

Finding optimal control strategies for invasive species: a density-structured model for *Spartina alterniflora*

CAZ M. TAYLOR and ALAN HASTINGS

Department of Environmental Science and Policy, One Shields Avenue, University of California, Davis, CA 95616–8755, USA

Summary

1. There are very few general guidelines available to improve the process of eradicating invasive species. We addressed the basic question of whether it is more efficient to prioritize the removal of outliers or core populations of an invasive grass, *Spartina alterniflora*.
2. We used a structured model in which the population of the invasive species is partitioned into different classes based on local conspecific density in order to investigate density-based eradication strategies.
3. The *Spartina* population at a Pacific coast estuary in Washington state, USA, is subject to an Allee effect: at low density plants produce fewer propagules than in high-density coalesced meadows. Plants at low density, however, are able to spread faster vegetatively. We used a genetic algorithm to find the optimal division of resources between removal of high-density and low-density plants. We explored the consequences of the Allee effect, contrasting financial budgets available for control operations and the inclusion of seedling control in addition to the control of mature plants.
4. We found that the optimal strategy was dependent on the annual budget available for control. At low and medium budgets, it was necessary to remove the low-density plants first to achieve eradication, but if more money was available then the optimal strategy was to prioritize high-density areas.
5. Without an Allee effect the optimal strategy would always be to prioritize the removal of fast-growing, low-density sub-populations. Seedling control did not change the optimal strategy but did, in some cases, reduce the cost of eradication.
6. *Synthesis and applications.* Given the uncertainty in future budgets allocated for control of invasive *Spartina*, we recommend a strategy that prioritizes the removal of low-density subpopulations of *S. alterniflora* over high-density subpopulations. The Allee effect in this system is not sufficiently strong to outweigh the importance of the rapid vegetative spread of the plants at low density.

Key-words: Allee effect, biological invasions, depensation, eradication, genetic algorithm, pollen limitation, *Spartina alterniflora*

Journal of Applied Ecology (2004) **41**, 1049–1057

Introduction

Invasive species are notoriously difficult and expensive to control or eradicate, and it is important to try to find the most efficient management strategies (Byers *et al.* 2002). Prevention is usually more cost-effective than post-entry eradication or containment (Mack *et al.* 2000; Rejmanek 2000; Leung *et al.* 2002), but obviously it is already too late to use this option for the many estab-

lished invasions. The dynamics of spread of invasive species have been successfully captured in various population models (reviewed in Hastings 1996; Higgins & Richardson 1996; Shigesada & Kawasaki 1997) but these have been used surprisingly infrequently to find optimal control strategies (Higgins & Richardson 1996; Higgins, Richardson & Cowling 2000).

Several aspects of control can be optimized. In agricultural crop–pest systems, the objective is often to find the best integration of control methods (biological, cultural and chemical) and the best within-season scheduling of pesticide application in order to maximize crop harvest and thus profit (Shoemaker 1981; Shoemaker 1982; Plant & Mangel 1987; Pandey & Medd 1991).

Correspondence: Caz M. Taylor, Department of Environmental Science and Policy, One Shields Avenue, University of California, Davis, CA 95616–8755, USA (fax +530 752 3350; e-mail cmtaylor@ucdavis.edu).

Optimal integration of control methods is also important for management of environmental weeds (Randall 1996; Buckley *et al.* 2004). When biological control agents are introduced to control an invasive species, one objective is to optimize the timing and size of releases in order to maximize the establishment of agents (Shea & Possingham 2000). Another objective is to find the most vulnerable life-history stages or transitions and thereby determine the best combination of biocontrol agents or other control techniques to reduce the population growth rate (Shea & Kelly 1998; Buckley, Briese & Rees 2003a,b). Barrier zones can be used to contain or slow the spread of an invasion, and a population model has been used to find the optimal number and placement of traps within such a zone for the control of the invasive gypsy moth (*Lymantria dispar*) (Sharov & Liebhold 1998b; Sharov, Liebhold & Roberts 1998). Deciding between different objectives, such as whether to eradicate, stop or slow the spread of an invasive species, requires economic long-term cost-benefit analysis (Sharov & Liebhold 1998a).

We address the question of whether it is more efficient to prioritize removal of young, low-density areas (outliers) at the edge of an invasion or older core population areas when using mechanical or chemical control methods (Moody & Mack 1988). Different approaches lead to different answers. The population biology approach suggests that, in general, outliers contribute the most to range expansion and should be removed first, whereas the metapopulation approach suggests prioritizing core populations that supply most of the new propagules (Hulme 2003).

Menz, Coote & Auld (1980) used a spatial simulation model to compare two control strategies: (i) inside-out (i.e. starting from the high-density centre of the invasion and moving to the lower density outliers); and (ii) the opposite, outside-in. They found that inside-out is cheaper when the spread rate is high, although they cautioned that this strategy needs a consistently high annual budget and incurs a higher risk of the invasion becoming unmanageable if the budget is not met every year. Wadsworth *et al.* (2000) found that prioritizing small satellite populations in riparian weeds was less efficient than controlling the highest density areas.

All other work on this question determines that it is better to prioritize outliers. Moody & Mack (1988) used a non-spatial simulation model of a plant spreading by multiple foci to address whether it is most effective to remove a proportion of the original 'main' invasion or a proportion of outliers, which they termed 'nascent foci'. They concluded that removing the outliers is a better strategy because such strategies lead to a longer time until the total area of the outliers exceeds the area of the main invasion (crossover time). However, maximizing the crossover time may not be the appropriate goal. It is, in fact, straightforward to construct scenarios in which strategies with a shorter crossover time produce faster or cheaper containment than those with longer crossover times. Both Higgins, Richardson & Cowling

(2000) and Grevstad (in press) used spatial simulation models of plant invasions to compare removal strategies that prioritize high-density sites with those that prioritize low-density sites, and both concluded that low-density sites should take precedence. Higgins, Richardson & Cowling (2000) further concluded that prioritizing removal of juveniles is more cost-effective than prioritizing removal of mature plants.

Direct simulation of different strategies is useful, and the most appropriate scheme in many cases but does not allow for mathematical or algorithmic optimization of strategies. In this study we used a genetic algorithm (Goldberg 1989) to find optimal density-based control strategies. Genetic algorithms belong to a class of algorithm known as stochastic global optimization (Torn & Viitanen 1999; Fouskakis & Draper 2002) that have the philosophy of using randomness in a constructive way to search globally for an optimal solution. These algorithms have been widely applied to engineering, economic and biological problems. The most common optimization technique for bio-economic problems, especially for pest control problems, is stochastic dynamic programming (SDP) (Bellman & Dreyfus 1962; Shoemaker 1981; Shoemaker 1982; Pandey & Medd 1991; Shea & Possingham 2000). However, SDP requires a model of low dimension, and for a structured population model the number of possible states of variables often exceeds the number that is computationally tractable (Shoemaker 1981).

Our population model is unusual in that it is structured by density. Structured population models usually partition the population into age, stage, physiological or size classes, under the rationale that the vital rates of individuals are age-, stage-, physiologically or size-dependent (Cushing 1998; Caswell 2001; De Roos, Persson & McCauley 2003). However, in some systems vital rates are dependent on conspecific density. When species are subject to an Allee effect (Allee 1958; Stephens, Sutherland & Freckleton 1999), also known as depensation, vital rates are depressed at low density. Several mechanisms can lead to an Allee effect, including diminished mate-finding opportunities in animals, pollen availability in plants and higher predation rates when conspecifics are few or widely spaced (Courchamp, Clutton-Brock & Grenfell 1999). Vital rates, such as fecundity and mortality, can also be suppressed at high densities due to intraspecific competition (often termed density-dependence). In our study system, the invasion of an intertidal grass into a Pacific estuary, space limitation and an Allee effect lead to an inherent trade-off between the removal of high-density and low-density plants. The low-density plants at the edge of an invaded area grow faster vegetatively because they are not subject to the space limitations of the high-density plants, but their isolation from one other leads to pollen limitation and reduced seed production (Davis *et al.* 2004a,b). While it is possible to have density-dependent vital rates in an age- or stage-structured model (Caswell 2001), we instead created a model in which the population is structured

into density classes in order to best represent these density-dependent vital rates (Taylor *et al.* 2004).

In this study, we extend the model to include annual plant removal and use it to find optimal partitioning of resources between the high-density main invasion and the low-density invasion edge. Additionally we consider the effect of seedling control, different levels of available annual resources, required time to eradication and the Allee effect in determining the optimal control strategies.

Materials and methods

SPECIES AND STUDY SYSTEM

Spartina alterniflora Loisel. is a perennial, intertidal grass native to Atlantic estuaries of North America. It was accidentally introduced into Willapa Bay, an estuary on the Pacific coast in the southern part of Washington State, about 100 years ago and has spread to occupy vast areas of mudflat that, prior to this invasion, had no emergent vegetation. *Spartina* now fringes the entire (43 × 10-km) estuary and affects 72 km² (Murphy 2003). If not checked, it is expected eventually to occupy the entire 230 km² of available mudflat in Willapa Bay. *Spartina* recruits from single seeds and grows rhizomatically into circular plants comprising a single genet (clone). Initial recruitment is at low density and clones grow circumferentially, increasing in diameter as rhizomes expand outwards. In time, clones merge to form dense continuous meadows. The process is reminiscent of bacterial colonies growing on a Petri plate. Seed of *Spartina* disperses great distances by floating on waterborne wrack in winter within Willapa Bay. Some goes out into the sea and the dominant current carries wrack northwards (Sayce, Dumbauld & Hidy 1997). Over the past decade seedlings have appeared at locations hundreds of kilometres north of Willapa Bay as far as the mouth of the Copalis River (Sayce, Dumbauld & Hidy 1997; Murphy 2003).

Attempts to control the spread started in the early 1990s, yet the population in Willapa Bay has continued to expand rapidly, despite the approximately \$1.6 million that was spent on control from 1998 to 2002 (Reeves 1998, 1999, 2000; Murphy 2001, 2002). An additional \$2.4 million was spent on control in 2003 and the state and federal agencies involved in the control programme believe that it will be possible to eradicate the population if this significantly larger effort can be sustained (Murphy 2003). Multiple methods of control are employed, including pulling seedlings by hand, attempting to remove adult plants mechanically by mowing, crushing and tilling, and spraying with herbicide (Murphy 2001, 2002, 2003).

Vital rates in *Spartina* are strongly dependent on the local conspecific density. Low-density *Spartina* individuals, because of their isolation from one another, are subject to pollen limitation and thus produce very little seed relative to the high-density individuals (Davis *et al.* 2004a,b). However, low-density plants are not

subject to the space limitation of plants in the high-density meadows and are able to spread much faster clonally (Taylor *et al.* 2004). Our model partitions a *Spartina* population into three classes: juveniles, low-density individual clones and high-density meadows (Taylor *et al.* 2004). This model structure allows us to most easily find the best density-based strategies.

DENSITY-STRUCTURED MODEL

We simulate the spread of *Spartina* in a 1-km² area of mudflat by partitioning the *Spartina* population into three classes representing different density stages: seedling, clone and meadow. The variables of the system represent the proportion of the total mudflat area occupied by seedlings, the proportion of the total mudflat area occupied by clones, the proportion of the total mudflat area occupied by meadows and number of distinct clones and meadows in the population. We define J_t as the proportion of the total available area occupied by juveniles or seedlings at time t , I_t as the proportion of the total available area occupied by clones, and M_t as the proportion of the total available area occupied by meadows. $(N_c)_t$ is the number of clones. $(N_m)_t$ is the number of meadows.

The area occupied at time $t + 1$ is given by three difference equations that are non-linear because the parameters are not constant:

$$J_{t+1} = (f_J)_t I_t + (f_M)_t M_t \quad \text{eqn 1}$$

$$I_{t+1} = J_t + (\mu_I)_t (1 - \eta_I) I_t \quad \text{eqn 2}$$

$$M_{t+1} = (\mu_M)_t \eta_I I_t + (\mu_M)_t M_t \quad \text{eqn 3}$$

The number of clones changes in the following way:

$$(N_c)_{t+1} = (N_c)_t + S J_t - \eta_I (N_c)_t \quad \text{eqn 4}$$

The number of meadows changes in the following way:

$$(N_m)_{t+1} = (N_m)_t - \frac{1}{2} (\eta_{MM})_t (N_m)_t + \frac{1}{2} (\eta_{II})_t (N_c)_t \quad \text{eqn 5}$$

where S ($= 1 \text{ km}^2$) is the total area of mudflat available, μ_I is the vegetative growth rate of clones and μ_M the equivalent for meadows. η is the rate at which clones coalesce into each other and into existing meadows to create more meadows, η_{MM} is the rate at which meadows coalesce into other meadows, and η_{II} is the rate at which clones merge into other clones. f_J is the total fecundity of clones per unit area. f_M is the total fecundity of meadows. The Allee effect is incorporated in that f_J is much smaller than f_M . If all these quantities were constant, we would have a linear stage-structured model but in fact we assume that the fecundities of clones (f_J) and meadows (f_M), the coalescence rates of clones into meadows (η , η_{MM} and η_{II}) and growth rates of both meadows (μ_M) and clones (μ_I) depend on the

area occupied by clones, the area occupied by meadows, the number of clones, the number of meadows and on four underlying fixed parameters. The growth rate and fecundities are density dependent; as the available mudflat fills up with *Spartina*, the vegetative growth rates and the establishment of new seedlings (which is incorporated into the fecundity parameters) decrease towards zero. A full description of this model and its development is given in Taylor *et al.* (2004) and in an online supplement to this paper.

The annual removal of juveniles, clones and meadows is modelled by subtracting proportions of the total mudflat area, $(R_J)_t$, $(R_I)_t$ and $(R_M)_t$, respectively, from equations 1, 2 and 3, and by subtracting from equations 4 and 5 a proportion of the number of clones and meadows equal to the proportion of clone and meadow area removed. If the area to be removed exceeds the existing area we remove all the existing area. We assume that $(R_J)_t$, $(R_I)_t$ and $(R_M)_t$ are areas of *Spartina* that are able to be permanently removed, not areas treated. So if, for example, the control treatment used is only 50% effective then two times R_M would need to be treated in order to remove R_M .

$$J_{t+1} = \max[(f_J)_t I_t + (f_M)_t M_t - (R_J)_t, 0] \tag{eqn 6}$$

$$I_{t+1} = \max[J_t + (\mu_I)_t (1 - \eta_I) I_t - (R_I)_t, 0] \tag{eqn 7}$$

$$M_{t+1} = \max[(\mu_M)_t \eta_I I_t + (\eta_M)_t M_t - (R_M)_t, 0] \tag{eqn 8}$$

$$(N_J)_{t+1} = \max \left[(N_J)_t + S J_t - \eta_I (N_J)_t - (N_J)_t \frac{(R_J)_t}{I_t}, 0 \right] \tag{eqn 9}$$

$$(N_M)_{t+1} = \max \left[(N_M)_t - \frac{1}{2} (\eta_{MM})_t (N_M)_t + \frac{1}{2} (\eta_{II})_t (N_I)_t - (N_M)_t \frac{(R_M)_t}{M_t}, 0 \right] \tag{eqn 10}$$

Finding optimal control strategies

DEFINITION OF CONTROL STRATEGY

If a control strategy is applied for a finite number of years (T), removal of seedlings, clones and meadows can be represented by three vectors of length T :

$$\bar{R}_J = [(R_J)_1, (R_J)_2, \dots, (R_J)_T]$$

$$\bar{R}_I = [(R_I)_1, (R_I)_2, \dots, (R_I)_T]$$

$$\bar{R}_M = [(R_M)_1, (R_M)_2, \dots, (R_M)_T]$$

Removal of juveniles takes place early in the season, whereas removal of clones and meadows is concurrent and thus competing. We therefore put an upper limit on the total area of adult plants, $(R_A)_t = (R_I)_t + (R_M)_t \leq R_{max}$, that can be removed in any given year, and find the optimal division between removal of clones and removal of meadows. Two vectors each of length T ,

(\bar{R}_A) and (\bar{P}_M) , comprise the control strategy. The elements of \bar{P}_M , $0 \leq (P_M)_t \leq 1$, are the meadow proportion of the total area removed in each time step.

We discretise the removal strategies to make it possible to optimize strategies using a genetic algorithm Goldberg 1989. Moreover, allowing the strategies to take continuous values delivers more precision than could actually be implemented. For every time step, we allow removal of 0%, 25%, 50%, 75% or 100% of the maximum, R_{max} , and allocate to meadow removal 0%, 25%, 50%, 75% or 100% of the area removed. So:

$$(R_A)_t = [0, 0.25, 0.5, 0.75, 1] \times R_{max}$$

$$(P_M)_t = [0, 0.25, 0.5, 0.75, 1] \times R_A$$

CONTROL OBJECTIVE AND SCENARIOS

Our goal is to find strategies that (i) eradicate the invasion within T years and (ii) minimize total effort and risk of colonization of other sites within the bay. For the latter, we use a multi-objective technique and minimize the product of the effort and risk. Eradication is chosen as a goal for each site because regrowth is certain if any *Spartina* is left at the end of the control programme. For each strategy we calculate the following.

AreaLeft: the area of the invasion left at the end of the strategy (after T years).

Cost: the total area that is removed during the control. We assume that there is a constant cost of removal per unit area. We also assume that the cost per unit area of removing meadow plants is equal to the cost per unit area of removing clones.

Risk: the total seed production during the control years. We assume that the risk of seed escaping from this site and colonizing other sites in the bay is linearly proportional to this number.

The objective function (which is to be minimized) of each strategy is give by:

$$Objective\ Function = \begin{cases} AreaLeft & \text{if } AreaLeft > 0 \\ Cost \times Risk & \text{if } AreaLeft = 0 \end{cases}$$

We are interested in finding optimal strategies and their associated cost and risk for five scenarios.

Base scenario: eradication must occur within 10 years. No control of seedlings is included and the population is subject to an Allee effect (fecundity of clones is much lower than fecundity of meadows).

With seedling control: this is the same as the base scenario except we add the removal of up to 100 seedlings per year.

No Allee effect: this scenario is the same as the base scenario except we take away the Allee effect by allowing the fecundity of the clones to be the same as that of the meadows. This scenario does not represent the true dynamics of the population and is designed to determine the consequences that an Allee effect might have on control decisions.

Table 1. Initial conditions at start of control for early, established and late invasions. Calculated from the model after 20, 40 and 60 years, respectively. Total area available is 1 km²

	Early invasion	Established invasion	Late invasion
Age of invasion (years)	20	40	60
Area occupied by juveniles (km ²)	1	82	4 000
Area occupied by clones (km ²)	511	10 771	50 400
Area occupied by meadows (km ²)	8	6 029	510 500
Number of isolated clones	3	193	9 620
Number of meadows	1	14	524
Total area occupied (km ²)	520	16 882	564 900
Percentage of available area occupied	0.05	1.7	56.5

Fast eradication: eradication must take place within 5 years otherwise this is the same as the base scenario.

Slow eradication: eradication must take place within 20 years otherwise this is the same as the base scenario.

OPTIMIZATION

Using the model without any removal, we calculate the initial state of a 20-year-old, 40-year-old and 60-year-old invasion labelled early, established and late, respectively. The initial conditions are shown in Table 1. The early invasion is dominated by uncoalesced clones, the established invasion has a significant area of both clones and meadows, and the late invasion is dominated by meadows. Control is then applied to the invasion for a specified (5-, 10- or 20-year) period. For every year there are 25 possible combinations of management options, leading to 25¹⁰ (c. 10¹⁴) possible control strategies for a 10-year control programme, 25⁵ (c. 10⁷) possible strategies for a 5-year programme and 25²⁰ (c. 10²⁸) possible strategies for a 20-year programme.

The genetic algorithm starts by randomly generating 10 000 control strategies. Each strategy is simulated in the model and the value of the objective function (described above) is calculated. Each iteration of the algorithm picks the 100 'best' strategies, i.e. those that produce the lowest values of the objective function, and uses a simple crossover function (Goldberg 1989) to generate 10 000 new strategies from every possible two-way recombination of the 100 best strategies. The crossover function generates a random crossover point, *cp*, for each vector ($\bar{\mathbf{R}}_A$ and $\bar{\mathbf{P}}_M$) of the two strategies to be recombined and generates new vectors by combining the first *cp* elements of the vector from one strategy with the last ($T - cp$) elements of the vector of the other strategy. There is also a small probability ($P = 0.05$) of mutation (to a value chosen randomly from a uniform distribution of the five possible values) for each element of both ($\bar{\mathbf{R}}_A$) and ($\bar{\mathbf{P}}_M$) to maintain diversity and improve the performance of the algorithm (Goldberg 1989). The algorithm terminates when an iteration does not reduce, within a tolerance of 10⁻⁶, any component (*AreaLeft*, *Cost* or *Risk*) of the current best value of the objective function.

We first calculated the minimal area that must be removed annually (R_{\max}) in order for eradication of an early, established and late invasion to be achievable.

We performed a binary search on the value of R_{\max} until we found the minimum value (to within 1% of initial invasion size) for which a strategy could be found to eradicate the invasion within T years. Since 1998, Washington State Department of Natural Resources has published yearly reports stating total expenditure and total area treated (Reeves 1998, 1999, 2000; Murphy 2001, 2003). We used these data to estimate the approximate cost of *Spartina* removal per square metre. We then translated the minimum R_{\max} value into an estimated minimum annual budget. We calculated the minimum R_{\max} and the minimal annual budget for each of the five scenarios described above.

We used the genetic algorithm to find the optimal division of resources between meadow and clone removal that could eradicate an established invasion at three annual budget levels (assuming an average value for the cost of removal per m²) corresponding to removal of 22%, 30% and 40% of the initial invasion. We repeated this for each of the five scenarios. We did not attempt to find the optimal control strategies for an early invasion that consists almost entirely of uncoalesced clones or for a late invasion that is dominated by meadows (Table 1). Only when the starting point of the invasion consists of large proportions of both clones and meadows is the optimal strategy of interest. We calculated the total expenditure and the relative risk of seeds from this site colonizing other sites for each of the optimal strategies for each budget level and each scenario.

Results

For an early invasion, at least 20% of the initial occupied area, or about 100 m², must be removed each year to effect eradication within 10 years. For an established invasion at least 22% of the initial occupied area must be removed annually, but this is about 3700 m². For a late invasion, at least 16% of the initial occupied area (approximately 90 000 m²) must be removed annually (Table 2). Calculations from the legislative reports gave a range of treatment costs of between \$0.05 m⁻² and \$0.13 m⁻² and an average of \$0.08 m⁻². Treatment was assumed in the reports to be about 50% effective, so the cost range for actual removal cost was between \$0.09 m⁻² and \$0.25 m⁻² and the mean was \$0.16 m⁻². Using these data, the minimum annual budget for eradicating a

Table 2. (a) Minimum area in terms of percentage of initial invasion that must be removed annually to effect eradication of the invasion. (b) Minimum annual budget needed to eradicate invasion assuming removal cost per square metre is \$0.09–\$0.25

	Early invasion	Established invasion	Late invasion
Initial size of invasion (m ²)	520	16 882	564 900
(a) Percentage initial invasion			
Base scenario (eradication within 10 years)	20	22	16
With seedling control	18	20	15
No Allee effect	25	23	16
Fast eradication (within 5 years)	33	39	38
Slow eradication (within 20 years)	16	17	8
(b) Minimum annual budget (\$)			
Base scenario (eradication within 10 years)	9–26	334–929	8 135–22 596
With seedling control	8–23	304–844	7 626–21 184
No Allee effect	12–33	349–971	8 135–22 596
Fast eradication (within 5 years)	15–43	593–1646	19 320–53 666
Slow eradication (within 20 years)	7–21	258–717	4 067–11 298

60-year-old invasion in 1 km² was between \$8100 and \$22 600. For a 40-year-old invasion, the minimum annual budget was \$330–\$930 km⁻², and for a 20-year-old invasion only \$9–\$26 km⁻² (Table 2b). Neither the Allee effect nor the inclusion of seedling control had a large effect on the minimum annual budget, except for an early invasion when the Allee effect increased the minimum budget needed. Faster eradication (within 5 years) increased and slower eradication (within 20 years) decreased the minimum annual budget dramatically, especially for a late invasion (Table 2).

For an established invasion, the type of strategy that was optimal depended a great deal on the annual budget. The best strategies (the ones that minimized the product of escapee risk and total expenditure) were ‘meadow-first’ strategies (Fig. 1b,c), but these required a high or medium annual budget (removal of 30% or more of the initial invasion, approximately \$800 assuming a cost of \$0.16 m⁻²). If a high annual budget was not available then it was necessary to remove the low-density clones first and focus in the second, third or fourth year on the meadows (Fig. 1a). Eradication using a meadow-first strategy was not possible when the budget was low (*c.* \$600 year⁻¹). Without the Allee effect (when fecundity of clones and meadows is identical), it was always better to remove faster growing clones first. Neither the addition of seedling control nor the desired eradication time qualitatively changed the optimal strategy under any of the conditions tested, although seedling control did substantially reduce the risk of colonization when the budget was low (Fig. 2b).

The annual budget also had a large effect on both the total expenditure and risk of colonizing other sites of the optimal strategy. Risk always decreased with increasing annual budget, whereas the lowest total expenditure (about \$4700 km⁻² for the base scenario) was the same when the annual budget was at its low or high value (Fig. 2a). Seedling control had a large effect on escapee risk when the budget was low, but the optimal strategy found in this case was more expensive by about \$500 over 10 years than for the base scenario (this did not

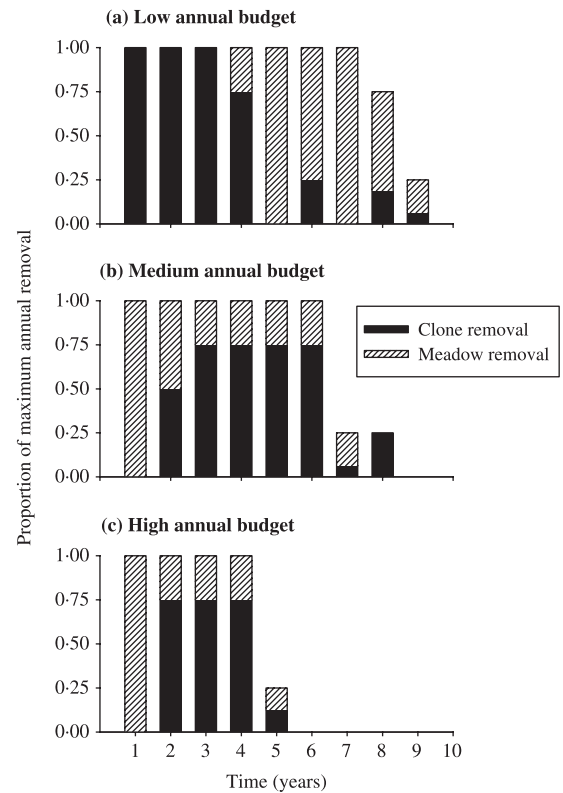


Fig. 1. Optimal strategies for eradication of an established (40 years) invasion when (a) annual budget is low (approximately \$600, corresponding to a maximum annual removal of 3700 m² or 22% of initial invasion), (b) annual budget is medium (approximately \$800, corresponding to a maximum annual removal of 5100 m² or 30% of initial invasion) and (c) annual budget is high (approximately \$1000, corresponding to a maximum annual removal of 6800 m² or 40% of initial invasion).

include the cost of removing the seedlings themselves). When the budget was medium or high, removing seedlings did not reduce the already low colonization risk but did result in strategies that were cheaper by \$600 and \$270, respectively (Fig. 2b). Removing the Allee effect always increased the escapee risk, increased the expenditure when the annual budget was low and

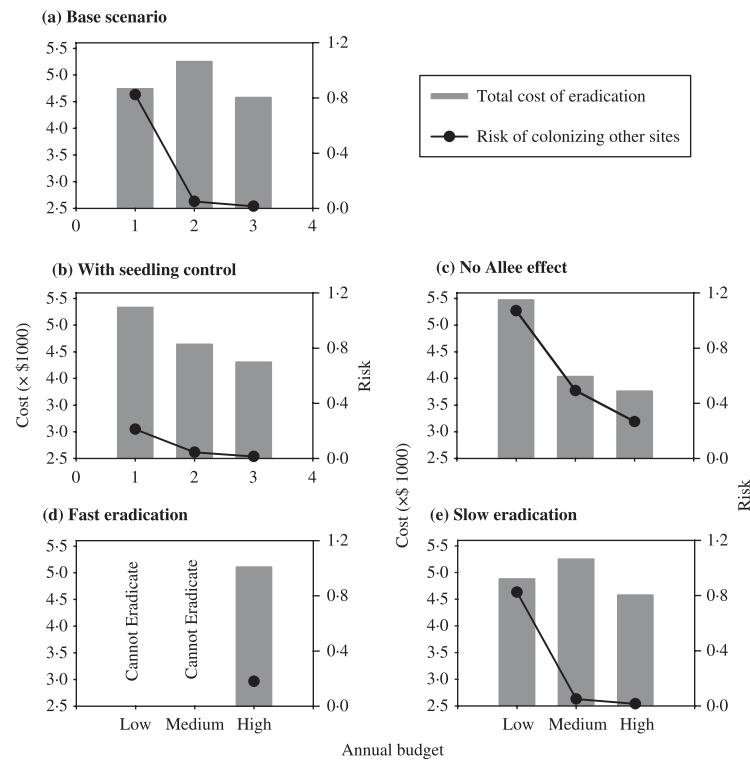


Fig. 2. Total expenditure and risk associated with the optimal control strategies for each of the five scenarios (a–e). Total expenditure (columns and left axes) in thousands of USA dollars, and number of thousands of potentially escaping seeds produced during control (circles and right axes). Assumes a removal cost of \$0.16 m⁻².

reduced the expenditure when the annual budget was medium or high (Fig. 2c). Faster or slower eradication had little effect on the expenditure or escapee risk. Fast eradication was only possible with a high annual budget. Slow eradication increased the expenditure when the budget was high (Fig. 2d,e).

Discussion

Although the best strategy that we found is to remove a large fraction of the area every year starting with the main invasion (meadow-first strategy), this is also the riskiest strategy as it requires large resources to be consistently available. When annual resources are lower, eradication is only possible if priority is given to the fast-growing low-density plants. This is the same conclusion that Menz, Coote & Auld (1980) reached, although for different reasons. Under Allee dynamics, as in *Spartina*, the strategy prioritizing the high-density meadows is optimal because it leads to a lower risk of new propagules. In other systems, prioritizing high density is optimal because of the inclusion of marginal (density-independent) costs or of costs of searching for infestations. If these costs are significant then removing high-density sites is likely to be more efficient (Menz, Coote & Auld 1980; Wadsworth *et al.* 2000). For a restricted annual budget or when there is no Allee effect, it is necessary to prioritize the fast-growing low-density plants, or the rate of spread of the invasion will exceed the rate of control (Moody & Mack 1988; Higgins, Richardson & Cowling 2000; Grevstad, in press). We

have shown that the optimal control strategy depends on both the biology of the invasive species and on the available annual commitment of resources.

We have previously shown that the Allee effect dramatically slows the rate of spread of *Spartina* (Taylor *et al.* 2004). We expected that eradication would be cheaper when the invasion was subject to Allee dynamics, and this was true when the annual resources were restricted (low annual budget). However, if high annual resources are available then the optimal strategy for a population with Allee dynamics is more expensive than for a population without Allee dynamics (Fig. 2a,c). The reason for this is found in the multiple-objective approach that we took. The more expensive strategy has a lower risk of escaping propagules than the less expensive strategy found for the non-Allee dynamics. There are two kinds of Allee effect, strong and weak (Wang & Kot 2001; Wang, Kot & Neubert 2002). With a strong Allee effect, growth rates become negative and the population will become extinct when it drops below a threshold density. For an invasive species with a strong Allee effect, eradication is easier because it is only necessary to reduce the population density to below this threshold (Liebhold & Bascompte 2003). *Spartina*, however, experiences only a weak Allee effect; the growth rates are lower at low density but never negative (Taylor *et al.* 2004). The weak Allee effect changes the optimal eradication strategy but does not always make eradication easier or cheaper.

The questions explored in this study are relevant to control of *Spartina* at a relatively small spatial scale.

The model simulates spread across a 1-km² site. The mudflats of Willapa Bay occupy about 230 km², about 72 km² of which is invaded to differing extents by *Spartina* (Murphy 2003). While the small-scale tactical questions addressed by this study are important for the optimization of control, a model of larger spatial scale would be needed to develop a full management plan for Willapa Bay (Mack *et al.* 2000; Grevstad, in press). In this system and in others the cost of control increases sharply with the length of time since invasion (Higgins, Richardson & Cowling 2000), as does the potential for propagule supply. A larger scale model is needed to explore whether control should focus on the recently invaded or more established sites or evenly throughout the bay. Lack of specific knowledge about the long-distance seed dispersal between sites in the bay has so far hampered development of such a model.

The control objective can radically change the strategy. We chose eradication as a goal because of the small spatial scale of this study and to minimize both cost and risk of escaping seeds. A goal of containment or slowing the spread may be more appropriate at a larger scale (Randall 1996; Sharov & Liebhold 1998a,b; Rejmanek 2000; Byers *et al.* 2002).

We structured our model by local density (uncoalesced clones and coalesced meadows) and by age (juveniles and adults). There is a long history in theoretical ecology of population models that are structured by age, physiological stage, some other physiological trait such as individual size (Metz & Diekmann 1986; Tuljapurkar & Caswell 1997; Cushing 1998; Caswell 2001), and occasionally by some other demographic trait (Lamberson *et al.* 1992; Waldstatter, Hadelér & Greiner 1988). The advantage of a structured model is that different classes can have different vital rates. It is well known that density of conspecifics can affect vital rates and it is therefore surprising that we were unable to find any other examples of density-structured models. The more common approach seems to be to use an age- or stage-structured model with density-dependent vital rates (Caswell 2001). We used difference equations to model discrete time, appropriate for an annually reproducing plant species, and a discrete set of possible states. To represent the individual's state as a continuous variable, integrodifference equations could be used for discrete time, and differential equations for continuously reproducing species. Such models could extend the concept of density structuring to include continuous time and/or continuous state.

MANAGEMENT RECOMMENDATIONS

We recommend that the agencies responsible for eradication of *Spartina* continue to prioritize the removal of low-density uncoalesced individuals, referred to as 'clone fields' in the legislative reports (Murphy 2003), over the high-density meadows. The vegetative spread of these low-density plants is so rapid that this strategy is necessary when resources are limited. Prioritizing

meadows is slightly cheaper when resources are high but the low-density-first strategy will also work and incurs less risk in the face of uncertain future budgets and uncertain efficacy of control techniques. These recommendations are consistent with results from comparing control strategies in a simple spatial model of *Spartina* that does not include the Allee effect (Grevstad, in press) and with general guidelines of weed control (Moody & Mack 1988; Hulme 2003).

Our results suggest that seedling control should continue to be considered as a possible adjunct control activity. Seedling removal used to be a component of the control plan (Murphy 2001) but is not mentioned in more recent reports (Murphy 2003). We do not have any data with which to estimate the cost of seedling control, but we can calculate the benefit of seedling control. Our model shows that when the annual budget is low, removing 100 seedlings km⁻² year⁻¹ from a 40-year-old invasion reduces the risk of escaping seed over a 10-year control programme by about 75%.

Acknowledgements

We would like to thank Janie Civile and Heather Davis for useful and insightful discussions. We are also grateful to Richard Wadsworth and to an anonymous referee for their help in improving this paper. This work was supported by a scholarship from the ARCS Foundation, San Francisco, and by the National Science Foundation Biocomplexity Grant No. DEB0083583 (P. I. Alan Hastings).

References

- Allee, W.C. (1958) *The Social Life of Animals*, revised edn. Beacon Press, Boston, MA.
- Bellman, R.E. & Dreyfus, S.E. (1962) *Applied Dynamic Programming*. Princeton University Press, Princeton, NJ.
- Buckley, Y.M., Briese, D.T. & Rees, M. (2003a) Demography and management of the invasive plant species *Hypericum perforatum*. I. Using multi-level mixed-effects models for characterizing growth, survival and fecundity in a long-term data set. *Journal of Applied Ecology*, **40**, 494–507.
- Buckley, Y.M., Briese, D.T. & Rees, M. (2003b) Demography and management of the invasive plant species *Hypericum perforatum*. II. Construction and use of an individual-based model to predict population dynamics and the effects of management strategies. *Journal of Applied Ecology*, **40**, 494–507.
- Buckley, Y.M., Rees, M., Paynter, Q. & Lonsdale, M. (2004) Modelling integrated weed management of an invasive shrub in tropical Australia. *Journal of Applied Ecology*, **41**, 547–560.
- Byers, J.E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale, W.M., Atkinson, I.A.E., Seastedt, T.R., Williamson, M., Chornesky, E. & Hayes, D. (2002) Directing research to reduce the impacts of nonindigenous species. *Conservation Biology*, **16**, 630–640.
- Caswell, H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation*, 2nd edn. Sinauer Associates, Sunderland, MA.
- Courchamp, F., Clutton-Brock, T. & Grenfell, B. (1999) Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution*, **14**, 405–410.

- Cushing, J.M. (1998) *An Introduction to Structured Population Dynamics*. Society Industrial and Applied Mathematics, Philadelphia, PA.
- Davis, H.G., Taylor, C.M., Civille, J.C. & Strong, D.R. (2004) An Allee effect at the front of a plant invasion: *Spartina* in a Pacific estuary. *Journal of Ecology*, **92**, 321–327.
- Davis, H.G., Taylor, C.M., Lambrinos, J.G. & Strong, D.R. (2004) Pollen limitation causes an Allee effect in a wind pollinated invasive grass. *Proceedings of the National Academy of Sciences*, **101**, 13804–13807.
- De Roos, A.M., Persson, L. & McCauley, E. (2003) The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecology Letters*, **6**, 473–487.
- Fouskakis, D. & Draper, D. (2002) Stochastic optimization: a review. *International Statistical Review*, **70**, 315–349.
- Goldberg, D.E. (1989) *Genetic Algorithms in Search, Optimization, and Machine Learning*. Addison-Wesley Publications Co., Reading, MA.
- Grevstad, F.S. (in press) Simulating control strategies for a spatially structured weed invasion: *Spartina alterniflora* in Pacific coast estuaries. *Biological Invasions*, in press.
- Hastings, A. (1996) Models of spatial spread: a synthesis. *Biological Conservation*, **78**, 143–148.
- Higgins, S.I. & Richardson, D.M. (1996) A review of models of alien plant spread. *Ecological Modelling*, **87**, 249–265.
- Higgins, S.I., Richardson, D.M. & Cowling, R.M. (2000) Using a dynamic landscape model for planning the management of alien plant invasions. *Ecological Applications*, **10**, 1833–1848.
- Hulme, P.E. (2003) Biological invasions: winning the science battles but losing the conservation war? *Oryx*, **37**, 178–193.
- Lamberson, R.H., McKelvey, R., Noon, B.R. & Voss, C. (1992) A dynamic analysis of northern spotted owl viability in a fragmented forest landscape. *Conservation Biology*, **6**, 505–512.
- Leung, B., Lodge, D.M., Finnoff, D., Shogren, J.F., Lewis, M.A. & Lambertini, G. (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **269**, 2407–2413.
- Liebhald, A. & Bascompte, J. (2003) The Allee effect, stochastic dynamics and the eradication of alien species. *Ecology Letters*, **6**, 133–140.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689–710.
- Menz, K.M., Coote, B.G. & Auld, B.A. (1980) Spatial aspects of weed control. *Agricultural Systems*, **6**, 67–75.
- Metz, J.A.J. & Diekmann, O. (1986) *The Dynamics of Physiologically Structured Populations*. Springer-Verlag, Berlin, New York.
- Moody, M.E. & Mack, R.N. (1988) Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology*, **25**, 1009–1021.
- Murphy, K.C. (2001) *Report to the Legislature: Progress of the 2001 Spartina Eradication Program*. Washington State Department of Agriculture, Olympia, WA.
- Murphy, K.C. (2002) *Report to the Legislature: Progress of the 2002 Spartina Eradication Program*. Washington State Department of Agriculture, Olympia, WA.
- Murphy, K.C. (2003) *Report to the Legislature: Progress of the 2003 Spartina Eradication Program*. Report no. PUB 805–110 (N/1/04). Washington State Department of Agriculture, Olympia, WA.
- Pandey, S. & Medd, R.W. (1991) A stochastic dynamic programming framework for weed control decision making: an application to *Avena fatua* L. *Agricultural Economics*, **6**, 115–128.
- Plant, R.E. & Mangel, M. (1987) Modeling and simulation in agricultural pest management. *SIAM Review*, **29**, 235–261.
- Randall, J.M. (1996) Weed control for the preservation of biological diversity. *Weed Technology*, **10**, 370–383.
- Reeves, B. (1998) *Report to the Legislature: Progress of the Spartina and Purple Loosestriple Control Programs*. Washington State Department of Agriculture, Olympia, WA.
- Reeves, B. (1999) *Report to the Legislature: Progress of the Spartina and Purple Loosestriple Control Programs*. Washington State Department of Agriculture, Olympia, WA.
- Reeves, B. (2000) *Report to the Legislature: Progress of the Spartina and Purple Loosestriple Control Programs*. Washington State Department of Agriculture, Olympia, WA.
- Rejmanek, M. (2000) Invasive plants: approaches and predictions. *Austral Ecology*, **25**, 497–506.
- Sayce, K., Dumbauld, B.R. & Hidy, J. (1997) Seed dispersal in drift of *Spartina alterniflora*. *Second International Spartina Conference* (ed. K. Patten), pp. 27–31. Washington State University, Pullman, WA.
- Sharov, A.A. & Liebhold, A.M. (1998a) Bioeconomics of managing the spread of exotic pest species with barrier zones. *Ecological Applications*, **8**, 833–845.
- Sharov, A.A. & Liebhold, A.M. (1998b) Model of slowing the spread of gypsy moth (Lepidoptera: Lymantriidae) with a barrier zone. *Ecological Applications*, **8**, 1170–1179.
- Sharov, A.A., Liebhold, A.M. & Roberts, E.A. (1998) Optimizing the use of barrier zones to slow the spread of gypsy moth (Lepidoptera: Lymantriidae) in North America. *Journal of Economic Entomology*, **91**, 165–174.
- Shea, K. & Kelly, D. (1998) Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications*, **8**, 824–832.
- Shea, K. & Possingham, H.P. (2000) Optimal release strategies for biological control agents: an application of stochastic dynamic programming to population management. *Journal of Applied Ecology*, **37**, 77–86.
- Shigesada, N. & Kawasaki, K. (1997) *Biological Invasions: Theory and Practice*, 1st edn. Oxford University Press, Oxford, New York.
- Shoemaker, C.A. (1981) Applications of dynamic programming and other optimization methods in pest management. *Ieee Transactions on Automatic Control*, **26**, 1125–1132.
- Shoemaker, C.A. (1982) Optimal integrated control of univoltine pest populations with age structure. *Operations Research*, **30**, 40–61.
- Stephens, P.A., Sutherland, W.J. & Freckleton, R.P. (1999) What is the Allee effect? *Oikos*, **87**, 185–190.
- Taylor, C.M., Davis, H.G., Civille, J.C., Grevstad, F.S. & Hastings, A. (2004) Consequences of an Allee effect on the invasion of a Pacific estuary by *Spartina alterniflora*. *Ecology*, **85** (in press).
- Torn, A. & Viitanen, S. (1999) Stochastic global optimization: problem classes and solution techniques. *Journal of Global Optimization*, **14**, 437–447.
- Tuljapurkar, S. & Caswell, H. (1997) *Structured Population Models in Marine, Terrestrial, and Freshwater Systems*. Chapman & Hall, New York, NY.
- Wadsworth, R.A., Collingham, Y.C., Willis, S.G., Huntley, B. & Hulme, P.E. (2000) Simulating the spread and management of alien riparian weeds: are they out of control? *Journal of Applied Ecology*, **37**, 28–38.
- Waldstatter, R., Hadel, K.P. & Greiner, G. (1988) A Lotka–Mckendrick model for a population structured by the level of parasitic infection. *Siam Journal on Mathematical Analysis*, **19**, 1108–1118.
- Wang, M.H. & Kot, M. (2001) Speeds of invasion in a model with strong or weak Allee effects. *Mathematical Biosciences*, **171**, 83–97.
- Wang, M.H., Kot, M. & Neubert, M.G. (2002) Integro-difference equations, Allee effects, and invasions. *Journal of Mathematical Biology*, **44**, 150–168.

Received 16 June 2004; final copy received 3 August 2004