

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 km² 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). Woolly 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 of 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 than 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 a 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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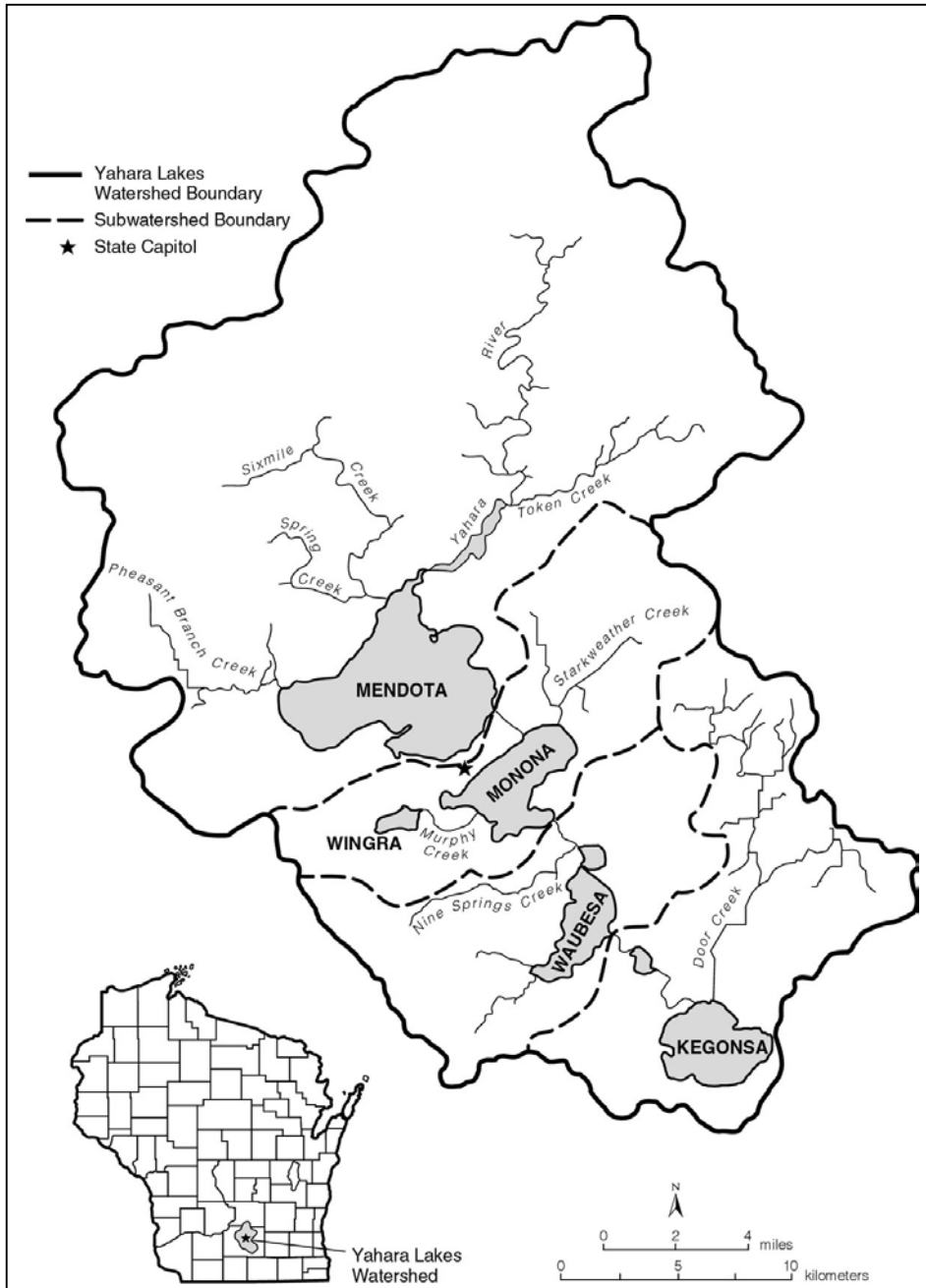


Figure 2. Hypothetical time series for an ecosystem variable (solid line), showing fluctuations around two regimes (dotted lines). (A) Effects of three unusually large perturbations. The second big perturbation is associated with a regime shift. Note that the peak of the third big perturbation is higher 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)

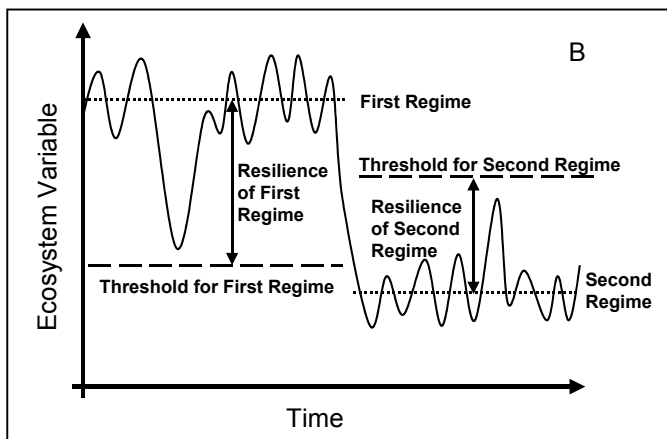
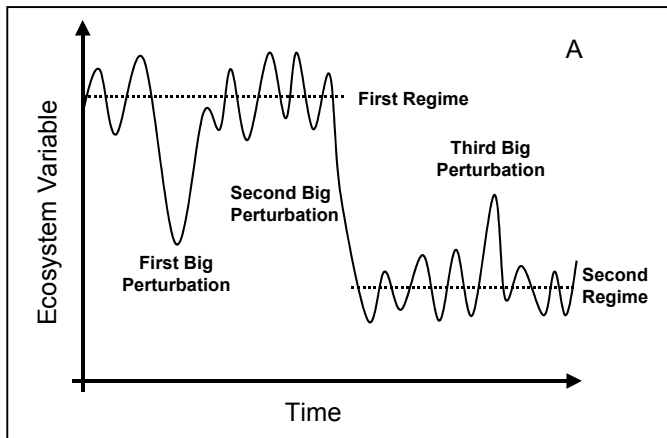


Figure 3. We observe a small subset of possible ecosystem behaviors. From a large set of possible ecosystem models, a small set is found to be consistent with the observed behavior. Together, the observations and the models set the scope for future predictions of ecosystem behavior. This scope is much smaller than the set of potential ecosystem behaviors. (Original)

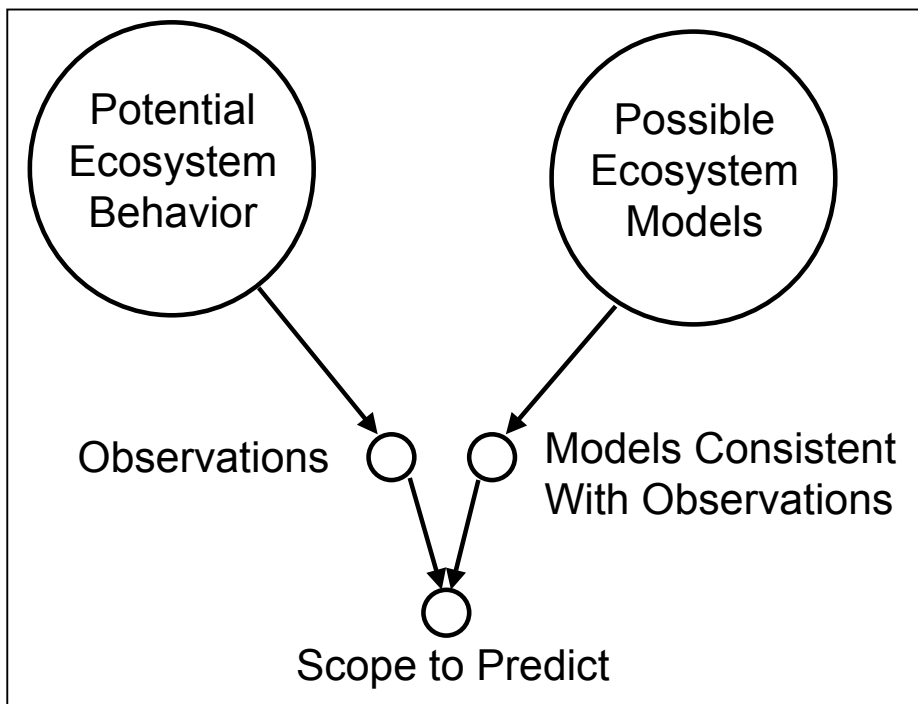


Figure 4. Spatial scales used in this book. (A) Many lakes on a landscape. (B) Focal scale: a single lake ecosystem showing boundaries: the shoreline, the sediment-water interface, and the surface of the lake. (C) Zones within a lake – littoral zone, sediments, epilimnion, hypolimnion. (Original)

