SUSTAINABLE EXPLOITATION OF BIOLOGICAL POPULATIONS

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For a system of nonlinear difference equations that models the dynamics of exploited biological populations, a locally optimal periodic solution is constructed. If this solution is unstable, a stabilizing feedback in the harvesting is introduced. The method is applied to an age-structured population model in fishery as well as to a host-parasitoid system for which the number of hosts and the number of introduced parasitoids should be minimized.

Keywords: optimal harvesting, system of nonlinear difference equations, fishery, host-parasitoid system, stabilizing feedback

1. Introduction

Harvesting of renewable natural resources such as fishery at sea, may be at risk because of a too intensive exploitation. This paper deals with optimal sustainable harvesting strategies. The dynamics of the biological populations involved is modelled by a system of nonlinear difference equations. Sustainability is implemented by the requirement that the solution to the system is periodic, so that after a time T all variables have returned to the initial state. Within this class of solutions we search for the locally optimal one in the neighborhood of a given periodic solution. For a survey of optimal harvesting we refer to (Clark, 1985).

In Section 2, an algorithm is developed that for difference equation models converges to a locally optimal solution. The method is related to that of De Gee and Grasman (1998) for differential equation models. If the optimal solution is unstable, a feedback law is introduced modifying the harvesting such that stabilization is achieved, see Section 3.

In Section 4, we study an example from fisheries and conclude that periodic harvesting with changing fishing effort may turn out to be more profitable. In Section 5, a host-parasitoid model is studied. Contrary to the usual problem of maximizing a harvest, the goal is here to have a minimal host population, which may cause damage to a crop, while the number of parasitoids, that are introduced, should also be as low as possible. This problem can be solved in the same manner as an optimal harvesting problem. The main difference is that these systems tend to be unstable, such as the well-known Nicholson-Baily model, while regular harvesting problems tend to have a stable optimal solution.

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2. Locally Optimal Solution under Periodicity Constraints

We consider the dynamics of n interacting populations x_i, $i = 1, \dots, n$ with harvesting; 'negative harvesting' is allowed (e.g. inoculation in biological pest control). The dynamical system is of the form

$$x(t+1) = f\big(x(t), u(t)\big), \tag{1}$$

where the control vector $u(t) = (u_1(t), \dots, u_m(t))$ represents the harvesting. It is assumed that $f(x, u)$ is differentiable in x and u.

In this study, we focus on periodic solutions of period $T \in \mathbb{N}$. For some $u(t)$ let an (un)stable periodic solution $\underline{x}(t)$ be given. Then the objective is to construct a periodic solution that locally maximizes (or minimizes) the performance index

$$J\big(u(0), \dots, u(T-1)\big) = \sum_{t=0}^{T-1} H\big(x(t), u(t)\big), \tag{2}$$

where the differentiable function $H(x, u)$ can be the profit of the harvest that is maximized or the cost of introducing a parasitoid (and the damage caused by the host) that should be minimized. For both the cases we will present an example in Sections 4 and 5, respectively. In the following it is assumed that the problem is of a type with the performance index doing worse for $|x|$ and/or $|u|$ tending to infinity.

Having a T-periodic solution to (1) given by $\underline{x}(t)$ we replace the control $u(t)$ by $u(t) + w(t)$. Assuming that $w(t)$ is small we consider the tangent linear system for $v(t) = x(t) - \underline{x}(t)$:

$$v(t+1) = F(t)v(t) + G(t)w(t) \tag{3}$$

with

$$F(t) = \left[\frac{\partial f_i}{\partial x_j}\right]_{\underline{x}(t), u(t)} \quad \text{and} \quad G(t) = \left[\frac{\partial f_i}{\partial u_k}\right]_{\underline{x}(t), u(t)}. \tag{4}$$

Clearly, the homogeneous system $v(t+1) = F(t)v(t)$ satisfies

$$v(t) = \Phi(t, t_0)v(t_0), \quad \Phi(t, t_0) = \prod_{\tau=t_0}^{t-1} F(\tau), \quad t > t_0. \tag{5}$$

Enforcing the periodicity constraint $v(0) = v(T)$ on the tangent linear system (3), the initial condition can be directly expressed in the perturbation of the control $w(t)$:

$$v(0) = \big[I - \Phi(T, 0)\big]^{-1} \sum_{t=0}^{T-1} \Phi(T, t)g(t)w(t). \tag{6}$$

In order to locally optimize (2), one has to compute the derivative of $J(u(0), \dots,$ $u(T-1))$ with respect to $u_j(t)$. There are various ways to carry out this calculation. One can compute directly

$$\frac{\partial J(u)}{\partial u_j(t)} = \sum_{k=1}^{n} \frac{\partial H(x, u)}{\partial x_k} \frac{\partial x_k}{\partial u_j(t)} + \frac{\partial H(x, u)}{\partial u_j(t)}$$

with $\partial x_k/\partial u_j(t)$ being the solution to (3)–(6) with $w_j(t) = 1$ and $w_i(\tau) = 0$ for $i \neq j$ and $\tau \neq t$. The adjoint method (Lawson *et al.*, 1995) is a useful alternative to compute the gradient of $J(u)$. Then only the adjoint of (3) has to be solved once, while in the above method mT systems of type (3) have to be evaluated. There are computer schemes that automatically generate the adjoint tangent linear systems (Giering and Kaminski, 1992). Yet another alternative is to work with an automatic differentiation package (Bischof *et al.*, 1992). Knowing the direction $w(t)$ in which we have to go, we make a step $\delta w(t)$ with a sufficiently small δ.

Next, using an implicit scheme we compute the periodic solution to the full nonlinear system for the control $u(t) + \delta w(t)$ with initial guess $\underline{x}(t) + v(t)$ and with $v(t)$ given by (3)–(6). Then the procedure is repeated until a local optimum is reached. Instead of this steepest ascent (descent) method, one may use a more efficient algorithm such as conjugate gradients.

The above methods apply to systems of high dimensions with a large number of parameters. The adjoint method is used in meteorology as a part of data assimilation procedure; there n and m are in the order of 10^3. For modelling the interaction and controlled harvesting of only a few biological populations, one may utilize as well some ad hoc approach.

3. Stabilizing Control

With the method presented in the previous section, we arrive at an optimal solution with a prescribed period T and a T-periodic control $u(t)$. This solution may be unstable. By an appropriate feedback the Lyapunov exponents of the linearized system can be brought to the left side of the complex plane. Stabilization can also be achieved by introduction of a feedback law as follows, see (Kwakernaak and Sivan, 1972, p.494). Let the optimal control be $u(t)$ which is necessarily a T-periodic vector function and let $x(t)$ be the corresponding solution. Then replacing the control $u(t)$ by $u(t) + w(t)$ with $w(t)$ sufficiently small, we study the tangent linear system (3) and consider the penalty function

$$\sum_{t=0}^{\infty} v^T(t)v(t) + \beta w^T(t)w(t), \quad \beta > 0 \tag{7}$$

with the feedback law

$$w(t) = -E(t)v(t), \tag{8}$$

where $E(t)$ is a T-periodic matrix function of the (backward) recurrent system

$$E(t) = \left[\beta I + G^T(t)\left[I + P(t+1)\right]G(t)\right]^{-1} G^T(t)\left[I + P(t+1)\right]F(t), \tag{9a}$$

$$P(t) = F^T(t)\left[I + P(t+1)\right]\left[F(t) - G(t)E(t)\right]. \tag{9b}$$

For a linear system the feedback (8) stabilizes the trivial solution $v = 0$. From Lyapunov's theorem (Verhulst, 1990) then follows the stability of the nonlinear system. In

(De Gee and Grasman, 1998) this is worked out for a differential equation model of a periodic prey-predator system with a feedback law working on the harvesting of both the prey and the predator. In Section 5, the present version of the method is applied to a host-parasitoid system with a feedback law acting through the introduction of parasitoids.

4. Rotational Harvesting in Fishery

As an example we study a fishery model for a population with three age classes: x_1 is the number of eggs, the number of juveniles is x_2 and x_3 is the number of adults. Eggs are produced at a rate α per adult. For the survival rate of the eggs we use the formula of Beverton and Holt (1959) meaning that there is competition within the first age class. In the first year the population satisfies

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = -(q + px_1)x_1 \tag{10}$$

with constant p and q. During the juvenile and adult stage the dynamics within one year is governed by the differential equation

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = -(m_i + f_i)x_i, \quad i = 2, 3, \tag{11}$$

where m_i is the natural mortality and f_i the fishing mortality which depends on the fishing effort u and the age-dependent catchability coefficient q_i:

$$f_i = q_i u, \quad i = 2, 3. \tag{12}$$

Thus, we obtain the following difference equation model for the fish population:

$$x_1(t+1) = \alpha x_3(t), \tag{13a}$$

$$x_2(t+1) = q\{p(e^q - 1)x_1(t) + qe^q\}^{-1} x_1(t), \tag{13b}$$

$$x_3(t+1) = \exp(-m_2 - f_2)x_2(t) + \exp(-m_3 - f_3)x_3(t). \tag{13c}$$

The parameter values we have chosen are presented in Table 1. There the average biomass w_i of a juvenile $(i = 2)$ and an adult $(i = 3)$ are also listed. The total yield equals the total catch of biomass,

$$Y(t) = w_2 c_2(t) + w_3 c_3(t), \tag{14}$$

where the catch c_j is given by (Daan, 1986)

$$c_j(t) = \frac{f_j}{m_j + f_j}\{1 - \exp(-m_j - f_j)\}x_j(t), \quad j = 2, 3. \tag{15}$$

Tab. 1. Parameter values for the model (13).

α	10^4
p	10^3
q	0.2

m_2	0.50
q_2	0.05
w_2	0.50

m_3	0.25
q_3	0.10
w_3	1.00

Starting with a zero fishing effort ($u = 0$) we find a stable optimal solution with period 1 for

$$u = 13 \quad \text{with} \quad Y = 401.2 \tag{16}$$

if we restrict u to the nonnegative integers. This solution can be taken as a starting value for finding an optimal solution to period 2. The result is a stable solution with

$$u_0 = 0, \quad u_1 = 29 \quad \text{and} \quad Y = 424.7, \tag{17}$$

where Y is the average yield per year. Periodic harvesting pays off in this model; the larger biomass of the adults explains this better result, see (Hilborn and Walters, 1992). If there are more independent populations of the fish species, a rotational harvesting scheme can be developed guaranteeing a constant supply to the market.

5. Host-Parasitoid Control

Biological pest control has increased in recent years not only because of the restrictions in the use of pesticides; it can also be economically an interesting option. In the following simple example we model its costs and benefits.

Larvae of an insect species (host) may cause severe damage to crops. A way to reduce their number is to introduce a parasitoid that deposit its egg (oviposition) in a larva which therefore dies, see e.g. (Jones *et al.*, 1994). We use the modified version of the Nicholson and Baily host-parasitoid (Beddington *et al.*, 1975; Edelstein-Keshet, 1988). Let x_1 be the host population and x_2 the parasitoid population. Then

$$x_1(t+1) = x_1(t) \exp\left\{ r\left(1 - \frac{x_1(t)}{K}\right) - a x_2(t) \right\} + d, \tag{18a}$$

$$x_2(t+1) = x_1(t)\Big\{1 - \exp\big(a x_2(t)\big)\Big\} + u. \tag{18b}$$

The damage to the crop per host is w_1 while the cost of bringing in one unit of parasitoids equals w_2, so that the total cost is

$$J(t) = w_1 x_1(t) + w_2 u.$$

The parameter d denotes the inflow of hosts; it is in this model the factor causing the damage to the crop. The parameter values are

$$a = 1, \;\; K = 5, \;\; r = 3, \;\; d = 0.1, \;\; w_1 = 1.25, \;\; w_2 = 1.$$

For $u = 0$ the system has a chaotic solution with an average yearly cost $J = 3.64$. Changing u we find a solution being quasi-periodic with an average cost $J = 2.79$, at $u = 1.266$. This solution is stable as can be concluded from its Lyapunov exponents being all strictly negative except for one being zero (Arnold and Wihstutz, 1986). Focusing on a constant optimal solution, we get a better result $J = 2.66$ for $u = 0.083$. However, this solution with equilibrium

$$(\underline{x}_1, \underline{x}_2) = (2.0653,\ 1.8105)$$

turns out to be unstable. Following the theory of Section 3 we have to introduce a feedback. Working (7)–(9) out with $\beta = 1$, we have to take

$$u = -E^T(x - \underline{x}) \quad \text{with} \quad E^T = (0.7107,\ 0.1045).$$

By running the model with this feedback, the correctness of the result is easily checked. If, due to external perturbations or observation errors, the control fails, the system will tend to a stable period-4 solution with average cost $J = 4.16$ which is more expensive than no control at all. Then it is advised to return to the optimal stable solution without feedback.

6. Concluding Remarks

In the same way as the Kalman filter can be extended to nonlinear systems (Jazwinsky, 1970), an optimization method and a stabilizing feedback can be designed for a class of problems in the field of sustainable harvesting of biological populations. In (De Gee and Grasman, 1998) the method applies to a system of nonlinear differential equations, while in the present study systems of nonlinear difference equations are considered. In population biology there are many problems for which the present method can be used. We already considered sustainable multispecies harvesting (De Gee and Grasman, 1998), while for difference equation models we took an example of optimally harvesting of an age structured population. The method also applies to other aspects of harvesting biological populations. An interesting case is biological pest control through the introduction of parasitoids, see Section 5. Another example of pest control, that can be analyzed in the same way, is that of roguing infected trees in orchards (Van den Bosch and De Roos, 1996). Furthermore, the use of herbicides and the effect upon the growth of weeds through the years and its consequences for the size of the crop can also be put in the present framework (Wallinga, 1998).

The model we developed can be extended with stochastic elements: it may be perturbed by noise and the observation of the state of the system may be incomplete and can also be corrupted by noise. Stochastic control theory (Kwakernaak and Sivan, 1972; Jazwinsky, 1970) offers tools to deal with these complications.

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