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Control theory and the management of ecosystems

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Summary

1. Control theory is a well-developed branch of mathematics and engineering that identifies optimal control policies for dynamic systems. While it should be useful for managing ecosystems, it is currently used only in certain fields of ecology and resource management, and only certain aspects of the theory are applied. Where optimal control policies have been determined, such as oceanic fisheries, the control policy often fails.

2. The goals of this study were to determine why control theory has not been used very much and why it fails, and also to improve its applicability to natural resource management. Control theory methods and assumptions were reviewed, and applications to agriculture, forestry and fisheries summarized. A comparison was made between control theory assumptions and the real ecological systems to which the method was applied. A fisheries example was developed to illustrate some improvements to the application of this technique.

3. It was shown that the paradoxical aspects of control theory in resource management result from the points of divergence of real systems from the assumptions of control theory. Because of non-linearities, noise, sampling difficulties, policy implementation error and other issues, ecosystems are neither readily observable nor easily controllable. This means that even theoretically correct control policies can lead to failure.

4. The fisheries example showed that measurement error and management lags can of themselves lead to the collapse of a fishery. It was shown that the costs of acquiring information and managing the system need to be incorporated explicitly into the control problem as decision variables. The solution to the fisheries control problem prevented extinction of the fishery by reducing sampling error and management lags to reasonable but non-zero levels.

5. Other suggestions are made for applying control theory with more success. By taking into account the deviations between the idealized control model and real systems, better resource management can be achieved. Control theory could also profitably be applied to the design of monitoring programmes, to model parameter estimation, and to other aspects of ecology and resource management where it is currently not being utilized.

6. *Synthesis and applications*. Control theory needs to be re-evaluated for its utility in natural resource management. It offers the potential for providing effective management policies. To achieve this potential, techniques borrowed from engineering must be expanded to incorporate the effects of state uncertainty (measurement error), environmental fluctuations (stochasticity), parameter uncertainty and policy implementation error.

Key-words: conservation, economics, exploitation, fisheries, forestry, optimal control, sampling, stability

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Introduction

The management of ecosystems is a pressing issue. Inefficient management in agriculture leads to leakage of chemicals into the environment. The passing of legislation to protect endangered species has led to the successful restoration of very few species. Overexploitation of fish stocks continues to be a problem world-wide. In all of these cases, basic research has not been sufficient to produce the desired outcomes.

Control theory, originally developed in electronics and engineering, is a methodology for achieving control over dynamic systems (Kirk 1998; Leigh 2004). It is used in rocket guidance systems and for designing stable aircraft, among many uses. It was confidently asserted 25 years ago (Halfon 1979) that control theory could be used in ecology and resource management. While the problem to be solved is identical in both cases, determine inputs to a dynamic system that will produce a desired outcome, the success of control theory in natural resource management has been uneven across disciplines and has fallen short of expectations. Analysis of this discrepancy has implications for ecosystem management. In this study, control theory concepts were reviewed, their application in various fields of resource management summarized, and a new approach to optimal control presented in the context of a fisheries example.

Control theory and ecology

The classic control problem is framed as follows. For a continuous time formulation, the system is given by:

$$\dot{x}_i = f_i(\boldsymbol{x}, \mathbf{u}) \quad \text{eqn 1}$$

where the $\dot{x}_i$ are rates of change for the state variables, the parameters are assumed fixed (e.g. are basic physical constants) and are hence not shown, and $\mathbf{u}$ is the intervention vector. The problem is to identify $\mathbf{u}$ of this augmented model such that some desired outcome is attained. In a rocket control problem, this might be the prevention of instabilities (wobble, spin) and the reaching of a target. In resource management, it might be the timing of pesticide application to maximize crop yield. In this formalism $\mathbf{u}_{it}$ might be the insect kill rate at a time t, which acts to reduce the state variable for the pest population. We can be more explicit in writing equation 1 as:

$$\dot{x}_i = f_i(\boldsymbol{x}, \mathbf{u}, \mathbf{p}) \quad \text{eqn 2}$$

by including the environmental parameter vector $\mathbf{p}$, which governs the rates. In ecological control problems, many of our interventions actually alter $\mathbf{p}$. We can partition our interventions $\mathbf{u}$ into $\mathbf{v}$ (those that affect parameters such as fertilization) and $\mathbf{w}$ (those that directly affect state variables, such as removal of biomass). If we designate $\mathbf{q}$ as the new (augmented) parameter set, then we get the algebraic relation:

$$\mathbf{q} = g(\mathbf{p}, \mathbf{v}) \quad \text{eqn 3}$$

and the new system:

$$\dot{x}_i = f_i(\boldsymbol{x}, \mathbf{w}, \mathbf{q}) \quad \text{eqn 4}$$

More detailed treatment of $\mathbf{v}$, $\mathbf{w}$, and $\mathbf{q}$ is given below, but it is clear that this aspect of ecosystem control introduces even more complexity than that posed by the non-linear relations of the ecosystem itself. Control theory methods have also been developed for discrete-time systems.

Several control theory concepts can be carried over to the ecosystem management problem to help clarify issues of resource management. These concepts include controllability, observability and identifiability. In control theory, a component is input controllable if given inputs allow that component to be regulated. In an ecological system, we might ask if manipulation of tree density can cause an alteration of herbivore abundance and thereby affect predator abundance. If so, then the predator population is at least partially controllable. This kind of question underlies every attempt to manage ecosystems, protect endangered species and extract natural resources. Thus the concept of input controllability applies to ecosystems. However, in contrast to classic control theory, control need not only be in terms of altered mass inputs but may also alter process rates (discussed below). It is rare for controllability to be specifically analysed for an ecological system. Yet a priori analysis of controllability could provide a method for feasibility analysis for proposed management actions, which at present are often undertaken based on general concepts (e.g. patch connectivity and source–sink dynamics).

The concept of observability (Cobelli, Lepschy & Romanin-Jacur 1979) is that if the outputs from a system uniquely define certain internal (not monitored) states, then those states are observable. Because ecological systems are not single valued (van Nes & Scheffer 2003), components that are not monitored cannot necessarily be inferred from other components. For example, a given predator population may be exploiting one of several herbivores, depending on their abundances. Predator numbers could be low because of disease, present low food levels or past low food levels. Thus, we cannot necessarily infer (observe) the herbivore population level from the predator population level, or conversely. We may be able to do this if we have a long time series of data that includes multiple components and we have a proper model of the system, but it is not guaranteed. Observability is rarely assessed explicitly in ecology.

Another concept is identifiability (Beck 1979; Cobelli, Lepschy & Romanin-Jacur 1979). In linear control theory, the structure and parameters of a system can be identified (parameters accurately estimated) from a sufficient set of system outputs (Leigh 2004; Walter *et al*. 2004). In ecology this is rarely true. Either the system has non-linearities (e.g. the functional response to prey density) or certain key processes are difficult to observe (e.g. root

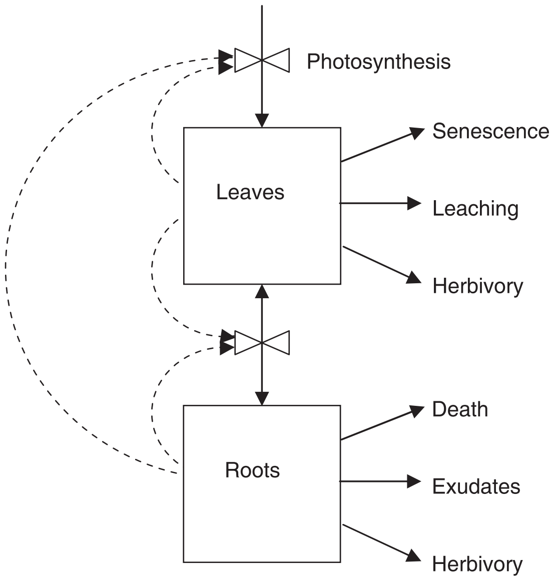

Fig. 1. A simple plant system showing mass transfers (arrows) and controls (bowties) on photosynthesis and translocation. Most of the mass transfers cannot be directly observed on a living plant, but must be inferred from experiments, as must the functional forms for flow controls.

respiration). In the latter case, the observable components do not define a unique system.

To clarify the concepts of observability, controllability and system identification, it is useful to consider a specific case. Figure 1 shows a simple plant model. The plant is conceived as growing alone and being similar to a grass with leaves and roots. The masses of leaves and roots both affect the rate of photosynthesis. Both leaves and roots are subject to death and herbivory. Leaves leach photosynthate and roots have exudates by which carbon is lost. Above-ground carbon is translocated below-ground. Observability for a plant like this is not intuitively obvious. We can sample the leaves and even the roots, but doing so requires destructive sampling. Various experimental methods have been devised to get around this problem, such as growing large numbers of plants and destructively sampling some of them at given times, or counting the number of leaves and their length and comparing this with regression models for biomass. Most of the transfers of mass in this system are not easily observable in a direct way. Leaves that die can be counted, but roots that die tend to become lost in the soil. The leaching of compounds from leaves and losses from roots via exudates are so hard to observe that for decades these processes were not suspected at all. These mass transfers have been identified following years of detailed experiments using tracers, careful observation and other methods. Some processes can be inferred from mass balance calculations (they are indirectly observable) but experimental error precludes this method for small magnitude transfers such as leaching from leaves. Some processes cannot be observed at all, such as the effect of root mass on photosynthesis. These processes must be inferred entirely from the use of models and a comparison of model output with experimental data.

System identification for such a system is again not entirely intuitive from an engineering standpoint. We do not have the exactly correct physical model for the growth of the plant. Even with error-free measurements of the states of the system, such as leaves and roots, we might still have an indeterminate system mathematically because we do not have direct estimates of the parameters governing processes, such as death, herbivory and photosynthesis. Thus, standard practice is to combine experimental estimates of some of the process rates with models containing free parameters that are then fit to experimental data. Because a physical model of the system is not available, and because many of the parameters are estimated indirectly, there is considerable sloppiness in this type of system identification procedure.

When considering system controllability, it is tempting to view the diagram in Fig. 1 as if all of the arrows could be manipulated. In fact, very few of the processes in this system can be directly manipulated. It is possible to add herbivores above-ground or kill them, but herbivory below-ground is almost impossible to control. Photosynthesis can be manipulated by altering the carbon dioxide content of the air, temperature, light levels and other factors, but translocation below-ground cannot be affected by experimental means. Thus, great care must be taken when moving from a diagram or model of an ecological system to questions of controllability and manipulation.

This is the fundamental problem of resource management. The system itself, although 'visible' in the literal sense, is not necessarily 'observable' in the systems theory sense. Without exact physical models of the system and with poor observability, system predictability is poor, as is our level of understanding.

A second major difficulty in controlling ecosystems is that feasible management options are generally extensive rather than intensive. The cheapest way to apply herbicide is aerially, but this method does not allow precision. Spot application of herbicide is possible, but costs much more. Larger timber harvest units have lower per volume harvest costs.

The manner in which control can be exerted on ecosystems puts serious constraints on what environmental or research management goals can be achieved. Highlighting the available options helps clarify why classic control theory does not always work in resource management. Manipulation of a biotic system can be achieved via three possible routes: state control, parametric (environmental) control and physical habitat control. State control is the addition or removal of biotic components. For example, mowing, burning, herbicide application, timber harvest, hunting, planting and stocking fish are in this category. Parametric control refers to alteration of environmental factors that influence organism vital rates and responses. For example, pollution, urban heat islands, fertilization and irrigation all alter organism growth and survival rather than their mass directly. Physical habitat control

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is the actual restructuring of the physical habitat. Examples include damming a river, addition of nest boxes, submerging cars to create coral reefs and installing drain tiles. These control actions can be characterized by spatial extent, intensity (degree of hunting or number of animals introduced), timing and spatial and/or temporal pattern. Only in the case of domesticated plants and animals do we expect any direct control over internal constants of the system, such as plant morphology and photosynthetic response.

In each of these dimensions, human interventions are generally extensive and not necessarily precise. It is not too hard to set hunting limits for deer that are enforceable, but it turns out to be very hard to get hunters to go precisely where the deer need to be shot or to change hunting limits rapidly. Thus hunting pressure is spatially uneven. It is very hard to design fishing nets that catch only the species desired (Vaca-Rodríguez & Enríquez-Andrade 2006). Cattle are controlled only generally by fencing them into large enclosures, but their daily movements cannot be controlled. Fire can be used, but not with spatial precision. Fire will burn too hot in some spots and will jump other spots. A forest can be fertilized, but only broadcast fertilization is economical.

In standard control theory, engineered systems can be built as designed based on analytic models. This is not necessarily true in ecology. Because models of ecological systems are non-linear, they cannot in general be solved analytically (Seppelt & Richter 1995). This means that simulation is necessary, which precludes the analytic generation of control equations. Finding an optimal control strategy then requires a link between the simulation and a non-linear optimizer of some sort, with no guarantee of finding an optimal policy. In fact, only *ad hoc* policies can be developed with this approach. As a simulation run over some time interval can take seconds to hours, and an optimization algorithm must call the simulation hundreds to thousands of times, it is clear that this approach can require a huge amount of computer time. It may even be impractical to use this approach with more realistic or spatial simulation models, in which case scenarios are often evaluated instead. In many cases when simulation and optimization are linked, a true control problem is not solved because the system is modelled near equilibrium rather than dynamically.

Resource management examples

How successful has the application of control theory to ecosystem control been, given the issues of observability, controllability and identifiability mentioned above? The answer depends greatly on the system being studied. Success can be thwarted by system complexity, difficulties of implementation and lack of follow-through.

AGRICULTURE

Agricultural systems are characterized by large, uniform patches of a crop. The farmer has control of the timing and amount of fertilizer, herbicide, pesticide and (maybe) water that can be applied. Models of crop growth and of insect pests have been successfully combined with economics to develop highly successful strategies for crop management (Ramirez & Saunders 1999; Shea & Possingham 2000; Shea *et al*. 2002; Rafikov & Balthazar 2005). It is noteworthy that extensive field tests of management strategies have been conducted. The models used for the agricultural system are usually both relatively complete and have terms that correspond closely to the real system. This is not always the case for other systems, as noted below.

FORESTRY

Forest management is similar to agriculture in that a crop is being grown. However, the value of the crop is lower and therefore the intensity of management is less. The primary intervention options are fertilization, herbicide application, site preparation, thinning, insecticide application in emergencies, fire exclusion and controlled burning. All of these are usually applied uniformly to the whole stand (or larger scale) because spatially detailed application is too expensive. The practice of forestry has developed through the interplay of stand growth models (Bugmann 2001; Robinson & Monserud 2003) and field experiments. In many forests, even extensive interventions will produce roughly the desired outcome (a merchantable stand of trees), although exceptions exist. Thus forestry is a commercially viable business. Economic analyses in forestry often follow a control theory approach (Chang 1998; Newman 2002; Crépin 2003; Rose & Chapman 2003; Sohngen & Mendelsohn 2003) even if analytic results are not available, but usually without explicit consideration of identifiability of models, observability of variables or controllability of the system.

RANGE MANAGEMENT

There are very few examples of optimal control applications in range management (Stigter & van Langevelde 2004). This is probably because, as a low-value activity, only extensive intervention measures are used. Further, only a few management interventions are feasible because of their cost.

FISHERIES

In contrast to agriculture and forestry, oceanic fisheries have been much more difficult to regulate. Once a crop or a stand of trees becomes established, it is safe to assume its long-term persistence. Forestry has not caused the extinction of the tree species being managed. This a crucial difference with fisheries. Analysis of fisheries management shows where control theory has run into difficulties.

An optimal control policy for a fishery was worked out some time ago (Cliff & Vincent 1973). For a population rate of change given by a logistic:

$$\dot{x} = rx\frac{(k-x)}{k} - u \qquad \text{eqn 5}$$

where u here is removals (harvest) of fish, r is the intrinsic rate of increase and k is carrying capacity. A constant effort policy:

$$u = \frac{rx}{2} \qquad \text{eqn 6}$$

where u is the harvest rate at each time, gives the system:

$$\dot{x} = rx\frac{(k-x)}{k} - \frac{rx}{2} \qquad \text{eqn 7}$$

which is stable, returns the population to the optimum level, $x = k/2$, as quickly as possible at any time t (Fig. 2a) and produces the maximum sustained yield.

While this is a nice result, and was believed to be true for many years, ocean fisheries have continued to collapse (Hutchings & Reynolds 2004) even though this approach was used. The reason for this serious discrepancy is that the real system deviates from the model in several key ways. The first problem is that the true growth rate varies over time (Senina, Tyutyunov & Arditi 1999; Kaitala, Jonzén & Enberg 2003; Rose 2004) but the control model assumes a constant or average r-value. If we designate this error by ε_1, we get:

$$\dot{x} = (r + \varepsilon_1)x\frac{(k-x)}{k} - \frac{rx}{2} \qquad \text{eqn 8}$$

which leads to the introduction of population fluctuations (Fig. 2b).

A second source of error is that the optimal policy $u = rx/2$ assumes that an accurate value for x is known at all times. In reality, the value of x must be inferred from sampling, which means that an error is introduced. System identification and state estimation are general problems for ecological systems (Jonzén *et al.* 2002; MacKenzie *et al.* 2003; van Nes & Scheffer 2003; Clark & Bjørnstad 2004), and are particularly problematic for oceanic fisheries (Charles 1998). Reported catch can even be intentionally biased (Watson & Pauly 2001) or may provide a misleading index of fish stocks (Charles 1998; Imeson, Van Den Bergh & Hoekstra 2002), for example because of fish schooling. We can introduce another random variable, ε_2, to capture this variability, which yields:

$$\dot{x} = (r + \varepsilon_1)x\frac{(k-x)}{k} - \frac{r(x+\varepsilon_2)}{2} \qquad \text{eqn 9}$$

With σ_1 (for ε_1) of 0·15 and σ_2 (for ε_2) of 20, the result (Fig. 2c) is larger oscillations but no extinctions out of 20 simulations of 1000 time steps.

Another complication is that lags may exist in the system. Once a fishing limit is set, it may take time to sample, analyse the data and make a policy change, or there may be resistance to fishing fleet reduction or a lag in fleet build-up (Charles 1998; Eisenack & Kropp 2001; Imeson, Van Den Bergh & Hoekstra 2002). Introducing an eight-time step lag (note that steps here are not years but are scaled by r) in the control policy equation 9 yields a 75% probability of extinction with these parameters (Fig. 2d). Note that even the latest control policy approaches for a fishery do not usually consider lags, fluctuations in r or error in sampling the fish population (Senina, Tyutyunov & Arditi 1999; Imeson, Van Den Bergh & Hoekstra 2002; Purohit & Chaudhuri 2002;

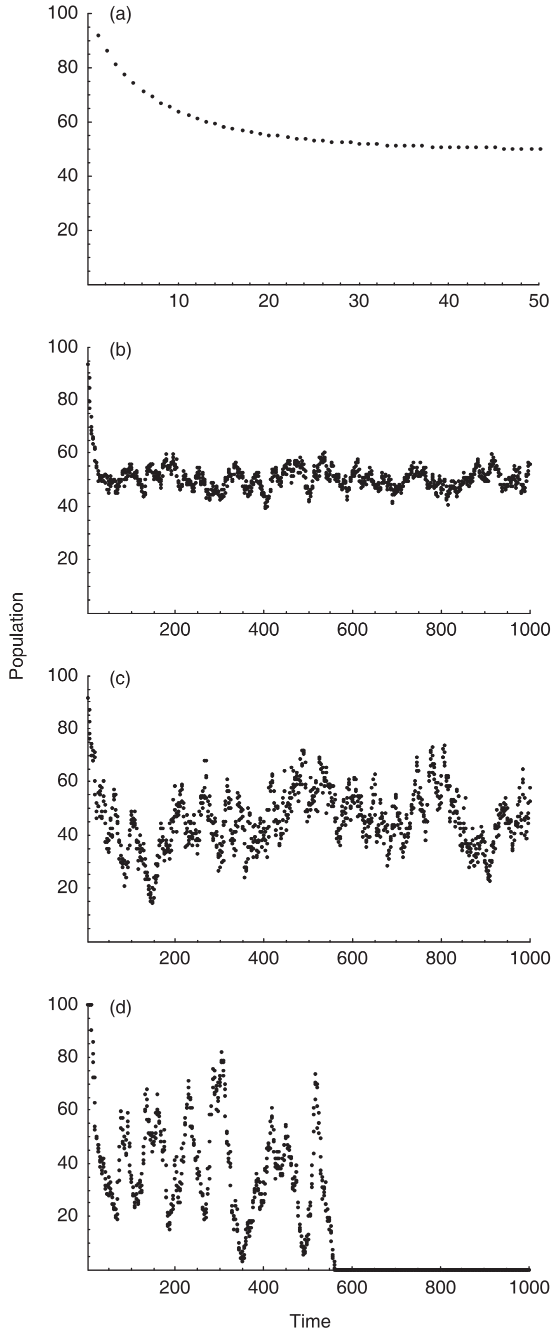

Fig. 2. Optimal control of a fishery. Parameters used were $k = 100$, $r = 0·15$. (a) Ideal noise-free case, showing rapid convergence to optimal population level for maximum sustained yield. (b) Effect of variability in true r ($\sigma = 0·15$) at each time step; no extinctions but fluctuations introduced. (c) Effect of population estimation error ($\sigma = 20$) plus variability in true r ($\sigma = 0·15$); no extinctions but wider fluctuations. (d) As in (c) but with an eight-time step lag between sampling and control; 75% of simulations led to extinction.

Clark & Hare 2004), or factor in only a single type of fluctuation or uncertainty (Senina, Tyutyunov & Arditi 1999; Runge & Johnson 2002; Kaitala, Jonzén & Enberg 2003; Katsukawa 2004). Shockingly, no study that includes the reduction of sampling error or lags as explicit control variables could be located.

A final factor that makes a fishery hard to control is that the system is really much more complicated than even this model (Brown *et al*. 2001; Bartell *et al*. 2003). For example, other competing species may become dominant after the species being fished drops to a low population level, creating a trap or hysteresis effect that keeps the fish population at a low level once it drops and prevents recovery (Folke *et al*. 2004; Rose 2004; van Nes & Scheffer 2004). Different recruitment equation forms can lead to different optimal control policies (Runge & Johnson 2002), as can the inclusion of competing species (Senina, Tyutyunov & Arditi 1999) and the joint harvesting of predators and prey (El-Gohary & Al-Ruzaiza 2002; Purohit & Chaudhuri 2002).

In the ocean, the fish do not stay in one place and the complexity of the system is much higher than for a crop. In addition, it is very hard to control exactly what the fishing fleet does. The poor observability of the system (in a literal sense) because of the fish being underwater and spread over thousands of square kilometres makes it hard to know when to take action. As a result of (i) system complexity, (ii) poor controllability, (iii) poor observability and (iv) lags, one major fishery after another has collapsed. Thus the assumptions of classic control theory are grossly violated and yet management has been based on models that have not been tested to see how they perform under the violation of key assumptions.

The above analysis throws a new light on the problem of ecosystem control. The overall control strategy in the absence of noise (equation 7) is not controversial but is completely subverted by the effects of sampling error and decision lags. One response to this situation has been to advocate more conservative management options (Roughgarden & Smith 1996; Senina, Tyutyunov & Arditi 1999), such as setting a higher minimum fish stock level. The analysis above, however, suggests that if stock level uncertainty and lags could be reduced, then stability and yield would both increase. The optimal management policy thus must consider the costs and benefits of reducing lags and stock uncertainty. As a first step, we can compute the production possibility frontier (Fig. 3) for both factors. The combination of high lag and high sample error (upper right) is very suboptimal, but the entire lower left portion of the graph is relatively flat, indicating that lag and sample error in this region do not affect harvest greatly.

To formulate the full control problem, it is necessary to consider both revenue and costs. With the system dynamics governed by equation 9, or some similar model, the revenue at time t is:

$$I\frac{rx_t}{2} \qquad \text{eqn 10}$$

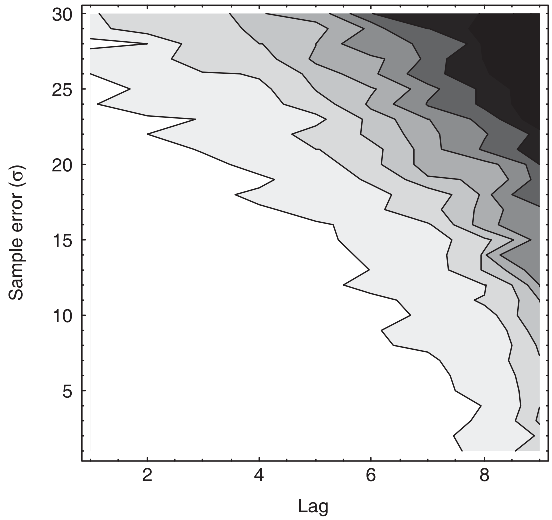

Fig. 3. Gross harvest response surface. Harvest calculated as the mean of 100 replicate stochastic simulations of 1000 time steps using equation 9 with a lag term. The σ term is sample error. The white region is relatively flat and shows that below a certain level the lag and sample error terms do not reduce yield.

where I is income per unit fish harvest. The cost of reducing uncertainty (ε_1) and lag (L) are clearly non-linear, because a sample error of 0 will cost infinitely more and rapid alterations in harvest levels will necessitate a larger administration or social cost (e.g. fleet regulation and catch monitoring). The costs at a level of lag and uncertainty will then be:

$$g(L) \qquad \text{eqn 11}$$

and:

$$h(\sigma_1) \qquad \text{eqn 12}$$

The complete control problem goal function is:

$$\max \sum \int \left(I\frac{rx}{2} - g(L) - h(\sigma_1) \right) \qquad \text{eqn 13}$$

where the integral is over the length of a simulation and the summation is over many replicate simulations to account for stochastic effects. Note that the control variables are how much to sample and how quickly to adjust the harvest, with the underlying harvest policy being taken from the deterministic case. The exact functional forms for g and h are at present unknown, because no one has studied the control problem in this way before. Thus equation 13 cannot be exactly solved at present either analytically or numerically. It is, however, possible to perform a qualitative analysis. We know that at 0 both cost functions (equations 11 and 12) go to infinity, because measuring an oceanic fish population with 0 error is impossible, and managing fleet size or fishing effort in real time (0 lag) is also virtually impossible. At the other extreme, a very large error term can be achieved cheaply by guessing at the population. In between, we know that a reasonable fish population

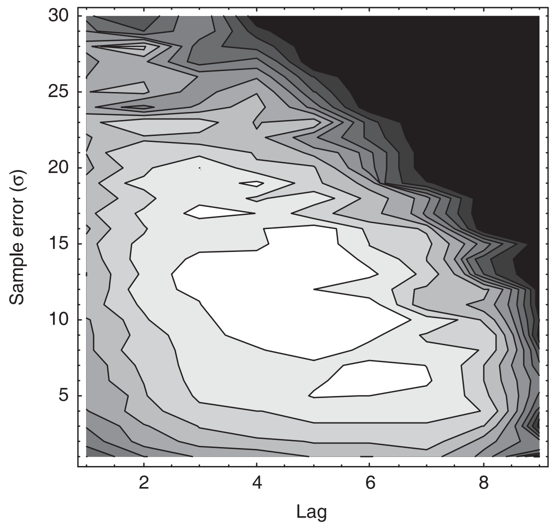

Fig. 4. Net profit response surface from equation 13. The white region is the maximal profit region. Negative profit regions were set to 0 (black) for better graphical display. Simulation conditions as in Fig. 3.

estimate or lag can be obtained for less than the value of the fish harvested, because this reflects current practice. Using general curves with these properties, we can evaluate equation 13. The result (Fig. 4) shows that there is an optimal region (white zone) with some lag and some sample error. The exact shape of this region will depend on parameters, but the general result should be robust. The precise optimum can be found, but this value may have little meaning because we know that precise implementation of a fishing policy is unlikely, and therefore a broader management target is more robust than a sharp peak. For this problem, extinction risk is factored in because it reduces long-term yield. Thus policies in the optimal region are also likely to reduce extinction risks. This approach provides a new perspective on optimal control problems in resource management, where deciding how much to spend on sampling and how rapidly to adjust harvest limits are in fact key decisions for resource managers. The novelty here lies not in the incorporation of stochasticity, for which various methods exist (Bagchi 1993), but in the shift in focus from the harvest policy alone to the harvest policy in the context of (i) information quality and (ii) policy implementation error (the lag effect). There are obvious extensions of these results to terrestrial exploitation systems, whether by hunting or wild plant harvesting.

CONSERVATION

In all of the above cases, we are primarily dealing with widespread or abundant species. Once weeds are controlled at emergence, arable crops largely dominate the site, as does a tree crop. Most fisheries are based on medium- to large-sized fish species that were abundant prior to human exploitation (Hutchings & Reynolds 2004). In the conservation field, this is not usually true. When formerly widespread species have been reintroduced, such as white-tailed deer *Odocoileus virginianus* Zimmerman, they have quickly become abundant with no further help. These are obvious conservation success stories. Most endangered species, however, were probably never superabundant. The California condor *Gymnogyps californianus* Shaw, for example, was brought back from extinction by captive breeding, but there are still not many of them. Species that are inherently rare are usually managed by 'protecting' them (Moore *et al*. 2003) but this strategy can backfire (Meek 2004), as, for example, when fire exclusion increases fuel loads and causes a catastrophic fire. This tendency to focus on nature reserves as a sole solution strategy is exacerbated by the fact that endangered species do not usually have an exploitable commercial value (like timber trees or deer) unless they attract tourism, and are thus not 'managed' in the same way as a harvested or hunted population. In addition, funds for endangered species recovery are often quite limited, so active management is uncommon (Wilhere 2002). More sophisticated control strategies are needed but are rarely developed. A positive example involves the management of the mallee-fowl *Leipoa ocellata* in Australia. This species depends on patchy habitat created by fire. Bradstock *et al*. (2005) showed by simulation that the amount of area burned and the fire interval interacted to produce a range of suitable habitat for this species. In this case optimal control involves the timing and extent of burning. It is probably feasible to implement this control strategy. Another example of successful ecosystem control is the kelp–otter–urchin system on the Pacific coast of North America. The decline of sea otters *Enhydra lutris* Linnaeus because of hunting caused sea urchin *Strongylocentrodtus polyacanthus* population increases and their grazing destroyed kelp beds (Simberloff 2004; Reisewitz *et al*. 2005). Understanding this system has led to interventions that have produced the predicted benefits to a large degree.

Why are there not more such success stories for endangered species? Solving an optimal control problem, either analytically or by numerical optimization, is only possible if the equations of state (equation 1) properly characterize the system (Runge & Johnson 2002). Many endangered species, however, are poorly understood. For example, a high percentage of declining amphibian species are declining for no known reason (Stuart *et al*. 2004). Even when recovery plans are undertaken, quantitative population data are usually not available (Harding *et al*. 2001). No reliable strategy for recovery is possible in such cases.

In other cases, the niche of the species is unusual and not easily understood or modelled. The red-cockaded woodpecker *Picoides borealis* Vieillot is an example of this problem (Simberloff 2004). Initial conservation efforts focused on this bird's need for pine trees large enough to have cavities in which to nest. Efforts to restore open pine forest with large trees have been successful (although limited in scope) but red-cockaded woodpecker populations are not really recovering. The foraging niche of this species may explain this puzzle (Simberloff

2004). The woodpeckers depend for food to a large degree on the arboreal ant *Crematogaster ashmeadi*, which does not make its own chambers but depends on galleries under bark, in twigs and in ground-level bark litter that are created by bark-mining caterpillars, beetles, termites and other insects. There are thus several complex interactions that are probably out of balance in current forests, but a path towards restoring them is inhibited by a lack of understanding. This means that this system cannot be properly modelled and therefore that no optimal control policy can be determined.

This appears to be a general problem. In spite of the attraction of traditional Lotka–Volterra population models, many real systems are more complex. In particular, they are complex in unpredictable and non-standard ways rather than just in degree of linkage (Brown *et al*. 2001). In contrast to electrical circuit components, which have known behaviours and which can be put together to form a predictably working device, the components of an ecological system often have unusual behaviours that can only be known with study. Ants on a plant might prey on aphids or farm them, with quite different consequences for the plant. This poses a real dilemma for the application of control theory to conservation, because such detailed natural history information is expensive to collect.

Conclusions

The above diagnosis of the application of control theory in ecology leads to some recommendations. Control theory clearly needs to be brought back into the spotlight for the management of ecosystems, whether for natural resources, amenity values or endangered species restoration. The design of monitoring programmes, field surveys (Ringold *et al*. 1999) and habitat conservation plans (Wilhere 2002) could benefit from consideration of concepts of observability (Field *et al*. 2004; Field, Tyre & Possingham 2005), although this is rarely done at present. Which components of the system when observed will provide information about other components? For example, at certain population levels of deer it is no longer necessary to sample the forest understorey to know that there is not much left. Such analyses can reduce sampling costs. Similarly, system identification concepts can help guide field data collection and experiments designed to parameterize a model (Walter *et al*. 2004). The few system identification-type studies that could be located (Lindley 2003; MacKenzie *et al*. 2003; Clark & Bjørnstad 2004; Wu, Fukuhara & Takeda 2005) are quite promising but very limited in number. Controllability analysis can be used to assess a priori whether given management actions can hope to influence a particular species or output, although no examples of this approach could be located.

Control theory should also be considered more seriously for the design of management guidelines and strategies. To overcome the problems presented in this paper, it is critical that the effect of discrepancies between the system model and control assumptions and the real world (Englund & Moen 2003; Jensen & Ginzburg 2005) be considered explicitly. There is often a gap between paper management plans and their implementation (Bellamy *et al*. 2001; Wilhere 2002; Stankey *et al*. 2003). For example, in the restoration of oceanic islands, removal of introduced pests (from domestic goats to snakes, rats, rabbits and birds) has been proposed as a restoration strategy. However, if every last animal is not removed, the pest population will rebound in just a few years. Removal of every animal is probably not possible, so such a policy is not feasible in the real world, even though mathematically it is a simple and optimal solution. Measurement error was shown in the fishery example to result potentially in oscillatory behaviour and management failure. It therefore needs to be considered explicitly. Some types of noise could be reduced if climate cycles (e.g. Pacific Decadal Oscillation) can be identified and factored into control policies in a feed-forward design (Yndestad 1997). Lags in response are a widespread problem in resource management. Conservation concepts when enshrined in law may take a long time to change even when everyone agrees they are out of date. For exploitation systems such as grazing systems and fisheries on public or common lands and waters, there is often resistance to reduction in harvest rates until evidence of damage and depletion is obvious and severe. More reliable forecasting based on better models and better control theory-based policies can help overcome this problem by increasing the public's confidence that predictions of future impacts are based on sound science. To cope with the reality that spatial pattern and heterogeneity can strongly influence many ecological processes, control theory needs to be extended to spatially explicit models (Hof & Bevers 1998; Akçakaya 2001). With whatever model is available, it is critical that the effect of uncertainty on the result be evaluated. For example, noise enters not only as stochastic weather over time but as uncertainty in the recruitment response equation form, as parameter estimation uncertainty and as error in implementation of the policy. The robustness of control strategies to these types of noise/error needs to be evaluated. Control strategy robustness can also be evaluated in terms of system bifurcation. If alternate stable states (Jasinski & Payette 2005) exist, the control policy can be tested for how well it prevents capture of the system by the low-yield regime. Finally, natural history does matter. Standard population dynamics models may not capture the key factors limiting a species, particularly endangered species. Management must begin with an understanding of the unique characteristics of the species. Overall, control theory offers tools and concepts indispensable to the practice of resource management.

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