University of New England

Graduate School of Agricultural and Resource Economics
&
School of Economics

Invasive Species in Aquatic Ecosystems: Economics and Matrix Population Models

by

Oscar Cacho

No. 2005-5

Working Paper Series in

Agricultural and Resource Economics

ISSN 1442 1909

http://www.une.edu.au/febl/EconStud/wps.htm

 ISBN 1 86389 947 2

Invasive Species in Aquatic Ecosystems: Economics and Matrix Population Models *

Oscar Cacho **

Abstract

When a biological invader is identified in an aquatic ecosystem rapid response is critical; particularly if the invasive organism has the ability to spread rapidly. The first response should be an attempt to contain the invasion while further information is gathered to evaluate whether eradication is feasible. Two aspects of the eradication v. containment decision are studied in this paper. First, the question of when it is optimal to eradicate an invasion is answered by developing and using a stochastic dynamic programming model based on a simple biological spread function. Second, the question of the best control options to be used in an eradication or containment program is related to the demographic characteristics of the invading organism, based on a stage-matrix population model. The sort of information required to calibrate the decision model for a specific invader is also discussed.

Key Words: biological invasions, optimal control, matrix population models, eradication

---

[*] Based on a Paper Presented at the Conference of the World Aquaculture Society, Honolulu, Hawaii, February 2004.

[**] Oscar Cacho is an Associate Professor in the School of Economics and in the Graduate School of Agricultural and Resource Economics at the University of New England.
Contact information: School of Economics, University of New England, Armidale, NSW 2351, Australia. Email ocacho@une.edu.au.

Introduction

Biological invasions are “the uncontrolled spread and proliferation of species… from their native geographic ranges to new ranges” (NRC, 2002: p. 14). These invasions are a global problem and, as well as causing considerable costs, their impact is a major component of global change. In some areas biological invasions represent major threats to ecosystems through mechanisms such as reductions in biodiversity and productivity and modification of habitat structure (Bax et al., 2001). In aquatic ecosystems this may in turn affect fisheries, tourism and other industries.

Three management technologies are generally employed to control pests: mechanical, chemical and biological (including habitat restoration). According to McEnnulty et al. (2000), one of the main constraints to eradication of invaders from aquatic ecosystems is the lack of highly specific control techniques. This means that early and accurate recognition of the pest is extremely important. Aquatic organisms are generally more difficult to control than terrestrial organisms because control techniques tend to be difficult to apply directly to the target species; thus significant collateral damage often arises from controlling aquatic invaders. McEnnulty et al (2000) discuss the case of Darwin Harbour in Australia, where *Mytilopsis sp*. was eradicated using chlorine and copper sulphate in three locked marinas. This resulted in high non-specific damage (everything was killed), but the authors argue that the potential cost of the invasion would have been much higher if left uncontrolled. For some benthic organisms such as molluscs, removal of adults (a mechanical methods) is feasible and may cause low collateral damages, but this methods is also labor intensive and therefore expensive.

Given the threats posed by exotic organisms, common sense dictates that when an invasion is discovered an attempt should be made to contain it immediately, to the extent possible, while assessing whether eradication is feasible. This requires rapid-assessment decision tools. Bioeconomic techniques provide an ideal infrastructure to develop these decision models. Bioeconomics is a theory of optimal management of renewable biological resources (Sharov and Liebhold, 1998) which has traditionally been applied in fisheries and aquaculture (eg. Clark, 1976, 1984; Allen at al. 1984, Cacho 1997 and references therein).

This paper deals with two aspects of the problem of managing biological invasions. First, the question of when it is optimal to eradicate an invasion is answered by developing and using a stochastic dynamic programming model based on a simple biological-spread function. Second, the question of the best control options to be used in an eradication or containment program is related to the demographic characteristics of the invading organism, based on a stage-matrix population model. The advantage of this approach is that it is possible to evaluate the effects of control options that target specific life stages; hence the method provides flexibility in the evaluation of alternative combinations of control options. The sort of information required to calibrate the decision model for a specific invader is discussed in the final section of the paper.

A model to evaluate the eradication decision

The model developed in this section is an implementation of the ideas presented by Olson and Roy (2002). The objective is to develop a model as simple as possible that captures the key features of a biological invasion and its management. There are three key variables that drive the invasion-control system: (i) the size of the invasion (y_t), (ii) the reduction in area invaded (u_t) achieved through control methods, and (iii) the size of the invasion after control is applied (x_t). Below, these three variables are measured in terms of area (ha), but they could also be expressed in terms of invasion density per unit area. The key variables are related to each other through three functions: the growth function, (Δy_t), the control-cost function ($C(u_t)$) and the damage function ($D(x_t)$).

The optimal control strategy is determined by solving the dynamic programming model:

$$V(y_t) = \min_{u_t}\left(C(u_t) + D(x_t) + \delta \cdot V\left(y_{t+1}\right)\right) \tag{1}$$

subject to:

$$y_{t+1} = x_t + \Delta y_t\left(x_t\right)\rho \tag{2}$$

$$x_t = y_t - u_t \tag{3}$$

Equation (1) is a recursive equation that finds the control strategy required to minimize the total cost of the invasion, in present value terms. The total cost includes the cost of control (C), the cost of damage (D) and the future cost of the uncontrolled invasion ($V(y_{t+1})$). The future cost is discounted using the factor $\delta = 1/(1+i)$ for the discount rate i. The optimisation is subject to the population dynamics of the invader (2) and to the effect of control on the spread of the invasion (3). The spread function is represented in equation (2) as $\Delta y_t(x_t)$. The variable ρ represents a random environmental disturbance ($0<\rho<\infty$), which may cause actual spread to be larger or smaller than its expected value.

In the pest-control literature it is common to maximise the net benefits of control, where benefits are expressed as the damage avoided by slowing down or eliminating the invasion. The model in equations (1) to (3) is exactly equivalent to one that maximizes net benefits, but it is more compact because damage is expressed as a component of the cost to be minimised. Note that the control cost (C) is a function of the amount of control applied (u_t), whereas damage (D) is a function of the size of the invasion after control has been applied (x_t).

In essence, equation (1) represents the present value of the cost of the invasion, which includes current control costs + current damage + discounted future costs of the remaining invasion. Control costs include not only normal costs such as labor and chemicals, but also the cost of damaging the environment and killing non-target organisms when control is applied. Recursive solution of equations (1), (2) and (3) leads to an optimal decision rule that can indicates the conditions under which eradication is optimal.

To obtain a model that can be solved numerically, specific functional forms need to be defined for the three key functions. The spread (growth) function can be conveniently represented by the logistic equation:

$$\Delta y_t = \alpha\, x_t \left[1 - \frac{x_t}{\kappa}\right] \tag{4}$$

and the simplest representation of the cost and damage functions is a liner function:

$$C(u_t) = \beta_C u_t \tag{5}$$

$$D(x_t) = \beta_D x_t \tag{6}$$

In these equations Greek letters represent parameters to be estimated for the particular invasion. The working hypothesis is that all four parameters (κ, α, β_C and β_D) are > 0. The implication of this hypothesis is that the invasion will eventually cover the entire area at risk if no control is applied. Definitions of the four parameters and their values are presented in Table 1. For simplicity it was assumed that the area at risk is 100 ha, so results can also be interpreted as percentages.

[TABLE 1 HERE]

The switching point

Inserting equations (4) to (6) into equations (1) and (2) and solving the dynamic model results in an optimal decision rule (optimal control). The optimal decision rule indicates the level of control (u_t) that should be applied for any given invasion size (y_t). Associated with the optimal control is the optimal state transition $y_t \rightarrow y_{t+1}$ which indicates whether the invasion increases ($y_t < y_{t+1}$), decreases ($y_t > y_{t+1}$) or remains stable ($y_t = y_{t+1}$) when subject to the optimal control. The optimal state transition should be interpreted by comparing it to a 45^0 'reference' line (Figure 1), representing the steady state (where $y_t = y_{t+1}$).

Figure 1 illustrates a convenient way of exploring the dynamics of the optimization system and identifying equilibrium points. If the optimal state transition lies below the reference line (dotted line in Figure 1) it is optimal to decrease the size of the invasion. Conversely, if the optimal state transition lies above the reference line it is optimal to allow the population to increase. The point at which the reference line is intersected from below (point *a* in Figure 1), indicates the 'critical' size of the invasion; to the left of point *a* eradication is optimal, to the right of point *a* it is optimal to allow the invasion to grow. Hereafter the critical point (*a*) is referred to as the *switching point*. The switching point occurs where the marginal cost of control equals the marginal cost of damage, with both costs measured in perpetuity and expressed in present-value terms.

[FIGURE 1 HERE]

The optimal state transition can be used to derive an optimal state path, which indicates the trajectory of the invasion through time under optimal control (Figure 2). In this example, with the assumed parameter values illustrated in Figure 1, an invasion under 55 ha should be eradicated within 8 years, whereas an invasion over 55 ha should be allowed to run its course. The switching point and optimal paths depend on a number of assumptions, including the values of the four parameters (Table 1) and the discount rate (i). So it is important to undertake sensitivity analysis.

[FIGURE 2 HERE]

A value of $\alpha = 0.2$ implies a slow-spreading invasion, whereby the whole area at risk is invaded within 50 years. Table 2 presents the switching points estimated for this invasion under a range of cost and damage values. For any given control cost, increasing damage causes the switching point to increase from zero to 100. For example if the control cost is $160/ha and damage is $4/ha, it is always optimal to do nothing (the switching point is zero), but if damage is $5/ha, it is optimal to eradicate invasions up to 32 ha in size.

[TABLE 2 HERE]

A value of $\alpha = 0.5$ implies a fast-spreading invasion, whereby the whole area at risk is invaded within 20 years. Under this assumption (Table 3) the results are similar to those discussed above in the sense that for any given control cost a higher damage parameter will result in a higher switching point. However, with a fast-spreading invasion, combinations of high control cost and low damage cost result in values of the switching point that are > 0, this is in contrast to values of zero for the slow-spreading invasion. For example, with a control cost of $240 and a damage of $4, the switching point is 0 ha for the slow invasion (Table 2), but it is 17 ha for the fast invasion (Table 3). This indicates that there is more pressure to reduce the fast invasion early on to avoid damage costs in the near future.

[TABLE 3 HERE]

The interaction between the invasion speed and damage costs when control costs are high ($240/ha) is further illustrated in Figure 3. At low damage cost the switching point for the fast invasion is greater than for the slow invasion; but at high damage cost the pattern reverses and the switching point is lower for the fast invasion. This implies that, when the control costs are high, a fast-spreading invasion discovered when it is fairly advanced (towards the right in Figure 3) is not worth controlling to the same extent as a slow invasion. These results also indicate that, for the fast invasion in its early stages (towards the left in Figure 3), the marginal cost of damage (in present-value terms) is higher than the marginal cost of control, and therefore it is optimal to eradicate invasions with damage costs as low as $4/ha.

[FIGURE 3 HERE]

An important question arising from the foregoing analysis is whether invasions can be characterized in terms of the four parameters: κ, α, β_C, and β_D. This is arguably the simplest possible description of the decision problem. As seen above, α determines the speed of spread, and slower invasions are only worth eradicating if the damage is high or the cost of control is low.

A common way of calculating the cost of controlling an invasion is to multiply the cost per ha (i.e. cost of labor and chemicals) times the area to be treated. This implies that the cost function is linear as expressed in equation (5). Similarly, damage is often calculated by multiplying the loss in the value of outputs per hectare caused by the pest times the total area invaded. This implies a linear damage function, as represented in equation (6). These assumptions are reasonable in some cases but may not be realistic for natural environments that have scarcity value. In these cases as the pristine area decreases the remaining un-invaded area may have a higher value per unit area, which would imply a damage function that increases at an increasing rate as the area invaded increases.

Life stages and control options

The model developed above provides a simple and convenient decision tool, but it abstracts away from important questions. The control variable (u_t) is expressed in terms of reductions in the area invaded. This says nothing about the techniques that should be used to control the invasion or the life-stages of the population that should be targeted. Matrix population models can help in this regard. Matrix models are a useful tool for investigating population dynamics (Caswell, 2001), they provide a convenient way of integrating demographic information regarding the different life-stages of an organism. Consider the life cycle of a hypothetical marine organism illustrated in Figure 4.

[FIGURE 4 HERE]

This particular organism has four distinctive life stages: egg, larva, juvenile and adult. Adults produce eggs according to their level of fecundity (F_4), a proportion of eggs (P_1) hatch into larvae, a proportion of these larvae (P_2) survive into juveniles, and a proportion of juveniles (P_3) survive into adults. The cycle is completed with the proportion of existing adults (P_4) that survive into the next time period. Given the demographic (survival and fecundity) parameters P_1, P_2, P_3, P_4 and F_4, the spread of this organism can be studied by creating a projection matrix. The structure of the projection matrix depends on the time step used to represent the population dynamics relative to the duration of the various life stages. If the time step is long enough to allow newly-laid eggs to hatch into larvae within a time period, we can represent the population as consisting of only three stages: larvae, juveniles and adults. The projection matrix is:

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & F_4 \times P_1 \\ P_2 & 0 & 0 \\ 0 & P_3 & P_4 \end{bmatrix} \tag{7}$$

Where the first row and column represent larvae, the second row and column represent juveniles and the third row and column represent adults. Columns can be interpreted as 'from' and rows as 'to', so the parameter in row 2 and column 1 (P_2) is the proportion of larvae (stage 1) that survive into juveniles (stage 2). The structure of the population at any time t is described by vector $\mathbf{x}_t$, which contains the number of individuals in each stage of the life cycle:

$$\mathbf{x}_t = \begin{bmatrix} x_{1t} \\ x_{2t} \\ x_{3t} \end{bmatrix} \tag{8}$$

where x_{1t} is the number of larvae, x_{2t} is the number of juveniles and x_{3t} is the number of adults at time t. Population growth and changes in population structure are calculated by performing the matrix multiplication:

$$\mathbf{x}_{t+1} = \mathbf{A}\ \mathbf{x}_t \tag{9}$$

Applying equation (9) recursively for any initial population $\mathbf{x}_0$, will result in exponential growth. The long-term dynamics of the population are described by the population growth rate (λ), which is related to the intrinsic rate of increase r asλ =e^r. This means that, to contain the invasion we must reduce λ to 1.0 (r = 0), and to eventually eradicate the invasion we must reduce λ to a value less than 1.0 (r < 0). The growth rate, however, is affected by the demographic parameters in **A**, and these effects are not uniform. The effects of demographic parameters on λ are measured by the elasticity matrix:

$$\mathbf{E} = \left(\frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \right) \tag{10}$$

To estimate λ, it is necessary to estimate the dominant eigenvalue of the **A**, Caswell (2001, pp. 107-108) shows how to perform this operation numerically.

As an example, consider a hypothetical invasive organism with the following projection matrix:

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & 200 \\ 0.08 & 0.40 & 0 \\ 0.01 & 0.20 & 0.80 \end{bmatrix} \tag{11}$$

This means that adults produce 200 live larvae ($A_{1,3}$) on average, there is an 8 percent probability that a larva will become a juvenile ($A_{2,1}$), a 1 percent probability that an early-maturing larvae will become an adult ($A_{3,1}$), a 20 percent probability that a juvenile will survive into an adult ($A_{3,2}$) and so on. The growth rate (λ) of this matrix is 2.35 > 1, this value is > 1, implying that the population will continue to increase if left unchecked. To control the invasion it is necessary to make $\lambda \leq 1$, and this can be achieved by targeting one or more life stages. The elasticity matrix corresponding to **A** in (11) is:

$$\mathbf{E} = \begin{bmatrix} 0 & 0 & 0.33 \\ 0.15 & 0.03 & 0 \\ 0.18 & 0.15 & 0.17 \end{bmatrix} \tag{12}$$

These elasticity values indicate that the most effective control option would be one that targets fecundity ($E_{1,3}$ = 0.33), followed by options that target adult survival (elasticities in row 3 range between 0.15 and 0.17). However, the most effective option is not necessarily the most efficient from an economic standpoint. Targeting fecundity may not be a viable option for the particular species in the particular environment being considered. For example, attempting to kill larvae by applying a chemical that will also kill coral may be unacceptable in a protected area, and the only option left may be the physical removal of adults (i.e. target $E_{3,3}$).

Information Needs

The control-cost function should be fairly easy to estimate, although the data are seldom readily available for existing eradication programs. The components of the cost function would be travel, labor, chemicals and equipment expenses. If other (non-target) organisms are also affected by the control technique, then the control-cost function should include these additional costs (i.e. reduced fish catches, reduced recreation).

Estimating the damage function is generally more difficult than estimating the cost function. Fortunately, sensitivity analysis results can answer questions such as: "For the given cost of control, what would be the minimum damage that would make it optimal to eradicate the invasion?" In Tables 2 and 3 this question may be answered by selecting the relevant control-cost column and moving down to find the switching point corresponding to the current invasion size. The "break-even" damage can then be read off the appropriate row. For example, assume a fast invasion with control cost of \$160/ha and a size of 50 ha when discovered; referring to the 4th column in Table 3 indicates that a switching point of 50 ha occurs when damage is \$7.50/ha, this is the break-even damage value for this invasion. This method eliminates the need for full biodiversity valuations to make pest-control decisions in natural ecosystems. However, it would still be necessary to place a lower bound on the value of the ecosystem under threat.

Linear cost and damage functions were assumed for simplicity in this example, but other functional forms may be more appropriate, this is an empirical question and the answer is likely to vary between cases.

The information required to estimate the spread function parameters may not be readily available for a particular species, but it should be possible to obtain rough estimates of the area at risk (κ) and the growth rate (α) from past experience, expert opinion and climate-matching. Furthermore, the exponential section of the spread function (4) can be estimated by solving the matrix model using equation (9).

In order to apply the elasticity matrix to the control decision it is necessary to know something about the cost of achieving a given reduction in the various demographic parameters, which in turn requires knowledge of the technologies available and their costs. This link is not made here, but the reader is referred to an example presented by Buhle et al. for an oyster drill (*Ocinebrellus inornatus*) invasion.

Summary and Conclusions

Biological invasions can be very costly and, when they occur in aquatic ecosystems, they are particularly difficult to control. Therefore it is important to have rapid-assessment decision tools. Such a tool is developed in this paper, in the form of a model that requires four parameters that represent the area at risk, the speed of spread, the cost of control and the cost of damage. Solution of the model for any given set of parameters yields a ‘switching point’: the critical size of the invasion below which it is optimal to attempt eradication.

Given the difficulty of estimating the cost of damage, particularly in natural environments, the paper shows how to perform sensitivity analysis to estimate the ‘breakeven damage’ that would make an eradication effort economically efficient. Thus avoiding the need to estimate a detailed damage function that may require calculation of biodiversity and other environmental values.

A weakness of the switching-point model is that the linkage between the level of control applied and its cost is abstract. Control is expressed in terms of invasion-area reduced, which gives no indication of the inputs required, the control techniques applied and the life stages targeted. This deficiency can be overcome by designing a matrix model based on demographic parameters that represent fecundity and survival of different life stages. In the tradition of fisheries bioeconomics, the model developed here was designed to be as simple as possible while capturing the essential biological and economic features of the problem. This makes the model amenable to empirical application and testing.

References

Allen, P.G., L.W. Botsford, A.M. Schuur and W.E. Johnston.1984. Bioeconomics of Aquaculture. Amsterdam: Elsevier .

Bax, N. Carlton, J.T., Mathews-Amos, A., Haedrich, R.L., Howart, F.G., Purcell, J.E., Rieser, A. and Gray, A. 2001. The control of biological invasions in the world's oceans. *Conservation Biology.* 15: 1234-46.

Buhle, E., Margolis, M. and Ruesink, J.L. 2004. Bang for the buck: cost effective control of invasive species with different life histories. Resource for the Future, Discussion Paper 04-06, April 2004.

Cacho, O.J., 1997. Systems modeling and bioeconomic modeling in aquaculture. *Aquaculture, Economics and Management*., 1:45-64.

Caswell, H. 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*. 2nd edition. Sinauer Associates, Sunderland, MA.

Clark, C.W. 1976. Mathematical bioeconomics. The optimal management of renewable resources. New York: John Wiley & Sons.

Clark, C.W. 1985. Bioeconomic modelling and fisheries management. New York: John Wiley & Sons.

McEnnulty, F.R., Baxc, N.J., Schaffelke, B and Campbell, M.L. (2000). A literature review of rapid response options for the control of ABWMAC listed species and related taxa in Australia. CSIRO Marine Research, Tasmania, Unpublished Manuscript. http://www.marine.csiro.au/crimp/Reports/publications.html accessed on 11 Aug 2004.

Olson, L.J. and Roy, S. (2002). The economics of controlling a stochastic biological invasion. *American Journal of Agricultural Economics*. 84: 1311-16.

NRC. 2002. *Predicting invasions of nonindigenous plants and plant pests*. National Academy Press, Washington DC.

Sharov, A.A. and Liebhold, A.M. 1998. Bioeconomics of managing the spread of exotic pests species with barrier zones. *Ecological Applications*. 8: 833-45.

Table 1. Parameter definitions and values tested in this study

Symbol	Values	Definition
κ	100	area at risk (ha)
α	0.2, 0.5	intrinsic rate of spread (1/yr)
β_C	80-300	cost of control ($/ha)
β_D	3-25	cost of damage ($/ha)
i	0.06	discount rate

Table 2. Switching points (ha)[a] for a slow invasion with cost and damage functions assumed linear (α=0.2, β_C and β_D vary).

Damage	Control cost, β_C ($/ha)				
β_D ($/ha)	80	120	160	200	240
3	44	0	0	0	0
4	64	38	0	0	0
5	85	50	32	0	0
7.5	100	85	59	44	32
10	100	100	85	64	50
15	100	100	100	100	85
20	100	100	100	100	100

[a] a value of 0 means eradication is never optimal, 100 means eradication is always optimal, other values indicate the maximum invasion size that should be eradicated.

Table 3. Switching points (ha)[a] for a fast invasion with cost and damage functions assumed linear (α=0.5, β_C and β_D vary).

Damage β_D ($/ha)	Control cost, β_C ($/ha)					
	80	120	160	200	240	300
3	42	27	21	16	11	7
4	52	38	27	23	17	13
5	62	45	36	27	23	17
7.5	87	62	50	42	36	27
10	100	78	62	52	45	38
15	100	100	87	71	62	52
20	100	100	100	94	78	65
25	100	100	100	100	99	78

[a] a value of 0 means eradication is never optimal, 100 means eradication is always optimal, other values indicate the maximum invasion size that should be eradicated.

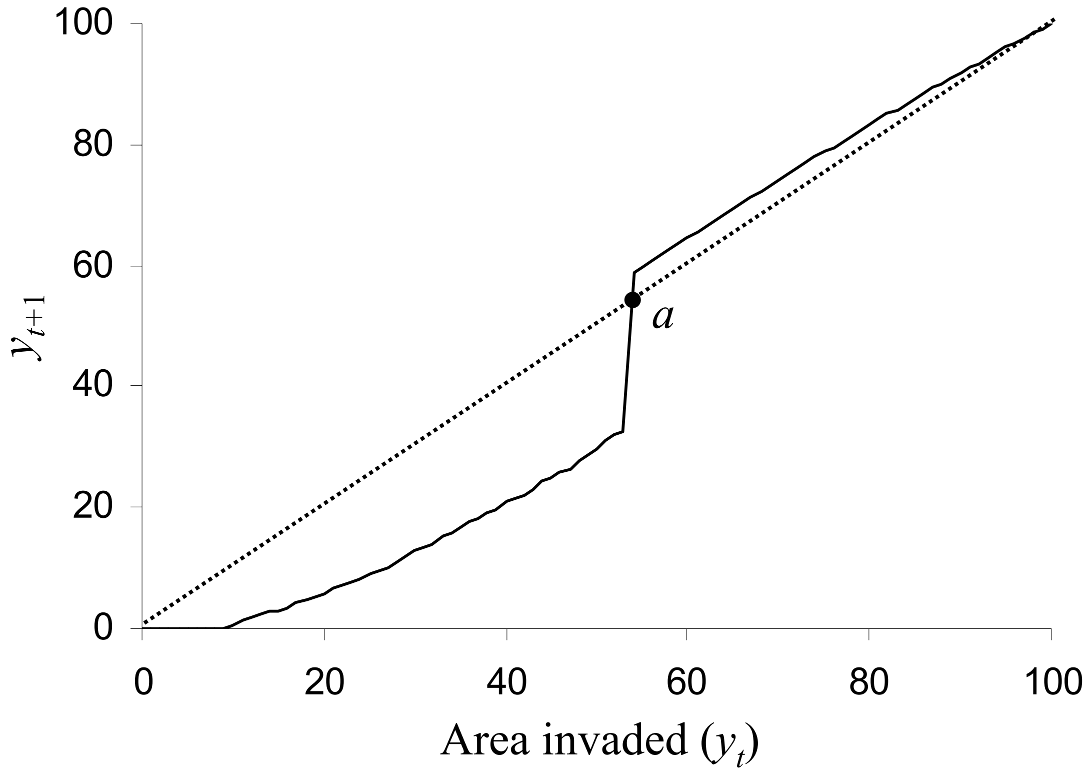

Figure 1. The optimal state transition (solid line) obtained by solving the DP model, *a* represents the switching point.

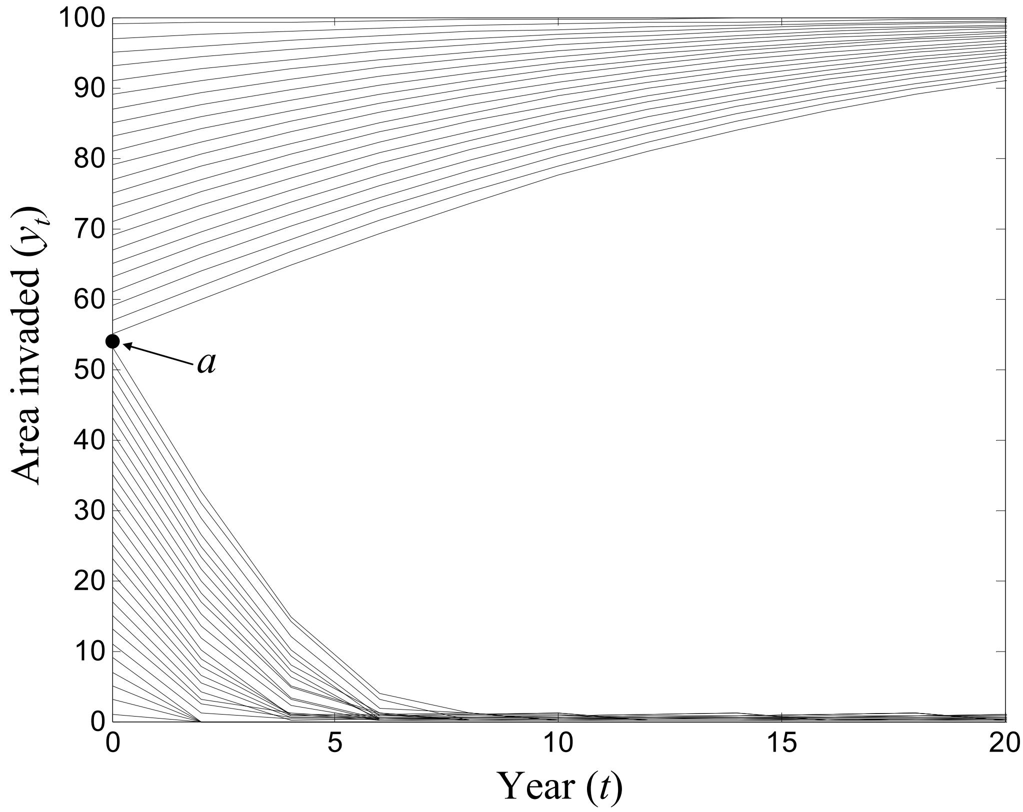

Figure 2. Optimal state paths for a range of starting values based on the optimal state transition illustrated in in Figure 1. Point *a* is the switching point.

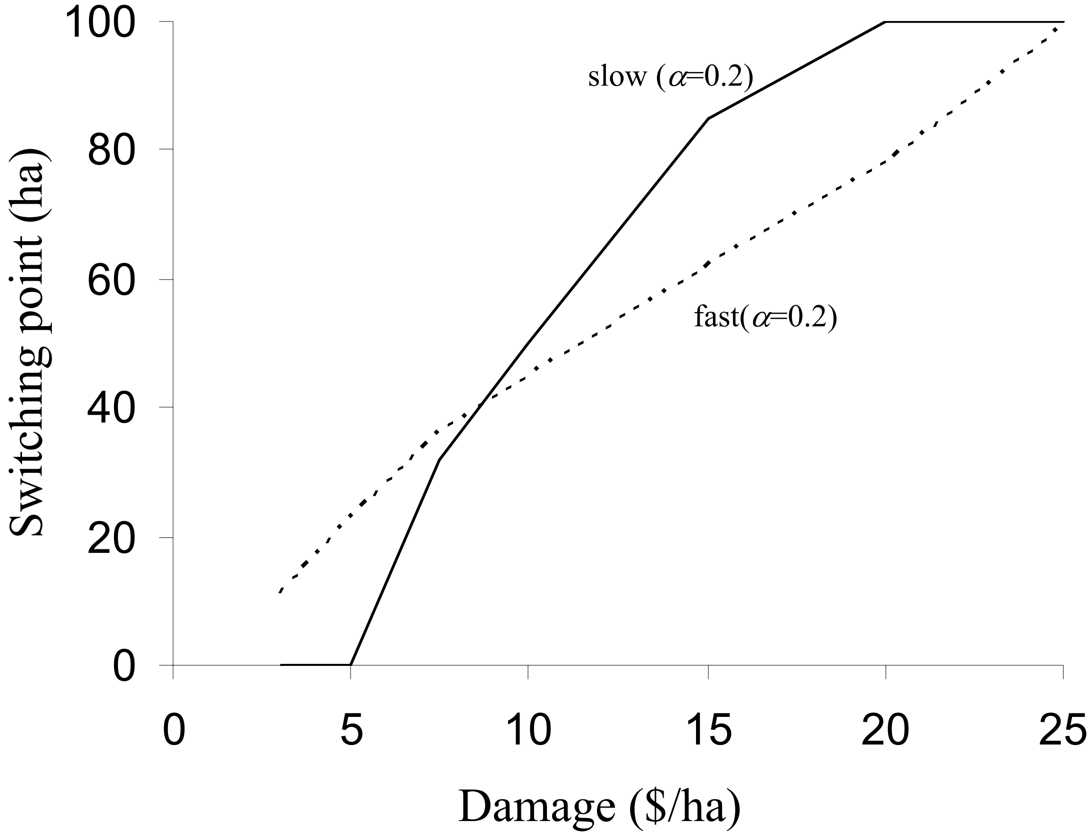

Figure 3. The effect of the damage parameter (β_D) on the value of the switching point for two different invasion speeds with a control cost of $240/ha.

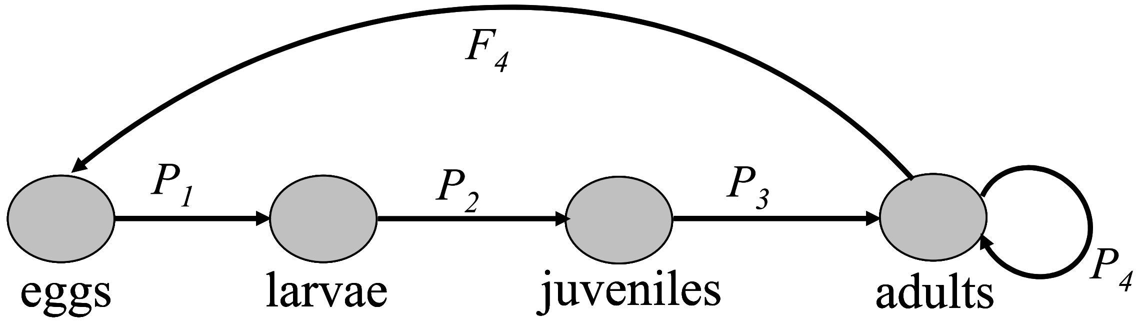

Figure 4. The life cycle of a hypothetical aquatic organism used as an example.