Allee effect and control of lake system invasion

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Abstract. We consider the model of invasion prevention in a system of lakes that are connected via traffic of recreational boats. It is shown that, in presence of an Allee effect, the general optimal control problem can be reduced to a significantly simpler stationary optimization problem of optimal invasion stopping. We consider possible values of model parameters for zebra mussels. The general N-lake control problem has to be solved numerically, and we show a number of typical features of solutions: distribution of control efforts in space and optimal stopping configurations related with the clusters in lake connection structure.

1 Introduction

The problem of controlling invasive species is very important for many regions in the world [30]. Ecological and economic impact of these species has been analyzed in a number of publications, see [24, 14] and references therein. Slowing down or stopping the invaders dispersal may reduce the corresponding impact. In this paper we consider a related model problem of controlling aquatic invaders.

For a number of invaders in the North America lakes, the major way of spreading is transportation with boating and fishing equipment [11]. This immediately suggests a way to slow down or stop the spreading by washing the equipment [22]. We assume that percentage of invader organisms killed during treatment depends on the amount of money given for treatment of a single boat. To compare treatment expenses with the losses due to invasion we can perform cost-benefit analysis. This brings us into the framework of bioeconomics and economic problems of cost-benefits analysis and optimal control [5, 21].

To set up a bioeconomics problem we need three basic components. First, we need a model for the invader population within each lake. To keep model tractable, we assume that each lake has a certain carrying capacity and, once the invader has been introduced in sufficient quantity, it grows and eventually reaches maximum. Then the lake becomes invaded and is a source of the invader for secondary invasions.

Second, we need information about boat transfer between the lakes, which causes the invader flow between the lakes. This can be described by the connectivity matrix, showing the intensity of the boat exchange between the lakes. Often the connection matrix can be approximated by so-called gravity models [27], which have been successfully applied to the problem of lake invasions by a number of authors [3, 1, 17].

Third, we need a model of boat treatment at the checkpoints. In this paper we use one proposed in [26]; with exponential dependence of the treatment efficiency on the finances allocated.

Note that complexity of the optimal control problem grows dramatically with the number of lakes. Even with 3-5 lakes, its complete analysis becomes practically impossible. However, for ecosystem valuation and determining the invasion costs infinite-horizon problems are often used [2, 21]. An optimal solution for such problems should converge to a steady state [12]. If convergence to the steady state is fast compared to the typical "discounting time" ρ_D^{-1} (inverse of discounting rate), then the steady state can contribute mostly to the overall cost/benefit analysis. This allows us to replace the analysis of a general control problem by analysis of the steady states. It is reasonable to assume that, under no control, all the lakes eventually are invaded, and there may be only two steady states, uninvaded and fully invaded. The control may allow to stop the invader somewhere in the middle. Then the problem of optimal controls becomes one of optimal invasion stopping.

Here we must note that the control cannot be perfect. Even if it were possible to make the number of invaders spread by boats equal to zero, there may be other mechanisms of spread. For example, zebra mussels can spread along with waterfowls with a very small probability [10]. Therefore the problem of invasion stopping may be solvable only if there is a critical population size, or equivalently, a critical invader flow, below which the invader population cannot establish. This means that there must be Allee effect for the invader [6, 28, 29], and we shall consider the class of models satisfying this condition.

The importance of Allee effect for spatio-temporal dynamics of biological invasions has been shown in [16, 13, 8]. It appears that in presence of the effect the invasion front can move slower, stop, or even reverse its direction. In the latter case the invader eventually goes extinct. Population dynamics at the invasion front becomes a competition between local extinction and incoming migration from the neighboring locations. For the invader to be able to spread, this migration flow must exceed a certain minimum value. In the present paper we consider qualitatively similar situation with two major differences: a) the invader migration flow is due to a human mediated transportation and 2) there is a possibility to control this flow and make it smaller than the minimum value required for the invader to spread.

The structure of the paper is the following. In Sections 2 to 5 we describe the model, and formulate two major problems: determining optimal allocation of resources for the given set of invaded lakes, and determining optimal set of invaded lakes where the invasion is to be stopped. These two problems are considered in Sections 6 and 7. The appendix contains technical details, including derivation of several formulas used in the main text, description of numerical techniques of solving the related optimization problems, and estimates of the model parameters for zebra mussels from available data in the literature.

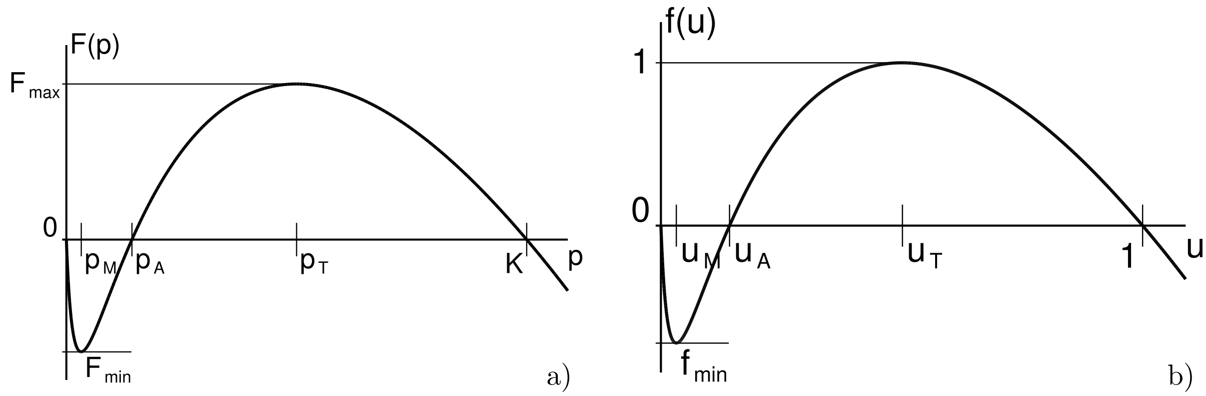

Figure 1: a) Typical form of $F(p)$ for Allee dynamics; b) Rescaled function and argument, $f(u) = F(Ku)/F_{\max}$, $u = p/K$.

2 The model

2.1 Individual lake dynamics and the Allee effect

For the invader population size p in a lake we use the classical differential equation population model [28]

$$\frac{dp}{dt} = F(p) + W_{\text{in}} - W_{\text{out}}, \tag{1}$$

where W_{in} and W_{out} are the incoming and the outcoming flows respectively, and F has the form shown in Fig. 1a. $F(p)$ is negative below the Allee threshold p_A and positive above it until the population reaches its carrying capacity K. The exact functional form is not important for our analysis. However, we shall assume that the following is satisfied:

- $F(p)$ is differentiable for $p \geq 0$;
- $F(p)$ has three zeroes $F(0) = F(p_A) = F(K) = 0$, $0 < p_A < K$, a minimum $F_{\min} = F(p_M)$, $0 < p_M < p_A$, and a maximum $F_{\max} = F(p_T)$, $p_A < p_T < K$,
- $F(p)$ is monotonic on all three intervals $0 \leq p < p_M$, $p_M < p < p_T$, $p > p_T$.

We denote $F_{\min} = F(p_M) < 0$ and $F_{\max} = F(p_T) > 0$. A typical example of such a function is cubic polynomial

$$F(p) = Rp(p - p_A)\left(1 - \frac{p}{K}\right) \tag{2}$$

with p_T and p_M given by the critical points

$$p_T = \frac{K + p_A + \sqrt{(K + p_A)^2 - 3Kp_A}}{3}, \qquad p_M = \frac{K + p_A - \sqrt{(K + p_A)^2 - 3Kp_A}}{3} = \frac{Kp_A}{3p_T}.$$

If $p_A \ll K$, which is typically the case then

$$p_T \approx \frac{2K}{3}, \qquad p_M \approx \frac{1}{2}p_A, \qquad F_{\max} \approx \frac{4}{27}RK^2.$$

For a system of N lakes each lake may have different carrying capacity K_i.

2.2 Invader flow between lakes and gravity models

We consider a system of N lakes with trailer boat traffic between them. We assume each boat that has been immersed into an invaded lake, and then has been transported to another lake, on average can carry a certain number of invader organisms η. The actual number of invaders picked up at the first lake is assumed to be proportional to relative invader density, that is to the proportion of the carrying capacity

$$u_i = \frac{p_i}{K_i}.$$

For each pair of lakes we assume known the mean number of boats per unit time transported from lake j to lake i, T_{ij}. Then the flow of propagules from lake j to lake i is $\eta T_{ij} u_j$. It is convenient to set $T_{ii} = 0$, then the incoming flow for the lake i is

$$W_{\text{in},i} = \eta \sum_{j=1}^{N} T_{ij} u_j, \tag{3}$$

and the outcoming flow is

$$W_{\text{out},i} = \eta \sum_{j=1}^{N} T_{ji} u_i. \tag{4}$$

In practice the coefficients T_{ij} are difficult to measure, because for N lakes there are $N(N-1)/2$ connections. However, it appears that in many economical and geographical problems the set of connections between the nodes of a transportation network can be reasonably approximated by the so-called gravity models [27], where it is assumed that

$$T_{ij} = m_i M_j \phi(d_{ij}), \qquad i \neq j, \qquad T_{ii} = 0,$$

where m_i characterize "attractiveness" of a network node, M_i its repulsiveness, and d_{ij} is the distance between nodes i and j. Then it is necessary to determine only $2N$ parameters m_i, M_i, and usually a few parameters related with $\phi(d)$. In most practical cases $\phi(d)$ is chosen to be either exponential

$$T_{ij} = m_i M_j \exp(-\beta d_{ij}), \tag{5}$$

or power law,

$$T_{ij} = m_i M_j (d_{ij}/d_0)^{-\gamma}. \tag{6}$$

The specific choice of $\phi(d)$ depends on the data — how fast the flow decays with the distance. Examples of extracting the gravity model coefficients from invasions data can be found in [3, 1, 17].

For the sake of simplicity, in numerical experiments below we assume that $m_i = M_i$, and hence the transportation matrix is symmetric, $T_{ij} = T_{ji}$.

2.3 Control of invader flows

To reduce the amount of the invader it is possible to wash boats at infected lakes after use, at uninfected lakes before use, or both. The result of washing can be described by a factor between 0 and 1 that shows how the number of propagules diminish after washing. Let the cost of washing one boat at the lake i before boat use be s_i, and after boat use be x_i. If cost equals zero, then there is no corresponding boat processing. It is clear, that it is not reasonable e.g. to wash boats before usage at already invaded lake, at least in case of a single invader. Nonetheless, to simplify notation it is convenient to consider both types of treatment at each lake. Below we shall see, that the optimal values of these redundant costs is zero, since they do not influence the invader flows.

The cost of washing may depend on its duration, or on the amount of the disinfectant used and so forth. We assume that the proportional reduction of carried invader organisms is related to the expenses as $\exp(-\kappa x_i)$ or $\exp(-\kappa s_i)$ respectively [26]. The exponential dependence has been chosen because the result of two successive independent washings with costs x_{ia} and x_{ib} is equivalents to a single treatment with the cost $x_{ia} + x_{ib}$. The amount of the propagules transported by one boat from lake j to lake i after the washing diminishes from η to $\eta \exp(-\kappa x_j - \kappa s_i)$, and the incoming flow for the lake i becomes $W_{\text{in},i} = \eta \sum_j e^{-\kappa s_i} T_{ij} e^{-\kappa x_j} u_j$.

We assume that at the washing checkpoints it may be hard to distinguish boats travelling from invaded to uninvaded lakes from all other boats, and therefore it is necessary to process all boats departing from or arriving to a certain lake. However, the overall traffic from invaded to uninvaded lakes we assume known. This allows us to estimate the necessary intensity of boats treatment.

Let us denote the number of boats arriving per unit time at lake i by A_i, and the number of boats leaving lake i per unit time by D_i,

$$A_i = \sum_{j=1}^{N} T_{ij}, \qquad D_i = \sum_{j=1}^{N} T_{ji}.$$

Therefore the total control cost per unit time at lake i is $D_i x_i + A_i s_i$.

2.4 The optimal control problem

Bioeconomic analysis uses either maximization of total present benefits or minimization of present costs. In our case we assume that uninvaded lakes are the sources of benefits, and the invader reduces the amount of these benefits, or produces negative benefits, or losses. We denote the losses per unit time at fully invaded lake i by g_i. For partially invaded lake ($p_i < K_i$) we assume that the losses are $g_i p_i / K_i$. The control costs are introduced in the previous section, hence total cost per time for the whole lake system is

$$E(t) = \sum_{i=1}^{N} \left(\frac{p_i(t)}{K_i} g_i + A_i s_i(t) + D_i x_i(t) \right). \tag{7}$$

Finally we come to an optimal control problem: find functions $x_i(t)$, $s_i(t)$, which minimize the total discounted cost

$$J = \int_0^\infty e^{-\rho_D t} E(t)\, dt, \tag{8}$$

where ρ_D is the discount rate, and $p_i(t) = K_i u_i(t)$ satisfy

$$\frac{dp_i}{dt} = F(p_i) + \eta \left(e^{-\kappa x_i} \sum_{j=1}^{N} T_{ij} e^{-\kappa x_j} \frac{p_j}{K_j} - D_i \frac{p_i}{K_i} \right)$$

3 Nondimensionalized model

It is more convenient to study a nondimensional model. Typically it contains only a few dimensionless parameters, that are combinations of the original dimensional ones. Some of the dimensionless parameters may appear to be very small or very large, which also simplifies the studies.

Let us introduce two parameters, the maximum possible invader flow within the whole lake system $W_{\max}$ and the total boat traffic within the lake system T_{tot},

$$T_{\text{tot}} = \sum_{i,j=1}^{N} T_{ij}, \qquad W_{\max} = \eta T_{\text{tot}}, \tag{9}$$

We expect that the flow will be small compared to the maximum possible growth rate $F_{\max}$. Based on scalings we introduce a small parameter

$$\epsilon = \frac{W_{\max}}{F_{\max}}.$$

Another small parameter arises from considering time scales. The ecological part of our bioeconomic model, which we now consider, has its characteristic time scale related to carrying capacity and the maximum growth rate: $t_K = K/F_{\max}$. However, our problem has two other time scales. One is $t_Y = 1\,\text{year}$, which is typical time scale for lifetime of many invaders and also a natural time unit in economical and financial applications. The other is $t_D = \rho_D^{-1}$, the inverse of the discount rate, which shows, how far into the future our planning of control and optimization extends. As we shall see below, a typical case is $t_K \ll t_Y \ll t_D$, and hence there is a small dimensionless parameter given by

$$\delta = \frac{t_K}{t_Y} = \frac{K}{t_Y F_{\max}}.$$

We need to use the same time scale both in ecological and bioeconomic part of our model, and we choose it to be t_Y.

Population dynamics. We nondimensionalize (1) taking for the new variable the population in proportion to carrying capacity $u = p/K$, rescaling F and introducing $f(u) = F(Ku)/F_{\max}$, and introducing dimensionless time $t' = t/t_Y$ relative to the scale t_Y. This yields

$$\delta \frac{du}{dt'} = f(u) + \epsilon \left(w_{\text{in}} - w_{\text{out}}\right), \tag{10}$$

where $w_{\text{in}} = W_{\text{in}}/W_{\max}$, and $w_{\text{out}} = W_{\text{out}}/W_{\max}$. The new nonlinear function $f(u)$ has maximum $f_{\max} = 1$ at $u = u_T = p_T/K$, a minimum $f_{\min}$ at $u = u_M = p_M/K$, and zeroes at $u = 0$, u_A, and 1, where $u_A = p_A/K$, Fig. 1b. As described above, we assume $u_A \ll 1$, which allows us to simplify some expressions. For example, in case of cubic function $F(p)$ (2) we obtain

$$f(u) = \frac{27}{4} u \left(u - u_A\right)(1 - u), \qquad u_M \approx \frac{1}{2} u_A, \qquad u_T \approx \frac{2}{3}, \qquad f_{\min} \approx -\frac{27}{16} u_A^2.$$

Since K may be different for each lake, small parameters ϵ and δ also may vary with the lake. However, in the subsequent analysis it is important that they are small, while specific value is not important. To simplify considerations, we shall assume these parameters equal for each lake. However, all formulas can easily be generalized for the case of lake-dependent parameters.

Invader flow. Defining the dimensionless flow rates

$$\tau_{ij} = \frac{T_{ij}\eta}{W_{\max}} = \frac{T_{ij}}{T_{\text{tot}}},$$

we observe from (9) that $\sum_{ij} \tau_{ij} = 1$ and hence $0 \leq \tau_{ij} < 1$. Thus τ_{ij} is interpreted as the proportion of the total possible flow between lakes that goes from lake i to lake j. Now the expressions for normalized flows are

$$w_{\rm in} = \sum_{j=1}^{N} \tau_{ij} u_j, \qquad w_{\rm out} = \sum_{j=1}^{N} \tau_{ji} u_i. \tag{11}$$

Control and costs. The natural scale for the control expenses per boat x, s is the control efficiency κ, therefore it is convenient to introduce dimensionless costs

$$x' = \kappa x, \quad s' = \kappa s.$$

The flows of arriving and departing boats we normalize by the total boat traffic $T_{\rm tot}$, then

$$a_i = \sum_{j=1}^{N} \tau_{ij}, \qquad d_i = \sum_{j=1}^{N} \tau_{ji}, \qquad A_i = T_{\rm tot} a_i, \qquad D_i = T_{\rm tot} d_i.$$

Then

$$E = \sum_{i=1}^{N} \left(u_i g_i + \frac{T_{\rm tot}}{\kappa} a_i s_i' + \frac{T_{\rm tot}}{\kappa} d_i x_i \right) = E_0 \sum_{i=1}^{N} \left(u_i g_i' + a_i s_i' + d_i x_i' \right), \tag{12}$$

where $E_0 = \kappa^{-1} T_{\rm tot}$ is the loss rate scale factor and $g_i' = \kappa g_i T_{\rm tot}^{-1}$ are the dimensionless losses at lake i. Finally, in the integral (8) we need to make a change to dimensionless time $t' = t/t_Y$, which introduces financial scale for total costs J_0 and dimensionless discounting factor ρ,

$$J_0 = T_{\rm tot} t_Y \kappa^{-1}, \qquad \rho = \rho_D t_Y.$$

If we introduce $E' = E/E_0$ and $J' = J/J_0$, this does not change the conditions for the minimum of total discounted costs.

The dimensionless problem. Eventually we come to the following dimensionless optimal control problem: find $x_i'(t')$ and $s_i'(t')$ that minimize

$$J' = \int_0^\infty e^{-\rho t'} E'(t')\, dt', \qquad E'(t') = \sum_{i=1}^{N} \left(u_i g_i' + a_i s_i' + d_i x_i' \right), \tag{13}$$

where $u_i(t)$ satisfy

$$\delta \frac{du_i}{dt'} = f(u_i) + \epsilon \left(\sum_j e^{-s_i'} \tau_{ij} e^{-x_j'} u_j - u_i d_i \right) \equiv \Phi_i(\mathbf{u}, \mathbf{x}', \mathbf{s}'). \tag{14}$$

Below we omit primes for brevity.

4 Critical flow

We start analysis of the model (10) by observing that, provided $\epsilon(w_{\rm in} - w_{\rm out})$ is sufficiently small and the initial lake population is also small, then the invader population in the lake will remain small (see also [13]).

Proposition 1. 1) If the net invader flow ϵw, $w = w_{\rm in} - w_{\rm out}$, is smaller than the maximum rate of population decline $|f_{\min}|$, and the population level is initially small, $u(0) < u_M$, then the invader population $u(t)$ remains below u_M for all $t > 0$. 2) If the net invader flow is large enough, $\epsilon w > |f_{\min}|$, the lake will eventually be invaded regardless of the size of initial invader population.

Proof. 1) The proof relies on the fact that $u(t)$ is a solution of an ordinary differential equation with bounded right hand side, and hence has to be a continuous function. Let us assume that for some t_2 $u(t_2) > u_M$. Since $u(0) < u_M$, due to continuity there has to be a moment when $u(t)$ takes the value u_M and is increasing. That is there must be such t_1 that $u(t_1) = u_M$ and $du/dt\,(t_1) \geq 0$. On the other hand

$$\delta \frac{du}{dt}(t_1) = f(u_M) + \epsilon w = -|f_{\min}| + \epsilon w < 0.$$

Hence such t_1 cannot exist, and this contradiction proves that $u(t) < u_M$ for all $t > 0$.

2) Now let us consider the second part of the proposition. According to the condition $\epsilon w > |f_{\min}|$, there exists positive constant $c = \min_{0 \leq u \leq 1}(f(u) + \epsilon w) > 0$. Then

$$\delta \frac{du}{dt} = f(u) + \epsilon w \geq c > 0, \quad u(0) \geq 0.$$

Using the properties of definite integral, and assuming that we consider t such that $u(t) \leq 1$,

$$\delta(u(t) - u(0)) = \delta \int_0^t \frac{du}{d\alpha} d\alpha \geq \int_0^t c\,d\alpha = ct, \qquad 1 \geq u(t) \geq u(0) + \frac{ct}{\delta}. \tag{15}$$

Therefore, at some moment $t_3 \leq \delta/c$ there must be $u(t_3) = 1$, and hence the lake will be fully invaded. Note that when $u > 1$ $f(u)$ may take values less than $f_{\min}$, and we cannot extend our analysis for u greater than 1. $\diamondsuit$

Proposition 1 shows that the value $|f_{\min}|$ plays critical role in the invasion process under Allee effect. For this reason let us introduce normalized critical flow or critical invader traffic

$$\tau_0 = \frac{|f_{\min}|}{\epsilon}. \tag{16}$$

Then $w = w_{\text{in}} - w_{\text{out}} > \tau_0$ guarantees invasion.

If we substitute explicit expressions for the invader flow into the condition $\epsilon(w_{\text{in},i} - w_{\text{out},i}) < |f_{\min}| = \epsilon\tau_0$, which guarantees the absence of invasion for the lake i, we obtain

$$\sum_j e^{-s_i}\tau_{ij}e^{-x_j}u_j - u_i \sum_j \tau_{ji} < \tau_0, \qquad u_i < u_A. \tag{17}$$

Note that in case $\sum_j e^{-s_i}\tau_{ij}e^{-x_j}u_j - u_A \sum_j \tau_{ji} > \tau_0$, when inequality sign in (17) is reversed, the lake i will eventually be invaded.

To obtain the critical flow in terms of arriving boats per year, we have to multiply τ_0 by T_{tot},

$$T_0 = \tau_0 T_{\text{tot}}, \tag{18}$$

In [1] this has been called "colonization threshold". It is natural to assume that this value has to be the same for all lakes.

Estimates of the model parameters for one of harmful aquatic invader are shown in Table 1; see the Appendix for details.

Table 1. Estimates of the model parameters for zebra mussels, see Appendix for details

parameter	description	estimate for zebra mussels
K	carrying capacity	10^9
$F_{\max}$	maximum growth rate	10^{12}year^{-1}
$t_K = K/F_{\max}$	characteristic time of growth	$3 \times 10^{-4}\text{year}$
$\delta = t_K/t_Y$	time factor	3×10^{-4}
u_A	Allee threshold	10^{-7}
T_{tot}	total boat traffic	10^5
T_0	invasion threshold	850 boats/year
τ_0	critical flow	$< 10^{-2}$
ϵ	flow factor	10^{-8}
κ	control efficiency	1boat/$
ρ_D	discount rate	$\sim 0.05\text{year}^{-1}$
g	scale for industrial losses	10^5\$/lake/year

5 Bioeconomic analysis and steady states

5.1 Dynamic optimal control task

The standard way to solve the above minimization problem is to use Pontryagin maximum principle [25]. It is convenient to use vector notation. Let us denote by $\mathbf{u}$, $\mathbf{x}$, $\mathbf{s}$ vectors of the lake state and controls respectively. In this notation (14) can be written as

$$\frac{d\mathbf{u}}{dt} = \delta^{-1}\Phi\left(\mathbf{u}, \mathbf{x}, \mathbf{s}\right).$$

Now we introduce the vector of adjoint variables or shadow prices $\mu = (\mu_1, \ldots, \mu_N)$, and the Hamiltonian

$$H = -E\left(t\right) + \delta^{-1}\left(\mu \cdot \Phi\right).$$

According to the maximum principle, μ should satisfy

$$\frac{d\mu}{dt} = \rho\mu - \nabla_u H = \rho\mu + \mathbf{g} - \delta^{-1}\nabla_u\left(\mu \cdot \Phi\right).$$

The optimal controls x_i, s_i are ones that maximize H at each moment of time.

General solution of this optimal control problem is complicated. However, it is known that for infinite horizon problems the solution must end at a steady state [12], which often is a fixed point [4]; that is for $t \to \infty$ $d\mathbf{u}/dt \to 0$, $d\mu/dt \to 0$, and hence $\mathbf{u} \to \mathbf{u}_*$, $\mathbf{x} \to \mathbf{x}_*$, $\mathbf{s} \to \mathbf{s}_*$. The controls x_i and s_i also tend to some constant values.

The dynamics then consists of a transient period t_{Tr}, during which the state and controls converge to the stationary values, and asymptotic period, during which $\mathbf{u} \approx \mathbf{u}_*$, $\mathbf{x} \approx \mathbf{x}_*$, $\mathbf{s} \approx \mathbf{s}_*$. Therefore

$$J = J_{Tr} + J_\infty = \int_0^{t_{\text{Tr}}} e^{-\rho t}E\left(t\right)dt + \int_{t_{\text{Tr}}}^{\infty} e^{-\rho t}E\left(t\right)dt \approx J_{Tr} + E_*\rho^{-1}e^{-\rho t_{\text{Tr}}}.$$

Below we shall assume that control can prevent invasions from the invaded lakes (u close to 1) to uninvaded ones ($u < u_M$). Then there should be no long transients in the system, related to long establishment period for flows close to critical one τ_0. Uninvaded lakes can be considered as already being in the asymptotic states. For the invaded lakes the dynamics practically does not depend on control and external flows, it is determined by $f(u)$, which is of the order 1. Therefore the transient time $t_{\mathrm{Tr}} \sim \delta$, and hence

$$J \approx O(\delta) + E_* \rho^{-1} e^{-\rho t_{\mathrm{Tr}}} \approx E_* \rho^{-1}$$

provided $\delta \ll \rho^{-1}$. As we have stated in the previous section, it is reasonable to assume that δ is a small parameter, so this assumption holds. Then minimization of J can be approximately replaced by minimization of E_* with respect to the choice of $\mathbf{u}_*$, $\mathbf{x}_*$, $\mathbf{s}_*$. That is, we replace dynamic optimal control problem by a static one.

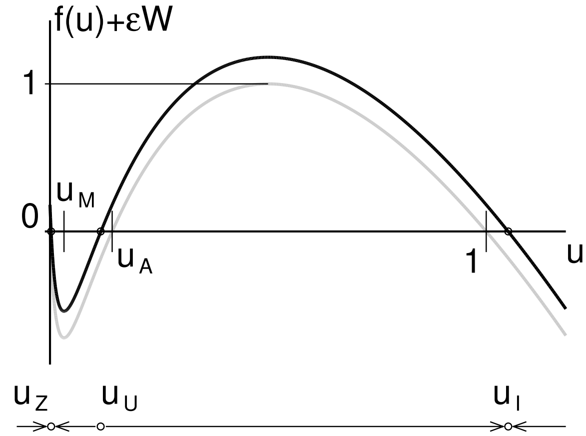

Figure 2: When the incoming flow is small, the equation $f(u) + \epsilon w$ has three roots, $u_Z < u_M$, $u_M < u_U < u_A$, and $u_I > 1$. u_Z and u_I are stable and correspond to uninvaded and invaded steady state. u_U is unstable. When the incoming flow increases, u_Z and u_U merge at u_M and disappear. Only u_I remains, and invasion becomes inevitable.

5.2 Simplification: static optimal control task

Instead of solving the dynamic optimal control problem, we can solve a static control problem, that is to assume that u_i, x_i, and s_i do not depend on time, and to find their values that minimize E under condition that $du_i/dt = 0$. This allows us to replace the search for minimum of functional J under differential constraints by searching minimum of a function under usual algebraic constraints. The latter problem is much simpler than the time-dependent one.

In the absence of external flows the equation $\delta du/dt = f(u) = 0$ has three roots. The same situation remains when the external flow $w = \epsilon(w_{\mathrm{in}} - w_{\mathrm{out}}) > 0$ is small, see Fig. 2. There are also three roots, u_Z, u_U, u_I, $0 < u_Z < u_M$, $u_M < u_U < u_A$, $u_I > 1$. The root u_U is unstable, and we shall not consider it. The roots u_Z and u_I correspond to uninvaded and invaded state of the lake respectively. When the incoming flow exceeds critical value $|f_{\mathrm{min}}| = \epsilon\tau_0$, the roots u_Z and u_U disappear, and only the invaded steady state remains.

The form for $f(u)$ means that $u_Z \approx 0$ and $u_I \approx 1$. Specifically, $|f'(1)|$ being of order 1 means that $u_I = 1 + O(\epsilon)$, and we know that $u_Z < u_A$, which is small. We also can neglect the outcoming flow and set $w_{\mathrm{out}} = 0$. For invaded lakes with $u = u_I$ both w_{in} and w_{out} are not important because they can only introduce perturbations to u_I of the order ϵ. For uninvaded lakes, when $u = u_Z \ll 1$, the outcoming flow $w_{\mathrm{out}} \sim u_Z$ is negligible compared to the incoming flow from the invaded lakes.

Substituting the expression (11) for w_{in} into the condition of Proposition 1 for invader flow $\epsilon\left(w_{\text{in}} - w_{\text{out}}\right) < \left|f_{\min}\right| = \epsilon\tau_0$ and neglecting w_{out} we obtain the condition on the incoming boat traffic for an uninvaded lake i:

$$\sum_{j=1}^{N} e^{-s_i}\tau_{ij}e^{-x_j}u_j \le \tau_0. \tag{19}$$

After these simplifications we come to the following problem.

Static optimal control problem. Find the optimal lake system configuration $\{u_i\}$ and the value of controls at each lake $\{x_i, s_i\}$ that minimize E (13) under the following constraints:

1) For each lake either $u_i = 1$, or $u_i = 0$ and (19) holds. Both cases can be combined in a single formula

$$(1-u_i)\sum_{j=1}^{N} e^{-s_i}\tau_{ij}e^{-x_j}u_j \le \tau_0, \qquad i = 1,\ldots,N; \tag{20}$$

2) For the originally invaded lakes $u_i = 1$;

3) $x_i \ge 0$, $s_i \ge 0$, $i = 1,\ldots,N$.

It is convenient to split it into two subproblems:

Problem 1 (Optimal control allocation in space for a given configuration of lakes). Let us set up a certain configuration of invaded and uninvaded lakes $U = \{u_1,\ldots,u_N\}$, where each $u_i = 0$ or 1, according to conditions 1 and 2. For this configuration U find x_i, s_i minimizing the control costs

$$E_C\left(U\right) = \min_{x,s}\sum_{i=1}^{N}\left(a_i s_i + d_i x_i\right) \tag{21}$$

under constraints 1 and 3.

Problem 2 (Optimal stopping configuration). Among all configurations U satisfying the constraint 2 find one which minimizes

$$E_{\min} = \min_{U}\left(E_C\left(U\right) + \sum_{i=1}^{N} u_i g_i\right). \tag{22}$$

The configuration U giving minimum to (22) and the respective x_i, s_i are the solution to the full problem. The proof is straightforward: if we assume the opposite, we obtain a contradiction.

The relation (20) immediately allows us to obtain the following statement.

Proposition 2. At the invaded lakes optimal $s_i = 0$, at the uninvaded lakes optimal $x_i = 0$. (As we have mentioned above, this proposition is intuitively obvious: it is useless to prevent invader flow into already invaded lakes, as well as to process boats after use in an uninvaded lake.)

Proof. Since for the uninvaded lakes $u_i = 0$, the corresponding x_i do not appear in the conditions (20). Therefore, for these x values we have minimum in (21) only under non-negativity constraint, which is $x_i = 0$. Similarly, for the invaded lakes $u_k = 1$, there are no conditions (20), hence for the corresponding s_k also minimum is reached at $s_k = 0$. ♢

6 Optimal control allocation for fixed configuration of invaded lakes (Problem 1)

The numerical technique for solving optimization problem with inequality constraints is described in Appendix. The algorithm is quite fast, and the problem can be solved for very big lake systems. Below there is example for a system of 1600 lakes. The actual pattern of spatial control allocation depends on many factors, such as the lake system structure, configuration of the invaded part, dependency of the connections τ_{ij} on distance. To demonstrate the major features of the solution we present results for several model situations.

We consider a number of identical lakes located at the nodes of one- or two-dimensional lattice. This demonstrates the features more clearly, without random distortions. We assume that invaded and uninvaded lakes are separated by a certain boundary, that is they do not alternate. The connection strength has been chosen according to the gravity models (6) and (5). The parameters of the gravity models have been chosen $m_i = m = 0.3$, $T_0 = 10^{-3}$, $\beta = 0.5$, $d_0 = 1$, $\gamma = 2$.

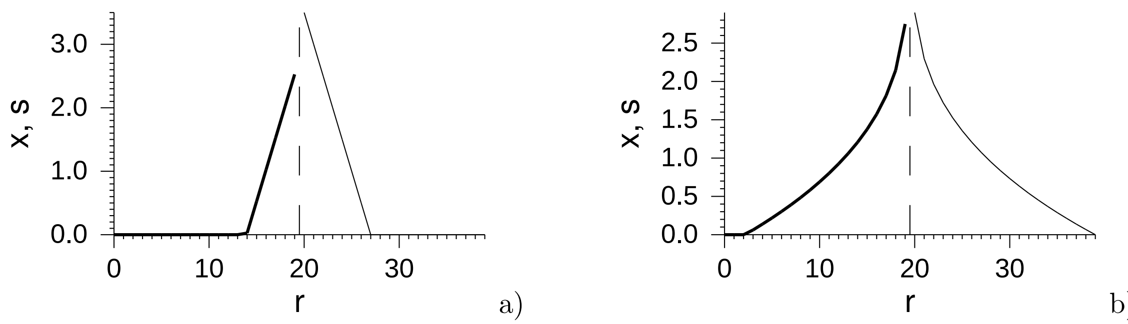

Figure 3: Examples of optimal control allocation in space for the system of linearly ordered lakes and connections T_{ij} for a) exponential gravity model (5), b) power-law gravity model (5). See section 6 for parameters and details.

In the first example $N = 40$ lakes were located at the same distance $h = 1$ from each other along the line. This gives $\tau_0 = 9.2 \times 10^{-5}$ for power gravity model and $\tau_0 = 9.6 \times 10^{-5}$ for exponential gravity model respectively. Examples of optimal distribution of control in space for one-dimensional lake systems are shown in Fig. 3. The left half of the lakes with the coordinates $r_i < 20$ (to the left of the dashed line) are invaded, so for $r < 20$ $x \geq 0$, $s = 0$, and for $r \geq 20$ $x = 0$, $s \geq 0$. Thick and thin lines show x_i and s_i for each lake respectively. Panels show the result for exponential (a) and power-law (b) gravity model. One can see that the intensity of control monotonically decreases with the distance from the invasion boundary. The size of this control region depends on the rate of decay of traffic with the distance. For the same maximum intensity m^2 exponential model gives significantly smaller size of the region.

Examples for controlling two-dimensional grids of lakes of the size 20×20 and 40×40 are shown in Fig. 4 and Fig. 5 respectively. The lakes are located in the points of regular grid with step 1. Invaded lakes are shown as dark circles, uninvaded — as light circles, and relative intensity of control at each lake is shown by the area of the overlaying square.

Fig. 4 shows the same feature as one-dimensional distribution — the most intense control is at the invasion front, and it decreases with the distance from the front. However, two-dimensional distribution brings one new component, the shape of the invaded region. When the interface boundary between invaded and uninvaded regions is not straight (panels a, d) then the control concentrates in convex part with the smaller area, while in the concave one the control is comparatively small. When the configurations of invaded and uninvaded lakes are symmetric (panel b), the control is close to symmetric as well. However, small deviation from symmetry (panel c), because the lakes at the diagonal are invaded, makes control visibly dominating within the smaller area.

Fig. 5 shows an example of a very large lake system of 1600 lakes, for which the optimal spatial

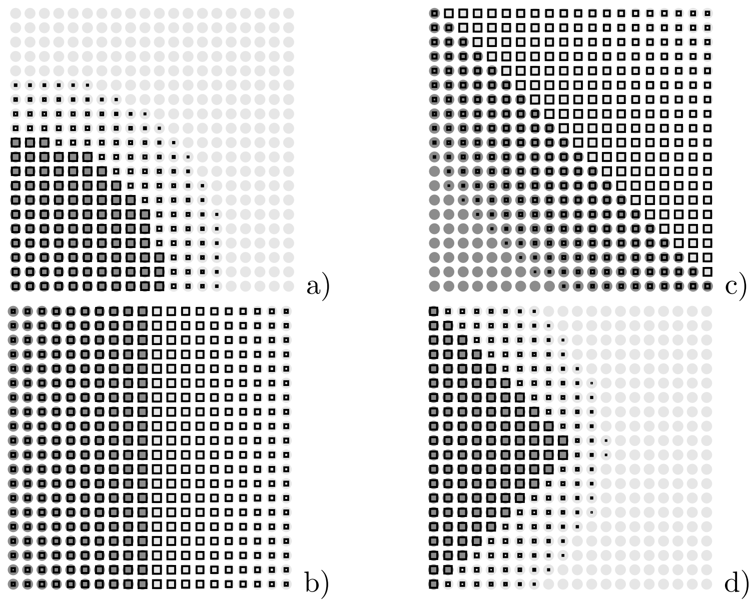

Figure 4: Examples of optimal control allocation in space for identical lakes forming 20×20 lattice. Parameters are the same as in Fig. 3. The connections are formed according to exponential gravity model (5). The invaded lakes are shown as dark circles, the uninvaded lakes as light circles, the area of squares is proportional to intensity of control at the given lake. See section 6 for details.

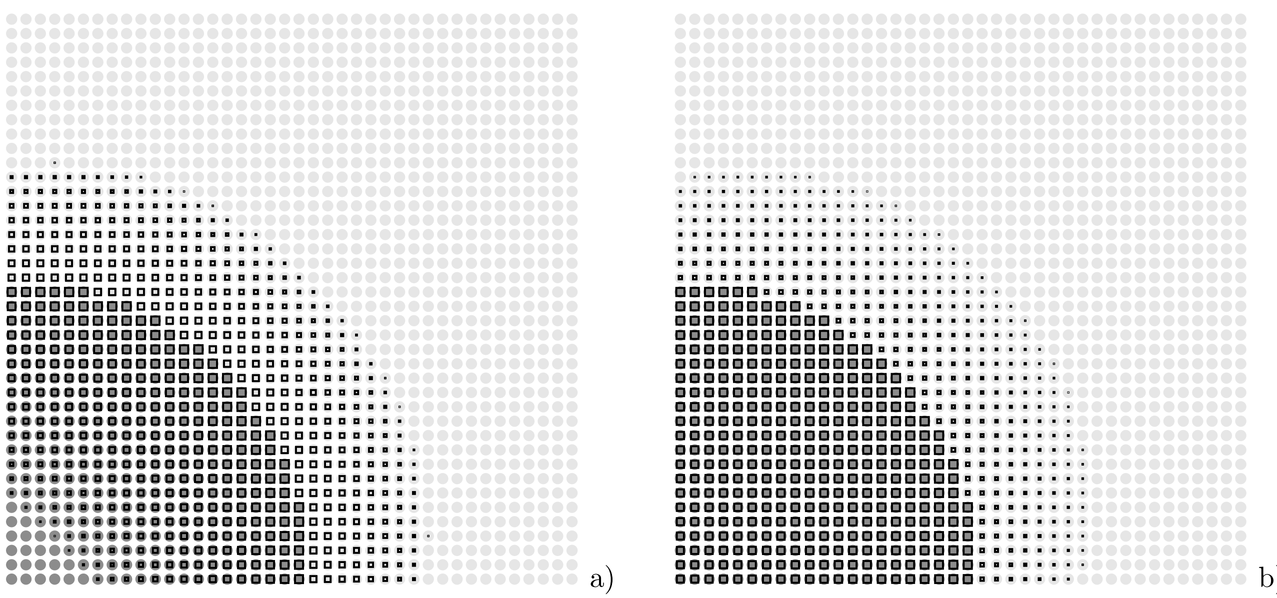

Figure 5: Examples of optimal control allocation in space for identical lakes forming 40×40 lattice. Parameters and notation are the same as in Fig. 4. The proportion of invaded lakes is the same as in Fig. 4a, however the size of the invaded region is greater, and curvature of the interface boundary is smaller. The connections are formed according to (a) exponential gravity model, same as as in Fig 4a, and (b) power-law gravity model. See section 6 for details.

control allocation can be obtained. Here the proportion of the invaded lakes is the same as in Fig. 4a, but size of the invaded region is greater, and the curvature of the interface boundary is smaller. This example also shows, how the optimal control distribution is influenced by spatial dependency of the boat travel intensity on the distance. For exponential dependency, when only local contacts are intense, the control is localized in the vicinity of the boundary. In case of power-law dependency it is necessary to control the bigger area, especially in the invaded region.

7 Optimal stopping configuration (Problem 2): lake clusters.

7.1 Configurations along most probable invasion path

To find the optimal configuration for invasion stopping we need to vary both the number of invaded lakes and the location of invaded lakes within the lake system. This makes analysis of all possible invasion configurations U a complicated task, because the number of configurations grows with N as 2^N, and for each configuration it is necessary to solve an optimization problem. If we assume that 10^6 is the maximum number of configurations that can be analyzed in practice, then direct searching through all possible configurations is limited by cases of $N < 20$.

However, different configurations arise with different probabilities in course of invasion development. Studies of invasion histories show that the invader usually spreads along directions of the most active traffic from the invaded lakes [3, 1, 17], that is along connections with the biggest τ_{ij}. Usually the number of such most probable invasion paths is much smaller than the total number of possible configurations. Therefore, it seems reasonable to study only configurations along these paths: it simplifies the task considerably and at the same time must cover all important configurations.

The idea to look at the sequences of configurations instead of analyzing each configuration separately has one almost obvious consequence. Suppose that the connection matrix τ_{ij} describes a clustered system of lakes. Namely, there are groups of lakes such that connections inside each group are significantly stronger than those between the lakes from different groups. In this case a typical invasion path is as follows: first invasion spreads within one group, then it jumps to another group and spreads within it, and so on. Since connections between the lakes in a group are strong, we can expect that stopping the invasion within the group should require more resources than preventing invasion spread between weakly connected clusters. Below we present two simple models that illustrate this idea, and show a simple criterion, when it may be optimal to abandon partially invaded group and switch to protecting other groups.

7.2 Two simple examples

7.2.1 Unstructured lake system (Model U)

We consider a uniform system of N lakes (Fig. 6a). Each lake is identical and connected to each other with the same strength; that is $\tau_{ii} = 0$, $\tau_{ij} = T$, $d_i = d_i = a = (N-1)\,T$, with the losses per lake $g_i = g$. We assume that $T > \tau_0$, and under no control all the lakes become invaded. Solution of this problem is presented in Appendix, and the total cost of stopping the invasion when M lakes are invaded is

$$E\,(M) = \min\{M, N-M\}\,a\ln\left(\frac{MT}{\tau_0}\right) + Mg.$$

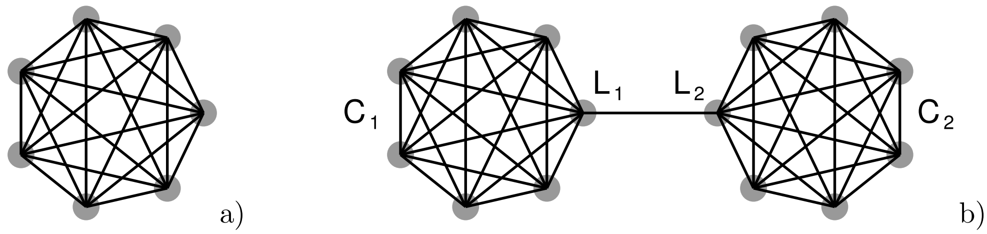

Figure 6: Configurations of identical lakes used in examples on optimal spatial stopping configuration. Circles show lakes, lines — nonzero connections between them. a) N lakes connected to each other with the same connectivity T. b) $N = N_1 + N_2$ lakes forming two clusters; all nonzero connections are equal T.

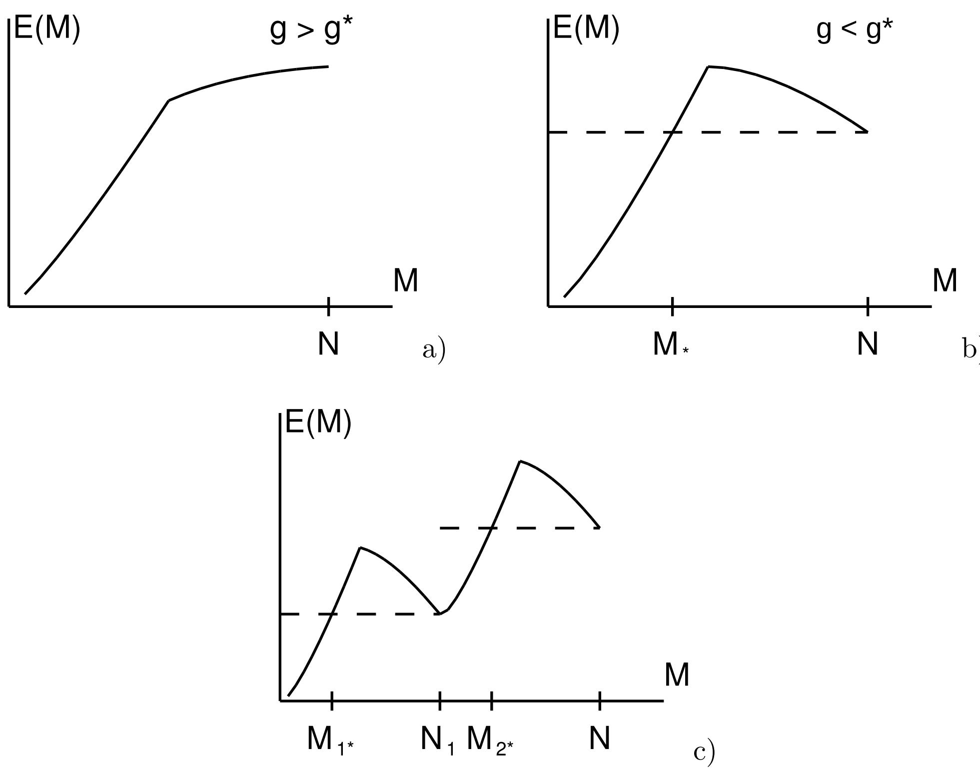

Figure 7: Total cost of invasion stopping after M lakes being invaded for configurations in Fig. 6a (panels a, b) and b (panel c). a)Invasion losses per lake are greater than the critical value g^*, optimal is to stop at the current M value for any M. b) same lakes configuration, but $g < g^*$. There is a critial value M_* above which optimal is no control at all; c) There are two clusters of lakes and small invasion losses, invasion of each clusters produces pattern similar to panel (b). There are two critical values, M_{1*} and M_{2*}, corresponding to the beginning of invasion of each cluster.

Optimal M corresponds to the minimum of $E(M)$ for $M \geq M_0$, where M_0 is the number of originally invaded lakes. There is a critical losses value

$$g_* = a \ln\left(\frac{(N-1)\,T}{\tau_0}\right).$$

One can observe a qualitative difference in the behavior of $E(M)$ for $g < g_*$ and $g \geq g_*$: in the former case there is an internal maximum of $E(M)$ for some $0 < M < N$, while in the latter case maximum of $E(M)$ is reached at $M = N$, see Fig. 7. Therefore we obtain solution for the optimal invasion stopping problem.

a) If the invasion losses are big, $g \geq g_*$, try to stop the invasion at the current $M = M_0$ for any M_0.

b) If the invasion losses are small, $g < g_*$, there exists a critical invasion level M_*, such that $E(M_*) = E(N)$, see Fig. 7. If $M_0 < M_*$, stop the invasion at $M = M_0$, otherwise the optimal policy is no control at all.

7.2.2 Clustered lake system (Model C)

We consider another system of identical lakes (Fig. 6b). All connections have the same strength T, but they form two clusters, containing N_1 and N_2 lakes respectively, and only one connection between the clusters. Let us denote the clusters by C_1 and C_2, the lake in C_1 that is connected to C_2 by L_1, and the lake in C_2 that is connected to C_1 by L_2. Within each cluster all lakes are interconnected like in the previous example, that is all lakes in C_1 except L_1 have N_1 connections, L_1 has $N_1 + 1$ connection, all lakes in C_2 besides L_2 have N_2 connections, L_2 has $N_2 + 1$ connections. In other words, there is a single "bridge" connection between the clusters. If one of the clusters is invaded, the only way for the invader to invade the second cluster is through this bridge.

Let us consider the following invasion scenario:

1) one lake in the cluster C_1 is invaded;
2) the invasion spreads inside C_1, and the last invaded lake is L_1;
3) the invasion jumps to the lake L_2 in the second cluster C_2;
4) the invasion spreads within C_2.

At each stage we estimate the control costs and total cost of invasion stopping.

The calculations of the stopping costs again can be found in the Appendix. The important difference with the previous case is that pure control costs (without accounting for the losses g) have a minimum at $M = N_1$, when the invasion jumps from one cluster to the other, and only one connection has to be controlled. If g is small enough, then $E(M)$ has a minimum too.

The existence of this minimum implies that there are two critical invasion levels, M_{1*} and M_{2*}, see Fig. 7c. Then the optimal control rules are: if $M_0 < M_{1*}$, then stop the invasion at M_0, otherwise retreat from the first cluster and protect the second one from the invader. If the second cluster is invaded, then stop if $M < M_{2*}$, otherwise do nothing.

If there are a number clusters, then there may be several critical values, depending on g_i and on actual structure of connections.

7.3 Model random configurations of lakes

For the next step we used a more complicated model. We generated two lake systems, containing $N = 50$ lakes of two sizes: many small lakes and a few big ones with 4 times bigger size. The connections between lakes were proportional to the product of their sizes, and the losses at each lake were proportional to its size. The lakes are located randomly, either as a single cluster, or four spatially separated clusters. One of the lakes has been chosen for the invader source. The subsequent invader spread has been random, but the probability to invade next lake was proportional to the total invader flow into the lake. Figure 8 shows the schemes of lakes allocation, one example invasion path, and cost of invasion stopping at each stage for 10 different paths.

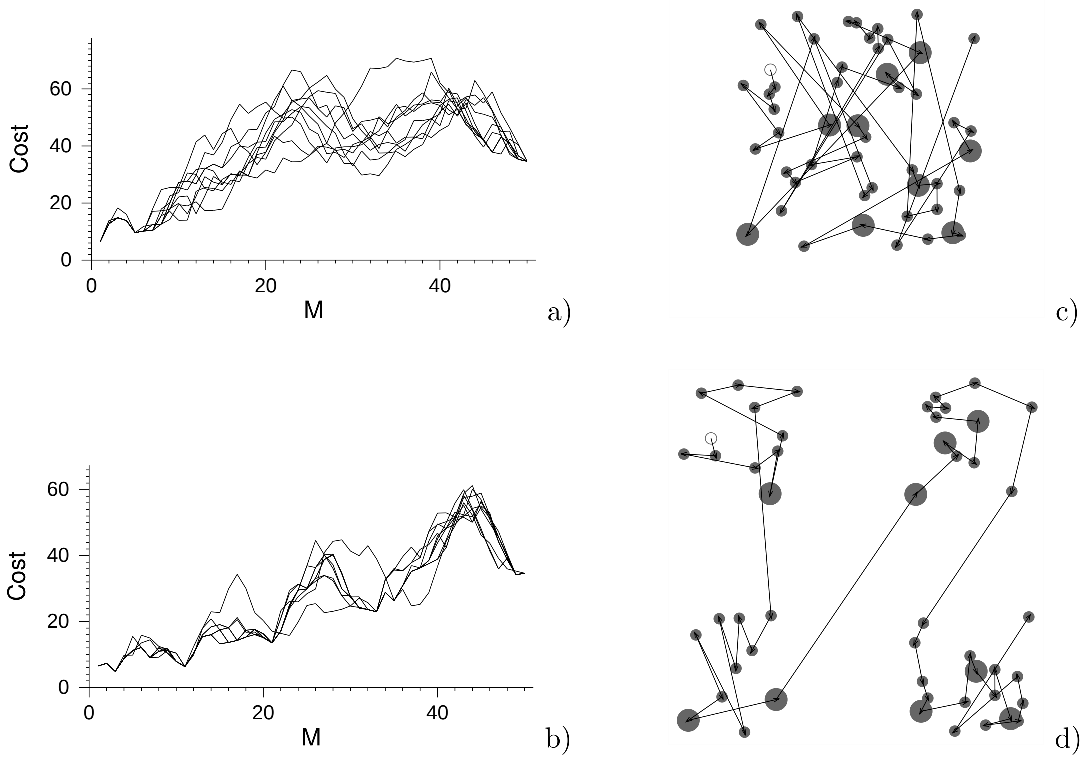

Figure 8: Model configuration of 50 different lakes randomly located without (a,c) and with (b,d) spatial clustering. Panels a and b show cots of invasion stopping after M lakes have been invaded along 10 probable invasion paths for configurations. Panels c and d show the relative lake size and location, the first invaded lake (empty circle), and one of the probable invasion paths.

The effect of spatial clustering is quite obvious, there is similarity between Fig. 8b and Fig. 7c. Therefore, like in the simple model, it is more efficient to stop invader between the clusters.

Splitting of a lake system into clusters may also help to make the problem of optimal invasion stopping tractable. First, one can consider the clusters as bigger units, and solve the stopping problem for them. After the cluster configuration has been selected, the accurate solution can be obtained. This may be a way to find a practical solution reasonably close to the optimum and in a reasonable time.

8 Conclusion

The main results of the paper are the following.

- We have derived the model for invasion spread and control in a lake system, and formulated the optimal control problem (Sect. 2 and 3). We present estimates of the model parameters for a harmful aquatic invader, zebra mussel (Appendix).
- Basing on the properties of infinite horizon optimal control problems and the existence of the critical flow in presence of Allee effect (Sect. 4), we have derived the constraint optimization problem for optimal invasion stopping (Sect. 5). The latter splits into problem of optimal spatial resource allocation for given configuraton of invaded lakes (problem 1) and problem of optimal invasion stopping or choice of optimal stopping configuration (problem 2).
- For problem 1 we developed an efficient numerical algorithm and applied it to a number of model lake configurations. The most intensive control is required at the boundary between invaded and uninvaded lakes. Spatial control allocation strongly depends on decay of boat transportation intensity with the distance between the lakes (Sect. 6).
- The complexity of problem 2 exponentially grows with the number of lakes, and for big lake systems it cannot be solved exactly. However, if the lakes form clusters, then the boundaries between clusters can be optimal places for stopping the invasion. As model examples show, if several lakes within a cluster are invaded, it may be better to abandon the cluster and to concentrate on prevention of invasion of other clusters. (Sect. 7).

The last point is in a good agreement with the 100-th meridian initiative [18] related with preventing spread of Zebra mussels to the basins of major western rivers in US. The eastern and some central rivers and lakes are already highly invaded. Due to Rocky Mountains, the connections between Eastern and Western water systems are weak, and prevention of zebra mussels invasion spread into the west appears to be the optimal strategy.

8.1 Acknowledgments

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9 Appendix

9.1 Characteristic parameter values: zebra mussels as an example

The model described involves a number of parameters. Their exact values may depend on specific situations. However we consider some typical values for a typical aquatic invader that spreads with the boat traffic and has Allee effect, the zebra mussel (ZM) [15] (Table 1).

Zebra mussels are small mussels with characteristic stripes on the shell [20]. Mean adult size is about 2cm. They live on hard substrate in relatively warm water mainly at the depths not exceeding 10m. In many aquatic systems of Europe and North America they settle in huge numbers, causing negative or even damaging consequences to industry and aquatic ecosystems. They clog water intakes and water processing facilities. When foraging they intensively filter water diminishing the amount of plankton and increasing the transparency of water. Both these effects cause strong perturbations for the ecosystems. Each female can produce up to 50000 offsprings, so quite soon after population establishment the mussels cover practically all suitable surfaces. They can colonize shells of other mussels causing their death of starvation, boats and ships immersed in the water for a long time, macrophytes and so on. And there are no predators, which are able to control their populations in efficient way. We attempt to determine parameters of our model for ZM using available data in the literature.

Carrying capacity K. It depends on the proportion of hard substrate at the lake bottom at the depths of several meters. Densities of ZM colonies at optimal conditions in the literature vary from $\sim 10^4$ to $\sim 10^6$ per square meter [20]. Characteristic size of a lake which is of interest for boating and fishing is $\sim 10^3$m, and its area $\sim 10^6$m^2. Assuming that only 10% of the bottom is suitable, we obtain $K \sim 10^9$.

Maximum growth rate $F_{\max}$. The actual function form of $F(p)$ for zebra mussels is unknown, so we try to estimate this value indirectly with the help of available physiological data and typical models of population growth. We approximate

$$F_{\max} = F(p_T) \approx \max_p \left(\frac{F(p)}{p} \right) p_T,$$

which is estimated from data by

$$\max \left(\frac{\Delta p/p}{\Delta t} \right) \frac{K}{2},$$

where $\frac{\Delta p/p}{\Delta t}$ is the maximum per capita growth rate estimated from the literature, and $p_T \approx K/2$ is a good approximation of the population size with maximum growth rate for most common population models. However, even if one takes $p_T = 0.01K$, the main conclusions remain the same.

Zebra mussels on average maturate during one year, adults spawn up to 4 time a year [20]. Average lifetime is 2-3 years. Therefore it is natural to analyze population increase during one mussel lifetime, and take $\Delta t = 3$ years.

$\Delta p/p$ in this case gives maximum possible number of offspring produced by one adult. It is known that on average one female produces $\sim 5 \times 10^4$ eggs. The gametes are released into water, where fertilization occurs. There are no estimates of fertilization efficiency in nature. Since 100% intersection of the gamete clouds is practically impossible, we assume that about 50% of eggs are fertilized. Mortality during larval stage is small, while during settlement it varies strongly, because survival depends on suitability of the bottom where settling occurs. We assumed 10% of bottom is suitable, which gives ∼90% mortality during settling. Then one spawning results in about 2500 offsprings. In 3 years we may expect 8 spawning events, so we may take $\Delta p/p \sim 2 \times 10^4$. During the same period all preexisting mussels must die, which gives mortality correction for $(\Delta p/p)_\mu = -1$, which is negligible compared to the number of new mussels.

Combining these values we obtain

$$F_{\max} \sim \frac{2 \times 10^4}{3} \times \frac{1}{2} \times K \sim 10^{12}\,\text{year}^{-1}$$

Characteristic time t_K and parameter δ.

$$t_K = K/F_{\max} \sim 3 \times 10^{-4}\,\text{year}$$

which gives

$$\delta = K/(t_Y F_{\max}) \sim 3 \times 10^{-4}, \qquad t_Y = 1\,\text{year}.$$

Colonization threshold T_0 has been estimated in [1] as

$$T_0 = 850\,\text{boats/year}.$$

Allee threshold u_A. The Allee effect arises because the mussels reproduce sexually, males and females release gametes into the water where fertilization goes on. Since mussels cannot move, to reproduce successfully they must be located close enough to each other [23]. Therefore, the critical population size depends not only on the number of individuals, but on their location as well. There may be situations, when two mussels located closely start a new population, and when several hundred evenly distributed over the lake go extinct. However, such extreme cases have a little probability, and we need a "typical" estimate. It seems natural to base upon the flow of mussels transported by boats. It is known, that the main way of spread is transportation of macrophytes with several attached mussels [11]. It has been estimated that about 1% of trailers carry weeds with mussels. Other source give estimate of average 2.2 mussels per macrophyte, however in a different situation [9]. Taking a critical flow $T_0 \sim 10^3$boats/year, we obtain that each year about 20 mussels must arrive. Assuming that arriving adults can survive for two years, we come to a typical size of population, which may start to grow: $p_A \approx 40$–50 individuals, or more roughly $p_A \sim 10^2$.

Flow factor ϵ. Using simultaneously expressions for τ_0 (16) and (18) we can write

$$\tau_0 = \frac{T_0}{T_{\text{tot}}} = \frac{|f_{\text{min}}|}{\epsilon} = \frac{1}{\epsilon}\frac{|F_{\text{min}}|}{F_{\text{max}}}$$

or

$$\epsilon = \frac{|F_{\text{min}}|}{F_{\text{max}}}\frac{T_{\text{tot}}}{T_0}.$$

The estimates for $F_{\text{max}} \approx 10^{12}\text{year}^{-1}$ and $T_0 \approx 10^3$ boat/year have already been given above. The rough estimate for F_{min} can be made from p_A and life duration for zebra mussels. If we take a small population of the size near $p_M < p_A \sim 10^2$, it will die out during 1–3 years, which gives upper estimate for $|F_{\text{min}}| \sim 10^2$. The hardest problem is to estimate the total boat traffic. According to [3, 1, 17], in Wisconsin there are 58000 registered boaters, however only about 10% of boaters do long travels, including transfers of the boat from lake to lake. Each boater can make several travels per year, and lake system can cover several states, so eventually it seems reasonable to estimate $T_{\text{tot}} \sim 10^5$boats/year, and in case of Wisconsin lake system one obtains

$$\epsilon \sim \frac{10^2}{10^{12}}\frac{10^5}{10^3} = 10^{-8} \ll 1.$$

The estimate remains small even if we increase T_{tot} and $|F_{\text{min}}|$ 10 times each. ϵ seems to be very small, however, the estimate for $|f_{\text{min}}|$, which is responsible for the possibility of invasion, appears to be even smaller,

$$|f_{\text{min}}| = \frac{|F_{\text{min}}|}{F_{\text{max}}} \sim \frac{10^2}{10^{12}} = 10^{-10}.$$

Critical traffic τ_0. Using estimates for colonization threshold T_0 and total boat traffic T_{tot} we obtain dimensionless colonization threshold

$$\tau_0 = T_0/T_{\text{tot}} \approx 10^{-2}.$$

However, numerical experiments show, that for a lake system with the number of lakes $N > 10$ typically all or almost all $\tau_{ij} < 10^{-2}$, and invasion spread becomes impossible. Typical τ_0 values resulting in a spatially distributed control structure is of the order 10^{-4} or even less. We can conclude that either our estimate of T_{tot} may need correction, or the estimate of T_0 corresponds to flows that significantly exceed τ_0 because for smaller flows establishment time becomes too big. This question may need further research.

Bioeconomic parameters include discount rate ρ_D, losses per year for each lake g_i, and the control efficiency κ. There are no exact data on the latter two parameters, so we tried to make estimates from available data.

Typical value of $\rho_D \sim 0.05\text{year}^{-1}$. Since $t_Y = 1\,\text{year}$, the dimensionless discount rate is also $\rho \approx 0.05$, and our assumption for static problem $\delta \ll \rho^{-1}$ holds.

The losses due to the invasion have four major components.

a) Industrial losses. In case of zebra mussels they are related with costs of cleaning water treatment facilities. Some data are available from [19]. For example, the mean treatment costs per year for Hydroelectric facilities are \$83000, fossil fuel generating facilities \$145000, drinking water treatment facilities \$214,000, nuclear power plants \$822,000. If we assume that each big lake has a drinking water treatment facility, this gives a corresponding g component about 2×10^5 \$/year.

b) Private losses. Many houses near lakes have individual water intakes, which are subject to zebra mussels impact. However, there are no estimates for the related expenses.

c) Ecological losses. Zebra mussels are filtering water very intensively for feeding. This results in major changes in planktonic content, and hence influences food chains and population structure of the lakes. Increasing water transparency causes changes in macrophytes population. Corresponding gains and losses have not been estimated yet.

d) Recreational losses. They are related with ecological changes (important for fishing), quality of the bottom and beaches covered with zebra mussel shells, and water clarity. No estimates are available at present, though corresponding techniques for c) and d) are being developed by environmental economists.

So, at present it is possible to make estimates only for big lakes with water treatment facilities, and this gives the order of magnitude for g.

To make a rough estimates for the control part, we can use the fact that zebra mussels in all stages almost instantly die after washing with 60^oC (140^oF) water. Therefore a treatment facility may be just like a car wash, and the costs may be comparable, say, \$3/wash. If we assume that the average efficiency of such a wash is about 90-95%, this gives $\kappa \sim 1\,\text{boat}/\$$, and $\exp(-3\kappa) \approx 0.05$.

Now, taking the example of Wisconsin lake system with $T_{\text{tot}} \sim 10^5$, and $g \sim 10^5\$$, we can evaluate the scale of dimensionless losses and financial factors E_0 and J_0,

$$g' = \frac{g\kappa}{T_{\text{tot}}} \sim 1, \qquad E_0 = \frac{T_{\text{tot}}}{\kappa} \sim 10^5 \frac{\$}{\text{year}}, \qquad J_0 = E_0 t_Y \sim 10^5\,\$.$$

9.2 Optimization with inequality constraints: penalty function and numerical technique

For a general optimization problem [7], find $\min F(u)$ under n restrictions

$$\Phi_i(u) \leq 0,$$

the solution u_* satisfies

$$\nabla F(u_*) + \sum_{i=1}^{n} \mu_i \nabla \Phi_i(u_*) = 0,$$

where for each i either $\Phi_i(u_*) = 0$ (point at the boundary of the domain of admissible u values) or $\mu_i = 0$ (internal point according to i-th criterion). So to find a solution it may be necessary to try up to 2^n different cases. For this reason for $n > 2$ often a method of penalty function is used. Let

$$P(x) = \begin{cases} Ax, & x \geq 0, \\ 0, & x < 0, \end{cases}$$

where A is big enough. Then the original problem is replaced by the problem of unconstrained minimization of

$$F(u) + \sum_{i=1}^{n} P(\Phi_i(u)) = \min. \qquad (23)$$

If $|\nabla F| \ll |\nabla P| = A$, the solution of (23) is close to that of original problem.

This penalty function $P(x)$ is nondifferentiable at $x = 0$, which may create problems in practical applications. We used a sequence of functions $G(x/\omega)$, which converge to P as $\omega \to 0$ with $A = \omega^{-1}$. This allows to obtain very accurate solutions for ω small. We used the penalty function

$$G(z) = z + \sqrt{z^2+1}, \quad G'(z) = 1 + \frac{z}{\sqrt{z^2+1}},$$

The incoming invader flow to the lake

$$w_i = \exp(-s_i) \sum_{j=1}^{N} \tau_{ij} \exp(-x_j)\, u_j, \qquad i = 1, \ldots, N.$$

We minimize

$$E = \sum_{1}^{M} d_i x_i + \sum_{M+1}^{N} a_i s_i + \sum_{M+1}^{N} G\left(\frac{w_i - \tau_0}{\omega}\right)$$

The simplest way is to use gradient descending, then we need only the derivatives

$$\frac{\partial E}{\partial x_m} = d_m - \frac{1}{\omega} \sum_{i=K+1}^{N} G'\left(\frac{w_i - \tau_0}{\omega}\right) \exp(-s_i)\, \tau_{im} \exp(-x_m), \qquad m = 1, \ldots, M,$$

$$\frac{\partial E}{\partial s_m} = a_m - \frac{1}{\omega} G'\left(\frac{w_m - \tau_0}{\omega}\right) \exp(-s_m) \sum_{j=1}^{K} \tau_{mj} \exp(-x_j), \qquad m = M+1, \ldots, N.$$

Minimizing is done iteratively with gradient descending: set $\mathbf{x}_0$, $\mathbf{x} = \{x_1, \ldots, x_M, s_{M+1}, \ldots, s_N\}$ then

$$\mathbf{x}_{n+1} = \max\{0, \mathbf{x}_n - \gamma \nabla E(\mathbf{x}_n)\}.$$

The choice of γ is important for efficiency, but this problem is standard, and we shall not discuss it here.

Most important was the fact that the convergence rate strongly depends on ω. For this reason we used a decreasing sequence of ω, first solve minimization problem for ω big, then reduce ω, use the previous solution as initial guess, and find the new minimum, and so on. This allowed us to combine fast convergence and reaching very small ω values about 10^{-9}, so the final solution after 30 ω-iterations has accuracy $\sim 10^{-6}$ or better.

9.3 Analysis of the Model U (unstructured lake system)

From symmetry it follows that controls at all invaded lakes $x_i = x$, and at all uninvaded lakes $s_i = s$, then the functional to be minimized is

$$E = Max + (N - M)\,as + Mg,$$

where g are losses per lake due to the invasion. The flow restriction under control is

$$e^{-s} MTe^{-x} = \tau_0, \qquad s + x \equiv z = \ln\left(\frac{MT}{\tau_0}\right) > 0.$$

For fixed M x and s can be easily found. Since the functional is linear in x and s, for $M < N - M$ $x = z$, $s = 0$, while for $M > N - M$ $x = 0$, $s = z$. Combining both cases, we obtain

$$E\,(M) = \min\{M, N - M\}\, a \ln\left(\frac{MT}{\tau_0}\right) + Mg.$$

For $M < N/2$ $E\,(M)$ is an increasing function. For $M > N/2$

$$\frac{dE}{dM} = \frac{N - M}{M} a + g - a \ln\left(\frac{MT}{\tau_0}\right),$$

which is a decreasing function of M, so the minimum of $E'\,(M)$ is achieved for $M = N$. Therefore, $E\,(M)$ can be decreasing for M close to N if g is small. The critical value g_* of g can be obtained from the condition that $E\,(N - 1) = E\,(N)$, that is

$$a \ln\left(\frac{(N-1)\,T}{\tau_0}\right) + (N - 1)\,g_* = Ng_*, \qquad g_* = a \ln\left(\frac{(N-1)\,T}{\tau_0}\right).$$

9.4 Analysis of the Model C (clustered lake system)

At each stage of the described scenario we estimate the control costs and total cost of invasion stopping.

1. The cluster C_2 does not participate in the estimates, for all lakes in $C_1 \backslash L_1$ $d_i = a_i = a = (N_1 - 1)\,T$, $d_{L1} = a_{L1} = N_1 T$. The functional to be minimized is

$$E = Max + (N_1 - 1 - M)\,as + a_{L1} s_{L1} + Mg, \tag{24}$$

and the flow constraints

$$e^{-s} MTe^{-x} = \tau_0, \qquad e^{-s_{L1}} MTe^{-x} = \tau_0, \qquad s + x \equiv z = \ln\left(\frac{MT}{\tau_0}\right) > 0.$$

Hence $s_{L1} = s$, and like in the previous example, we have

$$x = \begin{cases} z, & Ma < (N_1 - M)\,a + T \\ 0, & Ma > (N_1 - M)\,a + T \end{cases}, \qquad s = z - x,$$

$$E\,(M) = \begin{cases} Maz + Mg, & Ma < (N_1 - M)\,a + T \\ (N_1 - M)\,az + Tz + Mg, & Ma > (N_1 - M)\,a + T \end{cases}.$$

2. After L_1 has been invaded, only the bridge connection is dangerous, that is we have to control the incoming traffic on L_2 (s), or outcoming traffic on L_1 (x), or both. Since $d_{L2} = a_{L2} = N_2 T$,

$$E = d_{L1} x + a_{L2} s + N_1 g, \tag{25}$$

$$e^{-s} T e^{-x} = \tau_0, \qquad s + x \equiv z = \ln\left(\frac{T}{\tau_0}\right) > 0.$$

$$x = \begin{cases} z, & N_1 < N_2 \\ 0, & N_1 > N_2 \end{cases}, \qquad s = z - x,$$

$$E(N_1) = \min\{N_1, N_2\} Tz + N_1 g.$$

3-4. After L_2 has been invaded, the invasion spreads within C_2. To simplify consideration, we again assume that controls at all invaded lakes are equal to x, at all uninvaded lakes are equal to s, though there is no more complete symmetry between all invaded lakes, and the resulting solution is only close to true optimum. (Accurate analysis is possible, however it is very bulky and its results are very close to the expression presented below.) Then $a = d = (N_2 - 1) T$, $N = N_1 + N_2$,

$$E = (M - N_1) ax + Tx + (N - M) as + Mg, \tag{26}$$

and the flow constraints

$$e^{-s} (M - N_1) T e^{-x} = \tau_0, \qquad s + x \equiv z = \ln\left(\frac{(M - N_1) T}{\tau_0}\right) > 0.$$

$$x = \begin{cases} z, & (M - N_1) a + T < (N - M) a \\ 0, & (M - N_1) a + T > (N - M) a \end{cases}, \qquad s = z - x,$$

$$E(M) = \begin{cases} (M - N_1) az + Tz + Mg, & (M - N_1) a + T < (N - M) a \\ (N - M) az + Mg, & (M - N_1) a + T > (N - M) a \end{cases}.$$

Analyzing the overall $E(M)$ dependency one can see, that pure control costs (without g) have a minimum at $M = N_1$, when the invasion jumps from one cluster to the other. If g is small enough, then $E(M)$ has a minimum too.

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