Harvesting and Conservation in a Predator–Prey System

Jeljer Hoekstra

Jeroen C.J.M. van den Bergh

Harvesting and conservation in a predator-prey system

Jeljer Hoekstra and Jeroen C.J.M. van den Bergh

Department of Spatial Economics

Free University

De Boelelaan 1105

1081 HV Amsterdam

The Netherlands

email: jhoekstra@econ.vu.nl and jbergh@econ.vu.nl

Abstract

Optimal harvesting of prey in a predator-prey ecosystem is studied under the condition that the existence of the predator has value. Predators (birds) and humans (fishers) compete for prey (shellfish). The behavior of the system is studied and conditions for optimal control are deduced. Various optimal harvesting rates are identified for particular ecosystem characteristics, harvesting costs, the discount rate value, and value functions for birds. These optimal harvest rates are constant harvesting, at levels possibly leading to the extinction of birds, or oscillating harvesting, giving rise to oscillating stocks of birds and shellfish. The approach path towards an optimal regime is shown qualitatively and consists of alternating between harvesting maximally and not harvesting at all.

1. Introduction

The subject of harvesting in predator-prey systems has been of interest to economists, ecologists and natural resource managers for some time now. Most research has focused attention on optimal exploitation, guided entirely by profits from harvesting. Clark [1], Hannesson [2], Ragozin and Brown [3], and Ströbele and Wacker [4] derive golden rules for optimal steady-state harvesting in a multi-species context. In addition, Ragozin and Brown [3] study the approach path towards the optimal steady state. Semmler and Sieveking [5] show that an optimal constant harvesting effort can result in a trajectory that does not reach equilibrium but oscillates over time. Except for Tu and William [6], who consider the stability of an ecosystem for predator control programs in combination with harvesting of prey, no attention has been given to nature protection policies in multi-species systems. A critical review of different types of predator-prey relations is found in [7] and [8].

The present paper seeks to find optimal exploitation strategies for a predator-prey system, but differs in two respects from the previous studies. First, the ecosystem model is based on a more realistic specification of predation than the familiar Lotka-Volterra type. In particular, it includes search and handling of prey by predators in order to derive the ecosystem dynamics. Secondly, and more importantly, prey is harvested while predators are protected. More specifically, in contrast to other studies, we explicitly value the existence of a species, in this case the predator. Although the predator species is itself not harvested, incorporating its existence value is necessary because it is indirectly affected by the harvesting of its food.

Although the formal model analyzed will be fairly general, it is motivated by a specific conflict between shellfisheries and the conservation of bird species in the Netherlands. The theoretical analysis that follows was initiated by a large multidisciplinary research project to study the harvesting of cockles and mussels in the Dutch Wadden Sea. The Wadden Sea is a wetland, located in the north of The Netherlands, that extends to the east along the German and Danish coasts. The area is an important breeding ground for birds and a stopover for migrating birds. Birds preying on shellfish, such as oystercatchers and eiderducks come under the protection of national and EU law and international agreements by the countries bordering the Wadden Sea.

This paper is an endeavor to theoretically investigate the balance between exploitation and nature conservation. This balance is reflected in the social welfare function. The social welfare function consists of two terms. One expresses the income

generated by harvesting shellfish. The other represents conservation benefits derived from the presence of a certain amount of birds in the ecosystem. The optimal harvest rate maximizes the social welfare function. An optimal trajectory approaches either a fixed steady state or an optimal cyclic state [3]. The optimal harvest trajectory is divided into two parts: an end state and the approach path. We develop a method to find the optimal end state(s) and give necessary conditions for its (their) existence. In addition, we present a qualitative analysis of the approach path towards the end state.

We consider a simplified ecosystem containing only one general type of bird and one general type of shellfish. Birds depend entirely on shellfish for food. The amount of food eaten by birds has an upper limit, even if shellfish are abundant. The model can be used to describe general predator-prey ecosystems and even herbivore-plant systems, as long as their interactions obey what biologists refer to as a Holling type II functional response [9].

The structure of the paper is as follows. Section 2 describes the ecosystem model. Section 3 analyses the behavior of the ecosystem under fixed harvest rates. The end state of optimal harvesting is examined in Section 4. Section 5 provides a qualitative analysis of the approach paths to the end state. Finally, we discuss our results in Section 6.

2. The ecosystem model

The ecosystem model describes the interactive dynamics between predators (birds) and prey (shellfish). In the model the following assumptions are made. The rate at which new birds are born and the amount of birds that die due to starvation and other causes, control the net growth of the number of birds. The number of bird offspring is linearly related to the number of adults. Bird numbers decline when there is not enough food (shellfish) available, which is modeled through a decrease in the life expectancy of birds. The average lifetime of birds depends on their energy intake. Energy intake per bird ($\frac{e}{B}$) less than the reference level (e_0) reduces their lifetime linearly. The energy intake is limited by the time birds need to find and handle shellfish, which are considered the only source of food for birds.

The net growth rate of birds is described by the following equation. The first term expresses growth, which depends on the birth rate. The second term expresses decline, which depends on the average age that on turn depends on energy intake.

$$\frac{dB}{dt} = rB - \frac{e_0 B}{e}\frac{B}{b} = rB\left(1 - \frac{e_0 B}{reb}\right), \tag{1}$$

where

B : the number of birds;

r : the birth rate of birds;

e_0 : the reference energy intake rate per bird;

e : the total energy intake rate.

b : reference average bird age

Equation (1) is the logistic equation [9] and $\dfrac{reb}{e_0}$ is called the carrying capacity.

The energy intake depends linearly on the amount of shellfish eaten. It is given by:

$$e = cd , \tag{2}$$

where

c : the energy content of a shellfish;

d : the number of shellfish depleted,

The depletion depends on the time a bird needs to search for shellfish and the amount of time it needs to break open the shellfish and swallow its contents. The search time decreases as the number of shellfish becomes larger. This is expressed in the following equation:

$$d = \frac{B}{z/S + h} = \frac{BS}{z + hS} , \tag{3}$$

where

S : the number of shellfish;

z : the search time coefficient;

h : the handling time (per bird per shellfish).

This equation is known as Holling's disc equation [9]. Equation (3) shows that the amount of food intake per bird is asymptotically limited. Indirectly, therefore, also the life expectancy of birds has an upper limit.

Shellfish die due to being eaten by birds, being harvested by fishers or because of other factors such as lack of food, cold winters etc. Shellfish are recruited independently of the number of existing adult shellfish. New shellfish recruits arrive in the area through wind driven and tidal currents. Their survival depends on a number of factors such as the seabottom characteristics, food supply, temperature and preying fish. These factors are, however too complex to be included in our model. Measurements in the Wadden Sea do not show a strong relationship between

recruitment and the adult stock size of shellfish [10]. Therefore, recruitment is modeled as an exogenous variable that is independent of S. The number of shellfish is given by:

$$\frac{dS}{dt} = q - \frac{S}{a} - d - y, \tag{4}$$

where

q: the shellfish recruit rate;

a: the average shellfish age, if not eaten by birds or fished;

y: the shellfish harvest rate.

Substituting equations (2) and (3) in (1) and (4) and creating the parameter $K = \frac{rcb}{e_0}$, results in the following predator-prey system:

$$\frac{dS}{dt} = q - y - \frac{BS}{z + hS} - \frac{S}{a} = f_S(S,B) - y \tag{5}$$

and

$$\frac{dB}{dt} = rB\left(1 - \frac{z + hS}{KS}\right) = f_B(S,B). \tag{6}$$

The parameter K shows the time a bird needs to eat (find and handle) a unit of shellfish in equilibrium. If a bird needs more time, due to a long search time (z/S) because of low stock sizes of shellfish, the numbers of birds will decrease. If it needs less time, due to high shellfish numbers, the numbers of birds will increase.

Because we assume shellfish is the only food birds eat, the mass of birds can not increase more than the mass of eaten shellfish. This leads to an extra restriction on the ecological parameters because we do not allow the creation of mass. The condition is deduced in Appendix I.

3. Ecosystem behavior under fixed harvest rates

The behavior of non-linear systems can be characterized by standard equilibrium, stability and bifurcation analysis [11]. Stability analysis in predator-prey models has received widespread attention, in the case of Lotka-Volterra type models, e.g. May [12]. Brauer and Soudack [13] studied the behavior of a general predator-prey system (which includes Lotka-Volterra models and the model in this paper), where the predator is harvested at a constant rate. Dai and Tang [14] examine a more specific model in which predators and prey are harvested. These studies show that, depending

on parameter values a stable equilibrium, a limit cycle or a homoclinic[1] orbit is possible.

In the following analysis we show that the ecosystem model under study will approach equilibrium when the harvesting rate is kept constant. For sufficiently high harvest rates, the ecosystem changes to a one-dimensional system in which birds are extinct.

The ecosystem described here has two equilibrium points ($\dot{S}=0$, $\dot{B}=0$):

$$B_{e1} = (q-y)K - \frac{Kz}{(K-h)a}, \quad S_{e1} = \frac{z}{K-h} \tag{7}$$

and

$$B_{e2} = 0, \qquad S_{e2} = (q-y)a. \tag{8}$$

Note that, in the first equilibrium, the number of shellfish does not depend on the harvest rate, y. If the harvest rate increases, the number of shellfish in equilibrium does not decrease. Extra harvesting takes food away from birds therefore the ecosystem can sustain fewer birds.

In the second equilibrium, birds have become extinct. The first equilibrium can exist only when $(q-y)a > \dfrac{z}{K-h}$ and $K > h$, because the numbers of birds and shellfish need to be positive. When these conditions are not fulfilled, the system will reach the second equilibrium. As long as, $(q-y)a > \dfrac{z}{K-h}$, the condition for existence of the first equilibrium holds, fishers can fish and a certain bird population size can be sustained. Clearly, the number of shellfish in equilibrium is greatest when the birds have become extinct and fishing is stopped. Since q is independent of S, the double extinction of both birds and shellfish is not an equilibrium unless $y = q$.

Figure 1 shows the phase diagram of the system. It contains an example trajectory, the S- and B-isoclines, and the direction of the system's vector field. The B-isocline, i.e. the curve on which the number of birds does not change ($\dot{B}=0$), is given by $S = \dfrac{z}{K-h} = S_{e1}$ and by $B = 0$. The B-isocline separates the region where the number of birds increases from the region where it decreases. When $S \leq S_{e1}$, then $\dfrac{dB}{dt} \leq 0$; and, when $S \geq S_{e1}$, then $\dfrac{dB}{dt} \geq 0$. The number of shellfish does not change

---

[1] In a homoclinic orbit a seperatrix of a saddle point originates from that saddle point.

on the S-isocline ($\dot{S} = 0$), which is given by $B = \left(q - y - \dfrac{S}{a}\right)\dfrac{(z + hS)}{S}$. The S-isocline

separates regions of shellfish decrease from regions of shellfish increase. When

$B \geq \left(q - y - \dfrac{S}{a}\right)\dfrac{(z + hS)}{S}$, then $\dfrac{dS}{dt} \leq 0$; and, when $B \leq \left(q - y - \dfrac{S}{a}\right)\dfrac{(z + hS)}{S}$ then

$\dfrac{dS}{dt} \geq 0$. Combining these conditions leads to a vector field that indicates the direction
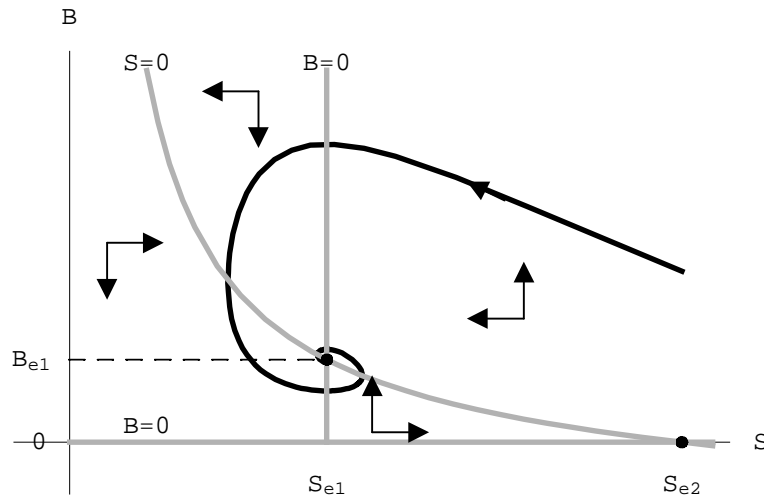
of the trajectories.

Figure 1: Phase diagram of the ecosystem under a fixed harvest rate.

Note: An example trajectory of the simple predator-prey system is shown. The isoclines are shown in gray and the equilibrium points as black dots. The arrows denote the direction of the trajectories.

The arrows show that a trajectory will either tend to, or originate from, or

circle around the first equilibrium, (S_{e1}, B_{e1}). In Appendix II we show that every

trajectory approaches equilibrium. The second equilibrium (equation (8)) is a saddle

point and can only be reached when the number of birds becomes zero. The S-isocline

depends on the harvest rate. When fishing increases, the S-isocline moves down and

the number of birds in equilibrium (B_{e1}) consequently declines. Figure 2 shows the

case when the harvest rate becomes so large: namely, $y > q - \dfrac{z}{(K - h)a}$, that the

isoclines do not intersect in the quadrant where S and B are positive. Then $(S_{e2}, 0)$ is
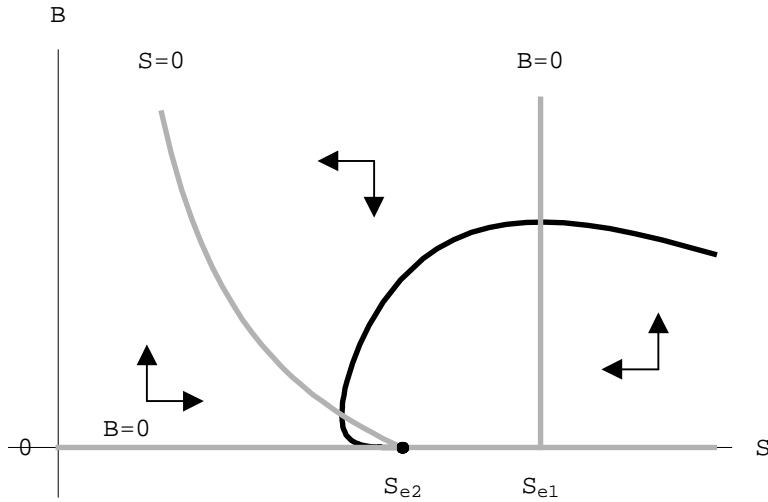
the only feasible equilibrium.

Figure 2: Phase diagram of the ecosystem under a high fixed harvest rate.

Note: The harvesting rate is so high that birds become extinct. The isoclines are shown in gray and the single equilibrium point as a black dot. The arrows denote the direction of the trajectories.

From the stability analysis (Appendix II) we know that the first equilibrium (S_{e1}, B_{e1}) is globally stable. This means that, starting from any point in the first quadrant ($S > 0$, $B > 0$), a trajectory will tend to the equilibrium. The equilibrium will be a stable node, meaning that the trajectory asymptotically approaches the equilibrium directly, if the birth rate of birds (r) is larger than the mortality rate of shellfish ($1/a$), or if S_{e1} and S_{e2} are either relatively far apart or relatively close together (Appendix II). Otherwise, the equilibrium will be a stable focus, i.e. the trajectory oscillates around the equilibrium with ever decreasing amplitude. Consequently, assuming the unharvested system has a stable node ($S_{e2} \gg S_{e1}$ and

$r > \dfrac{1}{a}$), increased fishing will change the equilibrium from a node to a focus and back again to a node until finally the birds become extinct.

One can get a feel for how the system behaves under dynamic (non-fixed) harvest rates if one considers such a system to approach a moving target: namely, the changing equilibrium because it depends on y.

The consequence of global stability is that fishing will not irreversibly change the system. As long as birds are not made extinct by excessive fishing of their food

supply, the system is able to recover. Once fishing is stopped, the system will asymptotically approach its natural equilibrium.

4. Optimal harvesting and ecosystem value

4.1 Problem formulation and necessary conditions

Suppose a governing body manages the fishery by setting quotas or by taking other measures to control shellfish harvesting. Its objective is to optimally exploit the resource, while taking into account the social value of the state of the ecosystem, expressed by the number of birds. When birds are not socially valued, it would be advantageous to catch shellfish until birds are extinct. The reason is that, in these circumstances either more shellfish are caught or a competitor is eliminated and harvest can therefore proceed at the same rate but, given the higher shellfish stock, at lower costs. The main question here is: What are the implications of a social valuation of birds on optimal harvesting? In order to address this issue, we assume that the governing body strives to maximize the following social welfare function, in which the value of birds in the ecosystem and the profits (revenues minus costs) of fishing are added and discounted over time:

$$ J = \max_{y} \int_{0}^{\infty} e^{-\delta t} (v(B) + py - c(S)y)\, \mathrm{d}t, \qquad (9) $$

here

δ :   the discount rate;

$v(B)$:   the value assigned to the state of the ecosystem;

p :   the price of a unit shellfish;

$c(S)$:   the cost of harvesting.

The price of shellfish is set constant, as we assume the amount harvested in this particular area will have a negligible influence on the overall supply of shellfish on the market. The cost of fishing is assumed to decrease with stock size, $\dfrac{\partial c(S)}{\partial S} \leq 0$,

and the value of birds to increase with their stock size, $\dfrac{\partial v(B)}{\partial B} \geq 0$. We assume that

the harvesting costs are linear in y. The interpretation is that labor can be hired at constant cost and is needed proportionally to the harvest rate. Later, we will relax this assumption (see Section 4.6). In addition, it is assumed that the existence of a fixed number of boats determines the maximum harvest rate (y_{max}). The value function of birds is assumed to be concave or S-shaped (see Figure AIII-1 in Appendix III).

Apply Pontryagin's maximum principle [15], the current value Hamiltonian is:

$$H = v(B) + py - c(S)y + \lambda_S (f_S(S,B) - y) + \lambda_B f_B(S,B). \tag{10}$$

The equations that form the necessary conditions for a solution are :

- the maximum condition:

$$\max_y H \Rightarrow \max_y (p - c(S) - \lambda_S)y, \quad 0 \le y \le y_{max}, \tag{11}$$

where, y_{max} is the maximum harvest rate;

- the familiar equations of motion for the state (5) and (6), which we repeat for clarity:

$$\dot{S} = \frac{\partial H}{\partial \lambda_S} = f_S(S,B) - y = q - y - \frac{BS}{z + hS} - \frac{S}{a} \tag{5}$$

and

$$\dot{B} = \frac{\partial H}{\partial \lambda_B} = f_B(S,B) = rB\left(1 - \frac{z + hS}{KS}\right); \tag{6}$$

- and the equations of motion for the co-state or shadow prices:

$$
\begin{aligned}
\dot{\lambda}_S &= \delta\lambda_S - \frac{\partial H}{\partial S} = \delta\lambda_S + \frac{\partial c(S)}{\partial S} y - \lambda_S \frac{\partial f_S(S,B)}{\partial S} - \lambda_B \frac{\partial f_B(S,B)}{\partial S} \\
&= \delta\lambda_S + \frac{\partial c(S)}{\partial S} y + \lambda_S\left(\frac{Bz}{(z + hS)^2} + \frac{1}{a}\right) - \lambda_B \frac{rBz}{KS^2}
\end{aligned} \tag{12}
$$

and

$$
\begin{aligned}
\dot{\lambda}_B &= \delta\lambda_B - \frac{\partial H}{\partial B} = \delta\lambda_B - \frac{\partial v(B)}{\partial B} - \lambda_S \frac{\partial f_S(S,B)}{\partial B} - \lambda_B \frac{\partial f_B(S,B)}{\partial B} \\
&= \delta\lambda_B - \frac{\partial v(B)}{\partial B} + \lambda_S \frac{S}{z + hS} - \lambda_B r\left(1 - \frac{z + hS}{KS}\right);
\end{aligned} \tag{13}
$$

- and because $S \ge 0$ and $B \ge 0$, the transversality condition:

$$\lim_{t \to \infty} \lambda_S \ge 0, \quad \lim_{t \to \infty} \lambda_B \ge 0. \tag{14}$$

Given the linear form of the harvesting cost function, $c(S)y$, the Hamiltonian (10) depends linearly on y with coefficient $(p - c(S) - \lambda_s)$. Consequently, its maximum value is reached for the extremes of y, i.e. the harvest rate must be either 0 or y_{max}. This leads to the rule that one must fish as much as possible when the shadow price of shellfish is sufficiently low ($\lambda_s < p - c(S)$), and not fish at all when the shadow price is sufficiently high ($\lambda_s > p - c(S)$). Furthermore, when $\lambda_s = p - c(S)$, the harvest rate is undetermined. In this case, three solutions for y are possible: namely, 0, y_{max} or $\tilde{y}(t)$ the singular control that maintains the condition $\lambda_s = p - c(S)$. So, the optimal control path will be bang-bang (i.e. harvesting

maximally or not harvesting at all or alternating between the two) or singular (i.e. keeping the revenues equal to the shadow price)

We assume there is a unique optimal path. After an initial period, the system will arrive at some end state. The optimal trajectory of the system will approach either an equilibrium or a cycle. Suppose the optimal path does not approach equilibrium, then it must cross itself. At this point, the optimal path must continue as it did before or it will not be unique. This implies a cycle. So, finally, the optimal trajectory will reach an equilibrium or a cycle. We call this the end state. The approach path is the beginning of the optimal trajectory until the end state is reached.

The remainder of this section is devoted to examining the end state. Remember that the harvest rate of an optimal trajectory and thus of the end state must be bang-bang, singular, or a combination of both. This means the following four end states are conceivable:

1) No harvesting: $y = 0$ and $p - c(S) \leq \lambda_s$. The end state is in equilibrium and the harvest rate is part of a bang-bang control (see Section 4.2).

2) Maximum harvesting: $y = y_{max}$ and $p - c(S) \geq \lambda_s$. The end state is in equilibrium and the harvest rate is part of a bang-bang control (see Section 4.3).

3) A singular state: $y = \tilde{y}(t)$ and $p - c(S) = \lambda_s$ (see Section 4.4). A singular harvest rate is applied. This can result in two types of singular equilibria (see Section 4.4.1): one in which birds exist (section 4.4.1.1), and one in which birds are extinct (see Section 4.4.1.2), or it can result in a limit cycle (see Section 4.4.2).

4) A bang-bang cycle, i.e. an oscillation controlled by a harvest rate that flips back and forth between the maximum, zero and possibly a singular harvest rate: $y = y_{max}$, when $p - c(S) > \lambda_s$; $y = 0$, when $p - c(S) < \lambda_s$; and, $y = \tilde{y}(t)$, $y = 0$, or $y = y_{max}$, when $p - c(S) = \lambda_s$. (see Section 4.5)

4.2 No harvesting: case 1

The first possibility is straightforward. Not harvesting is optimal, when in the equilibrium (S_{e1}, B_{e1}), the total cost of fishing ($c(S) + \lambda_S$) exceeds the price of shellfish. This means that, at any harvest rate the loss in social value of birds would be greater than the net gain from fisheries.

4.3 Maximum harvesting: case 2

The second possibility is to keep harvesting at the maximum level. In this case, the price of shellfish must exceed the total costs. If the maximum harvest level is

relatively small ($y_{max} < q - \dfrac{z}{a(K-h)}$, see equation 7), then the system will

asymptotically reach the equilibrium (S_{e1}, B_{e1}). But if $y_{max} \geq q - \dfrac{z}{a(K-h)}$ then the

system approaches the other equilibrium $(S_{e2}, 0)$, in which birds are extinct. The

condition $p - c(S) > \lambda_S$ and the transversality condition (14) imply that $p > c(S)$.

So, obviously fishing must make a monetary profit. For an end state in which

harvesting is at its maximum, the transversality condition (14) implies $c(S_{e1}) < p$, if

$y_{max} < q - \dfrac{z}{a(K-h)}$, or $c(S_{e2}) < p$, if $y_{max} \geq q - \dfrac{z}{a(K-h)}$.

4.4 A singular state: case 3

  The third possibility is an end state in which the total system (state and co-
state) is kept in a singular state. From the maximum condition (11), it follows that at
this end state we have to satisfy:

$$\lambda_S = p - c(S). \tag{15}$$

Substituting (15) and its derivative, $\dot{\lambda}_S = -\dfrac{\partial c}{\partial S}\dot{S} = -\dfrac{\partial c}{\partial S}(f_S - \tilde{y})$, in (12) gives the

following expression for λ_B in the singular state,

$$\lambda_B = \left((p-c)(\delta - \frac{\partial f_S}{\partial S}) + \frac{\partial c}{\partial S} f_S \right) \Big/ \frac{\partial f_B}{\partial S}, \tag{16}$$

provided $\dfrac{\partial f_B}{\partial S} \neq 0$ (i.e. $B \neq 0$). We take the time derivative of expression (16) for λ_B

and substitute it, together with (15), in (13). This eliminates both shadow prices and
we get the following expression that implicitly defines $\tilde{y}$, the harvest rate in the
singular state:

$$\left(\frac{\partial^2 c}{\partial S^2}(f_S - \tilde{y})f_S + \frac{\partial c}{\partial S}((2\frac{\partial f_S}{\partial S} - \delta)(f_S - \tilde{y}) + \frac{\partial f_S}{\partial B}f_B) - (p-c)\frac{\partial^2 f_S}{\partial S^2}(f_S - \tilde{y}) + \frac{\partial^2 f_S}{\partial B \partial S}f_B \right)\frac{\partial f_B}{\partial S}$$

$$-\left((p-c)(\delta - \frac{\partial f_S}{\partial S}) + \frac{\partial c}{\partial S}f_S \right)\left(\frac{\partial^2 f_B}{\partial S^2}(f_S - \tilde{y}) + \frac{\partial^2 f_B}{\partial B \partial S}f_B \right)$$

$$= (\delta - \frac{\partial f_B}{\partial B})\left((p-c)(\delta - \frac{\partial f_S}{\partial S}) + \frac{\partial c}{\partial S}f_S \right)\frac{\partial f_B}{\partial S} - \left(\frac{\partial v}{\partial B} + (p-c)\frac{\partial f_S}{\partial B} \right)\left(\frac{\partial f_B}{\partial S} \right)^2.$$

$$\tag{17}$$

  We have ignored a function's variable list so as not to further complicate the
expression. Equation (17) means that we can find the singular harvest rate for every

point in the phase diagram. Be aware, however, that $0 \le \tilde{y} \le y_{\max}$, and thus $\tilde{y}$ may not be not feasible for every value of S and B.

If a singular harvest rate is employed, an autonomous system results that describes the singular trajectories:

$$\frac{dS}{dt} = f_S(S,B) - \tilde{y}(S,B) \tag{18}$$

and

$$\frac{dB}{dt} = f_B(S,B). \tag{19}$$

Here $\tilde{y}(S,B)$ is the singular harvesting rate, implicitly given by equation (17). The singular system indirectly depends on the cost of fishing and the value of birds. In the next subsections (4.4.1 - 4.4.3), we consider various possibilities for a singular end state. These are: an equilibrium with coexistence of birds and shellfish; an equilibrium without birds; or, a limit cycle. From (18), it follows that, in equilibrium, $\tilde{y}(S_e, B_e) = f_B(S_e, B_e)$, which is independent of time. Thus, the singular harvest rate is constant at equilibrium. This means that the equilibria of the singular system must be equal to the equilibria under fixed harvest rates, as studied in section 3 (see equations (7) and (8)). Later, (see Section 4.4.2) we investigate the possibility that the singular system has a limit cycle, which means that $\tilde{y}(S,B)$ in the end state is not constant.

4.4.1 Equilibrium harvesting

From equation (18) and (19), it follows, that in equilibrium, $f_S - \tilde{y} = f_B = 0$. Substitution of this in (17) gives:

$$0 = (\delta - \frac{\partial f_B}{\partial B})\left((p-c)(\delta - \frac{\partial f_S}{\partial S}) + \frac{\partial c}{\partial S} f_S\right) - \left(\frac{\partial v}{\partial B} + (p-c)\frac{\partial f_S}{\partial B}\right)\frac{\partial f_B}{\partial S}. \tag{20}$$

Equation (20) is the golden rule of an optimal equilibrium. Clark[1] and Ströbele and Wacker [4] find two symmetric golden rules (one for each species) for the optimal harvesting of two interacting species, when both species are harvested. Ragozin and Brown [3] have generalized those results for harvesting n interacting species (n symmetric equations). The difference with our result in equation (20) springs from the fact that in our case the social welfare function depends on a species (birds) that is not harvested and therefore can not be directly controlled. Furthermore, we attach value to the number of predators remaining in the ecosystem instead of those harvested.

Equation (20) can be satisfied in many ways. Either the two main terms are non-zero and of equal size, or either (21) or (22), and (23) hold. First, however, we discuss the equilibrium when a combination of the following terms are zero:

$$(p-c)(\delta - \frac{\partial f_S}{\partial S}) + \frac{\partial c}{\partial S} f_S = 0 \qquad (21)$$

and

$$\delta - \frac{\partial f_B}{\partial B} = 0 \qquad (22)$$

and

$$\left(\frac{\partial v}{\partial B} + (p-c) \frac{\partial f_S}{\partial B} \right) \frac{\partial f_B}{\partial S} = 0 . \qquad (23)$$

Note that $\frac{\partial f_B}{\partial S} \neq 0$. Equation (21) is the standard golden rule for the harvesting of a single species [1]. It reflects the direct change in profit due to a change in the equilibrium shellfish stock, when birds are kept constant. The terms in (21) express the impact of a change in shellfish stock on social welfare through three channels:

- more interest on extra income from catching one unit more fish, $(p-c)\delta$;

- less future income through stock effects, i.e. less future harvesting, $-(p-c)\frac{\partial f_S}{\partial S}$;

- an increased cost of future harvesting due to stock effects, $\frac{\partial c}{\partial S} f_S$.

Note that, only if (21) is satisfied (and thus also (23) holds), can the optimal harvest rate in the present multi-species context equal the optimal harvest rate in the single species context. Expression (23) shows the indirect effect of a change in shellfish stock on social welfare that occurs via changes in the number of birds. A change in the number of shellfish changes the number of birds by a factor $\frac{\partial f_B}{\partial S}$. This results in a change of the value of birds by $\frac{\partial v}{\partial B}$. In addition, a change in bird numbers means a change in natural predation, so that the shellfish stock changes (by $\frac{\partial f_S}{\partial B}$). This is translated into value terms through the net benefit of extra fish to fisheries, ($p-c$). When (21) is satisfied, no direct gains can be made by a change in shellfish stock. Then (23) must hold too, so that neither can any gains be made through a change in bird numbers.

Secondly, equation (20) is satisfied when both (23) and an even more elementary golden rule, equation (22), hold. This means there are no marginal net

benefits due to a change in bird stock (23), because the marginal growth rate for birds exactly matches the discount rate. In other words, changing the harvest rate does not lead to extra net benefits because benefits (more value of more birds) cancel out against cost (the opportunity cost of waiting, i.e. the discount rate).

Third, to better understand (20) as a whole (both main terms are non-zero), one can use (16) to express equation (20) in terms of the shadow price for birds. This leads to the following recursive expression in λ_B:

$$\lambda_B = \frac{1}{\delta}\left(\frac{\partial v}{\partial B} + (p-c)\frac{\partial f_S}{\partial B} + \frac{\partial f_B}{\partial B}\lambda_B\right).$$

The shadow price of birds represents the marginal social benefit (or cost) of a marginal change in the number of birds. In simple terms, this is the price of an extra bird in the ecosystem. In equilibrium, it is equal to the discounted sum of three elements:

- a change in the direct value of birds, $\frac{\partial v}{\partial B}$;

- a change in net revenues of harvesting due to a change in the equilibrium shellfish stock, $(p-c)\frac{\partial f_S}{\partial B}$;

- a change in the number of birds due to a change in the number of offspring, valued against the shadow price, $\frac{\partial f_B}{\partial B}\lambda_B$.

4.4.1.1 Equilibrium harvesting when S=S$_{e1}$

Any equilibrium is located on the B-isocline , so that either $S = S_{e1}$ or $B = 0$. First, we consider an equilibrium on $S = S_{e1}$. In the next section (4.4.1.2), we will analyze an equilibrium on $B = 0$. From now on, our analysis is less general. We will explicitly use the growth functions from the ecological model, $f_S(S_{e1}, B_e)$ and $f_B(S_{e1}, B_e)$, as given in equations (5) and (6), respectively, to determine the location of the singular equilibrium of the harvested ecosystem. To find the optimal number of birds in equilibrium, we take the derivatives of $f_S(S_{e1}, B_e)$ and $f_B(S_{e1}, B_e)$ with respect to S and B, and substitute these together with the equilibrium value of S_{e1} (equation (7)), in (20). This gives us the following implicit solution for B_e:

$$B_e = \frac{K^2 z \delta \left((p - c(S_{e1}))(\delta + \frac{1}{a}) + \frac{B_0}{K} \frac{\partial c(S_{e1})}{\partial S} \right)}{K(K-h)^2 r \frac{\partial v(B_e)}{\partial B} - (K-h)^2 (p - c(S))(\delta + r) + K z \delta \frac{\partial c(S_{e1})}{\partial S}}, \tag{24}$$

where $B_0 = qK - \dfrac{KS_{e1}}{a} = qK - \dfrac{Kz}{(K-h)a}$ is the number of birds in the natural (non-

harvest) equilibrium.

Depending on the shape of $v(B)$ and the marginal costs of fishing at the

equilibrium (S_{e1}), one, several or no solution exist. In Appendix III, it is shown that

two types of coexistence (of birds and shellfish) equilibria exist, each characterized by

a particular set of necessary conditions.

The two types of equilibria can be explained as follows. A type I equilibrium

exists if, in the absence of birds, fishers would prefer to fish at a shellfish stock level

less than S_{e1}. In contrast, a type II equilibrium exists if fishers would prefer to fish at

a stock level higher than S_{e1}, in the absence of birds. In each case, birds are a

nuisance to fishers but in two different ways. In a type I equilibrium, birds decrease

the catch because they eat shellfish that fishers would like to have caught. In a type II

equilibrium, the birds increase the fishing costs by depleting the shellfish stock.

4.4.1.2 Equilibrium harvesting when B=0

Now, we consider the singular end state to be an equilibrium on the S-axis. Of

course, the system must be able to reach this state, so $y_{\max} \geq q - \dfrac{S_{e1}}{a}$ (see equation

(8)). Since $\dfrac{\partial f_B(S,0)}{\partial S} = 0$, the condition to derive equation (17) is not satisfied. For a

singular equilibrium on the S-axis, we must have $\tilde{y} = f_s(S_e, 0)$ (see equation (18)).

Given that the system is in equilibrium, it follows from (15) that $\dot{\lambda}_S = 0$. Substituting

$\dot{\lambda}_S = 0$, equation (15) and $B = 0$ in equation (12) eliminates λ_S and results in:

$$(p - c(S_e))(\delta - \frac{f_S(S_e, 0)}{\partial S}) + \frac{\partial c(S_e)}{\partial S} f_S(S_e, 0) = 0. \tag{25}$$

Again we have the well-known golden rule for harvesting in a single species

ecosystem [1]. This makes sense because birds are extinct, so they do not influence

the amount of shellfish in the end state. Equation (25) implicitly defines the number

of shellfish in the singular equilibrium.

Substituting $f_S(S_e, 0) = \dfrac{B_0}{K}$ and $\dfrac{\partial f_S(S_e, 0)}{\partial S} = -\dfrac{1}{a}$ in (25), then the Left Hand Size (LHS) of (25) increases monotonically as S increases. Hence, no more than one solution is defined by (25). If, for some S, the LHS of (25) is greater than zero, consequently $S > S_e$. This shows the interpretation of the type I and type II equilibria from the previous section and Appendix III. In this respect, note that, for a type I equilibrium, the LHS of (25) is greater than zero at S_{e1} and thus the optimum when birds are extinct is smaller than S_{e1}. For a type II system, the equilibrium lies to the right of S_{e1} and is not attainable unless birds are eliminated first.

4.4.2 Singular cyclical harvesting

Semmler and Sieveking [5] show that optimal constant harvesting may push a predator-prey system into cyclical behavior, whereas without harvesting the system would reach equilibrium. This does not hold for the system studied here.. As shown in Section 3 constant harvesting causes the ecosystem to reach an equilibrium. From the dynamic optimization literature, e.g. [16-19], it is known that a non-steady singular control can cause an optimal path to take the form of a limit cycle. Suppose such a limit cycle exists, then it is necessary to establish whether the associated singular control $\tilde{y}(t)$ is feasible, meaning that $0 \le \tilde{y}(t) \le y_{max}$. The trace condition [17] can be applied to rule out limit cycles. Otherwise, the Hopf bifurcation theorem [16, 18, 19] can be used to show that limit cycles are possible for certain combinations of parameter values. Both methods require the Jacobian of the singular system. The Jacobian must have purely imaginary eigenvalues for the Hopf-bifurcation. Because the system equations (18) and (19) consist of second-order partial derivatives of $f_S(S, B)$ and $f_B(S, B)$, determining eigenvalues is a cumbersome and tedious task. Therefore, we use a less traditional approach to determine the possibility of a limit cycle as the end state.

We can exclude limit cycles when $y_{max} \le q$. This follows from the stability analysis of the original system, because for any $y(t) < q$ no limit cycles can exist (equation (AII-4)). In order to have a limit cycle $y(t) \ge q$ for some t. Thus, $y_{max} \le q$.

Moreover, a limit cycle will follow a closed orbit around an equilibrium. Suppose the equilibrium exists, then we can use the transversality conditions (14) to determine the manifold on which an optimal limit cycle must circle. On this manifold, the shadow prices are strictly positive. From equation (15), it follows that a profit

must be made from the fishery throughout the singular limit cycle, and thus $S \geq S_0$, with $c(S_0) = p$. Furthermore, an extra condition for the existence of an optimal singular limit cycle can be derived from the knowledge that the shadow price of birds must be strictly positive along the limit cycle. Using (16), $\lambda_B > 0$ and $\frac{\partial f_B(S,B)}{\partial S} > 0$, we find that

$$\frac{\partial c(S)}{\partial S} f_S(S,B) > -(p - c(S))\left(\delta - \frac{\partial f_S(S,B)}{\partial S}\right). \tag{26}$$

At the B-isocline, equation (26) transforms to (AIII-8), which tells us the minimum value of B, for which λ_B is positive. Because the limit cycle circles around B_e, it will intersect $S = S_{e1}$ below the equilibrium , B_e , and above the minimum for which $\lambda_B > 0$. Therefore, also B_e must lie in the manifold where λ_B is positive. So, in order for the system to have an optimal singular limit cycle, it must have a singular equilibrium with positive λ_B. This means the equilibrium is either of type I, or that when it is of type II, equation (AIII-9) must hold (see Appendix III).

4.4.3 The influence of the discount rate and costs

The discount rate plays a pivotal role in establishing the singular solutions of the system. Suppose we have a system in which birds can become extinct:

$y_{max} > q - \frac{S_{e1}}{a}$. Then, for a large enough δ, equation (AIII-2) is satisfied, but not (AIII-4) so that we can have an end state in which birds are extinct. For a slightly smaller δ, (AIII-4) is satisfied, and (AIII-5) (just one equilibrium on $S = S_{e1}$) is not satisfied. Then the system has between one and three equilibria, one on the S-axis and none, one or two on the B-isocline. A limit cycle is also possible, provided $y_{max} > q$. If δ again becomes slightly smaller, then (AIII-5) is satisfied too and no more than two equilibria remain, one at $B = 0$ and one at $S = S_{e1}$. For a sufficiently small enough δ (AIII-6), the system can have an optimal type II equilibrium. This illustrates how δ serves as bifurcation parameter.

The costs at $S = S_{e1}$ can also serve as bifurcation parameter. Given the right cost function, every type of singular state is possible. This is relevant because fishers will try to reduce fishing costs, which will lead to new optimal end states. If the reduction leads to an increase in the marginal cost of fishing, the system will lose its type II equilibrium but it will gain a type I equilibrium and an equilibrium in which

birds are extinct. For low enough costs at $S = S_{e1}$, the singular system has only one type I equilibrium. For even lower costs, birds will become extinct.

This illustrates that the incentive of cost reduction can push the system to a different type of equilibrium. Equation (24) shows that through cost reduction the optimal number of birds, and consequently the optimal harvest rate, may go up or down, depending on how marginal costs change. The result of cost reduction could be lower optimal harvest rates, resulting in lower fishing revenues and possibly lower profits. In this case, policy makers would have a very difficult task. They would have to reward the higher efficiency of fishers by setting higher quota that reduce the income fishers can realize. Of course, the optimum value of the social welfare function increases when costs are reduced.

4.5   A bang-bang cycle: case 4

The last conceivable end state is one in which $y(t)$ continuously switches between 0 and $y_{\max}$. This is sometimes called pulse fishing. Pulse fishing can push the system into a cycle. We will call this a bang-bang cycle. A bang-bang cycle can also be realized by switching harvest rates between $y_{\max}, 0$, and $\tilde{y}(t)$, the singular control. Alternatively, a bang-bang control can move the system closer and closer to some point. We will discuss this in Section 5, when we examine approach paths.

Typically, a cycle will cross the B-isocline because, for every harvest rate, bird numbers increase to the right of it and decrease to the left of it. Figure 3 illustrates a typical bang-bang cycle.
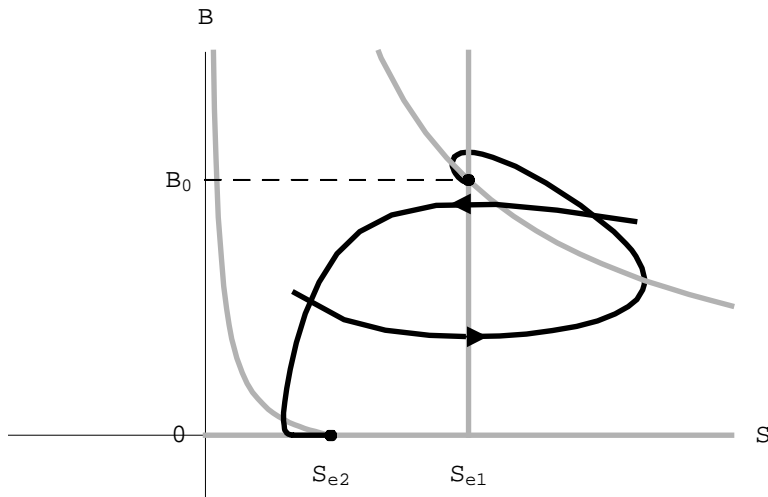
Figure 3: Phase diagram of a bang-bang cycle.

Note: The cycle is caused by alternating between maximum harvesting and not harvesting. The isoclines of the harvested and non-harvested system are shown in gray. The equilibria of both systems are denoted by a black dot. At the intersection of the two trajectories, the harvest rate is switched. Thus, neither the harvest nor the non-harvest equilibrium is ever reached and the bang-bang control is repeated for ever.

The phase diagram in Figure 3 shows that, when harvesting is stopped, the shellfish stock size increases while the bird population size keeps on decreasing. Only after a while, when $S = S_{e1}$, will bird numbers increase again. Also when the fishers start fishing to the right of the B-isocline ($S > S_{e1}$), bird numbers will increase in spite of fishing until the number of shellfish is S_{e1}. The simplest bang-bang cycle consists of two branches as in Figure 3: one on which is harvested and the number of shellfish declines, and another on which no fishing takes place and shellfish and birds recuperate.

4.6 Costs as a non-linear function of harvesting

Until now, we have assumed costs to increase linearly with the harvest rate. Suppose, however, that the cost function is non-linear in y: $c(S, y)$ instead of $c(S)y$. In this case, the maximum of the Hamiltonian is not at one of the extremes ($y = y_{max}$ or $y = 0$). Instead, an interior solution may exist. The maximum condition

21

becomes $\dfrac{\partial H}{\partial y} = 0 \Rightarrow p - \dfrac{\partial c(S, y)}{\partial y} = \lambda_s$, which replaces equation (15). The analysis

of the optimal end state is restricted to analysis of the singular state, leading to the same results for the equilibria and cycles, as derived in the previous sections, but with

$c(S)$ substituted by $\dfrac{\partial c(S, y)}{\partial y}$. Assuming, furthermore, that the Hamiltonian is

concave in S, B and y, the necessary conditions are also sufficient [15]. The optimal solution, the approach path and the end state are given by applying the singular harvest rate.

5. Qualitative analysis of approach paths

The harvest rate on the approach path (as elsewhere) is either bang-bang or singular. We will qualitatively describe how the system reacts under bang-bang control and it will automatically become clear when and how the singular control must be applied. We make use of the theory of variable structure systems [20] to describe the behavior of the ecosystem under bang-bang control. The optimal harvested ecosystem can be considered to consist of three subsystems: one in which $y = y_{max}$, one in which $y = 0$; and, one in which $y = \tilde{y}(S, B)$ (singular, equation (17)). These subsystems correspond to different regions in the phase diagram. A switching line separates the regions of maximum harvesting and no harvesting. The switching line is the projection on the (S, B)-phase plane of the points where the optimal trajectory of the four-dimensional state/co-state system (equations (5), (6), (12) and (13)) intersects the singular manifold, $p - c(S) = \lambda_s$.

Each subsystem has its own equilibrium points. The position of the switching line will determine if the equilibrium of a subsystem is located in the region where that subsystem is active. That means the equilibrium can be reached. If an equilibrium of a subsystem can be reached, it is called 'real'. If it can not be reached it is called 'virtual'. On one side of the switching line, $p - c(S) < \lambda_s$, so that no fishing occurs. On the other side, $p - c(S) > \lambda_s$ so that fishing occurs at the maximum rate. When as in Figure 4, the switching line is located such that the equilibrium of the harvested system lies in the region in which no harvest occurs, then the harvest equilibrium can not be reached. It is a virtual equilibrium, as opposed to the unharvested equilibrium which is a real equilibrium because it can be reached.

Suppose one of the equilibria is real and the other(s) is (are) virtual. Then the real equilibrium will be reached (see Figure 4). When all equilibria are real, one will be reached depending on the initial state (see Figure 5). If all equilibria are virtual equilibria, the system will experience bang-bang control (see Figure 6 and 7) until a state is reached where the singular harvest rate must be applied. A bang-bang cycle is a special case where two virtual equilibria exist and the bang-bang control must be applied infinitely. Generally, the system will end in equilibrium with a singular harvest rate.
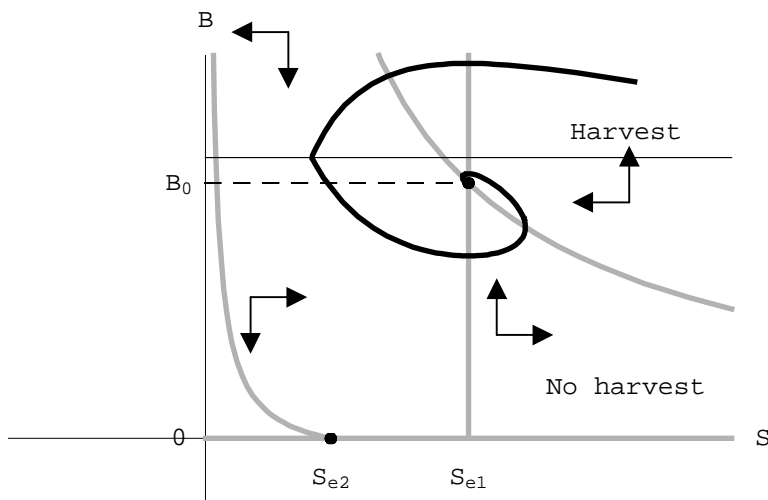

Figure 4: Phase diagram of a system with bang-bang control.
Note: The system has one virtual and one real equilibrium. The thick gray curves denote the isoclines of the harvested and non-harvested system. The thin line is the switching line. A trajectory will approach the real equilibrium.
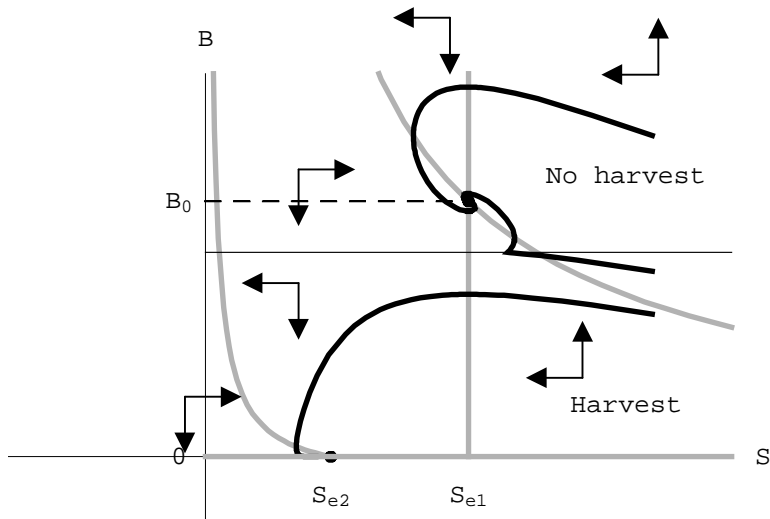
Figure 5: Phase diagram of a system with bang-bang control.

Note: The system has real two real equilibria. Three trajectories are shown. Depending on the initial condition the trajectory approaches the harvest or non-harvest equilibrium. The thin line is the switching line.
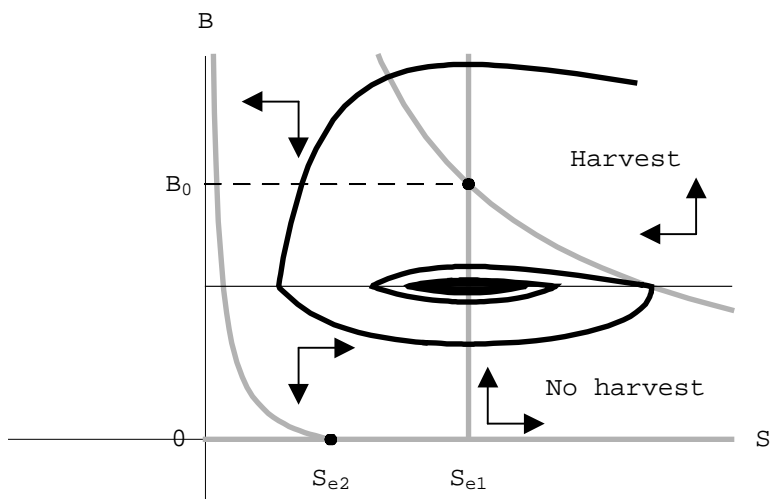

Figure 6: Phase diagram of a system with bang-bang control.

Note: The system has two virtual equilibria and approaches a point (the singular equilibrium) on the B-isocline. The thick gray curves denote the isoclines of the harvested and non-harvested system. The thin line is the switching line.

24

Suppose the trajectory on both sides of the switching line is directed towards the switching line and thus towards the other region. This is best seen in Figure 7, but it also happens in Figure 6. The system will arrive at the switching line and will not be able to leave, therefore it must slide along it. In effect, this means that the singular harvest rate is applied and the system follows a singular trajectory, because the system moves along a path on which $p - c(S) = \lambda_s$. Thus, in this case, (part of) the switching line is a singular trajectory. It has turned out to be difficult to prove or disprove whether in fact, the switching line must be a singular trajectory. A more complex switching line and resulting system behavior is possible if the system has several singular equilibria. An example is given in Figure 7. If we assume that the optimal trajectory ends in a singular equilibrium on the B-isocline then the switching line crosses or at least touches the B-isocline at the equilibrium. The examples in Figures 5-7 show that an end state is an equilibrium at the singular, the maximum or the minimum harvest rate. But in special cases, the approach path never reaches equilibrium. This means the end state is a limit cycle either singular or bang-bang (Figure 4).
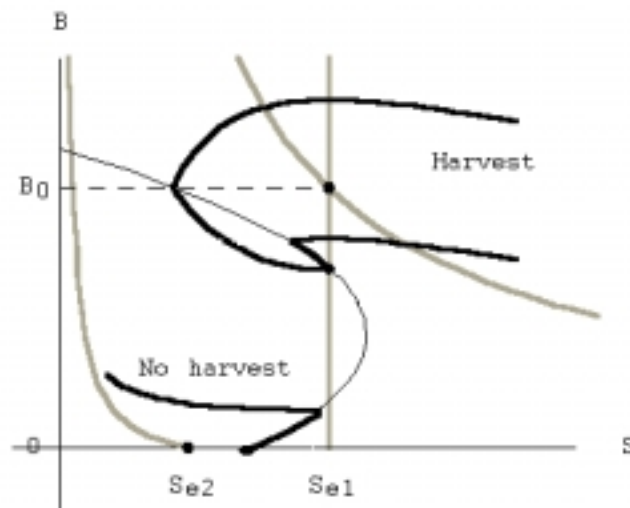

Figure 7: Phase diagram of a system with bang-bang control.

Note: The system has real two virtual equilibrium and approaches one of the singular equilibria, depending on the initial condition. The thick gray curves denote the isoclines of the harvested and non-harvested system. The thin black line is the switching line. Close to the singular equilibrium, the system cannot cross the switching line and must follow it under singular control.

6. Conclusion

This paper illustrates that several types of optimal harvesting solutions are possible in a predator-prey system when conservation of the predator species is considered valuable. The type of solution depends on economic parameters e.g. the maximum harvest rate, the discount rate, and the cost of fishing, as well as on ecological parameters such as the predator's search and handling time of prey. The final optimal harvest rate can be constant, resulting in an equilibrium, either with or without the predator species. For different economic and ecological parameters, the optimal harvest rate can become cyclical, resulting in oscillating populations of predator and prey species.

After an initial period the system reaches the end state. The end state can be one of three possibilities not fishing, fishing maximally, or fishing at a singular harvest rate. The necessary conditions for each possible singular end state are derived in Section 4. For some combinations of parameters, several end states can exist. In that case, the value of the welfare function and the initial conditions will determine which end state will be reached. But the most valuable end state will not necessarily be the optimal one. For a high discount rate, the path to an end state may be more valuable than the end state itself, even if this state lasts forever.

The paper illustrates the approach paths towards the end states. The approach path towards an equilibrium end state will usually consist of some period of bang-bang control followed by a singular harvest rate. Several possibilities are shown graphically. However, when the Hamiltonian has an interior maximum, the optimal solution is given by applying the singular harvest rate.

The optimum may not be stable over time. Fishers have an incentive to lower costs, because this will seem to increase their income. The regulator will encourage this because it is also beneficial to society. The social welfare function does indeed increase with lower costs. However, what happens to the socially optimal harvest rate depends on how the marginal cost at the equilibrium (S_{e1}) changes. If the optimal harvest rate decreases, tension between regulator and fishers will arise. Fishers will feel that increasing efficiency is punished.

Evidently, the results provide incomplete information for policy design. For example, the introduction of measures involves the administration of stock levels, harvest rate and so on. Moreover, then the measures have to be enforced. All this comes with a cost that we have ignored in specifying our welfare function and subsequently in defining the optimal state. For example, it may be much more costly to ensure a cyclical harvest rate than to maintain a constant harvest rate.

References

1.	C. W. Clark, "Mathematical Bioeconomics, " John Wiley & Sons New York (1976).

2.	R. Hannesson, Optimal harvesting of ecologically interdependent fish species, *Journal of Environmental Economics and Management* (1983), **10**, 329-345.

3.	D. L. Ragozin and G. J. Brown, Harvest policies and nonmarket valuation in a predator-prey system, *Journal of Environmental Economics and Management* (1985), **12**, 155-168.

4.	W. J. Ströbele and H. Wacker, The economics of harvesting predator-prey systems, *Journal of Economics* (1995), **61**, 65-81.

5.	W. Semmler and M. Sieveking, On the optimal exploitation of interacting resources, *Journal of Economics* (1994), **59**, 23-49.

6.	P. N. V. Tu and E. A. Wilman, A generalized predator-prey model: Uncertainty and management, *Journal of Environmental Economics and Management* (1992), **23**, 123-138.

7.	A. A. Berryman, The origins and evolution of predator-prey theory, *Ecology* (1992), **73**, 1530-1535.

8.	P. Yodzis, Predator-prey theory and management of multispecies fisheries, *Ecological Applications* (1994), **4**, 51-58.

9.	P. Yodzis, "Introduction to theoretical ecology," Harper & Row, New York (1989).

10.	J. van der Meer, A handful of feathers, Ph.D. thesis, Rijksuniversiteit Groningen, Groningen (1997).

11.	S. H. Strogatz, "Nonlinear dynamics and chaos," Addison-Wesley, Reading, Massachusetts (1994).

12.	R. M. May, Limit cycles in predator-prey communities, *Science* (1972), **177**, 900-902.

13.	F. Brauer and A. C. Soudack, Stability Regions and transition phenomena for harvested predator-prey systems, *Journal of Mathematical Biology* (1979), **7**, 319-337.

14.	G. Dai and M. Tang, Coexistence region and global dynamics of a harvested predator-prey system, *Siam Journal of Applied Mathematics* (1998), **58**, 193-210.

15. M. I. Kamien and N. L. Schwartz, "Dynamic optimization: the calculus of variations and optimal control, Vol. 4", Elsevier Science Publishers, Amsterdam (1981).

16. J. Benhabib and K. Nishimura, The Hopf bifurcation and the existence and stability of closed orbits in multisector models of optimal economic growth, *Journal of Economic Theory* (1979), **21**, 421-444.

17. W. A. Brock and J. A. Scheinkman, The global asymptotic stability of optimal control with applications to dynamic economic systems, *in* "Applications of control theory to economic analysis" (J. D. Pitchford and S. J. Turnovsky, Eds.), North-Holland Publishing Company, Amsterdam (1977).

18. E. J. Dockner and G. Feichtinger, On the optimality of limit cycles in dynamic economic systems, *Journal of Economics* (1991), **53**, 31-50.

19. F. Wirl, The cyclical exploitation of renewable resource stocks may be optimal, *Journal of Environmental Economics and Management* (1995), **29**, 252-261.

20. M. I. S. Costa, E. Kaszkurewicz, A. Bhaya and L. Hsu, Achieving global convergence to an equilibrium population in predator-prey systems by the use of a discontinuous harvesting policy, *Ecological Modelling* (2000), **128**, 89-99.

Appendix I: The balance of mass

The increase in the mass of birds must be less or equal to the mass of the depleted shellfish, $\frac{dB}{dt} = rB\left(1 - \frac{z+hS}{KS}\right) \le d = \frac{BS}{z+hS}$. For small numbers of shellfish, $S \le \frac{z}{K-h}$, this condition is true because $\left(1 - \frac{z+hS}{KS}\right)$ is negative. For large numbers of shellfish, $S > \frac{z}{K-h}$, the condition is true if

$$r \le \min_{S} \frac{S}{z+hS} \frac{KS}{KS-(z+hS)}.$$ If $K - 2h \le 0$ we find the minimum at $S \to \infty$ and

$r \le \frac{K}{h(K-h)}$, or (if $K - 2h > 0$) the minimum is at $S = \frac{2z}{K-2h}$, so that $r \le \frac{4}{K}$.

Appendix II: Stability analysis

From an analysis of the direction of the vector field, it follows immediately that $(S_{e2}, 0)$ is a saddle point. Equilibrium (S_{e1}, B_{e1}) is Lyapunov stable, when the real part of all the eigenvalues of the Jacobian, $Df(S_{e1}, B_{e1})$, are negative.

$$Df(S, B) = \begin{bmatrix} \dfrac{\partial f_S(S,B)}{\partial S} & \dfrac{\partial f_S(S,B)}{\partial B} \\[2mm] \dfrac{\partial f_B(S,B)}{\partial S} & \dfrac{\partial f_B(S,B)}{\partial B} \end{bmatrix}$$

Lyapunov stability means that a trajectory will stay within a finite distance from the equilibrium whenever it comes close enough to that equilibrium. The eigenvalues of $Df(S_{e1}, B_{e1})$ are:

$$\frac{1}{2aKz}\left(D \pm \sqrt{D^2 + 4aKrz(Kz+D)}\right), \tag{AII-1}$$

with $D = -(q-y)a(K-h)^2 - hz < 0$. $\tag{AII-2}$

A negative real part of the eigenvalue means that the equilibrium is stable. Equation (AII-2) shows D is negative. From equation (AII-1) we can see that the eigenvalue will have a negative real part if the square root term is smaller then D. That is the case when $Kz + D < 0$, which leads to

$$\frac{z}{(K-h)} < (q-y)a. \tag{AII-3}$$

This condition is satisfied because $S_{e1} < S_{e2}$ (Figure 1) so that the equilibrium is stable.

When the eigenvalue is complex, the equilibrium is a stable focus, meaning that the trajectory oscillates around the equilibrium with ever decreasing amplitude. If the eigenvalue is real, (S_{e1}, B_{e1}) is a node. This means the trajectory asymptotically approaches the equilibrium. The eigenvalue is real if the square root term is positive. The square root term, $D^2 + 4aKrz(Kz + D)$, is a parabola in D. For $r < \dfrac{1}{a}$, it has no roots and is positive. Thus, the equilibrium is a node if the birth rate for birds is smaller than the additional mortality rate for shellfish. For $r \geq \dfrac{1}{a}$, the parabola has two roots: namely, $D_1 = 2Kz(\sqrt{ar(ar-1)} - ar)$ and $D_2 = -2Kz(\sqrt{ar(ar-1)} + ar)$. The eigenvalues are real, i.e. the square root term is positive, for

$$D \geq D_1 \Rightarrow S_{e2} \leq \frac{2K(ar - \sqrt{ar(ar-1)}) - h}{K - h} S_{e1}, \text{ and for}$$

$$D \leq D_2 \Rightarrow S_{e2} \geq \frac{2K(ar + \sqrt{ar(ar-1)}) - h}{K - h} S_{e1}. \text{ Hence, the system has a node if the}$$

two equilibria are either close together or far apart.

We have proved that the system is locally stable by looking at the linearized system. We now prove that the system is also globally stable by showing that the system does not tend to a limit cycle. Using the Bendixson-Dulac criterion [11], we can prove that the system does not have a limit cycle in phase space. If such a closed trajectory C exists then $\oint_C \left(\begin{bmatrix} \dot{S} \\ \dot{B} \end{bmatrix} \cdot \bar{n}\right) dl = 0$, with $\bar{n}$ the outward normal on C. The dot product must equal zero because the trajectory follows C. Green's theorem yields: $\iint_A \nabla \cdot \left(g(S,B)\begin{bmatrix} \dot{S} \\ \dot{B} \end{bmatrix}\right) dA = \oint_C g(S,B)\left(\begin{bmatrix} \dot{S} \\ \dot{B} \end{bmatrix} \cdot \bar{n}\right) dl$, with A, the surface enclosed by C.

So, if we can find a function $g(S,B)$ for which the sign of the integrand is always positive or always negative over at least A, then the surface integral must be unequal

to zero. Consequently, this means C is not a trajectory. Taking $g(S,B) = \dfrac{(z+hS)}{KBS}$,

then
$$\nabla \cdot \left(g(S,B) \begin{bmatrix} \dot{S} \\ \dot{B} \end{bmatrix} \right) = \frac{\partial g(S,B)}{\partial S}(f_S(S,B) - y) + \frac{\partial g(S,B)}{\partial B} f_B(S,B)$$

$$= -\frac{hS^2 + (q-y)az}{aKBS^2} < 0.$$
(AII-4)

This implies the system has no limit cycles for $B > 0$ and $y_{\max} < q$.

By observing the vector field in Figure 2, it is clear that the equilibrium (S_{e1}, B_{e1}) must be globally stable. The system is locally stable, so any trajectory starting at an initial point in a neighborhood Ω of (S_{e1}, B_{e1}) will tend towards the equilibrium. Suppose that a trajectory starting at a point outside Ω moved away from the equilibrium. Due to continuity of the system, a trajectory starting on the border of Ω has to follow that border, which is impossible because it would imply the system has a limit cycle. Therefore (S_{e1}, B_{e1}) must be a globally stable equilibrium.

Appendix III: Conditions for a singular equilibrium on S=Se1

Equation (24) can be rewritten into equation (AIII-1) which allows for a graphical interpretation of the solution:

$$\frac{\partial v(B_e)}{\partial B} = R_\infty + \frac{Kz\delta\left((p - c(S_{e1}))(\delta + \frac{1}{a}) + \frac{B_0}{K}\frac{\partial c(S_{e1})}{\partial S} \right)}{(K-h)^2 rB_e},$$
(AIII-1)

where $R_\infty = \dfrac{(p - c(S_{e1}))(\delta + r)}{Kr} - \dfrac{z\delta \dfrac{\partial c(S_{e1})}{\partial S}}{(K-h)^2 r}$.

Figure AIII-1 shows equation (AIII-1) graphically. The Right Hand Side (RHS) of equation (AIII-1) is a hyperbolic function shown in black. It can be one of two different forms depending on the sign of the second RHS term. We call the RHS type I when the second RHS term is positive and type II when it is negative. The Left Hand Side (LHS) of equation (AIII-1), the marginal value of birds, is shown in gray. We consider two possible forms of the bird-value function: namely, an S-shaped and a concave function. The intersection point of a black and a gray curve defines a solution for equation (AIII-1). That is the singular equilibrium value of B.
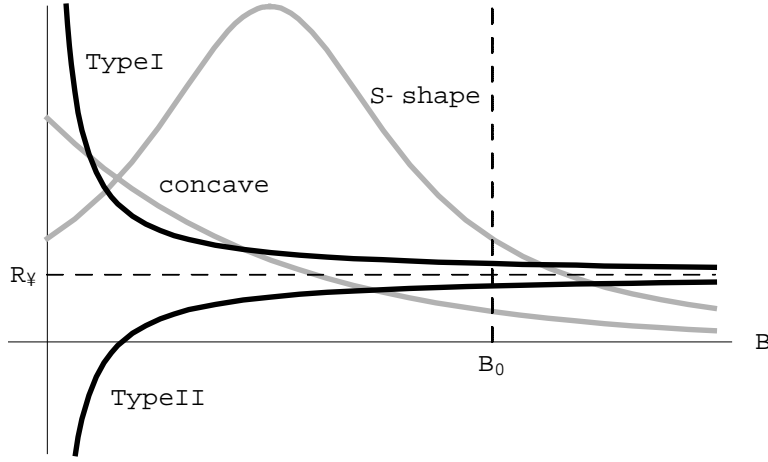
Figure AIII-1: Graphical representation of possible solutions to equation (AIII-1).

Note: The black curves denote the RHS of (AIII-1) for two types of hyperbolic functions. The gray curves denote the LHS of (AIII-1) for a concave and for an S-shaped bird-value function.

We call the solution a type I equilibrium when the RHS is of type I, meaning:

$$\frac{\partial c(S_{e1})}{\partial S} > -(p - c(S_{e1}))(\delta + \frac{1}{a})\frac{K}{B_0}, \tag{AIII-2}$$

and a type II equilibrium when the RHS is of type II, meaning:

$$\frac{\partial c(S_{e1})}{\partial S} < -(p - c(S_{e1}))(\delta + \frac{1}{a})\frac{K}{B_0}. \tag{AIII-3}$$

A type I (II) system means that if the system is in an optimal equilibrium with birds extinct, S is smaller (larger) than S_{e1}. For further discussion see Section 4.4.1.3, where singular equilibria on the S-axis are discussed.

From the graph in Figure AIII-1 and from the condition $0 < B_e < B_0$, we can deduce the following conditions for the solutions of equation (24) or (AIII-1). There can be 0,1 or 2 type I equilibria. The minimum of the LHS (gray) must be smaller than the maximum of the type I RHS (black), or the two curves will not intersect. Therefore, a necessary condition for the existence of a type I equilibrium is:

$$\max_B \frac{\partial v(B)}{\partial B} > (p - c(S_{e1}))\left(\frac{r + \delta}{Kr} + \frac{Kz\delta}{(K-h)^2 rB_0}(\delta + \frac{1}{a})\right). \tag{AIII-4}$$

The RHS of (AIII-4) equals the RHS of (AIII-1) for B_0, its minimum value. If $v(B)$ is concave, then $\max_B \dfrac{\partial v(B)}{\partial B} = \dfrac{\partial v(0)}{\partial B}$. There is only one type I equilibrium, when :

$$\frac{\partial v(B_0)}{\partial B} > (p - c(S_{e1}))\left(\frac{r+\delta}{Kr} + \frac{Kz\delta}{(K-h)^2 rB_0}(\delta + \frac{1}{a}) \right). \qquad \text{(AIII-5)}$$

This can be seen from Figure AIII-1.

When the RHS is of type II, up to 3 equilibria may exist. A necessary condition for a type II equilibrium is:

$$\min\left(\frac{\partial v(0)}{\partial B}, \frac{\partial v(B_0)}{\partial B} \right) < (p - c(S_{e1}))\left(\frac{r+\delta}{Kr} + \frac{Kz\delta}{(K-h)^2 rB_0}(\delta + \frac{1}{a}) \right). \qquad \text{(AIII-6)}$$

For a concave $v(B)$, no more than one equilibrium exists and (AIII-6) is also a sufficient condition. If $v(B)$ is S-shaped, up to three equilibria may exist. Equation (AIII-7) gives a necessary condition for the existence of more than one equilibrium:

$$\frac{\partial v(0)}{\partial B} < (p - c(S_{e1}))\left(\frac{r+\delta}{Kr} + \frac{Kz\delta}{(K-h)^2 rB_0}(\delta + \frac{1}{a}) \right). \qquad \text{(AIII-7)}$$

We are looking for possible end states. Not every singular equilibrium is a possible end state, because it may not be optimal. According to the transversality condition (14), the shadow price of birds needs to be positive for an optimal end state. Let us consider the singular end state on the B-isocline. Substituting $S = S_{e1}$ and equation (16) in $\lambda_B > 0$ leads to:

$$\tilde{B} > \frac{-K^2 z\left((p - c(S_{e1}))(\delta + \frac{1}{a}) + \frac{B_0}{K}\frac{\partial c(S_{e1})}{\partial S} \right)}{(p - c(S_{e1}))(K-h)^2 - Kz\dfrac{\partial c(S_{e1})}{\partial S}}. \qquad \text{(AIII-8)}$$

This equation defines the minimum number of birds on a singular trajectory for which the shadow price is positive, i.e. a lower bound to the number of birds in a singular coexistence end state. The denominator is positive, and, because B_e is positive and singular, an equilibrium of type I will satisfy (AIII-8). If the equilibrium is of type II, we can combine equation (24) with (AIII-8) to derive the following necessary condition that ensures the type II equilibrium is optimal:

$$\min\left(\frac{\partial v(0)}{\partial B}, \frac{\partial v(B_0)}{\partial B} \right) > \frac{\partial v(B_e)}{\partial B} > \frac{(p - c(S_{e1}))}{K}. \qquad \text{(AIII-9)}$$