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Simulating control strategies for a spatially structured weed invasion: *Spartina alterniflora* (Loisel) in Pacific Coast estuaries

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Abstract

Patterns in the spatial arrangement of invasive plant populations can provide opportunity for strategic placement of control efforts. Smooth cordgrass (*Spartina alterniflora*) is rapidly invading the intertidal mudflats of Pacific Coast estuaries. Its pattern of spread is distinctive. Seedlings establish in open mud and then grow vegetatively to form expanding circular patches, which dot the mudflats and eventually coalesce into a contiguous monospecific meadow. The invasion typically begins in the upper tide zone and then moves down the tidal gradient. A spatially explicit model was used to simulate the spread of *S. alterniflora* and compare various strategies for control in a situation where only a fraction of the total infestation could be controlled each year. A strategy of killing outlying patches first and then attacking the dense meadows (moving up the tidal gradient) led to eradication with up to 44% less time and effort than a strategy of attacking the dense meadows first and outlying patches second (moving down the tidal gradient). In the control of contiguous meadows located adjacent to the shoreline, the best strategy was to approach one end of the infestation, moving across the meadow to the other end. Suppression of seeds was not an effective control strategy. In general, effective control strategies were those that first eliminate the plant in areas where current or future vegetative growth is greatest. Application of these results in control programs for *S. alterniflora* and similar invasive species could greatly reduce the costs of control work and improve the likelihood of local or complete eradication.

Introduction

The realized and potential impacts of invasive non-indigenous plants have turned many natural areas into battle grounds for restoration. Rapidly invading weeds have proved particularly challenging to control. The development of efficient control strategies is necessitated by both the urgency to protect habitat before harm has been caused and the economic and environmental costs of mechanical and chemical control treatments.

One way that the management of invasive plants can be improved is by taking into account spatial patterning in the invasion of a landscape. Invasive plant populations are patterned in both the way they spread and in the spaces they invade. For example, most plant invasions involve spread at two spatial scales: long distance dispersal of seeds and local growth due to vegetative spread or local recruitment (Salisbury 1961; Baker 1974; Moody and Mack 1988). The result over time is a scattering of growing patches. Earlier invaded areas have relatively larger and denser patches and newly invaded areas, such as at the frontier of an invasion, have smaller and sparser patches. Habitat barriers and gradients also determine spatial patterning by funneling invasions into certain spaces and limiting their growth into others. The relevant question is where to place control treatments to maximize their effect on the weed population thereby minimizing the time and total cost necessary to reduce or eradicate the weed.

Theoretical population models are well developed in describing the patterns and rates of spread of invasive species, but have been remarkably underutilized for the purposes of strategizing control programs (Higgins and Richardson 1996; Dean 1998). An area of exception is the use of models to design patch spraying programs for weeds in agricultural fields (e.g. Audsley 1993; Cardina et al. 1997; Paice et al. 1998; Blumenthal and Jordan 2001). For environmental weeds invading the larger landscape, an exception is Moody and Mack's (1988) simple but insightful model demonstrating a clear advantage to controlling newly established outlying colonies in favor of large conspicuous infestations. Unfortunately, land managers are not always aware of this strategy, nor how much of a difference it could make within their particular weed control program. Lacking has been the application of Moody and Mack's concept in models tailored to specific weeds (Higgins and Richardson 1996). Moreover, there is a need for exploration of other forms of tactical approaches that take into account the spatial pattern of spread.

Invasion of the intertidal mudflats of Pacific coast estuaries by *Spartina alterniflora* (commonly called smooth cordgrass or Spartina) is a prime example of a spatially structured invasion in a relatively simple habitat for which strategic control efforts can be easily modeled and applied. *S. alterniflora* was introduced from the Atlantic coast of North America into Willapa Bay and North Puget Sound, WA and into San Francisco Bay, CA. In these areas it is a threat to birds, fish, and shellfish that depend on the open mud habitat (Simenstad and Thom 1995; Buchanan 1997; Sayce 1988). Round clonal patches dot the mudflats and spread vegetatively through rhizomes, eventually coalescing into expansive meadows (Figure 1). The upper tide zone tends to be invaded first because it is more favorable for seedling establishment. With time, plants establish further out from shore as growing upper tidal meadows serve as a source of increasing numbers of seeds. A distinctive upper boundary to the Spartina invasion is formed by the edge of the native salt marsh. Native forbs and grasses in this zone competitively exclude *S. alterniflora*. In Willapa Bay, where the *S. alterniflora* infestation is most advanced, the rate of invasion (increase in area covered) has been estimated at 17% per year (Reeves 1999). *S. alterniflora* can be found almost anywhere along the shoreline and far from shore in areas where wave energy is low and water depth is between approximately 0 and 3 m relative to the mean low water line (Feist 1999).

State and federal sponsored control programs are under way in Washington State, where more than $2 million annually is spent on control of *S. alterniflora* and the closely related *S. anglica*, which is invasive in Puget Sound (Murphy 2003). Available methods of control include hand pulling, tilling, crushing, herbicides, and biological control (Grevstad et al. 2003; Hedge et al. 2003). The difficulty and expense of controlling *S. alterniflora* coupled with its rapid rate of invasion dictate the need for the most efficient control tactics under an integrated weed management plan (Ebasco Environmental 1993). To this end, a spatially explicit stochastic simulation model was developed to address three questions: (1) should scattered outlying clones or dense meadows be controlled first?; (2) does the approach direction relative to the shape of the infestation and location of habitat barriers make a difference?; (3) how effective is seed suppression as a control tactic?

Materials and methods

Model

A grid-based model was created using Matlab® software to simulate the spread of *S. alterniflora* in a tidal mudflat. The model is in a class called interacting particle systems wherein the probabilistic fate of a grid cell in any time step is dependent on the state of neighboring cells. The grid dimension used in the simulations was 120 by 120 cells of 1 m^2 each. One axis of the model space follows a tidal elevation gradient, with the upper edge representing the native marsh boundary and the bottom edge representing the lower extent of *S. alterniflora* growth. All boundaries were considered to be absorbing, as would be the

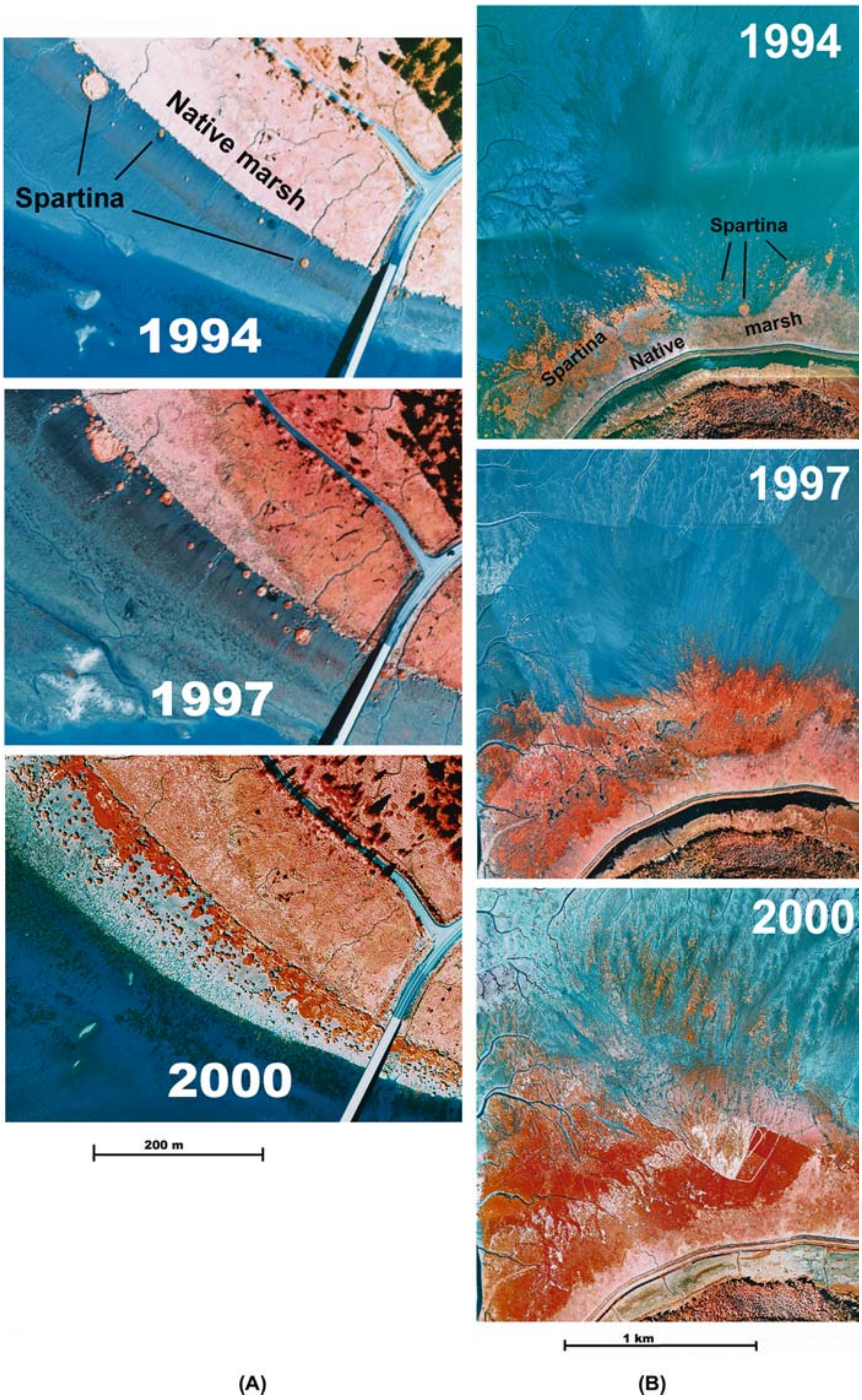

Figure 1. Illustrations of the pattern of invasion by *Spartina alterniflora* in sequences of color infrared aerial photographs taken in September 1994, 1997, and 2000. (A) Near mouth of Naselle River. (B) South Willapa Bay. Photos were compiled from aerial infrared photographs taken by Washington Department of Transportion and provided by the Washington State Department of Natural Resources.

case in a small cove or inlet bound on three sides by shoreline and one side by water too deep for *S. alterniflora* growth. Cells are considered either empty or occupied by *S. alterniflora*. They become occupied through vegetative spread from neighboring cells or by establishment of a seedling that dispersed from an occupied cell. Spread occurs primarily from the four immediately adjacent cells. Spread also can occur from the four neighboring corner cells but at 5% of the frequency of adjacent neighboring cells. This lower frequency of spread from corner cells allows for circular patch growth in a square grid universe. Spread rate was further adjusted by a factor of v to match field measures of vegetative growth (see below). If an empty cell is adjacent to more than one occupied cell then it has multiple independent chances to become occupied.

Estimates of vegetative growth were taken from color infrared aerial photographs obtained from the Washington Department of Natural Resources. These photographs, similar to those in Figure 1, were taken September of 1994, 1997, and 2000 at a scale of 1 : 6000 and covered the entire bay. Ten isolated clonal patches of varying sizes were selected from the 1997 photographs at each of seven sites throughout the bay. These same clones were located on the 1994 and 2000 photos. The diameter of each clone was measured for all three points in time so that there were two growth intervals for each clone. In some cases, the selected clones did not exist or were too small to be detected in 1994. Also, some clones could not be measured in 2000 because they had converged with other plants were no longer distinguishable. Omitting these cases, a total of 106 paired measurements from the two 3-year intervals were used to estimate vegetative growth rates. The mean increase in radius per year was 0.77 ± 0.034 m. Although growth rate varied among clones, it did not vary with the size of the clonal patch over a range of 0.9 to 57 m ($R^2 = 0.013$, $P = 0.25$). Setting the model parameter v to 0.70 led to model patches that grew at the measured rate of 0.77 m per year.

After spreading vegetatively, occupied cells produce seeds. Little is known about the actual dispersal distribution for *S. alterniflora* seeds, other than that they are dispersed by the tides and lead to a widely scattered distribution of seedlings (not tightly clumped). A Gaussian distribution was selected because of its relative simplicity (one parameter), its common use in dispersal models (e.g. van den Bosch 1990; Clark et al. 1999), and its reasonable fit to many wind/water dispersed seed shadows (e.g. Clark et al. 1999). The probabilistic rate of arrival in a given meter square is

$$s(d) = \frac{1}{\pi\alpha^2}\exp\left[-\left(\frac{d}{\alpha}\right)^2\right]$$

where d is the distance from the source and α is a parameter affecting dispersal distance. Because of the lack of certainty about seed dispersal distances, three levels of α were initially tested within a reasonable range (25, 50, and 100). Due to similarity in the outcome, only results for $\alpha = 50$ are presented. Seedling establishment was assumed to decline linearly with tidal elevation, a pattern consistent with aerial photo analysis by Feist (1999). The base seed survival rate was multiplied by the fractional distance along the tidal gradient. For example, a seed that lies half way between the lower and upper limit of Spartina growth is 50% as likely to establish as one that is at very upper edge of the elevation range.

Seedling survival rates were adjusted to allow the rate of increase in area in the model to match the observed overall rate of increase in area occupied by *S. alterniflora* in Willapa Bay. This rate has been reported by the Washington State Department of Agriculture to be 17% per year based on aerial photographs taken in 1994 and 1997 (Reeves 1999). This rate of increase also corresponds to the long term reported increase in Spartina coverage from 170 ha in 1984 (Ebasco Environmental 1992) to more than 3400 ha in 2003 (Murphy 2003). In the model, a match to this rate of increase was attained using a survival probability of 0.012 (measured during the time interval of $t = 20$–23). Examination of aerial photos clearly shows variation in rates of recruitment in different areas of the bay. The parameter estimate falls well within the observed range.

Large meadows or small outliers first

Simulated trials were used to compare the strategies of killing outlying clonal patches or large meadows first. A population was initiated from four occupied squares in the upper intertidal and was allowed to grow for 20 time steps (Figure 2).

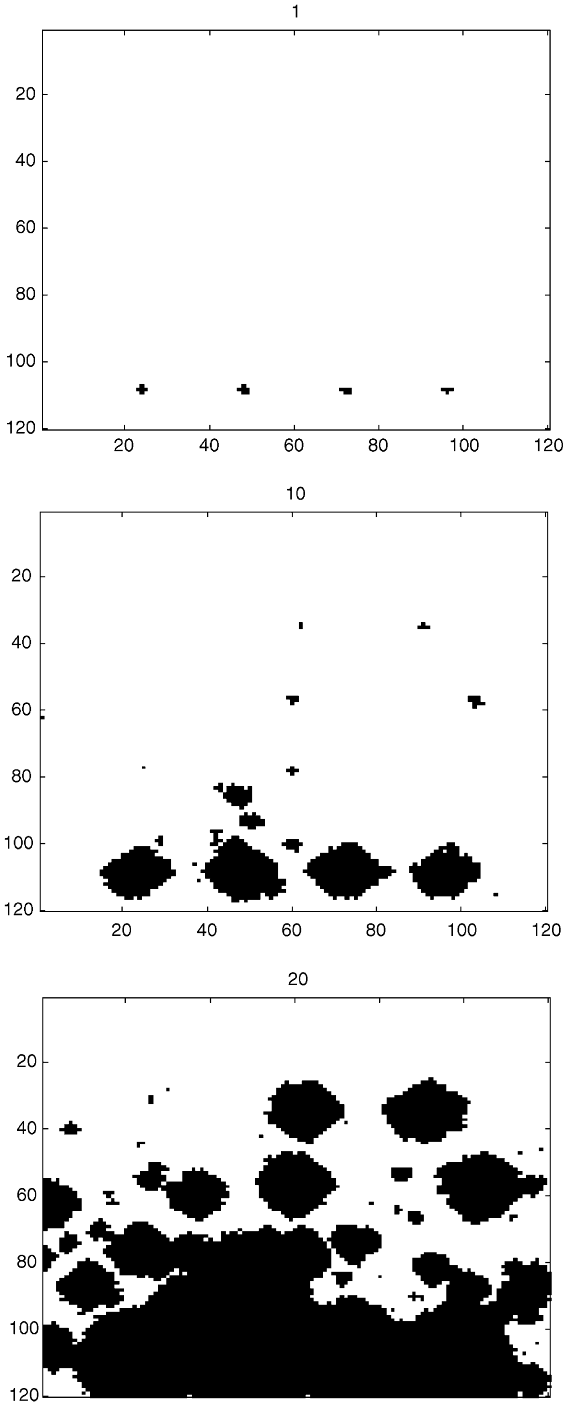

Figure 2. Simulated *Spartina alterniflora* distributions resulting from 4 initial plants at the end of years 1, 10, and 20 when no control is applied. Distributions similar to that in (C) were used as starting conditions in tests of control strategy efficacy.

At $t = 20$, two alternate control strategies were applied to identical starting conditions. In both cases, a fixed number of cells were removed each year. In the first strategy, occupied squares were removed row by row beginning from the lower tide zone and moving up the tidal gradient toward shore (Figure 3A). This removed sparse outlying patches first and then removed the larger contiguous meadow in the upper zone. In the second strategy, occupied squares were removed close to shore (upper tide zone) and then sequentially further from shore (Figure 3B). This removed the large contiguous meadow first and then the outlying clones. The level of control effort, measured as the number of squares removed each year, was varied from 500 to 1500. After treatments were applied, the remaining occupied cells continued to produced seed and grow vegetatively. The sequence of events was vegetative growth, followed by removal of controlled cells, followed by seed production and establishment of seedlings. The paired treatments were replicated 10 times for each of three levels of control effort. Each replicate pair of treatments used stochastic variants of $t = 20$ starting conditions.

Direction of approach for control of meadows

A simulated experiment was used to test the importance of the direction of approach for control work relative to the orientation of a growing meadow. To establish the starting conditions, the model was run for 20 years beginning with eight occupied cells. Seed production was set to zero in this experiment. After 20 years of growth, the initial clones had grown together into one oblong meadow with one side up against the upper boundary of growth (native marsh). Beginning in year 21, three alternate treatments were applied: (1) Removal of occupied cells beginning from the upper edge and subsequently moving down the tidal gradient; (2) beginning with the lower edge first and then moving up the tidal gradient; and (3) beginning at one end of the meadow, moving across it parallel to shore. As above, each of the three treatments was applied to identical initial conditions as a block. Each block was replicated 10 times using stochastic variants of the same starting conditions. The experiment was repeated for three levels of control effort: 200, 300, and 600 m^2.

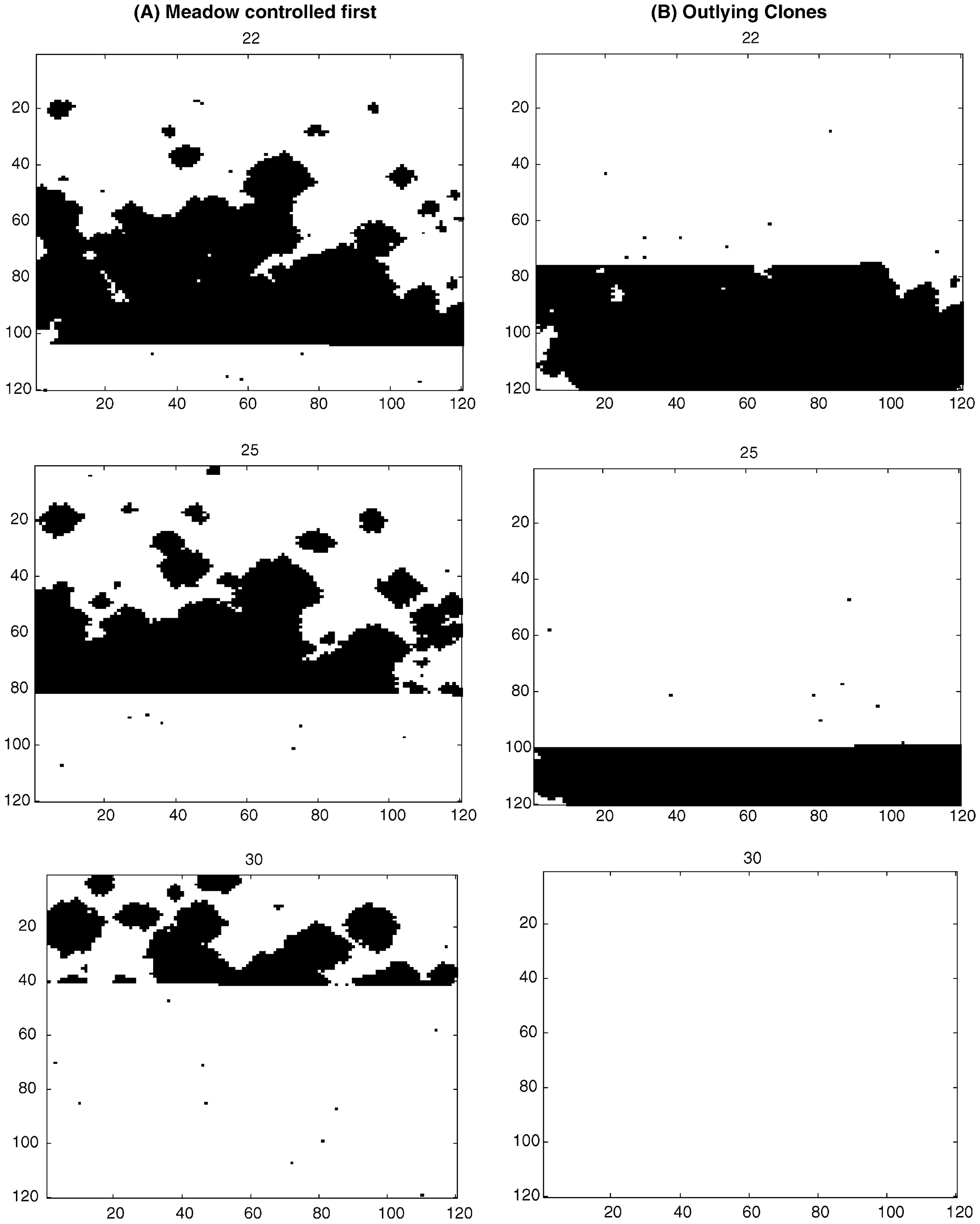

Figure 3. Simulated *Spartina alterniflora* distributions when control is applied to (A) meadows first or (B) outlying patches first.

Seed suppression

While completely killing *S. alterniflora* in the field is often difficult and costly, suppressing seeds can be achieved with much less cost and/or effort through mowing, crushing, or light spray with herbicide. But the effectiveness of seed suppression in slowing the invasion has been debated. To address this issue, the model was allowed to run for either 15 or 20 generations with normal seed production. In subsequent years, seeds were suppressed 0%, 50%, or 100%. Seed suppression was achieved by uniformly reducing the probability of seed survival from all sources. Each of the eight combination of invasion stage and level of seed suppression was replicated 10 times.

An additional test of the effectiveness of seed suppression was tried for a case in which there were no outlying clones in the infestation, but only a large meadow. Such would be the case after all outlying clones were controlled. The starting conditions were set up as for the tests of attack direction for meadows above. Seeds were then produced each year at either the normal rate, a 50% reduced rate, or not at all.

Results

Meadows or outliers

For all levels of yearly effort, a strategy of controlling outlying clones in the lower tide zone first and then moving toward the contiguous meadows in the upper tide zone was more effective than the reverse strategy. Both the number of years it took to control the plant population and the total cost of eradication measured in terms of square meters of plant material killed were substantially reduced when outlying clones were treated first (Figures 4 and 5). The advantage is particularly great when the level of yearly effort is low (Figure 5). For example, when 500 m^2 were controlled per year, the outliers-first strategy achieved eradication 16.6 years sooner on average than the meadows first strategy. In this case, the total cost of eradication using the outliers first strategy was 44% less than it was using the meadows first strategy. When a high level of yearly control was used (1500 m^2), the outlier strategy had a smaller advantage, achieving eradication in 5.8 ± 0.25, as opposed to 7.8 ± 0.25 years and using 24% less total effort. Results were not highly sensitive to the value of the dispersal parameter (Figure 6). For example, over the three levels of α, and for a yearly control effort of 1000, the number of years to eradication for the outliers-first strategy varied from 9.2 to 10.7 years. The difference in time to control corresponds with slight differences in the size of the initial infestation at the time control was first applied. In all three cases the outliers-first strategy consistently achieved control in 32–33% less time than the alternate strategy.

Approach direction for meadows

The approach direction for control work was found to be important even when there are no outlying patches but only one contiguous

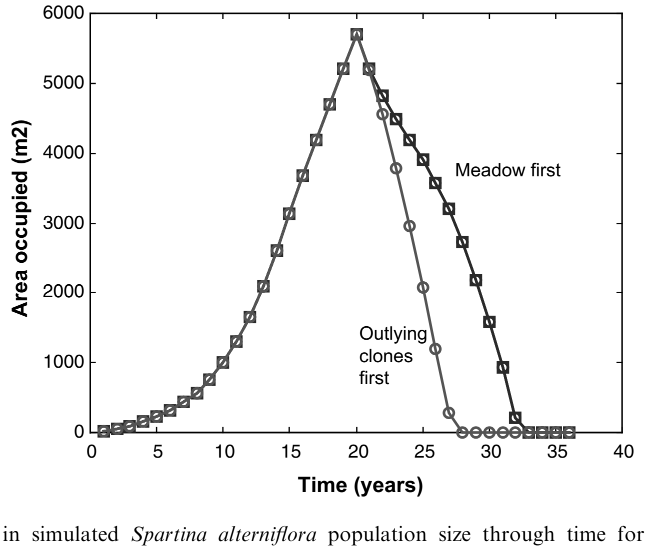

Figure 4. Example of change in simulated *Spartina alterniflora* population size through time for a meadows-first vs outlying-patches-first strategy. In both cases 1000 occupied cells were controlled each year beginning with year 21.

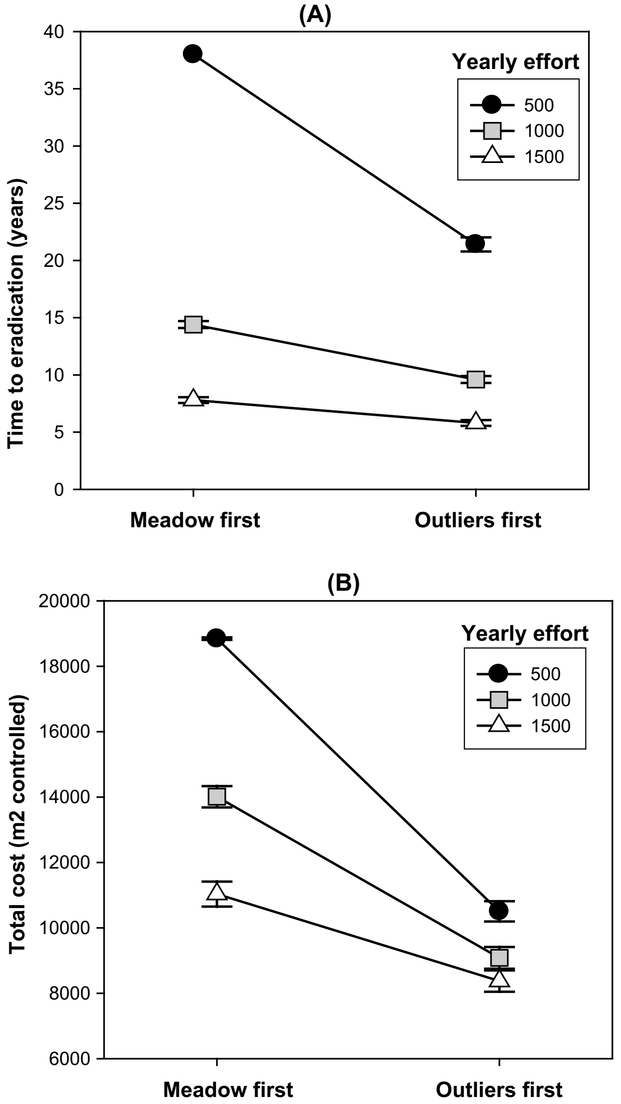

Figure 5. (A) Time to achieve eradication and (B) relative cost of eradication for meadow-first vs outliers-first strategies. Plots show mean and standard error of 10 replicate trials for each strategy and yearly effort combination.

meadow. When an oblong meadow is adjacent to the native marsh boundary (as is often the case for *S. alterniflora*), the least effective approach for control work was from the native marsh outward toward the water. The other two strategies achieved control faster, with control from one end and moving parallel to shore being slightly more effective than control from lower edge toward shore (Figure 7A). The advantage was most pronounced when yearly control was low and disappeared altogether when yearly control was high. With the lowest level of effort, 200 m^2 per year, the strategy of approaching from the upper tide zone failed to reduce the population at all, whereas the other two strategies achieved eradication after 14 and 16 years. The total cost of eradication was similarly affected (Figure 7B).

When this experiment was repeated for an oblong meadow situated in the open mudflat where it could grow freely on all sides, the advantage of controlling from the lower edge

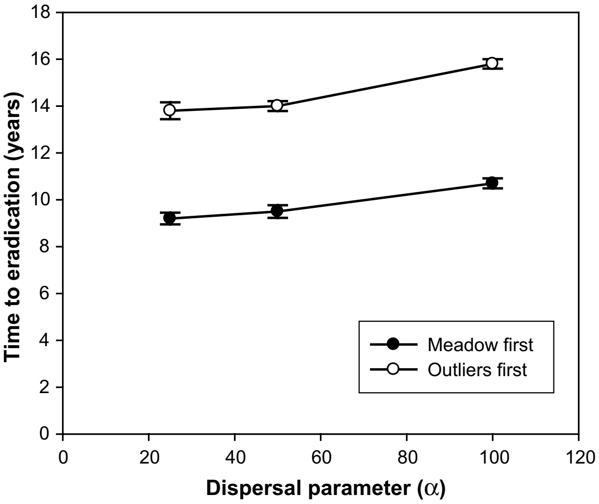

Figure 6. Influence of dispersal distance parameter (α) on the time to eradicate Spartina in simulations for meadow-first and outlier-first strategies, using a control effort of 1000 m^2 removed per year.

disappeared, while the advantage of approaching from one short end to the other was amplified.

Seed suppression

In general, suppressing seeds only slightly reduces the rate of increase in area covered by *S. alterniflora* (Figures 8A–C). Moreover, any benefit of suppressing seeds took many years to become visible. When an infestation is already widespread, the contribution of vegetative growth by already established scattered clones overwhelms any additional contribution from growth of new seedlings. Thus seed suppression was more effective when applied early on in the history of invasion before patches were widely scattered. When complete seed suppression was applied every year to an infestation that had been growing unsuppressed for 10 years, the area covered was 43% lower after 20 years of treatment than if it was left untreated (Figure 8A). When a 20 year old invasion was treated, it was only 7.4% smaller after 20 years (Figure 8C). Use of partial (50%) seed suppression was disproportionately less effective than full seed suppression in all cases.

Somewhat more effective results were obtained when seeds were suppressed in a solid meadow surrounded by uninfested (or prior controlled) mudflat. A meadow population that produced no seeds was 50% smaller after 20 years than an untreated population producing the full amount of seeds (Figure 8D).

Discussion

Since invading plants do not occupy new space randomly, neither should they be controlled randomly. Instead, as illustrated with simulations of *Spartina alterniflora*, strategic placement of control work that takes into account the patterns of spread can greatly reduce the amount of time and effort needed to locally eradicate a population. The use of an efficient control strategy is beneficial on multiple fronts. It reduces the financial cost of control. It reduces the extent of environmental harm caused by the weed. It reduces any environmental harm caused by control work itself. And it increases the possibility for completely eradicating the weed, a desirable but often challenging long term solution (Mack and Lonsdale 2002).

For the *S. alterniflora* control program, several approaches for improving effectiveness were revealed for a case where only a fraction of the population could be controlled each year. First, control is more effective if it first targets outlying clones in the lower tide zone and then moves up the tidal gradient to target the larger meadow. These results are congruent with expectations

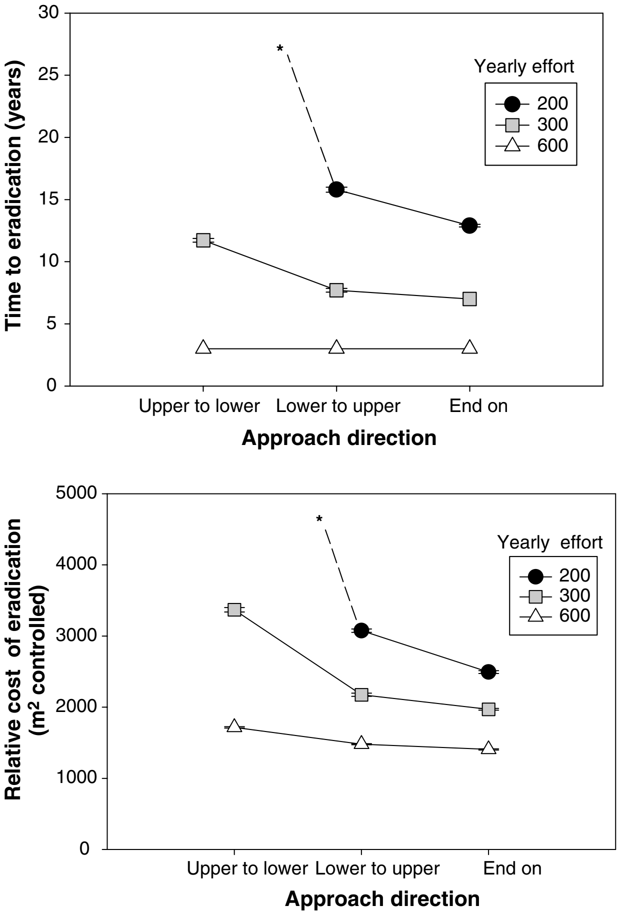

Figure 7. (A) Time to achieve eradication and (B) relative cost of eradication for control of an oblong meadow adjacent to the native marsh using three approach directions. Plots show mean and standard error of 10 replicate trials for each strategy and yearly effort combination.

based on the more generalized study by Moody and Mack (1988). The strategy is also congruous with the agricultural weed model of Blumenthal and Jordan (2001), who found that control effort is more effectively applied to sparse patches within agricultural fields rather than the more densely infested field margins. The outlier strategy is effective in these systems because it targets areas where current and future growth is greatest. In the Spartina system, it also has the advantage of not opening up the best seedling habitat in the upper tide zones until after much of the source for seeds has been controlled.

Second, when meadows are to be controlled with limited resources, treatment should begin with either the lower edge or, slightly better, one end of the meadow. Both approaches avoid opening a new growing edge that is otherwise bounded by the high native marsh. Strategies for controlling other infestation shapes and boundaries could be considered on a case by case basis. In general, the best strategy will be that which most rapidly reduces the amount of growing edge and avoids opening new edges currently bounded by habitat barriers.

Third, control of seeds alone is not likely to be effective in most situations and should be considered only if it can be accomplished at a very low cost and with a high level of effectiveness. Moreover, it should be used only after scattered clones have been eliminated and there are wide open spaces to keep free of Spartina. Because Spartina is a long-lived perennial that spreads vegetatively, reduction in the size of the infestation can only

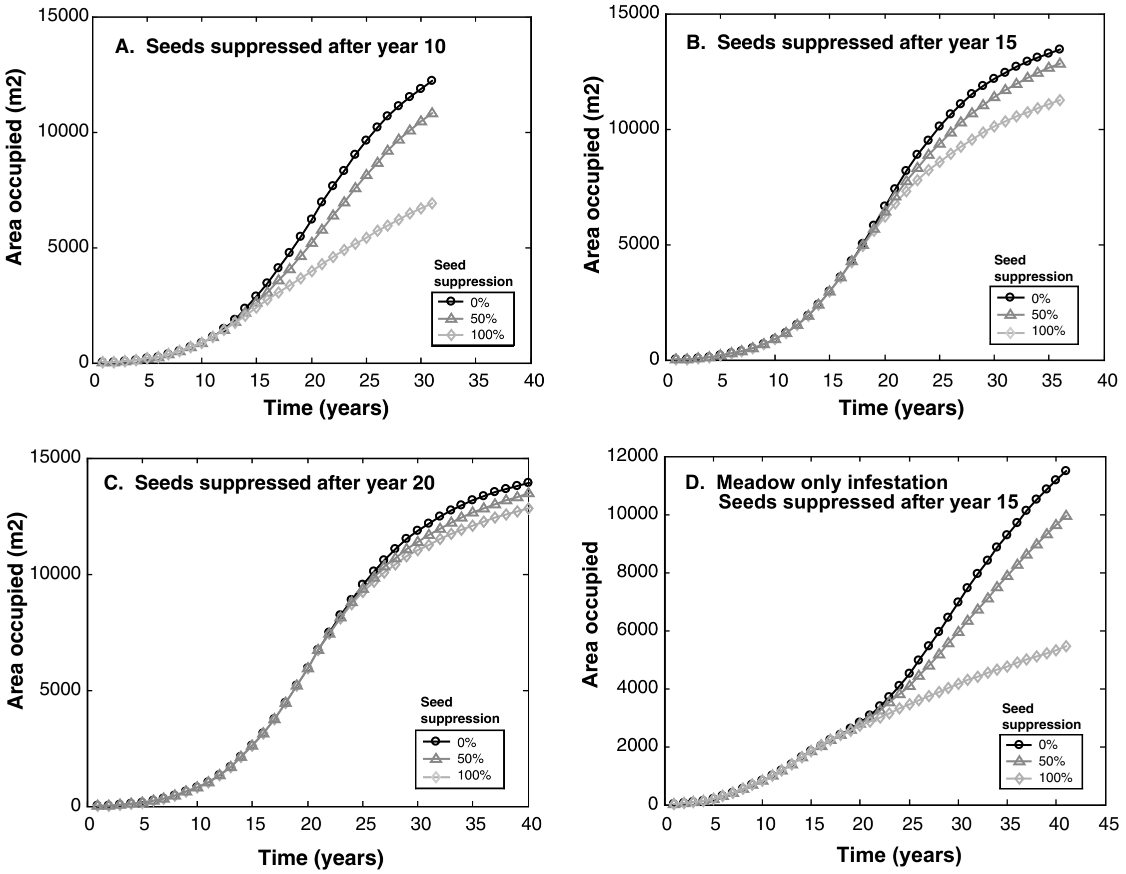

Figure 8. Examples of the growth of simulated *Spartina alterniflora* populations for which seeds were suppressed at levels of 0%, 50% and 100% every year for a 20 year period. Seed suppression treatment was applied to the invading population after 10 (A), 15 (B), and 20 (C) years of growth without any control. In (D) seed suppression was applied to a 15-year-old meadow surrounded by uninfested mudflat.

be accomplished by removing vegetative plant material. The outcome may well be different for annual plant that relies solely on seed for spread, such as many agricultural weeds.

The above recommendations have assumed that all areas of the invasion are similar in their cost of control per unit area of Spartina. Incorporating differences in the costs of control for isolated clones verses dense meadows would improve the model's capacity for strategic planning. However, costs were left out of the comparison because of ambiguity in estimating them. The cost of control depends on what tools are being used and where they are being used. For example, herbicides are known to be more effective in the upper tide zone where there is a longer dry time between high tides (Patten 2002). Crushing with a tractor works better on young plants in low tide zones, which do not have extensive root systems (T. Brownlee, Washington Department of Natural Resources, pers. comm.). For a given agency doing control work, the cost of control depends largely on what equipment is already owned by that agency. Moreover, the methodology for control work is still evolving and the costs are continuously changing. It is anticipated that land managers will consider the results of this study in combination with their own costs of control of different sections of the *S. alterniflora* invasion. The results of this study should be used to guide future development of methodology and equipment. The development of tools that can be effectively used against scattered outlying clones are strongly recommended.

Of the tools available for control of *S. alterniflora*, only biological control is not easily applied to delineated areas. Instead, the distribution of control will be largely determined by the dispersal and colonizing behavior of the biocontrol agent and the influence of habitat on herbivore impact. In light of the results of the model, a biocontrol agent would be most effective if it readily colonized and impacted outlying clones. Isaacson et al. (1996) used a model to show how biocontrol of tansy ragwort (*Senecio jacobaea*) in the Western United States was successful largely as a result of the agent's ability to colonize outlying patches. Similarly, Fagan and Bishop (2000) demonstrated a substantial slowing of the rate of re-invasion of lupines into the pumice plains of Mt. St. Helens due to heavy impacts of native herbivores on isolated patches at the frontier. Although dispersal distances of up to 200 m have been observed for the current Spartina biocontrol agent, *Prokelisia marginata* (Grevstad et al. 2003), it is unclear whether this planthopper will be able to control outlying patches in the lower tide zone. Winter survival in the low tide zones is unlikely and the insects would need re-colonize each spring (Denno et al. 1996; Grevstad et al. 2004). Selection of future biocontrol agents should consider agent ability to control outlying patches.

An remaining question is how strategies presented in this paper might be applied to an area-wide control program at a scale much larger than the isolated cove simulated with the model. Estuaries along the Pacific Coast are composed of many small semi-isolated coves and inlets as well as larger expanses of mudflats and long narrow stretches of Spartina habitat along channels and shorelines. Would it be better to eradicate *S. alterniflora* from one section of an estuary at a time or to eliminate all outlying patches from all areas and then move on to the meadows? At this larger scale, the shape of the seed dispersal function may become more of a factor than it was at the scale of an isolated cove. The rate of long distance dispersal between semi-isolated areas of the estuary would determine whether sites become re-colonized following local eradication. In other models where space is unlimited relative to seed dispersal, the shape of the tails of the seed dispersal function are known to greatly affect invasion rates (e.g. Kot et al. 1996; Woolcock and Cousens 2000). The amount and distribution of available habitat will also be important in that it largely determines dispersal survival (Ruckelshaus et al. 1997). An appropriate next step would be an estuary-wide model using improved estimates of long distance seed dispersal and actual remotely sensed Spartina and habitat distributions. This could be used to determine the optimal area-wide control strategy (see Higgins et al. 2000 for an example of an area-wide weed control model).

Although the main purpose of this study was to examine the spatial dimension of control application, it has also served to illustrate the importance of timing of control work. A greater effort applied early on can save a much larger effort later. In simulated *S. alterniflora* populations, use of higher levels of yearly control generally reduced total cost of eradication by 50–75%. The importance of controlling early has been emphasized in the literature (e.g. Hobbs and Humphries 1995; Mack and Lonsdale 2002) but too often neglected in the real world. In Willapa Bay, 170 ha of *S. alterniflora* were present in 1984 (Ebasco Environmental 1992), an amount that could have been completely removed in approximately half of one control season using the level of effort currently applied. Now, optimistic estimates call for a reduction of the more than 3500 ha to near zero in 6–8 years at a total cost of $12–15 million dollars (Murphy 2003). It is anticipated that the strategies modeled in this paper will help reduce these costs and make eradication more likely.

Acknowledgements

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