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Timescales and the management of ecological systems

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Human management of ecological systems, including issues like fisheries, invasive species, and restoration, as well as others, often must be undertaken with limited information. This means that developing general principles and heuristic approaches is important. Here, I focus on one aspect, the importance of an explicit consideration of time, which arises because of the inherent limitations in the response of ecological systems. I focus mainly on simple systems and models, beginning with systems without density dependence, which are therefore linear. Even for these systems, it is important to recognize the necessary delays in the response of the ecological system to management. Here, I also provide details for optimization that show how general results emerge and emphasize how delays due to demography and life histories can change the optimal management approach. A brief discussion of systems with density dependence and tipping points shows that the same themes emerge, namely, that when considering issues of restoration or management to change the state of an ecological system, that timescales need explicit consideration and may change the optimal approach in important ways.

management | timescales | *Spartina* | grazers

Ecologists and others are increasingly recognizing the importance of using models as a guide for managing ecological systems, and this need is even more important in the face of global change (1). In many ways, these efforts build on the relative success of the field of fisheries bioeconomics (2). It is important to recognize that many of the questions require ongoing actions and that the problem is a dynamic one, so time and timescales are a central part of the problem. The challenge of determining appropriate timescales is exemplified by issues arising in ecological restoration (3), and is especially critical given both the complexity of many systems and the need to act in the face of limited data. Specific examples, such as attempts to restore habitat for grassland butterfly communities (4), indicate the importance of understanding the role of time lags in understanding restoration as well as in making management decisions.

Another feature of ecological management is that decisions often have to be made in the face of limited data or knowledge of the systems, so the development of heuristics to guide decisions is an important step. In this spirit, here I will examine the role of timescales in ecological management using very simple models with the aim of elucidating general principles, and ignoring complications such as stochasticity until the discussion. The overall goal is to illustrate when and how it is important to consider time in management, recognizing that this includes both choice of actions and evaluation.

Several cross-cutting themes will emerge regarding the importance of understanding and including time. First, there are cases where it is simply important to recognize that the response of ecological systems to management actions must play out over time, so that any evaluation of response or success must take into account the time needed. Second, there are cases where the optimal management over time must take into account the dynamic response of the system. Ecological systems may be complex, so it is not surprising that temporal aspects play an important role. It may be less obvious that the same is true even for much simpler ecological systems.

The role of the temporal aspect of ecological processes shows up even in the simplest settings without density dependence. Mathematically, this means that the system is linear, and therefore it is possible to write a formula for an explicit solution describing the dynamics, although in some cases this representation can be too complex to interpret. Even in this context, one key theme here will show up: there are differences between trying to remove versus trying to restore, because with restoration the timescales of the biological systems enter explicitly.

I will proceed both by developing and presenting general approaches and by focusing on several specific examples. This is not, however, a comprehensive review. Important areas like epidemiology are not specifically covered; however, the principles and ideas I present should apply very broadly. I will begin with an overview of ideas from linear (density-independent) population dynamics that will play a role in what follows. Then, I will discuss how these ideas play out in systems like marine protected areas where the focus is on evaluation of management. Next, an approach for ongoing management of systems where density dependence need not be explicitly included will be developed in more detail. After discussing how these approaches are applied to issues arising in management of invasive species, I will contrast the heuristic guidelines with aspects that arise in restoration. Finally, I will briefly consider aspects where density dependence is important and consider aspects of tipping points, emphasizing the role played by biological timescales. Although the presentation here focuses on deterministic aspects, uncertainty is clearly an essential part of management, so a very brief section summarizes some of the issues involved. I will finish by summarizing the general conclusions from these relatively simple models while indicating how additional important issues could potentially change conclusions.

Density Independent Dynamics

The best understood models in ecology are the ones that ignore density dependence, which in discrete time are matrix models (5). Although similar ideas can be discussed for continuous time models, the fundamental ideas are not different, so here I will focus the discussion on discrete time models. For these models, a complete solution can be written down, and quantities such as the long-term growth rate can be calculated. Nevertheless, this solution does not necessarily provide the kinds of information most useful for management. Similarly, there are formulas for the sensitivity of the asymptotic growth rate to changes in parameters, but these formulas do not directly provide information about dynamics over shorter timescales (6). These shorter timescales may, however, be the ones most relevant for many ecological management

questions ranging from sustainable harvesting to control of invasive species to restoration (7, 8).

In the simplest settings, the dynamics of a species where density dependence can be ignored will be described by a linear model. Let the components of the vector N_t be the population level at different stages (or locations or both listed as a linear array), and let the entry m_{ij} in the matrix M give the per capita contribution of individuals in stage j to stage i in the next time step. Then the dynamics of the population are given by the following:

$$N_{t+1} = MN_t. \qquad [1]$$

The numbers after T years clearly can be written as follows:

$$N_T = M^T N_0, \qquad [2]$$

so a complete solution is known. Moreover, many properties of this solution are known (5) and can be used to guide any management decisions based on this model. An alternative way of representing the solution would be to express it as a sum of eigenvectors times eigenvalues raised to the power T, which also easily generalizes to other density independent descriptions of population dynamics.

Typically analyses of the matrix model [1] in management have focused on properties like the growth rate of the population, which can be easily calculated because it is the largest eigenvalue of the matrix M. Additionally, there are convenient equations (5) on the sensitivity of this growth rate (maximum eigenvalue) to changes in the entries of M (the demographic parameters). This ability to understand general aspects of the dependence of the growth rate of the population on life history parameters allows the determination of which life stages may be key for designing conservation strategies. A dramatic example (9, 10) of the use of sensitivity analyses is the development of turtle exclusion devices that reduce mortality on juvenile loggerhead sea turtles. For the conservation of a species, long-term growth rates may be the most important guide, and the sensitivity analysis showed that juvenile survival would have a dramatic effect on this long-term growth rate.

For other problems, however, this asymptotic behavior may not be informative over ecological timescales. The growth rate (eigenvalue) that determines the asymptotic behavior of the dynamics may not be informative over ecological timescales, as emphasized by Ezard et al. (6). Further complications arise when dealing with environments that are changing through time, but even in simple settings information is needed over shorter timescales.

One approach for dealing with dynamics over shorter timescales, rather than asymptotic behavior, has been to develop (11) an analysis of sensitivity for transient dynamics that parallels and extends the sensitivity analysis for long-term behavior (5). These newer results provide ways of computing how population dynamics over shorter timescales responds to changes in underlying parameters.

Marine Protected Areas

An important current issue is the recovery or restoration of overexploited fisheries and of coastal systems more generally, where for fisheries the goal is the return of a population to a state with reasonable representation of reproductive individuals and potentially harvestable individuals. More generally, the aim may be a return to an age distribution closer to that of an unexploited population. Because the focus is on overexploited populations, population levels will be low, so as a first step it may be reasonable to ignore density dependence. One approach that clearly has been widely used is the establishment of marine protected areas (12), where fishing is prohibited.

Understanding the response of a species to the establishment of a marine reserve is an important question (12). Here, the management action is clear-cut: establish a marine reserve. Prediction of the effect of the reserve depends on understanding the response of species to this action, and the simplest approach would be first to consider single species without the complications of species interactions. The simple age or stage structured model [1] forms the basis for understanding the response over time of a single species with sedentary adults (13) to the establishment of a marine protected area. The rationale for the establishment of marine protected areas is to remove negative human influences on marine species including fishing and other activities; for simplicity, I will refer to the negative influences as fishing. Before the establishment of the reserve, the matrix M includes both natural mortality and mortality due to fishing and afterward the fishing mortality is either removed completely or reduced. So, mathematically the question of determining the response becomes one of using Eq. 2 to determine the vector describing the population through time, starting with a population that has been the subject of fishing. Also, it is important when assessing the performance of any marine reserve to take into account the temporal aspect (14).

Even though a complete solution for the dynamics through time is possible, given the need to understand dynamics in the face of relatively limited data, it is important to understand heuristic aspects of this complete solution. Behavior of the population can be studied under two extreme cases, where all recruitment of new individuals is either from outside, an open population, or all recruitment comes from the local population, a closed population (13). The dynamics differ substantially for these two general cases, because in a closed population there will be a further lag in the response of the population until increased survivorship leads to more reproductive adults, which will in turn increase recruitment.

Because mortality from fishing typically is highly dependent on age, a fished population will be very far from the stable age distribution for an unfished population. Thus, in understanding the response to the removal of fishing, the transient dynamics are important. The problem of understanding the dynamics of the approach to the long-term stable age distribution was studied by Cohen (15), where a description of the distance between an observed age distribution and the stable age distribution was determined. This gets to the crux of the problem of understanding the transient behavior—the dynamics corresponding to eigenvectors other than the stable age distribution is important.

With a reduction in mortality, how will the dynamics of an age-structured population respond? For the fishery examples, where a discrete time approach may be natural, it is clearly a simple exercise to write an explicit description of the dynamics for a single species as is done above, but more usefully general conclusions can be drawn about the dynamics of the population. The timescale of recovery will in many ways be determined by the generation time of the species under consideration. If the population is closed so that recruitment mainly comes from within the population, as contrasted with an open population where recruitment is from outside, then the recovery can be much slower and involve essentially an oscillatory approach to the new dynamics. Here, the fact that a closed population recovers much more slowly is because recovery depends on the total growth rate, not the per capita growth rate, in a closed system of this kind. Conversely, if an open system lost population through dispersal more than it gained, the open system might recover more slowly. The overall conclusion is that care needs to be taken in judging outcomes on too short a timescale, and that quantitative assessments are possible.

Another way of analyzing the response of a fishery to the implementation of a marine reserve would be to consider the importance of shifted effort. Additionally, the transient sensitivity tools developed by Caswell (11) can be used to understand the response of the fishery to the implementation of a closed area (16). The analysis of this case (16) unequivocally demonstrates the importance of recognizing responses on different timescales as there is a short-term cost but a long-term benefit.

Ongoing Management and Density Independence

A second example where it may make sense to ignore the role of density dependence is in the control of an invasive species relatively early in the invasion. In the simplest settings, the dynamics of an invasive species that is relatively rare can be described by a linear model. As this approach can have widespread application and the previously published approaches can be generalized, I will present some of the details.

If management is added to the linear population model [1] as effort removing numbers the following year, the dynamics would be described by the following:

$$N_{t+1} = MN_t - H_t, \qquad [3]$$

where H_t is a vector where entry $h_{t,i}$ is the control of class i at time t. The classes could represent not only different ages or stages, but different spatial locations so the formulation is very general. Note that, obviously, the control H_t must be chosen so that all of the entries in N_{t+1} are nonnegative. Also, the equation above implies that the management described by H_t comes after the population dynamics in year t and before the census in year $t + 1$; this assumed separation of population dynamics and human action is essentially removed in the more general formulation below.

The key observation that leads to a simple understanding of the optimal approach is that because of the lack of density dependence or interactions among the different stages or locations, with control the population after T years is given by the following:

$$N_T = M^T N_0 - \sum_{i=0}^{T-1} H_i M^{T-1-i}. \qquad [4]$$

This equation verbally says that, after T years, the population could be found by taking what the population would be without management and subtracting the impact of the control in every year projected forward to year T. Here, the impact in year T of a control in the previous year is what the controlled part of the population would have grown to in year T.

Note that, alternatively, the management could be described in terms of a per capita effort affecting the numbers the following year, which would replace Eq. **3** by the following:

$$N_{t+1} = MN_t - C_t N_t, \qquad [5]$$

where C_t is a matrix, and Eq. **4** by the following:

$$N_T = M^T N_0 - \sum_{i=0}^{T-1} C_i N_i M^{T-1-i}. \qquad [6]$$

Most generally, C_t would be a matrix whose entries could even be negative, but could also be restricted to be diagonal or nonnegative or both. Finally, both kinds of management could be combined as follows:

$$N_{t+1} = MN_t - C_t N_t - H_t, \qquad [7]$$

and the population in year T would be as follows:

$$N_T = M^T N_0 - \sum_{i=0}^{T-1} H_i M^{T-1-i} - \sum_{i=0}^{T-1} C_i N_i M^{T-1-i}. \qquad [8]$$

This formulation of management with density independence could be used to answer a range of questions about optimal management. The specification of the question is an important step in determining management for invasive species as the cost of an invasive species is not the cost of its control but the damage it causes (17). Thus, one appropriate question would be to choose a management strategy that maximizes net present value, taking into account costs of damages from the invasive, costs of management actions, and discount rates. All of these aspects could be taken

into account in the formulation developed here. However, the basic ideas come through in simpler problems that may reflect how choices are made: minimize the cost of removing an invasive species over a fixed number of years with possible additional constraints. These additional constraints could be limits on the total amount spent, or the amount in a given year, or even restrictions on what classes or locations are dealt with.

If there were no additional constraints and any discount factor was ignored, the optimal approach would be simply to immediately remove all of the invasive species, so $H_0 = N_0$. However, complete removal in a single year is typically not possible, so the determination of an optimal strategy will result from the form of the constraints. This can be seen by noting that, if there is some cost of removal and a population is growing, it is clear that spending as much as possible as soon as possible is best.

The overall form of the problem ends up being to choose the control in any year, namely, the entries in the vectors H_t and matrices C_t. As developed previously (18–20), if the constraints are linear, then the problem falls into the class called linear programming problems. These ideas have been applied to specific problems involving the control of invasive species (18–20). As noted earlier (21), a slight generalization to quadratic control can be made with similar ease of computation of solutions.

With problems that fall into the category of linear programming, two important points arise. First, it is very easy to implement extremely fast solution methods to solve extremely large problems with continuous descriptions of both the variables and the population sizes. Second, one feature of the solution is known, namely, that the solution is at a vertex, meaning first that as much of the budget should be spent each year as possible. A second consequence of the solution lying at a vertex is that effort should not be split among different classes unless the maximum possible amount is spent on all but one of the classes that is being controlled. In other words, there should never be partial removal of more than one class.

Both from specific solutions and the general points regarding linear programming, general aspects of control of the spread of invasive species emerge. I will first consider the case where the problem specified is to find the most cost-effective means of removal of an invasive species in a spatial or nonspatial (possibly implicitly spatial) context. Here, removal should always use all of the available budget.

The problem of stopping the spread of a species is more complex than just indicated. If the species is growing slowly, budget constraints are not applied yearly but to the overall budget, and a discount rate that is greater than the growth rate of the species is taken into consideration; it can clearly pay to wait for removal. The problem becomes much more realistic if an actual cost of damages is included and discount rates are included as well.

An important and dramatic role of timescales emerges if the problem is made more realistic and aspects of restoration are included. In San Francisco Bay, an invasive salt marsh cord grass, which is a hybrid between the nonnative *Spartina alterniflora* and the native *Spartina foliosa*, has had a number of negative impacts, so there has been an ongoing program of removal of *Spartina*. Along the lines of the general principles outlined above, the approach had been to have the maximal possible effort each year.

However, there is an endangered bird species, Ridgway's rail (*Rallus obsoletus*), that has used the invasive *Spartina* as habitat. (Note that the common name has recently been changed from California clapper rail.) This has led to the requirement that sufficient habitat be provided for the endangered species. The habitat can either be the invasive *Spartina*, or the native *Spartina foliosa*. Thus, one aspect of management is the restoration of native *Spartina*. This problem can be analyzed using the linear programming approach outlined above, and the results from an analysis that does include density dependence (nonlinearity) are essentially similar (18, 20). The key aspect of this system is that California clapper rails requires mature plants for habitat and

only seedlings can be planted. Thus, there is a delay introduced by the biological feature of time to maturity for the cordgrass, and consequently the economically optimal approach for management changes. In effect, the biological constraint of a missing action, namely, the direct planting of "adult" native *Spartina*, changes the dynamics. This is essentially a timescale effect and leads to the result that the optimal management is to first remove the invasive as fast as possible until the constraint of maintaining habitat for the endangered rail is reached. Then there is a period of planting of native *Spartina* combined with slow removal of invasive while waiting for the native *Spartina* to grow, a period where smaller expenditures are the optimal solution, until the invasive is completely eradicated. This result of biological dynamics changing the optimal approach will appear below as well.

Density Dependence and Nonlinear Dynamics

With systems that include density dependence and nonlinearities, much more complex behavior is possible and the range of possible scenarios is almost unlimited. I will primarily consider systems that can possibly undergo critical transitions, or tipping points. These systems are typically thought of us having a slowly changing control parameter that changes the dynamics of the faster responding system. One example is shallow lakes where the control parameter could be thought of as nitrogen or phosphorus input, and the system state could be the amount of algae or chlorophyll (22). The two basic states would be oligotrophic or eutrophic, and the system would exhibit hysteresis as well. The literature on tipping points is vast (23) and has emphasized predicating critical transitions with the underlying rationale that the system could switch from a more desirable state to a less desirable state. Predicting systems that will undergo such a transition is a challenging issue, but obviously one reason for trying to do so is to take action to prevent a system from transitioning (22). Obviously, a proper treatment of this problem would require the inclusion of stochasticity and parameter changes through time, but many important ideas come through even from examining a deterministic version of the problem with parameters changing so slowly they can be assumed to be constant.

In the most basic situation, management would require changing the control parameter, such as nitrogen or phosphorous load in time. There clearly are timescale issues here, as action would need to be taken before the system transitioned into a state where recovery could not be achieved by a small change in the control parameter, but would require either a large change in the control parameter or the state variable or both. However, this observation may still understate the nature of the problem if the control parameter is itself one that has inherent biological dynamics. Two particular systems (24, 25), one marine and one terrestrial, that have been studied theoretically provide key insights into how temporal scales play an important role in thinking of management of systems that have tipping points and hysteresis.

In general, systems with tipping points have the dependence roughly illustrated in Fig. 1, where the final system state after a long time depends on the value of a parameter. Two important general aspects are that management can consist of changes in either the input parameter, or potentially changes in the system state corresponding to changes along either the horizontal axis or the vertical axis in Fig. 1, respectively. A second point is that dynamics near the unstable equilibrium as well to the right of the "tipping point" in Fig. 1 proceed slowly because in both cases the system is still near an equilibrium. This, often underappreciated, role of timescales and slow dynamics in systems with tipping points means that even when the outside influence (represented by the parameter) has changed so no desirable equilibrium exists, there can still be time to act.

In the description of grasslands (25) with exotics and natives that have different responses to and requirements for nitrogen, the final state of the system depends on the nitrogen level, with modifications possibly due to grazing and fire. Management actions that
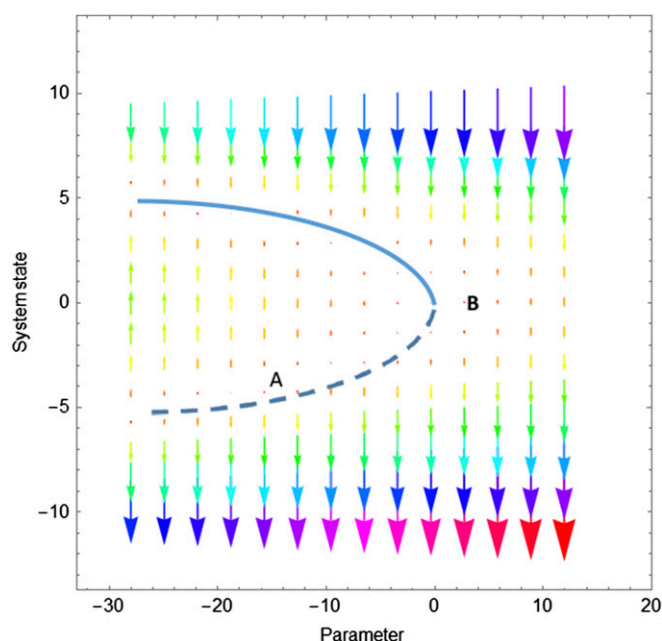

Fig. 1. Schematic diagram of a system with a tipping-point bifurcation showing the role of time. This abstraction represents parts of systems discussed in the text including a coral–algal grazer system, and a system with two plant species and grazing. This is a bifurcation diagram showing both equilibria and dynamics in the vertical direction as a function of a parameter that is varied in the horizontal direction. The solid line represents stable equilibria, and the dashed line represents unstable equilibria. The length (and color) of the arrows represents the speed of change of the system at those values of the system state and parameter. The state of the system will evolve both in response to changes in the parameter and changes in the system state. In choosing how to manage a system, it is important to recognize that the dynamics near either A or B are slow because at both the system is near an equilibrium. At any equilibrium, unstable or not, the rate of change is zero, so dynamics are slow near any equilibrium. Also, it is important to recognize that direct changes of system parameters or state may not be possible but may only occur in response to changes in other variables with biologically determined timescales. The dynamics in the figure are a generic system near a tipping point, namely, $dx/dt = -5*(a + x^2)$, where a is a parameter and x is the system state.

were considered included responses to or changes in nitrogen inputs on the one hand, and changes in grazing levels on the other. In analyzing this system, which embodies a more complex version of the bifurcation diagram in Fig. 1, including hysteresis, the different timescale of response of the system to changes in parameters (nitrogen level) or what essentially is a change in the state (vegetation changes due to fir or grazing) were compared. The model showed that direct changes in state may be the only way to led to changes on ecological timescales. Note that the management actions considered are not direct changes in the population level of the plants, but actions that lead to changes. This biologically sensible restriction has important consequences. This result embodies the idea that in a system represented by diagram like Fig. 1, that relative timescales of changes in the different axes may be key to understanding the dynamics of the system.

Another specific interaction that incorporates the same kinds of issues is the system of coral, algae, and grazers. In the simplest description of the system, there is a hysterias relationship where at high grazing levels the system is coral dominated (the desirable state), at low grazing levels the system is dominated by microalgae, and at intermediate grazing levels there are two stable outcomes (high and low coral cover) with an unstable equilibrium in between. Thus, heuristically, understanding management options in this system include the kinds of biological timescales arising in the

restoration problem for *Spartina* discussed above along with the complications of hysteresis.

In the simpler models of this system, the state of the system was described as the proportion of the habitat that was coral, macroalgae, or turf, and grazing was represented as a parameter (26), so management to reach a desirable outcome would involve changing the grazing level. However, grazing is a biological process and in the Caribbean is primarily due to feeding by parrotfish (26). In a more detailed study of the dynamics of coral–algal–grazer systems (24), the explicit dynamics of the grazer were included. Then the control (management option) is not an adjustment of grazing levels directly, but changes in fishing pressure, which leads to reductions in mortality for the grazer. Consequently, the response of the system is determined in large part by the demography and life history of the grazer, and rate of change in the system is constrained by this biologically realistic bound.

Uncertainty

Thus far, I have not explicitly included the role of uncertainty in management, which is a clear shortcoming. Instead, I have focused on developing heuristic understanding that may prove useful in the face of limited knowledge. Management of any system essentially consists of determining the current state of the system, then making predictions of the future state of the system as a result of any actions taken, and finally choosing an action that leads to the most desirable outcome. The role of uncertainty in all of these aspects has long been recognized in fisheries management (27), and these kinds of uncertainties certainly appear in any coupled human–ecological system. Especially with nonlinearities (density-dependent interactions), there is a limited ability to forecast system dynamics in time (28). System dynamics may not be known, and determination of system state may be difficult. Given the limited ability to predict for long times, adaptive management would be one approach (29). The issues that arise in the implementation of adaptive management would further reinforce the importance of recognition of the role of timescales.

Conclusions

Are there generalizations that emerge from the consideration of ecological timescales in management? Beyond the simple observation that timescales play a critical role, even these relatively simple systems have some common features. Especially in systems with hysteresis and tipping points as represented in Fig. 1, it is first important to recognize the difficulties in managing to change either system states or parameters as only indirect manipulation may be possible. Second, it is important to recognize that systems change slowly either near tipping points or near unstable equilibria, so prompt action (22) may allow recovery. Much caution is needed, however, in broadly applying any generalizations based on

systems that admittedly have been greatly simplified, leaving out important biological issues ranging from global change to stochasticity to spatial heterogeneity.

The challenge of managing ecological systems is becoming increasingly important, and there is a truly vast literature that I have only briefly described, leaving out many aspects. I have not attempted the impossible of trying to be comprehensive but have instead selected a very small number of case studies and particular approaches that highlight both general conclusions and challenges. Clearly, the necessity of explicitly including temporal aspects and the constraints of ecology lead to a difficult problem even before the inclusion of economic and other human aspects. Recognizing the issues arising even in the very simple systems covered here, the prospect of understanding how temporal issues play out on the global scale (30) is particularly daunting.

As I have been very selective in the methods and approaches discussed, it is important to recognize other powerful approaches for time-dependent optimization. The time-dependent control of dynamical systems is an intensively studied area with elegant mathematical approaches able to handle many difficult issues. However, for ecological problems, action is often needed in the face of relatively limited information. For problems with limited information, there are also well-developed approaches, such as partially observed Markov decision processes, which has been applied to ecological problems (31). However, because these approaches can only be strictly applied with rather coarse specifications of system states, it is important to develop heuristic understanding of control of ecological systems as I have done here. Alternatively, one could think of the ideas reviewed in the current paper as exact solutions to approximate (simple) models rather than approximate solutions to more detailed models; both approaches have their advantages.

Here, I have emphasized that an appreciation of the way that ecological dynamics enters into different management problems even in the context of very simple models can begin to provide essential information about the kinds of approaches needed for management and how ecological dynamics enters into assessments of the efficacy of management actions. Actual implementation of management approaches is a much more complex problem than described here, and as noted adaptive management (29) must play some role in real-world applications. Including more detailed aspects of the human dimensions of management problems (32) leads to even more complex problems with timescales that must be accounted for.

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