

Ecological Futures: Building an Ecology of the Long Now

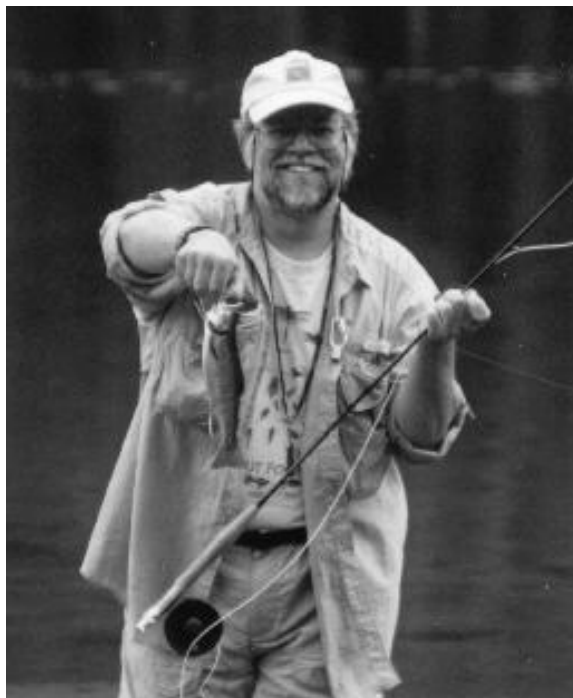
A paper based on a
Robert H. MacArthur Award Presentation
to the
Ecological Society of America
Annual Meeting at Madison, Wisconsin, 7 August 2001

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Date of this version: 13 December, 2001
Text file: Mac_Text8.rtf
Figure file: Mac_Fig3.ppt

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ABSTRACT

5 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.

10 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 which are potentially useful in forecasting. Eutrophication is an example of a problem for which ecologists created fundamental understanding, predictive capability, and new options for
15 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
20 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.

25 Key words: *Adaptive Management; Alternate States; Bayesian analysis; Ecological economics; Eutrophication; Fishery; Forecast; Long-term research; Optimal control; Prediction; Resilience; Scenario; Threshold; Uncertainty*

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, for actions that are reversible, and for 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). This paper assumes 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 (Clark et al. 2001, MacCracken 2001, Sarewitz et al. 2000). 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 contemporary 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 below) illustrates this approach.

Scaling Relationships are Cues to Prediction

5 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
10 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).

15 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
20 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
25 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

30 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 watershed and
turnover time proportional to the terrestrial soil phosphorus cycle (Reed-Anderson et al.
35 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).

40 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 (Vollenweider 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
45 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 1966, 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, 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 manipulated 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. 2001). 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 to predict chlorophyll in lakes? To address this question I calculated predicted probability distributions of chlorophyll for a hypothetical lake with moderate P inputs ($1.3 \text{ mg m}^{-2} \text{ d}^{-1}$) 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).

5 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 years. Learning was slow, not because of intellectual or resource limitations, but because causes were multiple, 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
10 understand them. As noted by Hilborn and Ludwig (1993), ecology isn't rocket science - it's much harder.

15 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. 1999). Nonpoint pollution is politically
20 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.

25 *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
30 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. 1999). Macrophytes can stabilize sediments and sequester nutrients, thereby suppressing phytoplankton until a disturbance (such as grazing or high water
35 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
40 connecting watershed, benthic and pelagic processes, ecologists discovered a richer set of dynamics.

45 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.

5

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 (Carpenter et al. 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, Hilborn and Walters 1992, Clark 1990). Although 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_t (adults) and W_t (habitat quality) 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 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 years 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 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 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 negativity 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 (Carpenter et al. 1999, Janssen 1998, 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. 2001). This model is programmed as a game which 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 representing resort owners, anglers, developers and the management agency. These groups negotiated to set harvest limits for each simulated year. The first 2 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" (VEMAP 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 1997) and this problem is compounded when the probabilities themselves are unknowable (Cooman and Walley 2000, Funtowicz et al. 1999).

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 versus 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 (van der Heijden 1996, Schwartz 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 3 or 4

scenarios that collectively represent a useful range of ambiguous and unknown outcomes (van der Heijden 1996, Schwartz 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 (VEMAP 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 (2000). 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 story-telling). 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). 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 current 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.

ACKNOWLEDGEMENTS

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.

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APPENDIX A. CALCULATION OF PROBABILITY DISTRIBUTIONS

The distributions shown in Fig. 5 were derived from data shown in Figs. 2-4 using standard normal theory for Bayesian analysis of linear regression models (Gelman et al. 1995). The posterior based on P load only (distribution 1 in Fig. 5) was calculated from the model

$$\log(A) = b_0 + b_1 \log(L) + \varepsilon \quad (\text{A.1})$$

Here A is chlorophyll, L is P load, b_i are regression coefficients, and ε is a normally-distributed error with mean zero and variance σ^2 . The regression coefficients and σ^2 are assumed to be unknown and must be estimated from data. The prior distribution for analysis of equation 1 was uniform for b_0 , b_1 , and $\log(\sigma)$ (Gelman et al. 1995).

A second prior (distribution 2 of Fig. 5) was needed for analysis of the model including both P load and crustacean mean length Z:

$$\log(A) = c_0 + c_1 \log(L) + c_2 Z + \varepsilon \quad (\text{A.2})$$

The c_i are regression coefficients, and ε is a normally-distributed error with mean zero and variance σ^2 . As before, the regression coefficients and σ^2 are to be estimated from the data. The joint posterior distribution obtained for b_0 and b_1 was used as the joint prior for c_0 and c_1 . The prior mean regression coefficient for the effect of Z was obtained by linear regression on the data in Fig. 3B fitting the model

$$\log(A) = a_0 + a_2 (Z - \check{Z}) + \varepsilon \quad (\text{A.3})$$

where \check{Z} is the mean of Z. The estimate of a_2 was used as the prior mean for c_2 . The prior variance of a_2 from this regression was 0.09. However, this is an underestimate of the variance of c_2 , because we cannot disentangle the role of P input (vs P concentration) in the data of Fig. 3. Therefore I calculated the prior variance according to Raftery et al. (1997) which was 0.9 in this case, reflecting greater uncertainty. The prior covariances of c_2 with c_0 and c_1 also followed Raftery et al. (1997). This leads to the prior shown as distribution 2 of Fig. 5. This prior was used to calculate the posterior based on P load and crustacean length (distribution 3 in Fig. 5) using equation 2 and the data of Fig. 4, following Gelman et al. (1995).

APPENDIX B. DEPENDSATION MODEL, ESTIMATION, AND POLICY CHOICE

The fish population model is

$$5 \quad A_{t+1} = - C_t + A_t \exp(G_t + N_t) \quad (B.1)$$

where A_t is adult stock in year t , C_t is harvest in year t , and population dynamics G_t and process noise N_t are given by

$$10 \quad G_t = k + f A_t (1 - m A_t - \{c (h/W_t)^q / [(h/W_t)^q + A_t^q]\}) \quad (B.2)$$

$$N_t = z - s^2/2, \text{ where } z \sim N(0, s^2) \quad (B.3)$$

15 Parameters are minimal population growth rate k , fecundity f , density-dependent mortality m , process variance s^2 , and those for mortality due to interspecific predation c , h and q . Maximum mortality due to interspecific predation is c , h scales the level of W at which interspecific predation occurs at half the maximum rate, and q is proportional to the slope of the interspecific mortality curve near this half-maximal point. W_t is the time series of habitat. Habitat is assumed to change more slowly than the fish population, so
 20 it makes sense to calculate steady-state fish populations for a given level of habitat. These are not true steady states because they change slowly over time as habitat changes (Rinaldi and Scheffer 2000).

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

$$30 \quad \exp \{f A(m A + \{c (h/W)^q / [(h/W)^q + A^q]\})\} = [A / (A + C)] \exp (k + f A) \quad (B.4)$$

The left side of equation B.4 is the total rate of natural (non-harvest) mortality. The right side is the total birth rate adjusted by the proportion of the population that is not harvested. The equilibria are the intersections of the sides of equation 4 plotted on the same axes (as in Fig. 6). For parameter sets that lead to two intersections, the lower
 35 equilibrium is the unstable threshold and the upper one is stable. The threshold level is inversely related to W . Discussions of similar models are presented by Clark (1990), Walters and Kitchell (2001) and Carpenter (2001).

40 The management problem is to sustain an optimal harvest level without crossing the threshold to collapse, given the challenges of stochasticity, possibly unknown parameters which must be estimated from data, and slow change in W which may be poorly known.

45 I assume that the manager does not know the true model, but instead fits approximate models to observed time series of A and W . Many approximate models are conceivable, but only two are analyzed here:

$$Y_t = b_0 + b_1 A_{t-1} + b_2 A_{t-1}^2 + \varepsilon_t \quad (\text{B.5})$$

$$Y_t = b_0 + b_1 A_{t-1} + b_2 A_{t-1}^2 + (b_3 / W_{t-1}) + \varepsilon_t \quad (\text{B.6})$$

5

The b_i are parameters to be estimated from data and the errors ε_t are normally distributed with mean 0 and unknown variance σ^2 . The response series Y is

$$Y_t = \log [(A_t + C_{t-1}) / A_{t-1}] \quad (\text{B.7})$$

10

The first approximate model includes density-dependence but no habitat effect (equation B.5). The second approximate model includes both density dependence and a habitat effect (equation B.6). Predicted one-step-ahead distributions of $A_{t+1} = -C_t + A_t \exp(Y_t)$ are obtained using the posterior distribution of Y_t . This posterior is calculated by analyzing equations B.5 and B.6 using standard normal theory with a prior uniform on the b_i and $\log(\sigma)$ (Gelman et al. 1995).

15

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

20

$$V = \sum \delta^t C_t \quad (\text{B.8})$$

where V is utility, the summation is over infinite time, δ is the discount factor, and C_t is catch in year t . The optimal policy can be found by maximizing the following expression with respect to harvest:

25

$$V(A_t) = C_t + \delta E [V(A_{t+1})] \quad (\text{B.9})$$

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

30

$$u(A, y) = A \exp(M_i) - y \quad (\text{B.10})$$

35

In equation 10, M_i is calculated from one of the fitted models (equations B.5, B.6). When the true model is used, M_i corresponds to G from equation B.2. When one of the fitted models is used, M_i corresponds to Y from equation B.5 or B.6. Because harvest cannot be negative, we set

40

$$C_t = u(A_t, y) \text{ if } u(A_t, y) \geq 0 \quad (\text{B.11a})$$

$$C_t = 0 \text{ if } u(A_t, y) < 0 \quad (\text{B.11b})$$

45

The models yield a distribution of future values of A_t . The distribution of $\log(A_t)$ is normal in the case of the true model, and Student-t in the case of the fitted models (Gelman et al. 1995). In computing policies we must account for the probability of obtaining each possible value of A_{t+1} given a particular value of A_t . This was done by
 5 computing probabilities on a discrete mesh, then weighting each possible value of A_{t+1} by its probability, as in Carpenter et al. (1999) Appendix C. Given these definitions, equation 9 can be computed for any given value of y . The value of y that maximizes V is computed by Brent's method (Press et al. 1989) over the interval $[0, A_t]$.

10 To account for uncertainty of model choice, the Bayesian model average utility, V_{BMA} , for a given y value is calculated over both fitted models (Raftery et al. 1997, Fernández et al. 2001):

$$V_{\text{BMA}}(y) = p V_D(y) + (1-p) V_H(y) \quad (\text{B.12})$$

15 V_D is the utility under the density-dependent model (equation B.5) given y , V_H is the utility under the habitat model (equation B.6) given y , and p is the posterior probability of the density-dependent model. The posterior probability p is computed by the method of Fernández et al. (2001), equations 2.12 and 4.1. In this exercise, there are only two
 20 models so the posterior probability of the habitat model is $1-p$. Bayesian model averaging generalizes to more than two models (Raftery et al. 1997, Fernández et al. 2001).

Fig. 1. Turnover time versus 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.

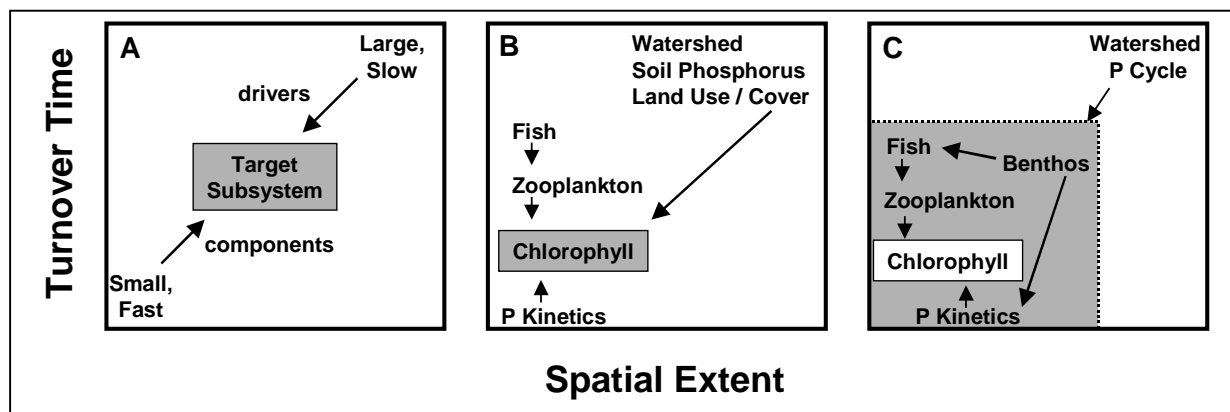


Fig. 2. Chlorophyll (mg m^{-2} , note log scale) versus P load ($\text{mg m}^{-2} \text{d}^{-1}$, note log scale) for the lakes sampled by Canfield and Bachmann (1981, open circles) and experimental lakes of Carpenter et al. (2001, filled triangles). The Canfield-Bachmann data are for true lakes with residence time greater than one year and no missing data ($n = 111$).

5

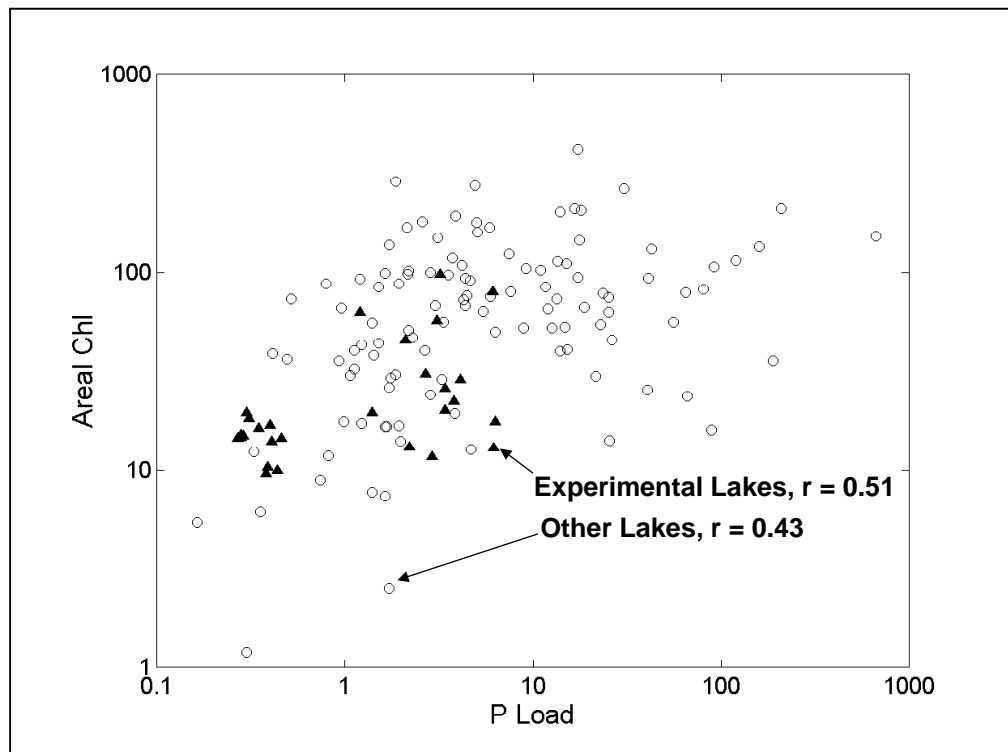


Fig. 3. Chlorophyll (mg m^{-2} , note log scale) versus (A) total P concentration at spring overturn (mg m^{-3} , note log scale) and (B) mean crustacean length (mm) for the lakes of Carpenter et al. (1991).

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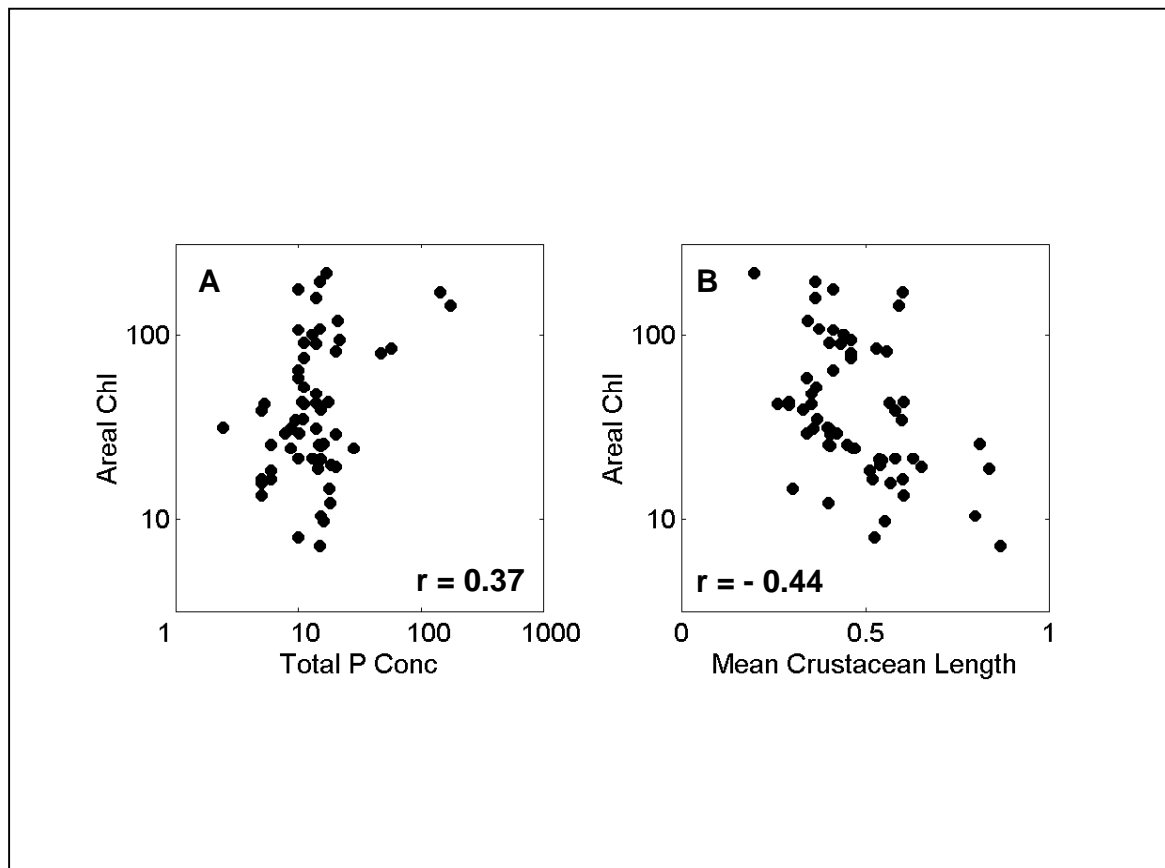


Fig. 4. (A) Chlorophyll (mg m^{-2} , note log scale) versus P load ($\text{mg m}^{-2} \text{d}^{-1}$, note log scale) from the whole-lake experiments of Carpenter et al. (2001). (B) Residuals from linear regression of data in panel A (chlorophyll mg m^{-2} , note log scale) versus mean crustacean length (mm).

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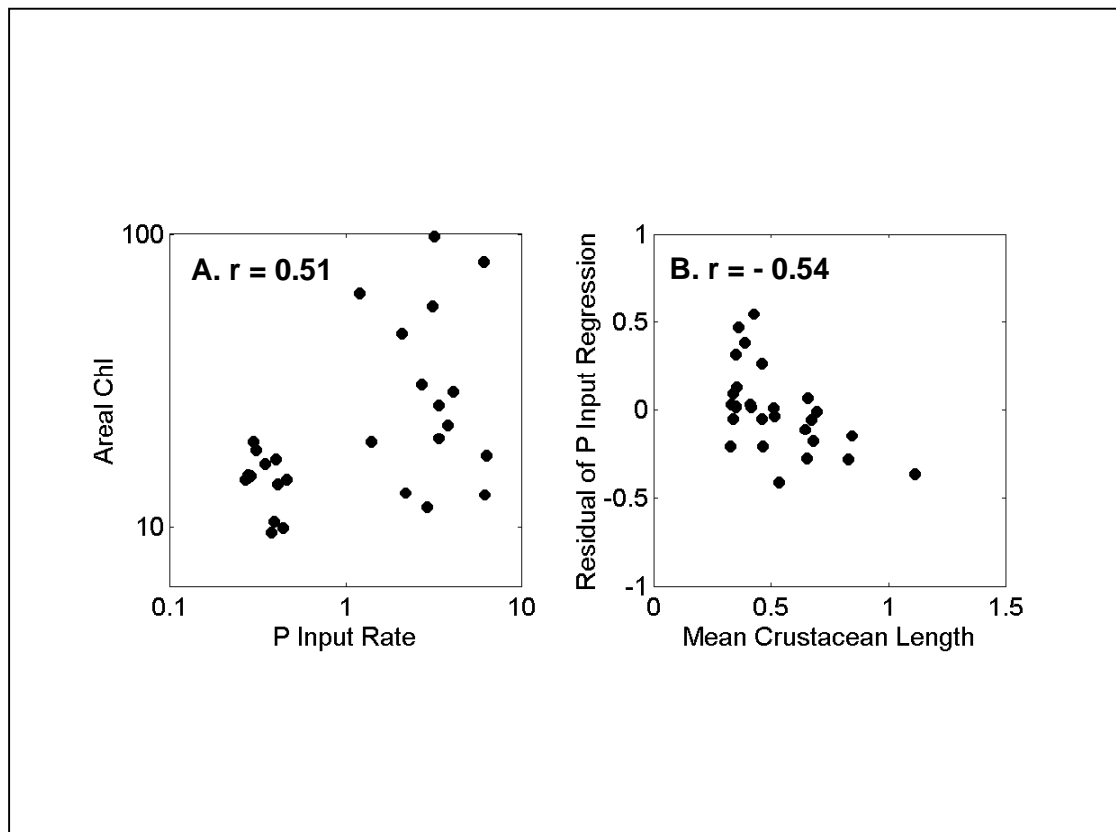


Fig. 5. Probability distributions of chlorophyll (mg m^{-2}) based on (1) P input alone (open circles in Fig. 2), (2) distribution 1 combined with the crustacean length effect based on Fig. 3B, and (3) all data in Figs 2, 3B and 4.

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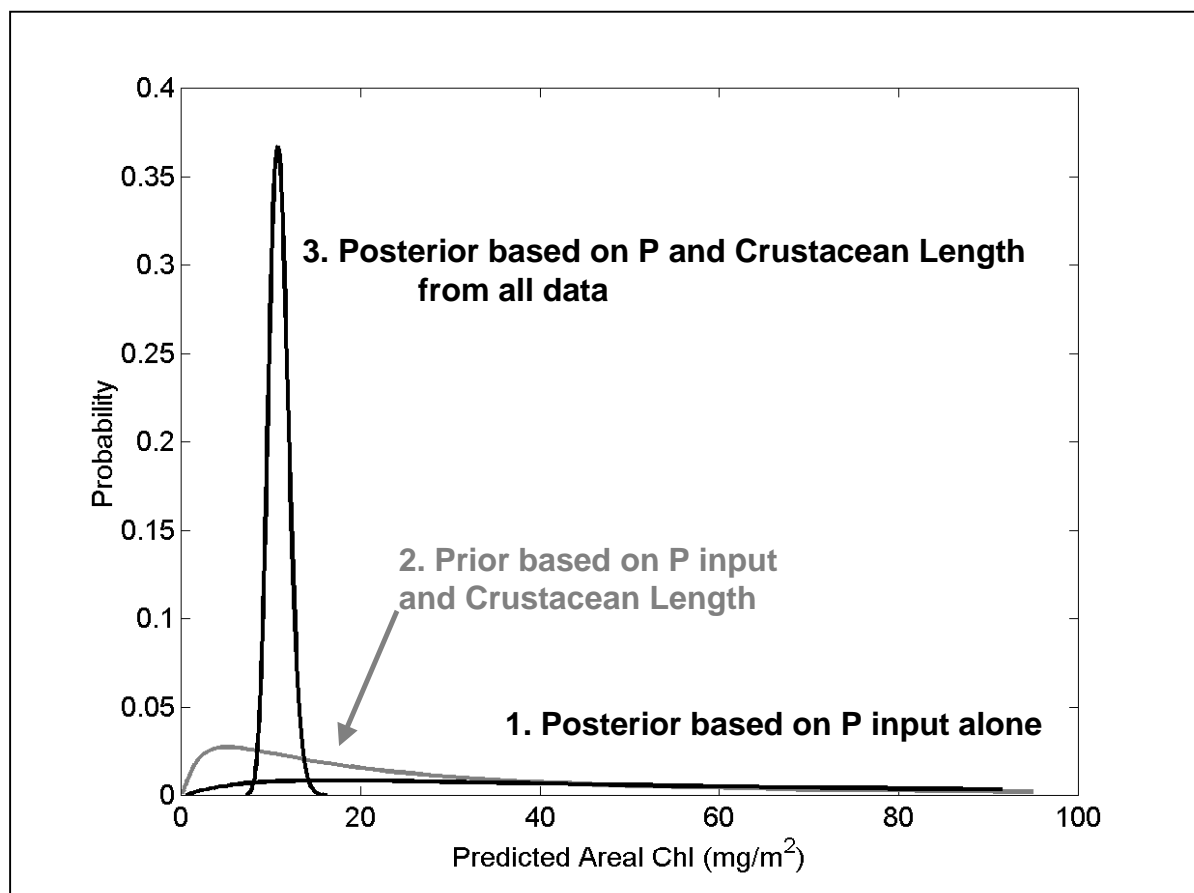


Fig. 6. Rates of birth and mortality (Appendix 2) versus fish population size for (A) abundant habitat ($W=1.5$) and marginal habitat ($W=0.5$). Dashed lines show equilibria; the left point is unstable, the right point is stable. The distance between the equilibria is the resilience. Parameter values: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

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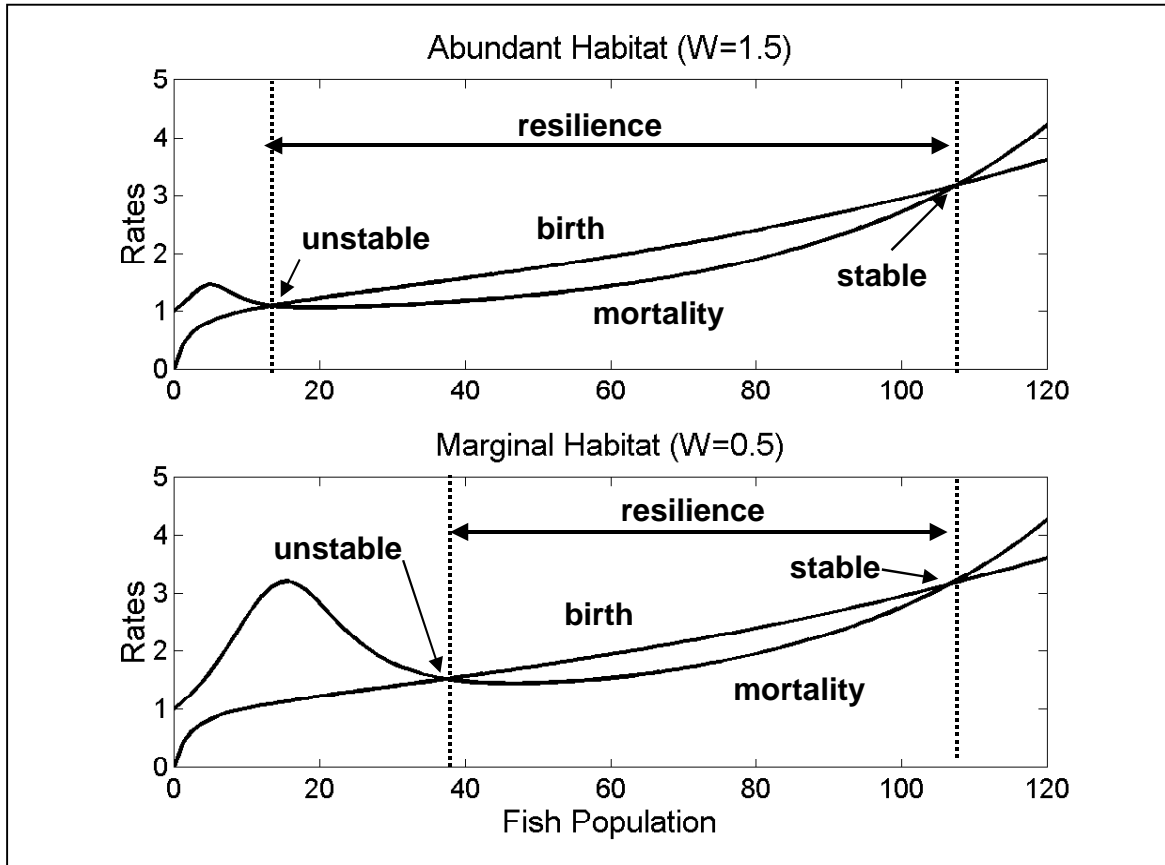


Fig. 7. Optimal policies versus stock size. Dashed lines show threshold (position of the unstable equilibrium). (A) Optimal harvest, (B) target stock size. Parameters: $s = 0.1$, $\delta = 0.98$; other parameters as in Fig. 6 except C is determined by stochastic dynamic optimization (Appendix 2).

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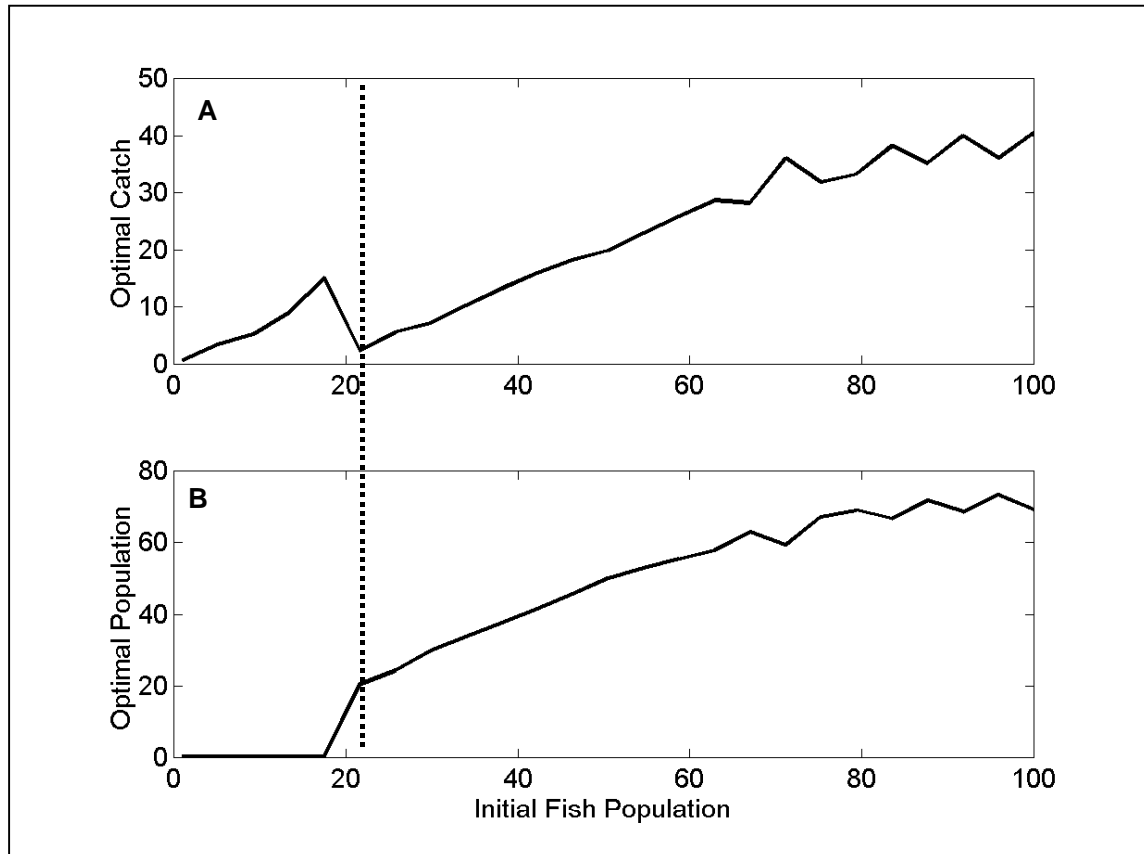


Fig. 8. Optimal harvest versus stock size under the true model (grey dashed line), density dependent model (grey solid line), and habitat model (black solid line). (A) data from strong manipulation, (B) data from weak manipulation.

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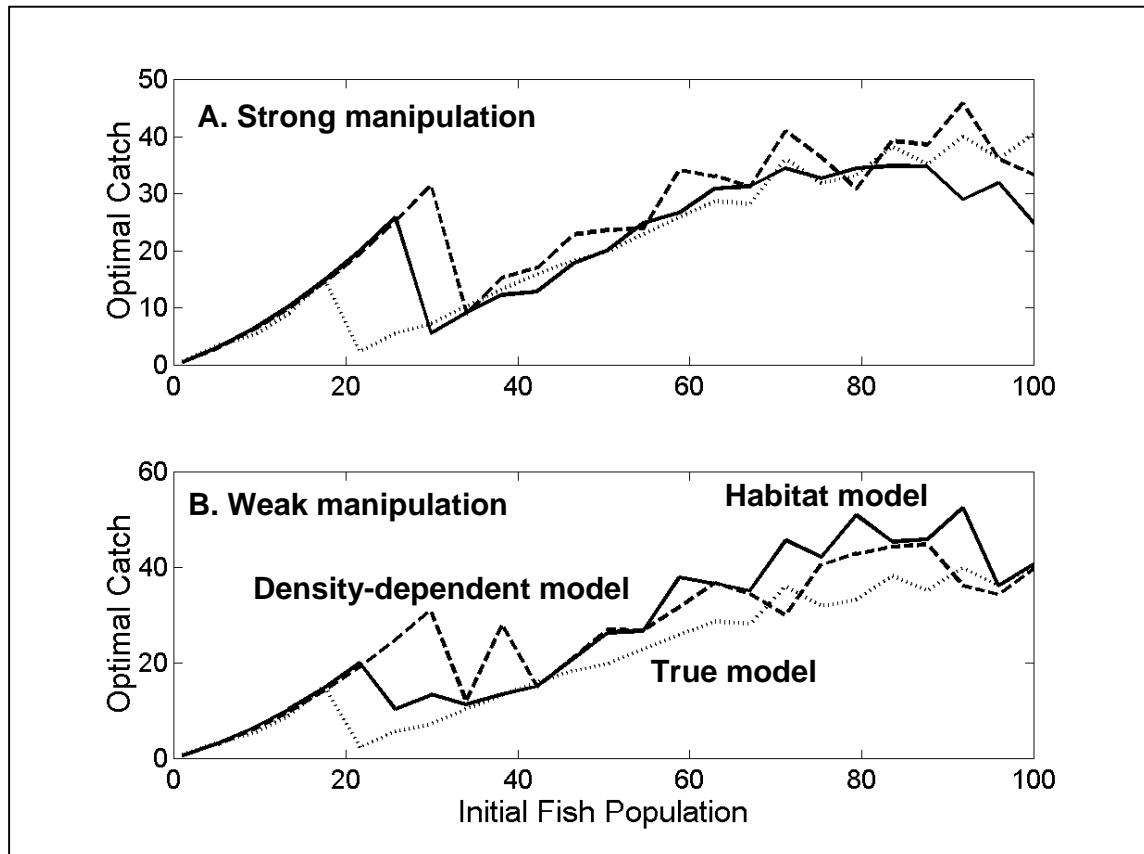


Fig. 9. Difference in utility obtained under the habitat model versus the density dependent model using data from strong manipulation (black line) or weak manipulation (gray line). (A) Marginal habitat ($W = 0.5$), (B) Good habitat ($W = 1.5$).

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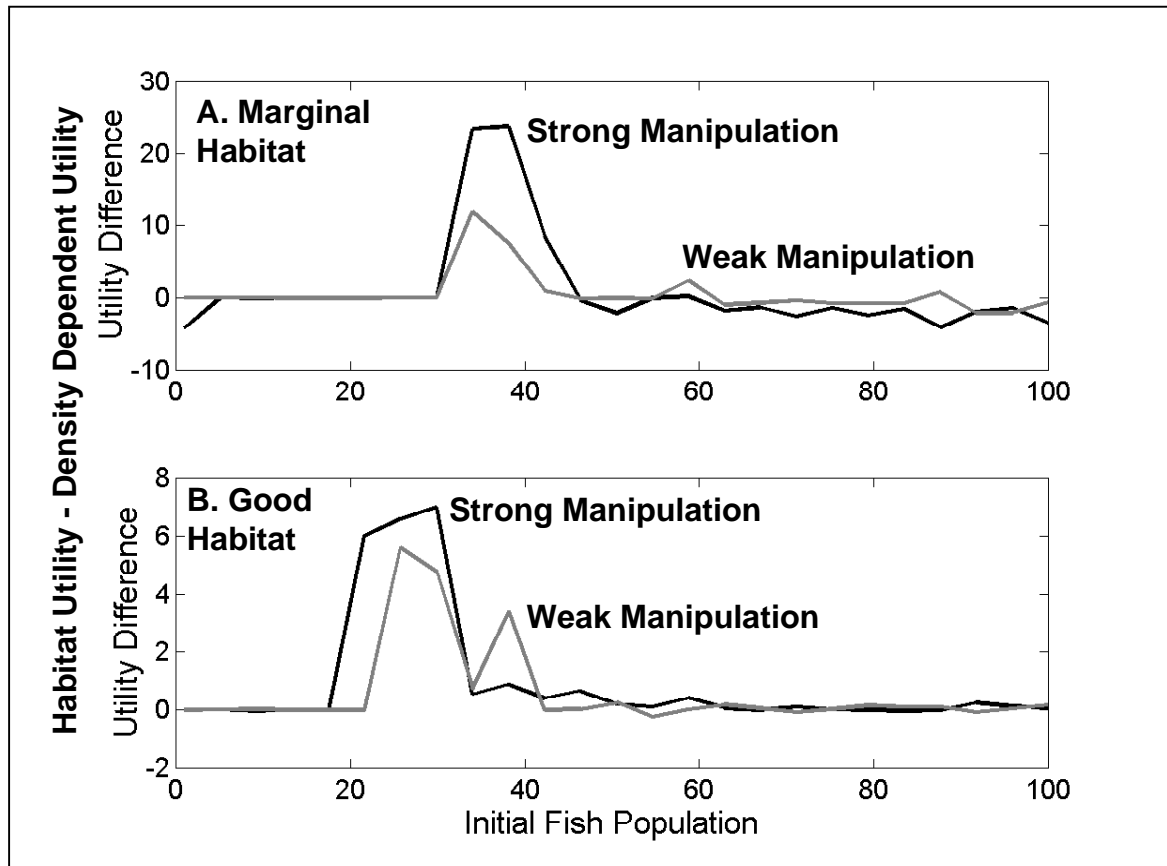


Fig. 10. Difference in utility obtained under the true model versus Bayesian model averaging using data from strong manipulation (black line) or weak manipulation (gray line). (A) Marginal habitat ($W = 0.5$), (B) Good habitat ($W = 1.5$).

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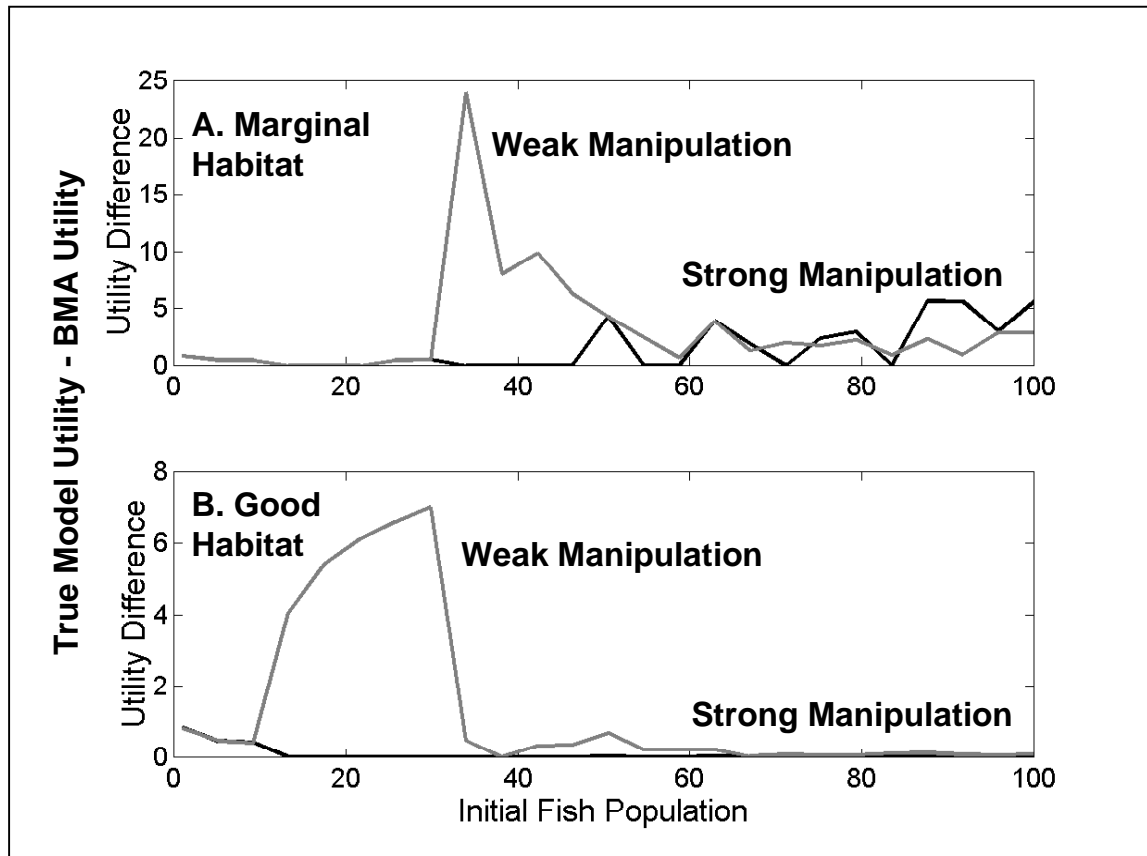


Fig. 11. Optimal harvest versus stock size for (A) the density-dependent model, (B) habitat model and (C) true model. Vertical lines show the threshold below which it is assumed that the population cannot be sustained. Data from strong manipulation.

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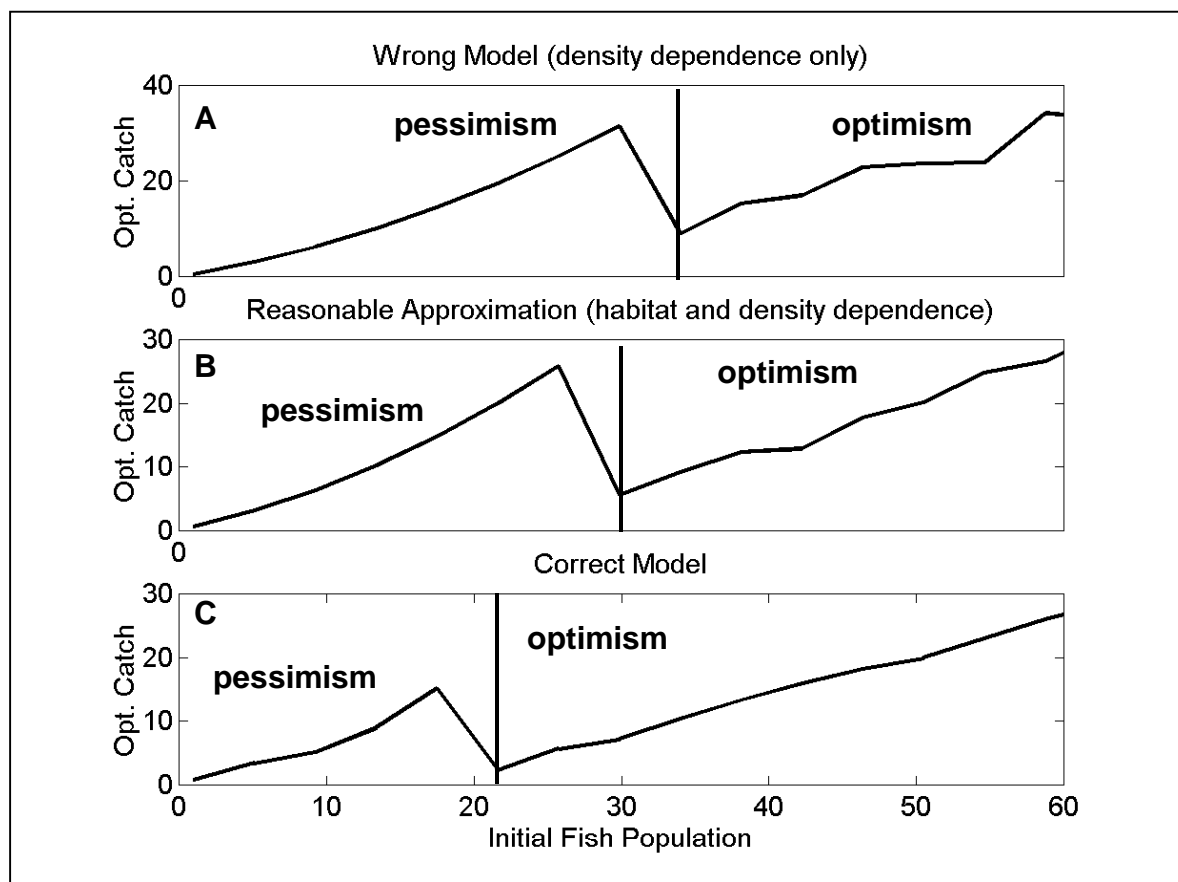


Fig. 12. Cycles from the fish management game plotted in 3 dimensions: stock size, human users per year, and size of the stable attractor (cf. Fig. 6). Cycles are numbered 1 through 4; the line becomes thinner and darker as time increases. Arrows show direction of flow.

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