



ELSEVIER

Contents lists available at ScienceDirect

Resource and Energy Economics

journal homepage: www.elsevier.com/locate/ree



Control and the management of a spreading invader

David Finnoff^{a,*}, Alexei Potapov^b, Mark A. Lewis^b

^a University of Wyoming, Department of Economics and Finance, 1000E University Avenue, Department 3985, Laramie, WY 82071, United States

^b University of Alberta, United States

ARTICLE INFO

Article history:

Received 28 April 2008

Accepted 3 March 2010

Available online 20 April 2010

JEL classification:

Q2, Renewable resources and conservation

Keywords:

Natural resources
Biological invasions
Invasive species

ABSTRACT

We consider the problem of management of an aquatic invader spreading in a lake system. We assume that each year the invader can be removed from a certain proportion of invaded lakes, which depends on the selected intensity of control. Control decisions are generated and compared for an optimally controlled system and for a static optimization across asymptotic steady states. Control close to eradication of the invasive species is always optimal for invasions with relatively high damages, low rates of density dependent spread and/or low chance of additional random introductions. Control to a highly invaded steady state is optimal for those invasions with low relative damages, high chances of random introduction and high levels of uncertainty in species location. In all other cases the optimal outcome depends upon initial conditions. Comparing the relative performance of the optimally controlled system and the static optimization demonstrates situations when the differences are small and when not. When invasions are acted upon in their later stages and across certain parameter combinations a static optimization provides a reasonable approximation of an optimally controlled system. The flip-side is that optimal policies directed at an invasion in its early stages tend to provide significantly savings. The savings vary across parameter combinations, yet in these situations little useful insight will be generated without consideration of a dynamically optimized system.

© 2010 Elsevier B.V. All rights reserved.

* Corresponding author.

E-mail address: finnoff@uwyo.edu (D. Finnoff).

1. Introduction

Economists have been studying the optimal management of biological nuisances for over three decades. While the bulk of the research has focused upon policies to combat agricultural pests Lichtenberg and Zilberman (1986), Archer and Shogren (1996), following Shogren (2000) there has been an explosion of research into the more general question of the economics of invasive species, extending the consequences of the pests beyond those in agriculture. Questions have emerged from this recent work: what are the linkages and the feedback loops between economic activity and the nuisance (Settle et al., 2002; Finnoff et al., 2005); what are the consequences of the nuisance (Pimentel et al., 1999; Zavaleta, 2000); what are its population dynamics (Eiswerth and Johnson, 2002; Gutierrez and Regev, 2005); what is its spatial spread (Sharov and Liebhold, 1998; Brown et al., 2002); what strategies exist to direct at the problem (Leung et al., 2002; Olson and Roy, 2006); and what are the enormous uncertainties inherent in each of these components (Olson and Roy, 2002; Horan et al., 2002; Eiswerth and van Kooten, 2002). These problems also have an additional dimensionality that policies in response to an invasive species can be directed at introductions (i.e. prevention) or at established populations (i.e. control). While a complete consideration of all these questions typically is beyond the scope of any single paper, to provide practical insight and be a contribution some care must be taken in their inclusion to any research in this area.

In this paper we consider some of these themes jointly in the optimal management of an invasive species following some initial introduction that is in the midst of a widespread dispersal. The research is pertinent because many current invasions have already occurred, some causing extensive damages to economic and ecological systems, and are spreading across large areas. Perhaps the best known example of such an invader is the freshwater mollusk, zebra mussel (*Dreissena polymorpha*), which currently costs US industries an estimated US\$100 million per year (Pimentel et al., 1999). Zebra mussels have spread rapidly across eastern North America¹ and are currently spreading across inland lakes and towards western river basins (Bossenbroek et al., 2001, 2007). The research is also useful to policy makers because the framework developed captures some necessary realities of the problem yet is basic enough to generate some analytical insight. It is also easily applicable using readily available data, as demonstrated with an application to the spread of zebra mussels.

The framework we develop considers the management of a system of interconnected lakes subject to nonindigenous species invasion. The invader may cause significant enough ecological and/or economic damage to attributes of the lake network that some sort of policy intervention may be warranted. In our model we simplify a complex stochastic process into a formulation that includes important effects on average, or proportionately. This allows the restatement of a stochastic problem in deterministic terms. The method permits the incorporation of intersecting biology and economics at a large scale, and allows for analysis of their joint influence on decision making and optimal invasion management.

In our model it is presumed that at least one lake has been invaded by the alien species with some damages, and the possibility exists that it can spread to other lakes. Unlike Potapov et al. (2007) who considered the optimal management of a spreading invader with strategies that worked only to slow the spread (only delaying the timing of a fully invaded network), we consider management policies which can not only slow the spread of the invasion, they are able to stop or reverse the process. For simplicity these strategies are lumped into a single management variable coined control. This is appropriate in cases of widespread invasions which may have already passed through the initial introduction and establishment of the invader. A strategy of control presumes there is a current nuisance to be controlled. Thus while this methodology may not be as appropriate for an ex ante consideration of invasion prevention, it does appear appropriate for the reality facing many regions. The method transforms a finite horizon problem into an infinite horizon problem and allows the possibility of long-run equilibria (steady states) other than a fully invaded system. Nonetheless, even with this refinement the transitional dynamics are complex, making a traditional analysis of the problem using the maximum principle (Pontryagin et al., 1962) complicated.

¹ http://cars.er.usgs.gov/Nonindigenous_Species/ZM_Progression/zm_progression.html.

The roots of the problem are that the dynamics can result in multiple steady states. Classic work (Davidson and Harris, 1981; Tahvonen and Salo, 1996; Rondeau, 2001) demonstrate methodologies to determine the optimal steady state in dynamically optimized systems, all of which requires the generation of an optimal transition path from specific initial conditions. In many problems this is an onerous task. In comparison we present a simple methodology that provides some analytical results and circumvents much of the complexity of a complete dynamic optimization. The turnpike property of infinite horizon problems (Haurie, 1976) is exploited with a focus on a static optimization across steady states. The methodology concentrates on the properties of the terminal state and not on initial transients. The use of this simple approach is appealing to those interested in providing clear and simple policy advice. Yet its use provides a trade-off in itself as it neglects an optimization across the transitions from initial states to the steady state but allows a clear view of the underlying characteristics of optimal long-run equilibria. Similar methodologies have been employed in applied work (for example see Burnett et al., 2006). While the problem is computationally simplified, a necessary question becomes what is lost? Finnoff et al. (2009) considered this comparison for a simple case of linear dynamics. They demonstrated that the simple approach always wastes some resources but the waste tends to be small. The waste is least for quickly spreading invasions, low rates of growth in marginal damages and high rates of growth in marginal costs. However, the assumption of a linear invasion process is at odds with ecological theory (Carpenter et al., 1999) and omits several of the most critical features of an invasion process to make the findings limited in scope.

Here we consider the management of a system subject to invasion from both dynamic and static perspectives. For either there is the possibility of multiple equilibria, the optimality of which may depend on initial conditions. A comparative benchmark with two stable steady states, one close to eradication and one close to complete invasion is used to illustrate the importance of key parameters through relative comparisons. While making general statements in this setting is problematic, for the situation considered it is shown that stringent control close to eradication of the invasive species is optimal for invasions with relatively high damages, low rates of density dependent spread and low chance of random introduction. Invasions that should be optimally controlled to a highly invaded steady state are those with low relative damages, high chance of random introduction and high levels of uncertainty in species location.

If the invasion has control policies initiated early in the invasion process then those with moderate to high rates of density dependent spread and low to moderate levels of uncertainty in species location should be optimally controlled close to eradication. If control policies are initiated later in the invasion process, the system should be controlled to a highly invaded steady state for invasions with moderate relative damages, moderate to high rates of density dependent spread, moderate chance of random introduction, and low to moderate levels of uncertainty in location of the invader.

In comparing optimization procedures, as expected dynamically optimal management always outperforms static management but there are situations when the differences are small. The differences are always small when the influence on the invasion process of density dependent spread is high and there is a high chance of the invader being randomly introduced throughout the system. Moreover, the differences are also small when invasions are acted upon in their later stages (i.e. high initial conditions) in situations when damages are relatively low, when the influence on the invasion process of density dependent spread is low, and when there is a low degree of uncertainty in the location of the invader. The flip-side is that optimal policies directed at an invasion in its early stages tend to provide significant savings. These savings are greatest when relative damages are low, the influence of density dependent spread is low and there is a high degree of uncertainty of the invaders whereabouts. Optimal policies directed at an invasion detected in its later stages with high relative damages will also provide significant savings. In these situations little useful insight will be generated without consideration of a fully optimized system.

To generate the comparison the problem is developed from both dynamic and static perspectives. Following some basic qualitative insights for both, each is applied (loosely) to the spread of zebra mussels across Wisconsin lakes. Numerical simulations are used to find the solutions to each problem across numerous variations in key parameters that characterize invasion processes. These solutions are compared and contrasted, and conclusions generated.

2. Dynamics of a spreading invader

The invasion process is modeled for the case of a network of interconnected lakes. An alien species has been introduced into one or several lakes, has become established and has started to spread to other lakes in the region. There are two main vectors of spread: spread due to “internal” factors within the system (dependent on the extent of the invasion i.e. movement via the natural mobility and migration of the species and/or “hitch-hiking” on human transportation within the system) and spread due to factors “external” to the system (such as the random chance the invader is introduced at any uninhabited point in the network). It is precisely this specification that differentiates an invasion process from a standard model of renewable resources. A standard model of renewable resources would not account for random introductions (when the initial conditions are absent of the invader) and neglect one of the more interesting aspects of the problem.

It is possible to derive a model of the spread of the invader if the total number of lakes N is assumed to be sufficiently large that it is possible to characterize the invasion process by a single variable, the proportion of lakes invaded p (invaded lakes N_I divided by all lakes, $p = N_I/N$). It is also necessary to assume there are enough lakes such that the change of p with time may be reasonably approximated by a continuous and differentiable function $p(t)$.

For the portion of the spread attributable to internal factors of the system, the average number of invader propagules that can be transported from any invaded lake to any given uninhabited lake per unit time (intensity of propagule transport) is assumed to be constant and given by A_1 . For an increment of time Δt , the mean number of propagules transported from each of the N_I invaded lakes to any other given lake is given $K = N_I A_1 \Delta t$. According to Jerde and Lewis (2007), the probability of a lake becoming invaded after arrival of K propagules is $P_I = 1 - \exp(-\omega K)$, where ω characterizes the species invasibility. For small Δt approximately $P_I = 1 - \exp(-\omega N_I A_1 \Delta t) \approx \omega A_1 N_I \Delta t$. The mean number of lakes that become invaded due to internal spread during Δt is $\Delta N_I = P N_R$, where $N_R = N - N_I$ is the total number of uninhabited lakes. Then

$$\Delta N_I = N_I(N - N_I)\omega A_1 \Delta t. \quad (1)$$

Dividing through by N , substituting for $\Delta p = \Delta N_I/N$, $N_I = Np$, and $\Delta N_I = N\Delta p$ allows Δp to be derived as

$$\Delta p = Ap(1 - p)\Delta t, \quad A = \omega A_1 N, \quad (2)$$

where A can be interpreted as the rate of spread attributable to internal factors (such as density dependent growth in the familiar case of logistic growth). Relying on the assumption that $p(t)$ is differentiable and Δt being sufficiently small, internal spread of the invader as represented by the internal invader flow from lake to lake can be represented by proportion of invaded lakes over time²

$$\dot{p} = Ap(t)(1 - p(t)). \quad (3)$$

In the context of metapopulation dynamics, this equation is equivalent to standard Levins model (Levins, 1969).

It is also possible for the invader to spread due to external factors such as random introductions or background propagule pressure, $b > 0$. The magnitude of this depends upon the area uninhabited, $(1 - p(t))$. Extending (3) to consider this case of external flow of the invader finds the equation of motion for the spread of the invader without human intervention as

$$\dot{p} = Ap(t)(1 - p(t)) + b(1 - p(t)), \quad A > 0, \quad b > 0, \quad p(0) = p_0. \quad (4)$$

The last term $b(1 - p(t))$ describes invasion spread due to external flow of the invader.

Human intervention in the invasion process is a program of control at invaded lakes which simply serves to reduce the proportion of lakes invaded (i.e. through local eradications).³ The effort that can be allocated for control is taken to be limited in the sense that there is a maximum control intensity

² Time derivatives are indicated by “dot” notation, i.e. $dp/dt = \dot{p}$.

³ In contrast (Potapov et al., 2007) considers interventions in human mediated transport between lakes.

per single lake, and maximum total control effort for the whole system. Let the control rate denoted by $H(t)$ and depend on both $p(t)$ and the amount of control effort $\tilde{h}(t)$ per unit time directed towards the invader. When implemented, $H(t)$ effectively reduces invader abundances and directly reduces the net change in proportion of lakes invaded, reducing $p(t)$. In this we assume away the irreversible nature of some invasions (for example see Potapov et al., 2007 where the spread can only be slowed, not stopped or reversed). The productivity of control effort is assumed to diminish towards zero as $p \rightarrow 0$ by the function $p(t)/(\alpha + p(t))$ so that the control rate is

$$\frac{\beta \tilde{h}(t) p(t)}{\alpha + p(t)} = \frac{h(t) p(t)}{\alpha + p(t)} = H(p(t), h(t)), \quad (5)$$

where β is control efficiency and $h(t) = \beta \tilde{h}(t)$ is effective control effort, measured in the units of control rate. For the sake of brevity below $h(t)$ is referred to as “control effort”. Function (5) arises naturally if one assumes a small uncertainty regarding whether the lakes are invaded or not (i.e. detection uncertainty). Then the effort is applied to the additional proportion $\alpha \ll 1$ of lakes. Hence the effort applied to invaded lakes would be $h(t)$ times the ratio $p(t)/(\alpha + p(t))$. Note that this function guarantees nonnegativity of p , since $H(0, h) = 0$.

With effort expended on an control program, (4) is thereby modified to become

$$\dot{p} = (Ap(t) + b)(1 - p(t)) - \frac{h(t) p(t)}{\alpha + p(t)} = F(p(t), h(t)), \quad (6)$$

$A > 0, b > 0, p(0) = p_0$.

3. Decision model

Let there be a resource manager charged with making choices/policies to maximize the net benefits associated with managing the lake network. The invader reduces the gross social benefits of all watersheds and causes environmental damages. To provide an analysis with as an insightful a message as possible we implement a common restriction over social benefits and environmental damages. Both are assumed to be enumerable, proportional to the total number of uninhabited and invaded lakes, and to have constant per unit valuations. The point is that the resource manager's objective is to maximize the benefits of the network net of the costs of environmental damages and costs of control by choosing the proportion of lakes to clean up. There is no locational specificity between invaded lakes and the manager is indifferent between them in the application of control.

Within these definitions, let the value of an uninhabited lake per unit time be constant and given by w_U . Similarly, let the value of an invaded lake per unit time be constant and given by w_I . The invader is assumed to cause damages such that $w_U > w_I$. In the proportional framework employed herein the average or expected value of the system at any time t is

$$(1 - p(t))w_U + p(t)w_I. \quad (7)$$

It is useful to notice that only the difference in value between invaded and uninhabited lakes

$$g = w_U - w_I, \quad (8)$$

influences changes in the expected value (7).⁴

The manager's control variable is (effective) control effort $h(t)$. While providing benefits as it reduces p , this is a costly strategy according to the convex cost function $C(h(t))$, $C'(h(t)) > 0$, $C''(h(t)) > 0$. Social welfare $W(t)$ is defined by the expected net benefits of the lake network

$$W = w_U - p(t)g - C(h(t)). \quad (9)$$

We assume that the cost function is zero with zero effort ($C(0) = 0$).

⁴ There are consequences of assuming g to be constant but these are deemed acceptable given the clear interpretation of the parameter and its potential ease of collection.

3.1. Optimal management

Optimal management is achieved by the resource manager choosing h to maximize the discounted stream of social welfare

$$J[h] = \max_h \int_0^\infty e^{-rt} W(t) dt, \tag{10}$$

where r is the discount rate. In the development of the method, it is useful to note that instead of maximizing W (9) one can minimize the associated expected invasion costs

$$J[h] = \min_h \int_0^\infty e^{-rt} (p(t)g + C(h(t))) dt, \tag{11}$$

The solution to (11) is referred to as the “optimal program” and is given by an optimal path to the terminal steady state. The optimal controls on this path minimize the total discounted cost of bringing the system to the steady state for any p_0 . Optimal controls for minimizing J can be obtained by the maximum principle (Kamien and Schwartz, 1991). The procedure follows from writing the current value Hamiltonian (omitting time notation)

$$\mathcal{H} = -pg - C(h) + \mu \left[(Ap + b)(1 - p) - \frac{hp}{\alpha + p} \right], \tag{12}$$

where μ is the costate variable (shadow price of the spreading invader). As costs are at their lowest when $p=0$, $\mu \leq 0$. μ should satisfy

$$\dot{\mu} = r\mu - \frac{\partial \mathcal{H}}{\partial p} = r\mu - \left[-g + \mu \left(A - 2Ap - b - \frac{\alpha h}{(\alpha + p)^2} \right) \right], \tag{13}$$

and the evolution of the state given by (6). For the optimal h , \mathcal{H} has to reach its maximum for each t , hence

$$\frac{\partial \mathcal{H}}{\partial h} = -C'(h) - \mu \frac{p}{\alpha + p} = 0, \tag{14}$$

it follows that $\mu = -C'(h)[(\alpha + p)/p]$.⁵

3.1.1. Optimal solutions

The solution to the problem is tricky and is helped by assuming a functional form for $C(h)$. Employing a quadratic form of $C(h) = (c/2)h^2$, $c > 0$ relates how marginal costs grow with h . Time differentiating (14) with this substitution, employing (13) and (6) finds

$$\dot{h} = -\frac{g}{c} \left(\frac{p}{\alpha + p} \right) + h \left[r - (A - 2Ap - b) + \frac{\alpha[A - Ap + (b/p) - b]}{\alpha + p} \right], \tag{15}$$

which provides the necessary changes in control effort through time along an optimal path.

Eqs. (6) and (16) form a dynamical system in $p-h$ space. To diagrammatically consider the extremal dynamics, Eq. (6) provides the $\dot{p} = 0$ isocline (the invasive species equilibrium condition) as

$$h = \frac{(\alpha + p)(Ap + b)(1 - p)}{p}, \tag{16}$$

⁵ The model is nonconvex and similar to a class of problems such as those considered by Tahvonen and Salo (1996), Rondeau (2001) and Horan and Bulte (2004). As demonstrated throughout this work, multiple equilibria are common in these problems and sufficiency conditions have to “checked” on a case by case basis. The method elegantly documented by (Rondeau, 2001) is applied in this paper.

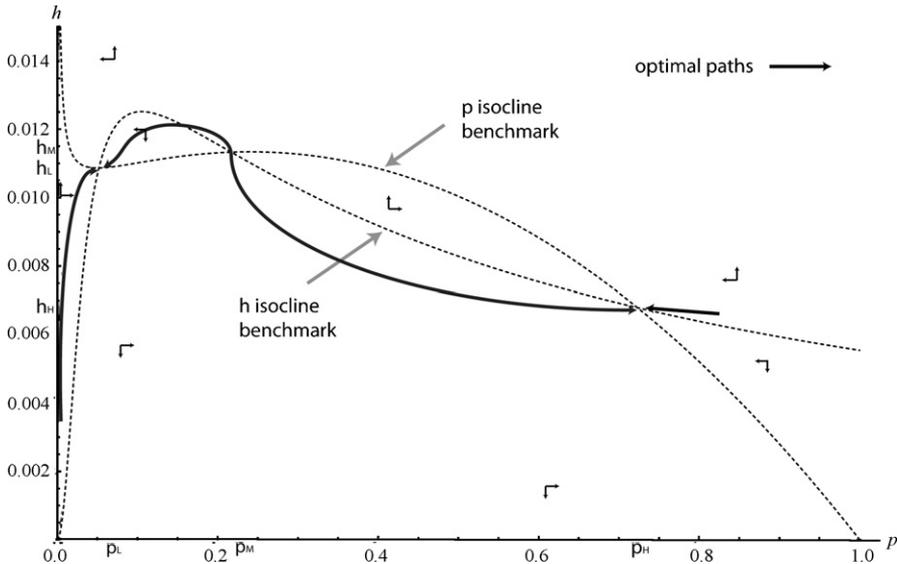


Fig. 1. Multiple steady states and optimal paths.

The control isocline $\dot{h} = 0$ is found from Eq. (15)

$$h = \left[r - (A - 2Ap - b) + \frac{\alpha[A - Ap + (b/p) - b]}{\alpha + p} \right]^{-1} \frac{g}{c} \left(\frac{p}{\alpha + p} \right), \tag{17}$$

Both (16) and (17) are highly non-linear making the possibility of numerous steady states likely and analytical solutions unlikely. To generate phase diagrams a comparative benchmark parameter set was constructed for an application of the zebra mussel spread across lakes in Wisconsin and is detailed in Appendix A sketch of the phase diagram for the comparative benchmark is given in Fig. 1 and is similar to Fig. 3 in Tahvonen and Salo (1996) in that it provides general principles for many other topologies that could occur.

The comparative benchmark consists of two saddle point steady states (one at low levels of invasion at (p_L, h_L) and one at high levels of the invasion at (p_H, h_H)) that lie on either side of an unstable focus (moderate level of invasion (p_M, h_M)).⁶ The directions of movement follow from (6) and (15) and optimal paths (dashed lines with arrows) sketches of solutions generated in a discrete version of the model.⁷

Which steady state and path are optimal depends upon the initial conditions p_0 . For an invasion detected in its early stages ($p_0 = p_0^e < p_M$) the optimal path directs the system to the low steady state (p_L, h_L) . For invasions detected in their later stages ($p_0 = p_0^l > p_M$) the system is optimally controlled to arrive at the high steady state (p_H, h_H) . In the immediate neighborhood of (p_M, h_M) there is a threshold in the optimality of either stable steady state. Rondeau (2001) and Tahvonen and Salo (1996) elegantly demonstrated methods to assess which steady state would be optimal in the vicinity of such thresholds but the tact employed here was more brute force: across a range of initial conditions in this region the model was run repeatedly to narrow down the range to arrive at the

⁶ Using the data in the comparative benchmark the Eigenvalues of the low and high steady states invasion are real and of alternating sign, while the Eigenvalues of the intermediary steady state are complex with positive real parts. The intermediary steady state corresponds to a “Skiba” point although we were unable to derive this analytically.

⁷ Mathematica version 7.0 was employed to determine all candidate steady states. Optimal paths to steady states were found in GAMS using the CONOPT solver from the same initial conditions, across all parameter variations. In addition to the results presented in the paper we re-ran the model across a wide range of initial conditions to check the instability of the “Skiba” point.

Table 1
Equilibrium states p_i , controls h_i and present value costs J across parameter variations.

Equilibrium	p_L	h_L	$J_{p_0=p_0^e}$	p_M	h_M	p_H	h_H	$J_{p_0=p_0^l}$
Parameter								
Benchmark	0.0520	0.0109	38	0.2169	0.0113	0.7232	0.0068	172
g_{LV}			12			0.9611	0.0011	36
g_{HV}			54					533
A_{LV}	0.2062	0.0087	34					157
A_{HV}	0.0159	0.0128	52	0.3539	0.0295	0.9772	0.0025	194
b_{LV}	0.0064	0.0028	3					160
b_{HV}			131			0.9509	0.0034	189
α_{LV}	0.0194	0.0104	34	0.2365	0.0113	0.7207	0.0068	172
α_{HV}			45			0.7346	0.0066	172

threshold (approximately (p_M, h_M)). Initial conditions that result in optimal paths converging to p_L (i.e. those for $p_0^e < p_M$) have lower cumulative costs J than those that converge to p_H (i.e. those for $p_0^l > p_M$).

Alternative topologies that relate to the specific characteristics of invasion processes can be seen by variations in g/c , A , b , and α . An application of the Implicit Function theorem to the steady state expressions of (6) and (15) provides intractable results for comparative statics on the steady states. Without analytical results a numeric comparison was made to the benchmark. Each of these parameters was varied above (by five times) and below (to one-fifth) its benchmark value so that for each parameter there are low values (subscript LV) and high values (subscript HV) in addition to the benchmark. Equilibrium values of the level of invasion and control effort over the three potential types of steady state $((p_L, h_L), (p_M, h_M), \text{ and } (p_H, h_H))$ for each parameter variation are given in Table 1. Also given in the table are the present value costs J (Eq. (11)) for optimal paths from initial conditions $(p_0 = p_0^e, p_0^l)$. As parameters are varied the shape of one or both isoclines can be altered, the number of steady states can be changed, the location of steady states that exist can be shifted and control patterns for optimal paths altered in turn.

The steady state influence of g/c (damages per growth rate of marginal costs) is obvious and only influence the $\dot{h} = 0$ isocline. Low relative damages make control effort for any level of p less worthwhile, pivoting down the $\dot{h} = 0$ isocline towards the horizontal axis and result in a single, highly invaded equilibrium (p_H, h_H) . High relative damages have the reverse effect and increase the value of control effort. This pivots the $\dot{h} = 0$ isocline upwards and towards the vertical axis, leaving only a single, almost eradicated equilibrium.

The effects of spread parameters are not so obvious. Fig. 2 shows that high levels of A_{HV} (high degree of internally driven/density dependent spread) serve to increase the curvature of both isoclines. The peak in the $\dot{p} = 0$ isocline is “pulled” up and two discontinuities introduced to the $\dot{h} = 0$ isocline.⁸ The result is that the low invasion steady state declines (p moves closer to the origin and eradication as h rises) and the highly invaded steady state moves closer fully invaded (p rises towards 1 as h declines). The two saddle points and the unstable focus remain but have diverged in their relative position. The intuition is that if the invader is spreading very quickly in a density dependent fashion, there is only a narrow range of very early detection levels at which it is optimal to control it at a high rate and “pin” the invasion at a very low level. If this type of invasion is detected at any other initial condition (i.e. $p_0 > p_{L,AHV}$) then invader spreads so quickly that it is optimal for the manager to almost give up and only lightly control the invasion to an almost fully invaded steady state.⁹

Low A (omitted from the figure) brings the peaks and troughs of each isocline together (reduced curvature in relation to the benchmark) which makes the two saddle points converge into a single saddle point at a rather moderate level of invasion. In this case the invader is spreading slowly enough that a relatively low level of control is able to hold the invader at a moderate level. Thus while damage costs are higher than an eradication equilibrium, control costs are so much lower that it is optimal to allow the invader to spread a bit and pin it at a moderate level.

⁸ With $\dot{h} = 0$ for A_{HV} in the interval $0.02 < p < 0.3$ the function is negative, positive for the rest of p .

⁹ We appreciate invaluable comments by Rick Horan’s on this point.

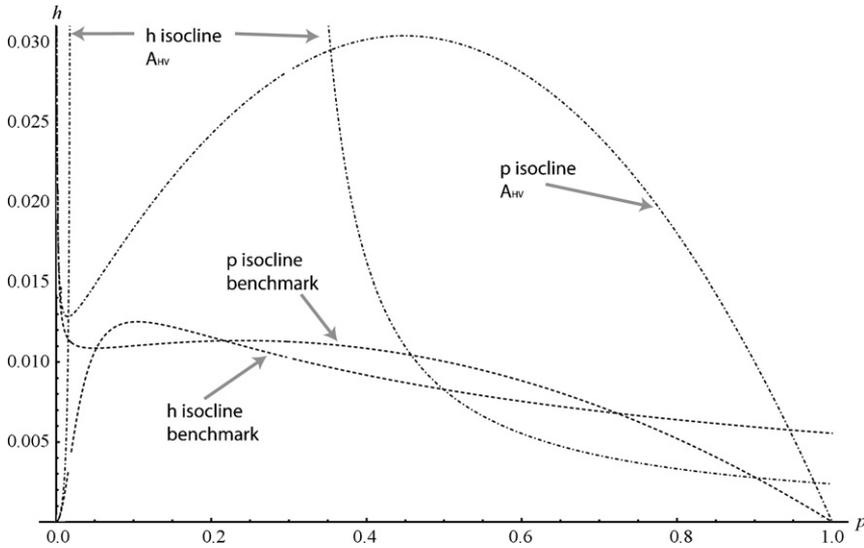


Fig. 2. Isoclines for variations A.

The greater the chance of random introduction (high b) reduces the density dependent spread effect and increases the rate of spread significantly. In the $p - h$ space, higher b causes the $\dot{p} = 0$ isocline to pivot upwards on the h -axis and to have less of the “S” bend. The $\dot{h} = 0$ isocline loses a pronounced peak and pivots downward. The shifts push the (single) steady state close to a fully invaded system as shown in Table 1. The greater the external flow into the system the less useful is a long-run control strategy. Changes for lower b are in reverse, with the clear importance of the control strategy (given relatively high influence of density dependent spread) holding the invasion at a low level.

Increased detection uncertainty reduces the curvature of each isocline, moving the low saddle point (p_L) towards the high saddle point (p_H , converging for α_{HV}). Higher levels of uncertainty in the presence/absence of the invader make control effort on average less effective across the system. This makes the highly invaded steady state p_H the only long-run outcome at high levels of α .

Optimal paths associated with the parameter variations follow those of the comparative benchmark in cases with three steady states (A_{HV} and α_{LV}). In these cases, when the invasion is detected in its early stages (p_0^e) then the system is optimally controlled to converge to the lower steady state (p_L, h_L). If the invasion is detected in its later stages (p_0^l) the optimal path converges to the highly invaded steady state (p_H, h_H).

With parameter variations that result in only a single saddle point initial conditions do not influence the terminal state. Control of the invasion process to (p_L, h_L) will be optimal for invasions with g/c_{HV} and b_{LV} . Invasions that should be controlled to (p_H, h_H) are those with g/c_{HV} , b_{HV} , and α_{HV} . When the total costs J (net present value, Eq. (11)) of these steady states and their transition paths are compared what becomes clear is that higher levels of each key characteristic lead to invasions that have higher total costs. In addition, invasions that are detected (or acted upon) in their later stages end up costing significantly more than those detected early. The most costly/worst situations are those when an invasion is detected late in its spread and has very high relative damages (g/c_{HV}) or high density dependent spread (A_{HV}). In all cases early detection and action would save a significant amount of resources.

3.2. Static management

Deriving the optimal program of management was difficult, requiring a solid grounding in differential equations, control theory, and methods of numeric simulation. In comparison we offer a

Table 2

Static equilibrium states p_i^S , controls h_i^S and present value costs J^S across parameter variations.

Equilibrium	p_L^S	h_L^S	$J_{p_0=p_0^e}^S$	p_M^S	h_M^S	p_H^S	h_H^S	$J_{p_0=p_0^e}^S$
Parameter								
Benchmark	0.0226	0.0111	42					177
g_{cLV}^e	0.0370	0.0109	38	0.3994	0.0109	0.9111	0.0025	37
g_{cHV}^e	0.0115	0.0119	55					722
A_{LV}	0.0280	0.0105	38					159
A_{HV}	0.0133	0.0129	53	0.5040	0.0345	0.9702	0.0032	194
b_{LV}	0.0055	0.0029	4					170
b_{HV}			132			0.9279	0.0015	190
α_{LV}	0.0098	0.0105	36					176
α_{HV}	0.0539	0.0124	55					181

less computationally intense program of static management that implicitly analyzes the problem by exploiting the properties of infinite horizon problems. With this class of problems, the optimal trajectory has to end at a steady state, where p and h do not depend on time. Neglecting the initial transients and focusing on just the steady states, it is possible to consider $W(t)$ as time-independent so that social welfare is simply

$$S[h] = \max_h W \int_0^\infty e^{-rt} dt = r^{-1} W. \tag{18}$$

The solution of this problem is straightforward as it is a static optimization across possible steady states to find the one with minimum costs into perpetuity. The problem then is to find p^S, h^S such that discounted welfare S is maximized.

The first step is to derive the static steady states. They are the roots of the equation resulting from (6) when \dot{p} equals zero, as given by the $\dot{p} = 0$ isocline (Eq. (16)). The equation is cubic, making an explicit solution impossible. It is only possible to state that it may have from 1 to 3 roots on $[0, 1]$. Substituting (16) for $h(p)$ into W

$$W(p, h(p)) = -pg - \frac{c}{2} \left(\frac{(\alpha + p)(Ap + b)(1 - p)}{p} \right)^2, \tag{19}$$

has a first order condition

$$\frac{dW}{dp} = -g - c \left(\frac{(A - \alpha A - b)p^2 - 2Ap^3 - \alpha b}{p^2} \right) = 0, \tag{20}$$

and second order condition

$$\frac{d^2W}{dp^2} = -c \left(\frac{-2Ap^4 + 2\alpha b p}{p^4} \right) = -c \left(-2A + \frac{2\alpha b}{p^3} \right) < 0, \tag{21}$$

that requires $-2A + 2\alpha b/p^3 > 0$ or $\alpha b/p^3 > A$. Each solution of (20) corresponds to a fixed level of p^S and so h^S as given in Table 2. The present value of total management costs are also given in the table and calculated for initial conditions ($p_0 = p_0^e, p_0^l$). These include costs of transition and those incurred at the steady states over an infinite horizon (denoted by J^S).

In each case with multiple solutions, the solution with the smallest p yielded the smallest instantaneous steady state cost W but not necessarily smallest present value cost J^S from the early and late initial conditions. Comparing Tables 1 and 2 shows the potential for similar outcomes, and those that significantly diverge. Consider the benchmark with two stable steady states (p_L, h_L) and (p_H, h_H) under optimal management and a single steady state (p_L^S, h_L^S) in the static case. The static steady state level of invasion is less than optimal ($p_L^S < p_L$) and control more than optimal ($h_L^S > h_L$). These relationships are maintained across all stable steady states if $r > 0$, and is analytically demonstrated by Finnoff et al. (2009) in a linear model.

Static management primarily targets (almost) eradicated steady states. Only with a very high chance of random introduction (b_{HV}) is the highly invaded steady state a sole maximum under static management. However the influence of key parameters for static management follows that of optimal management. The comparative static effects of variations in underlying parameters can be determined through an application of the Implicit Function Theorem on Eq. (20). Higher damages per growth in marginal costs g/c lowers p^S

$$\frac{\partial p_S}{\partial (g/c)} = -\frac{-1}{-c(-2A + (2\alpha b/p^3))} < 0, \quad (22)$$

while the influence of A on P_S is

$$\frac{\partial p_S}{\partial A} = -\frac{1 - \alpha - 2p}{-c(-2A + (2\alpha b/p^3))} \geq 0, \quad (23)$$

and depends on the magnitude of p_S . For large p_S (i.e. a highly invaded steady state) an increase in A increases p_S . For small p_S an increase in A lowers p_S . These are the same effects as shown in Table 1 for optimal management.

In the same fashion it can be shown that

$$\frac{\partial p_S}{\partial b} = -\frac{(-1 - (\alpha/p^2))}{-c(-2A + (2\alpha b/p^3))} > 0, \quad (24)$$

and

$$\frac{\partial p_S}{\partial \alpha} = -\frac{(-A - (b/p^2))}{-c(-2A + (2\alpha b/p^3))} > 0, \quad (25)$$

also following Table 1. While the steady states from static management will not coincide with those of optimal management (as long as $r \neq 0$) the implications of variations in invasion characteristics are maintained.

However there are differential dynamic consequences. Whether or not the static equilibrium is attainable or not depends upon the initial conditions. Fig. 3 illustrates the benchmark phase-plane for the optimal and static solutions. The single benchmark equilibrium (p_L^S, h_L^S) from Table 2 corresponds to the furthest left intersection of h^S and the $\dot{p} = 0$ isocline at p^S .¹⁰ This point lies to the left (lower p) and above (higher h) than the low optimal equilibrium (p_L, h_L) at the left most intersection of the two isoclines.

The static rule over applies control (at constant levels h^S for both initial conditions) in relation to the optimal steady state controls (for both initial conditions) but the consequences depend on the initial conditions. In this benchmark case with initial condition p_0^e the steady states are relatively close yet the transition paths very different. The optimal path initially employs a very low level of control (in relation to h^S) that rises to stop the invasion at p_L . With an invasion detected in its later stages (p_0^l) the realized steady state under static management is the furthest right intersection of h^S with the $\dot{p} = 0$ isocline. In this case the magnitude of the over employment of control is not as large but the realized steady state is significantly less than optimal (although the realized steady state $p_0 = p_0^l$ turns out to be at a much higher level of invasion than the target steady state p_L^e). This shifts costs away from damages due to the invader to control costs. This may be appealing yet is not an optimal mix and results in waste of resources.¹¹

Just how much static management wastes depends not only on the differences in steady states, but also on transitional costs. To compare the relative performance of the two management strategies the corresponding static problem was solved for each of the optimal problems (across parameter

¹⁰ The other intersections of h^S and the $\dot{p} = 0$ isocline do not satisfy the static first order condition 20 but in the dynamics are potential (non-optimal) steady states.

¹¹ It would of course be possible to get to p_L^e on another path by varying control from h^S , for example on a Most Rapid Approach Path (MRAP). But this would require a more sophisticated decision making process than static management, making the extra effort of optimal management worthwhile.

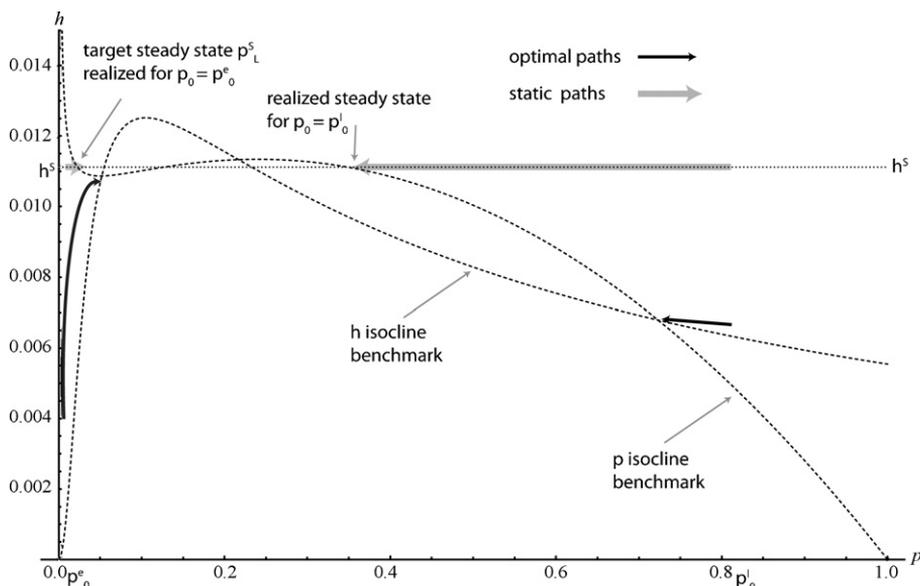


Fig. 3. Optimal and static equilibria and paths.

Table 3

Relative differences in total costs.

Initial condition	p_0^e	p_0^l
% Difference in Costs	$\left(\frac{S-J}{J}\right)$	$\left(\frac{S-J}{J}\right)$
Parameter		
Benchmark	8.9%	3.0%
α_{CLV}	201.2%	1.5%
α_{CHV}	0.9%	35.4%
A_{LV}	13.9%	1.0%
A_{HV}	2.8%	0.1%
b_{LV}	3.4%	6.2%
A_{HV}	0.5%	0.4%
α_{LV}	3.6%	2.2%
α_{HV}	21.5%	5.2%

variations and initial conditions).¹² Total costs of static management always exceed those of optimal management $S > J$, but in varying degrees depending on characteristic and initial condition. To make the comparison clear the percentage difference in cost of static management S over that of optimal management J (as a percentage of optimal costs $((S - J)/J)$) were calculated and shown in Table 3.

Table 3 demonstrates a great deal of variation in the relative performance of static management. In relation to the benchmark as shown in Fig. 3, while the steady states are relatively close for an invasion detected in its early stages (p_0^e) there is a greater difference in costs in comparison to detection in its later states (p_0^l). This is due to differences in transition costs being larger at the start of the planning horizon for p_0^e than those for p_0^l . When the invader is detected in its early stages of spread the control costs are much greater than those under optimal management (which are almost zero at p_0^e in the

¹² Mathematica version 7.0 was employed to determine all candidate solutions and determine the global optimum. Paths to steady states were then simulated in GAMS using the fixed level of h^s and Eq. (6) from the same initial conditions, across all parameter variations.

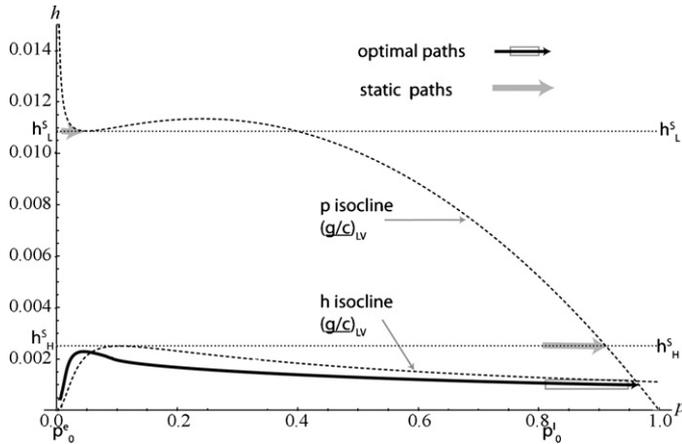


Fig. 4. Static and dynamic equilibria for g/c_{LV} .

benchmark). This large difference in control costs occurs close to the beginning of the planning horizon and is not heavily discounted. If the invasion is detected in its later stages, static control is also over applied, but not by such an extent (given the high levels of invader) and so the differences in costs of management are less.¹³

Across the parameters, optimal management tends to outperform static management when invasions are detected in their early stages (p_0^e) for similar reasons. The exceptions are for $(g/c)_{HV}$ and b_{LV} when the performance of static management is relatively worse with invasions that are detected in their late stages (p_0^l). This is due to both steady states being nearly eradicated (p_L) and the large amount of p that has to be reversed from the high initial condition. In these cases the optimal path applies control at a higher rate than the static rate until the steady state is attained and has a much shorter time of transition. While the static level of control is low (and less costly) the transition is long which allows high damages to persist and drive up static costs.

Static management performs relatively well for either initial condition when the rate of internal spread is high (A_{HV}), there is a high chance of random introduction into the system (b_{HV}) and there is a low amount of detection uncertainty (α_{LV}). In each of these cases the static and optimal steady states for both initial conditions are relatively close and transition paths similar. The relative performance of static management in other cases depends on initial conditions and the differences in steady states.

Fig. 4 illustrates the variance in differences for the case of g/c_{LV} .

There is only a single steady state for optimal management (p_H, h_H) at the intersection of the isoclines as given in Table 1. Static management has three possible solutions, the two relevant shown in the figure by dashed lines (h_L^s and h_H^s). For an invasion detected early (p_0^e) static management would target (p_L^s, h_L^s) given by the upper left intersection of the light dashed line and the $\dot{p} = 0$ isocline. The static steady state is almost eradicated while the dynamic is almost fully invaded. The constant level of static control is much greater than the optimal level of control (which first rises with the invader and then decreases gradually to a level a tenth of the static level). Under static management the system is directed to a steady state very different than optimal and coupled with large initial cost differences the relative performance is poor.

For an invasion detected in its later stages (p_0^l) static management would target (p_H^s, h_H^s) or the lower right intersection of the heavy dashed line and the $\dot{p} = 0$ isocline. Here the differences between the two steady states are not nearly as large nor are the differences in transition paths (where the

¹³ Differences at the beginning of the planning horizon influence the present value of costs by a much greater extent than those at the end of the planning horizon, placing a greater weight on differences in transition costs than steady state costs if transition times are lengthy.

optimal path follows that of the low initial condition but is drawn slightly below to differentiate it in the figure) with more similar costs.

In summary, by definition optimal management always outperforms static management, but there are situations when the differences are small. If invasions are detected early in their progression, on average optimal management can provide significant savings while static management performs reasonably well when invasions are detected and acted upon in their later stages. But there is so much variability in the relative performance of static management that prescriptions by characteristic and initial conditions are likely to be of more use than sweeping generalities.

The specification of a more realistic invasion process over (Finnoff et al., 2009) provides significant insight. Making a differentiation between internally motivated (density dependent) and externally motivated (random introductions) spread has important implications, namely that across a wide range of density dependent spread rates invasions detected early in their progression should all be optimally managed. But across this same range if the invasion is detected in its latter stages static management will provide a close approximation. However, when external inputs to spread are an important driver of the invasion process, optimal management provides less of an improvement over static management. Taken together, these components of the spreading process can work to alleviate the other, making generalizations tricky. What can be said is that if internal factors are more relatively important than external, and the invasion is detected early, optimal management will be clearly superior. The opposite holds if external factors are dominant, and static management provides a close approximation.

Another important differentiation is the inclusion of some uncertainty in the specific location of the invader. When this uncertainty is low, static management and its implications provide a reasonably close approximation of optimal management. However, when this uncertainty is high, optimal management will provide significant savings over static management.

4. Conclusion

Invasive species pose an interesting problem from an economic point of view as there are certain characteristics of the problem that differentiate it from a standard question in the management of renewable resources. Here we consider the effect of characteristics specific to a simple invasion process and the implications of these characteristics on management of the system from both dynamic and static perspectives. Results indicate that stringent control of the invasion process close to eradication is optimal for relatively high damages, low rates of density dependent spread and low chance of random introduction. Invasions that should be controlled to a highly invaded steady state are those with low relative damages, high chance of random introduction and high levels of uncertainty in species location.

If the invasion has control policies initiated early in the invasion process then those with moderate to high rates of density dependent spread and low to moderate levels of uncertainty in species location should be controlled close to eradication. If control policies are initiated later in the invasion process, the system should be controlled to a highly invaded steady state for invasions with moderate relative damages, moderate to high rates of density dependent spread, moderate chance random introduction, and low to moderate levels of uncertainty in location of the invader.

In comparing optimization procedures, as expected dynamically optimal management always outperforms static management but the differences are small when there is a high degree of density dependent spread and/or there is a high chance of the invader being randomly introduced throughout the system. The differences are also small in most cases when invasions are acted upon in their later stages (i.e. high initial conditions) when damages are relatively low, when the influence on the invasion process of density dependent spread is low and when there is a low degree of uncertainty in the location of the invader. In these situations some useful insights can be derived without having to fully characterize the optimization of the initial transients of the dynamical system. This is of practical use as it allows a clear and concise view of the long-run equilibrium and the influence of critical parameters on this state, uncluttered by the complexity of a optimal characterization of the initial transients.

The flip-side is that optimal policies directed at an invasion in its early stages tend to provide significantly savings. These savings are greatest when relative damages are low, the influence of density dependent spread is low, and there is a high degree of uncertainty of the invaders whereabouts. In these situations little useful insight will be generated without consideration of a fully optimized system.

While our results are intuitively plausible, our mathematical formulation and analysis has allowed us to generate specific policy prescriptions that can be applied to invasion problems such as zebra mussel. Our model is necessarily simplistic, as our goal has been to outline the basis principles of optimal application of control effort. More realistic models would include the cost of monitoring lakes for invasion status, and alternate strategies such as treating boats before they enter uninhabited lakes after they leave infected lakes (Potapov et al., 2007).

Acknowledgments

The authors would like to thank Rick Horan and two anonymous reviewers for many helpful suggestions and ISIS group members for useful discussions. This research has been supported by a grant from the National Science Foundation (DEB 02-13698). ML also acknowledges support from a Canada Research Chair, and NSERC Discovery and Collaborative Research Opportunity grants.

Appendix A

A.1. Application data

To generate phase diagrams for several interesting cases a comparative benchmark parameter set was constructed for an application of the zebra mussel spread across lakes in Wisconsin. The primary vector of long distance zebra mussel dispersal is from the transportation of recreation and fishing boats (Johnson et al., 2001). Let the mean boat traffic between two lakes be denoted by T , and the mean number of mussels transported by one boat by η . Then the intensity of the mussel transport $A_1 = \eta T$. According to (2), $A = \omega A_1 N = \omega \eta TN$, where ω characterizes the invasibility of the invader and N is the number of lakes in the system that are attracting for boaters. We can estimate T by dividing the total boat traffic within the lake system T_{tot} by the number of lake pairs $N(N-1) \approx N^2$, so $T \approx T_{tot}/N^2$. The values of ω and η are unknown. However we can estimate their product using the “colonization threshold” T_0 introduced in Bossenbroek et al. (2001). For the intensity of boat traffic less or equal to $T_0=850$ boats/year the probability of lake invasion P_I is between 0 and 20% for the period since the beginning of the mussel spread. We take the medium value $P_I=0.1$. This result was related to a time interval between 5 and 10 years: the study was done in 1999, the spread of zebra mussels started around 1988, and some time could be expected to be required for the propagule pressure on the lakes to form. Taking the time interval $t_I=5$ years, we obtain that

$$P_I = 1 - \exp(-\omega \eta T_0 t_I), \quad \omega \eta T_0 t_I = -\ln(1 - P_I) \approx P_I,$$

therefore

$$\omega \eta \approx \frac{P_I}{T_0 t_I}.$$

Combining estimates for T and $\omega \eta$ we come to.

$$A \approx \frac{P_I T_{tot}}{N T_0 t_I}.$$

According to Buchan and Padilla (1999) there are 58,000 registered boaters in Wisconsin. However about 90% of these boaters do not pull their trailers over long distances, and some of them do not transfer the boat from lake to lake. On the other hand each boater may make several trips per year, and the lake network can cover several states. It seems reasonable to estimate $T_{tot} \sim 10^5$ boats/year. The

number of lakes in the lake system that are of essential interest for boaters we take as $N \sim 10^2$. Then for the case of lakes in Wisconsin

$$A \approx \frac{0.1 \times 10^5}{10^2 \times 850 \times 5} \text{ year}^{-1} \approx 0.02 \text{ year}^{-1}.$$

An estimate for the background propagule pressure b in this setting can be found from the trailer boat trips between two remote regions (assuming the regions are remote enough that the trips are not part of internal spread). According to Fig. 3 in Maclsaac et al. (2004), only about 10% of boaters travel distances more than 500 km, which we can relate to the interaction between lake systems. Taking into account a higher mortality rate for propagules on longer trips, in many cases it is reasonable to assume that b is between $0.01A$ and $0.1A$. However, in certain cases, b can be greater. For example, the Michigan, Wisconsin, Illinois, Indiana and Ohio lake system considered in Bossenbroek et al. (2001) have the invaded Great Lakes as its part or its neighbor. This may create a much higher propagule pressure, comparable to A . For Wisconsin lakes b may therefore be big because of the proximity of the Great Lakes, such that we take $b = 0.5A \approx 0.01 \text{ year}^{-1}$.

For the necessary valuation data, in a study of the 2,072-acre Delavan Lake in Walworth County, Wisconsin (Eiswerth et al., 2005) find that the removal of a restoration program for the lake would result in a decline in water quality resulting in a reduction of regional expenditures close to \$6 million per year. In the absence of superior data we extrapolate from this estimate and let $g \approx$ \$6 million. Without any control cost information, the value of c was calibrated to provide a comparative benchmark with three steady states. A discount rate of $r=3\%$ was employed in the simulations.

References

- Archer, D.W., Shogren, J.F., 1996. Endogenous risk in weed control management. *Agricultural Economics* 14, 103–122.
- Bossenbroek, J.M., Kraft, C.E., Nekola, J.C., 2001. Prediction of longdistance dispersal using gravity models: zebra mussel invasion of inland lakes. *Ecological Applications* 11 (6), 1778–1788.
- Bossenbroek, J.M., Johnson, L.E., Peters, B., Lodge, D.M., 2007. Forecasting the expansion of zebra mussels in the United States. *Conservation Biology* 21 (3), 800–810.
- Brown, C., Lynch, L., Zilberman, D., 2002. The economics of controlling insect-transmitted plant diseases. *American Journal of Agricultural Economics* 84, 279–291.
- Buchan, L.A.J., Padilla, D.K., 1999. Estimating the probability of long-distance overland dispersal of invading aquatic species. *Ecological Applications* 9, 254–265.
- Burnett, K., Kaiser, B., Pitafi, B.A., Roumasset, J., 2006. Containment of invasive species: illustrations from Hawaii. *Agricultural and Resource Economics Review* 35, 63–77.
- Carpenter, S.R., Brock, W., Hanson, P., 1999. Ecological and social dynamics in simple models of ecosystem management. *Conservation Ecology* 3 (2), 4 (online).
- Davidson, R., Harris, R., 1981. Non-convexities in continuous-time investment theory. *Review of Economic Studies* 48, 235–253.
- Eiswerth, M.E., Johnson, W.S., 2002. Managing nonindigenous invasive species: insights from dynamic analysis. *Environment and Resource Economics* 23, 319–342.
- Eiswerth, M.E., van Kooten, G.C., 2002. Uncertainty, economics, and the spread of an invasive plant species. *American Journal of Agricultural Economics* 84 (5), 1317–1322.
- Eiswerth, M., Kashian, R., Skidmore, M., 2005. What is the value of a clean and healthy lake to a local community? Prepared by the Fiscal and Economic Research Center at the University of Wisconsin-Whitewater, <http://www.wisconsinlakes.org/AboutLakes/PDFs/DelavanLakeStudy.pdf>.
- Finnoff, D., Shogren, J.F., Leung, B., Lodge, D., 2005. The importance of bioeconomic feedback in invasive species management. *Ecological Economics* 52, 367–381.
- Finnoff, D., Lewis, M.A., Potapov, A.B., 2009. Second best policies in invasive species management: when are they “good enough”? In: Perrings, C., Mooney, H., Williamson, M. (Eds.), *Bioinvasions and Globalization: Ecology, Economics, Management, and Policy*. Oxford University Press.
- Gutierrez, A.P., Regev, U., 2005. The bioeconomics of tritrophic systems: applications to invasive species. *Ecological Economics* 52., 383–396.
- Haurie, A., 1976. Optimal control on an infinite time horizon. The turnpike approach. *Journal of Mathematical Economics* 3, 81–102.
- Horan, R.D., Perrings, C., Lupi, F., Bulte, E.B., 2002. Biological pollution prevention strategies under ignorance: the case of invasive species. *American Journal of Agricultural Economics* 84 (5), 1303–1310.
- Horan, R.D., Bulte, E., 2004. Optimal and open access harvesting of multi-use species in a second-best world. *Environmental & Resource Economics* 28 (3), 251–272.
- Jerde, C.J., Lewis, M.A., 2007. Waiting for invasions: a framework for the arrival of non-indigenous species. *American Naturalist* 170 (1), 1–9.
- Johnson, L.E., Ricciardi, A., Carlton, J.T., 2001. Overland dispersal of aquatic invasive species: a risk assessment of transient recreational boating. *Ecological Applications* 11 (6), 1789–1799.

- Kamien, M.I., Schwartz, N.L., 1991. *Dynamic optimization: the calculus of variations and optimal control in economics and management*. North-Holland, Amsterdam.
- Leung, B., Lodge, D.M., Finnoff, D., Shogren, J.F., Lewis, M.A., Lamberti, G., 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proceedings: Biological Sciences (formerly Proceedings Royal Society London B)* 269, 2407–2413.
- Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15, 237–240.
- Lichtenberg, E., Zilberman, D., 1986. The econometrics of damage control: why specification matters. *American Journal of Agricultural Economics* 68, 261–273.
- MacIsaac, H.J., Borbely, J.V.M., Muirhead, J.R., Graniero, P.A., 2004. Backcasting and forecasting biological invasions of inland lakes. *Ecological Applications* 14, 773–783.
- Olson, L.J., Roy, S., 2002. The economics of controlling a stochastic biological invasion. *American Journal of Agricultural Economics* 84 (5), 1311–1316.
- Olson, L.J., Roy, S., 2006. *The Economics of Controlling a Biological Invasion*. Working Paper, University of Maryland <http://www.wam.umd.edu/126houdini/cwp.html>.
- Pimentel, D., Lach, L., Zuniga, R., Morrison, D., 1999. Environmental and economic costs of nonindigenous species in the United States. *Bioscience* 50, 53–65.
- Pontryagin, L.S., Boltyanskii, V.G., Gamkrelize, R.V., Mishchenko, E.F., 1962. *The Mathematical Theory of Optimal Processes*. Wiley.
- Potapov, A.B., Finnoff, D.C., Lewis, M.A., 2007. Optimal control of biological invasions in lake networks. *Natural Resource Modeling* 20 (3), 351–379.
- Rondeau, D., 2001. Along the way back from the brink. *Journal of Environmental Economics and Management* 42 (2), 156–182.
- Settle, C., Crocker, T.D., Shogren, J.F., 2002. On the joint determination of biological and economic systems. *Ecological Economics* 42 (1–2), 301–311.
- Shogren, J.F., 2000. Risk reductions strategies against the “explosive invader”. In: Perrings, C., Williamson, M., Dalmazzone, S. (Eds.), *The Economics of Biological Invasions*. Edward Elgar, Northampton, MA.
- Sharov, A.A., Liebhold, A.M., 1998. Bioeconomics of managing the spread of exotic pest species with barrier zones. *Ecological Applications* 8, 833–845.
- Tahvonen, O., Salo, S., 1996. Nonconvexities in optimal pollution accumulation. *Journal of Environmental Economics and Management* 31 (2), 160–177.
- Zavaleta, E., 2000. The economic value of controlling an invasive shrub. *Ambio* 29 (8), 462–467.