the best efforts of lake managers. A new nonpoint pollution program launched in the mid-1990s appears to be underfunded and insufficient. Now the lake’s hydrology appears to be changing in fundamental ways. Development has decreased groundwater recharge and increased runoff, severing the lake’s connections to groundwater while increasing the variability of runoff, nutrient inputs, and water levels. As I write this chapter (2002), Lake Mendota appears to have entered a new era of more variable ecosystem dynamics. Water levels fluctuate more widely. *Daphnia pulicaria* still dominates the zooplankton and provides some control of nuisance algae, but its population could collapse quickly if a
planktivorous fish like cisco again becomes abundant in the lake. The lake is vulnerable to invasions by a number of species, such as zebra mussels and the toxic cyanobacterium *Cylindrospermopsis raceborskii*, which could change water clarity in either direction. After more than a century of ecosystem management and limnological research, the future of Lake Mendota seems more uncertain than ever.

**Changing Baselines of Ecosystem Dynamics**

The history of Lake Mendota (Martin 1965, Mollenhoff 1982, Brock 1985, Kitchell 1992, Lathrop et al. 2002, Carpenter et al. 2004) illustrates a pattern common to the history of all ecosystems. Change is endless. Any choice of baseline is arbitrary. Certain regimes are discernable – a regime of clear water, a regime of algae blooms, a regime of fish species replacement, and perhaps now a regime of variable hydrology. Within each regime, dynamics may be somewhat repeatable and predictable. The transition between regimes, while easy to discern in retrospect, is hard to predict in advance. For example, the hydrologic problems that now preoccupy scientists and managers of Lake Mendota were undreamed of when the first nutrient management plans were devised in the 1950s.

The ever-changing nature of ecosystems is richly illustrated by many long-term ecological studies. Ecologists usually think about two sorts of changes, gradual changes and saltational ones, or regime shifts. Ecosystem change is gradual most of the time. Regime shifts, or big changes that seem to occur during a relatively short
period of time, are infrequent. They are often traced to events which are interpreted as shifts from one type of dynamics to another: nutrient-poor to nutrient-rich; grassland to woodland; before versus after the top predator was lost. Even though regime shifts are infrequent, when they occur they draw the attention of ecologists and often have significant impacts on people who live in an ecosystem or depend on it for their livelihoods. Regime shifts are an exciting topic for ecological research and have important consequences for society, despite being a relatively uncommon type of ecological change.

The history of Lake Mendota illustrates a second pattern seen in many managed ecosystems during the 20th century, a trend of increasingly frequent management interventions to cope with new and unexpected ecosystem changes (Gunderson et al. 1995). Success in diverting sewage was followed by failure of the initial nonpoint pollution control program, a successful food web manipulation with partial improvements in water clarity, a new nonpoint pollution control program which appears to be bogging down in fiscal constraints, and growing awareness that hydrologic change and impending species invasions are the next big challenges. The old problems are unsolved when the new ones arise, and the frequency of new problems is increasing. There is an association, and perhaps a positive feedback, between the frequency of management interventions and the frequency of big changes in the ecosystem. This pattern suggests that management is not altering the fundamental causes of unwanted ecosystem change. In fact, management may be making these changes worse. If we understood the root causes of big changes in ecosystems, perhaps we could devise
approaches to management that increase the capacity of ecosystems to maintain
themselves in desirable regimes.

**Regime Shifts, Thresholds and Resilience**

A regime shift is a rapid modification of ecosystem organization and dynamics, with
prolonged consequences. “Rapid” and “prolonged” are relative terms; the time required
for the change is much shorter than the time that the ecosystem spends in the regimes
before and after the change. In many cases regime shifts involve multiple factors.
Often, they involve changes of internal feedbacks as well as changes in external
drivers. During a regime, a particular set of internal feedbacks tends to maintain the
regime. The change of internal feedbacks is the key difference between a regime shift
and an ecosystem change which is merely driven by external forcing. These internal
feedbacks determine the threshold for change, *i.e.* the point beyond which the
ecosystem will change from one regime to another. The thresholds are closely related
to the concept of resilience for a given regime.

**Resilience and Thresholds**

Ecosystem dynamics are always changing. Thus, the state of an ecosystem in a given
regime can be viewed as a random variable with a particular probability distribution.
Two ecosystem regimes with fluctuations are presented in Fig. 2A. The solid line is the
time series of an ecosystem variable, such as biomass of primary producers or
population of a predator. The dotted lines show the means for each regime. A given regime could exhibit cycles or some more complicated pattern over time. Regimes with a constant mean are shown here for the sake of simplicity.

While ecosystem dynamics always fluctuate, some perturbations are bigger than other ones. The perturbations may be a result of extrinsic forcing (for example, a year with variable climate), internal factors (for example, cyclic population dynamics of a keystone species), or some combination of causes. Three big perturbations occur in the hypothetical time series of Fig. 2A. The first of these does not cause a regime shift; the ecosystem variable returns to the first regime. The second big perturbation is large enough to cause a shift to the second regime. This shift is a surprise, in the sense that previous fluctuations have not caused a consistent change in the mean of the time series (see the following section). The third big perturbation does not cause a shift back to the first regime, even though it rises above the trough of the first big perturbation. Therefore the failure of the system to revert to the first regime may also come as a surprise. Evidently the threshold for regime shift is different for the two regimes. This phenomenon, called hysteresis, is common in ecological regime shifts. In hysteresis, the conditions required to change a system in one direction are different from the conditions required to change the system back to the original state. Many examples of hysteresis in ecosystems will be discussed in this book.

A perturbation must cross a threshold to cause a regime shift. Thresholds for the hypothetical time series are shown as dashed lines in Fig. 2B. Thresholds are formed
by the feedbacks that act to maintain a particular regime. Often they are related to ecosystem variables that change more slowly than the variable of interest. For example, in the case of a lake subject to algae blooms, such as Lake Mendota, the y-axis of Fig. 2B might be water clarity. The fluctuations are caused by variability in nutrient inputs due to weather, while the threshold is determined by the amount of nutrients in the sediment. Sediment nutrient levels change relatively slowly. They control nutrient recycling, which determines the threshold (Chapter II). In the case of a fish population, the y-axis of Fig. 2B could be fish biomass, while the fluctuations are caused by variable water temperatures and the threshold is determined by the number fallen trees in the lake that provide habitat for the fishes. The number of trees in the lake changes more slowly than fish population dynamics. In both the water clarity and fish examples, feedbacks between variables with different turnover times give rise to ecosystem thresholds.

Resilience is the magnitude of perturbation required to cross a threshold (Holling 1973, Carpenter et al. 2001a). It can be measured as the distance from the mean value to the threshold for a given regime. In this case, it has the same units as the ecological variable under study. Alternatively, resilience can be measured as the distance from the mean to the threshold, divided by the standard deviation of the fluctuations. This measure of resilience is dimensionless, because the units of numerator and denominator are the same. This stochastic resilience measure represents the distance to the threshold in units of the average fluctuation.
Another definition of resilience is common in the ecological literature but will not be used in this book. Resilience is sometimes defined as the rate of return to a particular regime after a perturbation (Pimm 1984). This quantity was called stability by earlier theorists (Holling 1973, May 1973). The return-time definition of resilience is used in ecological studies that are concerned with small changes in the neighborhood of one specified regime. This definition is not relevant to discussions of regime shifts, because regime shifts are concerned with perturbations that cross boundaries, not with rate of return to a baseline state. In this book, resilience means the magnitude of disturbance required to cause regime shift.

In ecosystems, the feedbacks that determine the thresholds can also change over time (Fig. 2C). Because the thresholds are related to slowly-changing variables, they are not usually constant. Therefore, resilience changes over time. A perturbation that fails to cause a regime shift at one time may trigger a regime shift at a different time, depending on changes in the threshold. Many important regime shifts in ecosystems have been caused by slow change in a threshold, followed by an unusually large random perturbation which moved the ecosystem past the threshold into a new regime (Scheffer et al. 2001a).

In Lake Mendota, the regime shift from a clear-water state to the turbid state is well defined. Although we have no limnological data from before the regime shift, paleolimnological studies document the changes. The sediments show a sharp transition during the mid-19th century from buff-colored carbonate-rich deposits to black.
sludge (Murray 1956). This change is associated with shifts in phytoplankton and zooplankton fossils (Hurley et al. 1992, Kitchell and Sanford 1992, Kitchell and Carpenter 1993). Modeling studies indicate that phosphorus inputs to Lake Mendota increased more than ten-fold after settlement by Europeans (Soranno et al. 1996). High phosphorus inputs are maintained by elevated levels of phosphorus in watershed soils, caused by excessive applications of fertilizer (Bennett et al. 1999). In addition, recycling from sediments exceeds phosphorus inputs during summer and is sufficient to maintain the eutrophic state of the lake (Soranno et al. 1997). In summary, Lake Mendota has shifted from a regime of low phosphorus inputs, low recycling, low algal biomass, and clear water to a regime of high phosphorus inputs, high recycling, high algal biomass and turbid water. Lake Mendota appears to have crossed a threshold. Recycling could maintain eutrophication for many years, even if external phosphorus inputs were drastically reduced. However, despite excellent data this threshold is difficult to measure and the rate of recovery of the lake from eutrophication is hard to forecast (Chapter III).

In ecosystems, many variables are changing at the same time. The multiplicity of changes may make regimes difficult to discern. In Lake Mendota the regime shift from clear to turbid water is accompanied by changes in the food web that could also be described as regime shifts. For example, the important planktivorous fish cisco tends to be abundant for periods of about 10 years, and absent for longer periods of time in between episodes of abundance (Rudstam et al. 1993). As noted earlier, regimes of cisco abundance or rarity affect algae concentrations and water clarity. The
introductions of carp and drum, the invasion of Eurasian milfoil, and some of the extirpations of fish species, may be irreversible. Thus the history of Lake Mendota can be seen as multiple overlapping and interacting regime changes. Such a pattern probably holds for all ecosystems (Likens 1989, Botkin 1990, Gunderson et al. 1995, Foster 2000).

**Alternate Stable States**

The definition of regime shifts used in this book is related to the ecological concept of alternate stable states (Lewontin 1969, Holling 1973, Ludwig et al. 1997, Carpenter 2001). The theory of alternate stable states is simple and elegant. It is used in a number of the models in this book, and may turn out to explain a number of limnological phenomena. However, alternate states are only one among many potential explanations for regime shifts in ecosystems. I wish to consider phenomena that may have a wider range of explanations and models. In most cases, we are not sure about which mathematical model is appropriate for apparent shifts among regimes. Complex systems have many types of attractors, such as various types of cycles (Guckenheimer and Holmes 1983, Kuznetsov 1995). To be useful, models must be simple, and simple models will describe some, but not all, types of ecosystem behavior. Alternate stable states are a particular type of model appropriate for a certain subset of regime shifts but not others. For this reason, I prefer to use the term “regime shifts” for a general class of big ecosystem changes, regardless of the appropriate mathematical model.
Ecological Surprise

A surprise is something that takes us unaware. After we have been surprised, we can sometimes learn what caused the surprise. Serendipitous learning of this sort is reflected in the scientific dictum that “chance favors only the mind that is prepared” (Louis Pasteur, quoted by Vallery-Radot 1927). For example, scientists have learned a great deal about ecosystem succession and multiple pathways of vegetation dynamics by studying recovery from large, infrequent disturbances such as hurricanes and volcanoes (Turner and Dale 1998).

Surprises are an inevitable consequence of growing scientific understanding in an ever-changing world. Science builds understanding retrospectively, by devising explanations of past events that appear consistent with all available data. It is natural to build future expectations on this retrospective understanding. But change is endless in ecosystems. Some key processes change slowly from a human perspective, and also ecosystems have evolving components which create novelty (Levin 1999). Consequently ecosystems will always surprise us. Ecosystem models that explain the past may not be very good at predicting the future (Carpenter 2002).

Scientific debates that lead to improvement in models to explain the past usually push models to an intermediate level of complexity (Burnham and Anderson 1998, Walters 1986). If the model is too simple, it will miss important factors and feedbacks necessary to explain past events. If the model is too complex, it will be so difficult to
understand that it is not useful for explanation. Also, the model will fail on statistical
grounds, because the available data (always limited in some ways) will not allow
estimation of all the necessary parameters. The balance between the need for
sufficient complexity on the one hand, and the need for transparency and statistical
identifiability on the other, lead to models of intermediate complexity. Yorque et al.
(2002) call this the “rule of hand” – the best ecological models will have about as many
variables as the fingers on one hand.

Ecosystem models are always based on small samples of ecosystem behavior
(Fig. 3). These are vastly more limited than the ecosystem itself, which is more
complex than we can grasp. There will always be slowly changing variables that are
assumed constant, or critical processes that are omitted from the models. Thus the
scope for prediction is always limited in comparison with the true range of potential
ecosystem behavior. The small scope of model behaviors, relative to the wide scope of
possible ecosystem behaviors, sets the stage for surprises when the models are used
to predict the future (Carpenter 2002).

Limnology has encountered a number of surprises in the past century. None of
these discoveries was predicted by the dominant perspectives prior to the discovery,
although surely there were some individual scientists who anticipated that each of these
discoveries might be made. A few limnological surprises are as follows.
Cultural eutrophication is not easily reversible: Eutrophication is a syndrome of toxic algal blooms, anoxia and fish kills caused by over-fertilization of lakes with phosphorus. Because of recycling of phosphorus from sediments, and other ecological interactions, reduction of phosphorus input is often not sufficient to restore lakes which have been eutrophied by phosphorus pollution (Chapter II).

Dilution is not the solution to pollution: For many pollutants in many regions of the world, the dilution capacity of freshwaters has been exhausted, or will soon be exhausted (World Water Council 2002). In the case of biomagnified toxic pollutants such as mercury and halogenated organic compounds, the tendency of the chemicals to concentrate in sediments and accumulate up the food chain leads to severe environmental problems even at very low levels of pollution. While fresh water is a renewable resource, demand is outstripping the renewal rate in many regions of the world (Postel 1997).

Freshwater systems are unusually vulnerable to species loss and invasion: The biota of lakes and streams has an unusually high proportion of endangered species, and unusual susceptibility to species invasion, compared to other ecosystem types (Lodge 2001). Perhaps this vulnerability is related to the insular nature of freshwater ecosystems.

Dam building promotes water-borne disease: Dam construction on tropical rivers has repeatedly caused snail populations to expand and led to outbreaks of schistosomiasis.
Although this should no longer be a surprise, potential outbreaks of disease are often underestimated during the planning of large water projects (Ross et al. 1997).

*Indirect uses massively increase the human footprint on freshwater.* Humanity’s impact on freshwater availability for ecosystems depends far more on indirect uses of water, such as evapotranspiration by forests needed for carbon sequestration and paper products, than on direct extraction of water (Jansson et al. 1999). This discovery may have increasing importance in water resource planning for development (World Water Council 2000).

Of course, all of these were surprises because they were not anticipated by the models that prevailed prior to discovery of the surprise. Once the surprise has been discovered, models can be revised or invented to account for it. The next surprise will be something completely new. Yet, even though future ecological surprises are unknowable, we might learn about planning for the possibility of surprise by studying past experiences with surprise.

In this book, regime shifts are studied as examples of ecological surprises. Regime shifts are a good model system because changes occur relatively rapidly, have large ecological and social consequences, and are difficult to predict in advance. In particular, I am interested in events that are known to be possible, but have poorly understood thresholds. Examples include lake eutrophication, collapse of predator populations, or species invasions. In these cases, economic or political forces may set
management targets that come close to thresholds without crossing them. How practical is it to manage an ecosystem that is close to a threshold? By considering experiences with managing hundreds of lakes near thresholds, we may extract useful lessons for managing unique, singular systems, such as the global climate system or the thermohaline circulation of the oceans (Broecker 1987). This book shows that it is very difficult to manage close to thresholds, even for types of ecosystems in which powerful replicated experiments can be performed. If the cost of crossing a threshold is high, it is best to stay a long way from the threshold.

Parallel Work in Related Fields

Research on abrupt shifts in complex systems is found throughout the sciences, and will not be reviewed in a comprehensive way in this book. Instead I will focus on certain types of abrupt changes in lakes. However, I wish to mention several areas of research that seem closely related to the work that will be described in future chapters. Thinking about research in parallel areas helps draw some boundaries around the subject of this book.

Regime Shifts in Oceanography

In oceanography, a regime shift is defined as a prolonged change in the coupled ocean-atmosphere system (Mantua et al. 1997, Minobe 1997). Such physical regime shifts are often closely associated with changes in ecosystem organization (Anderson and Piatt...
1999, Karl 1999, Naiman et al. 2002, Chavez et al. 2003). The ecological regime change may be the result of physical forcing entirely, and changes in the ecological feedbacks that maintain a particular regime are not necessarily strong. The definition of regime shift used in this book is different, because I focus on the internal feedbacks that maintain regimes. This usage of regime shift corresponds to that of Steele (1996, 1998). Steele notes that shifts in climate and ocean physics often trigger ecological regime shifts, but also describes how ecological feedbacks change in ways that affect the responses of marine communities to fishing. In its focus on ecological as well as physical feedbacks, the usage of regime shifts by Steele aligns with the usage in this book.

Other authors have pointed out that ecological feedbacks can alter physical systems, consistent with the view of regime shifts adopted here. Atmospheric dynamics respond to changes in vegetation, for example, leading to changes in climate (Scheffer et al. 2001a, Higgins et al. 2002). In lakes, food web change affects light penetration, heat budgets, and thermal stratification of the water column (Mazumder et al. 1990, Carpenter and Kitchell 1993). This book considers one example of a feedback from ecology to a biogeochemical process: the effect of production and respiration on phosphorus recycling.

Regime Shifts in Econometrics and Statistics
Economists have developed many models of human behavior that include interdependencies of individual decisions that are not mediated by markets. A generally-accessible example of such a model is the mathematical representation of paradigm change in science by Brock and Durlauf (1999). Testing of such models of human behavior is the subject of a sophisticated literature in econometrics (Brock and Durlauf 2001). While the term “regime shift” is not always used in this literature, the sorts of dynamics exhibited by the models are consistent with the topic of this book.

The term regime shift also arises in statistics, where it pertains to tests for abrupt changes in model structure over time (Gregory and Hansen 1996, Ostermark et al. 1999). The intervention analyses used in ecology are related to this literature (Rasmussen et al. 1993). The methods often focus on shifts in a particular model parameter, or a few parameters, over time. The models are purely statistical; usually there is no attempt to include ecological mechanisms. Clearly these approaches are relevant to the study of ecological regime shifts. However, these methods are not used in this book, because my objectives are different. In particular, I am interested in understanding the multiple causes of regime shifts, using multiple types of data. For these purposes, I have emphasized partly-mechanistic models, Bayesian methods for combining sources of information, and studies of patterns in data that cannot be explained by a particular model.

**Confronting Models with Data in Population Ecology**
This book has some parallels with the merger of long-term population studies and time series analysis that is ongoing in population biology (Dennis et al. 1995, Ives 1995, Kendall et al. 1999, Ives et al. 2003). For example, Kendall et al. (1999) stress a 3-step process of (1) defining, and mathematically analyzing, plausible models (and perhaps discarding some candidates that cannot produce the qualitative behavior of interest); (2) estimating parameters, possibly from experimental data, or possibly by fitting the models to long-term data; (3) simulating an extensive set of time series using the fitted stochastic models, and comparing their statistical properties (such as means, variances, autocovariance function, and so forth) to data. Importantly, Kendall et al. (1999) discuss the continuum from purely statistical, abstract, non-mechanistic models (which they term “phenomenological models”) to purely ecological mechanistic ones. They point out that the most useful models are likely to be semi-mechanistic (Ellner et al. 1998) or process-based. Such models lie somewhere in the middle of the continuum, combining plausible ecological mechanisms with some purely statistical features. Many of the models used in this book are of this type. They attempt to describe plausible ecological processes at observable scales.

Hilborn and Walters (1992) stress the importance of testing statistical methods with artificial data which were simulated by the process of interest. One can then ask whether the statistical method can detect the correct mechanism in the simulated data. This approach is used in several instances in this book.
The study of alternate states seems to be undergoing a renaissance in community ecology. Petraitis and Latham (1999) describe how alternate states of communities can be studied experimentally by manipulating spatial scale and the arrival of species belonging to the different states. This focus on scale is also reflected in landscape studies of alternate states and resilience in plant communities (Peterson et al. 1998, Peterson 2002a,b). This literature is an important reference point for this book, even though the book focuses more on ecosystem processes than community ones, and more on temporal scaling than spatial scaling.

Overview of the Book

This final section provides some personal comments on my purpose in writing the book, the rationale for the book’s focus on lakes, four overarching questions for this Excellence in Ecology book, and an overview of the chapters to come.

Purpose

In my view, the most exciting research in ecology today involves regime shifts. Studies of regime shifts are challenging, for many reasons. Regime shifts occur infrequently. The ecosystems involved are often large. Relevant field experiments are difficult, so when they are possible the results are usually informative. There are multiple explanations for most regime shifts. Sorting among these possibilities requires synthesis of diverse types of information. Such synthesis creates opportunities for
novel models and statistical analyses that sometimes lead to surprising or even useful discoveries. I hope that this book proves to be a useful contribution to the literature on synthesis of long-term whole-ecosystem data using models and statistics.

Regime shifts are an important topic for ecosystem management. When ecosystems are behaving in familiar ways, their dynamics may seem simple and benign. When not much happens in an ecosystem, no one notices. Constructed environments and long supply chains with diffuse feedbacks separate people from nature most of the time. Yet people are deeply and intimately dependent on ecosystems for their health and livelihoods. When big changes occur, human dependencies upon ecosystems are exposed. Social-ecological systems have collapsed in the past, with substantial human costs (Redman 1999). It would be naïve to assume that such collapses will not occur in the future.

Ecosystem management frequently fails. Even the apparent successes tend to be short-lived, and create vulnerabilities that lead to future failures. Many of these failures are traceable to the false assumption that ecosystem dynamics can be predicted and controlled. Study of regime shifts exposes some difficulties of managing ecosystems through rigid controls. Efforts to suppress variability of ecosystems can prevent learning, erode resilience, and increase impacts of later regime shifts (Holling and Meffe 1996, Folke et al. 2002a,b). Many recent global agreements have expressed concern for managing ecosystems sustainably, which means building the resilience of social-ecological systems. In order to build resilience, we must understand it. Regime
shifts focus attention on resilience and transformation. Ultimately, sustainability means learning to adapt to the variability and transformations of ecosystems. This adaptive process calls for flexibility and innovation. I hope that this book contributes to the creative thinking that will be needed to build a more adaptive approach to ecosystem management.

Why Lakes?

Of all the ecosystems in the world, I have chosen to focus this book on lakes. Lakes cover only 1.9% of earth’s surface and contain less that 0.26% of earth’s freshwater (Shiklomanov 1998, Kalff 2002). Why devote a book to such an inconspicuous type of ecosystem? Some of the reasons are pragmatic. Ecosystems are richly complex, and the study of ecology is correspondingly difficult. It takes a long time to learn about your favorite ecosystem. I have spent nearly 30 years studying lakes, and it makes sense to think about regime shifts in the ecosystems I know best. Also, the opportunity to write this book arose from a prize in limnetic ecology. I am grateful for the opportunity to contribute to a series of thoughtful books about lakes by many distinguished colleagues.

Other reasons to choose lakes are conceptual. Lakes have proven to be an extraordinarily rich arena for ecosystem research which has yielded a surprisingly large number of fundamental concepts (Carpenter 1988b). For example, limnology has made key contributions in the trophic-dynamic concept (Lindeman 1942), explanations for species diversity despite the homogenizing force of competitive exclusion (Hutchinson
1961), resource-based competition theory (Tilman 1982), approaches for whole-ecosystem experiments (Likens 1985), trophic cascades (Carpenter et al. 1985) and the theory of ecological stoichiometry (Sterner and Elser 2002).

For my purposes, lakes offer 2 particularly important conceptual advantages. First, although lakes are as spatially heterogeneous as any ecosystem, regime shifts of lakes can be understood even if a great deal of spatial detail is suppressed. This book will employ 3 primary scales for analysis of lake ecosystems.

The focal scale in space is the volume of a single lake. In addition, the book considers 2 other spatial scales. One is the set of lakes found on a landscape, or in a lake district (Fig. 4). The basic concepts of landscape limnology are described by Magnuson and Kratz (2004). Lakes are modular ecosystems, that is they are to some extent replicate ecosystems on the landscape and in some respects separate lakes behave autonomously. Modularity is an important component of resilience in landscapes (Levin 1999) and turns out to be a key factor for the models of ecosystem management studied in this book. The third and final scale is that of the major zones within a lake (Kalff 2002). Four zones within a lake are necessary for the arguments in this book: (1) the nearshore shallow waters of the littoral zone which provide critical habitat for small fishes, (2) the sediments, and in the offshore deep waters (3) the upper mixed layer of water (epilimnion) and (4) the deep layer of water (hypolimnion). The distinction between epilimnion and hypolimnion can only be made in lakes that are deep enough to stratify thermally during the summer. The two layers are separated by a
narrow layer through which water temperature changes rapidly, the thermocline. This zonation within lakes is described in basic textbooks of limnology such as the one by Kalff (2002).

The second conceptual advantage is that regime shifts in lake ecosystems are clearly tied to feedbacks among processes with different turnover times. Different time scales are important in terrestrial regime shifts, but because of the powerful role of spatial heterogeneity it may be difficult to isolate the role of different time scales in terrestrial ecosystems. Because many regime shifts in lakes can be understood using only a few spatial scales, it is possible to focus on the role of time scales. Thus lakes offer an unique opportunity to learn about the role of feedbacks across time scales.

The final reason to focus this book on lakes is the importance of fresh water in human affairs. Fresh water is a key limiting factor for human life. Although lakes are a relatively small fraction of the biosphere, they are a large fraction of the renewable freshwater that is available for human use (Shiklomanov 1998). Most of earth’s freshwater is locked in ice caps, soil or groundwater that is difficult to access, or dissipates in floods that cannot be captured for human use. Lakes, in contrast, offer available freshwater as well as living resources. In addition to providing water for drinking, agriculture, industrial use and recreation, lakes support wildlife, waterfowl and fisheries that are critical resources for people with substantial economic value (Postel and Carpenter 1997).
Questions

As explained in this chapter, the book will consider both the basic science of regime shifts in lakes and the management implications. Four overarching questions will be addressed. Two of the overarching questions focus on issues of basic ecology, as follows.

*How can we build understanding of ecological regime shifts?* Regime shifts are difficult to study, because they are rare events that occur in large ecosystems. What types of research approaches are most likely to expose the processes that lead to regime shifts?

*Can regime shifts be anticipated?* As we build understanding of regime shifts of a particular type, such as eutrophication or predator collapse, what are the prospects for predicting regime shifts in advance? This question is closely related to the issue of measuring thresholds.

Two further overarching questions address issues of applied ecology and ecosystem management.

*How should planning and policy account for the possibility of regime shifts?* If we can learn to measure thresholds, it might be possible to use this information to guide management decisions. How should management systems change, given information about thresholds and regime shifts?
When is management for regime shifts compatible with learning? Environmental management generally involves the stabilization of ecosystem processes, but we must observe variance in key drivers in order to fit models and estimate thresholds. What are the tradeoffs between learning and management? How can learning and management be coordinated?

Chapters to Come

The history of change in Lake Mendota demonstrates several ecological processes. Among these are the effects of nutrient enrichment, the resilience of algae blooms conferred by in-lake nutrient recycling, abrupt shifts in biomass of keystone predators, and cascading effects from top predators to primary producers. These processes are known from many lakes, and aspects of them will be described more fully in this book. Of the many types of big changes in lakes, three in particular – enrichment, collapses of predator populations, and trophic cascades – will be studied further. Chapter II reviews the literature about these processes, and introduces some of the common models.

While it is easy to define regime shifts using time series (Fig. 2), it is not necessarily easy to characterize regime shifts using such data. Chapter III uses a simple simulation model to investigate the data demands for detecting regime shifts using time series. How long must ecosystems be observed, and what are the effects of observation error? In some cases it may be possible to supplement time series data
with other types of data, such as comparative studies of many lakes. Can we increase our insight into regime shifts by combining comparative and time-series data?

Ecosystem experiments have proven to be a powerful method for studying eutrophication and trophic cascades. In ecosystem experiments, a single factor is changed in a massive way, so causes and responses can usually be identified more clearly than in other types of ecosystem studies (Carpenter 1998). Chapter IV analyzes data from experimental lakes to investigate the possibility of regime shifts. Two different models – one linear, the other nonlinear and capable of predicting regime shifts – are fitted, and their predictions and residuals are examined to evaluate the possibility that regime shifts occurred in the experimental lakes.

Ecosystem experiments yield substantial insights, and could therefore be useful in management. Can experiments be used to improve information about thresholds, and thereby design management programs that successfully avoid thresholds? Chapter V considers this problem for a single lake ecosystem subject to eutrophication. It compares trial-and-error, precautionary, and experimental styles of management with respect to their ability to avoid thresholds and provide more accurate estimates of the threshold.

In situations where many similar lakes exist in the same region, it might be possible to experiment on a few lakes and apply the information to all the lakes. How accurately can thresholds be measured using replicated experiments? Is it possible to
gain enough information to manage optimally in such a situation? Or is better knowledge of the threshold best regarded as a guardrail for precautionary management? These questions are addressed in Chapter VI, using a model for a fishery distributed across many lakes of a landscape.

The final chapter summarizes the lessons from the book. Regime shifts are an exciting research frontier of ecology. Analysis of regime shifts requires data at multiple scales, and data collected using several different approaches. Ecosystem experiments are a particularly powerful way to study regime shifts. While ecologists are likely to make significant progress in understanding regime shifts, prediction will remain difficult. It is very difficult to anticipate regime shifts in advance, even when we know what to look for. Regime shifts can be completely novel, therefore unpredictable, and the novel and unpredictable ones are likely to be important. We are likely to be surprised over and over again. When attempting to predict ecosystem dynamics, the possibility of regime shifts should be kept in mind, even if historical data or statistical analyses indicate that regime shifts are unlikely. In other words, it is critical to keep a wide variety of models in play, despite statistical criteria which tend to narrow the set of models under consideration. If we can use scientific information to broaden our thinking about the future, to consider a wide diversity of potential futures, and to imagine new and innovative approaches for ecosystem management, we are more likely to build resilient interactions among people and ecosystems.
Summary

Long-term observations of ecosystems show that eternal change is the norm. Big changes are infrequent, but when they occur they have important consequences for ecosystems, and often for people.

A regime shift is a rapid modification of ecosystem organization and dynamics, with prolonged consequences. In some cases, a threshold separates different regimes, and regime shift occurs when the ecosystem crosses a threshold. Thresholds often depend on slowly-changing variables. Consequently thresholds are not constant. They change over time. Resilience is a measure of the distance between the typical value of an ecological variable within a regime, and the threshold for that regime. Thus, resilience is a feature of a particular regime, with respect to changes in a particular variable. Because ecosystem states and thresholds change over time, resilience changes over time.

The book focuses on three important types of regime shifts which have been well-documented in lakes: enrichment, collapses of predator populations, and trophic cascades that transmit variability of top predator populations throughout a food web.

The book addresses 4 main questions. (1) How can we build understanding of ecological regime shifts? (2) Can regime shifts be anticipated? (3) How should
planning and policy account for the possibility of regime shifts? (4) When is management for regime shifts compatible with learning?
Figures

Figure 1. Watersheds of the Madison Lakes, Wisconsin, U.S.A. from Lathrop 1992.

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Figure 2. Hypothetical time series for an ecosystem variable (solid line), showing fluctuations around two regimes (dotted lines). (A) Effects of three unusually large perturbations. The second big perturbation is associated with a regime shift. Note that the peak of the third big perturbation is higher than the trough of the first big perturbation. (B) Thresholds (dashed lines) and resilience (length of arrows) for each regime. (C) Thresholds (dashed lines) change over time, due to the dynamics of variables that change more slowly than the ecosystem dynamics shown by the solid line. (Original)
Figure 3. We observe a small subset of possible ecosystem behaviors. From a large set of possible ecosystem models, a small set is found to be consistent with the observed behavior. Together, the observations and the models set the scope for future predictions of ecosystem behavior. This scope is much smaller than the set of potential ecosystem behaviors. (Original)
Figure 4. Spatial scales used in this book. (A) Many lakes on a landscape. (B) Focal scale: a single lake ecosystem showing boundaries: the shoreline, the sediment-water interface, and the surface of the lake. (C) Zones within a lake – littoral zone, sediments, epilimnion, hypolimnion. (Original)
II  REGIME SHIFTS IN LAKES

Introduction

Lakes are an exceptionally promising type of ecosystem for research on regime shifts. All lakes are similar in fundamental ways, so it is possible to observe regime shifts over and over, compare case studies to test ideas about underlying causes, or even create regime shifts experimentally. The possibilities for comparison and experimentation make it easier to understand the processes that lead to regime shifts, or those that maintain the resilience of particular regimes. This modular feature of lakes is a great advantage for studying regime shifts. Similar opportunities are offered by only a few other types of ecosystems, such as small watersheds and oceanic islands.

This book will focus on three types of regime shifts that have been observed repeatedly in lakes: eutrophication, large changes in fish populations or communities, and coordinated shifts in food web structure (trophic cascades). These types of regime shifts emphasize pelagic phenomena, and in this respect connect to previous Excellence in Ecology volumes by Cushing (1996) and Reynolds (1997). My selection of examples is necessarily arbitrary and incomplete. For example, benthos of lakes, and benthic-pelagic interactions, will likely prove to be a rich arena for regime shifts (Paine 1994) building upon the excellent examples provided by Scheffer (1997) and Jeppesen et al. (1998). Ecological stoichiometry provides several cases of multiple
stable states (Sterner and Elser 2002) and growth of that field seems likely to yield more examples in the future.

The primary goal of this chapter is to review observations of regime shifts in whole lake ecosystems. The study of regime shifts starts with patterns observed in the dynamics of whole lakes, as well as experimental and comparative studies aimed at understanding the processes that produce the patterns. In addition, the chapter introduces some models addressed in later chapters. The models are introduced graphically and conceptually. Mathematical versions of the models are presented in later chapters.

This chapter contains three main sections, corresponding to the three types of regime shifts that will be addressed by the book. Each section describes a phenomenon in a general way, discusses processes for the regime shifts, reviews examples, and presents a model graphically.

Phosphorus and Eutrophication

Definition and causes

Lake phosphorus cycles exhibit two different regimes, as seen in the history of Lake Mendota (Chapter I). Each regime tends to be stabilized by a distinct set of feedbacks. In one regime, phosphorus inputs, phytoplankton biomass, and phosphorus
regeneration from sediments are relatively low. The water is relatively clear. Such lakes are called oligotrophic. Lakes in the contrasting regime are called eutrophic (Smith 1998). Eutrophic lakes have high phosphorus inputs, high phytoplankton biomass, turbid water, and high return rates of phosphorus from sediments. Eutrophication is a syndrome caused by over-enrichment with phosphorus (Smith 1998). Eutrophication leads to excessive plant production, blooms of toxic cyanobacteria (also called blue-green algae), increased frequency of anoxic events, and fish kills. Species of macrophytes, invertebrates, and fishes may be extirpated. Eutrophication also occurs in flowing waters and oceans (Smith 1998). The oceanic phosphorus cycle appears to have alternate states caused by biogeochemical mechanisms similar to those described below for deep, thermally stratified lakes (Van Cappellen and Ingall 1994).

Excess inputs of phosphorus are the most common cause of lake eutrophication (Schindler 1977). In this respect, lakes differ from many other ecosystems in which nitrogen is the most limiting mineral nutrient. Nitrogen can also be an important nutrient in lakes, but, unlike phosphorus, nitrogen can be fixed from the atmosphere. Thus if phosphorus is abundant, nitrogen rarely remains a limiting factor for long. There are exceptions, such as lakes in which nitrogen fixation or assimilation is limited by trace metals (Vitousek and Howarth 1991). Increasingly, ecosystems are enriched by nitrogen applied as fertilizers or derived from atmospheric pollutants (Vitousek et al. 1997a, Howarth et al. 2002). Increased availability of fixed nitrogen could promote phosphorus limitation in some circumstances.
Excess phosphorus inputs to lakes usually come from sewage, industrial discharges, and agriculture. In North America and Western Europe, nutrient runoff from agricultural and urban lands has become the most important phosphorus source as municipal and industrial sources have been curtailed (Carpenter et al. 1998a). Agriculture is particularly important as a source of phosphorus pollution. Excessive fertilizer use causes phosphorus to accumulate in soils (Bennett et al. 2001). During runoff events, phosphorus-enriched soils are washed into lakes, where some of the phosphorus dissolves and is taken up by algae. In some cases, soil particles become saturated with phosphorus and dissolved phosphate ions are carried to lakes in surface- or groundwater (Carpenter et al. 1998a, Bennett et al. 2001). Although phosphorus may be rapidly stripped from the water by sinking particles, it can also be recycled rapidly from sediments or by animals.

Once it enters the lake, phosphorus stimulates algal growth, including blooms of toxic cyanobacteria. Decay of algae consumes oxygen, and can thereby create anoxic episodes which suffocate living organisms. Rooted aquatic plants may be lost due to shading by algae suspended in the water. Fish species may be lost due to anoxic events. Loss of rooted plants also reduces food supply and habitat for fishes (Olson et al. 1998). The vegetation provides substrate for invertebrates which are consumed by fishes. Vegetation also shelters fishes from predators.
Recycling of phosphorus is critical for maintaining plant production of lakes. In many lakes, primary producers obtain more of their phosphorus from recycling than from inputs. Phosphorus is recycled by several mechanisms in lakes. Recycling by animals (excretion or egestion) can supply a significant fraction of the phosphorus demand for phytoplankton growth during summer. Both herbivorous zooplankton and fishes are potentially important sources of phosphorus to phytoplankton (Carpenter et al. 1992, Schindler and Eby 1997, Elser et al. 1988). Recycling from sediments stabilizes eutrophication, especially in deep lakes (see below). In shallow water, wind-mixed waters can resuspend sediments and thereby move phosphorus from sediments into the water. However, P may also be removed as it sorbs to sediment particles which re-settle to the bottom of the lake.

**Shallow lakes: a special case**

Shallow lakes are not thermally stratified. They can mix to the bottom at any time of the year. Also, shallow lakes may support beds of rooted aquatic plants (macrophytes) that cover most of the area of the lake. Consequently, in shallow lakes, a unique set of processes affects the transition between clear and turbid water (Scheffer 1997, Jeppesen et al. 1998). These processes are different from those described in the previous section, which can occur in any lake. Because of these unique mechanisms of transition between regimes, shallow lakes can be considered as a special case.
Transitions between clear-water and turbid states of shallow or non-stratified lakes are the most thoroughly studied regime shifts in limnology (Scheffer 1997, Jeppesen et al. 1998). In the turbid state, phytoplankton are the dominant primary producers. Rooted aquatic plants are sparse, because of shading by phytoplankton. Also, bottom-feeding fishes uproot the macrophytes, and some waterfowl eat macrophytes. Phosphorus release from sediments may be rapid, because the sediments are exposed to waves and are easily resuspended. In the clear-water state, macrophytes, periphyton, and their epiphytes are the dominant primary producers and phytoplankton concentrations are low. Recycling of phosphorus to phytoplankton is slow, because the rooted plants stabilize sediments and monopolize nutrients during the growing season. In addition, phytoplankton may be grazed heavily by zooplankton. The macrophytes provide the zooplankton with a refuge from fish predation. Regime shifts between turbid and clear water in shallow lakes have been the subject of a rich diversity of limnological studies and an influential body of models and theory.

Deep lakes: biogeochemical basis of alternate states

In most temperate lakes, temperature gradients create two layers during the growing season: an upper, well-mixed layer of warm water called the epilimnion, which floats on a lower, colder more isolated layer or hypolimnion (Fig. 4). Mixing of water, energy, and solutes between the epilimnion and hypolimnion is limited. One of the largest material fluxes between the layers is the downward flux of sedimenting particles.
The layering of deep lakes creates a process for alternate states that is completely different from the one seen in shallow lakes. During summer stratification, waters of the hypolimnion cannot be reoxygenated by contact with the atmosphere. Thus the oxygen content of the hypolimnion depends on the initial endowment of oxygen at the onset of stratification, and the rate that oxygen is depleted by organic matter decay. If the hypolimnetic water remains oxygenated, phosphorus is bound by insoluble complexes with iron and is therefore not available for recycling to primary producers (Mortimer 1941, 1942). If the hypolimnetic water becomes anoxic, however, the iron is chemically reduced to a soluble form and phosphate is released into the water (Mortimer 1941, 1942). Turbulence at the upper edge of the hypolimnion, or mixing episodes that entrain hypolimnetic water into surface waters, make this dissolved phosphate available to phytoplankton in the epilimnion (Soranno et al. 1997).

This process requires a sufficient iron to bind phosphate when the hypolimnion is oxygenated. In many lakes, there is sufficient iron available. Under some conditions, for example lakes that have received high inputs of sulfate from atmospheric pollution, low availability of iron may limit this mechanism (Caraco et al. 1991). In such lakes, phosphate recycling may be high even while the hypolimnion is oxygenated, because there is insufficient iron to bind the phosphate in sediments.

In most lakes, therefore, oxygen concentration of the hypolimnion acts as a regulator of phosphorus release from sediments. The oxygen concentration of the hypolimnion is affected by the production of phytoplankton in the upper waters of the
lake. As the phytoplankton die, they sink, and the greater the production of phytoplankton the greater the flux of sinking organic matter to the hypolimnion. If the flux of decomposing material into the hypolimnion is low, then the rate of oxygen consumption in the hypolimnion is also low and the hypolimnion may remain oxygenated through the summer. If the hypolimnion remains oxygenated, recycling of phosphorus is low. In contrast, if the flux of decomposing material is sufficiently large, then oxygen depletion will be fast enough to deoxygenate the hypolimnion during the summer. Once the hypolimnion is anoxic, phosphate recycling can be rapid.

This process creates the possibility of alternate states. When phosphorus inputs are low, phytoplankton production is low, the hypolimnion remains oxygenated, phosphorus recycling is low, and the clear-water state of the lake is reinforced. When phosphorus inputs are high, the feedbacks shift. Phytoplankton production is high, the hypolimnion is deoxygenated, phosphorus recycling is high, and the turbid-water state of the lake is reinforced. As phosphorus inputs increase from low to high rates, there is an increase in the frequency of anoxia, from essentially zero at low rates of phosphorus input to nearly 100% of the summer at high rates of phosphorus input (Reckhow 1979). Thus the recycling flux rises from near zero to a maximal rate over the gradient of phosphorus inputs (Carpenter et al. 1999b).

To predict the annual recycling of phosphorus in a lake, one needs to know the daily rate of phosphorus release from sediments (Nürnberg 1984) and the duration of anoxia during summer stratification. Rates of P release from sediments have been
reviewed by Nürnberg (1984) and are reasonably predictable (see Chapter III). What controls the duration of anoxia in stratified lakes? The rate of hypolimnetic oxygen depletion increases with phosphorus and algal biomass of the lake, and with hypolimnetic water temperature, and decreases with thickness of the hypolimnion (Cornett and Rigler 1980, Charlton 1980). According to these empirical models, the number of days per summer that a hypolimnion is anoxic should increase with phosphorus concentration and temperature, and decrease with thickness of the hypolimnion (Carpenter et al. 1999b). Other analyses reach similar conclusions (Nürnberg 1995). The probability of anoxia is a sigmoid function of phosphorus concentration (Reckhow 1979). This probability is directly related to the amount of time that sediments are overlain by anoxic water. Thus, the mass of phosphorus recycled each year in a lake should be a sigmoid function of the phosphorus concentration, increase directly with hypolimnetic water temperature, and decrease with thickness of the hypolimnion. This relationship is developed quantitatively later in this Excellence in Ecology book.

Recovery from eutrophication: delays and irreversibility

We now have decades of experience with managing eutrophication in hundreds of lakes around the world (Cooke et al. 1993). Case studies of projects to reverse eutrophication reveal a mix of successes and failures. These studies illuminate the processes that stabilize eutrophication, as well as strategies for breaking down the resilience of the eutrophic condition and restoring clear water.
In some cases, eutrophication has been halted or reversed by reducing phosphorus inputs (Edmondson 1991). Success is most common in lakes that are deep, with cold, oxygen-rich deep waters. In other cases, successfully-managed lakes have rapid flushing rates. Whether deep or rapidly flushed, these lakes have great capacity to dilute phosphorus and maintain oxygenated conditions. Also, some lakes which recovered rapidly from eutrophication were eutrophic for only a few years. Such lakes may not accumulate a large mass of phosphorus in the sediments.

Lake Washington (Washington, USA) is a well-known example of eutrophication that responded directly and rapidly to decreased inputs of phosphorus (Edmondson 1991). Eutrophication symptoms were recognized during the 1950s, and the problem was traced to sewage discharges. Diversion of effluent began in 1963, and by 1967 almost all (99%) of the sewage effluent had been diverted from the lake. Notable improvements in water quality occurred within a year of completing the diversion. By 1971, Secchi disk transparency exceeded that of the 1950s. By 1975, Secchi transparency had increased from 1.0 m to 4.0 m, total phosphorus decreased from 70 to 16 mg m\(^{-3}\), and chlorophyll decreased from 35 to 4 mg m\(^{-3}\) (Edmondson 1979).

In many cases, however, the degree of eutrophication has not responded to reductions of phosphorus input (Sas 1989, UN National Research Council 1992). Instead, rapid, efficient recycling of phosphorus within the lake has maintained eutrophication despite reductions of inputs. In some of these cases, eutrophication has
eventually been reversed by removing phosphorus from the lake (e.g. by dredging) or immobilizing phosphorus (e.g. by adding aluminum sulfate to sediments). In other cases, eutrophication could not be reversed.

Shagawa Lake (Minnesota, USA) is an example of a lake that did not respond to reductions of phosphorus input. Like Lake Washington, Shagawa Lake suffered eutrophication due to sewage inputs. Poor water quality prompted limited sewage treatment in 1911, but water quality continued to deteriorate. Treatment improvements in 1952 failed to improve water quality. Finally, in 1973, a new treatment plant was built which decreased phosphorus inputs by more than 80% (Larsen et al. 1979, 1981). Phosphorus loading models predicted that annual average total phosphorus concentration should drop from 51 to 12 mg m\(^{-3}\), but the concentration dropped only to 29 mg m\(^{-3}\). More importantly, summer concentrations of total phosphorus and chlorophyll remained unchanged, and severe blooms of blue-green algae continued to occur. The cause was efficient release of phosphorus from lake sediments during periods of anoxia (Larsen et al. 1981). Over a long period of time, it is possible that sediment phosphorus will be depleted and summer algal blooms will decline, as occurred in other lakes with delayed responses to reduced phosphorus input (Welch et al. 1986). However, by 1991 --18 years or 24 complete hydrologic flushings after the reduction of phosphorus input-- the lake had not yet recovered (US National Research Council 1992).
Model for eutrophication

The literature reviewed so far suggests that lake water quality can be likened to an old-fashioned pan balance (Fig. 5). The two pans of the balance represent clear water or turbid water with high concentrations of algae. The ecosystem (black ball in Fig. 5) can lie in either pan. Disturbances to the ecosystem, such as runoff events triggered by big rainstorms, may affect the ecosystem but only a rather large disturbance will move the ecosystem between pans. If excess phosphorus is added to a clear lake, it will slowly build up in the sediments. Eventually, phosphorus accumulates to the point where the lake is highly vulnerable to any disturbance that increases phosphorus in the water. After such a disturbance, algae concentrations will increase and the decay of these algae will trigger phosphorus recycling that grows more algae. The resulting feedback tips the lake into a self-sustaining eutrophic state with turbid water due to growth of algae. Once the lake is eutrophic, it is necessary to reduce phosphorus inputs and perhaps also disturb the lake by some management intervention to tip the balance back toward clear water.

One can also construct a graphical model that captures the features of eutrophication represented by the physical model of the pan balance. The graphical model is consistent with, but simpler than, other models for lake eutrophication (Reckhow and Chapra 1983; Chapra and Reckhow 1983; Scavia and Robertson 1979). The model presented here is designed to capture the essential patterns and processes of eutrophication with minimal complexity. This chapter will explain the model using
graphs. Mathematical versions of the model will be presented in Chapters III and V. More detailed expositions of this model are presented by Carpenter et al. (1999b), Dent et al. (2002), and Ludwig et al. (2003).

The model incorporates mass balance for phosphorus (P) in a watershed-lake system (Fig. 6). Land use and land cover affect P content of watershed soils. In many watersheds, agricultural fertilizers and manures are the most important source of P to the soil (Bennett et al. 2001). Phosphorus input, or loading, from the watershed to the lake is carried in runoff driven by precipitation events and snowmelt (Soranno et al. 1996). For a given watershed, the parameters that link soil P concentration, climate, and loading depend on local topography and hydrologic flow paths (Soranno et al. 1996).

The amount of P in the water is affected by the watershed or release from lake sediments, and loss due to hydraulic outflow or sedimentation (Fig. 6). P in sediment may be released to the overlying water, or may be buried in layers of sediment that are too deep to be recycled. P concentrations in lake water are highly correlated with phytoplankton biomass (Schindler et al. 1978, Canfield and Bachmann 1981), and for the purposes of this model lake water P and algal biomass are assumed to be interchangeable. The model does not calculate phytoplankton biomass, but instead assumes that it is directly related to P mass or concentration in the water.
Stability of the model depends on processing of $P$ by outflow and sedimentation (straight line), and inputs plus recycling (curved lines) (Fig. 7). Equilibria occur where source curves (inputs plus recycling) intersect loss lines (outflow plus sedimentation). At stable equilibria, or attractors, the $P$ declines to the equilibrium after a small increase in $P$, because losses exceed sources. Also, the system increases to the equilibrium after a small decrease in $P$, because sources then exceed losses. At unstable equilibria, or repellers, the $P$ increases to a higher equilibrium point after a small increase in $P$, or decreases to a lower equilibrium point after a small decrease in $P$.

Two hypothetical lakes are shown in Fig. 7A. Lake 2 has higher average input from the soil (intercepts of curved lines) and a higher maximum rate of recycling (height of curved lines). Both lakes have identical outflow and sedimentation. Both lakes have three equilibria. The middle one is an unstable repeller, and the upper and lower ones are locally stable attractors. The steady state at low $P$ concentration is the clear-water state, and the steady-state at high $P$ concentration is the turbid or eutrophic state.

Resilience of a state is measured by the distance (in $P$ units) from a stable steady-state to the unstable steady state. The resilience of the clear-water state is greater for Lake 1 than for Lake 2. Resilience is related to the size of a stochastic shock that the system can absorb without changing states. A shock which moves the system from one stable state past the unstable steady state will shift the system to the other stable state. For example, a $P$ input event that is larger than the resilience of the...
clear-water state will push the lake past the unstable steady state, and recycling will then drive the P level to the eutrophic steady state.

Soil P affects the probability distribution of input events to the lake (Fig. 7B). These input events are driven by variable and unpredictable storms and snowmelt, so we model them as a random variable. The logarithm of input event magnitude can often be described by a Student-t or gamma distribution (Carpenter et al. 1999b, Reed-Anderson and Carpenter 2002). The logarithm of annual inputs often fits a Student-t distribution (Reckhow 1979, Lathrop et al. 1998, Carpenter et al. 1999b). The watershed of Lake 2 has high-P soils causing a higher mean input rate and broader distribution of stochastic shocks. Because the resilience of the clear-water state is low for Lake 2, there is a relatively high probability of a shock large enough to move Lake 2 out of the clear-water state. In contrast, the watershed of Lake 1 has low-P soils causing a relatively low mean input rate. The probability distribution has low variance, so large input events are rare. Because the resilience of the clear-water state for Lake 1 is rather large, there is a low probability that a random input event will shift Lake 1 to the turbid state.

In summary, the eutrophication model describes clear- and turbid-water states of lakes, as well as the probability distribution of P inputs. The shift from clear to turbid water usually involves shrinkage of the resilience of the clear-water state (e.g. Lake 1 to Lake 2 in Fig. 7A) as well as a large P input event. The shrinkage of resilience can be caused by P buildup in sediments, increased P inputs, or both. The reverse shift – from
turbid to clear water – requires expansion of the resilience of the clear-water state (e.g. Lake 2 to Lake 1 in Fig. 7A). The increase in resilience involves a reduction in P inputs. Reducing the mean P input rate usually decreases the variance as well, so large P input events are less frequent. In addition, some lakes have been manipulated to increase the P outflow rate or decrease P recycling (Cooke et al. 1993), both of which increase resilience of the clear-water state.

According to the model, measures of susceptibility to eutrophication are related to resilience. For example, the P recycling rate or the P input distribution are better measures of eutrophication than the P concentration in the water (Beisner et al. 2003a). P recycling rate is related to resilience, and the P input distribution is related to the probability of shocks that exceed resilience. P concentration in the water, in contrast, is a rapidly-changing variable that may not accurately indicate resilience.

This model can represent the behavior of most case studies of lake eutrophication, and all current methods for managing P in lakes (Carpenter et al. 1999b). For example, P management methods may decrease inputs, reduce recycling by dredging sediments or treating them with aluminum sulfate to precipitate the P, reduce recycling by oxygenating the hypolimnion, or remove P by increasing the hydraulic flushing rate (Cooke et al. 1993). All of these can be represented by manipulating or fitting the appropriate parameters of the model. Riparian buffers (shoreline vegetation that can intercept nutrient inputs before they reach the lake) affect the mean and variance of P inputs (Weller et al. 1998, Reed-Anderson and Carpenter.
Effects of these parameters can be represented in the model by modifying the distribution of P inputs. Biomanipulation, a management method based on trophic cascades (see below), can also be represented in the model, by increasing the rate of removal of P from the lake water or decreasing the rate of recycling. In terms of the P cycle, biomanipulation works by decreasing P availability to phytoplankton. This occurs by increasing flux to sediments, sequestering P in bodies of animals, or decreasing flux of P from littoral sediments to pelagic water (Carpenter et al. 1992, Schindler et al. 1996, Jeppesen et al. 1998). The role of trophic cascades in the P cycle of lakes leads us to consider regime shifts connected to fish population dynamics and food webs.

Depensatory Dynamics in Aquatic Food Webs

Pelagic Regime Shifts

Since Ricker’s (1963) famous paper about “big effects from small causes”, many of the case studies of big changes in pelagic ecosystems have come from studies of fish and fishing. Long-term observations of fish stocks sometimes exhibit sharp changes that suggest regime shifts (Steele 1996, 1998). Even in the absence of direct scientific observation, changes in fish resources may be recorded, perhaps in harvest records or archeological information. A change in a fish stock may have notable human consequences without large ecological impacts (Steele 1998). However, many changes due to fishing have significantly altered marine food webs (Steele 1996, Jackson et al. 2001). Similar changes have occurred in freshwater ecosystems subject
to sport fishing (Post et al. 2002), although interactions of fishing with other factors such as species invasion and eutrophication must also be considered when interpreting long-term changes in lake food webs (Kitchell and Carpenter 1993).

Sizeable changes in fish stocks have occurred ever since there were fisheries (Jackson et al. 2001). Even in prehistoric times large marine vertebrates such as whales, manatees, seals, crocodiles, jewfish, swordfish, sharks, and rays have been extirpated from coastal ecosystems, or driven to functionally trivial populations, by overfishing (Jackson et al. 2001). Over time scales of decades to centuries, these changes in top predators cascaded through near-shore marine communities. Often, unfished species became abundant, and later were fished by humans. In some cases, population expansions of unfished species led to overcrowding and epidemic disease. Climatic changes at decadal to millennial scales may trigger or enhance regime shifts in marine food webs. Furthermore, coastal eutrophication may interact with food web shifts to intensify ecosystem changes (Jackson et al. 2001, Scheffer et al. 2001a). For example, eutrophication may create turbid or anoxic water which causes die-offs of benthic organisms or fish kills. Massive and ongoing changes in marine ecosystems over thousands of years suggest that it is impossible to define a baseline equilibrial state (Steele 1998).

Changes driven by fishing can cascade through an entire food web (see later section on trophic cascades). In the Black Sea, industrial fishing began about 1970 and depleted stocks of top predators such as dolphins, bluefish, bonito and mackerel
(Daskalov 2002). Stocks of planktivorous fishes (such as anchovy and sprat) increased during the 1970s, and became a target for the fishery in the 1980s. At the same time, the Black Sea was subject to species invasions, as well as eutrophication by anthropogenic nutrient input (Zaitsev and Mamaev 1997). Jellyfish biomass, especially that of the exotics *Mnemiopsis* and *Beroe*, increased as fish biomass declined. Biomass of herbivorous zooplankton decreased, in part due to predation by jellyfish. Phytoplankton biomass increased, and dense blooms became frequent. The decline in water transparency caused a decrease in benthic algae, especially the formerly dominant red alga *Phyllophora*. Oxygen content declined, leading to hypoxia and loss of benthic animals and plants. The post-1970 regime differed from the pre-1970 regime at every level of the trophic system. After 1970, large pelagic predators were rare, pelagic planktivorous fishes and blooms of jellyfish were common, herbivorous zooplankton biomass was low, phytoplankton biomass and bloom frequency increased, and benthic communities were degraded. These shifts had at least three drivers: overfishing, species invasions, and eutrophication.

In lakes, species invasions are an increasingly important factor in ecosystem change (Kolar and Lodge 2000). Ecosystem impacts of invasion may interact with those of fishing, eutrophication, and climate change. In the Laurentian Great Lakes, extensive food web changes were attributed to fishing and invasion (Christie 1974). Following invasion of the sea lamprey, stocks of lake trout and burbot declined. This decline was followed by increases in the prey species of these top predators, such as deepwater cisco and the exotics rainbow smelt and alewife. Lake herring declined,
apparently due to predation of juveniles by rainbow smelt. Thus the major changes in Great Lakes ecosystems prior to the 1950s were driven by overfishing and lamprey invasion. Resilience of Great Lakes ecosystems to subsequent invasions was reduced by loss of the top predators, lake trout and burbot.

Species invasions also cause significant changes in smaller lakes (Kolar and Lodge 2000, Lodge 2001). Sparkling Lake (Wisconsin, USA) was invaded by rainbow smelt (Osmerus mordax) in 1982 (Hrabik et al. 1998). The native planktivore, cisco (Coregonus artedii), did not recruit successfully after the smelt introduction, and was functionally eliminated from the food web by 1987. Predation by smelt on young-of-the-year cisco was an important factor in the cisco decline. Piscivorous fishes in Sparkling Lake also declined in abundance after the smelt introduction (unpublished data, North Temperate Lakes LTER site, http://lter.limnology.wisc.edu). A second invader, rusty crayfish (Orconectes rusticus) which entered the lake in 1985, may have contributed to piscivore declines by eliminating macrophyte beds that provided crucial habitat for juvenile fishes (Lodge et al. 2000, Wilson 2002). However, smelt invasions have caused stocks of walleye (Stizostedion vitreum) to collapse in other lakes (Gilbert 2002). Although walleye feed on smelt, walleye fail to recruit within four to six years of smelt invasion in some lakes, and eventually the population of walleye disappears from the lake. These patterns suggest that the predation impact of smelt on juvenile walleye is less than that of adult walleye on smelt. Case histories of smelt invasion suggest an important role for size-specific predation in regime shifts of lake fish communities.
Rusty crayfish also appear to play an important role, perhaps by degrading fish habitat and also by consuming fish eggs (Lodge et al. 2000).

**Processes and Models**

Regime shifts in lake or marine ecosystems appear to have multiple causes, including fishing, eutrophication, habitat alteration, and climate change. In fisheries stock analysis, much attention has focused on the possibility that overfishing may increase the vulnerability of a population to other factors, or directly trigger the collapse of a population to a low level. Many simple population models, such as the logistic equation, predict higher per-capita population growth rates at low population densities. This phenomenon is called compensation. But what if per-capita population growth rates decrease when the population falls below some critical level? This phenomenon is called depensation or the Allee effect (Asmussen 1979, Hilborn and Walters 1992, Frank and Brickman 2000). Predictions of food web dynamics can be quite different for compensatory and depensatory models.

Detection of depensation in time series of single populations has proven difficult (Myers et al. 1995). Statistical problems are numerous, including short time series, lack of data at extremely low and high population densities, and large observation errors (Hilborn and Walters 1992). Liermann and Hilborn (1997) devised a test statistic for depensation and calculated its probability distribution for 115 fish stocks, each of which was studied for 15 or more years. Results spanned a wide range, from strong
depensation to hypercompensation (i.e. extreme increase in per-capita population growth at low densities). However, most of the mass of the probability distributions lay on the depensatory side, indicating significant probability of depensation. Thus it is inappropriate to assume that depensation will not occur. These authors conclude that fish stock analyses should use models that include the possibility of both depensation and hypercompensation. At low population sizes, both collapse and explosive growth are possible.

What might cause depensation in fish populations? Suggested mechanisms include reduced reproductive success, inbreeding, impaired aggregation, inefficiency of food location, or predator-prey interactions with multiple domains of attraction (Asmussen 1979, Emlen 1984, Hilborn and Walters 1992). De Roos and Persson (2002) presented a general model of size-structured predation for two species that prey on each other in a size-dependent manner. Larger individuals of each species eat smaller individuals of the other species. If larger individuals of one species become rare for some reason, that species’ recruitment can be eliminated by predation from the other species, leading to a depensatory collapse.

Walters and Kitchell (2001) proposed a mechanism that follows from the strong size-selectivity of aquatic trophic interactions. According to this “cultivation-depensation” process, high adult densities of a particular fish species suppress predation on juveniles of that species, by either consuming predators directly or by changing predator behavior (Fig. 8). Low adult densities, however, fail to suppress
predators, leading to heavy predation on juveniles and negative population growth. They argued that certain regime shifts in marine food webs, such as the collapse of North Atlantic cod stocks, could be explained by cultivation-depensation. Other examples are discussed by Post et al. (2002) and de Roos and Persson (2002).

Figures 8 and 9 present results from a simple model for a food-web process of depensation that is similar to that of Walters and Kitchell (Carpenter 2001, 2002). For certain combinations of parameters, the fish population has two steady states (Fig.9A). The upper steady state is stable. The lower steady state is not stable. If the population is perturbed below the lower steady state, it will collapse to zero. Three different stability outcomes are possible, depending on the parameters that control rate of harvest of the adult fishes, and the rate of predation on juvenile fishes (Fig. 9B). If the harvest rate of adults is sufficiently high, there is no stable steady state and the fish population collapses to zero. If both harvest rate of adults and predation on juveniles are sufficiently small, there is no unstable steady state, there is no depensation, and the population has only a positive stable steady state. There is an intermediate range of parameters that yields two steady states, one stable and the other unstable, as depicted in Fig. 9B.

Habitat changes, such as loss of rooted aquatic plants, may affect rates of interspecific predation in ways that cause depensation (Carpenter and Gunderson 2001, Carpenter 2002). An example of how habitat change might affect the predation rate on juvenile fishes is shown in Fig. 8B. If the mortality curve for juveniles responds to
habitat as in Fig. 8B, the system can gradually change from one stability domain to another, with potentially catastrophic consequences for the fish population (Carpenter 2002). If this mechanism is embedded in a more complex food web model, changes that resemble regime shifts can occur (Walters and Kitchell 2001). If such changes occur in a model for stock assessment and management decisions that affect harvest rates, very complex dynamics can occur (Carpenter and Gunderson 2001). A relatively simple version of this model will be studied in more detail in Chapter VI. In the remainder of this chapter, we will turn to the implications of shifts in fish populations for lower trophic levels in lakes.

**Trophic Cascades**

Annual phosphorus input is a reliable predictor of mean pelagic chlorophyll during the growing season. Chlorophyll is a commonly-used measure of phytoplankton biomass, and a correlate of primary production rate. Concentration of phosphorus during spring mixing is frequently used as an index of P input rate. Fig. 10 shows one of many published relationships between this indicator of P input and chlorophyll. Generally, such plots show significant correlations, yet a substantial proportion of the variance in chlorophyll cannot be explained by nutrients. Trophic cascades can explain a significant amount of the missing variance (Carpenter and Kitchell 1993, Carpenter et al. 2001b).
Trophic cascades connect fishes to phosphorus and phytoplankton, as follows. In the absence of piscivorous fishes, planktivorous fishes may be abundant. These fishes feed size-selectively on zooplankton, eliminating the larger-bodied herbivores. In contrast, lakes with abundant piscivorous fishes have few planktivorous fishes. Large-bodied zooplankton can thrive, and are often the dominant pelagic herbivores when planktivorous fishes are rare (but see Elser et al. 1998). The effect of fishes on total zooplankton biomass may be small, but the shift in body size has significant implications for chlorophyll (Fig. 10B). Larger-bodied herbivores tend to have higher per-capita grazing rates, broader diets, and lower recycling rates of P than smaller-bodied ones (Gliwicz 1980, Peters and Downing 1984, Elser et al. 1988). Often, the largest herbivores in lake plankton are species of *Daphnia*, which have rapid numerical response, broad diets, and high physiological requirements for P (Gliwicz 1980, Elser et al. 1996). The latter characteristic of *Daphnia* causes their excreta to be P-deficient, and thereby promotes P-limitation which contributes to the inverse relationship between *Daphnia* biomass and chlorophyll (Sterner et al. 1992, Sterner and Elser 2002). In general, a trophic cascade is a series of reciprocal predator-prey linkages that alters biomass or productivity across more than one link of a food web (Pace et al. 1999). The term was introduced to ecology by Paine (1980) and applied to lakes by Carpenter et al. (1985).

**Comparisons and Experiments**
The discovery and demonstration of trophic cascades and their effects on phytoplankton biomass took a long time. Hrbacek et al. (1961) showed that differences in algal biomass among fishponds could be attributed to the effects of fishes on the food web. The impact of size-selective predation by fishes was described by Brooks and Dodson (1965), who noted the implications for phytoplankton. Shapiro et al. (1975) introduced the idea of biomanipulation – a management tool to mitigate nuisance algae blooms by reconfiguring the food chain. In whole-lake experiments, the fish components of two nearby lakes were exchanged. Piscivorous bass were moved from Peter Lake to Tuesday Lake (Michigan, USA), and an equal biomass of planktivorous minnows was moved from Tuesday Lake to Peter Lake. This reciprocal transplant of fish biomass caused large and opposite shifts in the zooplankton community, chlorophyll, and primary production (Carpenter et al. 1987, Carpenter and Kitchell 1993). These experiments manipulated only the food web, and employed an unmanipulated reference lake to screen for possible confounding effects of weather or other factors. They showed that food web manipulations alone could create approximately three-fold changes in primary producer biomass and production, as well as changes in nutrient cycling and plankton community structure.

At the whole-lake scale, manipulation strength is a critical factor in the experimental outcome. Manipulation strengths of several successful whole-lake experiments were shown to be within the range of typical variation of predator populations (Carpenter et al. 1991). A number of whole-lake manipulations have produced significant food web effects from manipulations within the range of natural
variability of predator populations (Carpenter et al. 1987, McQueen et al. 1989, Hansson et al. 1998, Carpenter et al. 2001b). Manipulations must be strong enough to create a detectable change in noisy data (Carpenter 1988a,b, 1989; Hansson et al. 1998). Weak manipulations are uninformative, because lack of effect could be explained by either absence of a cascade, or a high level of noise in the data. Thus, manipulations that approximate the range of natural range of fish community composition are most likely to provide informative yet reasonably realistic results.

Biomanipulations are changes in food web structure to improve water clarity through trophic cascades (Shapiro et al. 1975, Carpenter et al. 1985). Some biomanipulations were combined with other types of interventions to improve water quality, so interpretation of food web effects is not straightforward, but nevertheless some conclusions may be drawn. In a broad review of case studies, Hansson et al. (1998) concluded that biomanipulation was most useful as a trigger for secondary processes that reduced recycling of nutrients. In other words, biomanipulation may cause a regime shift, but the shift may be unstable unless other ecosystem changes such as reduced P loading are implemented as well. Hansson et al. (1998) stressed the importance of rapid, massive manipulation of fishes, which may be difficult in large lakes. Kitchell (1992) and Lathrop et al. (2002) described the even greater challenges of biomanipulating an eutrophic lake when an additional trophic level – human anglers – is prominent. Despite the complications of coping with an additional human trophic level, they found significant effects of food web change on the ecosystem of Lake Mendota.
The interaction of trophic cascades with nutrient enrichment has been debated. Some authors have argued that cascade effects are weak in highly enriched lakes (Benndorf 1995, Reynolds 1994). Comparative studies suggest that both nutrients and trophic cascades have powerful impacts (Fig. 10), but impacts of changing these factors cannot be inferred from comparative studies alone (Carpenter et al. 1991). Simple stoichiometric models of grazer-algae-nutrient systems in chemostats demonstrate multiple stable states consistent with trophic cascades (Sterner and Elser 2002). While nutrients and food web structure can be manipulated independently in enclosures or small containers, it may be difficult to extrapolate results of container experiments to whole ecosystems in the field (Carpenter 1996, Schindler 1998, Pace 2000). The keystone grazer *Daphnia* has a high physiological requirement for phosphorus, suggesting that at least moderate levels of this nutrient are required for trophic cascades to occur (Elser et al. 1998, Sterner and Elser 2002). Collectively, these patterns suggest that effects of nutrients and cascades on lake productivity may interact in complex ways.

The combined effects of nutrient enrichment and trophic cascades on primary producers were studied by manipulating nutrients and food web structure independently in whole-lake experiments. These experiments showed that trophic cascades had strong impacts on primary producers across a range of nutrient loading rates (Carpenter et al. 2001b). Both inorganic N and P were added in a ratio designed to maintain P limitation of phytoplankton. At the highest P input rates, inorganic P accumulated in the
surface waters of the lakes, indicating that some other factor (perhaps light transmission) was limiting algal growth. Thus, the experiments spanned a range of situations from unenriched P-limited conditions, through enriched but still P-limited conditions, to conditions under which P was saturating.

Algal biomasses of a planktivore-dominated lake and a piscivore-dominated lake were compared over the full range of nutrient input rates (Fig. 11). Results for an unenriched reference lake are also presented. Each data point is the mean for an annual growing season. Over the range of experimental nutrient loadings, the planktivore-dominated lake had about three times more chlorophyll than the piscivore-dominated lake (Fig. 11). Primary production was about six-fold greater in the planktivore-dominated lake than in the piscivore dominated lake (Carpenter et al. 2001b). Similar differences were seen if the phytoplankton responses were calculated per unit volume instead of per unit area (Carpenter et al. 2001b).

This brief summary has stressed the whole-lake studies of trophic cascades that used comparative and experimental approaches. Most of the discussion about ecosystem impact of cascades has centered on studies using one of these two approaches. However, long-term data sets also offer important insights, and are especially pertinent to considerations of models for trophic cascades. Models of cascades should be consistent with data from long-term studies.

Long-Term Observations of Trophic Cascades
Long-term observations of fisheries are more abundant in the literature than long-term data for entire pelagic food webs. Here I define “long-term” as spanning more than one lifespan of the longest-lived species in the food web. In pelagic ecosystems, this longest-lived species is usually the top carnivore, a fish species. A few selected examples are reviewed here. I have chosen lakes which were not manipulated experimentally during the time period of study. One lake (Lake Mendota) was subjected to a management intervention near the end of the period of study, but this intervention only intensified the natural event described below (Lathrop et al. 2002).

Winterkill eliminated the top carnivore, largemouth bass (*Micropterus salmoides*), from Wintergreen Lake (Michigan, USA) in 1978 (Mittelbach et al. 1995). Following extirpation of the bass, planktivorous fish abundance increased and large-bodied herbivorous zooplankton declined. The ecosystem remained in this state until largemouth bass were reintroduced in 1986. As the bass population grew, planktivore abundance decreased about 100-fold, zooplankton biomass increased about ten-fold, large-bodied *Daphnia* returned to a prominent role in the food web, and water clarity increased substantially. These limnological changes are similar to those in European lakes from which fishes were removed (Scheffer 1997, Jeppesen et al. 1998). In Wintergreen Lake, however, the changes were caused by a cascade driven by a top carnivore. In another case study of partial winterkill, part of the populations of both piscivores and planktivores were killed (McQueen et al. 1989). The partial kill of both trophic levels led to responses that were weaker and more short-lived than those
observed by Mittelbach et al. (1995), but there were qualitatively similar responses in the zooplankton (McQueen et al. 1989).

The impacts of a dominant planktivore, cisco (*Coregonus artedii*), were documented for Lake Mendota using time series data (Rudstam et al. 1993). In years of low cisco biomass, zooplankton were dominated by large-bodied *Daphnia pulicaria*. Biomass of this zooplankton increased earlier in the spring, and lasted longer into the summer, than biomass of the zooplankton that dominated when cisco were abundant. Low levels of cisco were associated with a longer period of clear water during spring and early summer, apparently a consequence of heavy grazing by *D. pulicaria*. In years of high cisco abundance, spring and summer zooplankton were dominated by the smaller-bodied *D. galeata mendotae*. During spring, *D. galeata* biomass develops at warmer water temperatures than those required by *D. pulicaria*. Consequently, when cisco are abundant, grazer biomass develops later in the spring. *D. galeata* can escape control by cisco, overgraze their resources, and cause a clear water phase. However, *D. galeata* are more susceptible to starvation than *D. pulicaria*, and their biomass consequently drops to low levels after the clear water phase. This causes grazing pressure on phytoplankton to be low through most of the summer when cisco are abundant.

Some long-term analyses of trophic cascades demonstrate cyclic changes in lake food webs. Yellow perch (*Perca flavescens*) in Crystal Lake (Wisconsin, USA) oscillated, with individual age classes dominating the population for periods of about
five years (Sanderson et al. 1999). These authors considered diverse possible causes for the cycles, and concluded that inter-cohort predation was a key factor. When juvenile perch are present in the lake, they cannibalize young-of-the-year (YOY) perch and prevent recruitment. This process tends to form a single age class of juvenile perch. By the time the cohort reaches reproductive maturity, its reproductive impact on YOY outweighs any impact of predation. Adult perch may be less abundant than juveniles, and benthic prey may partially replace YOY prey in adult perch diets. Thus, in the absence of juvenile perch, a new year class of perch can survive.

The yellow perch cycles have complex effects on plankton (Sanderson 1998). In years when juvenile perch were absent, Daphnia dominated the zooplankton and chlorophyll concentrations were lower than in years when juvenile perch were abundant. Similar cycles, and similar ecosystem consequences, are known from population dynamics of other fishes such as vendace (Hamrin and Persson 1986) and pink salmon (Shiomoto et al. 1997).

Similar processes of age-class interaction were noted in a study of Paul Lake (Michigan, USA), an undisturbed reference lake for whole-lake experiments on trophic cascades (Post et al. 1997). Cannibalism by largemouth bass suppressed recruitment. As bass densities declined due to gradual mortality of adults, a window of opportunity opened for recruitment in which YOY bass were abundant enough to survive predation by the adult bass remaining in the lake. Zooplankton are a major diet item for YOY
bass in their first summer. The large cohort of zooplanktivorous YOY bass had predictable effects on lower trophic levels (Post et al. 1997).

Annually-resolved pigment concentrations from laminated lake sediments exhibited cycles with periods of three to five years (Carpenter and Leavitt 1991). The cycles were pronounced for fossil pigments that tend to be deposited in zooplankton feces, but no cycles were evident for pigments that have multiple sources or mainly terrestrial sources. The pattern in the sediment record is consistent with a trophic cascade triggered by periodic year classes lasting 3 to 5 years. This period corresponds with the lifespans of the top carnivores of this lake’s food web (Carpenter and Leavitt 1991).

These case studies suggest that cyclic trophic cascades in lakes tend to be synchronized with the lifespans of the top predators. Pink salmon and vendace have lifespans of two years, corresponding with the food web cycles (Hamrin and Persson 1986, Shiomoto et al. 1997). The mix of species in the lake studied by paleolimnological methods had lifespans of three to five years, corresponding with the cycles found in the sediment archive (Carpenter and Leavitt 1991). Yellow perch lifespans are variable and may be somewhat longer than the five-year cycle described by Sanderson et al. (1999). Other studies are not long enough to assess the existence of cycles, but do demonstrate food web regimes that correspond to the duration of a predator cohort.
Models

Numerous mathematical models have been used for describing trophic cascades. Two of these will be discussed here. The first uses simple equations, most linear, to represent the year-to-year dynamics of food webs over a long period of time (Carpenter 1988a, 1989). The second uses more complicated nonlinear mathematics, and is intended to represent dynamics of plankton within an ice-free season (Scheffer et al. 1997, Scheffer et al. 2000b, 2001b).

A pelagic food chain model with four dynamic variables (Fig. 12) includes piscivorous fishes, planktivorous fishes, zooplankton, and phytoplankton (Carpenter 1988a, 1989). There are two external factors: littoral zone resources (e.g. benthic invertebrates) consumed by fishes, and stochastic physical-chemical drivers (e.g. climate effects on nutrient loading or fish recruitment). Food resources from the littoral zone can sustain fish stocks through fluctuations in pelagic resource levels, and thereby maintain fish predation with significant implications for pelagic communities (Schindler and Scheuerell 2002). Exogenous stochastic forcing is assumed to be independent for fish recruitment and phytoplankton. The planktivore component implicitly includes two species, an obligately planktivorous fish and juvenile piscivores. Recruitment of juvenile piscivores is proportional to adult piscivore biomass, but cannibalism of juvenile piscivores also increases with adult piscivore biomass. When adult piscivores are abundant, they can consume all of their progeny. When adult piscivores are at low abundance, some juveniles can escape cannibalism and survive to adulthood. In
consequence, a large year class of piscivores can occur only when the abundance of the previous year class has declined by natural mortality or fishing. This phenomenon creates cycles in the time series of phytoplankton and zooplankton, driven by the life cycle of the top carnivore in the food chain. The period of the cycle is about the same length as the top carnivore life history (Carpenter 1988a). In the year that the large year class is created, high planktivory leads to high phytoplankton biomass. Once the juvenile planktivores recruit to the piscivore compartment, planktivory is low, so zooplankton biomass increases and phytoplankton biomass decreases. This situation will persist until the adult piscivore biomass has declined to the point where a new year class can form. Model results include cycles with periods about equal to the life history length of the top carnivore.

A model of trophic cascades with just two dynamic variables, phytoplankton and zooplankton, exhibits multiple attractors (Scheffer 1997, Scheffer et al. 1997, 2000b, 2001b). Some of these attractors are stable points and others are stable cycles. The model’s attractors are shown in a three-dimensional space of algal biomass, planktivorous fish biomass and zooplankton biomass (Fig. 13). These results were obtained for a rather high level of phosphorus input. They show complex effects of changes in planktivorous fish biomass. At low levels of planktivorous fish biomass, phytoplankton and zooplankton oscillate in a predator-prey cycle (grey surface at low fish biomass). When planktivorous fish biomass grows to the level of point O₁, the predator-prey cycle intersects a repeller (denoted by the dashed line). The ecosystem moves to a stable attractor on the solid line between points F₀ and F₁. Along this line,
phytoplankton biomass is high and zooplankton biomass is low. At relatively high fish biomass, a strong decrease in phytoplankton biomass could shift the system to a stable attractor between points $F_2$ and $H$. Such a perturbation of phytoplankton biomass could occur after a heavy rain that flushed the lake, for example. If fish biomass remains between $F_2$ and $H$ (solid line), the system is stable, with low phytoplankton and zooplankton biomass. If the fish biomass is between points $H$ and $O_2$, there is a stable predator-prey oscillation of phytoplankton and zooplankton (grey surface). If fish biomass is at point $O_2$, the predator-prey oscillation again intersects a repeller on the dashed line, and the system moves to a stable point on the solid line between $F_0$ and $F_1$, with high phytoplankton biomass and low zooplankton biomass.

The crash to a low zooplankton – high algae state when oscillations cross the dashed line in the region between $O_1$ and $O_2$ has important implications for seasonal plankton changes in eutrophic lakes. This model behavior resembles a pattern that occurs in many eutrophic lakes, in which a springtime phase of heavy grazing and clear water gives way to a summer phase of low grazing and high biomass of algae. The ecological explanation for the zooplankton crash involves two different mechanisms. First, the zooplankton numbers decline, due largely to depletion of their food, and second, the zooplankton population is trapped at this low level by fish predation. Eventually, population oscillations make the zooplankton more vulnerable to overexploitation by planktivorous fish. In this sense, the oscillations have the same effect as external perturbations: they increase the probability that the system will shift from one state to another. As lakes become progressively enriched, temporal variability
of plankton tends to increase, and to some extent this increase may be related to predator-prey cycles. This model suggests how such cycles, in the presence of planktivorous fish, can lead to collapse of zooplankton populations and to blooms of phytoplankton unrestrained by grazing.

Summary

Even though regime shifts are not common, many have been observed in limnology. This chapter describes three types of regime shifts known from many examples in lakes: eutrophication, depensatory shifts in fish populations or fish community composition, and the shift in food webs between dominance by piscivores and large-bodied grazers versus planktivores and small-bodied grazers (trophic cascades). Anthropogenic drivers such as phosphorus input, habitat alteration, species invasions and overfishing are often factors in regime shifts.

Scientific analysis to understand regime shifts is difficult, because the events are not common and causes are usually multiple. Lakes may be an especially good study system for regime shifts, because there are many lakes in the world, and therefore many opportunities to observe regime shifts. Long-term study is necessary, but not sufficient, to understand regime shifts. Cross-system comparisons and whole-ecosystem experiments also play important roles. All three of these approaches – long-term study, comparative study, and whole-ecosystem experiments – have been important in understanding regime shifts in lakes. Because multiple scientific
approaches are necessary to understand regime shifts, synthesis of many studies is required. In this respect, the study of regime shifts is similar to many other problems in ecology (Pickett 1999, Ford and Ishii 2001).

The examples described in this chapter show that it is difficult to generalize about regime shifts. The cases do have a few features in common. All seem to involve more than one spatial or temporal scale (watershed and lake in eutrophication; slow-turnover adult fish and rapid-turnover juvenile fish in fishery regimes; two to four trophic levels with a wide range in turnover rate for trophic cascades). All seem to involve the interaction of slowly-changing and rapidly-changing variables. In eutrophication, the turnover time of phosphorus ranges from about a century in watershed soil, to decades in sediment, to much less than a year in lake water. Both fishery regimes and trophic cascades involve food web components with very different turnover times. All of the cases involve stochastic factors: climate-driven runoff pulses and mixing events in eutrophication, and stochastic recruitment events in fishery regimes and trophic cascades.

Simple mathematical models have been useful for understanding regime shifts in lakes and many other types of ecosystems (Carpenter 2001, Scheffer et al. 2001a). Selected examples of useful models are summarized in this chapter. A comprehensive review would require a much longer document. Nevertheless, the few examples presented here illustrate some of the diversity of models that have been used to describe lake regime shifts. Using the models we can understand which dynamics can
be explained by our abstractions, and which cannot. We can also attempt to explain
observations in a post-hoc way. But to what extent are such models useful for
anticipating the future? Can regime shifts be predicted? The next four chapters will
address the use of models for description, prediction and management of regime shifts.
Figures

Figure 5. Pan balance model of eutrophication. The left and right sides of the pan balance represent clear and turbid water, respectively. The ball represents the ecosystem, which can lie in either pan. External shocks such as weather events will not shift the ball between pans, if the shocks are sufficiently small. As phosphorus is added to the lake and builds up in the sediments, the lake becomes more vulnerable to shocks that may shift it to the turbid, eutrophic side of the balance. (Original)
Figure 6. Major pools and flows of phosphorus in lake eutrophication (boxes and black arrows). Gray arrows show effects of major drivers, climate and land use and cover.

(Original)
Figure 7. (A) Phosphorus flux rates versus water phosphorus concentration. Straight line shows outflow plus sedimentation fluxes. Curved lines show P loading from watershed (intercept) plus recycling from sediments for 2 hypothetical lakes. Steady-states occur where inputs balance outputs, i.e. where the lines intersect. At the stable steady states, a slight increase in P causes outputs to exceed inputs, and a slight decrease in P causes inputs to exceed outputs. In either case, the lake returns to the stable steady state. At the unstable steady states, a slight change in P tips the P level toward either the higher or lower steady state. (B) Probability distributions of phosphorus input (or loading) for the 2 hypothetical lakes. In each curve, likelihood of a given input rate is plotted against input rate. The area under both curves is the same (one). (Original)
Figure 8. Size-selective predation leading to depensation in the model of Carpenter (2001). A. Food web relating adults and juveniles of a piscivorous fish population to a second species (forage fish) which is consumed by adult piscivores but consumes juvenile piscivores. B. Mortality rates of juvenile piscivores versus population density of adult piscivores. Juvenile mortality has two components, intraspecific (density-dependent) mortality and predation by the forage fish. Dashed line shows predation mortality of juvenile piscivores caused by an increase in the amount of habitat usable for refuge from predation by the juvenile piscivore. (Original)
Figure 9. Alternate stable states in the model presented in Figure 5 (Carpenter 2001).

A. Rates of fecundity and mortality versus adult density. B. Bifurcation diagram showing rates of predation on juveniles and harvest of adults that lead to the three possible stability conditions – stable persistence; alternate states (critical depensation); or collapse of the fish population. Reproduced by permission of © Blackwell Publishing Company.
Figure 10. Chlorophyll concentration (photic zone mean, mg m\(^{-3}\)) versus (A) total phosphorus concentration (mg m\(^{-3}\)) at spring overturn and (B) mean length of all zooplankton (mm) for Wisconsin and Ontario lakes studied by Carpenter et al. (1991). Each point is the mean of two to six years of data for one lake. Total phosphorus and zooplankton mean length are not significantly correlated (r = 0.14). Reproduced by permission of © Springer-Verlag, New York.
Figure 11. Chlorophyll density (integrated vertically through the photic zone, mg m$^{-2}$) versus phosphorus input rate (mg m$^{-2}$ d$^{-1}$) for an unmanipulated reference lake (X) and lakes with food webs dominated by planktivores (open circles) and piscivores (closed circles) (Carpenter et al. 2001b). Error bars show ± standard error. Reproduced by permission of © Ecological Society of America.
Figure 12. Flow chart of the trophic cascade model of Carpenter (1988a). Open boxes denote state variables, shaded boxes denote external influences. Black straight arrows indicate consumption, gray straight arrows indicate recruitment processes, dashed line indicates non-predatory mortality of piscivores (including fishing and natural mortality), and curved black arrows indicate stochastic effects. (Original)
Figure 13. Stability manifolds for the trophic cascade model of Scheffer et al. (2000b). Reprinted from Scheffer (1999). Reproduced by permission of © Resilience Alliance.
III ANALYSIS OF REGIME SHIFTS: ROLES OF STOCHASTICITY AND EXPERIMENTS

Introduction

Statistical methods are powerful for analyzing frequent events, but weak for analyzing uncommon events such as regime shifts. The rarity of regime shifts poses deep problems for both understanding and prediction. For any given regime shift, many different models are equally appropriate. There are straightforward statistical methods for sorting among rival models, but these depend on observing many regime shifts. Without extensive data, it may be difficult to decide which model is most appropriate. Consequently, there is considerable doubt about our ability to predict future regime shifts on the basis of any particular model.

This chapter addresses some statistical problems posed by regime shifts, using both models and data. A minimal model, which represents no particular ecosystem but is transparent and easy to understand, is used to explore the detectability of alternate equilibria using time series data. Then, an example using field data is introduced. This example illustrates the use of time-series data and comparative data together to estimate parameters for regime shifts.

There are three parts to the chapter. First, a graphical model of regime shifts is used to explain some of the implications of experimental manipulations and sources of
error that affect the detection of regime shifts. Second, a minimal model is presented for drawing inferences about regime shifts from time series of ecosystems. The model is designed to address issues such as duration of time series, ability to perform informative experiments, the effects of stochastic shocks, and the effects of observation error. This minimal model suggests that it is difficult to characterize regime shifts. In particular, there is considerable risk that analysis of a typical data set will conclude incorrectly that the system has only a single stable point. The third part of the chapter presents an analysis of a well-studied ecosystem, Lake Mendota, to demonstrate the challenges of assessing regime shifts for a real data set. The case for regime shifts in the eutrophication of Lake Mendota depends not only on time series, but also on detailed process measurements, a comparative multi-lake data set, and historical information.

**Detecting Regime Shifts: A Graphical Model**

Ball-and-cup diagrams (Fig. 14) have often been used to describe alternate stable equilibria of ecosystems. Alternate stable states are one of many potential causes of regime shifts, as described in Chapter I. In the ball-and-cup diagram, the topography represents slowly changing variables (Fig. 14A). The basins are stable points, and the hilltops are thresholds. For simplicity, only two basins and one threshold will be shown here, but any number of basins and thresholds are possible. The ball represents the level of an ecosystem variable that changes more rapidly than the topography changes. In the case of lake eutrophication, the amount of phosphorus in the lake sediments is
represented by the topography, and the water quality (turbidity, phosphorus in the water, or biomass of phytoplankton) is represented by the ball (Chapter II). Shifts among equilibria can be caused by external shocks that move the ball from one basin to another (Fig. 14B). The shock can be a stochastic event, such as a violent storm, or a deliberate manipulation caused by an experiment or a management action. Changes in slow variables can alter the topography and shift the ecosystem to another basin (Fig. 14C). For example, slow buildup of phosphorus in sediments of a lake shrinks the basin of the clear-water regime and moves the lake toward the turbid-water regime (Chapter II).

Now consider an observer who wishes to determine whether the ball-and-cup system has one basin or two. The observer measures the rapidly-changing variable, which corresponds to the horizontal position of the ball (Fig. 15). This measurement and its uncertainty are represented by the horizontal error bars in Fig. 15. Observation error (the standard deviation of measurements of the position of the center of the ellipsoid) increases the length of the error bar. If the center of the ellipsoid is in only one basin throughout the period of observation, and the observation error is smaller than the basin, the observer may conclude that the system lies in a rather narrow range (Fig. 15A). On the other hand, if the center of the ellipsoid stays in one basin but the observation error is larger than the basin, the observer may conclude that the system occupies a broad range (Fig. 15B). Although the observations may extend to two or more basins, the observer would be uncertain about the number of basins.
Experiments make it easier to perceive the number of basins, especially if the observation error is smaller than the basin (Fig. 15C). The experimental perturbations lead to observations that are clustered, and the clusters correspond roughly to the basins. If natural events that can cause regime shifts are rare, experiments may be a rapid and effective way to determine the number of regimes.

Process variance is the term used for the variance shocks that affect the location of the ball. If the center of the ball lies in one basin but the ball is subject to small random disturbances, the observer will perceive some variability in the location of the ball. However, this variability is not created by measurement errors but instead it is caused by the small random changes in the location of the ellipsoid. These variations are called process variance, or process errors, to distinguish them from observation errors (Hilborn and Mangel 1997). The distinction between process error and observation error will be made in a mathematical model in the next section.

Process variance can make it easier to perceive the number of basins (Fig. 15D). Essentially, the random shocks act as “natural experiments”. The observer perceives clusters of observations, which correspond roughly to the locations of the basins. For the observer to perceive the two basins, the frequency of shifts between basins must be not too fast and not too slow. If the shifts between basins are very frequent, then it does not matter that there are two basins. The system acts as if the topography was flat. If the shifts between basins are very infrequent, then we have the same situation as in Fig. 15A and the observer perceives only one basin.
In summary, this pictorial model captures the essential ideas of regime shifts in a simple way. The topography represents the slowly-changing ecosystem variables and the position of the ball represents the rapidly-changing ones. The basins are the different regimes and the hilltops are the thresholds. We imagine a human observer who wishes to know how many regimes exist in the system using measurements of the position of the ball. Observation errors, or noisy measurements, blur the location of the ball. Random disturbances, or process errors, change the location of the ball and therefore cause variability in measurements. Experiments can significantly improve the observer’s ability to perceive the number of basins. Process errors can also improve perceptions, if disturbances that shift the system between basins are not too frequent and not too rare. In the next section, we will explore these ideas further using a mathematical model.

Prospects for Identifying Alternate Equilibria: A Simulation

In ecological modeling, the term “minimal model” is used for models that are just complex enough to represent the abstraction under study, but no more complex than necessary (Scheffer and Beets 1994). In this section, a minimal model of a system with alternate equilibria is used to study the effects of observation error and experimentation on the ability to detect alternate equilibria. Like the pictorial model of the previous section, this minimal model includes a simple one-dimensional representation of an ecosystem with alternate equilibria subject to process error, and an observer who
samples the system with varying degrees of observation error. The observer can also perturb the system experimentally. The minimal model is mathematical, so it can represent the processes of gathering and analyzing data for a variable system subject to alternate equilibria. Using this model, I examined the probability of correctly detecting alternate equilibria with and without experimental manipulation, with different magnitudes of observation error.

**A Minimal Model for Studying Alternate Equilibria in Time Series**

This section presents a mathematical model that will be used to explore possibilities for detecting alternate equilibria in time series. The model is as simple as possible, yet contains key features of ecosystem data relevant to the analysis of regime shifts. Thus the model includes a dynamic system with alternate equilibria and process variance, a sampling process with observation error, and an analytical procedure for inferring the number of equilibria. This model is an arbitrary, deliberately simplified representation of a time-varying system with two stable equilibria. The simplicity of the model is useful for demonstrating some general points about detecting alternate equilibria, even though the model does not represent any particular ecosystem. The model first appeared in Carpenter (2001).

The model assumes that time series, of varying length, can be observed for the ecosystem of interest. The ecosystem is subject to stochastic shocks, similar to the effects of climatic variability on ecosystems. The observations are subject to
measurement error, as occurs in actual ecological data. In some simulations it is possible to perform experiments intended to switch the ecosystem between regimes. The simulated ecosystem has two different equilibria and an unstable threshold, but this fact is unknown to the investigator. Instead, the investigator must evaluate statistical evidence for the regime shifts. Artificial data sets are generated using the ecosystem model. Then, these artificial data are analyzed for evidence of alternate equilibria (Fig. 16). This model uses a large number of simulations to measure the probability of detecting alternate equilibria when in fact alternate equilibria are the true situation.

The simple ecosystem model is as follows. Time series data sets of an ecosystem variate $X$ were calculated by repeated simulations with the difference equation

$$X_{t+1} = X_t - \beta_0 (X_t - \beta_1)(X_t^2 - \beta_2) + v_t$$

Equilibria are calculated by setting $X_{t+1} = X_t = X^*$ and solving for the equilibria $X^*$. If $\beta_2 < 0$, there is one stable real equilibrium ($X^* = \beta_1$) and two complex equilibria. The complex equilibria are of no ecological significance, and can be ignored. If $\beta_2 > 0$, there
are three real equilibria ($\beta_1, \beta_2^{0.5}$, and $-(\beta_2)^{0.5}$). The largest and smallest of these three are attractors, and the intermediate one is a repeller.

Measurements of ecological time series data are of course imperfect, so it is desirable to include observation errors in the simulation exercise. Observations of $X$, symbolized by $Y$, were simulated as

$$Y_t = X_t + w_t$$  \hspace{1cm} (2)

where $w_t$ is observation error (normally distributed with mean zero and standard deviation $s_w$).

For simulations shown in this chapter, parameter values were $\beta_0 = 0.1$, $\beta_1 = 1$, $\beta_2 = 0.16$, $s_w = 0.1$ or $0.0001$, and $s_v = 0.05$. Thus there were two stable points at $X = -0.4$ and $X = 1$, and one unstable point at $X = 0.4$.

Two types of data sets were generated, non-experimental data and experimental data. To generate non-experimental data, simulations of a given number of time steps were calculated from a randomly-chosen starting point on the interval between the two stable points. Duration of the time series was varied to represent different durations of long-term ecological studies. For experimental data, an infinite number of experimental designs can be imagined, and one approach was chosen arbitrarily for this book. Trials with several different experimental designs indicated qualitatively similar results in all
cases. To generate experimental data, simulations were re-started at a new random starting point every 12 time steps. This represents manipulations that regularly re-set the initial conditions of the ecosystem. For both non-experimental and experimental scenarios, 1000 independent data sets were simulated.

The probability of identifying alternate equilibria was calculated for each simulated time series. Time series were fit to a cubic polynomial

\[ Y_{t+1} = b_0 + (1 + b_1) Y_t + b_2 Y_t^2 + b_3 Y_t^3 + \varepsilon_t \] (3)

The \( b_i \) are the regression parameters. \( \varepsilon \) is the model error, which is assumed to be normally distributed with mean zero and variance to be estimated from the data. Note that Equation 1 expands into a cubic polynomial like Equation 3. The estimated parameters \( b_i \) are functions of the unknown parameters \( \beta_i \), and the observed model error \( \varepsilon \) is a function of the unknown process and observation variances.

To account for observation error, the entire trajectory was fitted by least squares to Equation 3 (Hilborn and Mangel 1997). That is, for a given set of parameter values, the entire time series was simulated starting with the first observed value. Then the sum of squared differences between simulated and observed time series was calculated. The optimal parameter values were taken to be those that minimized this sum of squared differences.
Once the parameter estimates were calculated, the equilibria \((Y_{t+1} = Y_t)\) were calculated as the roots of the polynomial

\[
0 = b_0 + b_1 Y_t + b_2 Y_t^2 + b_3 Y_t^3
\]  

This polynomial has either one real root and two complex roots (indicating one stable equilibrium), or three real roots (indicating three equilibria). In the latter case only two of the equilibria are stable. The probability of detecting alternate equilibria was calculated as the proportion of simulated data sets that yielded three real roots.

**Detection of Alternate Equilibria**

In the time series simulated without experimental manipulation, the probability of detecting alternate equilibria was relatively low (Fig. 17A). In the absence of manipulation, the system is not likely to leave the initial regime over the course of a simulation. Therefore, the analysis is likely to detect only one of the two stable equilibria. In simulations with larger observation error, the probability of detecting both stable equilibria is near 0.5 and does not change perceptibly as sample size increases. This phenomenon was illustrated by the ball-and-cup diagrams with large observation error. Errors in measuring the value of \(X\) can be interpreted as shifts between equilibria.

In simulations with low observation error, the probability of detecting both stable equilibria is about 0.4 for small sample sizes, and declines to about 0.25 for large
sample sizes. This decline occurs because parameter estimates are increasingly precise for large sample sizes, but the system occupies only one stable domain. There is an increasingly precise characterization of a narrow range of the system’s potential dynamics. This leads to the conclusion that the system has only one stable equilibrium, because the other stable equilibrium is unlikely to occur in any given time series.

In the time series simulated with experimental manipulation, alternate equilibria are more likely to be detected (Fig. 17B). Each time the system is reset experimentally, there is a chance that it will be moved to a different domain of attraction. With low observation error, the probability of detecting alternate equilibria climbs above 0.9 for the longer time series. As the time series get longer, one observes more switches between domains of attraction and parameter estimates become more precise. With high observation error, however, the probability of detecting alternate equilibria hovers between 0.5 and 0.6, and actually appears to decline slightly for longer simulations. Even though experimental manipulation switches the system between domains of attraction, and more switches occur in longer time series, the high observation error makes it difficult to determine that switches have occurred.

As was illustrated using the ball-and-cup model, certain magnitudes of process error have an effect comparable to experimental manipulation (Carpenter 2001). The random shocks of process error can switch the system between stable domains, thereby increasing the probability that alternate equilibria will be detected. If process errors are too small, the shocks will not switch the system between stability domains.
and therefore will not increase the probability of detecting alternate equilibria. If process errors are too large, the system can jump between stability domains frequently. If the shift between stable equilibria occurs frequently due to process error, then the probability of detecting alternate equilibria will be low. Of course, such alternate equilibria may have no ecological significance. A system that rapidly switches between alternate equilibria due to process error is simply noisy. It does not settle into any regime for more than a few time steps. Even though there are multiple equilibria, they have no practical significance for the dynamics of the system.

Despite its simplicity, this exercise illustrates important points about detecting alternate equilibria. The ecosystem must switch between equilibria during the period of study. Ideally several regime shifts should be observed. Regime shifts can be produced by natural variability (represented by process error in this model) or by experimental manipulation. The data must be high quality. Observation error obscures the actual state of the system, and increases the difficulty of detecting alternate equilibria. Overall, this exercise suggests caution in using time series data alone to conclude whether or not alternate equilibria exist. The statistical power to detect alternate equilibria will be low for most ecological time series.

In reality, the ecologist searching for evidence of alternate equilibria faces many difficulties that are not represented by the simple exercise presented here. In this exercise, the investigator knows the true system structure. The choice between fitted models is a simple dichotomy between a single stable equilibrium and double stable
equilibria. Thus, detection of alternate equilibria hinges entirely on estimating the parameters correctly. These simplifications are useful for exposing some of the problems in detecting alternate equilibria, which are actually made more severe by the complications of studying real ecosystems. In actual research, there are many plausible models, the set of models may or may not include a good approximation to the true system structure, and many parameters are unknown and must be estimated from data. In ecosystem studies, conclusions about the absence of alternate states must always be suspect. It is plausible that the observations are simply not up to the task.

Multiple Lines of Evidence: A Case Study

This third and final section of the chapter considers the detection of alternate states in field measurements from ecosystems. The previous section showed that it is difficult to detect multiple equilibria from time series data alone. The most convincing examples of multiple states in ecosystems rest on multiple lines of evidence, including long-term observations, experiments, and comparative studies (Carpenter 2001). This section will combine long-term and comparative data to explore features of alternate equilibria in an eutrophic lake.

To illustrate how several kinds of evidence can be used to assess the possibility of multiple equilibria, I will consider the eutrophication of Lake Mendota (Wisconsin, USA). For this lake, relatively long time series data are available, and a number of measurements have been made of key process rates. Also, some large management
manipulations have been performed in attempts to improve water quality (Carpenter et al. 2004). These manipulations may increase the probability of detecting transitions between states in Lake Mendota, if such transitions have occurred. It turns out that comparative studies (measurements made on a large number of similar lakes) are important for the analysis of Lake Mendota.

Lake Mendota is among the world’s best-studied lakes (Brock 1985, Kitchell 1992, Carpenter et al. 2004). It is culturally eutrophic due to excessive phosphorus inputs from its watershed (Soranno et al. 1996, Bennett et al. 1999). The eutrophic state is stabilized by phosphorus accumulated in watershed soils, sediments of tributary streams, and sediments of the lake itself (Bennett et al. 1999, Reed-Anderson et al. 2000). The hypolimnion of Lake Mendota is anoxic for about 60 to 90 days each summer so there is significant potential for phosphorus recycling (Nürnberg 1995).

Direct measurements of internal phosphorus recycling show that it can exceed inputs by several-fold (Stauffer 1974, Soranno et al. 1997). On the basis of these publications, the model of eutrophication presented in Chapter II seems plausible for Lake Mendota.

Do phosphorus dynamics in Lake Mendota correspond to qualitative patterns that are expected from the eutrophication model of Chapter II? To examine some correlations relevant to this question, I analyzed the phosphorus budget time series presented by Lathrop et al. (1998). These authors measured phosphorus budgets for Lake Mendota for 21 consecutive years. The lake’s P budget can be described by the equation
\[ P_{t+1} = P_t + L_t + R_t - S_t - X_t \]  \hspace{1cm} (5)

The subscript denotes year, which starts on 15 April of each calendar year in this data set (Lathrop et al. 1998). \( P \) is mass of phosphorus in the lake, \( L \) is annual input of phosphorus from the watershed, \( R \) is recycling from sediments, \( S \) is sedimentation and \( X \) is export in surface water flowing out of the lake. All quantities are measured in kg. Lathrop et al. (1998) directly measured \( P \), \( L \) and \( X \), with \( P \) measured on 15 April each year and \( L \) and \( X \) measured for the annual cycle beginning 15 April. Thus net recycling \((R_t - S_t)\) can be calculated by difference. In addition, average summer \( P \) mass was estimated using data from Lathrop and Carpenter (1992) and unpublished data of the North Temperate Lakes LTER site (http://lter.limnology.wisc.edu).

If the eutrophication model of Chapter II is appropriate, we would expect \( P \) content of the lake water to be directly related to recycling. Four indicators of recycling were examined for correlations with summer \( P \) mass in the lake (Fig. 18). Annual change in \( P \) mass \((P_{t+1} - P_t)\) is directly related to summer \( P \) mass, as expected (Fig. 18 A). Net recycling \((R_t - S_t = P_{t+1} - P_t - L_t + X_t)\) is also directly related to summer \( P \) mass (Fig. 18 B). Two additional indices of recycling can be calculated from residuals. Residuals from the regression of the quantity \((P_{t+1} + X_t)\) versus \( L_t \) represent the amount of \( P \) accumulated through the year that cannot be explained by inputs. \( P \) recycling is the likely mechanism for such accumulation. These residuals are directly correlated with summer \( P \) mass (Fig. 18 C). An alternative indicator of recycling is the regression
of the quantity $(P_{t+1} - P_t + X_t)$ versus $L_t$. These residuals should measure the increment of P mass during the year that cannot be explained by load. This surrogate for recycling is also directly correlated with $P_t$.

All of the rough indicators of recycling shown in Fig. 18 are directly correlated with P mass in the overlying water during summer. These results are consistent with the feedbacks invoked in the regime-shift model for lake eutrophication (Chapter II). According to this model, high P mass in the water during summer increases the duration and spatial extent of anoxia in the hypolimnion of the lake. Anoxic conditions increase the solubility of phosphate, thereby increasing the flux of phosphate from sediments to the overlying water.

While these budget analyses are consistent with the eutrophication model of Chapter II, they suffer from the problem that phosphorus in the water column may turn over many times during the year. For example, Soranno et al. (1997) showed that recycling and sedimentation exceed annual inputs, suggesting that each phosphorus atom cycles several times a year between sediments and the overlying water. Thus the measures of net recycling from budget data may miss a substantial amount of phosphorus flux with significant implications for eutrophication.

Ludwig et al. (2003) addressed the fast dynamics of sedimentation and recycling by using a continuous time model, which was then integrated to calculate the annual fluxes. Their continuous time model for dynamics of P in the water column is
\[ \frac{dP}{dt} = L - (s + h) P + r \left[ \frac{P^q}{m^q + P^q} \right] \]  

(6)

Here \( L \) is the continuous input rate, \( s \) and \( h \) are rate constants for sedimentation and hydrologic outflow, respectively, \( r \) is the maximum recycling rate, and \( m \) is the P mass in the water for which recycling is half the maximum rate. The parameter \( q \) sets the steepness of the recycling versus P curve when \( P \approx m \). To integrate this differential equation over one year, Ludwig et al. (2003) assume that the recycling term (in square brackets) is approximately constant over the year. The resulting difference equation is

\[ P_{t+1} = c P_t + \left[ \frac{(1 - c)}{s + h} \right] \{L + r \left[ \frac{P_t^q}{m^q + P_t^q} \right]\} \]  

(7)

where \( c = \exp (-s - h) \). While this difference equation is a rough approximation, it does accommodate the fact that annual P flux to sediments may be substantially greater than the average mass of P in the lake, because the mass of P in the lake is the result of a rapid dynamic equilibrium between sedimentation and recycling.

For the purposes of this chapter, I focused on the recycling parameter \( r \). If there is a threshold for eutrophication, it will depend on \( r \). Measurements of \( r \) have been made in many lakes (Nürnberg 1984) so \( r \) is a good choice for illustrating the benefits of combining information from different studies.
The unknown parameter $r$ was estimated by fitting Equation 7 to data using Bayesian inverse modeling. Details of Bayesian inverse modeling are presented in the Appendix. It is one of the methods available for estimating parameters using data from two or more independent sources. By convention, the first source of data is summarized as a probability distribution called a prior distribution (Appendix).

The prior distribution for $r$ was calculated from data published by Nürnberg (1984, her Table 6). She presents 14 lakes with anoxic hypolimnions for which the mean $r$ is $5.11 \text{ g m}^{-2} \text{ y}^{-1}$ with a standard error of 0.68. It was also necessary to provide a prior distribution for the parameters $s$ and $m$. Because these are unknown, I used a prior that was rather uninformative (i.e. had a high variance). For $s$, I used a mean of 2 with standard deviation 0.5. For $m$, I used a mean of equal to the maximum observed P value (2.3) with standard deviation half as large as the mean. These choices are arbitrary. However, the outcome was not sensitive to small changes in these values. The value of $q$ was fixed at 8, near the value estimated by Carpenter et al. (1999b). The choice of $q$ had only a weak effect on the outcome, over the range of $q$ values from 4 to 20.

The second source of data was the time series data of Lathrop et al. (1998), which was described previously in this chapter. Using Bayesian inverse modeling (Appendix), the time series information was combined with the prior distribution to estimate probability distributions for $r$, $s$ and $m$. Probability distributions that contain information from both sources of data are called posterior distributions (Appendix). The
posterior distribution for the parameter $r$ is most interesting, because it reflects the impact of the prior data from Nürnberg (1984).

One-year-ahead predictions from Equation 7 are similar to observations, although there is considerable scatter (Fig. 19; correlation of observations with one-year-ahead predictions $= 0.61$). Parameter estimates were $s = 0.48$, $r = 5.1$, $m = 3.4$, and $\sigma = 0.32$. While this equation fits the data, it appears to underestimate both sedimentation and recycling. The quantities $c$ and $(1 - c) / (s + h)$ are 0.51 and 0.72, respectively. These suggest that about half the standing stock of $P$ and three quarters of the load plus recycling carry over from year to year. In contrast, sediment trap and entrainment studies suggest that the standing stock of $P$ may turn over several times each summer due to sedimentation and recycling (Soranno et al. 1997). Annually-resolved data may simply be unable to represent the fast dynamics of these processes during the summer season.

The prior distribution for $r$ (Nürnberg 1984) had a heavy impact on the fit of Equation 7 (Fig. 20). The distribution of $r$ estimated by Nürnberg (1984) for 14 lakes is sharply defined. In contrast, the likelihood function based on time series for Lake Mendota alone is flat and diffuse. Consequently, the posterior distribution that combines the Lake Mendota data with Nürnberg’s data is similar to Nürnberg’s distribution. Nürnberg’s estimate of $r$ is $5.11 \text{ g m}^{-2} \text{ y}^{-1}$ and the posterior estimate was $5.07 \text{ g m}^{-2} \text{ y}^{-1}$.
The threshold for eutrophication of Lake Mendota depends heavily on the estimated parameter r. These calculations show that the time series data for Lake Mendota are not very informative about r. A wide range of r values is possible (none are very probable), based on the time series alone. When time series data are combined with the comparative data from Nürnberg (1984), however, the probability distribution of r is considerably narrower. This more precise estimate of r will lead to a more precise estimate of the threshold. Because the calculation of the threshold is complicated, and is not needed to demonstrate the value of multiple sources of data, it will not be presented in this book. Interested readers will find a more complete analysis of the Lake Mendota time series, including probabilities of various types of dynamics, in Stow et al. (1997), Lathrop et al. (1998) and Carpenter et al. (1999b).

Summary

A simple pictorial ball-and-cup model illustrates the basic features of one explanation for regime shifts, alternate stable equilibria. The pictorial model also illustrates the effects of observation error, process error, and experiments on the perception of alternate equilibria. Observation error represents uncertainty in the measurements of the variables that indicate the state of an ecosystem. Process error represents the effects of external shocks that disturb the state of an ecosystem. Experiments are useful for testing the possibility of alternate equilibria because they can produce changes in ecosystem state that are large relative to observation and process errors. Also, it is
often easier to infer the causes of ecosystem change when they are associated with a direct manipulation of a particular variable.

A minimal mathematical model was created to study the possibility of detecting alternate equilibria. The mathematical model represents the same situation illustrated by the ball-and-cup model. Results of the mathematical model show that it is difficult to identify and predict regime shifts using time series data alone. Experiments were helpful for revealing alternate equilibria, especially when observation errors were relatively small.

Regime shifts can often be understood using multiple lines of evidence. In lake eutrophication, for example, our understanding of transitions between the clear-water and turbid-water states derives from long-term observation, comparative study of large numbers of lakes, responses of water clarity to whole-lake manipulation of driving factors, and knowledge of the underlying biogeochemical mechanisms (Chapter II). A dynamic model consistent with these mechanisms appears to fit time series data from Lake Mendota. Fit of the model was improved substantially by including a comparative, multi-lake data set for a key recycling parameter. This analysis demonstrates one statistical method for combining data from multiple sources to analyze regime shifts. In general, models grounded in several types of evidence may be the most powerful method available for analyzing and understanding regime shifts.
Statistical methods are powerful for frequent events, but regime shifts are infrequent by definition. Regime shifts are therefore difficult to characterize statistically unless many events can be observed, and this requires long time series, whole-ecosystem experiments, observations of many similar systems subject to similar regime shifts, and careful process studies. In ecosystem studies, conclusions about the absence of alternate states must always be suspect. It is likely that the observations are simply not up to the task.
Figures

Figure 14. (A) Ball-and-cup model for an ecosystem with two stable equilibria. (B) An external disturbance shifts the system between states. (C) A change in the topography shifts the system between states. Arrow shows the uplift that causes the left basin to shrink, moving the ball to the right basin. (Original)
Figure 15. Ball-and-cup diagrams illustrating how observation error, experiments, and process errors can affect perception of the number of basins. The observer measures the horizontal position of the center of the ball. The perceived position of the ball is shown by the horizontal error bars. The black circles show the actual position of the ball. (A) Low observation error, with the ball in one basin throughout the period of measurement. (B) High observation error, with the ball in one basin throughout the period of measurement. (C) Low observation error, with experimental manipulation of the position of the ball. (D) Low observation error, with random shocks (high process variance) that disturb the position of the ball. (Original)
Figure 16. Flow chart of the simulation exercise for estimating the probability of detecting alternate equilibria. A. Simulations with no experimental manipulation. B. Simulations with experimental manipulation, in this case random resetting of the time series after 12 time steps. (Original)
Figure 17. Proportion of 1000 simulations with two alternate stable equilibria versus number of time steps simulated, with observation standard deviation 0.1 (solid line) or 0.0001 (dashed line). A. Simulations without experimental manipulation. B. Simulations with experimental manipulation. (Original)
Figure 18. Indicators of recycling versus mass of phosphorus in the water of Lake Mendota during summer. A. Annual change in P mass ($P_{t+1} - P_t$). B. Net recycling ($P_{t+1} - P_t - L_t + X_t$). C. Residuals from the regression of ($P_{t+1} + X_t$) versus $L_t$. D. Residuals from the regression of ($P_{t+1} - P_t + X_t$) versus $L_t$. (Original)
Figure 19. Observed P mass in Lake Mendota versus one-year-ahead prediction using the fitted equation 7 (triangles). Units of both axes are g m\(^{-2}\) y\(^{-1}\). Line shows observations equal to predictions. (Original)
Figure 20. Probability distributions for the recycling parameter $r$ from the 14 lakes studied by Nürnberg (1984) and the time series data for Lake Mendota. The distribution for the Lake Mendota data is a marginal distribution, integrated over the prior distributions of the other parameters. (Original)
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 \( \frac{L_{\text{max}} - L_t}{L_{\text{max}}} \) where \( L_t \) is the mean crustacean length observed in the sample from a lake on date \( t \), and \( L_{\text{max}} \) 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 \( L_{\text{max}} = 1.5 \) 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 = \( \log(\text{chl}_{t+1} / \text{chl}_t) / \Delta t \) and net zooplankton biomass growth rate = \( \log(\text{ZB}_{t+1} / \text{ZB}_t) / \Delta t \). 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 biomass growth rate, the candidate predictors were phosphorus input rate, chlorophyll, chlorophyll squared, chlorophyll per unit phosphorus load, and net zooplankton biomass growth rate.
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

\[-\log(L_0) = 0.5 \left[ (\beta - B_0)' S_0^{-1} (\beta - B_0) + k \log(2 \pi) + \log (|S_0|) \right]\]

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

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

In the above equations, \(\beta\) is the vector of parameters to be estimated. The prior estimates of these parameters are \(B_0\) with covariance matrix \(S_0\). \(E_A\) and \(E_Z\) 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 \((\beta, s_A, and s_Z)\) 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

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 $\Delta t$ (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: $D = 10^{-8}$; $m = 0.01$; $q = 6$.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Prior mean</th>
<th>Prior std. dev.</th>
<th>Posterior mean</th>
</tr>
</thead>
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<tr>
<td>$r$</td>
<td>0.4</td>
<td>0.01</td>
<td>0.00025</td>
</tr>
<tr>
<td>$k$</td>
<td>300</td>
<td>30</td>
<td>298</td>
</tr>
<tr>
<td>$g$</td>
<td>0.3</td>
<td>0.1</td>
<td>0.045</td>
</tr>
<tr>
<td>$h_A$</td>
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<td>5</td>
<td>202</td>
</tr>
<tr>
<td>$a$</td>
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<td>0.05</td>
<td>0.75</td>
</tr>
<tr>
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<td>0.5</td>
<td>1.02</td>
</tr>
<tr>
<td>$h_Z$</td>
<td>7</td>
<td>0.3</td>
<td>8.8</td>
</tr>
<tr>
<td>$s_A$</td>
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<td>--</td>
<td>0.56</td>
</tr>
<tr>
<td>$s_Z$</td>
<td>1</td>
<td>--</td>
<td>0.83</td>
</tr>
</tbody>
</table>
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)
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)
V  CAN WE PREDICT_THRESHOLDS WITHOUT CROSSING THEM?

Introduction

Previous chapters discussed the retrospective analysis of regime shifts. By retrospective, I mean the backward-looking process of examining data, fitting models, and drawing inferences about which models are appropriate descriptions of the ecosystem’s behavior. The retrospective study of regime shifts is difficult, primarily because regime shifts are relatively uncommon events. Nevertheless, regime shifts can be discerned in ecosystem data, particularly when long-term observations are supplemented with ecosystem experiments, comparisons of many ecosystems, or studies that provide properly-scaled measurements of key process rates.

This chapter turns to the prediction of regime shifts. To predict, additional assumptions are needed. For example, it is necessary to assume that we have the appropriate model for the regime shifts, that we can predict the trends of extrinsic drivers, and that parameter values are stable (or at least have predictable trends). These conditions are difficult to meet, and the additional uncertainties contributed by the added assumptions are hard to evaluate. Nevertheless, prediction of regime shifts is a necessary step in hypothesis testing. As the study of regime shifts becomes a more rigorous part of ecology, ecologists will want to test hypotheses about regime shifts by predicting where and when they should occur. Thus research on prediction will help to
advance the basic science of regime shifts. The consideration of uncertainties and how they should be propagated over time is one of the most important research frontiers in this area (Clark et al. 2001, Carpenter 2002).

**Today’s Actions Affect Tomorrow’s Predictions**

Ecosystem managers may also need to predict regime shifts, and this need raises further complications because actions based on predictions can change the future. In management, the backward-looking understanding of regime shifts merges with the forward-looking capability to manipulate ecosystems. By choosing actions based on predictions of future ecosystem conditions, managers affect how the ecosystem changes and thereby affect learning, by influencing the new observations available for fitting predictive models.

The cycle of retrospective model fitting and forward-looking manipulations could either improve or inhibit our ability to predict regime shifts. In Chapter IV the deliberate manipulations of the experimental lakes revealed a regime shift in plankton dynamics at a certain critical level of the planktivory index. The experimental manipulations were designed to produce large changes in ecosystem dynamics. Such manipulations could be used by managers to improve understanding of ecosystem dynamics, with benefits for future management (Walters 1986, Kitchell 1992). What if instead the manipulations had been designed to maintain the ecosystem in a particular condition, as is often the goal of ecosystem management? In this case, the range of ecosystem responses...
would have been limited, and the ability to discern the regime shift would have been compromised. This reveals a fundamental conflict between the scientific goal of understanding regime shifts and management to avoid them.

The conflict might be sidestepped if it is possible to anticipate regime shifts without actually changing regimes. The purpose of this chapter is to explore that possibility, using a specific example for a lake. In order to address the possibility of anticipating regime shifts, we must consider both the retrospective analysis of available data and the capacity to look forward. Whole-lake experiments in which the manipulations are chosen for purely scientific reasons, like those described in Chapter IV, are relatively rare because few lakes are available for experimentation and few funding agencies are willing to support such large interdisciplinary experiments. Instead, most ecosystem experiments are undertaken by managers, or by collaborative teams of scientists and managers. In these situations, the benefits of better information about regime shifts are balanced against the costs of potential damage to ecosystem resources. This more complicated, but also more realistic, situation is considered in this chapter.

Before turning to the lake case study, I will discuss a global problem of predicting abrupt climate change. In this situation, costs of crossing a threshold are high, data to estimate the threshold are sparse, the system of interest is large, unique, and cannot be replicated, and experimental manipulations to cross the threshold would be unwise even if they were possible. This global problem is analogous in many ways to the problem of a clear-water lake subject to eutrophication. In the lake case, costs of crossing the
threshold are high, data are often sparse, and experimental manipulations to find the threshold may be risky. Because of these similarities, study of the lake management problem may build intuition about the global climate problem. The main difference between the global problem and the lake problem is that many lakes are available for comparison and experimentation. Thus, experimentation using a few lakes to learn about thresholds may have significant benefits for managing the whole population of lakes on a landscape. That idea will be developed further in the next chapter. The present chapter focuses on the case of a unique resource for which little prior information is available. Most of the information about the threshold must be obtained from the ecosystem being managed, but experimentation could cause the ecosystem change that we wish to avoid. Is it possible to learn enough about the threshold to avoid crossing it?

**Continent at risk of ice age**

Global pollution of the atmosphere has created a risk of abrupt climate change (Alley et al. 2003). One pattern of concern involves catastrophic cooling of Europe. Europe’s climate is moderated by the North Atlantic thermohaline circulation, a current system that carries warm water from the tropics to northern latitudes. On a handful of occasions in the past, the northward extent of warm surface water has been pushed southward by melting of arctic ice (Taylor 1999). The cold fresh water from the melted ice floats above the warmer but more saline (and therefore more dense) tropical water, pushing the warm water below the surface of the North Atlantic ocean. This change in
circulation reduces the flux of heat from the ocean to the atmosphere. The heat of the eastward-flowing winds to Europe is diminished. Europe cools rapidly and then becomes covered by glaciers. These cooling events can be triggered in less than 10 years, and the subsequent glaciations of Europe last hundreds of years (Rahmstorf 1997, Taylor 1999). The events are analogous to eutrophication: underlying causes build slowly and gradually, the regime shift is rapid, and the consequences last a long time.

Currently, warming of Earth, caused at least in part by human burning of fossil fuels, is causing rapid melting of polar ice. This melting could cut off the heat pump to Europe by the same mechanisms that have occurred in the past (Broecker 1987).

The problem is analogous to lake eutrophication, but larger in scale. Nearly a billion people live in Europe. Glaciation of Europe would be a massive disaster. All of humanity uses the atmosphere to dilute pollutants, including the gases that contribute to global warming and melting of polar ice. How can these competing interests be resolved? What is the threshold rate of climate warming to change thermohaline circulation? How much fossil fuel burning is acceptable if we wish to avoid glaciation of Europe (Broecker 1987)? As in the lake case, the management problem is to estimate the threshold and construct policies to stay away from it (Deutsch et al. 2002, Heal and Kriström 2002).

Lake at risk of eutrophication
A lake in an agricultural region is valued for water supply, fishing, and recreational use. It is also used to assimilate polluted runoff from farms. People are aware that the lake could become eutrophic due to phosphorus pollution (Chapter II). If this occurs, the drinking water supply, fish populations and recreational opportunities would all be impaired or lost. On the other hand, agriculturalists need the lake to dispose of phosphorus pollution from excess manure and mineral fertilizers. Thus there are competing uses for the lake water (Fig. 32). One interest group would like to decrease phosphorus inputs to reduce risk of eutrophication and maintain clean water for drinking, fishing and recreation. A different interest group would like to increase agricultural output, which will increase phosphorus pollution. How should these competing goals be balanced?

In practice, the tradeoffs are settled through political competitions (Fig. 32) with varying degrees of scientific input (Scheffer et al. 2000a). The scientific questions center around the location of the threshold for eutrophication, and the economic costs and benefits of the various uses of the lake such as drinking water, pollution dilution, fishing and recreation. Frequently the costs of eutrophying the lake far outweigh the benefits of using the lake to dilute pollution, because the value of clean water is high and reversing eutrophication is expensive or impossible (Wilson and Carpenter 1999, Carpenter et al. 1999b). Thus, in most cases a rational manager will seek to avoid crossing the threshold to eutrophication.
If the location of the threshold is known, then one can estimate how much pollution is acceptable if eutrophication is to be avoided (Carpenter et al. 1999b, Ludwig et al. 2003, Peterson et al. 2003). One sure way to find the threshold is to cross it, but this is undesirable because of the long time lags involved in recovery from eutrophication. Thus the manager faces the dilemma of avoiding an unknown threshold. One interest group will favor very low phosphorus pollution to be sure to avoid the threshold, while the other interest group will favor higher rates of phosphorus pollution. The political tension could be resolved by economic arguments if the location of the threshold could be predicted. Can this be done without crossing the threshold?

The remainder of this chapter uses a simulation model of a managed lake to explore the possibility of anticipating regime shifts before they occur. The next two sections of the chapter describe the motivation for the model and the details of its construction. Then, model results are presented and discussed. The general conclusion is that it is very difficult to anticipate a regime shift without causing it to happen, even with rather bold experiments. Indeed, the most informative experiments cause a regime shift. On the other hand, a few simple, precautionary management rules make it possible for management to prevent unwanted regime shifts. Such precautionary management is not always compatible with experimentation on a particular ecosystem.

Motivation for the Model
A regime shift in lake water clarity, as introduced in the previous section “Lake at risk of eutrophication”, provides a case study for this chapter. Eutrophication is a significant societal problem that is a focus of applied ecology and ecosystem management in many parts of the world (Carpenter et al. 1998a). The regime shifts involved in eutrophication are reasonably well understood (Chapters II and III). Slowly-changing variables, such as soil or sediment phosphorus, could provide “leading indicators” of future eutrophication (Bennett et al. 2001), so there is a possibility of anticipating regime shifts before they occur. Many case studies of eutrophication have been published, and this rich literature can be used to improve estimates of parameters necessary to predict the regime shift (see Chapter III). Eutrophication causes substantial economic losses (Wilson and Carpenter 1999) and reversal of eutrophication is expensive (Cooke et al. 1993), so economically rational management should strive to avoid the regime shift to eutrophication (Carpenter et al. 1999b, Ludwig et al. 2003). Thus eutrophication is a situation in which experimentation to measure thresholds may come into conflict with the need to avoid crossing the thresholds.

To focus discussion, consider a lake subject to possible eutrophication through the phosphorus cycling mechanisms discussed in Chapter II (Fig. 33). The manager attempts to balance competing political and economic pressures while avoiding eutrophication of the lake. Phosphorus concentration in the water is the central concern. The phosphorus concentration in the water can change rapidly in response to more gradual changes in phosphorus in the lake sediments and the soils of the watershed. Management often focuses on controlling the mean rate of phosphorus
input to the lake, although there may also be uncontrollable stochastic fluctuations due to weather. Management can act at several scales, ranging from in-lake manipulations of phosphorus concentrations, to manipulations of inputs from tributary streams and riparian land, to manipulations of soil phosphorus in the watershed. To simplify the model for this chapter, I assumed that management actions would control the mean annual input at the point of entry to the lake (Cooke et al. 1993). In practice, this corresponds to point source controls such as sewage treatment, direct manipulations of tributary streams (e.g. diversion of tributaries), or installation of riparian buffers to intercept phosphorus inputs (Osborne and Kovacik 1993).

The model (described below) assumes that the economically optimal management would avoid the regime shift to eutrophication. However, the model does not compute an optimal policy. Instead, the management algorithms attempt to avoid crossing the threshold, implicitly assuming that this is close to the optimal strategy. This simplifying assumption is appropriate for the case of a lake with good water quality subject to P inputs that may increase in the future (Carpenter et al. 1999b, Ludwig et al. 2003). In the case of a lake which is already eutrophic, or a lake in which sediment phosphorus has accumulated to the point where eutrophication is inevitable, it may be economically optimal to use the lake as a dump for pollutants and abandon any uses for drinking water, fishing or recreation (Ludwig et al. 2003). Such a conclusion is highly sensitive to the choice of economic discount factor used in the computation of the optimal strategy (Ludwig et al. 2003). The situation in which it is economically optimal to pollute the lake is not considered in this chapter.
Management, in the model, operates by simple rules that seek to avoid the threshold. In some cases, the rules also seek to improve parameter estimates. These simple rules are a plausible representation of typical strategies of managers in the field. Most lake managers are aware of the possibility of a regime shift, and act to avoid eutrophication. Most managers do not perform an economic cost-benefit analysis at each time step. They know that economic analyses generally show that the clear-water state is far more valuable than the eutrophic one (Carpenter et al. 1999b, Wilson and Carpenter 1999), and they assume that clear water is economically preferable. However, managers are continually pressured by some interest groups to increase phosphorus inputs to the lake, and to justify their targets for phosphorus inputs (Scheffer et al. 2000a). This creates a tension between increasing the phosphorus input while avoiding the threshold of eutrophication. This tension is addressed in different ways by the management strategies described below.

I will assume that the manager invests in observations of the concentration of phosphorus in the lake water and the amount of phosphorus in the sediment (Fig. 33). Because I have assumed that phosphorus input control occurs immediately upstream of the lake, this chapter will not address phosphorus content of soils. Although soil phosphorus content is perhaps the best control variable for managing eutrophication (Bennett et al. 2001), my points about anticipation of regime shifts can be made without including the complications of soil phosphorus in the model. I assume that the manager fits a predictive model for the ecosystem to available data at each time step. Based on
this predictive model and specified goals for phosphorus in the lake, the manager chooses an input target for the next time step. The precision of the model predictions depends on the data that are available to fit the model. This creates a tension between experimentation to improve the data and the risk that the experiments might create a regime shift. How much can the manager learn about the threshold without crossing it? And how will different management strategies affect learning and risk?
Model

For the purposes of this chapter, I built a simple model of a lake ecosystem subject to eutrophication, interacting with a management system that attempts to avoid eutrophication (Fig. 34). The manager observes the lake, and fits a model which is used to predict the future condition of the lake. Given these predictions, a phosphorus input target is chosen using a specified management strategy.

In building this model, a number of specific assumptions were necessary and these are detailed below. The rationale for these assumptions follows from the overarching goal of the exercise, which is to explore the possibility of anticipating thresholds before they occur. We shall see that this proves very difficult. The major assumptions of the model were chosen to make it easier to anticipate thresholds. In reality, it will be more difficult to anticipate thresholds than it is in this model. Because it is difficult to anticipate regime shifts in the model, and the model is biased in favor of anticipating regime shifts, the results strongly suggest that regime shifts will be difficult to anticipate in actual management situations.

The model (Fig. 34) combines an ecosystem model of phosphorus dynamics in lake water and sediment, a statistical model for dynamic learning of unknown parameters, and a policy for choosing phosphorus inputs (Fig. 34). Each year, a mean input target is set for the lake based on current information. The actual phosphorus input is subject to random shocks around the mean, due to random effects such as
weather. Given the actual input, levels of phosphorus in sediments and water are calculated using the ecosystem model. We assume that the managers of the ecosystem do not know the parameters for the dynamics of the ecosystem, and must estimate them from data. Based on observed time series, parameters for an estimated model for ecosystem dynamics can be calculated at each time step. Managers choose the mean input target for the next year using their estimated model and a management strategy.

The remainder of this chapter presents details of the model in four subsections. The first three subsections present the ecosystem model, the statistical model for observing the ecosystem and predicting its future condition, and the management strategies to be compared. Because the model is stochastic, it is difficult to draw conclusions about the management strategies from a single run of the model. Therefore Monte Carlo simulations were conducted to characterize the distribution of outcomes under each management strategy. The methods for the Monte Carlo simulations are described in the fourth subsection.

Ecosystem Model

Dynamics of phosphorus in sediment and water followed the model used by Dent et al. (2002) and Ludwig et al. (2003). Dynamic equations are

\[
M_{t+1} = M_t + s P_t - b M_t - r M_t \left[ \frac{P_t^q}{m^q + P_t^q} \right]
\]

(8)
\[ P_{t+1} = P_t + L \exp[z_t - (\sigma^2 / 2)] - (s + h) P_t + r M_t \left[ P_t^q / (m^q + P_t^q) \right] \]  

(9)

M is mass of phosphorus in the lake sediments and P is mass of phosphorus in the lake water (both subscripted by time and with units g m\(^{-2}\)). L is mean P input flux (g m\(^{-2}\) y\(^{-1}\)) and \(z_t\) is the annual disturbance of P input which is assumed to be normally distributed with mean zero and variance \(\sigma^2\). The quantity \(\sigma^2 / 2\) is subtracted from \(z_t\) to cause the mean value of \(\exp[z_t - (\sigma^2 / 2)]\) to be unity (Hilborn and Mangel 1997). Thus realized P input each year is a lognormally distributed random variate with mean L. Parameter definitions and values used for simulations are presented in Table 3.

I assume that P mass in the water is directly proportional to phytoplankton biomass. This assumption is corroborated by many limnological studies. In lakes where primary production is controlled by phosphorus, most of the phosphorus is contained in plant biomass during the growing season (Kalff 2002).

This model has three equilibria: a stable clear-water regime (low P or oligotrophic), a stable turbid regime (high P or eutrophic), and an unstable point at intermediate P (Chapter II; also see Dent et al. 2002, Ludwig et al. 2003). If the lake is in the clear-water regime, a large random input event can shift P level above the unstable point into the turbid regime. Once the lake has entered the turbid regime, the excess P accumulates in sediments and is repeatedly recycled to the overlying water.
Therefore, several years of low P input are required to shift the lake from the turbid regime to the clear-water regime.

The critical P input rate declines with the mass of phosphorus in the sediment (Fig. 35). The critical P input rate is the threshold for transition from the clear-water regime to the turbid regime, which was discussed in Chapter II. P input events larger than the critical P input rate will shift the lake from the clear-water regime to the turbid regime. The threshold for the opposite transition – from the turbid regime to the clear-water regime – occurs at much lower P input rates (Carpenter et al. 1999b). This chapter concerns the transition from clear water to the turbid regime.

Parameter values were chosen to place the ecosystem in the clear-water regime, but near the threshold for transition to the eutrophic regime (Table 3). This is the region where information about the critical P input rate is most useful for maintaining clear water (Carpenter 2001). The critical P input rate can be calculated from the parameters of the ecosystem model. The precision of the estimate of the critical P input rate is directly related to the information available to estimate the parameters.

**Statistical Estimation**

The goal of the statistical component of the model is to simulate a plausible scheme for monitoring the ecosystem, updating parameter estimates for an ecosystem model, and drawing inferences to guide management decisions. These goals could be met in many
ways. The approach described below is arbitrary, but plausible. Where necessary simplifications were likely to introduce bias, the model is biased in favor of correctly predicting the threshold. Thus the analysis is likely to be overly optimistic about prospects for predicting the threshold. As noted above, the chapter concludes that it is difficult to predict the threshold. Because the analysis was designed to be overly optimistic, this pessimistic conclusion is likely to be robust.

I assumed that the manager knows the correct structural model (Equations 8 and 9) and must estimate the parameters from time-series data. In an actual application, the correct structural model would be unknown, and model selection would add uncertainty to the analysis (Peterson et al. 2003). In the real world of lake management, then, predicting the threshold is even more difficult than my model suggests.

I assume that the manager measures P mass in the lake water and P input each year, a common practice in lake management programs. Observation error is assumed to be negligible for P mass in the water, as can occur in monitoring programs with extensive replication. Errors in P input measurements, however, are likely to be nontrivial because of the high temporal variability of input events. Log(P input) is assumed to be observed with normally-distributed errors (mean zero, standard deviation 0.07). M is rarely measured in lake management programs, so there is little precedent for designing a statistical approach. I assumed that managers invested in a spatially-intensive sampling program which estimated M with a coefficient of variation of 12.5%.
This is perhaps overly optimistic, but if so it biases the model in favor of successful predictions. In preliminary simulations, changes in M over time were too small to be useful for updating parameter estimates. Therefore, dynamics of M were ignored in the estimation.

Parameter estimates were updated each year using Bayesian nonlinear dynamic regression (Appendix). This method is appropriate because slow changes in M could be captured as slow drift in the parameters. The Bayesian scheme can be computed rapidly (an advantage for Monte Carlo analyses, see below) and makes it easy to experiment with the precision of prior information available to the manager. Estimates of mean parameter values from Bayesian nonlinear dynamic regression had only trivial differences from maximum likelihood estimates using 30 years of simulated data. However, the Bayesian nonlinear dynamic regression does not adequately represent the full posterior distribution of the parameters (because of the Taylor approximation employed in the updating, see Appendix). This would be important if the lake was to be managed by optimal control methods which require integrations over such a posterior distribution (Carpenter et al. 1999b, Ludwig et al. 2003, Chapter VI). The model presented here does not include optimal control, so a full analysis of the posterior distribution is not essential.

Bayesian nonlinear dynamic regression was implemented with an observation vector of two elements, log(P input) and P. Parameters to be estimated are log(\(\lambda\)) (corresponds to log(L)), \(\theta\) (corresponds to \(1 - (s + h)\)), \(\rho\) (corresponds to \(r \, M_t\)), and \(\eta\)
(corresponds to m). For simulations presented here, the prior distributions of the parameters were assumed to be Student-t distributions with one degree of freedom and mean values as in Table 3. Scale factors were calculated assuming coefficients of variation of 10\% for $\log(\lambda)$, 20\% for $\theta$ and $\rho$, and 30\% for $\eta$. This prior distribution represents an informative parameter distribution, as might be estimated from a multi-lake data set. Initial parameter estimates were drawn randomly from the prior distribution. Note that $q$ is assumed to be known precisely. This is unrealistic, and biases the analysis toward successful prediction of the threshold.

Management Strategies

Five management strategies were compared (Table 4). In the Trial-and-Error strategy, the manager attempts to find a P load rate that balances the need to avoid regime shift with the pressure from constituents who wish to increase P inputs to the lake. The water quality is deemed acceptable if the P level in the lake remains below 1. The manager attempts to find the P loading rate that will maintain this P level by making small adjustments to the P load depending on the current level of P in the lake.

In the passive strategy, the manager simply holds the P load rate at a fixed target value that is deemed acceptable. In practice, this would be a level that balanced the interests of constituents who wish to increase P inputs to the lake with those who wish to maintain the lake in the clear-water state.
In the passive precautionary strategy, the manager reduces the P load to the lake if key indicator variables are too high. One indicator variable is last year’s P load to the lake. If it exceeds the expected P load plus a standard deviation, the next year’s P load is scaled back to compensate for the impact of the exceptionally high load in the preceding year. A second indicator variable is the recycling rate estimated from the model, which is directly related to the possibility of regime shift. If the estimated recycling rate can account for more than 1% of the P in the lake water, then load is scaled back to compensate for the impact of recycling.

In the passive precautionary strategy, the decisions of the manager depend on the predictions of P loading and the estimates of recycling. Both of these indicators will be more accurate if the estimates of model parameters are more precise. The precision of the parameter estimates could potentially be improved by experimentation.

In the experimental strategy, P input rates are selected from an experimental design. Using exploratory simulations, I investigated alternative experimental designs. The one used here is relatively simple, and yields data that can provide relatively precise parameter estimates in 20 or 30 years. It is not feasible to obtain accurate parameter estimates with less than about 20 years of data.

In the actively adaptive precautionary strategy, the precautionary rules are combined with the experimental design. If the key indicators (P load rate and recycling rate) are too high, the precautionary rule is applied and P load is decreased to 25% of
the nominal value. If the key indicators are acceptably low, then P load is selected randomly from the experimental design. Thus experiments are performed only when conditions are thought to be safe.

Monte Carlo Analyses

This model includes stochastic shocks at each time step. To understand the behavior of the model, it is useful to study the frequency distribution of a large number of simulations. These distributions were obtained by running the model 1000 times from the same initial conditions for a given management strategy. The outcome represents the frequency distribution obtained from randomly-chosen sequences of stochastic shocks under a particular management strategy.

Results

Management Strategies and Regime Shifts

Choice of management strategy had strong effects on the probability of regime shift to the eutrophic state (Table 5). Under the trial-and-error and experimental strategies, the probability of eutrophication was high, roughly 70%. Under the actively adaptive precautionary strategy, the probability of eutrophication was somewhat reduced. Under the passive strategy, the probability of eutrophication was lower still. The passive precautionary strategy had the lowest probability of eutrophication, about 5%.
Management Strategies, Regime Shifts and Learning

Parameter estimates were improved by experimentation. Time series presented in Figs. 36 and 37 are from a model run in which management was experimental, but no regime shift occurred. P and L exhibit variability due to the experimental treatments (Fig. 36A,B). One-step-ahead predictions of P and log(L) were reasonably accurate. Although recycling was high in a few years, it was not sufficient to trigger a regime shift (Fig. 37C). The time series of P load treatments is presented in Fig. 37A. Experimental treatments have some effect on parameter estimates (Fig. 37B-D). The most notable improvement is seen in $\eta$ (estimator of m), where the estimate draws closer to the nominal value and the standard deviation declines. The mean value of $\rho$ (estimator of $r_M$) changes slightly in the direction of the nominal value, but the standard deviation grows. Changes in the estimate of $\theta$ (estimator of $1 - (s+h)$ ) are negligible.

Parameter estimates improved sharply if a regime shift occurred (Figs. 38 and 39). The regime shift was triggered by a larger-than-expected input event in year 10, coincident with a jump in recycling the same year. The estimates of recycling parameters $\rho$ (estimator of $r_M$) and $\eta$ (estimator of m) improved immediately (Fig. 39). Mean parameter estimates moved closer to the nominal values, and standard deviations shrank. The estimate of $\theta$ (estimator of $1 - (s+h)$ ) deteriorated after the regime shift, moving slightly away from the nominal value with slightly larger standard
deviation. After the regime shift, the estimate of recycling (which depends only on \( \rho \) and \( \eta \)) and the estimate of the threshold for regime shift are markedly more accurate.

The improvement of parameter estimates after a regime shift makes sense. After the regime shift has occurred, we have some basis for evaluating where the regime shift occurs. We also have measurements across a wide range of P levels, which leads to more precise parameter estimates.

Recycling rate typically increased one or two time steps prior to the regime shift (Fig. 38). Any indicator that depends on the second derivative of observed P in the water will jump prior to a regime shift. Sometimes the signal is helpful in preventing a regime shift (e.g. Fig. 36 at Time steps 6 and 15). In other cases, the reduction in P inputs following the signal is insufficient to prevent a regime shift (e.g. Fig. 38).

Active adaptive management consistently improved the estimates of recycling rate (Fig. 40A). Bias is the difference between the recycling rate estimated by the manager and the true recycling rate. Under active adaptive management, bias clusters more tightly around zero than under passive management. However, most of the power of active adaptive management derives from the regime shifts that it creates (Fig. 40B). When we compare simulations in which a regime shift occurred, the bias of recycling rate is about the same for the passive strategy and the active adaptive strategy. Simulations in which no regime shift occurred have much higher frequency of large bias (whether positive or negative) than simulations in which a regime shift occurred. There
are some minor differences between the passive strategy and the active adaptive strategy, but the least-biased estimates of recycling occur in simulations with regime shifts.

Discussion

The management strategies were chosen to explore two tensions. The tension between those who wish to increase inputs to the lake and those who wish to avoid the regime shift is illustrated by the trial-and-error strategy. This strategy has a high probability of shifting the lake to the eutrophic state. Trial-and-error is a poor way to manage a system subject to regime shifts. This leads to the second tension, that between the need for precaution and the desire to learn about the regime shift. Knowledge of the regime shift should assist the manager in setting limits or targets on $P$ loading, but gaining this knowledge runs the risk of regime shift. The experimental management strategy was as risky as trial-and-error. The actively adaptive strategy was better, but still had a high risk of regime shift.

The model used in this chapter was deliberately biased in favor of successfully measuring model parameters and the threshold, while avoiding crossing the threshold. The model assumes that the correct dynamic equations for the ecosystem are known, prior parameter distributions are informative, regular monitoring programs are in place, and the manager can rapidly (within one time step) change $P$ inputs to desired levels. All of these assumptions are optimistic. The assumption of rapid controllability of $P$
inputs is not realistic. Even under these favorable conditions, it was not possible to improve estimates of parameters without crossing the threshold. In a more realistic situation, prediction of thresholds will be far more difficult.

Experimental or actively adaptive management improved parameter estimates, but the improvement is due almost entirely to the regime shifts caused by the manipulations. For the ecosystem model analyzed here, it is very difficult to improve parameter estimates without causing a regime shift. Similar conclusions were reached by Walters (1986) and are evident in the statement that “To find out what happens to a system when you interfere with it, you have to interfere with it (not just passively observe it).” (Box 1966).

Implications for lake management

Certain indicators can help to prevent regime shifts if rapid, extreme management responses are possible. Indicators related to the second derivative of P in the water, such as recycling rate, were useful leading indicators in this model. However, the lead time of the advance warning is short, only one time step. By the time the indicator changes, the slow variable of sediment phosphorus is taking effect and eutrophication may not be avoidable. Also, an unlucky stochastic shock could tip the system toward eutrophication even if appropriate management action is taken. By the time the indicator changes, there is a chance, but not a certainty, that swift, massive reductions in P input can prevent the regime shift. In the case of real lakes subject to
eutrophication, such swift and massive responses are not likely because of the difficulties of controlling nonpoint P inputs (Carpenter et al. 1998a). If it were actually implemented for lakes at risk of eutrophication, the management system described in this chapter would have a high failure rate.

Precautionary management can prevent most regime shifts in this model. The simulations employ simple rules that were effective for reducing the probability of a regime shift. These rules, however, assume that draconian steps can be taken within a year to reduce P inputs. In real management situations, such rigorous year-by-year management of P inputs is not possible. Instead, policies to avoid regime shifts should maintain low levels of P in watershed soils and lake sediments, and thereby create a large domain of attraction for the clear-water regime (Carpenter et al. 1999b, Bennett et al. 2001, Dent et al. 2002). Such policies would also reduce P loads. For eutrophication, precautionary policies maintain the resilience of the clear-water regime: minimize point source inputs of P, reduce levels of P in watershed soils, and maintain riparian buffers (Carpenter 1998).

Implications for actively adaptive management

In these simulations, I have not attempted to find the experimental design that is optimal, in the sense of maximizing the probability of detecting the threshold. Such experimental designs are discussed by Walters (1986) and Wieland (2000). Optimal experimental designs may lead to better parameter estimates than the designs
employed here. However, such designs are unlikely to alter the conclusion that the best way to determine the threshold for a regime shift is to cause a regime shift.

If the only way to learn about a regime shift is to observe one, then experimental management as practiced in this chapter is unsafe for any specific ecosystem. However, there are other approaches to actively adaptive management. Even for singular ecosystems it may be possible to assess the processes that maintain the stability of the regime that the manager prefers. This assessment could involve safe experiments that do not create regime shifts but do explore aspects of the system that may improve management. For example, in a model of eutrophication that included agricultural practices and soil P, as well as sediment and water P, the threshold for regime shift was a moving target (Carpenter et al. 1999a). In simulations with this model, frequent experimentation with agricultural practices provided information about the sensitivity of the lake which could be used to adjust the risk of regime shift. In this more realistically complex model, active adaptive management proved useful for assessing options that could avoid an undesirable regime shift. Active adaptive management has other important advantages that are not addressed in this chapter. For example, it fosters flexible and open institutions and multi-level decision systems that allow for learning and tend to increase the likelihood of successful management (Gunderson et al. 1995, Ostrom et al. 1999, Berkes et al. 2002, Folke et al. 2002a, b).

While certain types of experiments are dangerous for individual ecosystems, the situation may be quite different for a set of modular ecosystems such as landscapes.
with a large number of lakes (Levin 1999). Multi-lake comparative data sets have proven extremely useful for understanding the P cycle and eutrophication in lakes (Schindler et al. 1978, Reckhow and Chapra 1983, Rigler and Peters 1995). In the context of this model, the multi-lake data would provide prior distributions for the parameters. Simulations presented in this chapter suggest that informative prior distributions are extremely useful for estimating recycling rates or the threshold for regime shift. Prior distributions of parameters changed little over time in these simulations unless a regime shift occurred.

The value of comparable data sets from multiple ecosystems adds another dimension to adaptive ecosystem management. In cases where a large number of similar ecosystems are available, it may be possible to experiment on a few ecosystems to obtain data that are informative about thresholds in other ecosystems. While comparative analysis is one of the pillars of ecosystem ecology (Cole et al. 1991), comparative ecosystem studies have rarely been used to estimate thresholds and this appears to be an important research frontier. The method of Bayesian inverse modeling (Appendix) is a natural method for combining comparative ecosystem data with local time-series observations to estimate parameters for thresholds or other ecosystem properties.

Summary
This chapter considers the problem of managing a single ecosystem subject to regime shift, given limited prior information about the threshold for change to an undesirable regime. Is it possible to learn the location of the threshold without crossing it? What are the tradeoffs between precaution to avoid the regime shift and experimentation to learn the location of the threshold? This is a generic problem in ecosystem management. In this chapter it was explored using the example of a clear-water lake subject to eutrophication.

Trial and error is a risky strategy for managing systems subject to regime shift. It combines high probability of regime shift with slow rates of learning about the ecosystem.

There is a conflict between precautionary management and experimental management. Precautionary management can prevent regime shifts, but provides little information about the location of thresholds. Experimental management can reveal the location of thresholds, at the cost of crossing them. Experiments that manipulate P input prove risky. Other types of experiments, such as those to measure the rate of P recycling or other key parameters, may provide useful information with less risk. The appropriate design for such studies will differ among ecosystems and management circumstances.

When managing a single ecosystem, the parameters for predicting a regime shift can be learned, but this learning seems to require observing a regime shift. If the new
regime is highly undesirable, then precautionary management to minimize risk of regime shift is preferable to experimentation. In the simulations presented in this chapter, precaution and learning are incompatible. One can either create a regime shift and thereby learn the location of the threshold, or attempt to avoid the threshold and thereby leave its location shrouded in uncertainty. In a world with growing demand for ecosystem resources, it will be difficult to justify precautionary policies without better knowledge of thresholds. Such knowledge comes hard. The precautionary manager will have difficulty building information about the threshold necessary to rationalize the precautionary policies. Thus there is great risk that precautionary policies will give way to trial-and-error.

The situation is different when a large number of similar ecosystems are to be managed, as is the case for most lakes. The example of Lake Mendota (Chapter III) showed that information from other lakes was extremely helpful in predicting recycling, a key parameter for predicting regime shifts. Information from other lakes can narrow the probability distribution of parameter estimates, and would in fact dominate the analysis unless a regime shift occurred. Thus information from multiple lakes will improve the performance of management strategies that depend on accurate predictions of ecosystem thresholds.

For modular ecosystems with many separate replicates on the landscape, active adaptive management may offer significant advantages. Information useful for managing all the ecosystems on the landscape could be gained by subjecting only a
few of the ecosystems to experiments. The most powerful experiments will cause regime shifts. Such experiments yield the greatest amount of information about ecosystem behavior. Even though they may cause costly damage to the manipulated ecosystems, the information can be used to improve the management of a much larger number of ecosystems on the landscape. Such risky experiments may be warranted, particularly if the damage can be contained, would not spread to other ecosystems, and could be reversed. Prospects for managing a large number of modular ecosystems subject to regime shifts will be explored further in the next chapter.
### Tables

Table 3. Parameters for the lake phosphorus model: symbols, definitions, units and values used in simulations.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
<th>Units</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>b</td>
<td>Burial rate</td>
<td>y(^{-1})</td>
<td>0.001</td>
</tr>
<tr>
<td>h</td>
<td>Outflow rate</td>
<td>y(^{-1})</td>
<td>0.15</td>
</tr>
<tr>
<td>L</td>
<td>Mean P input flux</td>
<td>kg m(^{-2}) y(^{-1})</td>
<td>0.7</td>
</tr>
<tr>
<td>m</td>
<td>Half-saturation for recycling</td>
<td>kg m(^{-2})</td>
<td>2.4</td>
</tr>
<tr>
<td>q</td>
<td>Exponent</td>
<td>dimensionless</td>
<td>8</td>
</tr>
<tr>
<td>r</td>
<td>Recycling rate</td>
<td>y(^{-1})</td>
<td>0.019</td>
</tr>
<tr>
<td>s</td>
<td>Sedimentation rate</td>
<td>y(^{-1})</td>
<td>0.7</td>
</tr>
<tr>
<td>(\sigma^2)</td>
<td>Variance of annual disturbance to P input flux</td>
<td>dimensionless</td>
<td>0.1225</td>
</tr>
</tbody>
</table>
Table 4. Algorithms used to choose P input rates under the five management strategies. "Nominal value" refers to parameter values in Table 3. The vector of experimental P load levels contains 10 P load levels evenly spaced between 0.1 and 2.

<table>
<thead>
<tr>
<th>Strategy</th>
<th>Algorithm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trial-and-Error</td>
<td>If the observed P is less than 1, increase P load by 10%; otherwise decrease P load by 10%</td>
</tr>
<tr>
<td>Passive</td>
<td>Hold the P load at the nominal value</td>
</tr>
<tr>
<td>Passive adaptive, with precaution</td>
<td>If the observed P load is greater than one standard deviation above the prediction, OR estimated recycling accounts for more than 1% of the P in the lake water, reduce P load to 25% of the nominal value; otherwise hold the P load at the nominal value</td>
</tr>
<tr>
<td>Experimental</td>
<td>Draw the P load level randomly from the vector of experimental P load levels</td>
</tr>
<tr>
<td>Active adaptive</td>
<td>If the observed P load is greater than one standard deviation above the prediction, OR estimated recycling accounts for more than 1% of the P in the lake water, reduce P load to 25% of the nominal value; otherwise draw the P load level randomly from the vector of experimental P load levels</td>
</tr>
</tbody>
</table>
Table 5. Probability of regime shift to eutrophication under the five management strategies.

<table>
<thead>
<tr>
<th>Strategy</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trial-and-Error</td>
<td>0.69</td>
</tr>
<tr>
<td>Passive</td>
<td>0.23</td>
</tr>
<tr>
<td>Passive adaptive, with precaution</td>
<td>0.05</td>
</tr>
<tr>
<td>Experimental</td>
<td>0.70</td>
</tr>
<tr>
<td>Active adaptive, with precaution</td>
<td>0.56</td>
</tr>
</tbody>
</table>
Figures

Figure 32. Societal decisions about phosphorus inputs to lakes are often decided by political competition between agricultural interests who use water for pollution dilution and other interest groups concerned with use of water for drinking, fishing, and recreation. (Original)
Figure 33. Schematic diagram for the interaction of a manager (left) with an ecosystem (right). The ecosystem is the same as in Figure 5. (Original)
Figure 34. Flow chart for simulations of lake phosphorus system with parameter updating and decisions. (Original)
Figure 35. Critical P input rate versus phosphorus mass in sediment (g m⁻²). P input rates above the critical value shift the lake from the clear-water regime to the turbid regime. (Original)
Figure 36. System dynamics from a simulation with active management and no regime shift. (A) Phosphorus in lake water (triangles observed, lines one-year-ahead forecasts ± standard deviation). (B) Phosphorus input (triangles observed, lines one-year-ahead forecasts ± standard deviation). (C) Proportion of lake water phosphorus from recycling, estimated from model fitted to observations. (Original)
Figure 37. Interventions and parameter estimates from a simulation with active management and no regime shift. (A) Management intervention as a proportion of baseline phosphorus input. (B) – (D) show parameter estimates (crosses true but unknown value, lines estimate ± standard deviation. (B) $\theta = 1 - (s+h)$ (C) $\rho$ (D) $\eta$. (Original)
Figure 38. System dynamics from a simulation with active management and a regime shift. (A) Phosphorus in lake water (triangles observed, lines one-year-ahead forecasts ± standard deviation). (B) Phosphorus input (triangles observed, lines one-year-ahead forecasts ± standard deviation). (C) Proportion of lake water phosphorus from recycling, estimated from model fitted to observations. (Original)
Figure 39. Interventions and parameter estimates from a simulation with active management and a regime shift. (A) Management intervention as a proportion of baseline phosphorus input. (B) – (D) show parameter estimates (crosses true but unknown value, lines estimate ± standard deviation. (B) $\theta = 1 - (s+h)$ (C) $\rho$ (D) $\eta$. (Original)
Figure 40. (A) Bias in estimating maximum recycling rate $r_M$ (Estimated $r_M$ – true $r_M$) versus rank for simulations with passive management versus active management. (B) Bias in estimating $r_M$ versus rank for simulations with or without a regime shift, and with passive or active adaptive management. (Original)
VI FORECASTING AND DECISION FOR MULTIPLE ECOSYSTEMS SUBJECT TO

REGIME SHIFTS

Introduction

All lakes have some essential similarities. The interaction of the phosphorus and carbon cycles is a key process for the functioning of nearly all lake ecosystems. Size-structured predation governs food web dynamics in nearly all lakes. Such repeatable patterns of biogeochemistry, food web organization, and other processes mean that information from one lake is often transferable to a different lake. Because of these fundamental similarities among lakes, lakes are to some extent substitutable or exchangeable for purposes of scientific inference. These similarities are the basis of comparative limnology (Cole et al. 1991, Rigler and Peters 1995). Other types of ecosystems, such as small watersheds or islands, may also be replicates in some respects. This degree of similarity among ecosystems provides ecosystem managers with potential approaches to the dilemma discussed in Chapter V.

Chapter V considered the possibility of anticipating regime shifts in advance for a single ecosystem, by monitoring key indicators and updating a dynamic model. The probability of measuring the threshold was low, unless a regime shift occurred. It proved difficult or impossible to learn the threshold for the regime shift without crossing it and transforming the ecosystem. If the regime shift is costly and difficult to reverse, then a cautious policy that minimizes risk of regime shift may be preferable to a learning
policy that attempts to locate the threshold. Thus, in unique ecosystems subject to regime shifts, there is a dilemma between precaution and experimentation. Social-economic pressures to exploit the ecosystem may oppose precaution, but in the absence of information about the location of the threshold, one does not know which policies may cause a regime shift.

Prospects for measuring the threshold might improve, however, if many ecosystems are available for study and information is transferable among ecosystems. If a large number of similar ecosystems are available, it may be possible to use a few of them for experimentation, to gain information about the threshold and avoid unwanted regimes in the majority of ecosystems. That possibility is explored in this chapter. As in Chapter V, I will use an ecosystem model combined with models for learning and management to ask whether and how experimental learning might improve prospects for managing ecosystems subject to regime shifts.

A Landscape of Lake Fisheries

Consider a landscape with many lakes and fisheries subject to exploitation and management (Fig. 41). This general situation occurs in many regions of the world. For example, the walleye fishery of northern Wisconsin includes hundreds of lakes, which are managed using models calibrated with regular studies of a subset of 125 lakes (Beard et al. 2003a,b). Marine fisheries have also been assessed using the assumption that information on different stocks is exchangeable (Liermann and Hilborn 1997).
This chapter considers a set of similar lakes with exploited fisheries (Fig. 41). The dynamics within each lake ecosystem resemble those described in Chapter II for depensation in fish populations (Fig. 8). A piscivorous fish population is subject to harvest (Fig. 41). Juvenile piscivores are consumed by other species of fishes (forage fish), which are preyed upon by adult piscivores. As discussed in Chapter II, predator-prey interactions of this type can exhibit cultivation-depensation dynamics, in which recruitment of the piscivore depends on the capacity of adult piscivores to control the forage fish population (Walters and Kitchell 2001).

The piscivore stock collapses if the adult population falls below a certain critical level (Fig. 41). This phenomenon, called critical depensation or the Allee effect (Allee 1931, Begon et al. 1986), is marked by negative population growth rates when the population drops below the threshold for critical depensation. Critical depensation has important implications for resource management and conservation because it implies that population sizes well above zero may be nonviable (Dennis 1989, Stephens and Sutherland 1999). If this is true, then sustainable policies must maintain population levels well above the threshold, to ensure that stochastic events do not take the population below the threshold.

In the model used in this chapter, the critical depensation threshold depends on the availability of nearshore habitat for juvenile piscivores. Predatory interactions (shaded box in Fig. 41) occur primarily in nearshore habitat, such as rooted aquatic
plants or trees fallen into the lake. If adequate habitat exists for juvenile piscivores, they suffer little mortality from predation by forage fishes. As habitat availability declines, the mortality of the juvenile piscivores increases. This phenomenon is discussed in Chapter 2 and illustrated in Fig. 8. The role of habitat in fish recruitment is important, because shoreland development practices are altering fish habitat and growth in some lakes (Christensen et al. 1996, Olson et al. 1998, Schindler et al. 2000). The documented effects of habitat on fish growth suggest potentially important impacts on size-structured predation and fish community change.

In aquatic ecosystems, size-selective interspecific predation creates many situations in which critical depensation is possible (Chapter II; de Roos and Persson 2002, Walters and Kitchell 2001). The location of the threshold may depend on life history characteristics of the fishes as well as characteristics of the habitat. Factors which may drive a population across the threshold include fishing, invasion of exotic species or weather during key times of the fishes’ life history (Chapter II).

Although critical depensation is potentially widespread in aquatic food webs, and is profoundly important for management, it has proven difficult to quantify thresholds in advance of population collapses, or even to detect depensation statistically (Liermann and Hilborn 1997). This difficulty has led to controversy in both fishery management and conservation. Presence or absence of depensation has implications for the structure of ecosystem models and for harvest or conservation derived from them (Pascual et al. 1997, Runge and Johnson 2002). The problem, then, is one of choosing
which model is most appropriate for decisions (Peterson et al. 2003). Ecosystem manipulations should be helpful in determining which model is most appropriate (Walters 1986, Petraitis and Latham 1999, Carpenter 2002).

I assume that the manager’s task is to sustain the fisheries by regulating harvest rates. A program of monitoring and modeling is in place to guide the process of regulating harvest. Experiments using a subset of the lakes can be conducted to estimate the depensation threshold, and this information can be used to manage all the lakes of the landscape (Fig. 41). To assess the value of the information obtained from the experiments, it is necessary to measure the performance of the management system. I will use the expected future harvest over infinite time to measure management performance. Sport fisheries usually have substantial economic benefits which are largely related to expenditures on equipment and travel (Postel and Carpenter 1997). It seems reasonable to assume that expected future harvest over infinite time is an appropriate indicator of the total net economic benefits of managing the fishery.

Model

The model was designed to be as simple as possible, while retaining the necessary features demanded by the goals of this chapter (Fig. 42). These features include an ecosystem subject to regime shift, the possibility of different types of experiments to gain information about the threshold, plausible statistical models with different
implications for management, and an explicit process for choosing harvest policies. The model first appeared in Carpenter (2002).

There is one state variable, a harvested fish population subject to critical depensation. The depensatory process depends on the quality of habitat, represented by the number of fallen trees in the littoral zone of the lake. The habitat is assumed to change slowly relative to the fish population. I assume that both the fish population and the number of fallen trees can be manipulated experimentally. Such experiments are presently underway in lakes of northern Wisconsin http://biocomplexity.limnology.wisc.edu/).

In this chapter, I will consider two contrasting experimental designs, one which yields little information and another which is highly informative. Data from experimental manipulations are fitted to two statistical models which (1) provide reasonably good fits to simulated data but (2) yield different estimates of the threshold and have sharply different implications for policy choice.

Population dynamics of the adult piscivores follow

\[ A_{t+1} = A_t \exp(G_t + N_t) - C_t \]  

(10)

where \( A_t \) is adult stock in year \( t \), \( C_t \) is harvest in year \( t \), \( G_t \) is a function for population dynamics, and \( N_t \) is a function for stochastic shocks.
Population dynamics $G_t$ are given by

$$G_t = k + f A_t (1 - m A_t - \left\{ \frac{c (h/W_t)^q}{(h/W_t)^q + A_t^q} \right\} )$$  \hspace{1cm} (11)

Parameters include minimum population growth rate $k$, fecundity $f$, density-dependent mortality $m$, and three parameters for mortality due to interspecific predation on juvenile piscivores, $c$, $h$ and $q$. $W_t$ is the amount of habitat available for juvenile piscivores in year $t$. Maximum mortality due to interspecific predation is $c$, $h$ determines the level of $W$ at which interspecific predation occurs at half the maximum rate, and $q$ determines the slope of the interspecific mortality curve near this half-maximal point. $W_t$ is the time series of habitat. The interspecific predation term $\left\{ \frac{c (h/W_t)^q}{(h/W_t)^q + A_t^q} \right\}$ is plotted against adult stock for two different levels of habitat in Fig. 8B. Interspecific predation on juvenile piscivores declines with adult population size, because the adults suppress the forage fishes that prey on the juveniles. Also, as the amount of habitat for juvenile piscivores ($W$) increases, predation on juvenile piscivores declines.

Process noise $N_t$ represents stochastic effects on population dynamics due to factors such as weather. This term is given by

$$N_t = z - s^2/2, \text{ where } z \sim N(0,s^2)$$  \hspace{1cm} (12)
The process variance is $s^2$. The noise term in equation 12 is adjusted by subtracting $s^2/2$ so that the mean value of $e^N$ is zero (Hilborn and Mangel 1997).

In the following, I refer to the true system dynamics as the dynamics given by equations 10 to 12. The deterministic portion of the true dynamics is calculated by setting $N_t = 0$.

For certain parameter values a threshold value of $A$ can exist, below which the population collapses to zero, and above which the population reaches a stable point. This can be seen at equilibrium by rearranging the deterministic part of the model (Equations 10 and 12) as

$$\exp \left\{ f \left( m A + \{ c \ (h/W)^q / \left[ (h/W)^q + A^q \right] \} \right) \right\} = \left[ A / (A + C) \right] \exp (k + f A) \quad (13)$$

The left side of Equation 13 is the total rate of natural (non-harvest) mortality. The right side is the total birth rate adjusted by the proportion of the population that is not harvested. In this model, habitat is assumed to change more slowly than the fish population. This is the case in lakes where habitat is provided by trees fallen into the lake (Christensen et al. 1996), because tree population dynamics are generally slower than those of fishes. In that case it makes sense to calculate steady-state fish populations (see below) for a given level of habitat, as shown in equation 13. These are not true steady states because they change slowly over time as habitat changes (Rinaldi and Scheffer 2000).
When the left side and right side of equation 13 are plotted on the same axes (as in Fig. 43 described below), the intersections correspond to equilibria. In many cases, parameters lead to two intersections. In these cases, the lower equilibrium is an unstable threshold (the depensation threshold) and the upper one is stable. The threshold level is inversely related to \( W \). Discussions of similar models are presented by Clark (1990), Carpenter (2001, 2002) and Walters and Kitchell (2001).

The management challenge is to sustain the fishery without crossing the threshold to collapse, given the complications of stochasticity, possibly unknown parameters which must be estimated from data, and slow change in \( W \) which may be poorly known.

The manager uses a subset of the lakes for ecosystem experiments to fit models for the piscivore population dynamics. The manager is aware that both population size and habitat may have important effects on the dynamics. Two types of experiments are considered, one in which contrasts are weak and another in which contrasts are strong. The experiments and their outcomes are described in the next section.

I assume that the manager does not know the true model, but instead fits approximate models to observed time series of \( A \) and \( W \). Many approximate models are conceivable, but only two particularly interesting ones are analyzed here. In
subsequent text, I refer to these as the estimated models. The first of these, referred to as the simple model, is a lag-1 autoregressive model with density dependence:

\[
Y_t = b_0 + b_1 A_{t-1} + b_2 A_{t-1}^2 + \varepsilon_t
\]  

(14)

The second estimated model, referred to as the habitat model, is the simple model augmented with a term that accounts for habitat effects

\[
Y_t = b_0 + b_1 A_{t-1} + b_2 A_{t-1}^2 + (b_3 / W_{t-1}) + \varepsilon_t
\]  

(15)

In extensive simulations, the simple habitat term, \(b_3 / W_{t-1}\), produced reasonably good fits to data, leaving little pattern in the residuals. Thus the habitat term represents an estimator of habitat effects that might well be obtained from empirical regression analyses of data generated by equations 10 to 12. The \(b_i\) are parameters to be estimated from data and the errors \(\varepsilon_t\) are assumed to be normally distributed with mean 0 and unknown variance \(\sigma^2\). The response series \(Y\) is

\[
Y_t = \log \left( \frac{(A_t + C_{t-1})}{A_{t-1}} \right)
\]  

(16)

Predicted one-step-ahead distributions of \(A_{t+1} = A_t \exp(Y_t) - C_t\) are obtained using the posterior distribution of \(Y_t\). This posterior is calculated by analyzing equations 14 and 15 using Bayesian multiple linear regression with a prior distribution that is uniform on the \(b_i\) and \(\log(\sigma)\) (Appendix; Gelman et al. 1995).
For the purposes of this chapter, I assume that management follows an optimal control policy. That is, the manager estimates the population size that leads to the maximum expected yield over infinite time, and adjust harvest to stabilize the population at that optimal level. Harvest policies of this type have many difficulties, both in theory and practice (Walters 1986, Hilborn and Walters 1992, Ludwig et al. 2001). In this chapter they are used as a benchmark to show how the difficulties of estimating thresholds can lead to extirpation of valuable populations. The analyses presented here depict only one of the difficulties of optimal control policies for living resources. For a broader view of the problems with optimal management of natural resources, and some alternatives, see Gunderson and Holling (2002).

If management follows an optimal control policy, the goal is assumed to be maximization of utility $V$ derived from harvest (Clark 1990), defined here as

$$ V = \sum \delta^t C_t \quad (17) $$

In words, the performance of the fishery, $V$, is assumed proportional to the total future discounted harvest for all time. The summation is over time from the present to infinity, $\delta$ is the discount factor, and $C_t$ is catch in year $t$. The economic discount factor $\delta$ ($0 < \delta < 1$) measures the manager’s preference for current versus future harvest. For example, if $\delta = 0.98$ then 100 fish this year are considered to be as valuable as 98 fish next year, or $100 \times 0.98^2 \approx 96$ fish in two years. Discount factors are controversial in
natural resource management (Heal 1997). For the purposes of this book, expression 17 is offered as an arbitrary benchmark for performance of the management system that is similar to the performance measures used by many other authors. Note that the economic discount factor used in this chapter is different in meaning from the statistical discount factor used in Bayesian nonlinear dynamic regression (Appendix).

The optimal policy can be found by maximizing the following expression with respect to harvest:

\[ V(A_t) = C_t + \delta \mathbb{E}[V(A_{t+1})] \]  

(18)

where \( \mathbb{E} \) is the mathematical expectation operator, which corresponds to the mean over the posterior distribution of \( V(A_{t+1}) \) (Clark 1990). This expected value depends on the policy choice \( C_t \). The optimal policy is found by establishing a target population size \( y \) and moving to that level as quickly as possible (Clark 1990). Define \( u(A,y) \) as the harvest that will move the population to a target level \( y \) in one time step

\[ u(A,y) = A \exp(M_i) - y \]  

(19)

In equation 19, \( M_i \) is calculated from one of the fitted models (Equations 14 or 15), or from the true model (Equations 10 to 12). In the latter case, \( M_i \) corresponds to \( G \) from equation 11. When one of the fitted models is used, \( M_i \) corresponds to \( Y \) from equation 14 or 15. Because harvest cannot be negative, we set
\[ C_t = u(A_t, y) \text{ if } u(A_t, y) \geq 0 \quad (20A) \]

\[ C_t = 0 \text{ if } u(A_t, y) < 0 \quad (20B) \]

Each model yields a distribution of future values of \(A_t\). The distribution of \(\log(A_t)\) is normal in the case of the true model, and \(\text{Student-t}\) in the case of the fitted models (Gelman et al. 1995). In computing policies we must account for the probability of obtaining each possible value of \(A_{t+1}\) given a particular value of \(A_t\). This was done by computing probabilities on a discrete mesh, then weighting each possible value of \(A_{t+1}\) by its probability, as in Carpenter et al. (1999b) Appendix C. I used a mesh of 50 grid cells uniformly distributed over the interval \([\log(\hat{A}) - 4 \, s_{\log(\hat{A})}, \log(\hat{A}) + 4 \, s_{\log(\hat{A})}]\) where \(\log(\hat{A})\) is the expected value of \(\log(A)\) and \(s_{\log(\hat{A})}\) is the standard deviation for the prediction of \(\log(A)\). Given these definitions, equation 18 can be computed for any given value of \(y\). The value of \(y\) that maximizes \(V\) is computed by Brent’s method (Press et al. 1989) over the interval \([0, A_t]\).

When the experimental data do not clearly favor one model over another, model uncertainty may have a significant influence on policy calculations for resource management (Walters 1986, Peterson et al. 2003). Model uncertainty refers the probability that a given model is true. It is different from parameter uncertainty, which relates to the probability distribution of parameters, and from the error term of the model, which relates to the probability distribution of model residuals. Like parameter
uncertainty and the model error term, model uncertainty affects the uncertainty of predictions.

To account for the effect of model uncertainty on predictions, I calculated a third estimate of optimal population size by Bayesian model averaging, or BMA (Raftery et al. 1997, Fernández et al. 2001). BMA is a weighting method, in which the impact of each model on the policy is weighted according to the credibility of the model. The credibility is based on the model's fit to data. According to this procedure, the Bayesian model average utility, \( V_{BMA} \), for a given \( y \) value is calculated over both fitted models (Raftery et al. 1997, Fernández et al. 2001) as:

\[
V_{BMA}(y) = p \ V_D(y) + (1-p) \ V_H(y) \quad (21)
\]

\( V_D \) is the utility under the simple density-dependent model (Equation 14) given \( y \), \( V_H \) is the utility under the habitat model (Equation 15) given \( y \), and \( p \) is the posterior probability of the simple density-dependent model. The posterior probability \( p \) is computed by the method of Fernández et al. (2001, using her equations 2.12 and 4.1). In this exercise, there are only two models so the posterior probability of the habitat model is 1-\( p \). The optimal population size is computed by finding the target level \( y \) which maximizes \( E[V_{BMA}(y)] \). As described above for the individual models, this expectation was computed over a discrete mesh, assuming a Student-t distribution for the predictive distribution of the two estimated models. The value of \( y \) that maximizes \( E[V_{BMA}(y)] \) is computed by Brent's method (Press et al. 1989) over the interval \([0,A_i]\).
Results

The birth and death rates of the fish population for three different habitat conditions were calculated using Equation 13 (Fig. 43). In all cases the birth and death rate curves cross at two values of A. The right intersection point is stable: at slightly larger values of A, deaths exceed births and drive the population down to the intersection point, while at slightly smaller values of A, births exceed deaths and drive the population up to the intersection point. This stable value of A is the same for all three habitat conditions. The left intersection point, the threshold for collapse of the fish stock, is unstable. At slightly larger values of A, births exceed deaths and drive the population toward the right intersection point. At slightly lower values of A, deaths exceed births and the population is driven extinct. This threshold occurs at increasingly large population sizes as the habitat deteriorates.

Two simulated experiments were calculated to fit the approximate models of equations 14 and 15 (Table 6). In each experiment, fish stock size and habitat condition are manipulated in a number of lakes, and then the fish dynamics are observed for two years. The “strong contrast” experiment is an example of data which might derive from an aggressive program of experimental management. It substantially reduces the model uncertainty. The “weak contrast” experiment represents data which poorly discriminate the models. Note, however, that even this rather uninformative experiment assumes that 6 manipulated lakes are studied. Also, in these simulations I have
assumed that observation error is negligible due to intensive sampling. Thus even the “weak contrast” data in this exercise are substantially better than those available for most lake management decisions.

Posterior probabilities of the two fitted models were calculated by the method of Fernandez et al. (2001) (Table 6). The weak-contrast experiment does not discriminate the two models; each has a posterior probability near 0.5. The strong-contrast experiment detects the habitat effect. Consequently, given the strong-contrast experiment there is a high posterior probability for the habitat model and a low posterior probability for the simple model.

The experiments differed sharply in their estimation of the threshold (Table 7). With strong-contrast data, the estimated threshold was within about 10 fish / ha of the true threshold. The estimated threshold decreased as habitat quality increased, consistent with the true ecosystem dynamics. Standard deviations of threshold estimates were 11 to 14 fish ha\(^{-1}\), reflecting the magnitude of uncertainty about the location of the threshold. With weak-contrast data, the estimate of the threshold was much more uncertain. The mean estimate was negative in all cases. There was no clear trend of the threshold with changing habitat conditions. In practice, this would be interpreted as evidence for only one positive intersection of the birth and death curves, the stable one (Fig. 43). The analyst would conclude, incorrectly, that depensatory collapse was not possible for this fish stock. However, the standard deviations are quite large, indicating considerable uncertainty about the location of the threshold.
I compared the performance of optimal management using weak-contrast data and strong-contrast data for lakes with the three habitat conditions shown in Fig. 43. In each case, I will compare optimal population targets as a function of fish population size (Figs. 44 to 46). These targets are computed under 4 models: the fitted simple model, the fitted habitat model, the Bayesian average of these two fitted models, and the true model. In each case, it is interesting to assess the performance of the models near the threshold for fish population collapse.

When the fish habitat is poor, the threshold for collapse occurs when the fish population declines to about 50 fish ha\(^{-1}\) (Fig. 43A). Note that in this case the habitat level used for the policy calculations was a treatment level in the experiments (Table 6). Given the true system dynamics, the policy calculations show correctly that the population must drop to zero if the initial stock size is less than about 50 fish ha\(^{-1}\) (Fig. 44D). With weak-contrast data, under which the simple model is credible (Table 6), the simple model indicates that positive populations can be maintained with initial stock sizes as low as about 42 fish ha\(^{-1}\) (Fig. 44A). With strong-contrast data, the simple model indicates that positive populations can be maintained from initial stock sizes as low as nearly 20 fish ha\(^{-1}\), but the credibility of the simple model is very low if the contrast in the data is strong. The habitat model is close to the correct threshold with weak-contrast data (Fig. 44B). With strong-contrast data, the habitat model incorrectly indicates that positive fish populations can be maintained when the initial stock is as low as about 42 fish ha\(^{-1}\). The Bayesian model average gives similar results for both weak-
and strong-contrast data (Fig. 44C). It indicates incorrectly that positive stocks can be maintained if the initial stock is as low as about 42 fish ha\(^{-1}\).

When the fish habitat is moderate, the threshold for collapse occurs at a fish population of about 22 fish ha\(^{-1}\) (Fig. 43B). In this case, the habitat level used for the policy calculations is not included in either experiment, but is close to one of the experimental treatments used in the strong-contrast data (Table 6). Given the true population dynamics, the policy calculation is close to the true threshold (Fig. 45D); the small error is attributable to the mesh interval used for initial stock sizes. The simple model is close to the true threshold given strong contrast data (Fig. 45A), but of course this model has low credibility under the strong contrast data. With weak contrast data, the simple model indicates, incorrectly, that the threshold is about 40 fish ha\(^{-1}\). The habitat model indicates that the threshold is about 30 fish ha\(^{-1}\) for both weak- and strong-contrast data (Fig. 45B). The Bayesian model average indicates that the threshold is between about 30 and 40 fish ha\(^{-1}\), depending on the data set (Fig. 45C).

When the fish habitat condition is high, the threshold for collapse occurs at a fish population of about 17 fish ha\(^{-1}\) (Fig. 43C). In this case, the habitat level used for the policy calculations is included in the strong-contrast data set, but must be extrapolated in the weak-contrast data set (Table 6). Given the true population dynamics, the shift in policy occurs below the true threshold (Fig. 46D). This is a conservative policy, in the sense that a population below the threshold is underharvested and may recover due to a fortunate stochastic shock. The simple model overestimates the true threshold under
both data sets (Fig. 46A). The habitat model accurately estimates the threshold for the strong-contrast data set, and overestimates the threshold for the weak contrast data set (Fig. 46B). The Bayesian model average also gets the threshold about right given the strong-contrast data, and overestimates the threshold given the weak-contrast data (Fig. 46C).

To assess the overall performance of the estimated models, the difference in optimal stock sizes between the true model and the Bayesian model average was calculated (Fig. 47). This difference is zero when the estimation is perfect. Note that, in every case, the deviation between true and estimated models is greatest near the threshold. True threshold values were about 50 fish ha\(^{-1}\) for poor habitat, 22 fish ha\(^{-1}\) for moderate habitat, and 17 fish ha\(^{-1}\) for good habitat (Fig. 43). With weak-contrast data, the performance is significantly worse. The estimated model routinely underestimates optimal population size, an error that will lead to overharvest.

**Discussion**

The model is a highly simplified representation of fish management. The simplifications were designed to investigate the effects of ecosystem experimentation on inference about thresholds and optimal harvest policies based on these inferences. The exercise shows that thresholds are difficult to measure without strong experimental manipulations that yield high-contrast data. Even when such data are available,
uncertainty is high near the threshold and policy choices are strongly affected by this uncertainty.

There are several assumptions that have strong effects on these findings. First, the model assumes that factors governing fish dynamics are the same across lakes, so the model and parameter estimates apply to all the lakes on the landscape. If it is not appropriate to describe the lakes using a common model, then the management problem is more similar to the case described in Chapter V, where each ecosystem is unique. This issue could be explored using a hierarchical Bayesian model (Gelman et al. 1995), in which the parameters for the threshold of a particular lake were viewed as a sample from a meta-distribution of parameters for the set of lakes on the landscape.

The model assumes that the threshold is constant over time. In reality, the threshold could move slowly over time due to changes in habitat, food web composition, or other ecological factors that were not included in the model. If the threshold moves over time, then repeated experiments will be necessary to track the changes. In general, this will increase uncertainty for model predictions and policy choices at any given time.

It is assumed that the habitat and harvest can be manipulated independently in entire lakes. Such replicated, multi-factor ecosystem experiments are rarely possible. Most ecosystem experiments have involved one or two manipulated ecosystems and one or two reference (or control) ecosystems (Carpenter et al. 1995, Carpenter 1998).
When an ecosystem experiment reveals something important, the experiment tends to be repeated by different research groups in different regions (Carpenter 1998). This type of replication leads to especially robust inferences, because it samples across regional differences in ecosystems as well as differences in methodology and practice among research groups. However, this type of replication takes a long time. It leads to inferences more slowly than the experiments assumed in this model. Slow inference could lead to much greater uncertainty about the location of the threshold, especially if the threshold is moving over time.

Some of the experimental manipulations assumed in the model are drastic ones that involve massive changes to habitat, deliberate overharvest of fish stocks, or severe reductions in harvest of fish stocks. While these extreme treatments are the most important ones for identifying the threshold, they are the most difficult ones to conduct. Extreme manipulations often face political barriers (Walters 1997, Carpenter 1998). When extreme manipulations are omitted, the situation is similar to the “weak contrast” situation shown in this chapter: high uncertainty, poorly-characterized thresholds, underestimate of optimal stock sizes, and overharvest with risk of inadvertent collapse. Ironically, a manager who avoids extreme manipulations will promote overharvest and risk collapse of fish stocks in most of the lakes on the landscape. While the extreme manipulations will damage some ecosystems, they lead to better policies in many other ecosystems. For the manager who is responsible for a landscape of lakes, there are significant advantages in investing in a few extreme experimental treatments.
Data and inference about thresholds

This exercise shows that analyses of thresholds demand excellent data. Given strong-contrast data, it may be possible to locate the general neighborhood of a threshold and take appropriate management action.

Even with excellent data, however, it is very difficult to locate the threshold with precision. This modeling exercise employed simplifying assumptions that made it easier to locate the threshold. Despite these assumptions, there was considerable variability in estimates of the threshold. Uncertainty about the threshold resulted from the process variance of the fish dynamics and uncertainty about which model was appropriate. In a more realistic situation, there would be additional sources of uncertainty, including observation error and dynamics of other slowly-changing variables (in addition to W) that could cause the threshold to shift over time. Also, I have assumed that whole-ecosystem observations for similar lakes are available for fitting the models. In reality, it might be necessary to estimate some parameters using data from small-scale experiments. In this case there are additional uncertainties due to extrapolating parameters from one scale to another. Therefore, this chapter has presented a rather optimistic scenario for estimating thresholds. In most practical situations, the uncertainties will be substantially larger than portrayed here.

In most cases, the estimated models underestimate the size of the population that can be sustained in the neighborhood of the threshold. Put another way, the
estimated models tend to indicate that the threshold occurs at a population size larger than the true threshold. The impact of this overestimate on decisions would depend on the goals of the manager. A manager who was purely interested in optimal yield would assume that the population should be driven extinct from starting levels below the apparent threshold, but above the true the threshold. This error would lead to extirpation of stocks that are in fact potentially sustainable. A manager who sought to avoid thresholds, however, would behave more conservatively. Such a manager would harvest cautiously at stock sizes well above the true threshold, because of the fitted models’ overestimation of the true threshold. These very different outcomes depend entirely on the managers’ preference for maximizing expected present value of harvest versus avoiding the threshold for collapse.

**Effect of the threshold on policy choice**

Near the threshold, there is a sharp change in the optimal control policy. Above the threshold, the policy is to sustain a positive fish stock. Below the threshold, the policy is to harvest all remaining fish and drive the stock to zero. When the model for fish dynamics is estimated from data, the estimated location of the threshold has a powerful effect on policy choice. In any particular situation, the decision depends on the initial stock size, the choice of model for fish dynamics, and the estimates of parameters for that model, including parameter variances and the model variance.
The “use them or lose them” feature of the optimal control solutions occurs in many analyses of this type (Clark 1990, Ludwig et al. 2003). It is a consequence of the arbitrary decision to maximize net future discounted harvest. If this goal was replaced by a different goal, such as to avoid the threshold, different policies would result (Limburg et al. 2002). If the goal is to avoid collapse, one would sharply reduce harvest at stock sizes well above the threshold. At lower stock sizes, one would try to rebuild the population, for example by stocking or creating connections to refuges.

**Implications for experimental management**

If the goal of management is to avoid the threshold, ecosystem experiments can significantly improve the information for choosing management targets. The experiments also show the cost of crossing thresholds in direct and powerful ways. Thus ecosystem experiments combined with precautionary management appear to be a promising approach for modular ecosystems like lakes.

A landscape of similar ecosystems offers interesting possibilities for actively adaptive experimental management. By using a subset of the available ecosystems for strong-contrast experiments, it is possible to gain substantial information about regimes and thresholds. However, it is risky to use this information for optimal control near the threshold. If the goal of management is sustaining the ecosystem, then a more precautionary approach is necessary. In this case, the precautionary choices are informed by relatively precise information about the location of the threshold. The
precautionary manager should recognize that the location of the threshold is uncertain and that the threshold might be moving. The experimental results are best used to design rough guidelines and simple rules for maintaining the system in desired regimes.

Strong-contrast data provide better information about the location of the threshold, and thereby lead to policies that are more likely to avoid the threshold while coming close to maximizing the long-term yield of the fishery. With weak-contrast data, the performance of the management system is significantly worse. One can reach the erroneous conclusion that there is no threshold. At best the estimate of the threshold will have high variance. The resulting policies aim for stock sizes that are too low. Consequently, stocks are overharvested, leading to frequent collapses as thresholds are crossed. These unwanted stock collapses are a direct result of weak-contrast data.

Extreme manipulations are necessary to create strong-contrast data. These extreme manipulations will damage some ecosystems, and for this reason they may be opposed by the public and by some managers. However, strong-contrast data are a good investment when it is possible to manipulate a few ecosystems to obtain information that is useful for managing many ecosystems. Weak-contrast data can lead to far more damage as ecosystems are over-exploited due to poor knowledge of thresholds.

Summary
Actively adaptive experimental management has great potential for landscapes with a multiplicity of similar ecosystems. While lakes are the focus of this chapter, analogous approaches may be possible for other types of modular ecosystems, such as small watersheds or islands. Experimentation on a subset of the ecosystems can reveal which regimes are possible and provide rough estimates of the thresholds. Such information is valuable for maintaining desired regimes.

Management actions may cross thresholds inadvertently when thresholds are poorly known. Results of this chapter show that poor knowledge of the threshold leads to overly aggressive harvest policies that increase the risk of crossing the threshold. This may occur in many situations where policies push ecosystem state near to unknown thresholds. It may be possible to devise utility functions that lead to less risky choices when a threshold is more uncertain (Heal and Kriström 2002).

Successful experiments involve strong manipulations that cross thresholds in some ecosystems. Such experiments yield data with strong contrasts between experimental treatments. While locations of thresholds will be uncertain after even the best experiments, experimental estimates of thresholds lead to better policy choices within the framework described in this chapter. Prospects for maintaining a desired regime are improved when experimental estimates of thresholds are employed in precautionary policies that seek to avoid thresholds.
To provide useful information about thresholds, thresholds must be crossed in some experimental ecosystems. This means that some ecosystems will be damaged by the manipulations. This damage must be weighed against the improved performance of management for the other ecosystems of the landscape. If extreme manipulations are not performed, the weak-contrast data that result lead to a number of policy problems related to high uncertainty. Within the framework of this chapter, weak-contrast data lead to erroneous conclusions about absence of a threshold, or large errors in estimating the location of the threshold. The consequence is overexploitation with high risk of inadvertently crossing the threshold to an unwanted regime. Avoidance of extreme manipulations has severe consequences, leading to ecosystem damage that far exceeds the potential impact of the experiments.

Even under the best conditions, estimates of threshold location for real ecosystems will have substantial errors. Given the complexity of ecosystems, and the challenges of experimenting with them, it seems unlikely that precise quantitative measurements of any important threshold will be attainable. Nevertheless, ecosystem experiments that cross thresholds lead to rough estimates of threshold location that could be extremely useful in management. Such experiments reveal the levels of exploitation that can be maintained without a costly regime shift. Policies that seek to avoid collapse by maintaining ecosystems far from thresholds, and well within desirable domains, may succeed. If management seeks to avoid the threshold, this implies a different utility function with a heavy penalty for transcending the threshold (Heal and Kriström 2002). Thus, the combination of experimentation on a subset of ecosystems
with precautionary management appears to be a promising management approach for modular ecosystems such as lakes, small watersheds or islands.
Tables

Table 6. Description of the simulated experiments.

<table>
<thead>
<tr>
<th>Contrast</th>
<th>Number Of Lakes</th>
<th>Initial Fish Stocks (A)</th>
<th>Habitat Conditions (W)</th>
<th>Posterior probability for Simple Model</th>
<th>Posterior probability for Habitat Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weak</td>
<td>6</td>
<td>10, 55, 100</td>
<td>0.4, 1.4</td>
<td>0.49</td>
<td>0.51</td>
</tr>
<tr>
<td>Strong</td>
<td>25</td>
<td>10, 32, 55, 77, 100</td>
<td>0.4, 0.75, 1.1, 1.45, 1.8</td>
<td>0.01</td>
<td>0.99</td>
</tr>
</tbody>
</table>

Table 7. Estimated threshold (fish ha\(^{-1}\)) for an unharvested fish population given the weak-contrast and strong-contrast data sets described in Table 6. Means and standard deviations (in parentheses) are presented. The threshold was estimated using the simple model (Equation 14) and the habitat model (Equation 15) at three habitat levels, assuming C = 0. Means and standard deviations of the threshold were calculated by parametric bootstrapping from the multivariate Student-t distribution of estimated parameters and the Student-t distribution of residuals (Efron and Tibshirani 1993).

<table>
<thead>
<tr>
<th>Contrast</th>
<th>Simple Model</th>
<th>Habitat Model</th>
<th>Habitat Model</th>
<th>Habitat Model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>All W values</td>
<td>W = 0.4</td>
<td>W = 0.8</td>
<td>W = 1.8</td>
</tr>
<tr>
<td>Weak</td>
<td>-58.1 (1530)</td>
<td>-19.4 (277)</td>
<td>-14.3 (250)</td>
<td>-18.9 (249)</td>
</tr>
<tr>
<td>Strong</td>
<td>26.2 (14.1)</td>
<td>40.3 (11.6)</td>
<td>27.1 (11.8)</td>
<td>18.2 (11.3)</td>
</tr>
</tbody>
</table>
Figures

Figure 41. Overview of the system analyzed in this chapter. Many similar lake fisheries on a landscape are subject to management. A subset of the lakes is available for experimentation to gain information about fish population dynamics and possible thresholds. (Original)
Figure 42. Flow chart of model calculations presented in this chapter. (Original)

Experimental Design
(Weak Contrast Data versus Strong Contrast Data)

Simulate Ecosystem Dynamics using True (but Unknown) Model

Fit Alternative Models to Simulated Data
(Simple Model versus Habitat Model)

Calculate Optimal Harvest Policies for Models:
Fitted Simple Model
Fitted Habitat Model
Bayesian Average of Fitted Models
True Model
Figure 43. Vital rates from the deterministic part of the fish population model (births solid line, deaths dashed line; both in fish ha\(^{-1}\) y\(^{-1}\)) versus population size (fish / ha). A. Poor habitat (W = 0.4). B. Moderate habitat (W = 0.8). C. Abundant habitat (W = 1.8). Values of other parameters are C = 4, q = 4, k = 0.1, f = 0.01, m = 0.01, c = 10, h = 10. (Original)
Figure 44. Apparently optimal population size (fish / ha) versus initial fish population (fish / ha) in simulations with poor habitat (W = 0.4). In panels A-C, optimal population sizes are calculated by fitting models to data with weak contrast (dashed line) or strong contrast (solid line). A. Simple model with density-dependence. B. Habitat model, with density dependence and a habitat effect. C. Bayesian model average of the simple model and the habitat model. D. Optimal population size calculated from true system dynamics. Values of parameters as in Fig. 1. Additional parameter values are s = 0.1, \( \delta = 0.98 \). (Original)
Figure 45. Apparently optimal population size (fish / ha) versus initial fish population (fish / ha) in simulations with moderate habitat ($W = 0.8$). In panels A-C, optimal population sizes are calculated by fitting models to data with weak contrast (dashed line) or strong contrast (solid line). A. Simple model with density-dependence. B. Habitat model, with density dependence and a habitat effect. C. Bayesian model average of the simple model and the habitat model. D. Optimal population size calculated from true system dynamics. Values of parameters as in Fig. 1. Additional parameter values are $s = 0.1$, $\delta = 0.98$. (Original)
Figure 46. Apparently optimal population size (fish / ha) versus initial fish population (fish / ha) in simulations with abundant habitat ($W = 1.8$). In panels A-C, optimal population sizes are calculated by fitting models to data with weak contrast (dashed line) or strong contrast (solid line). A. Simple model with density-dependence. B. Habitat model, with density dependence and a habitat effect. C. Bayesian model average of the simple model and the habitat model. D. Optimal population size calculated from true system dynamics. Values of parameters as in Fig. 1. Additional parameter values are $s = 0.1$, $\delta = 0.98$. (Original)
Figure 47. Difference between estimated optimal population size and the optimal population size (fish / ha) computed from the true system dynamics versus the initial population (fish / ha). The y-axis value is calculated as the estimated optimal population size from Bayesian model averaging minus the optimal population size if the true system dynamics were known. Solid lines show results with strong-contrast data set, and dashed lines show results with weak-contrast data set. A. Poor habitat (W = 0.4). B. Moderate habitat (W = 0.8). C. Abundant habitat (W = 1.8). All other parameters as in Figs. 2 – 4. (Original)
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...
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).

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<tr>
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<th>Known Regime Shift</th>
<th>Novel Regime Shift</th>
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<tr>
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<td>Modular</td>
<td>Singular</td>
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<td><strong>Examples</strong></td>
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<td>Piscivore collapse</td>
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<td>Trophic cascades</td>
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<td><strong>Strategies for</strong></td>
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<td><strong>Strategies for</strong></td>
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<td>memory and creativity</td>
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<td>Build institutions that learn and adapt rapidly</td>
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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)
Regime shifts are among the most exciting research frontiers in ecology. They bring long-term and spatially-extensive ecological research together with theory, modeling and statistical approaches that are at the forefront of ecology today. Regime shifts, like many important topics of ecological research, demand a synthetic approach. Thus there are tremendous opportunities for small interdisciplinary teams to make crucial advances in the understanding of regime shifts.

Regime shifts are also a key topic in applied ecology. Ecosystem management is devoted to maintaining desirable ecosystem regimes, avoiding transitions to undesirable ecosystem regimes, and inventing new ways to adapt to novel ecosystem regimes. Thus regime shifts are crossroads of ecology and management.

The choice between globally-stable and multiple-attractor models of ecosystems is a key dilemma (Fig. 52). We generally have limited information about potential attractors and the state of the ecosystem. This uncertainty is depicted by the large and shifting balls and thick, fuzzy topography of the ball-and-cup diagram labeled “observations” in Fig. 52. Because the data are limited, many different inferences are plausible, and the various models have diverse implications for management decisions. Two simple extremes are shown (Fig. 52). An analyst may favor a linear model of global stability, which implies that resilience is infinite. It may further be assumed that
the desired ecosystem state (position of the ball) can be attained by controlling the position of the ecosystem through continued exogenous pressure (grey arrow). Alternatively, an analyst may conclude that there are multiple attractors, although they are not very well defined, and that the ecosystem could be managed by increasing resilience of the desired attractor, even if we are uncertain about its characteristics. The variability, or at least some of it, may be due to the intrinsic dynamics of the ecosystem, and may even be essential for building resilience.

A central message of this Excellence in Ecology book is that alternate attractors are difficult to discern yet cannot be neglected by ecologists. Fundamental work on regime shifts and alternate attractors will lead to important new insights about ecosystem change. In management, practices that ignore the possibility of regime shifts risk unpleasant surprises. A narrow focus on controlling and stabilizing ecosystem dynamics may increase the risk of crossing thresholds, while diminishing variance that is necessary for estimating where the thresholds lie.

Intensive control of ecosystems seems to increase frequency of regime shifts and perhaps promote the emergence of novel regimes. Why? Are there ways to increase ecosystem resilience, and reduce the frequency of unwanted regime shifts? How do management and ecological regime shifts interact? How do management practices change the resilience of ecosystems? Can management institutions invent better ways to address ecosystem regime shifts before they occur? These are among the most important questions facing ecology today. Yet, in a sense they are old
questions, because people have encountered ecosystem regime shifts at many times in the past.

Humanity's search for an ideal environment has meandered over time, and has never approached a stable condition. While the details differ among cultures, biogeographic regions, and eras of history, there have always been tensions between exploitation and nurturing of ecosystems, and between controlling and inventive styles of management. Control provides security, but it also leads to dependency. Control gets easier as systems are simplified, but simplification creates fragility and vulnerability. When ecological regimes change and old management systems break down, the future depends on innovative new approaches. Innovation arises from multiple human perspectives, heterogeneous landscapes, diverse biotic communities, and modular ecosystems. People nurture these seeds of creativity by instinct, even as they strive for greater predictability and control. So we move from one to the other – from control to innovation, simplification to diversification, efficiency to creativity, breakdown to renewal – seeking a point of balance that is not attainable. Instead, we find endless change, an ongoing dance with nature which sustains us and inspires us. Regime shifts are part of the dance, the big changes in rhythm that seem to transform everything. If we understand that surprises are coming, we are more likely to adapt and dance onward.
Figure

Figure 52. Observations provide uncertain information about ecosystem state (circles) and potential regimes (curves). Two possible inferences and management actions are shown for maintaining desired ecosystem conditions. Noisy data might support the idea that the system is globally stable and controllable (left), or the idea that the system has multiple attractors (right). If there are multiple attractors, it may be possible to increase resilience of a desirable attractor. (Original)
APPENDIX: BAYESIAN REGRESSION METHODS

Introduction

Many of the regressions presented Chapters III to VI derive from Bayesian statistics. Bayesian methods are less familiar than some other statistical approaches in ecology, and for this reason it is appropriate to provide some methodological background. This Appendix provides a brief summary of the Bayesian regression methods that are employed for many analyses presented in the book.

Methods presented below come from the Bayesian theory for normally-distributed random variables (Gelman et al. 1995). Bayesian methods can be used for any probability distribution. The methods shown here are but a narrow subset of the possibilities.

The explanations in this Appendix assume that the reader is familiar with matrix algebra. Matrix algebra is explained in many elementary mathematics texts. The matrix algebra needed to follow most statistical calculations is explained in many textbooks, for example Draper and Smith (1981).

Prior Probabilities and Bayes’ Theorem

The task of each Bayesian analysis is to build a model for the relationship between parameters (θ) and observables (y), and then calculate the probability distribution of parameters conditional on the data, p(θ|y). In addition, the Bayesian analysis may calculate the predicted distribution of unobserved data.
Bayesian statistics begins with a model for the joint probability distribution of \( \theta \) and \( y \), \( p(\theta,y) \). \( \theta \) may be a single parameter or a vector of many parameters, and \( y \) may be a vector of observations of a single variable or a matrix with multiple observations of many variables. The function \( p \) is a probability distribution. An example of a model is the familiar one for estimating the mean and variance of a normally distributed population, in which \( p(\theta,y) \) is a normal distribution with mean and variance given by the parameter vector \( \theta \), and \( y \) is a sample of independent measurements.

Using the definition of conditional probability (Mangel and Clark 1988, Howson and Urbach 1989), \( p(\theta,y) \) can be decomposed into two components:

\[
p(\theta,y) = p(\theta) \, p(y|\theta) \tag{A.1}
\]

By convention, \( p(\theta) \) is called the prior distribution of \( \theta \) (i.e. the distribution prior to observing the data \( y \)) and \( p(y|\theta) \) is called the likelihood function (i.e. the likelihood of observing the data given a particular parameter value \( \theta \)). Bayes’ theorem provides the posterior probability distribution \( p(\theta|y) \) (i.e. the distribution of \( \theta \) obtained after observing \( y \) and combining the information in the data with the information in the prior distribution):

\[
p(\theta|y) = p(\theta) \, p(y|\theta) / p(y) \tag{A.2}
\]

Equation A.2 provides a probability distribution of \( \theta \) given observations of the data \( y \).
In this equation, \( p(y) \) is the sum (or integral) of \( p(\theta) p(y|\theta) \) over all possible values of \( \theta \). For discussions of these basic points of Bayesian analysis, see Mangel and Clark (1988) or Howson and Urbach (1989).

**Subjectivity**

Bayesian probabilities are sometimes called subjective probabilities. It is important to understand exactly what is meant by “subjective” in this context.

Decision analyses are often unique. The situation in which one is making the decision may occur only once. It cannot be replicated, so there is no possibility for measuring probabilities by repeated sampling. Nevertheless, Bayesian analysis may be used to compute the probabilities needed to make decisions. Because these probabilities cannot be measured by repeated sampling, they are called “subjective” and they represent a degree of belief in a particular outcome. For thorough discussions of this notion of subjectivity in the context of decision making, see Lindley (1985), Howson and Urbach (1989) and Pratt et al. (1995).

Also, if there is no basis in observed data for estimating the prior probability distribution, then the analyst may simply assume a particular prior distribution. The consequences of this assumption can be tested by sensitivity analyses that compare the response of the posterior distribution to different assumptions about the prior distribution. Most commonly, a *noninformative* prior distribution is assumed. A noninformative prior distribution assigns the same probability to each possible value of the parameters. If the number of observations is at least moderately large, a noninformative prior distribution will have negligible impact on the
posterior distribution. If the data y are limited, however, the choice of prior distribution may have a substantial impact on the posterior distribution. In this case, sensitivity analysis is needed to evaluate the consequences of different assumptions about the prior distribution.

**Further reading**

This Appendix is not intended to be a thorough review of Bayesian methods. Readers who are interested in Bayesian methods should consult one of the many excellent texts on the topic. Howson and Urbach (1989) describe the Bayesian approach to scientific reasoning from a philosophical perspective. The book clarifies the similarities and differences between Bayesian inference and other types of statistical inference. Bernardo and Smith (2000) give a thorough summary of Bayesian theory. On a more practical level, Gelman et al. (1995) provide a user’s guide to Bayesian calculations. Their book covers several of the statistical models most familiar to ecologists from a Bayesian perspective. It is oriented toward application of statistics more than toward theory. Many of the methods presented by Gelman et al. (1995) can be computed using the software package WINBUGS which is available from the Internet (URL: http://www.mrc-bsu.cam.ac.uk/bugs/welcome.shtml).

Bayesian time-series methods are also called dynamic regressions, because the parameter estimates are updated over time in a dynamic way. Pole et al. (1994) have written a practical guide to Bayesian time series analysis using models that are linear in the parameters. They also provide software for calculating Bayesian dynamic regressions. Detailed descriptions of their algorithm as implemented for ecological analyses are presented in appendices to Cottingham and Carpenter (1998) and Lamon et al. (1998). West and Harrison (1989) present the nonlinear
Bayesian statistics are used extensively in decision analysis. A brief introduction to decision theory was written by Lindley (1985). His book also covers many basic aspects of Bayesian statistics. The book by Pratt et al. (1995) is as much a textbook of Bayesian statistics as it is a book about decision theory. Decision theory is most familiar to ecologists as a method in behavioral ecology. Mangel and Clark (1988) provide an excellent introduction while Clark and Mangel (2000) have written an updated and wider survey of the uses of dynamic optimization models in ecology.

**Bayesian Linear Regression**

**Linear Regression with Noninformative Prior**

In linear regression, the observations consist of a response variable in a vector $y$ and one or more predictor variables in a matrix $X$. The vector $y$ has $n$ elements, corresponding to $n$ observations. The matrix $X$ has $n$ rows, corresponding to the observations, and $k$ columns corresponding to the number of predictors. If the regression includes an intercept, one of the columns of $X$ is a column of ones. The parameters are the regression coefficients $\beta$ and the error variance of the fitted model, $\sigma^2$. The model that relates observations and parameters is written:

$$(y \mid \beta, \sigma^2, X) \sim \text{Normal}(X \beta, \sigma^2 I) \quad (A.3)$$
In words, this model states that the distribution of $y$ given parameters $\beta$ and $\sigma^2$ and predictors $X$ is a normal distribution with mean $X \beta$ and variance $\sigma^2$. The identity matrix is $I$. A normal distribution is completely specified by its mean and variance.

Once the model is specified, the Bayesian analysis seeks the posterior distribution for the parameters and a predictive distribution for the model’s predictions. The analysis begins with a prior distribution. A noninformative prior distribution that is commonly used for linear regression is

$$p(\beta, \sigma^2) \propto 1/\sigma^2 \quad (A.4)$$

In words, this expression means that the joint probability distribution of $\beta$ and $\sigma^2$ given $X$ is a flat surface with a constant level proportional to $1/\sigma^2$. In many situations encountered in ecology, the outcome is not overly sensitive to this choice of prior distributions. For example, if the prior value of $\sigma^2$ is sufficiently large and the observations are many and informative, the effect of the likelihood will overshadow that of the prior distribution. It may be desirable to explore the sensitivity of the posterior distribution to the choice of prior distribution.

The posterior distribution of $\beta$ given $\sigma^2$ is

$$\beta | \sigma^2, y \sim \text{Normal}(\beta_E, V_{\beta} \sigma^2) \quad (A.5)$$
Expression A.5 states that the probability distribution of \( \beta \) given \( \sigma^2 \) and \( y \) is normal with mean \( \beta_E \) and variance \( V_\beta \sigma^2 \). The parameters of this normal distribution are computed from

\[
\beta_E = (X' X)^{-1} X' y \tag{A.6}
\]

\[
V_\beta = (X' X)^{-1} \tag{A.7}
\]

The apostrophe (‘) denotes matrix transposition.

The marginal posterior distribution of \( \sigma^2 \) (i.e. the integral over all possible values of \( \beta \) of the joint distribution of \( \beta \) and \( \sigma^2 \)) is

\[
\sigma^2 \mid y \sim \text{Inverse } \chi^2 (n - k, s^2) \tag{A.8}
\]

Expression A.8 says that the probability distribution of \( \sigma^2 \) given \( y \) follows an inverse \( \chi^2 \) distribution. The inverse \( \chi^2 \) distribution, presented by Gelman et al. (1995), is fully defined by two parameters, the degrees of freedom and the scale factor. In this case there are \( n - k \) degrees of freedom (where \( n \) is the number of observations of \( y \) and \( k \) is the number of parameters to be estimated, i.e. the number of columns of \( X \)). The scale factor \( s^2 \) is computed by

\[
s^2 = (y - X \beta_E)' (y - X \beta_E) / (n - k) \tag{A.10}
\]

Note that \( y - X \beta_E \) is the vector of residuals, or deviations of observations from predictions.
The marginal posterior distribution of β given y is written

$$\beta \mid y \sim \text{Multivariate Student t} \,(n - k, \, \beta_E, \, s^2) \quad \text{(A.11)}$$

The multivariate Student t distribution (presented by Gelman et al. 1995) has three parameters, the degrees of freedom n - k, the mean $\beta_E$, and the scale factor $s^2$. This distribution is derived by integrating the posterior distribution of $\beta$ given $\sigma^2$ (A.5) over all possible values of $\sigma^2$ (A.8).

Regressions are often fitted in order to make predictions. The predictive distribution, $y_p$, given a new set of predictors $X_p$ has mean

$$E(y_p \mid y) = X_p \beta_E \quad \text{(A.12)}$$

The marginal posterior distribution of the variance of this prediction is

$$\text{var}(y_p \mid \sigma^2, \, y) = (I + X_p \, V_{\beta} \, X_p') \, \sigma^2 \quad \text{(A.13)}$$

where I is the identity matrix. This variance formula has two components, I $\sigma^2$ for sampling variance of the new observations and $X_p \, V_{\beta} \, X_p' \, \sigma^2$ for uncertainty about $\beta$. The marginal posterior distribution of $y_p$ given y is

$$p(y_p \mid y) \sim \text{Multivariate Student-t} \,[n - k, \, X_p \, \beta_E, \, (I + X_p \, V_{\beta} \, X_p') \, s^2] \quad \text{(A.14)}$$

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Ecologists usually use Bayesian regression analysis to calculate the probability distribution of $\beta$ or the probability distribution of predictions for new observations $X_p$. The probability distribution of $\beta$ is given by A.11 with $\beta_E$ computed by equation A.6 and $s^2$ computed by equation A.10. The probability distribution for new observations is given by A.14 with $\beta_E$ computed by equation A.6, $V_\beta$ computed by equation A.7 and $s^2$ computed by equation A.10.

The multivariate Student t distribution commonly arises in Bayesian regression. A number of useful properties of the univariate and multivariate Student t distributions are presented by Gelman et al. (1995), including the equation for ordinates of the distributions. These authors also explain how to compute a random sample from a Student t distribution. Probabilities are computed by integrating the Student t distribution using the incomplete beta function, as explained by Press et al. (1989). Many scientific software packages include subroutines for computing random samples and probabilities from the univariate and multivariate Student-t distributions.

The rationale for Bayesian regression analysis is different from the rationale for classical regression (e.g. Draper and Smith 1981). The Bayesian analysis is focused toward a conditional posterior distribution for the parameters and a predictive distribution for the model. The classical analysis focuses on point estimates of parameters or predictions, as well as the variances of these point estimates. The classical analysis is derived by a different sequence of steps which involve maximization of a likelihood function for model errors (Burnham and Anderson 1998). Despite these differences, the computations turn out to be similar to the
Bayesian analysis using the noninformative prior of equation A.4. The classical estimates of $\beta$ and $\sigma^2$ are $\beta_E$ and $s^2$, respectively. The classical standard error estimate for $\beta$ is $V_\beta s^2$. The classical prediction for new data is $y_p = X_p \beta_E$ with variance $(I + X_p V_\beta X_p') s^2$.

**Linear Regression with Informative Prior**

Bayesian analysis can be used to combine two different sources of information in a single model to estimate parameters or make predictions. The results can then be combined with a third source of information to improve the parameter estimates or predictions. This process can be repeated over and over again to combine information from any number of sources. Combining multiple sources of information is one of the most important uses of Bayesian statistics in ecology (Hilborn and Mangel 1997). Ecologists frequently have information from diverse experiments or field observations that could be combined to make predictions under a single model. Bayesian statistics offer a family of methods for such mergers of information. One of these methods is linear regression with an informative prior distribution.

In linear regression with an informative prior distribution, there are two statistically-independent data sets that provide information about the model to be analyzed. We assign one data set to be the prior, and use the other data set for the likelihood.

Usually it is convenient to assume that the prior distribution of the $k$ regression parameters is multivariate Student-t. This distribution has three parameters, a vector of mean regression parameters, a matrix with variances along the main diagonal and covariances elsewhere, and degrees of freedom. In this case, the mean vector contains the $k$ prior estimates.
of the mean regression parameters ($B_0$) and the $k \times k$ parameter covariance matrix $S_0$, model variance $s_0^2$ and degrees of freedom $n_0$. For the second data set, we have a $n_1 \times 1$ response vector $y_1$ and a $n_1 \times k$ matrix of predictors $X_1$.

The posterior can be computed by treating the prior as additional data points, and then weighting their contribution to the posterior (Gelman et al. 1995). The weights are inversely proportional to the variance of the prior parameter estimates. To perform the computations, construct a new vector of observations $y$, predictor matrix $X$, and weight matrix $\Sigma$ as follows:

$$\begin{align*}
y &= [y_1 \: B_0]' \tag{A.15} \\
X &= [X_1 \: I_k]' \tag{A.16} \\
\Sigma &= [I_{n_0} \: 0 \: : S_0] \tag{A.17}
\end{align*}$$

Here $I_k$ and $I_{n_1}$ stand for the identity matrices of dimension $k$ and $n_1$, respectively. $0$ denotes the zero elements necessary to fill out the square matrix $\Sigma$, which has $I_{n_1}$ as the upper left elements and $S_0$ as the lower right elements.

The posterior estimate of the parameters follows a multivariate Student-t distribution (Gelman et al. 1995). The mean vector $\beta_E$ is

$$\beta_E = (X' \: \Sigma^{-1} \: X)^{-1} \: X' \: \Sigma^{-1} \: y \tag{A.18}$$
The scale matrix is \( s^2 V \) with \( n-k \) degrees of freedom, where \( n \) is the number of observations, \( k \) is the number of parameters estimated from the data, and

\[
V = (X' \Sigma^{-1} X)^{-1}
\]  

(A.19)

The variance \( s^2 \) with \( n_0 + n_1 - k \) degrees of freedom is calculated as

\[
s^2 = \frac{(n_0 s_0^2 + n_1 s_1^2)}{(n_0 + n_1)}
\]  

(A.20)

where the variance \( s_1^2 \) is calculated as

\[
s_1^2 = \frac{(y - X \beta_E)'(y - X \beta_E)}{(n_1 - k)}
\]  

(A.21)

Predictions for new data \( X_p \) using the regression for both existing data sets also follow a multivariate Student t distribution:

\[
p(y_p | y) \sim \text{Multivariate Student-t} \left[ n_0 + n_1 - k, X_p \beta_E, (I + X_p^T V X_p^{'}) s^2 \right]
\]  

(A.22)

In this distribution \( X_n \) is the new set of predictors, \( \beta_E \) is computed with A.18, \( V \) is computed with A.19 and \( s^2 \) is computed with A.20 and A.21.

In summary, the linear regression with two independent data sets is computed as follows. First, express the results from the first data set as a multivariate Student t distribution for the

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parameters. This distribution follows from a Bayesian regression analysis of the first set of data using noninformative priors. Then, form the new response vector, predictor matrix, and weight matrix using A.15 – A.17. The posterior distribution of parameters from both sets of data is multivariate Student t with mean given by A.18, covariance matrix $s^2 V$ computed using A.19 and A.20, and $n_0 + n_1 - k$ degrees of freedom. Predictions for new data follow the multivariate Student t distribution given by A.22.

**Bayesian Inverse Modeling**

Methods covered so far in this appendix are appropriate for models in which the response variable is a linear function of the predictors. Some models in this book involve nonlinear functions of the predictors. Parameters of these models can be estimated by various methods. The method used here estimates parameters from multiple data sets using Bayes’ theorem. Earth scientists call this method Bayesian inverse modeling (Jackson and Matsu’ura 1985). “Inverse modeling” is a term used by physical scientists to describe parameter estimation for complex models, often in situations where the models are poorly constrained by data.

The general form of the nonlinear models used in this book is

$$y = f(\beta, X) + E, \ E \sim N(0, \sigma^2) \quad (A.23)$$

where $f$ is some nonlinear function, $y$ is a vector of observations of the response variable, $X$ is a matrix of predictors, $\beta$ is a vector of parameters, and $E$ is a vector of residuals (deviations of $y$
from model predictions). Usually the errors are assumed to be normally distributed as shown in A.23. In this situation, $E$ can be written as a function of the unknown parameters, $E = y - f(\beta, X)$.

In this book, equations like A.23 were fit to multiple sources of data using Bayes’ theorem, as described below. Before explaining that method, however, it is useful to mention the maximum likelihood method for estimating the parameters of A.23. The unknown parameters $\beta$ and $\sigma^2$ (the variance of the residuals) can be found by minimizing

$$\text{log}(L) = 0.5 \left( \frac{E' E}{\sigma^2} + n \log (2 \pi \sigma^2) \right)$$  \hspace{1cm} (A.24)

This function is called the negative log likelihood function (Hilborn and Mangel 1997). The values of $\beta$ and $\sigma^2$ that minimize A.24 will maximize the likelihood $L$. The likelihood of a single residual is its y-axis value from the normal distribution of residuals. The likelihood of all the residuals taken together is the product of the likelihoods of the individual residuals. The log likelihood, then, is the sum of the logs of the likelihoods of the individual residuals. Equation A.24 is the negative log of that collective likelihood. Computationally, it is more convenient to minimize the negative log likelihood than it is to maximize the likelihood.

This book uses a conceptually different, though computationally similar, method for estimating parameters of nonlinear models. This approach combines multiple sources of information using Bayes’ theorem. Bayesian inverse modeling is the name given by geophysicists to the process of pooling two types of measurements for the same parameter (Jackson and Matsu’ura 1985). In Bayesian inverse modeling, a prior distribution for certain
parameters is combined with data from a second, independent source to calculate a posterior
distribution for the parameters. By an argument analogous to the one used for pooling data to
estimate parameters for linear models, Jackson and Matsu’ura (1985) show that parameters of a
nonlinear model can be estimated by minimizing the sum of a negative log likelihood plus the
negative log prior probability density:

\[-\log(L_P) = -\log(L_0) - \log(L_1) \quad \text{(A.25)}\]

$L_P$ stands for the negative log posterior density that results from pooling a prior ($L_0$) probability
distribution from the first data set and a likelihood ($L_1$) from the second data set. The prior
distribution for the parameters has mean $B_0$ and covariance matrix $S_0$. As above, $E = y - f(\beta, X)$.
The negative log of the prior distribution is

\[-\log(L_0) = 0.5 \left[ (\beta - B_0)' S_0^{-1} (\beta - B_0) + k \log(2\pi) + \log(|S_0|) \right] \quad \text{(A.26)}\]

where $\beta$ is the vector of parameters to be estimated. The negative log likelihood function from
the second set of data is

\[-\log(L_1) = 0.5 \left[ (E' E / \sigma^2) + n \log(2\pi\sigma^2) \right] \quad \text{(A.27)}\]

In summary, to estimate parameters of a nonlinear model from two data sets, first obtain
parameter estimates $B_0$ and an approximate covariance matrix $S_0$ for the data set which will
provide the prior distribution. Often, the covariance matrix contains only the prior variances,
with zeros elsewhere. The prior parameters $B_0$ and $S_0$ can be estimated by minimizing a negative log likelihood such as A.24 and then bootstrapping the covariance matrix of parameters, for example (Efron and Tibshirani 1993). Then, compute the pooled parameter estimates by minimizing the negative log probability density A.25 over the parameters $\beta$ and $\sigma^2$. Several computational methods are available for minimizing the negative log probability density (Press et al. 1989). Results reported in this book used the simplex method of Nelder and Mead (1964).

This method is an approximation, and there is no guarantee that it will work. It is a good idea to examine plots of the likelihood against each parameter, as well as the usual plots of residuals recommended in statistics textbooks (e.g. Draper and Smith 1981). Often the approximation seems reasonable.

The posterior probability distribution of the parameters will not resemble a standard distribution, such as the multivariate normal or multivariate Student t distribution. It is possible to calculate an approximate covariance matrix for the parameters by various methods, such as linearizing near the optimal parameter estimates or bootstrapping (Draper and Smith 1981, Efron and Tibshirani 1993). Full Bayesian analysis of the posterior distribution may be difficult. Unlike the linear case in the preceding section, it is not possible to write a general summary of Bayesian results for nonlinear models.

**Bayesian Dynamic Regression**

Previous sections showed how Bayesian methods can be used to estimate parameters from two or more data sets. This approach can be used to update parameter estimates using
sequential monitoring data in a process called Bayesian Dynamic Regression (Pole et al. 1994, West and Harrison 1989). Suppose that an ecosystem is observed at regular intervals in time, and that some error is associated with each observation. Prior to making a new observation, one can predict the next state of the system using a model for the observations so far. This predictive distribution is a prior distribution conditional on the time series data observed so far. Then new observations provide a second estimate of the state of the system, which may be summarized in a likelihood function. The prior distribution and the likelihood are combined by Bayesian dynamic regression into new posterior distributions for the parameters, the current state of the system, and the predictive distribution for the next time step. Then the process is repeated for successive time steps. The result is a regularly-updated calculation of the conditional posterior density of the parameters and the predictive probability distribution of future ecosystem states.

Chapters IV and V use nonlinear Bayesian dynamic regressions, meaning that the predictions of the regression model are a nonlinear function of the parameters. Theory is well developed for linear Bayesian dynamic regression models, in which the predictions are a linear function of the parameters (Pole et al. 1994, West and Harrison 1989). Nonlinear Bayesian dynamic regressions are still an active area of research. I used the algorithm of West and Harrison (1989). It adapts the well-understood linear case to nonlinear models by using the first-order terms of a Taylor expansion of the model in the neighborhood of the most recent observation.

In dynamic regression, the relationship between observations and unknown parameters is described by an observation equation
\[ Y_t = F_t(\theta_t, X_t) + w_t \quad \text{(A.28)} \]

The observation equation relates system state variables, \( Y_t \), to parameters \( \theta \), and observed regressors \( X_t \). The parameters \( \theta \) are not observed directly, but can be estimated from the observations of system state \( Y_t \) and predictors \( X_t \). Changes in the parameters over time are described by a *system equation*:

\[ \theta_t = g_t(\theta_{t-1}) + v_t \quad \text{(A.29)} \]

\( F \) and \( g \) are functions (possibly nonlinear) of the parameter vector \( \theta \). \( F \) and \( g \) must be differentiable. We assume that observation and process errors \( w \) and \( v \) are independent and normally distributed with means of zero and standard deviations \( s_w \) and \( s_v \), respectively. Note that \( \theta \) receives a random shock \( v_t \) at each time step. We assume that this random drift in \( \theta \) can be represented by inflating the variance of our estimate at each time step (or, equivalently, discounting the precision of our estimate at each time step). We will specify a parameter \( \delta \) (\( 0 < \delta < 1 \)) to discount the precision (i.e. increment the variance) of \( \theta \) at each time step. Maximum-likelihood estimates of \( \delta \) typically lie between 0.95 and 0.99. In practice, it turns out that results are not very sensitive to \( \delta \) when \( \delta \) is near 1 (Pole et al. 1994, West and Harrison 1989).

At the beginning of any time step \( t \), we have posterior information which consists of the current estimate of \( \theta \), \( m_{t-1} \), the covariance of this estimate \( C_{t-1} \), and the current degrees of freedom \( n_{t-1} \). These are the parameters of a multivariate Student t distribution for \( \theta_{t-1} \) given data.
available through time t-1. For the first time step, before any observations are made, the values of m, C and n will depend on the amount of prior information. If there is no prior information, the diagonal elements of C (which correspond to the parameter variances) can be set to a large number. The computations can be repeated with different values for the initial parameter variance to assess the sensitivity of the outcome to assumptions about the prior. Usually the effects of the prior are negligible after the first few observations have been made.

The sequence of calculations for any time step t is as follows. First, calculate the prior estimate for \( \theta_t \), \( a_t \), which is

\[
a_t = g_t(m_{t-1})
\]  

with covariance matrix \( R_t \) calculated as

\[
R_t = G_t C_{t-1} G_t' + ((1/\delta) - 1) C_{t-1}
\]

\[ (A.31) \]

\( G_t \) is the matrix of partial derivatives of \( g_t \) with respect to each parameter (element of \( m_{t-1} \)), evaluated at the posterior values for time t-1. In the linear case, \( G \) is simply the matrix of predictors at the previous time step.

Next, calculate the one-step ahead forecast of the system state \( Y_t \), which will be labeled \( f_t \):
\[ f_t^* = F_t(a_t) \]  (A.32)

The covariance matrix for the one-step ahead forecast is calculated as

\[ Q_t = H_t' R_t H_t + S_{t-1} \]  (A.33)

\( H_t \) is the matrix of partial derivatives of \( F_t \) with respect to each element of \( a_t \), evaluated using the prior estimates for time \( t \). The marginal distribution of the predictions is multivariate Student \( t \), with \( n_{t-1} \) degrees of freedom and scale matrix \( Q_t S_{t-1} \). In the linear case, \( H \) is simply the vector of parameter estimates at time \( t, a_t \).

At this point, the new observation is made and the parameters are updated as follows.
The prediction errors are \( E_t = Y_t - f_t \). It is convenient to calculate a matrix \( A_t = R_t H_t Q_t^{-1} \). Then the updated parameter vector is

\[ m_t = a_t + A_t E_t' \]  (A.34)

with degrees of freedom

\[ n_t = \delta n_{t-1} + 1 \]  (A.35)

and covariance matrix
\[ C_t = R_t - A_t Q_t A_t' \] (A.36)

The updated covariance matrix for the estimate of current system state is

\[ S_t = \left[ n_{t,1} S_{t-1} + E_t Q_t^{-1} E_t' \right] / n_t \] (A.37)

The calculations A.30 to A.37 are repeated for each time step.

In summary, the Bayesian dynamic regression is computed as follows. Before any data are observed, a prior multivariate Student t distribution is chosen for the parameters. This distribution may be based on data, or it may be a prior with low information content (large diagonal elements in the covariance matrix). At the beginning of each time step, prior estimates of the parameters are calculated by A.30 and A.31. Prior forecasts of the system state variables are computed using A.32 and A.33. Then, the new data are observed. One then calculates the updated parameter distribution (A.34 – A.36) and the new covariance matrix for the estimate of current system state (A.37). The sequence A.30 – A.37 is repeated at each time step.
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