



An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species

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Numbers of non-indigenous species—species introduced from elsewhere—are increasing rapidly world-wide, causing both environmental and economic damage. Rigorous quantitative risk-analysis frameworks, however, for invasive species are lacking. We need to evaluate the risks posed by invasive species and quantify the relative merits of different management strategies (e.g. allocation of resources between prevention and control). We present a quantitative bioeconomic modelling framework to analyse risks from non-indigenous species to economic activity and the environment. The model identifies the optimal allocation of resources to prevention versus control, acceptable invasion risks and consequences of invasion to optimal investments (e.g. labour and capital). We apply the model to zebra mussels (*Dreissena polymorpha*), and show that society could benefit by spending up to US\$324 000 year⁻¹ to prevent invasions into a single lake with a power plant. By contrast, the US Fish and Wildlife Service spent US\$825 000 in 2001 to manage *all* aquatic invaders in *all* US lakes. Thus, greater investment in prevention is warranted.

Keywords: stochastic dynamic programming; non-indigenous; exotic species; risk assessment

1. INTRODUCTION

Non-indigenous species are increasing worldwide (Sala *et al.* 2000), are one of the top causes of global biodiversity loss and environmental change (Mack *et al.* 2000; Lodge 2001) and are economically expensive (e.g. estimated to cost the US\$137 billion year⁻¹; Pimentel *et al.* 1999). Recent efforts across many countries have highlighted the urgent need for more rigorous and comprehensive risk-analysis frameworks for non-indigenous species so that prevention and control strategies can be targeted appropriately (McNeely *et al.* 2001; National Invasive Species Council 2001).

To develop an appropriate framework, we need to recognize that risk analysis of species invasions is inherently an interdisciplinary problem, involving ecology, economics and mathematics. Ecosystem conditions and species' characteristics determine whether a nonindigenous species will establish itself in a new location and whether it will cause damage (although these conditions may be difficult to quantify; Mack et al. 2000). Economic conditions influence the transport of nonindigenous species, and influence the resources that are spent on preventing an invasion versus control after an invasion. Reasonable resource expenditure is, in turn, influenced by the expected consequences of the invader. Thus, ecological and economic parameters together define non-indigenous species risks, with mathematics providing the techniques that allow the most rigorous analysis possible. Accounting for the ecological and economic links and feedbacks is now critical in invasion biology (Perrings et

We use stochastic dynamic programming (SDP; Bellman 1961) as the mathematical basis underlying our riskanalysis framework. SDP is efficient (finds global solutions to exponentially complex problems in linear time), permits uncertainty to be included in the analysis and has the flexibility to incorporate the entire invasion process, including biology and economic components. Furthermore, management responses change with environmental and economic conditions, and the responses, in turn, moderate the environment and economy. In the SDP framework we can explicitly incorporate such forecasted interactions based on the best available data. We can identify the combination of prevention and control efforts that maximizes social welfare given uncertain invasion events. SDP has been useful in other management contexts (Shea & Possingham 2000), but this application to merge the ecology and economics of species invasions is novel.

The conceptual underpinnings of the framework focus on processes common to all species invasions in all ecosystems (the ecology column of figure 1a): a species is transported in a pathway and is released into a new environment, where it may establish, spread and become abundant, with environmental and economic impact. Success at each step in this invasion process is probabilistic, and only a small proportion (but a large absolute number) of species survive the entire process and cause an impact. Ecological forecasts of success or failure at each transition interact with the economic circumstances associated with each transition (figure 1a). Social welfare (benefits minus

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al. 2002; Simberloff 2002) and requires an interdisciplinary effort to unite risk assessment with risk management (Committee on Environment and Natural Resources 1999).

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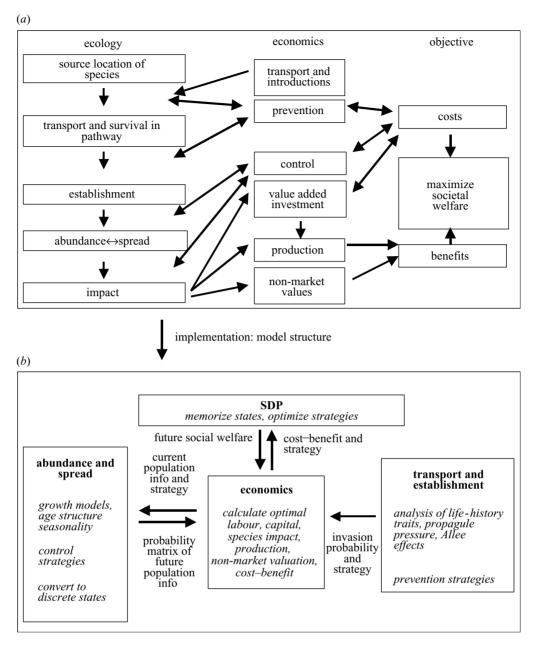


Figure 1. Bioeconomic framework for invasions. (a) The conceptual approach to the ecological and economic components of a generalized invasion process. Both economic input and ecological states change over time and influence one another. Our goal is to determine the optimal set of strategies that maximize welfare, where welfare can be a function of both market and non-market values. (b) Implementation of the conceptual approach through an operational model structure. The boxes and bold text represent modules, within which details (italic text) may be hidden (encapsulated) and modified without affecting the entire model. Plain text represents the interfaces (information passed between modules).

costs) is determined jointly by ecological and economic processes (figure 1a).

By contrast, traditional risk analysis considers risk assessment (determining environmental goals, such as reducing invader abundance to a specified level) and risk management (determining methods to reach those goals) separately (Simberloff 2002). Such separation implicitly assumes that the benefits of prevention and control are negligible below the level specified in the risk assessment. Our perspective, however, is that it is important to determine quantitatively the benefits of incremental improvements in the environment relative to the costs of achieving them, thereby recognizing explicitly the interaction between ecology and economics. In our conceptual frame-

work, the level of risk society should accept occurs when the projected damages are less than the costs associated with prevention and control. This framework may be applied at different scales: for a nation, a region or a local area.

We implement the conceptual model (figure 1a) into the computational SDP model, breaking the conceptual model into four operational modules (figure 1b). The 'abundance and spread' and 'transport and establishment' modules contain the biological aspects of an invasion and their interaction with control and prevention strategies. The functions encapsulated within these modules include processes such as recruitment and survival. Importantly, these processes represent details that may differ depending

on the biological system, but do not affect the overall structure of the model. Only the movement between states (e.g. uninvaded, invaded, population density of invader) needs to be passed to the economics module. The economics module determines the costs and benefits of each state, and analytically determines the optimal labour and capital investment. The SDP module keeps track of the future states that have been calculated and determines the optimal strategies based on the economic benefit—cost analysis of the current state and the accumulation of future states based on expected trajectories.

We first present a hypothetical example to demonstrate the general application of our framework, so that its properties are not obscured by the idiosyncrasies that are inherent in specific biological systems. We then test the utility of our framework on the real-world example of the invasions by zebra mussels (Dreissena polymorpha) of uninvaded lakes. We examined zebra mussels for the following reasons: they currently cost US industries an estimated US\$100 million year⁻¹ (Pimentel et al. 1999); power plants and water firms continue to experiment with new control measures and schedules in an effort to maximize the benefits of zebra mussel control; zebra mussels have enormous environmental impacts (Ricciardi & Rasmussen 1998; Lodge 2001); and prevention of new infestations remains timely because zebra mussels are still expanding their range within North America (Bossenbroek et al. 2001).

2. MATERIAL AND METHODS

(a) Hypothetical example

We used a logistic growth model allowing uncertainty (ε)

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(\frac{1-N}{\kappa}\right) + \varepsilon. \tag{2.1}$$

SDP required discrete states (θ) , defined here as discrete levels of population abundance $(\theta = N)$. We modelled probability of invasion (I') per time interval as a function of base rate invasion probability (I) and prevention effort (E)

$$I' = Ie^{-\Lambda E}. (2.2)$$

Welfare (w) for any given state is a function of production (Q), price per unit of production (p) and the cost (C) per unit of labour (L), capital (K), prevention (E) and control (X):

$$w = pQ - C_{L}L - C_{K}K - C_{E}E - C_{X}X, \tag{2.3}$$

Production (Q) followed an economic Cobb–Douglas functional form (Archer & Shogren 1996), relating labour, capital investment and damage due to the pest (G).

$$Q = \alpha L^a K^b G(N)^c, \tag{2.4}$$

$$G(N) = 1 - e^{-\lambda/N},$$
 (2.5)

$$N_{t+1} = N_t e^{-\nu X}. (2.6)$$

We extended the usual economic models by integrating damage with an explicit biological model. We determined optimal labour (L^*) analytically as follows:

$$L^* = \left(\frac{\alpha p a K^b G^c}{C_L}\right)^{1/(1-a)} = \frac{a p Q^*}{w}.$$
 (2.7)

 K^* was analogously calculated. The welfare (w) of each state (θ) was used in the SDP calculation

MAX
$$W_{\theta,t} = w_{\theta,X,E} + \sum P_{\theta,X,E,i} W_{i,t+1},$$
 (2.8)

where W was the cumulative welfare from the end time horizon (T) to the current time (t), and P was the probability of moving from a state θ to state i, given strategies X and E (chosen to maximize W). W was calculated by moving backwards from t = T to t = 1. Thus, for each state at each time interval, we knew the optimal strategies and future trajectories.

(b) Zebra mussel invasion

(i) Biological sub-model

Seasonally dependent recruitment rates were determined by counting settled postveligers on artificial substrates from a power plant (electronic Appendix A, available on The Royal Society's Publications Web site). We obtained age-dependent survival estimates from the literature (Akcakaya & Baker 1998) (electronic Appendix A). Estimates were skewed and non-negative, and were $\log(X+1)$ transformed (Zar 1984). Rates were converted to monthly bases. We used a point estimate of growth rate (ΔS) (Akcakaya & Baker 1998) as follows:

$$\Delta S = 16.3 - 0.343S,\tag{2.9}$$

where S is the size (in mm). We modified growth to monthly rates occurring during May–October. We related volume to size by measuring water displacement and regressing shell length versus displacement (electronic Appendix A). We collapsed recruitment and survival rate distributions, age structure, seasonality, growth rates and size–volume relation (biological details) into a few variables directly causing industrial impacts to avoid the 'curse of dimensionality' (Bellman 1961) and keep SDP efficient. Here, we defined SDP states (θ) as each possible control scenario and the associated total zebra mussel volume, which could then be related to damage estimates and control strategy. Based on nuclear power industry data, we used a point estimate of zebra mussel control cost ($C_{\rm X}$ = US\$1.6 million) and effectiveness (95% reduction in abundance of all age classes) (E. C. Mallen, personal communication).

(ii) Economic sub-model

Based on data from six power plants from 1994 to 2000 (electronic Appendix B, available on The Royal Society's Publications Web site), we estimated the price per unit of production (p), cost of labour $(C_{\rm L})$ and cost of capital $(C_{\rm K})$ using regression techniques (electronic Appendix C, available on The Royal Society's Publications Web site). We assumed firms made choices to maximize their welfare (equation (2.3)). The production function (equation (2.4)) and optimal labour (equation (2.7)) were expressed in regression form as:

$$ln(Q) = ln(\alpha) + aln(L) + bln(K) + \varepsilon, \qquad (2.10)$$

and

$$\frac{1}{pQ^*} = a\frac{1}{C_L L^*} + \varepsilon. \tag{2.11}$$

Optimal capital was analogously calculated. We estimated a, b and α using SURE (seemingly unrelated regression equations) (Zellner 1962).

Zebra mussels reduce production (i.e. cause damage) by clogging pipes and reducing water flow. We modelled flow as being linearly related to production and pipe cross-sectional area (A),

and therefore damage (G^c) was proportional to reduction in pipe area.

$$V_{\rm o} = \pi l \left(\frac{1D}{2}\right)^2 \tag{2.12}$$

and

$$V_{\rm zm}$$
 = surface area $\sum d_i v_i = \pi l D \sum d_i v_i$, (2.13)

where $V_{\rm o}$ was the pipe volume without zebra mussels (m³), l was the pipe length (m), D was diameter (m), d was the density (individuals m $^{-2}$) and v was the volume of an individual zebra mussel (m³). We summed over all the age classes i (simplified to homogeneous sizes within an age class). The proportional reduction in flow was

$$G^{c} = \frac{A_{o} - A_{zm}}{A_{o}} = \frac{V_{o} - V_{zm}}{V_{o}}$$

$$G^{c} = 1 - \sum_{i} d_{i}v_{i} \frac{4}{D} [MIN = 0].$$
(2.14)

Annual production, labour and capital costs were converted to monthly values, whereas zebra mussel control was expressed as the cost per event. Welfare was determined using equations (2.3) and (2.8). The coefficient c was not estimated explicitly, because our estimate of damage was externally derived rather than fitted from industry data.

(iii) Probability of invasion

To estimate invasion probability, we considered 95 at-risk lakes in Michigan monitored over 7 years from before invasion (http://www.msue.msu.edu/seagrant/zmfiles/). A total of 56% of the lakes remained uninvaded ($U_t = 0.56$). If the invasion probability was constant, $U_t = e^{-pt}$, where p was the probability of invasion per time interval, and t was time: $p = -\ln(U_t)/t$. Given monthly time-intervals, $p = -\ln(0.56)/(7 \times 12) = 0.007$, i.e. a 0.7% probability of being invaded each month.

(iv) Simulations

To determine the optimal control strategy after invasion, we ran the simulation for 120 monthly time intervals (10 years) with the two possible control strategies at each time-step (do nothing or perform a control event). To determine the acceptable prevention expenditure for a given initial invasion probability and a given proportional reduction in invasion probability, simulations were conducted at a range of prevention expenditures, in increments of US\$1000. These results were for quasi-stationarity, i.e. the time-frame where the welfare of each state plateaued, and, therefore, the strategies became constant for each state.

3. RESULTS

In our hypothetical example, we compared a lake that was initially uninvaded with an invaded lake, simulated over 25 years. For the uninvaded lake, we also examined a shorter (e.g. politically driven) time-frame (5 years). In each of the scenarios (figure 2), we considered the consequences for cumulative welfare of alternative strategies (figure 2a-c) and examined the average optimal welfare and the associated optimal expenditures on control (figure 2d-f), labour, capital and prevention (figure 2g-i) over time. We also derived the invasion probabilities associated with optimal management strategies for 5 and 25 year durations (figure 2j-l).

In our example, the cost of optimal control in the invaded lake reduced welfare by one-half relative to welfare in a lake in which optimal prevention measures were adopted before an invasion (figure 2a versus figure 2b); thus, under these model assumptions, prevention would be a good investment. Additionally, 'subopt', 'random' and 'do nothing' represented null strategies, which society could also apply; the optimal strategies resulted in the highest cumulative welfares, demonstrating internal model consistency and that the SDP works within the constraints of the model (figure 2a-c). In the invaded lake, the optimal investment in control declined over time because control was effective; low welfare was acceptable in the first few years to maximize welfare over the long term (figure 2e). Time-frame was a major determinant of the optimal strategy. With a 5 year time horizon and an uninvaded lake, the optimal strategy was to spend nothing on either prevention (figure 2i) or control (figure 2f). Our modelling framework thus permitted an explicit demonstration of the consequences of long-term environmental perspectives versus short-term political perspectives for optimal control.

Investments in labour and capital were influenced by the initial environmental state, representing another level of interaction between ecological and economic parameters (figure 2g versus figure 2h). The level of risk of invasion that society should accept changed over time, but was never reduced to zero because the cost of achieving the last increment of risk reduction was not offset by the extra benefits (figure 2j-l). In all scenarios, the acceptable risk increased toward the end of the time horizon because the costs beyond the time horizon were excluded from consideration (figure 2j-l). While these results reflect one hypothetical parameter set, they demonstrate that the modelling framework is useful for examining the interaction of ecological and economic factors, and for providing quantitative guidance for public policy.

Next, we tested the application of our framework to a real-world problem—zebra mussel invasions in lakes. We modelled changes in zebra mussel population over time, using rates of recruitment, growth and survival structured by age or size and seasonality. We focused on the impact on industry of reduced water intake efficiency caused by fouling of pipes by zebra mussels. Although lake-wide control of established zebra mussels is currently impossible, industry applies toxins to pipes to reduce fouling (see Deng (1996) for these and other methods). We used the model to choose between alternative control strategies in terms of when and how often power plants should perform control efforts using toxins. As prevention of zebra mussel spread to uninfected lakes is possible through public education and the management of boat traffic (Johnson et al. 2001), we also considered how much society should be willing to pay to reduce the probability of invasion of currently uninvaded lakes, to maximize the net benefits. We considered spread by boat traffic, as this is the primary vector of zebra mussel spread to inland lakes (Johnson et al. 2001).

Results illustrated that after invasion the optimal strategy for our modelled power plant is to perform one control event per year in September (different plants may have different optimal strategies). Control is now conducted twice per year in the power plant that provided us with

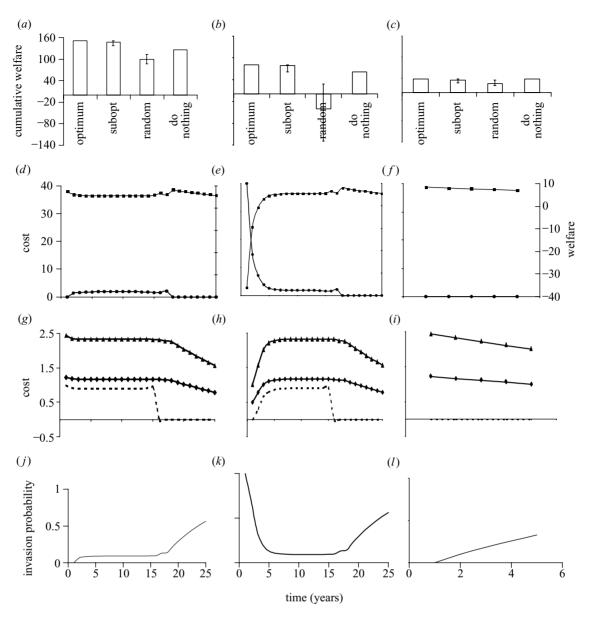


Figure 2. An analysis of a hypothetical invasion. Each datum was a projected value at each time interval, weighted by the probability of being in a state, summed across all states. The panels show the projected cumulative welfares (a-c), optimal welfare (squares) and control expenditure (circles (d-f)), labour (triangles), capital (diamonds) and prevention expenditure (dashed line (g-i)), and the invasion probability that society should accept for optimal welfare (j-l). 'Optimal' used optimal strategies, 'subopt' used random strategies during one time interval, 'random' used random strategies at all intervals and 'do nothing' spent nothing. The error bars represent one standard deviation. Shown for 25 year uninvaded (a, d, g and j), 25 year invaded (b, e, h and k) and 5 year uninvaded (c, f, i and l) time horizons.

data, but moving to a single control event in September is currently under consideration.

On the question of preventing new lakes from infestation, society should implement prevention policies when $C_E < E(W_{0,t} - W_{1,t})$, where C_E is the cost of prevention, E is the absolute reduction in probability of invasion and $W_{0,t}$ and $W_{1,t}$ are the cumulative welfares given optimal control and prevention strategies summed from time t to the time horizon of an uninvaded lake and newly invaded lake, respectively. Using data from 95 lakes, we derived an estimate for probability of invasion of 0.7% per month (see § 2b(iii)). As empirical estimates of the costs or effectiveness of particular prevention strategies do not yet exist, we modelled how much society should be willing to pay to reduce the probability of invasion by a given amount, considering only damages to industry. We determined the

level of expenditure at which the costs of prevention equalled the benefits of reducing invasions by a given probability (i.e. society would derive a net benefit if expenditures below this level achieved a given effectiveness of prevention). For example, assuming a constant probability of invasion of 0.7% per month, our analyses indicated that to reduce the probability by 10% it would be beneficial for society to pay up to US\$27 000 month⁻¹ (US\$324 000 year⁻¹) on prevention for a single lake containing the modelled power plant (figure 3).

4. DISCUSSION

Our hypothetical example and our real-world example with zebra mussels for a single generic power plant demonstrate the utility of our quantitative framework for ask-

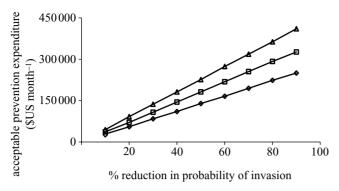


Figure 3. Acceptable expenditure for prevention. The graph shows the prevention expenditure (in US\$) that society should accept to obtain a given reduction in the probability of invasion, given an initial probability of invasion. We simulated three initial probabilities of invasion per month: 0.7% (diamonds: result based on 95 lakes), 10% (squares), and 20% (triangles). For each, we simulated a reduction in invasion due to prevention of 10%–90%. Acceptable expenditure increased linearly with reduction in invasion probability. Heterogeneous slopes indicated an interaction between reduction due to prevention and the initial probability of invasion.

ing key questions and guiding policy. For instance, our analysis for zebra mussels suggests that it would be beneficial to spend up to US\$324 000 year⁻¹ to obtain a modest reduction in the probability of zebra mussel invasion into a single lake containing our modelled power plant. The actual cost of such a reduction would probably be much lower (e.g. a full-time manned inspection station would cost less). For comparison, in 2001 the US Fish and Wildlife Service distributed to all states combined a total of US\$825 000 for prevention and control efforts for all aquatic non-indigenous species *in all lakes*. Thus, although separate analyses would need to be done for different lakes and different industries, and could also include alternative methods of prevention, these results suggest that prevention is currently underfunded.

There are a number of challenges that remain to be addressed to improve policy decisions further.

- (i) For a comprehensive accounting of social benefits, it is important to consider non-market values. While we recognize the challenges of nonmarket valuation (Brown & Shogren 1998; Costanza 2000; Heal 2000; Ludwig et al. 2001), policymakers can benefit from more information about probable values that are attached to ecological services. Invaders have the potential to influence biodiversity, aesthetics, recreation and property values. For instance, zebra mussels are decimating native mussels, 60% of which are already endangered (Ricciardi et al. 1998), which may increase the amount that society is willing to pay for prevention. Conversely, zebra mussels may improve water clarity, which may be positively valued (Effler & Siegfried 1998). The analysis of positive and negative impacts on ecosystems will allow a more accurate depiction of the true consequences of invasive species.
- (ii) We have only considered risk-neutral optimizations.Society may be risk averse towards some potential

- invaders. Quantification and understanding of such preferences would allow better assessment of the amount society should spend on prevention.
- (iii) We should expand analyses to incorporate multiple species simultaneously. Although species-specific assessments are the core of screening protocols for intentional pathways of introduction, other pathways, especially unintentional pathways, such as ballast water in ships, carry hundreds of species at a time (Aquatic Sciences Inc. 1996). Risk analyses on multiple species would be useful to understand better the risks created by the pathway.
- (iv) The framework should be extended to permit largescale heterogeneous landscapes, where the environment and optimal policy may differ between areas, and where policies in one local area may have ramifications in others.

Such analyses can use available information to facilitate the interaction between risk assessors and managers (Committee on Environment and Natural Resources 1999), provide quantitative rationale for policy decisions and help policymakers allocate society's resources most efficiently. Efficient resource allocation is crucial given that inadequate funding to achieve environmental objectives is the norm (Brown & Shogren 1998). Furthermore, even if limited to market values, bioeconomic cost-benefit analysis of non-indigenous species can strengthen the rationale for actions that achieve environmental goals (Van Wilgen et al. 2001). For example, our zebra mussel analysis—based only on market values of damage to industry—suggests that a much higher value should be placed on prevention than is currently spent. Greater prevention will protect the environment while also protecting industry.

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