

PERSPECTIVES

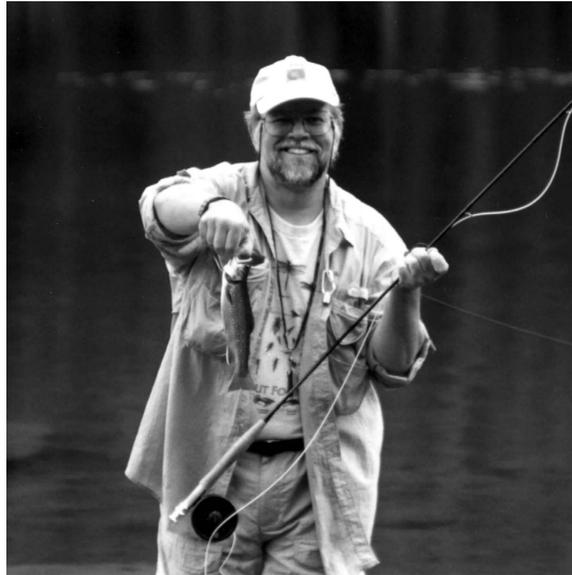
THE ROBERT H. MACARTHUR AWARD LECTURE

Ecology, 83(8), 2002, pp. 2069–2083
© 2002 by the Ecological Society of America

ECOLOGICAL FUTURES: BUILDING AN ECOLOGY OF THE LONG NOW¹

STEPHEN R. CARPENTER

Center for Limnology, 680 North Park Street, University of Wisconsin, Madison, Wisconsin 53706 USA



STEPHEN R. CARPENTER, MacArthur Award Recipient, 2000

Abstract. Ecosystem dynamics unfold into the future but are understood by examining the past. A forward-looking ecology, which assesses a broad range of possible future ecosystem states, is the complement of long-term, historical approaches to ecology. Together they are the ecology of the long now. The “long now” of ecosystems includes historical influences that shape present ecologies, and the future consequences of present events.

As a step in testing theories by their consequences, prediction is widely used in ecology. Ecologists have developed, criticized, and improved many predictive theories. Ecologists also have developed many empirical relationships that are potentially useful in forecasting. Eutrophication is an example of a problem for which ecologists created fundamental understanding, predictive capability, and new options for management.

Ecologists frequently justify their research funding through appeals to improved predictability. This goal is sometimes attainable and in any case motivates a considerable body of insightful research. However, in many cases of environmental decision making, what ecologists cannot predict is at least as important as what can be predicted. It is important to assess the full range of changes in ecosystems that may plausibly occur in the future, and the implications of these changes. The paper discusses some ways that ecological information can be used to improve understanding of the future consequences of present choices.

Key words: *adaptive management; alternate states; Bayesian analysis; ecological economics; eutrophication; fishery; forecast; long-term research; optimal control; prediction; resilience; uncertainty.*

Manuscript received 17 August 2001; accepted 10 December 2001; final version received 22 January 2002.

¹ Presented 7 August 2001 in Madison, Wisconsin, USA.

INTRODUCTION

Ecology cannot ignore context. Biogeography, landscape ecology, and satellite images have helped us appreciate the multiscale nature of spatial interactions. Spatial dynamics were the focus of one of Robert MacArthur's enduring contributions, *Geographical Ecology* (1972). History matters in ecology, so context also involves time. Events far in the past influence present ecological phenomena. Paleoecology, evolutionary biology, and long-term ecological research have shown us the ever-changing variety of the natural world—"the long now." The historically based branches of ecology are an important foundation for this paper, although my goal is to look forward in a way that is informed by the past. The phrase "long now" expresses the history dependence of the current state of ecosystems, and the impact of current ecological processes and human action on future ecosystems.

Stewart Brand (1999), in *The Clock of the Long Now*, asks, "How do we make long-term thinking automatic and common instead of difficult and rare? How do we make the taking of long-term responsibility inevitable?" Long-term perspectives are important in ecology, and ecology can contribute to environmental problem solving by helping to advance long-term thinking.

Why a forward-looking ecology? There are important, fundamental, scientific opportunities in research about the future of ecological systems. When we take forecasting seriously, we look for connections between slow and fast processes, or between rare events and ecological transformations. Such connections are fundamental for understanding ecological systems. They lead to multicausal, integrative explanations. Sometimes they improve ecologists' ability to predict, although this may turn out to be less important than the understanding that derives from research that continually formulates, criticizes, and improves predictive models. Science itself is a forward-looking undertaking and scientific knowledge is part of the endowment we leave to future generations. In ecology, where many crucial variables change slowly, a legacy of long-term observation and experiment takes on special importance. These are the shoulders we provide for future ecologists to stand upon.

Growing human demands on the environment are changing ecosystems in unprecedented ways with long-lasting consequences (Vitousek et al. 1997). Will future generations have access to resilient, functional ecosystems? The ecology of the long now helps us understand how present ecosystem states came to be, how present decisions impact future ecosystems, and how systems of people and nature might be perpetuated.

Despite the usefulness of prediction as a tool for advancing ecological research, the future of integrated systems of people and nature is beyond the traditional scope of ecology. This calls for new forms of ecological research as well as creative ways of coping with an

ever-changing environment (Gunderson and Holling 2001). Science is as much about clear articulation of what we do not know, and what we can do about it, as it is about the known. In ecology, what we do not know, yet could and should know, leads to creation of new research. In ecosystem management, what we do not know also affects choices. For example, it may suggest policies that are precautionary, actions that are reversible, and institutions that promote learning and adaptation. Acknowledgement of what we do not know should lead to actions informed by awareness of our ignorance, and thereby improve the legacy we leave for the future.

This paper presents some principles and goals for forward-looking ecology. It starts by recognizing an important class of predictions in ecology: those that are made possible by cross-scale interactions. These are illustrated with a case history: the understanding of lake eutrophication. The paper then addresses ecological uncertainty and prospects for coping with it. At present, forecasts for coupled systems of people and nature have large variances, as well as uncertainties that are unknown. Nevertheless, it may be possible for ecologists to help frame scenarios for the range of possible outcomes, as well as discover actions that are robust to diverse plausible futures.

PREDICTION AND ECOLOGY

Prediction is important in the practice of ecology

Prediction, in the sense of stating an explicit expectation about the outcome of a study, may be a universal feature of ecological research (Ford 2000). In ecology, there has been considerable argument about the philosophy and uses of prediction (Peters 1991, Pickett et al. 1994). In this paper, I assume that prediction and understanding are intertwined in the ways ecologists think (Pickett et al. 1994, Ford 2000) and that both theoretical and pragmatic needs will cause prediction to persist as a component of ecology (Pace 2001).

The terms "prediction" and "forecast" have different meanings for different professional communities (Sarewitz et al. 2000, Clark et al. 2001, MacCracken 2001). In this paper, I will use prediction and forecast interchangeably to mean the future probability distribution of an ecological variable, conditional upon initial conditions, parameter distributions, distributions of extrinsic drivers, and the choice of model used to make the calculations. Ecologists use both theoretical and phenomenological approaches to prediction. Theoretical predictions are based on a theory of a process or mechanism. Phenomenological predictions are based on curve fitting or pattern recognition without an attempt to represent underlying mechanisms. Many ecological predictions, including the examples discussed in this paper, are a pragmatic hybrid of theoretical and phenomenological approaches. Ecological models are frequently developed or tested by predicting the con-

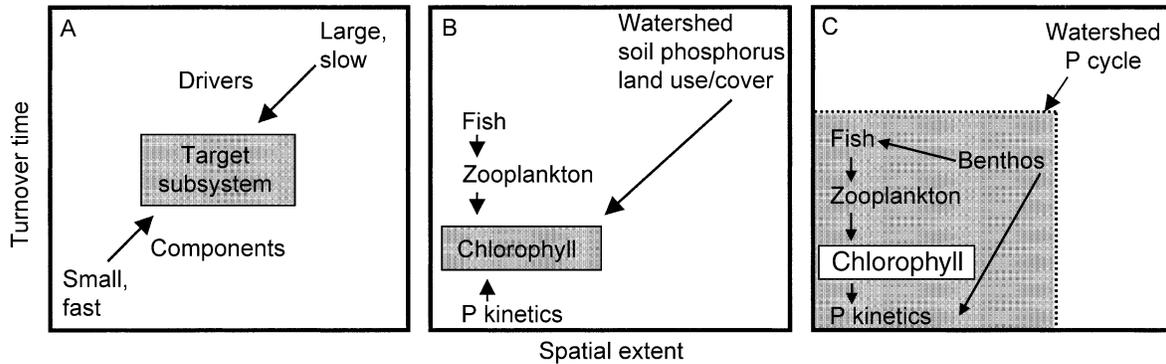


FIG. 1. Turnover time vs. spatial extent. (A) The minimal scales considered to predict a given target subsystem. (B) Scaling relationships for predicting lake chlorophyll from nutrient inputs and the food web. (C) Scaling relationships for predicting lake chlorophyll when benthic–pelagic interactions are considered.

temporary value of a variable from simultaneous values of other variables. By assuming that contemporary relationships hold across time (Pickett 1989), ecologists sometimes use contemporary models to make future predictions. The lake eutrophication example (presented in Prediction and ecology: Example: prediction of primary producers in lakes) illustrates this approach.

Scaling relationships are cues to prediction

Hierarchical organization is a key to understanding ecosystems (Allen and Starr 1982, O'Neill et al. 1986, Levin 1992). Each component of an ecosystem can be characterized by a typical spatial extent and turnover time (or return time in the case of a stochastic event; Turner and Dale 1998). A particular ecological question can often be answered by addressing a small number of dominant scales (O'Neill et al. 1986, Gunderson and Holling 2001). These dominant scales suggest the kinds of predictions that are possible and the drivers and equilibrium relationships that can be used to predict (Stommel 1963, Levin 1992). O'Neill et al. (1986) assert the importance of identifying processes at three scales: the focal scale for which predictions are to be developed; the scale of larger, more slowly changing processes which act as drivers or parameters; and the scale of smaller, more rapidly changing processes (Fig. 1A).

The range of turnover times in ecosystems spans at least 12 orders of magnitude, from the split-second cycling of limiting nutrients to the millennial weathering of rock formations, from generations of bacteria to generations of redwoods (Hotchkiss et al. 2001, Reed-Anderson et al. 2001). The coupling of fast and slow across multiple time scales creates the history dependence of ecology, driven by slow variables and the endless evolution of novelty (Botkin 1990). Thus ecological predictions are specific to particular time horizons. It is possible to build predictive models for a given time horizon, by treating slow variables as if they were parameters. Over longer time horizons, these “parameters” become variables. Such differences in turnover time can be exploited to decompose ecosystem

models into tractable components (Rinaldi and Scheffer 2001). In practice, parameter drift due to slow variables in ecological time series can be handled by data assimilation methods that discount past information (Walters 1986, Doney 1999, Cottingham et al. 2000).

Example: prediction of primary producers in lakes

Production of lake phytoplankton is the focus of a rich literature on ecological prediction. The focal scale is a year in a lake (Fig. 1B). Input of nutrients from the watershed is an important driver, with spatial extent corresponding to the terrestrial soil phosphorus cycle (Reed-Anderson et al. 2000). Food web dynamics are another important factor, at the spatial extent of the lake and with turnover time proportional to the life cycle length of the apex predators (Carpenter and Kitchell 1993).

By the 1960s, it was clear that phosphorus input was correlated with phytoplankton biomass as measured by chlorophyll (Fig. 2). Models based on phosphorus input rate, mean depth of the lake, and hydraulic retention time were commonly used to assess trophic state (Voltenweider 1976). The correlation of P input and chlorophyll across sets of lakes does not prove that manipulation of P input would change trophic state. Whole-ecosystem fertilization experiments established that P input rate controlled chlorophyll and primary production (Schindler 1977).

Phosphorus–chlorophyll plots exhibit considerable scatter. Many limnologists suspected that food web structure was a factor in this residual variability (Hrbacek 1961, Brooks and Dodson 1965, Shapiro et al. 1975). The mechanism of food web effects was thought to be trophic cascades: the abundance of large piscivorous fishes determines the magnitude of size-selective planktivory, which determines the size structure of herbivorous zooplankton and the magnitude of grazing (Carpenter et al. 1985).

Comparative data from many lakes are consistent with the food web hypothesis (Fig. 3). Chlorophyll is directly related to total P concentration at spring mixis,

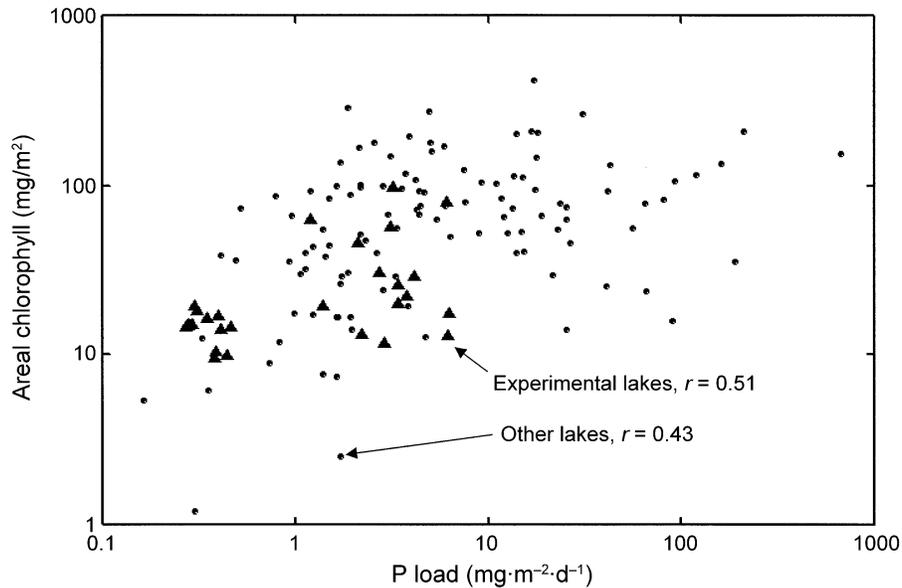


FIG. 2. Chlorophyll vs. P load for the lakes sampled by Canfield and Bachmann (1981, circles) and experimental lakes of Carpenter et al. (2001, triangles); note log scales. The Canfield-Bachmann data are for true lakes with residence time greater than one year and no missing data ($n = 111$).

which is a surrogate for P input rate. Chlorophyll is inversely related to mean crustacean length, an index of both size-selective planktivory and grazing rate. When a linear regression is fit to the chlorophyll–total P relationship (Fig. 3A), the residuals are significantly correlated with mean crustacean length ($r = -0.52$, plot not shown).

Correlations alone do not prove whether food web manipulation changes chlorophyll in lakes. Whole lake experiments and biomanipulations of many lakes demonstrated that food web manipulations controlled chlorophyll concentrations (Carpenter and Kitchell 1993, Hansson et al. 1998). Whole-lake experiments in which both phosphorus input and the food web were manip-

ulated show strong effects of both factors (Fig. 4). The experimental lakes data are overlaid on the comparative data set in Fig. 2 to show that the patterns are roughly consistent. The experimental results show that food web manipulation causes substantial changes in chlorophyll (Carpenter et al. 2001a). Studies by many authors have elaborated the mechanisms involved in trophic cascades. For example, the stoichiometry of grazers controls the nutrient limitation of phytoplankton and thereby influences the magnitude of cascades (Elser et al. 1996, 1998) and phosphorus flow through consumption of benthic invertebrates is crucial for maintaining fish predation (Schindler et al. 1995).

How has this body of research affected our ability

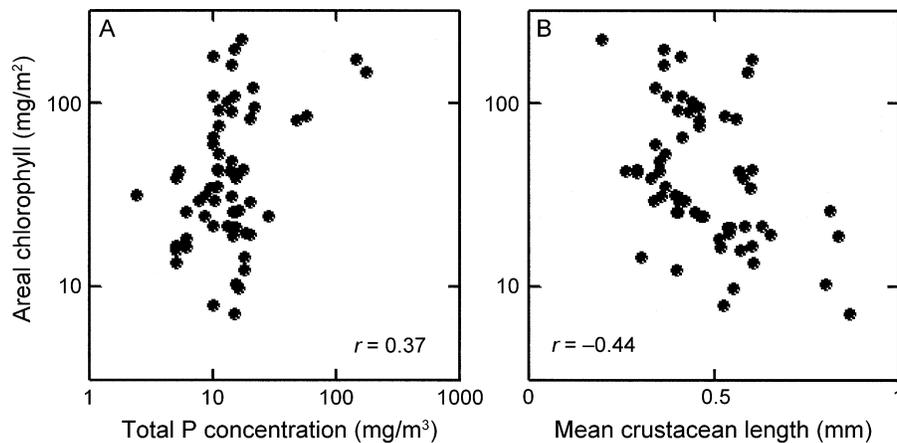


FIG. 3. Chlorophyll vs. (A) total P concentration at spring overturn and (B) mean crustacean length (mm) for the lakes of Carpenter et al. (1991); note log scales.

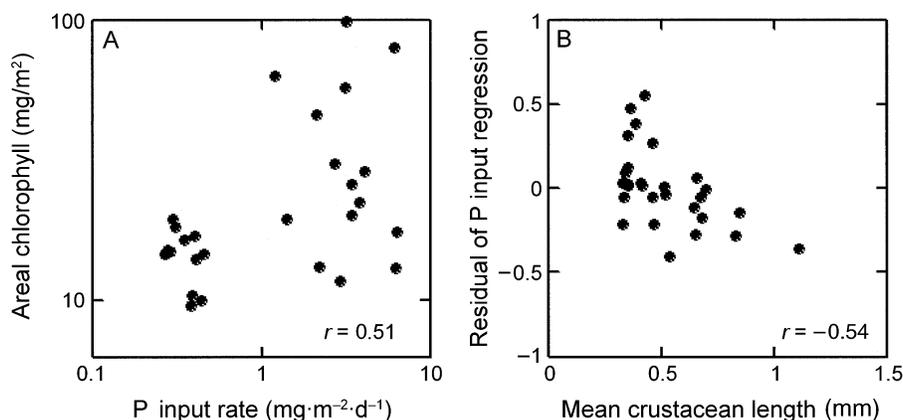


FIG. 4. (A) Chlorophyll vs. P load from the whole-lake experiments of Carpenter et al. (2001); note log scales. (B) Residuals from linear regression of data in panel (A) vs. mean crustacean length (mm).

to predict chlorophyll in lakes? To address this question, I calculated predicted probability distributions of chlorophyll for a hypothetical lake with moderate P inputs ($1.3 \text{ mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) and large crustaceans (1 mm) (Appendix A). The predictions based on P input only have a broad, flat distribution that suggests high uncertainty about chlorophyll (Fig. 5, distribution 1). The prediction narrows somewhat when information about the slope of the grazer effect from Fig. 3 is included (Fig. 5, distribution 2). However, this slope is highly uncertain because P input rate was not directly measured for the lakes shown in Fig. 3, and P concentration can be affected by food web structure. The experimental lake data (Fig. 4) overcome this problem. When they are included, the predicted distribution becomes

much narrower (Fig. 5, distribution 3) although it still conveys some uncertainty about future chlorophyll.

Powerful science with unfulfilled implications

In the eutrophication example, science worked. Scientists discovered relevant mechanisms at the whole-lake scale, improved predictions (as shown by narrowing of the predictive distributions), and created new options for management of lake chlorophyll (change phosphorus input; change the food web; or both).

These successes took a long time. The research summarized in the previous section represents the effort of scores of scientists around the world during more than 50 yr. Learning was slow, not because of intellectual or resource limitations, but because causes were mul-

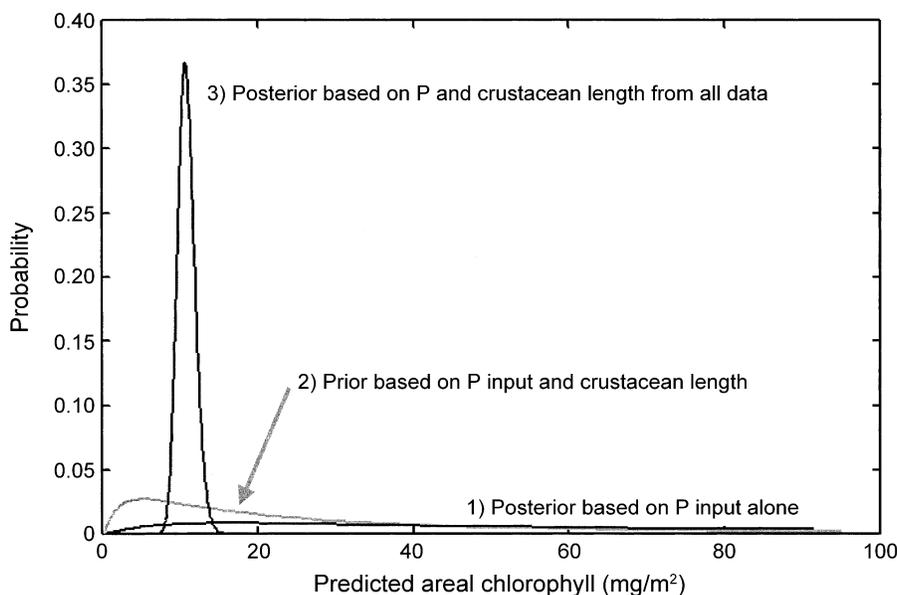


FIG. 5. Probability distributions of chlorophyll based on (1) P input alone (circles in Fig. 2), (2) distribution 1 combined with the crustacean length effect based on Fig. 3B, and (3) all data in Figs. 2, 3B, and 4.

tiple, many hypotheses (some initially promising but ultimately unproductive) were considered, and many years of data were needed to understand ecosystem responses. Slow dynamics are crucial in ecosystems, and it takes time to understand them. As noted by Hilborn and Ludwig (1993), ecology isn't rocket science—it's much harder.

Policy impact included successes such as the ban on phosphate detergents and reduction of P inputs to ecosystems such as the Laurentian Great Lakes. Most of the successes apply to readily identifiable and manageable point sources of pollution such as industrial and municipal discharges. However, eutrophication remains a widespread problem, often due to nonpoint pollution (Carpenter et al. 1998). Economic analyses frequently show that nonpoint pollution control would increase net social welfare (Wilson and Carpenter 1999, Carpenter et al. 1999b). Nonpoint pollution is politically contentious, because sources are diverse and mitigation often requires intervention on private lands. So far the United States has failed to implement effective policies for reducing eutrophication due to nonpoint pollution, despite sophisticated scientific understanding of the problem.

Research discovered new possibilities of ecosystem change

As limnologists were creating predictive capability and understanding of lake eutrophication, evidence developed showing nonlinear state changes in lakes. All of these phenomena can be simulated using models that include benthic–pelagic interactions (Fig. 1C). The benthos adds spatial complexity, intermediate turnover times, and a richer set of interactions. Phosphorus recycling from sediment can stabilize eutrophy and delay or prevent recovery when phosphorus inputs are reduced (Carpenter et al. 1999b). Macrophytes can stabilize sediments and sequester nutrients, thereby suppressing phytoplankton until a disturbance (such as grazing or high water level) reduces macrophyte cover and shifts the lake to a turbid state (Scheffer et al. 1993). The littoral zone provides refuge and alternate prey for fishes, creating the possibility of collapsing predator–prey cycles related to changing refuges (Scheffer 1998, Rinaldi and Scheffer 2001). Littoral habitat also provides mechanisms for alternating states of planktivore and piscivore dominance (Carpenter 1988). By connecting watershed, benthic and pelagic processes, ecologists discovered a richer set of dynamics.

Thresholds and multiple self-sustaining states are known from many aquatic and terrestrial ecosystems (Carpenter 2001, Scheffer et al. 2001). Demonstrating thresholds and multiple states is difficult. The best-documented examples rest on multiple types of evidence, including experiments to demonstrate differences among states in controlling processes, temporal observations of state changes, comparisons of ecosystems in different states, and fitting of models. As in

the lake eutrophication case, progress is slow. State changes are infrequent events, and it may take a long time to observe enough of them to draw conclusions. Causes are multiple. The systems are large and complex, evoking multiple competing hypotheses. It takes many years for scientists to sort through these to gain a synthesis of the plausible causes (Pickett et al. 1994, Ford 2000). Thus the possibility of long-lasting or irreversible state shifts in ecosystems adds significantly to the difficulties of prediction.

PREDICTION AND DECISION

A minimal model

How should ecological predictions, and the processes of improving them, interact with decision making? This question will be explored using a case study. In the Northern Highland Lake District of Wisconsin, recreational development is altering lakeshore ecosystems. Riparian forests are replaced by lawns, and fallen trees are removed from littoral habitats (Christensen et al. 1996). Angling effort is directly correlated with development (S. R. Carpenter, *unpublished data*). Fish growth rates are inversely correlated with development (Schindler et al. 2000). Development is also associated with introductions of rusty crayfish, which remove macrophytes and directly consume fish eggs (Lodge et al. 2000). Thus development brings a suite of changes in nearshore habitats and angling which may cause losses of fish diversity and production. A simple model of this system focusing on a harvested fish population provides a heuristic for learning and decision in systems that may exhibit alternate states.

Criteria for choosing the model were (1) simplicity, the model should include just enough complexity to address alternate states, learning, and decisions, but no more (Gunderson and Holling 2001); (2) an ecosystem service subject to management; (3) a social–ecological framework for the service. In the model (Appendix B), the ecosystem service is a harvested fish population. The ecosystem context includes a food web, as well as habitat necessary for juvenile growth and survival, such as reefs in marine systems or fallen trees in freshwater. These minimal considerations lead to a model with two alternate states. Convenient approximations to this model can be fit by regression. Harvest can be managed via optimal control to study the consequences of that type of management. Other goals of management, such as enlarging the domain of attraction of a preferred stable state, can also be studied using the model. While a number of models could have been chosen for this exercise, the one presented here is sufficiently rich to address learning and management in an ecosystem context, yet transparent enough for understanding. An additional advantage is that similar models are well studied and have many applications to living resources (Ludwig and Hilborn 1983, Walters 1986, Clark 1990, Hilborn and Walters 1992). Although

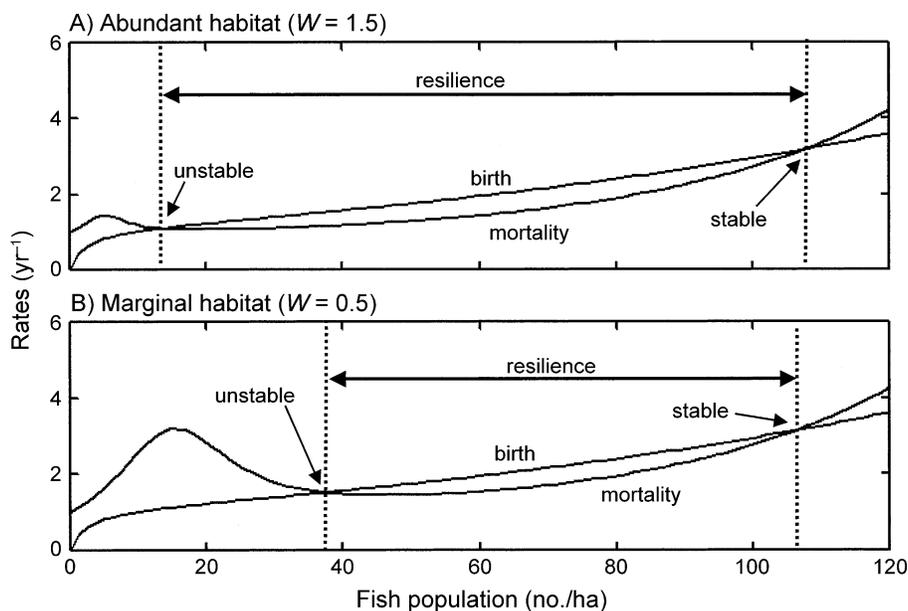


FIG. 6. Rates of birth and mortality (Appendix B) vs. fish population size for (A) abundant habitat ($W = 1.5$) and marginal habitat ($W = 0.5$). Dotted lines show equilibria: the left point is unstable; the right point is stable. The distance between the equilibria is the resilience. Parameter values: $k = 0.1$, $f = 0.01$, $m = 0.01$, $c = 10$, $h = 10$, $q = 4$, $C = 2$.

this analysis focuses on a living resource, analogous conclusions derive from biogeochemical models in which the ecosystem service is processing of a pollutant (Carpenter et al. 1999a, b).

The model (Appendix B) centers on dynamics of adults of the harvested population. Juveniles of the harvested population are consumed by a second species, while adults of the harvested population prey upon this second species. Walters and Kitchell (2001) point out that this interaction creates alternate outcomes of cultivation (when adults suppress the second species and facilitate juvenile recruitment) or depensation (when low adult densities allow the second species to flourish and consume all juveniles before they recruit to adulthood). The rate of juvenile mortality due to predation by the second species depends on the quality of habitat, which can change over time due to natural processes or human intervention.

For appropriate parameter values, there are two steady states (Fig. 6). The right-hand steady state is stable. The left-hand steady state is unstable, and the population of adults (A) collapses toward zero if it moves below the left-hand steady state. Thus the left-hand steady state is the threshold between collapse and persistence of the population. The distance between the two steady states is resilience, the magnitude of disturbance that the population can withstand and still persist (Holling 1973, Gunderson and Holling 2001). Resilience is directly related to the quality of the habitat

Learning and choice

Harvest policies calculated using optimal control criteria have two domains of behavior (Fig. 7). To the

right of the threshold, optimal control seeks a positive population level that provides maximum expected yield over infinite time. To the left of the threshold, the optimal policy is "use them or lose them." Because the population is collapsing anyway, the remaining individuals are harvested as quickly as possible.

In reality, a science-based manager would not know the position of the threshold, and would rely on research to approximate the dynamics by fitting models. For the purposes of this paper, it is interesting to explore two fitted models, a density-dependent one with no habitat effects, and a model with an additional parameter to approximate habitat effects (Appendix B). While both models can estimate a threshold, only the second model can capture the dependency of resilience on slow changes in habitat.

The performance of the fitted models depends entirely on the quality of the data used to fit them. In general, there are two types of problems with ecological data: the measurements of A , (adults in year t) and W_t (habitat quality in year t) will be noisy (observation error), and the range of A and W levels available for fitting the models will be limited (poorly conditioned design matrix, as occurs when experimental or natural variation is observed across only a limited range). Impacts of observation error can be reduced by better methods and more intensive sampling. Impacts of both observation error and poor design can be reduced by deliberate manipulation of A and W . An extensive literature addresses the effects of observation error on estimation and optimal control in living resource management (Ludwig and Hilborn 1983, Walters 1986). This important problem must be considered in actual

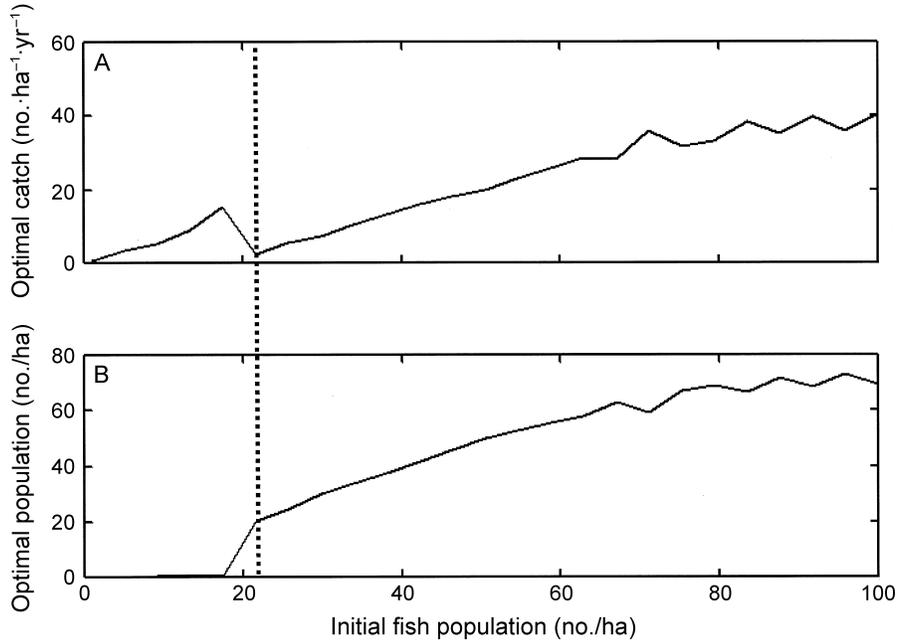


FIG. 7. Optimal policies vs. stock size. Dotted line shows threshold (position of the unstable equilibrium): (A) optimal harvest; (B) target stock size. Parameters: $s = 0.1$, $\delta = 0.98$; other parameters are as in Fig. 6 except harvest is determined by stochastic dynamic optimization (Appendix B).

PERSPECTIVES

applications. In this exercise, I wish to focus on the design problem, and can do so more clearly if observation error is ignored. To address the design issue, two types of data sets were generated to fit the models, one with weak contrasts in A and W and one with manipulations of both A and W over a wide range. In the resulting data sets, A and W were uncorrelated. Both data sets had 2 yr of simulated observations from 25 lakes. The weak manipulation failed to discriminate the

two models (posterior probabilities of each were ~ 0.5). The strong manipulation clearly identified the habitat model as superior, with a posterior probability > 0.99 .

When the models were fitted to data from strong manipulations, optimal policies were similar to those calculated from the true model (Fig. 8A). The most important differences occurred near the threshold, where both fitted models tended to overharvest. The density-dependent model overharvested more than the

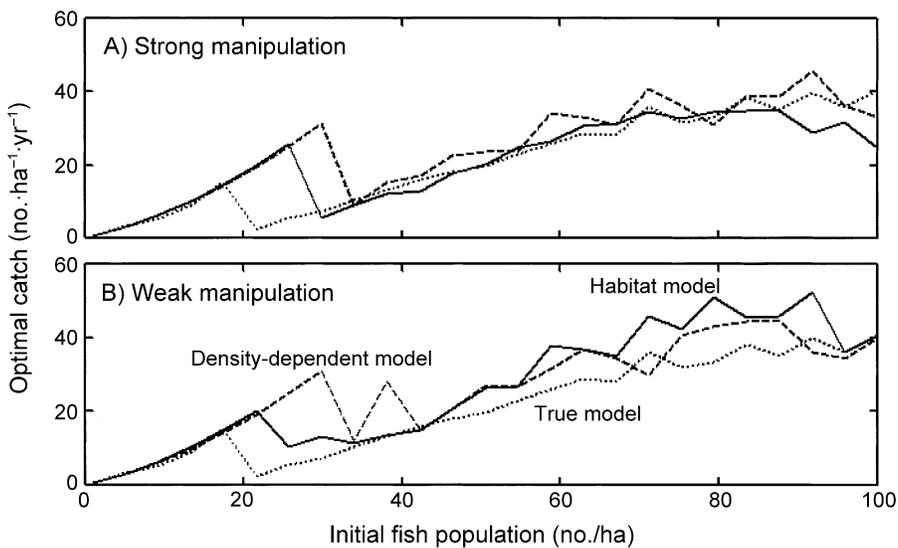


FIG. 8. Optimal harvest vs. stock size under the true model (dotted line), density dependent model (dashed line), and habitat model (solid line): (A) data from strong manipulation; (B) data from weak manipulation.

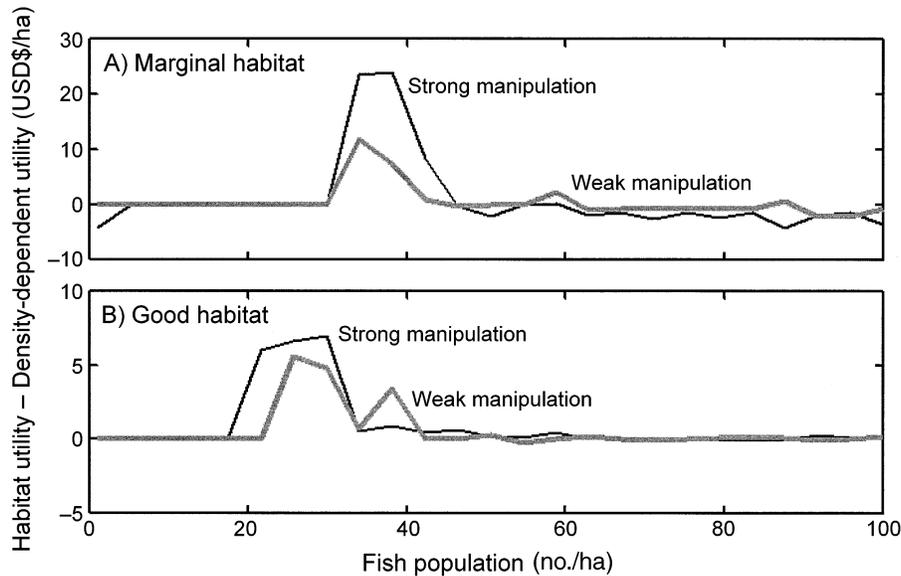


FIG. 9. Difference in utility obtained under the habitat model minus that obtained under the density-dependent model vs. fish stock using data from strong manipulation (black line) or weak manipulation (gray line): (A) marginal habitat ($W = 0.5$); (B) good habitat ($W = 1.5$).

habitat model. When the models were fit to data with weak contrast, both fitted models tended to overharvest relative to the true model (Fig. 8B). The density-dependent model overharvested the most in the neighborhood of the threshold, which would increase the risk of collapse. The habitat model recommended the largest harvests at relatively high stock sizes.

How well do the fitted models perform? For a given model, the optimal policy is the harvest schedule that maximizes expected future catch (utility, as defined in Appendix B). The optimal policies calculated under each fitted model can be used to calculate the true utility obtained from each policy. The net benefit of using the habitat model is the difference between the utilities obtained under each policy (Fig. 9). The difference in performance between the models is greatest near the threshold. Good ecological information matters most when the risk of collapse is greatest.

The habitat model provides a precautionary signal to the manager even when the data are weak. This signal can be built into decision making by calculating expected future catches over both fitted models. Each model's contribution to the forecast is weighted by its posterior probability (which will be largest for the best-fitting model). This procedure is known as Bayesian model averaging (Raftery et al. 1997, Fernández et al. 2001).

In our example, the true model is known so the true utility obtained under Bayesian model averaging can be calculated. This will always be less than the utility obtained by managing under the true model, because the fitted models are always an imperfect approximation. The difference is a measure of the performance lost due to ignorance of the true model (Fig. 10). With strong

manipulation, the performance loss is modest. With weak manipulation, there is a large performance loss near the threshold—exactly the region where good information matters the most. The performance loss is greatest when the habitat is marginal (note that the threshold occurs at a higher fish population when W is lower). The underperformance of the fitted models is due to overharvesting in the neighborhood of the threshold.

This example shows that quality of data is paramount. High-quality data increase the chance of getting the model right, and thereby discovering new management options in manipulating habitat, the slowly changing variable that controls resilience. In this case, high quality is obtained by observing annual change in whole ecosystems across a wide range of variability in A and W . In practice, this wide range would be obtained by comparing a suite of lakes across broad gradients of A and W , or by whole-lake experiments that created large and independent changes in A and W . In general, data quality is the magnitude of independent contrast among the drivers thought to be important in the ecosystem.

The model reveals an important paradox of learning for ecological thresholds. In the long run, knowledge of the threshold and the underlying mechanism would improve the fishery and decrease the chance of collapse. Experimental manipulations of habitat and harvest are the best way to learn about the threshold. However, some of the experimental treatments run the risk of collapsing the fishery. In practice, then, one should experiment only when collapse is unlikely. Safe experiments are likely to be better than no experiments at all, but may be less informative than experiments that put the resource at risk. For modular ecosystems, such as lakes, islands or

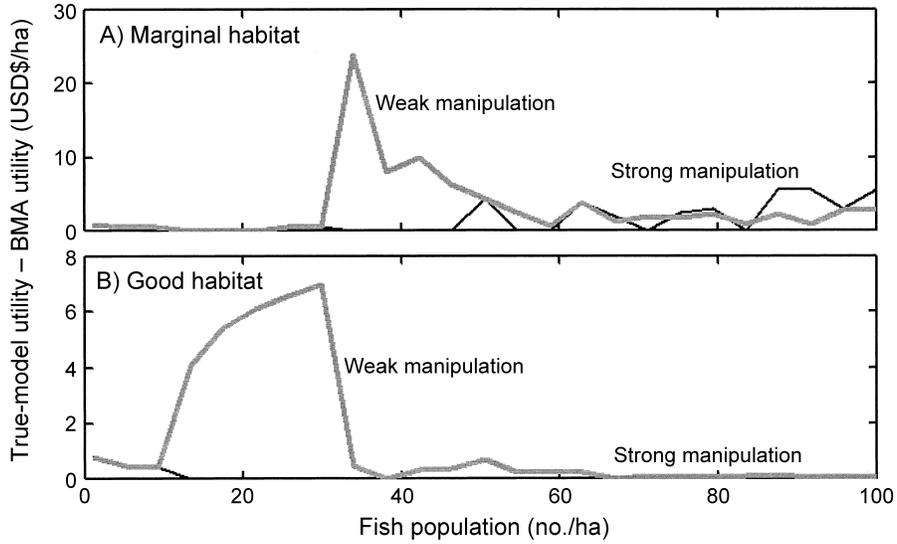


FIG. 10. Difference in utility obtained under the true model minus that obtained under Bayesian model averaging vs. fish stock using data from strong manipulation (black line) or weak manipulation (gray line): (A) marginal habitat ($W = 0.5$); (B) good habitat ($W = 1.5$).

small watersheds, it may be possible to experiment on a few ecosystems to gain information that applies to many ecosystems. For ecosystems that are large and unique, cautious experiments that attempt to learn while avoiding thresholds may be the best option.

The model is also a metaphor for the link between human attitudes and action. Recall that the preferred choice (i.e., the optimum harvest) is destructive (use them or lose them) below an estimated threshold, and

constructive (build a sustainable stock) above the threshold. Choice depends on whether the decision maker thinks the world is getting worse, or getting better. The threshold between pessimism and optimism depends on the choice of models, and the better models have a larger domain of optimism (Fig. 11). In the realm of human action where prophecies can become self fulfilling, should ecologists foster pessimism or optimism? Warnings have value, but unrelenting neg-

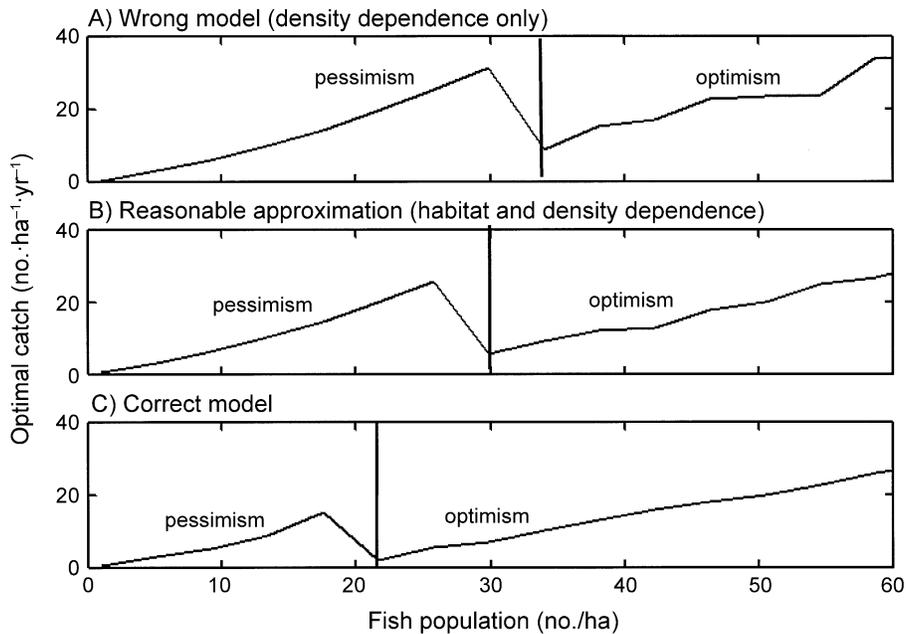


FIG. 11. Optimal harvest vs. stock size for (A) the density-dependent model, (B) habitat model, and (C) true model. Vertical lines show the threshold below which it is assumed that the population cannot be sustained. Data are from strong manipulation.

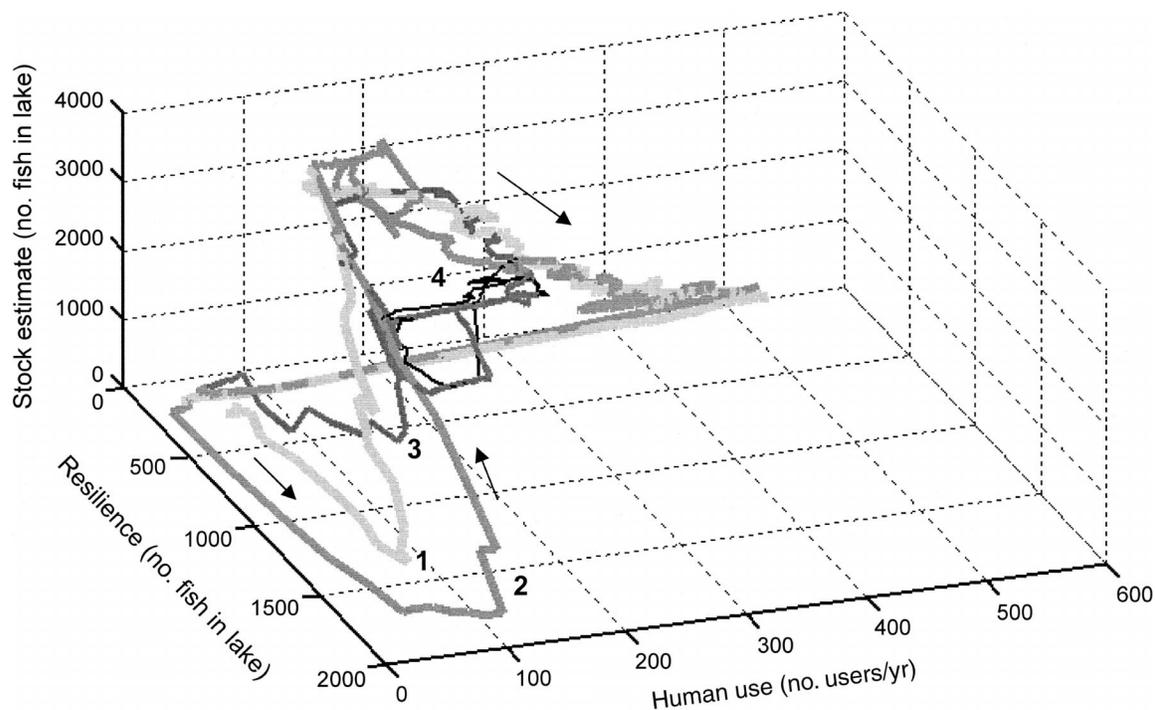


FIG. 12. Cycles from the fish management game plotted in three dimensions: stock size, human users/yr, and size of the stable attractor (cf. Fig. 6). Cycles are numbered 1 through 4; the line becomes thinner and darker as time increases. Arrows show direction of flow.

activity has an effect on listeners that may be different from our intent. Constructive solutions that evoke optimism may come closer to our goals.

Ecological prediction and social dynamics

A more realistic analysis considers multiple decision makers, with diverse goals and beliefs, each learning about the ecosystem and social system while making choices. The implications of this added complexity for ecosystem management have been examined in several studies (Janssen 1998, Carpenter et al. 1999a, Janssen et al. 2000). A living resource model (similar to the one of Appendix B) has been embedded in a model of a recreational lake community including resident anglers, tourists, and a science-based management agency (Carpenter and Gunderson 2001, Carpenter et al. 2002). This model is programmed as a game that can be played by one or many players. The objective is to sustain the fish stock and the recreational economy that depends upon it. The players can manipulate harvesting while attempting to learn the underlying ecological dynamics.

Results typically exhibit cycles (Fig. 12) that resemble the adaptive cycle of Holling (1986, Gunderson and Holling 2001). Useful axes for understanding these cycles are the size of the fish stock, the number of people using the ecosystem each year, and ecosystem resilience (as in Fig. 6). The results shown here were generated by a class of students playing the game interactively. The students were divided into groups rep-

resenting resort owners, anglers, developers, and the management agency. These groups negotiated to set harvest limits for each simulated year. The first two cycles had high amplitude, with a boom in human use followed by collapse of the stock, followed by a severe drop in human activity. By the third cycle, negotiations led to more cautious harvest policies. The students discovered that careful, brief experiments (to determine the current sensitivity of stock to harvest, and of human response to fishing opportunity) were useful. By the fourth and final cycle, the oscillation was modest, striking a balance between stock size and human use while maintaining resilience that was large relative to the stochastic shocks experienced by the system. The group dynamic also changed over time. Initially, debates were intense and it was difficult for the players to find acceptable compromises. Gridlock prevented changes in policy, and gridlock was broken only by massive crashes. As the players gained understanding of their collective action problem, it became easier to reach consensus on experimental policies. Stock declines became smaller and less frequent.

While this game is simplistic, it demonstrates several tenets of ecosystem management in complex, ambiguous situations. Avoid fixing on putatively optimal policies. Build social flexibility for exploring multiple options. Prefer reversible actions. Experiment when it is safe to do so. Seek leading indicators of ecological dynamics, such as resilience. Resilience and its surrogates reside in the slowly changing variables.

COPING WITH THE LIMITATIONS OF
ECOLOGICAL FORECASTS

Some important uncertainties are irreducible

What are the limits of ecological prediction? All quantitative ecological predictions are probabilistic. Often variances are large. Sometimes new research can improve predictions in a reasonable amount of time. For example, where fast variables to be forecast are embedded in slowly changing processes, research may increase predictive capability, as in the case of lake eutrophication. In other cases, slowly changing variables may expose thresholds, and thereby cause surprising dynamics that are hard to predict (Rinaldi and Scheffer 2000, Scheffer et al. 2000, Carpenter 2001). Ecological processes that generate unpredictable dynamics include evolution of resistance in pests or spread of newly invasive species. While we expect that resistance will evolve and species will invade, predicting specific instances of evolution or invasion is difficult.

The future dynamics of ecosystems are contingent on drivers that are outside the domain of ecology, such as climate change, human demography, or globalization of trade. The probability distribution of ecological predictions depends in part on the distributions of such drivers, but future driver distributions may be unknown or unknowable. Therefore the uncertainty of the ecological predictions cannot be calculated. The shortcomings of other disciplines' predictions are described by Sarewitz et al. (2000) for the geosciences and Sherden (1998) for climate, demography, and economics. These books offer strong cautions for predictive ecology. Ecologists can and should consider the ecological consequences of the major trends of our time, such as climate change, human population, and the global economy. Such projections, however, do not have the status of fully quantified probabilistic predictions. Ecologists have been appropriately frank about this shortcoming, reflected in words like "projection" (Melillo et al. 1995) and "scenario" (Nakicenovic and Swart 2000, Sala et al. 2000).

Coupled social–ecological systems are exceptionally difficult because of unknown feedbacks and unpredictable human actions. Suppose, for example, that ecologists could generate credible predictions of ecosystem services on time horizons relevant to human action. People would then act upon the forecasts, perhaps in surprising ways (e.g., unforeseeable technological innovations), and sometimes cause the forecasts to be wrong. Because of the reflexive interactions of people and ecosystems, forecasts for ecosystems that are affected by human action (i.e., all ecosystems of earth at the present time) are highly uncertain. Even the uncertainties are uncertain, because we do not know the set of plausible models for the dynamics of the probability distributions. Conveying uncertainty is difficult (Anderson 1998) and this problem is compounded

when the probabilities themselves are unknowable (Funtowicz et al. 1999, Cooman and Walley 2000).

The usual tools of decision analysis do not apply to problems in which objectives are ambiguous and there are multiple, contradictory approaches, each one plausible from a particular viewpoint (Funtowicz et al. 1999, Ludwig 2001, Ludwig et al. 2001). The appropriate models cannot be identified. Each interest group may construct models convenient to its preferences, but there is no basis for assigning greater credibility to one model vs. another. Diverse definitions of social welfare are in play, and many different actions appear equally likely to meet social goals. The role of scientists in such an ambiguous decision setting is different from our role in situations where the probabilities and preferences are known. In the latter case, finding the optimal path is a purely technical problem. In the ambiguous case, science can help envision possible futures and discover robust win–win options. This is closer to the role of science in scenario exercises.

Imagining the possible

Scenarios are a method for bringing future considerations into present decisions when prediction is not possible (Schwartz 1996, van der Heijden 1996). Their purpose is to broaden perspectives, open new questions, expose possibilities for surprise, and raise challenges to conventional thinking (Greeuw et al. 2000). A scenario is a narrative of a possible future. The scenario is not a prediction; it is a plausible future that merits consideration. Scenarios are considered not singly but in sets of three or four scenarios that collectively represent a useful range of ambiguous and unknown outcomes (Schwartz 1996, van der Heijden 1996). Differences among the scenarios embrace a range of ambiguous, uncontrollable aspects of the future. The scenarios provide a framework for finding robust decisions that have acceptable consequences no matter how events turn out. Scenarios may not lead to a unique optimal decision. Instead, they make it possible to compare possible actions in light of diverse models, multiple causes, and ambiguous, uncontrollable aspects of the future.

Scenarios encourage action, whereas uncertainties sometimes lead to doubt, inaction, and further analysis. Honest and accurate assessment of uncertainty is an important function of science, yet we need more than just a measure of uncertainty. Scenarios present the range of possibilities in tangible, evocative statements about alternative futures. By bringing alternative possibilities to life in the form of realistic narratives, scenarios may motivate action. Scenarios bring science into decisions that must be made now, rather than after further research.

The scenario approach has already had an impact on ecological research and environmental management. Examples include scenarios of future biodiversity and ecological responses to climate change (Melillo et al.

1995, Sala et al. 2000). Environmental scenarios were presented by Raskin et al. (1998) at a global scale, and at continental scale for Australia by Cocks (1999). Ecological information has also been included in scenarios developed for other purposes. For example, U.S. Central Intelligence Agency (2000) scenarios consider ecosystem services that affect environmental security.

In scenario exercises, ecologists play the dual roles of imagining and disciplining accounts of the future. A plausible scenario is consistent with state-of-the-art ecological understanding. Fair, insightful criticism by ecologists is therefore a necessary step in the construction of scenarios. This type of activity is familiar to scientists. We are less familiar with our role in creating scenarios that evoke insight and change (although this activity has similarities to teaching or storytelling). The success of a scenario exercise depends on many factors, not just the quality of the ecological input. Yet, scenarios of future environments demand information that can only be provided by ecologists.

Everything we do must first be imagined. How can scientists improve the processes of creativity and renewal that lead to adaptive responses? One approach attempts to build both ecological resilience and institutions that foster learning and innovation (Gunderson and Holling 2001). Resilience can be manipulated to collapse undesirable ecosystem structures, or to make desirable ones more robust (Carpenter et al. 2001*b*). In principle, individual decision making could be aligned with ecological factors to reinforce desirable ecosystem states. Understanding how this might be achieved in practice requires input from ecologists, other disciplinary specialists, and the individuals living in the social-ecological system.

ECOLOGICAL FUTURES AND THE FUTURE OF ECOLOGY

Scenarios are more than science. Unlike scientific theories, models, or hypotheses, scenarios are not tested (in the sense of determining consistency with extant or readily attainable data). Instead, alternative policies are tested for robustness against a set of diverse scenarios. Even though scenarios are not scientific constructs, science must play a central role, both in creating scenarios and ensuring that they are consistent with current ecological understanding.

Ecologists must embrace a bipolar stance toward prediction. At one pole, ecologists strive to expand our capabilities to forecast ecological change for spatial extents and time horizons of human action (Clark et al. 2001). A culture of prediction and rigorous assessment of probabilities will improve the science of ecology. Development of predictive capability will take time. As in the case of lake eutrophication, progress will be deliberate and painstaking because ecosystem dynamics are slow, causes are multiple, and hypotheses are numerous and difficult to discriminate. Some kinds of ecological prediction are impossible given our cur-

rent capabilities. Nevertheless, prediction has an important role in ecological research and also contributes to various tools for environmental problem solving, including scenarios.

At the opposite pole, ecologists must acknowledge the shortcomings of ecological predictions and frankly admit when prediction is inappropriate. This implies a broader perspective on the uses of ecology, which will expand the field and increase its impact.

Faced with uncertainty and ambiguity, decision makers have a number of options, only one of which is to learn (Stein and Fineberg 1996). Other options involve making choices that are robust to a range of possible futures, and seeking ways to cope with uncontrollable change and unpredictable surprise. In these areas, ecological expertise is underused. Some ways that ecologists can help cope with the ambiguous and uncontrollable are (1) Understand how ecological persistence derives from connections of slowly changing processes or disturbance regimes to more rapidly changing processes. These connections are especially relevant for creating and maintaining robustness to cope with future change. They require sustained ecological research because dynamics are slow and regime shifts are infrequent (Likens 1992). (2) Provide blunt assessments of the uncertain outcomes of proposed environmental interventions. Emphasize the importance of evaluating any policy proposal (including the status quo) against a wide range of plausible outcomes, hedging bets, choosing reversible actions, experimenting, monitoring, and learning. (3) Develop scenarios of future ecologies on time horizons meaningful to people (years to decades). What worlds are possible, and how might they be attained? How are these future outcomes a legacy of present decisions? These challenges to ecologists suggest new research agendas—on prediction at scales relevant to human action, limits of prediction, construction of insightful scenarios, and discovery of robust options for ecosystem management. These goals follow from the ecological discovery that “now” extends a long time into the future.

ACKNOWLEDGMENTS

I am indebted to three groups of colleagues. For their contributions to understanding the field sites where I work, I thank Jon Cole, Jon Foley, Tom Frost, Jim Kitchell, Tony Ives, Tim Kratz, John Magnuson, Mike Pace, and Monica Turner. The MAPLE scenarios group at U.W. Madison (Darren Bade, Doug Beard, Bea Beisner, Elena Bennett, Graeme Cumming, Lisa Dent, Paul Hanson, Tanya Havlicek, Jeff Houser, and Garry Peterson) was exceptionally helpful during the writing of this paper. The Resilience Network, especially Buz Brock, Carl Folke, Lance Gunderson, Buzz Holling, Don Ludwig, Brian Walker, and Frances Westley, has transformed my thinking about the uses of ecology. The whole-ecosystem experiments were performed at the University of Notre Dame Environmental Research Center. Buz Brock and Don Ludwig provided useful critiques of the calculations presented here. Joel Cohen, Buzz Holling, Ann Kinzig, Don Ludwig, Mike Pace, Brian Walker, and an anonymous referee provided helpful reviews. This research was sponsored by the National Science Foundation, the A. W. Mellon Foundation, and the J. S. McDonnell Foundation.

LITERATURE CITED

- Allen, T. F. H., and T. B. Starr. 1982. *Hierarchy: perspectives for ecological complexity*. University of Chicago Press, Chicago, Illinois, USA.
- Anderson, J. 1998. Embracing uncertainty: the interface of Bayesian statistics and cognitive psychology. *Conservation Ecology* 2(1). [Online, URL: <http://www.consecol.org/vol2/iss1/>.]
- Botkin, D. 1990. *Discordant harmonies*. Oxford University Press, London, UK.
- Brand, S. 1999. *The clock of the long now: time and responsibility*. Basic Books, New York, New York, USA.
- Brooks, J. L., and S. I. Dodson. 1965. Body size and composition of plankton. *Science* 150:28–35.
- Canfield, D. E., and R. W. Bachmann. 1981. Prediction of total phosphorus concentrations, chlorophyll *a*, and Secchi depths in natural and artificial lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 38:414–423.
- Carpenter, S. R. 1988. Transmission of variance through lake food webs. Pages 119–138 in S. R. Carpenter, editor. *Complex interactions in lake communities*. Springer-Verlag, New York, New York, USA.
- Carpenter, S. R. 2001. Alternate states of ecosystems: evidence and its implications. Pages 357–383 in M. C. Press, N. Huntly, and S. Levin, editors. *Ecology: achievement and challenge*. Blackwell, London, UK.
- Carpenter, S. R., W. A. Brock, and P. C. Hanson. 1999a. Ecological and social dynamics in simple models of ecosystem management. *Conservation Ecology* 3(2):4. [Online, URL: <http://www.consecol.org/vol3/iss2/art4/>.]
- Carpenter, S. R., W. A. Brock, and D. Ludwig. 2002. Collapse, learning and renewal. Pages 173–194 in L. Gunderson and C. S. Holling, editors. *Panarchy: understanding transformations in human and natural systems*. Island, Washington, D.C., USA.
- Carpenter, S. R., N. F. Caraco, D. L. Correll, R. W. Howarth, A. N. Sharpley, and V. H. Smith. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications* 8:559–568.
- Carpenter, S. R., J. J. Cole, J. R. Hodgson, J. F. Kitchell, M. L. Pace, D. Bade, K. L. Cottingham, T. E. Essington, J. N. Houser, and D. E. Schindler. 2001a. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. *Ecological Monographs* 71:163–186.
- Carpenter, S. R., T. M. Frost, J. F. Kitchell, T. K. Kratz, D. W. Schindler, J. Shearer, W. G. Sprules, M. J. Vanni, and A. P. Zimmerman. 1991. Patterns of primary production and herbivory in 25 North American lake ecosystems. Pages 67–96 in J. Cole, S. Findlay, and G. Lovett, editors. *Comparative analyses of ecosystems: patterns, mechanisms, and theories*. Springer-Verlag, New York, New York, USA.
- Carpenter, S. R., and L. H. Gunderson. 2001. Coping with collapse: ecological and social dynamics in ecosystem management. *BioScience* 51:451–458.
- Carpenter, S. R., and J. F. Kitchell. 1993. *The trophic cascade in lakes*. Cambridge University Press, London, UK.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35:634–639.
- Carpenter, S. R., D. Ludwig, and W. A. Brock. 1999b. Management of eutrophication for lakes subject to potentially irreversible change. *Ecological Applications* 9:751–771.
- Carpenter, S. R., B. H. Walker, J. M. Anderies, and N. Abel. 2001b. From metaphor to measurement: resilience of what to what? *Ecosystems* 4:765–781.
- Central Intelligence Agency. 2000. *Global trends 2015: a dialogue about the future with nongovernment experts*. [Online, URL: <http://www.cia.gov/publications/global-trends2015/index.html>.]
- Christensen, D. L., B. R. Herwig, D. E. Schindler, and S. R. Carpenter. 1996. Impacts of lakeshore residential development on coarse woody debris in north temperate lakes. *Ecological Applications* 6:1143–1149.
- Clark, C. W. 1990. *Mathematical bioeconomics: the optimal management of renewable resources*. Wiley, New York, New York, USA.
- Clark, J. S., et al. 2001. Ecological forecasting: an emerging imperative. *Science* 293:657–660.
- Cocks, D. 1999. *Future makers, future takers: life in Australia 2050*. University of New South Wales Press, Sydney, Australia.
- Cooman, G., and P. Walley. 2000. The imprecise probabilities project. [Online, URL: <http://ippserv.rug.ac.be/>.]
- Cottingham, K. L., J. A. Rusak, and P. R. Leavitt. 2000. Increased ecosystem variability and reduced predictability following fertilisation: evidence from paleolimnology. *Ecology Letters* 3:340–348.
- Doney, S. C. 1999. Major challenges confronting marine biogeochemical modeling. *Global Biogeochemical Cycles* 13:705–714.
- Elser, J. J., T. H. Chrzanowski, R. W. Sterner, and K. H. Mills. 1998. Stoichiometric constraints on food-web dynamics: a whole-lake experiment on the Canadian shield. *Ecosystems* 1:120–136.
- Elser, J. J., D. R. Dobberfuhl, N. A. MacKay, and J. H. Schampel. 1996. Organism size, life history, and N:P stoichiometry. *BioScience* 46:674–684.
- Fernández, C., E. Ley, and M. F. J. Steel. 2001. Benchmark priors for Bayesian model averaging. *Journal of Econometrics* 100:381–427.
- Ford, E. D. 2000. *Scientific method for ecological research*. Cambridge University Press, London, UK.
- Funtowicz, S. O., J. Martinez-Alier, G. Munda, and J. R. Ravetz. 1999. Information tools for environmental policy under conditions of complexity. *European Environment Agency, Environmental Issues Series Number 9*, Luxembourg.
- Greuw, S. C. H., M. B. A. van Asselt, J. Grosskurth, C. A. M. H. Storms, N. Rijkens-Klomp, D. S. Rothman, and J. Rotmans. 2000. *Cloudy crystal balls*. European Environment Agency, Copenhagen, Denmark.
- Gunderson, L. H., and C. S. Holling, editors. 2001. *Panarchy: understanding transformations in human and natural systems*. Island, Washington, D.C., USA.
- Hansson, L. A., H. Annadotter, E. Bergman, S. F. Hamrin, E. Jeppesen, T. Kairesalo, E. Luokkanen, P. A. Nilsson, M. Søndergaard, and J. Strand. 1998. Biomanipulation as an application of food-chain theory: constraints, synthesis, and recommendations for temperate lakes. *Ecosystems* 1:558–574.
- Hilborn, R., and D. Ludwig. 1993. The limits of applied ecological research. *Ecological Applications* 3:550–552.
- Hilborn, R., and C. J. Walters. 1992. *Quantitative fisheries stock assessment*. Chapman and Hall, London, UK.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1–23.
- Holling, C. S. 1986. Resilience of ecosystems; local surprise and global change. Pages 292–317 in W. C. Clark and R. E. Munn, editors. *Sustainable development of the biosphere*. Cambridge University Press, Cambridge, UK.
- Hotchkiss, S., P. M. Vitousek, O. A. Chadwick, and J. Price. 2001. Climate cycles, geomorphological change, and the interpretation of soil and ecosystem development. *Ecosystems* 3:522–533.
- Hrbáček, J. M., V. Dvoraková, V. Korinek, and L. Procházková. 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of the metabolism of the whole plankton association. In-

- ternationale Vereinigung für Theoretische und Angewandte Limnologie **14**:192–195.
- Janssen, M. 1998. Modeling global change: the art of integrated assessment modeling. Edward Elgar, London, UK.
- Janssen, M. A., B. H. Walker, J. Langridge, and N. Abel. 2000. An adaptive agent model for analysing co-evolution of management and policies in a complex rangeland system. *Ecological Modelling* **131**:249–268.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* **73**:1943–1967.
- Likens, G. E. 1992. The ecosystem concept: its use and abuse. Ecology Institute, Oldendorf/Luhe, Germany.
- Lodge, D. M., C. A. Taylor, D. M. Holdich, and J. Skurdal. 2000. Nonindigenous crayfishes threaten North American freshwater biodiversity: lessons from Europe. *Fisheries* **25**:7–20.
- Ludwig, D. 2001. The era of management is over. *Ecosystems* **4**:758–764.
- Ludwig, D., and R. Hilborn. 1983. Adaptive probing strategies for age-structured fish stocks. *Canadian Journal of Fisheries and Aquatic Sciences* **40**:559–569.
- Ludwig, D., M. Mangel, and B. Haddad. 2001. Ecology, conservation, and public policy. *Annual Review of Ecology and Systematics* **32**:481–517.
- MacArthur, R. H. 1972. *Geographical ecology: patterns in the distribution of species*. Harper and Row, New York, New York, USA.
- MacCracken, M. 2001. Prediction versus projection—forecast versus possibility. *WeatherZine* 26. [Online, URL: <http://sciencepolicy.colorado.edu/zine/archives/1-29/26/guest.html>.]
- Melillo, J. M., et al. 1995. Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO₂ doubling. *Global Biogeochemical Cycles* **9**:407–437.
- Nakicenovic, N., and R. Swart, editors. 2000. *Emissions scenarios*. Cambridge University Press, London, UK.
- O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. *A hierarchical concept of ecosystems*. Princeton University Press, Princeton, New Jersey, USA.
- Pace, M. L. 2001. Prediction and the aquatic sciences. *Canadian Journal of Fisheries and Aquatic Sciences* **58**:1–10.
- Peters, R. H. 1991. *A critique for ecology*. Cambridge University Press, London, UK.
- Pickett, S. T. A. 1989. Space-for-time substitution as an alternative to long-term studies. Pages 110–135 in G. E. Likens, editor. *Long-term studies in ecology*. Springer-Verlag, New York, New York, USA.
- Pickett, S. T. A., C. Jones, and J. Kolasa. 1994. *Ecological understanding*. Academic, New York, New York, USA.
- Raftery, A. E., D. Madigan, and J. A. Hoeting. 1997. Bayesian model averaging for linear regression models. *Journal of the American Statistical Association* **92**:179–191.
- Raskin, P., G. Gallopin, P. Gutman, A. Hammond, and R. Swart. 1998. Bending the curve: toward global sustainability. PoleStar Report Number 8. Stockholm Environment Institute, Stockholm, Sweden.
- Reed-Anderson, T., S. R. Carpenter, and R. C. Lathrop. 2001. Phosphorus flow in a watershed-lake ecosystem. *Ecosystems* **3**:561–573.
- Rinaldi, S., and M. Scheffer. 2001. Geometric analysis of ecological models with slow and fast processes. *Ecosystems* **3**:507–521.
- Sala, O. E., et al. 2000. Global biodiversity scenarios for the year 2100. *Science* **287**:1770–1774.
- Sarewitz, D., R. A. Pielke, Jr., and R. Byerly, Jr. 2000. *Prediction—science, decision making, and the future of nature*. Island, Washington, D.C., USA.
- Scheffer, M. 1998. *Ecology of shallow lakes*. Chapman and Hall, London, UK.
- Scheffer, M., S. Carpenter, J. Foley, C. Folke, and B. Walker. 2001. Stochastic events can trigger large state shifts in ecosystems with reduced resilience. *Nature* **413**:591–596.
- Scheffer, M., S. H. Hosper, M. L. Meijer, and B. Moss. 1993. Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution* **8**:275–279.
- Schindler, D. E., S. R. Carpenter, K. L. Cottingham, X. He, J. R. Hodgson, J. F. Kitchell, and P. A. Soranno. 1995. Food web structure and littoral zone coupling to pelagic trophic cascades. Pages 96–105 in G. A. Polis and K. O. Winemiller, editors. *Food webs: integration of pattern and dynamics*. Chapman and Hall, New York, New York, USA.
- Schindler, D. E., S. I. Geib, and M. R. Williams. 2000. Patterns of fish growth along a residential development gradient in North Temperate lakes. *Ecosystems* **3**:229–237.
- Schindler, D. W. 1977. The evolution of phosphorus limitation in lakes. *Science* **195**:260–262.
- Schwartz, P. 1996. *The art of the long view*. Doubleday, New York, New York, USA.
- Shapiro, J., V. Lamarra, and M. Lynch. 1975. Biomanipulation: an ecosystem approach to lake restoration. Pages 85–96 in P. L. Brezonik and J. L. Fox, editors. *Water quality management through biological control*. University of Florida, Gainesville, Florida, USA.
- Sherden, W. A. 1998. *The fortune sellers: the big business of buying and selling predictions*. John Wiley, New York, New York, USA.
- Stein, P. C., and H. V. Fineberg. 1996. *Understanding risk*. National Academy, Washington, D.C., USA.
- Stommel, H. 1963. Varieties of oceanographic experience. *Science* **139**:572–576.
- Turner, M. G., and V. H. Dale. 1998. Comparing large, infrequent disturbances: what have we learned? *Ecosystems* **1**:493–496.
- Van der Heijden, K. 1996. *Scenarios: the art of strategic conversation*. Wiley, New York, New York, USA.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* **277**:494–499.
- Vollenweider, R. A. 1976. Advances in defining critical loading levels for P in lake eutrophication. *Memorie dell'Istituto Italiano di Idrobiologia* **33**:53–83.
- Walters, C. 1986. *Adaptive management of renewable resources*. MacMillan, New York, New York, USA.
- Walters, C., and J. F. Kitchell. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Sciences* **58**:1–12.
- Wilson, M. A., and S. R. Carpenter. 1999. Economic valuation of freshwater ecosystem services in the United States, 1977–1997. *Ecological Applications* **9**:772–783.

APPENDIX A

An appendix outlining the calculation of probability distributions is available from ESA's Electronic Data Archive: *Ecological Archives* E083-037-A1.

APPENDIX B

An appendix outlining the depensation model, estimation, and policy choice is available from ESA's Electronic Data Archive: *Ecological Archives* E083-037-A2.