Management of populations in conservation, harvesting and control

Katriona Shea and the NCEAS Working Group on Population Management

Conservation, harvesting and pest control are three aspects of the same general problem: population management. All three involve intervention with the aim of regulating population size and growth in some way, yet the dissociation of these disciplines is pervasive. Recent developments and a comparison of approaches show the potential of a synthetic paradigm.

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In conservation, we aim to minimize the chance that a population declines to extinction. In harvesting, we seek to maintain exploited populations at productive levels. In control, we attempt to decrease the numbers of a pest below some critical 'damage threshold'. The common thread is the regulation of population size and growth rate under some management regime. However, these goals are often thought about as separate issues, as illustrated by the proliferation of books on 'conservation' and 'pest control', and the relative autonomy of the fisheries management literature. All three areas have strong theoretical constructs, including conceptual and mathematical models, that have developed relatively independently. There are many commonalities and much can be gained from an examination and synthesis of the theoretical underpinnings, objectives and tools, whereas the differences are great enough that each has something to learn from the others.

A major objective of conservation biology is to identify species at risk and determine appropriate management actions to protect such species. Modelling has focused on estimating extinction probabilities and minimum viable population size to guide management actions, such as designing reserves. A popular tool has been Population Viability Analysis (PVA), which uses process-based simulations to calculate the likely fate of threatened populations[1,2]. The consideration of spatial aspects of population dynamics is prevalent, and includes concepts such as metapopulations, patchy environments, source–sink dynamics and edge effects[3,4]. Formal decision-making tools are just beginning to be used in this area[5,6].

Fisheries science is driven by the need to regulate fishing to achieve sustainable yields. Management strategies for achieving this goal are chosen using past experience to anticipate how the fishery might respond to different levels of harvesting. The tactical decisions, such as setting a catch quota, are made recurrently based on periodic assessments of the status of stocks. Consequently, work has focused on two areas: developing reliable methods for estimating stock abundance, and designing strategies that can cope with natural variability and uncertainty about the likely consequences of harvesting[7]. Estimation of abundance is achieved using statistical models to fit time-series data on catch and abundance indices. Models are also used to evaluate payoffs, costs and information gain associated with alternative management strategies. Because management decisions can be modified as managers collect new data and learn more about the fishery, fisheries were the natural place for adaptive management to grow and develop[8,9] (Box 1).

Pest (including weed) management involves the use of a variety of approaches, including various forms of physical control, spraying of pesticides, and biological control. These approaches tend to rely on the empirical, but there are exceptions. 'Expert systems' are sometimes developed, incorporating simple decision rules or simulation models that indicate, for example, optimal timing of chemical application with respect to plant phenology, weather, levels of infestation and natural enemies[10]. Biological-control theory focuses on stabilizing the interactions in pest–control agent systems[11,12], although it is rare for the success of a released control agent or the subsequent population dynamics to be routinely monitored in a quantitative manner. Integrated pest management (IPM) is an holistic process aimed at using our understanding of population dynamics to integrate multiple control approaches[13,14].

The three fields of conservation, harvesting and control exist within a common conceptual framework that can be applied to the management of all kinds of populations. The scope is huge (e.g. harvesting includes forestry and animal harvesting, as well as fisheries, and control is intimately related to epidemiology), so here we select three aspects of population management where a more frequent dialogue across discipline boundaries would be fruitful.

Decision theory as a tool for population management

Academics often remark that their theories 'provide insight', 'offer guidance' or 'illuminate possibilities'. Some of the theories are nice ideas but are any of them useful? To be useful in the real world, these ideas have to be part of a decision-theory framework[15] (Box 2) – there needs to be a clear statement of the objectives, constraints and tradeoffs inherent in the problem. Here, we briefly explore the past, present and future of decision theory in the fields of harvesting, control and conservation.

The first step in making a management decision is to determine its purpose. The management objective may be simple, such as maximizing the revenue from a harvested resource, minimizing the time a pest is at economically damaging levels, or minimizing the chance a species becomes extinct. Alternatively, it may be complex and hard to define, such as managing

Box 1. Adaptive management

Adaptive management is an approach used to guide ecological intervention in the face of uncertainty about the system. The main idea is that management actions are taken not only to manage, but also explicitly to learn about the processes governing the system. This new information is then used to improve understanding of the system and hence to inform future management decisions. Monitoring is a key component. A plan for learning is fundamental – just to say 'oh that didn't work, let's try something else' is not adaptive management.

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Box 2. What is decision theory?

Decision theory is a framework within which people responsible for management attempt to achieve explicitly stated objectives. This sort of theory is used extensively by other professionals, such as engineers and financial advisers, to make decisions. In some disciplines, decision theory uses complex mathematical tools that generally go under the banner of 'mathematical programming'. However, decision-theory is much broader and it includes qualitative methods, such as 'multi-criteria assessment' or 'ecological risk assessment'[2]. We should think of decision theory as a framework for objective management, rather than as a set of mathematical tools. In a disciplined approach to decision theory we need to define the following:

- A clear statement of management objectives, or at least a list of indicators of policy performance.
- A list of the management options, which can be expressed in terms of control variables.
- Variables that describe the state of the system (e.g. population size).
- Equations that describe the dynamics of the state variables.
- Constraints that bound the decision variables and state variables.
- All the parameters needed to describe the above, preferably with some notion of the variability around each.

the number of deer in a park to maximize overall 'community' benefit. This latter objective would need clarification – for example, defining the community, measuring benefit to different sectors and possibly expressing those benefits with a single currency. The process of defining an objective is important and nontrivial.

Fisheries managers have had a head start because of an obvious economic imperative to their objective. When mathematical programming was still in its infancy, fisheries ecologists built population models with decision theory and optimization in mind, and the objective of maximizing sustainable yield[16–18]. Modelling approaches have become more sophisticated, however, and include looking at risks of 'catastrophes', such as stock collapse, and making use of Bayesian methods to acknowledge uncertainties when evaluating policy choices[19].

Weed and pest control experts also deal with explicit costs and benefits as they try to maximize sustainable yields from agriculture. Because control decisions are inevitably sequential and state-dependent, stochastic dynamic programming (SDP) is an appropriate tool. SDP is a powerful algorithm for solving complex, stochastic, state-dependent optimization problems of the type commonly encountered in population management. Consider, for example, decisions about pesticide use. During the course of a season a farmer might need to make weekly decisions about whether or not to spray. These decisions should depend on the state of the system (e.g. pest abundance, pest stage, crop state and time of year), as well as potential rewards (e.g. the anticipated sale price of the crop). The outcome of these decisions will mainly depend on stochastic events, such as rainfall, temperature and fluctuations in commodity prices. There seem to be few applications of SDP to pest control[10,20] but 'expert systems' amount to heuristic approximations of state-dependent decision-making in a stochastic system[10].

Conservation biologists sometimes have clear objectives, such as minimizing the probability of extinction of a specific species. However, for many problems in conservation, especially ecosystem and multispecies management, the objectives are often unclear or complex, and hard to express mathematically[5,6,21–23]. The range of conflicting objectives perceived by conservation ecologists has possibly been the single most important obstacle to the application of decision theory to conservation. It is important to realize that many of the 'grand' theories of conservation biology, such as island biogeography or metapopulation theory, are useless to managers outside a decision-making framework. Consider one of the major problems in conservation: minimizing the chance of extinction of a species restricted to a fragmented habitat. Constructing corridors that allow movement has been advocated but, even if we assume that corridors are useful in a particular case, is this sufficient to make a decision? The construction of a corridor costs both time and money. The question is not whether a corridor is useful but whether its construction is the best use of resources to achieve the objective. That same effort might be better spent on expanding one fragment of the habitat. Advocating only one solution breaks a fundamental rule of decision-making: that of listing all the management options.

Enthusiasm for decision theory, however, needs to be tempered by reality. There is a wide range of analytically and computationally complex tools for optimizing management, but the benefits of finding the optimal strategy can be marginal. Intuition, rules of thumb, multicriteria assessment and experience can often lead to decisions that are robust and almost as successful, especially when system responses are difficult to predict. Different decision-making approaches can coexist – indeed, many rules of thumb have been derived from more complex mathematical optimization methods. Mathematical tools aside, we strongly recommend the decision-theory framework for all population managers. At a minimum, this involves a clear statement of objectives and an evaluation of the possible consequences of alternative management options.

Combining process-based models and time series data

Management of populations cannot help but be improved by a better understanding of the processes that drive the observed dynamics. One way to accomplish this is to develop competing process-based models, each of which represents a different view of the mechanisms that drive the dynamics, and then build up confidence in the competing models by comparing their predictions with actual observations. This approach underlies adaptive management, in which the results of past management actions are used to reappraise the credibility of the competing hypotheses[24].

Time series of estimated population abundance are one source of data for testing competing process-based models. Indeed, in systems where manipulative experiments are not feasible, they may be the only source. In these circumstances, it can often be useful to develop process-based models with the explicit intent of testing them against time series data. Various statistical methods, both traditional and new, exist for measuring the explanatory power of process-based models against time series data[25]. A key strength of this combined approach is that time series can be used to evaluate models that contain important state variables (e.g. abundance by age) that are not actually observed, or processes (e.g. the effect of age or density on a vital rate) that are not measured directly[26]. The method also allows all sources of information to be integrated within a unified estimation protocol[27]. This applies to data as diverse as results from particular experiments, field estimates of vital rates, independent estimates of carrying capacity, or prior knowledge of any sort.

Different versions of this combined approach are used in fisheries[27], which is at one end of an information continuum. Long time series of some index of abundance may be available, such as catch per unit of effort (CPUE), sometimes separated into year classes. Models and time-series data are occasionally used to explore competing hypotheses concerning, for example, density dependence in recruitment, growth and mortality[26].

Conservation is typically at the other end of the information continuum from fisheries. There is usually some information available on key processes, including habitat use, fecundity, age-related death rates, and dispersal (even if the parameters are sometimes 'borrowed' from closely related species). Long time series are usually scant, however, particularly if species are rare or endangered. We believe that obtaining such data would be a useful addition to conservation programs, especially if they are collected with the aim of testing competing models of the processes underlying the population dynamics. Such a time-series approach is quite different from the current common practice in population modelling for conservation, which focuses on estimating demographic parameters and their variances at a point in time, and projecting population sizes into the future on the basis of these estimates[28]. Any of a number of different processes might be responsible for an observed decline, such as response to continuously declining carrying capacity, delayed response to previously lowered carrying capacity, or trends in population parameters[29]. Each explanation has its own management implications, but these differences are typically not explored in PVA analyses.

Pest control is the area in which process-based models are most fully developed, and where most use could probably be made of testing explanations against time-series data. Process-based models are the basis of expert systems[10] and have also been used in attempts to explain successful biological control and to guide the selection of natural enemies[30,31]. However, alternative process-based models are not usually assessed, and there is no procedure for assembling monitoring data on pest and natural enemy abundance and using the resulting time series in a formal statistical framework to evaluate the predictability of the models. Even where data have been collected[32], it is frequently for too short a period and the data are typically compared more or less informally with a model of interest, rather than being used formally to explore the credibility of competing explanatory models.

The fundamental constraint to applying a process-based time-series fit to a model is simply the lack of time series data. The differences among fields arise, at least in part, from the frequency at which management decisions are made. Thus, fisheries researchers have long time series partly because fish are caught more or less continuously, but also because decisions about quotas are needed each year. In contrast, decisions about species preservation or decisions to use a particular biological control agent on a particular pest are usually made just once (although this has been criticized[9]).

Box 3. Population management: a joke of a science?

There were four population ecologists shivering and starving, trapped in the boreal winter – a conservation biologist, a fisheries scientist, a theoretical ecologist and a pest manager. A moose appeared on the horizon and came thundering towards them – 1000 kg of warm edible flesh. Each scientist drew on his or her expertise and dealt with the moose using all their respective discipline's wisdom:

- The conservation biologist couldn't decide on an objective. He died wondering whether the moose's existence was more important than his own.
- The fisheries scientist used the wrong model. Based on her prior knowledge of elk, she predicted that more moose would be coming, so she starved in anticipation of a herd that never appeared.
- The theoretical ecologist drew out his laptop and quickly wrote a program to calculate the optimal distance at which to shoot the moose. His calculations proved that the optimal distance was an imaginary number, and he would have been successful had the moose entered imaginary space.
- The pest manager knew immediately that the moose had to be killed – the only question was with what – pesticide or natural biological control? She opted for the environmentally friendly biological control and released a wolf, which turned around and ate her.

Space in population management

Population management needs to address spatial considerations at two levels. First, managers should be aware of spatial heterogeneity and the scale at which population processes occur when planning. Second, management options themselves could be spatially explicit. Variability in space, both in environmental and population processes, is of fundamental importance to population dynamics, and managers need to understand and manage this variability.

In some senses, conservation biologists have been most concerned with spatial issues. The first question a wildlife manager often asks about a threatened species concerns its distribution and abundance. Fieldwork is directed at partitioning habitat into classes according to the observed densities of the population. Although density is important, partitioning the landscape into classes according to population processes – changing birth, death and movement rates – is more so. A frontier of population management is understanding the implications of habitat heterogeneity on demographic rates and managing it accordingly. For example, the source–sink concept[4] is beginning to have a profound effect on conservation biology as we seek to manage habitat not on the basis of population density but on its ability to consistently sustain source populations[33].

There is also a large body of theory and data on the role of corridors and edges in conservation[34], and conservation biologists have long been interested in the size and spatial arrangement of protected areas[3,35] (although it is important not to lose sight of the fact that it is total habitat area and quality that is fundamental to the persistence of a species). Two reserve design issues that have been discussed at length in the conservation literature include the effects on populations of dispersal and reserve isolation, and of reserve size. Populations in large reserves are buffered from extinction caused by demographic and environmental variability but could be vulnerable to a single catastrophic event, whereas those in many small reserves can spread risk with respect to catastrophes (depending on the spatial scale) but are more likely to go extinct in isolation[36–38].

In pest control, there is an extensive literature on the effectiveness of biocontrol agents that respond to spatial heterogeneity in either the environment or pest density[39–41]. There is also some theory on the role of spatial processes, such as how spatial staggering of planting and harvesting can lead to improved control of rice pests by generalist predators that move from field to field as harvesting proceeds[42]. Increasingly, habitat heterogeneity is being managed to expedite control. For example, attempts to increase the ambient level of natural enemies have included intercropping or planting species along the edges of fields that attract or maintain natural enemies, and there is field evidence that planting pattern and intercropping do lead to better control[43,44].

In forestry, although tree harvesting theory is highly developed with regard to size distributions of trees and economics[45], the spatial impact of harvesting on forest pest outbreaks is poorly understood. For example, Roland and Taylor[46] have shown that the fly parasitism rates of forest tent caterpillar (*Malacosoma disstria*) are strongly depressed in logged forest, leading to longer, more intense pest outbreaks. To minimize economic loss, forest managers might be able to learn from spatial pest control and reconsider the spatial arrangement and timing of harvest events.

Fisheries management has made less use of spatially explicit approaches, even though the study of spatial processes has always been central to fisheries science. Basic knowledge about spatial processes has mostly been used to delineate management stock units, each of which could be viewed as a 'dynamic pool' isolated from the rest[17]. Most theory and management have been developed for the big industrial fisheries that target rather mobile species (e.g. tuna, plaice, cod and haddock[7]). Although it is true that spatial structure might not be so 'apparent' or persistent in some of these stocks, spatial structure could be more relevant than we have traditionally acknowledged: the effect of fishing is not simply diluted in the pool, as fisheries models commonly assume. Certainly, fisheries based on organisms with a relatively stationary adult phase (e.g. scallops, urchins and abalone) will benefit from more explicit spatial management[47–49], such as areas closed to fishing. The size and placement of closed areas should, at least in part, be determined by recruitment patterns, the habitat preferences of adults, and fish movement among areas.

Is population management a unified science?

Because pest control, conservation biology and fisheries science all attempt to manage population size, it would seem that these three disparate fields are really part of one scientific discipline: the science of population management (Box 3). Consequently, these branches of applied ecology would do well to borrow insights and tools from one another. Ironically, the opposite is the case: on many university campuses, conservation biology, forestry, fisheries science and pest control are taught in different academic departments, with no overlap among the students. This is unfortunate. The potential for cross-fertilization and integration among the fields is by no means restricted to the subjects discussed here. Other relevant areas include evolutionary issues (genetic bottlenecks, evolution of resistance in pests, selection of life history traits and the development of genetically manipulated organisms), considerations of uncertainty (demographic, environmental and economic stochasticity, catastrophes, and ignorance about population processes), and the issue of nontarget impacts of management plans. Fisheries biologists and conservation biologists can discuss working with time series data. Pest control researchers and fisheries biologists can talk about the benefits of mechanism-based models. Conservation biology can infect pest control and fisheries management with its attention to spatial detail. Ecologists in all fields should use developments in disciplines not traditionally their own and take part in the integration of population management.

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Designer snails

The Algorithmic Beauty of Sea Shells (2nd edn)

by Hans Meinhardt

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Mollusc shells, especially those from the marine tropics, often display complex and beautiful color patterns. Multicolored bands, oblique sets of lines, chevrons, dots, triangles and combinations of these are superimposed on the regularly coiled shells of gastropods, bivalves and the pearly nautilus. In burrowing species, at least, the adaptive value of shell pigmentation is puzzling because the patterns are never seen in life by other members of the same or other species. Perhaps because of this, intraspecific variation in color pattern tends to be high even though basic themes are repeated over and over within and among species.

Many biologists and mathematicians have attempted to make sense of these bizarre patterns, starting with Waddington and Coe in 1969 (Ref.1) and including Wolfram's models based on cellular automata[2]. But Hans Meinhardt has done by far the most extensive research and has probably come closest to an explanatory model. Because very little is actually known about the physiological mechanisms of the pattern formation, Meinhardt uses computer simulations to test *ad hoc* models against the variety of actual patterns in nature. This is a dangerous strategy, of course, but the results are truly impressive. Using a fairly simple model based on the nonlinear dynamics of pigment production and inhibition, plus diffusion to neighboring sites, Meinhardt has successfully simulated virtually the entire range of molluscan color patterns. These are documented by scores of color photographs of actual shells with matching simulations. The result is not only convincing but also makes a beautiful volume. The success of Meinhardt's model is such that the real world must use something close to this algorithm.

A disk is provided containing a DOS-executable program whereby one can reproduce the simulations illustrated in the book or explore other possibilities within the parameter space defined by the basic equations. The program is easy to use and the disk includes the full source code so the user can read, trouble-shoot or change the algorithm.

Meinhardt's simulations are shown as two-dimensional plan views, appropriate to his mission because it avoids the distortion of the pattern being superimposed on the curved, spiral surface of the shell. However, a special chapter by Prusinkiewicz and Fowler adds the third dimension. The color pattern algorithm is combined with earlier work on computer representation of spiral shell forms[3] to produce a series of truly remarkable graphics. Photographs of real shells are shown alongside simulations. The shell geometries and color patterns are matched so perfectly that it is often hard to tell which is which. This is not only scientifically important, but also further adds to the beauty of the book.

Throughout *The Algorithmic Beauty of Sea Shells*, Meinhardt emphasizes that he is using color patterns in shells only as a vehicle to learn about a host of other developmental systems in which oscillations, traveling waves and similar phenomena are common. The great advantage of using shells is that the pigmentation generally occurs during accretionary growth of the shell, so that the adult shell carries a complete historical record of the process. With the time dimension preserved, validation of the model is far more rigorous than if the time sequence had to be inferred. In the final chapter, curiously titled as an appendix, Meinhardt explores the potential applications of his activator–inhibitor model to a wide variety of problems posed by development in other animal and plant groups. At the very least, this should provide a valuable source of hunches for people working with problems as far afield as limb buds in vertebrates and vein patterns in leaves.

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Natural CO_2 springs: obstacle or opportunity?

Plant Responses to Elevated Carbon Dioxide: Evidence from Natural Springs

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Aside from its influence on the climate system, the increasing concentration of atmospheric CO_2 has direct effects on plants and ecosystems via photosynthesis[1–3]. Since the middle of the 1980s, there has been a flood of research designed to evaluate and predict such direct CO_2 effects. Recently, however, strong concerns have been expressed as to whether we can sufficiently predict plant and ecosystem responses to rising CO_2 levels purely from experiments of short-term, ambient versus double-ambient CO_2 concentrations, which have predominated in the field[4–6].

Natural CO_2 Springs is the product of a workshop on 'Carbon Dioxide Springs and Their Use in Biological Research' in 1993. It provides an excellent overview of ongoing and planned research at sites near naturally occurring CO_2 springs from Iceland to central Africa but with a focus on Italy. In the field of CO_2 research, debate still rages about the scientific value of ecological experiments conducted using this natural form of atmospheric CO_2 enrichment. Indeed, the debate permeates the entire book, with nearly all of the 18 chapters comprehensively but repetitively discussing the advantages and disadvantages of using CO_2 springs.