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Bang for buck: cost-effective control of invasive species with different life histories

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Abstract

Strategies for controlling invasive species can be aimed at any or all of the stages in the life cycle. In this paper, we show how to combine biological data on population dynamics with simple economic data on control costs options to determine the least costly set of strategies that will prevent an established invader from continuing to increase. Based on biological data alone (elasticities of matrix population models), effective control strategies are sensitive to both life history and rate of population growth. Adding economic considerations, however, can cause the optimal control strategy to shift, unless the costs of intervention are the same across life stages. As an example, we apply our methods to oyster drills (*Ocinebrellus inornatus*), an economically important aquaculture pest that has been accidentally introduced worldwide. Control efforts are applied to local tidelands through manual removal of adults, although the life history characteristics of the species indicate a low population elasticity for adult survival. Aquaculturists are making bioeconomic decisions to remove adults vs. egg capsules, because of the relative ease of controlling each stage.

Keywords: Control costs; Elasticity; Matrix model; Species invasion

1. Introduction

Harmful nonindigenous species exact a tremendous toll on ecological and economic well-being, and prominent attempts to quantify their costs assign about 15% of the total to control efforts (Pimentel et al., 2000, 2005). Because resources for dealing with invasive species are limited, it is essential to select cost-effective methods for control. Across entire landscapes, for example, removal of newly emerged populations has been shown both theoretically and empirically to be a better strategy for managing invasive plants than reduction of the size of well-established populations (Moody and Mack, 1988; Cook et al., 1996). In this paper, we examine the

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significance of different life histories—ranging from short-lived, rapidly reproducing species to species with high survivorship but low fecundity—for the optimal design of control strategies.

Effective control should target the weak link in the life cycle. This phase is where demographic reductions most effectively reduce population densities or slow spread. How can ecologists identify this weak link? This question has already been explored in depth—but inversely—to manage threatened and endangered species. For species in decline, managers are interested in the smallest improvement through the life cycle—in survival, growth, or reproduction—that most improves population growth. Specifically, such issues have been explored with what ecologists call "elasticity analysis" of matrix population models (Heppell et al., 2000). These models describe the dynamics of stage-structured populations in discrete time intervals (Caswell, 1989). In their standard formulation, they assume that per capita rates of survival and fecundity do not change with population density. In economics, the term "elasticity" refers to the responsiveness of any variable to changes in another if both are measured in percentage changes, so in order to prevent confusion, we will refer to elasticities of matrix models as "population elasticities". The population elasticities characterizing any species are functions of that species' "transition matrix" **A**, of which each element a_{ij} is the fraction of a population at stage j in the life cycle expected to survive to stage i (or the expected number of offspring produced by an individual at stage j). The population elasticities e_{ij} are defined as

$$e_{ij} = \frac{\partial \ln\lambda}{\partial \ln a_{ij}} = \frac{a_{ij}}{\lambda}\frac{\partial \lambda}{\partial a_{ij}} \tag{1}$$

where λ, the dominant eigenvalue of **A**, gives the discrete time multiplicative rate of change in population abundance, that is the ratio of population sizes at time $t+1$ relative to time t. Population elasticities thus represent the proportional effect on population growth (λ) achieved by a proportional change in a given demographic parameter (a_{ij}). Across all transitions, elasticities sum to unity.

Long juvenile periods are associated with high population elasticity of juvenile survival, and long life spans are associated with high population elasticity of adult survival (Benton and Grant, 1999; Heppell et al., 2000). Applied to the case of species in decline, conservation of endangered species with a long prereproductive phase is likely to be achieved by protecting juveniles; long-lived species are likely to be conserved by protecting adults. However, in contrast to endangered species dynamics, most invasive species are rapidly increasing in abundance or, if populations have stabilized, would increase in abundance if their densities were reduced. Population growth itself can markedly influence the results of population elasticity analyses, so rules of thumb developed for enhancing endangered species with different life histories may not be directly applicable to invasive species.

For many species, several control options are available that target different life stages, for instance, reproductive output (e.g., release of sterile males, biological control by seed predators; Shea and Kelly, 1998) or adult survival (e.g., hunting or poisoning of mammals invading islands; Courchamp et al., 2003). The relative effectiveness of these options is generally judged in terms of reduced population growth of an invasive species, an issue mostly addressed by biologists. Sometimes, a purely ecological approach can have immediate implications. For instance, although population growth rate of a thistle invading New Zealand was most influenced by transitions involving seeds, seed predators introduced as biocontrol agents were unlikely to reduce seed survival enough to make the population decline (Shea and Kelly, 1998). In general, however, selecting the optimal method to control an invasive species will require explicit consideration of the costs of each alternative.

In this paper we (1) explore relative contributions of reproduction, juvenile survival and adult survival to population growth of invading species (λ>1) with two- or three-stage life histories through population elasticity analysis, and (2) show how to identify the combination of life stage interventions that will minimize the total cost of halting population growth. We also apply this framework to a real example of control of oyster drills (*Ocinebrellus inornatus*), direct-developing marine snails that cause economic harm by preying on small oysters.

We stress that this analysis applies only to the question of *how* to control an established invader, leaving aside the matter of whether the invasion is worth controlling. It assumes linear population dynamics of an established invader. We do point out a parameter emerging in our analysis (a Lagrange multiplier) that could be compared to the social cost incurred if the invasion proceeds, but we do not pursue the matter further. Assessing that social cost is complicated by all the well-known difficulties in valuing ecosystem services (Boyd and Wainger, 2003), as well as the empirical challenges of accurately describing both ecological (Barbier, 2001) and socioeconomic (Perrings et al., 2002) responses to the invasion. Modeling ecological costs may be especially complex if the relationship between invader abundance and damage is nonlinear, as, for instance, when per capita effects change with density (Ruesink, 1998). The value of the whole comparison is in any case conditional on acceptance that benefit–cost criteria are appropriate to conservation decisions. The cost minimization problem on which we focus, by contrast, is important even to a resource manager who believes that conservation must be pursued without regard to human values.

2. Methods

2.1. Population elasticities of matrix population models

Matrix population models summarize a schedule of life history events for a species, specifically reproduction, growth, and survival (Caswell, 1989). They can be used to project the asymptotic growth rate of the population (dominant eigenvalue, λ) and to assess the population elasticities (proportional sensitivities) indicating relative contributions of different matrix elements to λ. The success of some invasive species has been attributed to a suite of life history characteristics and, in particular, high rates of population growth that allow species to increase from an initially small incursion (Richter-Dyn and Goel, 1972). High population growth rates have been achieved by invasive species that escape natural enemies (improve adult survival or fecundity; Maron and Vilà, 2001; Mitchell and Powers, 2003; Torchin et al., 2003), have short juvenile periods (Rejmanek and Richardson, 1996), or reproduce rapidly, often via asexual reproduction (Reichard and Hamilton, 1997; Kolar and Lodge, 2002).

A 2×2 transition matrix **A** describes a two-stage life history, in which newborn individuals mature into adults following a single juvenile (nonreproductive) phase (Fig. 1A). Here, we will assume that the juvenile stage lasts one year (a_{11}=0) and adults can survive and reproduce over multiple years (a_{22}>0), hence

$$\mathbf{A} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} = \begin{bmatrix} 0 & f \\ j & a \end{bmatrix} \tag{2}$$

where j denotes juvenile-to-adult survival, a adult survival, and f fecundity. The asymptotic rate of population growth $\lambda(\mathbf{A})$, which is the ratio of population sizes between successive time steps, is the dominant eigenvalue of **A**. Similarly, for a 3×3 transition matrix describing a three-stage life history (young, juvenile, adult; Fig. 1B), the rate of population growth $\lambda(\mathbf{A})$ is the dominant eigenvalue of the matrix. We calculated population elasticities using a formula given by Caswell (1989, p. 121)

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle} \tag{3}$$

where **w** is the right eigenvector and **v** is the left eigenvector of the matrix **A**, and $\langle \mathbf{w}, \mathbf{v} \rangle$ is their inner or dot product.

We varied adult survival (0.05 to 0.95), duration of the juvenile period, and fecundity independently to determine elasticities across a range of life history strategies (two- and three-stage) and population growth rates. All scenarios were developed in Matlab 5.3.

2.2. Minimizing costs of invaders

To reduce an invasive species' density requires that demographic parameters be altered until the population declines [$\lambda(\mathbf{A})<1$]. We assume it is sufficient that the population be frozen, i.e., that $\lambda(\mathbf{A})=1$. The reason for this assumption is that there is no solution to the problem of minimizing cost subject to a strict inequality: for any solution yielding allowable λ_0, there will be another that yields $\lambda_0+\varepsilon<1$ for which cost is lower. The problem would be essentially unchanged

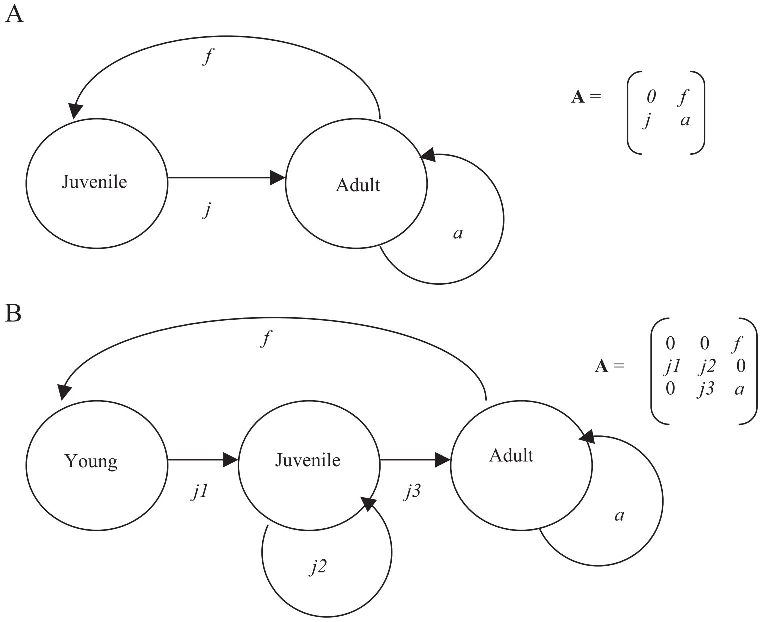

Fig. 1. Life cycle diagram for (A) two-stage life history with a 1-year nonreproductive juvenile period and (B) three-stage life history with a two- or more year juvenile period. Transitions among stages of the life cycle are shown as arrows where f=per capita fecundity, j=juvenile survival, and a=adult survival.

if some particular *rate* of decline were required, e.g., $\lambda \leq 0.8$, and the boundary case of $\lambda \leq 1$ seems to us the best choice for illustration.

As a simple case, we also assume that each transition probability can be reduced from its pre-intervention level $\hat{a}_{ij}$ to a chosen level a_{ij} and kept there in perpetuity at cost $c_{ij}(a_{ij})$. Relaxation of this assumption, which will require the methods of optimal control theory, is deferred to future work. Clearly, it must cost more to drive a given transition probability to a lower level, so $c'_{ij}(a_{ij})<0$. A policy-maker chooses a set of interventions to minimize total cost subject to $\lambda(\mathbf{A}) \leq 1$. Since we are abstracting from the details of the intervention strategies, this is equivalent to choosing the a_{ij} directly to minimize the Lagrangian

$$L = \sum_{ij \in I} c_{ij}\left(a_{ij}\right) + \mu(1 - \lambda(A)). \qquad (4)$$

The summation occurs over those elements of **A** that can be changed, which defines the *intervention set* denoted I. In a two-stage life history with a juvenile period of 1 year, for example, there are three elements in which intervention is possible; the element representing the probability that juveniles will remain juveniles is inalterably zero and is thus not an element of I. In the oyster drill example considered below, juvenile survival is also not an element of I, which represents a judgment prior to formal analysis that intervention at this stage will not be efficient. That judgment could be checked with the tools described herein, but only after control technology is designed from which the cost function $c(j)$ can be estimated. In this case, and in many cases, it probably makes more sense to treat interventions not contemplated by the biologists in the field as though they were impossible, rather than to expend the effort to generate cost functions for processes that appear *a priori* impractical. Recalculation if a new control technology is invented is straightforward.

The new variable μ, where $\mu<0$, is a *Lagrange multiplier* and measures the cost savings that could be achieved if it were deemed permissible for $\lambda(\mathbf{A})$ to rise a bit above one. That is, μ is a function of the whole cost structure representing expenditure on the last unit of the most costly intervention, where a "unit" is normalized across interventions in terms of the impact on the population, so that at the optimally chosen **A**

$$\mu = \max_{ij \in I} \left\{ c'_{ij}\left(a_{ij}\right) \lambda'\left(a_{ij}\right) \right\}. \tag{5}$$

For a cost minimization problem, the value of μ does not influence results. As demonstrated below, μ is eliminated by division from the expressions for optimal **A**. Economists will recognize this as formally identical to the elimination of the unobservable utility term from a set of consumer demand equations (Silberberg and Suen, 2001). If the problem is not to minimize control cost but to maximize social welfare, allowing for the possibility that not controlling is optimal, the value of μ should be compared to the social damage of invasion.

In general, the solution to Eq. (4) must satisfy the set of first order conditions given by $\lambda(\mathbf{A})=1$ and

$$\left.\begin{array}{l} \left[c'_{ij}\left(a_{ij}\right) - \mu \dfrac{\partial \lambda}{\partial a_{ij}} \right] \left(\hat{a}_{ij} - a_{ij}\right) = 0 \\ c'_{ij}\left(a_{ij}\right) - \mu \dfrac{\partial \lambda}{\partial a_{ij}} \leq 0 \end{array}\right\} \forall ij \in I \tag{6}$$

where $\hat{a}_{ij}$ is the transition probability if no intervention occurs. The top line of Eq. (6) thus states that for each ij in the intervention set, either a_{ij} is left alone (i.e., $\hat{a}_{ij} - a_{ij}=0$) in which case $c_{ij}=0$, or $c'_{ij}(a_{ij})=\mu\lambda'(a_{ij})$. The bottom line of Eq. (6) indicates which of these must hold; if $c'_{ij}(a_{ij})<\mu\lambda'(a_{ij})$ for all $a_{ij}<\hat{a}_{ij}$, then marginal costs of control outweigh the marginal benefits of reduced population growth, and the choice must be to leave a_{ij} at $\hat{a}_{ij}$. This represents a situation in which the cost of the smallest possible reduction in a transition probability achieves less than an equally costly reduction in some other transition.

Consider the two-stage life cycle of transition matrix (2), depicted in Fig. 1A, where intervention is possible either to reduce adult survival or reduce reproductive output. The dominant eigenvalue of this matrix is given by

$$\lambda(A) = \frac{1}{2}\left[a + \left(a^2 + 4fj\right)^{1/2} \right]. \tag{7}$$

If it is optimal to intervene in both stages, then (dividing the one first-order condition by the other)

$$\frac{c'_a(a)}{c'_f(f)} = \frac{\partial \lambda}{\partial a} \Big/ \frac{\partial \lambda}{\partial f} \tag{8}$$

which states that the ratio of marginal costs must equal the ratio of impacts on population growth.

The right side of Eq. (8) is the *marginal benefit ratio* (MBR) of adult survival to fecundity: that is, it measures the relative impact on population growth of unit reductions in a and f. It is important to be clear about what is meant by a "unit"; we refer to the natural units of the population matrix, i.e., individuals per individual. We are thus comparing in this ratio the impact of removing, for example, one in a thousand adults with removing one in a thousand offspring. The changes in transition probabilities are absolute, not proportional as in the case of population elasticity analyses. The left side of Eq. (8) is the *marginal cost ratio* (MCR), that is, the relative cost of achieving these absolute changes in different transition probabilities.

Each additional increment of control is likely to be slightly more expensive than the previous; that is, reducing transition probabilities is an increasing marginal cost activity because it becomes more difficult to find individuals as they become rarer. Accordingly, we assume that the cost of altering each parameter increases logarithmically as the parameter is reduced below its intrinsic value $\hat{a}_{ij}$ set by the biology of the organism:

$$c_{ij}\left(a_{ij}\right) = \kappa_{ij}\left(\ln\hat{a}_{ij} - \ln a_{ij}\right) = \kappa_{ij}\left(\ln\frac{\hat{a}_{ij}}{a_{ij}}\right) \tag{9}$$

where κ_{ij} is a scalar relating change in survival or fecundity to dollars spent. Note that although the MCR in Eq. (8) refers to the marginal cost of absolute changes in a_{ij}, the cost itself depends on the proportional decrement in the transition probability. This functional form of c_{ij} can be derived by assuming that individuals experience an instantaneous mortality rate δ_{ij} from time t to $t+1$, and this rate increases linearly from a baseline value $\hat{\delta}_{ij}$ with money spent on control, so that $a_{ij} = \exp\left(-\delta_{ij}\right) = \exp\left[-\left(\hat{\delta}_{ij} + \frac{c_{ij}}{\kappa_{ij}}\right)\right]$. Using the cost function (9) and expression (7) for $\lambda(\mathbf{A})$, the joint first-order condition (8) becomes

$$\frac{f\kappa_a}{a\kappa_f} = \frac{a + \left(a^2 + 4fj\right)^{1/2}}{2j}. \tag{10}$$

Because of increasing marginal costs of control, the most cost-effective way to achieve $\lambda=1$ for some-invaders will involve control of several life stages. As one transition is reduced ever further, there will come a point at which condition (10) is fulfilled. From that point onwards, it is efficient to put effort simultaneously into reducing several life stages.

We used this framework to find the values of a and f minimizing the total cost of an invasion that is growing rapidly (λ=1.2). We explored two-stage life histories ranging from short-lived species with high fecundity (f large, a small) to long-lived species with low fecundity (f small, a large). Because survival and fecundity will in general be reduced from very different baselines, we explored relative control costs of control (κ_a/κ_f) ranging from 0.01 to 100. These ratios correspond to scenarios where reducing adult survival to some fixed percentage of its baseline value is up to 100 times as difficult as a similar change in fecundity, and vice versa.

2.3. Cost-effective control of oyster drills

Oyster drills (*O. inornatus*) have been accidentally introduced to many aquaculture areas with Pacific oysters (*Crassostrea gigas*). We have been studying dynamics and impacts of oyster drills in Willapa Bay, Washington, for the past year and have developed the following preliminary assessments. Oyster drills have a two-stage life history. Adults lay clumps of bright yellow benthic egg capsules, and about 10 juvenile (2 mm) oyster drills emerge from each capsule. Juveniles grow rather rapidly (>2 mm/month) and many reach reproductive size (27 mm) by the following year. Adult survival rates, based on small sample sizes, probably do not exceed 30% annually. Based on preliminary results, the population matrix for *Ocinebrellus* is:

$$\mathbf{A} = \begin{bmatrix} 0 & 160 \\ 0.005 & 0.3 \end{bmatrix} \tag{11}$$

which gives λ=1.06, an annual increase of 6% in population abundance.

The only control technologies currently available are based on manual removal. In terms of a two-stage life cycle, the destruction of egg capsules reduces fecundity, and the collection of adults reduces adult survival. Reducing juvenile survival is not feasible because newly hatched individuals are small and cryptic. The MBR for the two remaining interventions, calculated by inserting the numbers from the population matrix (11) into the right side of Eq. (10), is 211. In this case, it is more than 200 times more effective to control the invasion by reducing adult survival from, say, 0.3 to 0.29 than by reducing fecundity from 160 to 159.99. However, the choice of control techniques also depends on the marginal costs of achieving these changes. In practice, such a number can only be estimated by scaling down the cost of considerably larger interventions.

We based MCR on surveys where we recorded all drills and egg capsules that we observed, which reflects the ease of capturing each stage. Drills were repeatedly marked and recaptured, leading to estimates of adult density of about 30 m^{-2}. We were able to find about 20% of these individuals in an hour searching an area of 4 m^2. The relative ease of finding egg capsules vs. snails varied through the year due to seasonal reproduction, with a peak in ratio of eggs to drills in midsummer at 10 (Nemah) or 25 (Peterson Station; Fig. 2). At a third location where we did not mark and recapture individuals, eggs/drill=60. The right eigenvector of the population matrix (11) is the stable stage distribution (0.9934, 0.0066). This stable

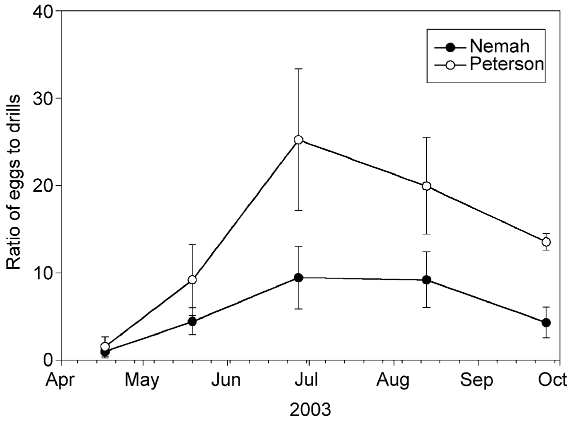

Fig. 2. Ratio of eggs to adult oyster drills, *O. inornatus*, in 2003 at two sites in Willapa Bay, Washington. The “egg” phase actually represents the number of juvenile drills that would emerge from egg capsules found during the survey, where, on average, 10 juveniles emerge from each capsule.

stage distribution indicates that the actual egg/drill ratio is 150. In most cases, then, we found fewer eggs (1/15, 1/6, and 2/5 at the three sites) than would be expected from the intrinsic dynamics of *Ocinebrellus*—eggs were more difficult to find or more ephemeral than adult snails. Specifically, finding 10–25 eggs per drill would cause reproductive declines of just 2–8% (20% of 1/15 or 2/5) in an hour of searching 4 m^2. We used our estimates of search efficiency (proportion of the population collected per unit time in a known area) for adult and juvenile drills to solve Eq. (9), which gave κ_a=4.5 and 12≤κ_f≤49 at peak egg capsule densities across three sites. (The κ are measured in hundredths-hour of labor per percent reduction in transition.)

3. Results

3.1. Population elasticities of invaders

Given life cycles characteristic of invasive species, population elasticities are highly dependent on both population growth (λ) and demographic rates. For two-stage life histories, adult survival elasticities were small for life histories with low adult survival: because the relationship between adult survival and elasticity is concave-up, the proportional sensitivity of population growth to adult survival was always less than the survival parameter itself (Fig. 3A–C). The adult survival elasticity also declined steadily as population growth rate increased. For the two-stage

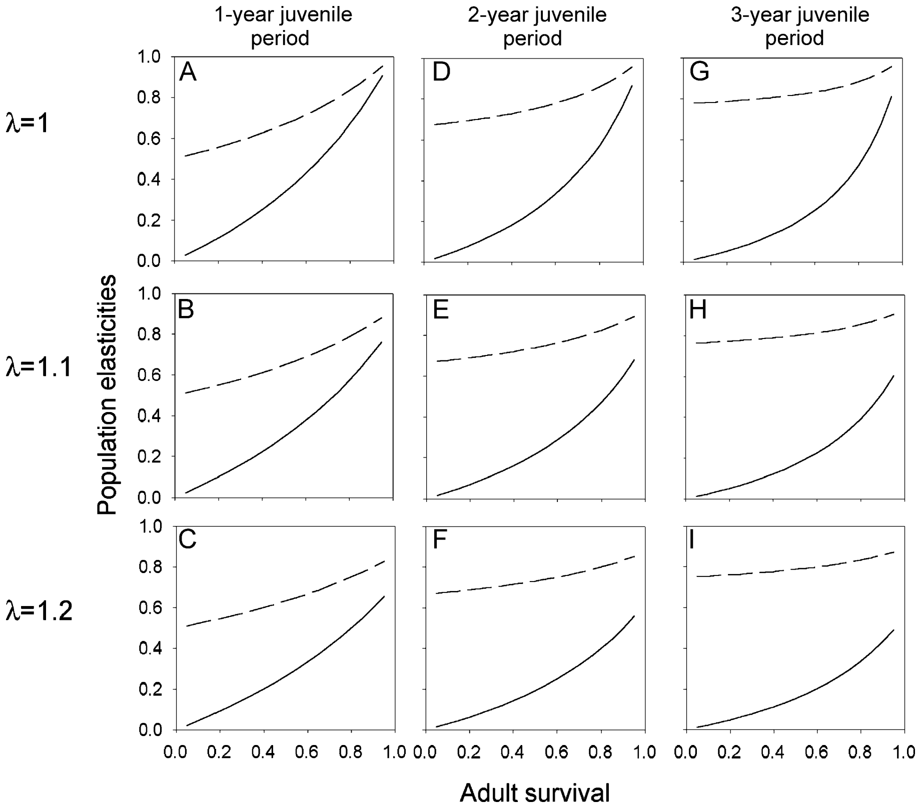

Fig. 3. Population elasticities of three stages of the life cycle, calculated across life histories and population growth rates (λ). Lines show cumulative elasticity from adult survival (solid line), juvenile survival (dashed line), and fecundity (always sums to one). Each panel shows elasticities from high-fecundity to high-survival life histories, where population growth is held constant. Population growth increases from the top row of panels (λ=1) to the bottom row (λ=1.2). The length of the juvenile period varies across columns: (A–C) 1 year (j=0.5), (D–F) 2 years ($j1$=$j3$=0.71), (G–I) 3 years ($j1$=0.71, $j2$=0.59, $j3$=0.41). In all cases, the proportion of offspring that reach adulthood is 0.5, but the time it takes to reach adulthood varies.

case, fecundity and juvenile survival had identical population elasticities, because they affected a single pathway of the life cycle.

Population elasticity analyses of three-stage life cycles gave results similar to the two-stage case. Adult survival elasticities were large only when adult survival was high, particularly if populations were growing rapidly (Fig. 3D–G). In the three-stage case over the range of parameterizations we examined, elasticities for juvenile survival always exceeded those for fecundity. This occurred because we always assumed that half of the individuals born reached adulthood, but the number of time steps required to reach adulthood varied. Longer juvenile periods expose individuals to prereproductive survival rates for more time steps. Consequently, the population elasticity for juvenile survival, which was the sum of contributions from several transitions among prereproductive stages, increased with the length of the juvenile period.

O. inornatus has a life history with low adult survival and a moderate rate of increase. The population elasticity for adult survival, calculated by using parameters from Eq. (11) in Eq. (3), is 0.17. Elasticities for fecundity and juvenile survival are both 0.42, suggesting that the most effective stage for intervention from a biological perspective is to reduce reproduction.

3.2. Minimizing costs of controlling invaders

We consider next the implications of life history features for the mix of interventions that will minimize the cost of stabilizing an invader's abundance. We focus our bioeconomic analyses on rapidly invading species (λ=1.2) and examine control strategies across a range of demographic values that could generate this high invasion rate. As the population elasticity analysis suggests, short-lived, high-reproduction species are in general more effectively controlled by reducing fecundity, whereas adult survival is more cost effective for long-lived, low-reproduction species (Fig. 4). However, the details of the optimal strategy are quite sensitive to the relative costs of intervention at different life history stages.

For each life history scenario, there is a range of relative control costs (κ_a/κ_f) in which the optimal intervention includes reducing both fecundity and survival. The range of relative costs where a mixed control strategy is optimal depends on the invader's life history pattern. For long-lived, low-fecundity invaders, it was optimal to reduce adult survival alone unless $\kappa_a/\kappa_f \geq 1.25$ (Fig. 4C). At still higher cost ratios ($\kappa_a/\kappa_f \geq 10$), a strategy targeting only fecundity became optimal. In contrast, mixed strategies were favored for short-lived, highly fecund species only when reductions in fecundity were very costly relative to reductions in survival (Fig. 4A). Species with intermediate survival and fecundity gave more symmetric patterns, with mixed strategies favored when the relative costs of proportional changes in survival and fecundity were roughly

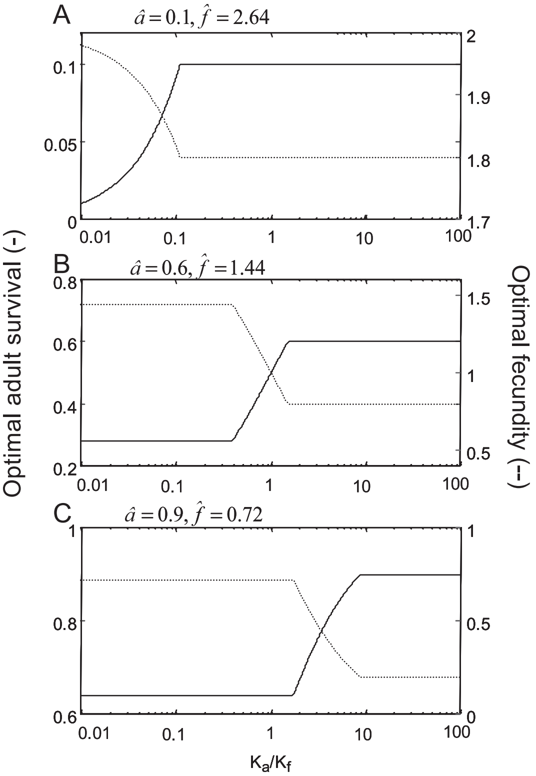

Fig. 4. Adult survival and fecundity values that minimize the costs of invasion control, found by minimization of Eq. (9). The optimal strategy depends on the relative costs of control at each life history stage, as illustrated here by varying the ratio κ_a/κ_f (note logarithmic x-axis scale). Thus, a ratio of 1 means it is equally costly to reduce either survival or fecundity to a given fraction of its baseline value. Results are shown for three life history scenarios: (A) $\hat{a}$=0.1, $\hat{f}$=2.64, (B) $\hat{a}$=0.6, $\hat{f}$=1.44, (C) $\hat{a}$=0.9, $\hat{f}$=0.72. With no intervention, λ=1.2 in all cases.

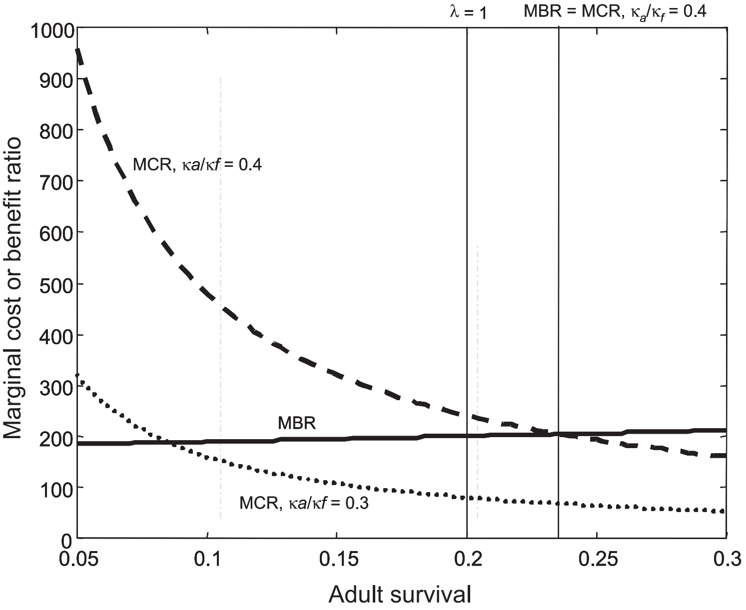

Fig. 5. Costs and benefits of reducing adult survival of oyster drills, *O. inornatus*. The marginal benefit ratio (MBR) and marginal cost ratios (MCR) are calculated according to Eq. (10) for cost ratios κ_a/κ_f=0.3 or κ_a/κ_f=0.4. Adult survival (a) is varied while fecundity (f) and juvenile survival (j) are held constant at baseline values. Vertical lines indicate values of a for which λ=1 or MCR=MBR, respectively.

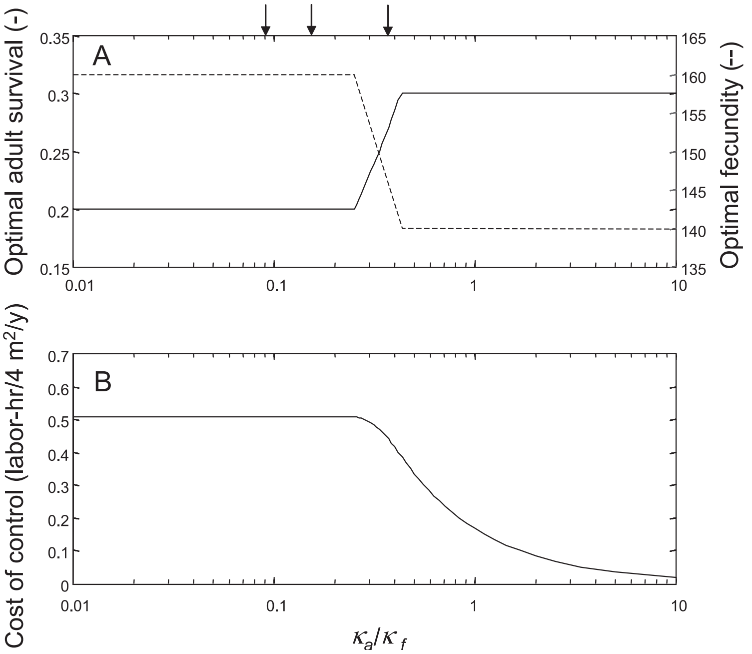

Fig. 6. Optimal adult survival and fecundity values and control costs across a range of cost parameter ratios for oyster drills, *O. inornatus*. Baseline demographic parameters are taken from transition matrix (11). Cost parameters κ_a and κ_f are estimated as described in Section 2.3. Here, κ_a=5 and κ_f is varied from 0.5 to 500. Arrows indicate κ_a/κ_f=0.09, 0.15, and 0.375, corresponding to field collection data from Peterson Station, Nemah, and Stackpole, respectively. (A) Optimal survival and fecundity values. (B) Annual cost of control per 4 m^2 of invaded area.

equal (Fig. 4C). These differences across life histories reflect changes in the MBR, i.e., the marginal contributions of survival and fecundity to λ, and are thus qualitatively consistent with population elasticity analyses.

3.3. Cost-effective control of oyster drills

We used the estimated population matrix for *O. inornatus* in Eq. (11) to calculate the MBR as a function of adult survival a, with fecundity and juvenile survival held at their preintervention levels. Two marginal cost curves are shown (Fig. 5), based on the parameterization in Eq. (10) with cost parameter ratios (κ_a/κ_f) of 0.3 and 0.4. In the case where κ_a/κ_f=0.4, the optimal policy includes effort expended against fecundity (Fig. 5). This is visible in that the intersection of the MCR and MBR is at around a=0.24, a level at which the population is still growing. To halt population growth, some further action is needed, and the equality of MCR and MBR means that it is now efficient to combine attacks on both life stages. In the case where κ_a/κ_f=0.3, the efficient solution involves no efforts to reduce fecundity. This is visible in that the marginal cost of reducing adult survival lies below the marginal benefit ratio all the way from the natural survival level of 0.3 to the level required for stabilizing population, ~0.2. In this case, the full optimal policy cannot be illustrated in Fig. 5, because the curves are drawn with fecundity fixed.

Fig. 6A shows the most cost-effective strategies for controlling oyster drills across a range of MCR, the results of simultaneously solving Eq. (10) and $\lambda(\mathbf{A})$=1 for a and f. Based on the efficiency of field collections of egg capsules and adult drills, we estimated κ_a=4.5 and κ_f=12, 30, and 49 at three collection sites, giving κ_a/κ_f of 0.375, 0.15, and 0.09, respectively. As shown in Fig. 6A, a mixed strategy should be pursued whenever the marginal cost of a proportional reduction in adult survival is approximately 0.25 to 0.45 times the cost of changing fecundity. This range corresponds to the lower range of κ_f values consistent with field data. As egg capsule removal becomes more expensive relative to adult drill removal, the optimal strategy shifts to targeting only adults while the total annual cost of control per unit of invaded area increases (Fig. 6B).

4. Discussion

Based on population elasticity analysis, the most effective method for reducing the growth rate of an established invasive species depends on both its life history and its rate of increase (Fig. 3). Rapidly increasing species with short life spans show high elasticities for fecundity and juvenile survival, indicating that control efforts should target these life stages. For an invasive species (λ>1), control by removing adults would likely only be effective if adult survival were naturally high. Control by removing juveniles would be particularly effective when pre-reproductive periods were long, in which case juveniles would be susceptible to this method of control for several time steps.

Results from population elasticity analysis, however, do not account for the fact that control efforts targeting different stages of the life cycle can have different costs. The optimization approach allowed economic considerations to be added to the biological question of how to control the invasion. The relative costs of control substantially influenced solutions to the cost minimization problem. Changes in cost can switch which stage should be the target of control efforts by demanding that more expensive interventions yield a correspondingly greater return in terms of reduced population growth. For example, management strategies should target adult survival when the marginal cost of lowering fecundity is high, even if the invader's life history alone might suggest otherwise (Fig. 4A). One result of the bioeconomic analysis matched population elasticities well: the least-cost strategy to stop an invasion varied with invader life history. In Fig. 4, when costs to reduce each life stage were equal (κ_a/κ_f=1), it was optimal to reduce fecundity for high-fecundity invaders (Fig. 4A), and reduce adult survival for high-survival invaders (Fig. 4C). Mixed interventions, in which optimal control was achieved by changing two parameters simultaneously, were best over a range of moderate survival and fecundity values. This mixed strategy could not be predicted by population elasticities, which only reflect small proportional changes in each transition rate, with all other matrix elements held constant.

A current limitation of our analysis is that it does not effectively incorporate the costs of damage due to the invader itself. We assume that successful control occurs when the invader's population stabilizes (λ=1). In practice, if a population stabilizes at high density, its impacts likely remain substantial. Intervention to reach this stable population size thus does not accrue any benefit in terms of reduced invasion impacts. However, it is certainly possible to change the conditions of Eq. (4) constraining λ to be, say, $\leq$0.8, so that the invader declines. We also assume that the population matrix (Eq. (2)) contains demographic parameters that do not vary with population density. Demographic values may change over the course of control, for instance, because birth rates improve when an invader is at lower densities and resources are not limiting. Conversely, Allee effects or stochastic disturbances that disproportionately reduce the growth rates of small populations might aid in controlling or eradicating an invasion (Keitt et al., 2001; Liebhold and Bascompte, 2003). In such cases, the optimal intervention predicted by linear matrix models could be periodically reevaluated based on new ecological information.

We have framed our analysis to address the bioeconomic question of cost-effective ways to stabilize the population of an established invader. We compare the relative costs and benefits of intervening at different phases of the life cycle. As the case study of oyster drills indicates, this framework is most likely to apply to control of an invader in a local area where its impacts are not tolerable. Previous analyses have emphasized intervention at different stages of the invasion, and most lead to recommendations of early intervention, before the invader has become abundant and spread widely. For instance, Naylor (2000) provided an economic assessment of costs to prevent invasions, control early incursions, and control well-established invaders. Her analyses suggest that early intervention minimizes the total control costs. Similarly, Sharov and Liebhold (1998) found that eradicating or slowing the spread of an invader became less optimal as the invasion progressed, although the optimal bioeconomic strategy also depended on invader impacts and the discount rate.

The importance of a bioeconomic approach is illustrated by the invasion of oyster drills. Based on population elasticities, population growth was most sensitive to changes in reproduction. The population elasticity for fecundity was 0.42 (equivalent to the elasticity for juvenile survival in this two-stage life history), and for adult survival, it was just 0.17. In contrast, control cost was minimized by reducing adult survival over a range of realistic MCR based on how easily we found egg capsules vs. adults in field surveys (Fig. 6). Currently, control efforts target adults, the phase that is easiest to remove, despite its lower population elasticity. Likewise, our models suggest that intervention in adult survival is optimal except during periods of peak reproduction. Evidently, aquaculturists have been making qualitative bioeconomic decisions in the absence of the quantitative framework provided here.

This bioeconomic approach to the control of invasive species indicates that economics can alter the "rules of thumb" for control of invasive species based on biological information alone. Knowledge of the organism's life cycle and dynamics, as well as information on the relative costs of controlling different stages, are required for cost-effective decisions about how to control invasive species.

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