Bang for the 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 cost options to determine the least costly set of strategies that will halt an invasion. We then apply our methods to oyster drills *(Ocinebrellus inornatus)*, an economically important aquaculture pest that has been accidentally introduced worldwide. If the costs of intervention were the same across life stages, extermination of adults would be an inefficient way to control species with the population dynamics characteristics of invaders. In the oyster drill case, however, efficient control targets adults because they are much easier to find.

Key Words: Invasive Species; Bioeconomics; Control Strategies

JEL Classification Numbers: Q10, Q2, Q22

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INTRODUCTION

Harmful nonindigenous species exact a tremendous toll on ecological and economic wellbeing, and prominent attempts to quantify their costs assign about 15% of the total to control efforts (Pimentel et al. 2000). Because resources for dealing with invasive species are limited, it is essential to select cost-effective methods for control. Across entire landscapes, for example, removing newly emerged populations has been shown both theoretically and empirically to be a better strategy for managing invasive plants than reducing well-established populations (Moody and Mack 1988; Cook et al. 1996). In this paper we examine the 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 increases the population. Specifically, such issues have been explored with what ecologists call "elasticity analysis" of matrix population models (Heppell et al. 2000). In economics, *elasticity* refers to any logarithmic derivative, so to prevent confusion we will

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refer to the objects of that analysis as "population elasticities." The population elasticities characterizing any species are functions of that species' "transition matrix" **A**, of which each element a_{ij} measures the fraction of a population at stage *j* in the life cycle expected to survive to stage *i*. The population elasticities e_{ij} are defined as

$$e_{ij} = \frac{\partial \ln \lambda}{\partial \ln \alpha_{ij}} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}$$
(1)

where λ is the overall rate of change in population abundance, and also the dominant eigenvalue of **A**. Population elasticities thus represent the effect on population growth (λ) achieved by a proportional change in a given demographic parameter (a_{ij}). Across all transitions, elasticities sum to unity.

For endangered species, 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 (Heppell et al. 2000). Accordingly, 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, such as reproduction (e.g., release of sterile males, biological control by seed predators; Shea and Kelly 1998) or adult survival (e.g., manual removal of large individuals). The relative effectiveness of these options is generally judged in terms of reduced population growth of the invasive species, an issue mostly addressed by biologists. Sometime, a pure biology approach can have immediate implications. For instance, although population growth rate of an invasive thistle in New Zealand was most influenced by transitions involving seeds, seed predators introduced as biocontrol agents were unlikely to be able to reduce seed survival enough to make the population decline (Shea and Kelly 1998). Similarly, in an illustration below we will argue

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that trying to kill juvenile oyster drills is so obviously inefficient that the option can be left out of economic analysis. In general, however, the comparison of life stage interventions 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 ($\lambda > 1$) 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),* a direct-developing marine snail that causes economic harm by preying on small oysters.

We stress that this analysis applies only to the question of *how* to stop an invasion, leaving aside the matter of whether the invasion is worth stopping. 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) and is likely to be especially complex if the relationship between invader abundance and damage is nonlinear—for instance, if 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.

METHODS

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 (Noy-Meir 1975). High population growth rates have been achieved by invasive species that escape natural enemies and thereby 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

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

where *j* denotes juvenile-to-adult survival, *a* adult survival, and *f* fecundity. The asymptotic rate of population growth $\lambda(\mathbf{A})$ 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 the strategy proposed by Caswell (1989, 121)

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

where w is the right eigenvector and v is the left eigenvector of the matrix A, and $\langle w, v \rangle$ 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.

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—that is, that $\lambda(\mathbf{A}) = 1$.

As a simple case, we also assume that each transition probability can be reduced from its preintervention 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 ($c'_{ij}(a_{ij}) > 0$). A policymaker chooses a set of interventions to minimize total cost subject to $\lambda(\mathbf{A}) = 1$. Since we are abstracting from the details of the intervention strategies, this is equivalent to choosing the a_{ij} directly to minimize the Lagrangian

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

$$\tag{4}$$

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 one 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 is known as a *Lagrange multiplier*, and it 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

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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 population, so that at the optimally chosen **A**

$$\mu(\mathbf{C}(\mathbf{A})) = \max_{ij \in I} \{-c_{ij}'(a_{ij})\lambda'(a_{ij})\}.$$
(5)

For a cost minimization problem, the value of μ is irrelevant. 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 (4) must satisfy the set of first-order conditions given by $\lambda(\mathbf{A})=1$ and

$$\begin{bmatrix} c'_{ij}(a_{ij}) - \mu \frac{\partial \lambda}{\partial a_{ij}} \end{bmatrix} (\hat{a}_{ij} - a_{ij}) = 0$$

$$c'_{ij}(a_{ij}) - \mu \frac{\partial \lambda}{\partial a_{ij}} \ge 0$$

$$\forall ij \in I$$
(6)

where \hat{a}_{ij} is the transition probability if no intervention occurs. The top line of (6) thus states that for each *ij* in the intervention set, either a_{ij} is left alone (in which case $c_{ij} = 0$) or $c'_{ij}(a_{ij}) = \mu \lambda'(a_{ij})$. The bottom line of (6) indicates which of these must hold; if $c'_{ij}(a_{ij}) < \mu \lambda'(a_{ij})$ for all $a_{ij} < \hat{a}_{ij}$, then 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. Note that from (5) it is not possible for $c'_{ij}(a_{ij}) > \mu \lambda'(a_{ij})$ for all life stage transitions.

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

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

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

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

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

The right side of (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 (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. Accordingly, we assume that the cost of altering each parameter increases logarithmically as the parameter is reduced below its intrinsic value \hat{a}_{ii} set by the biology of the organism:

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

where κ_{ij} is a scalar relating change in survival or fecundity to dollars spent. Note that although the MCR in (8) refers to the marginal cost of absolute changes in a_{ij} , the cost itself depends on the proportional decrement in the transition probability. In the case of survival parameters, this functional form of c_{ij} corresponds to assuming that individuals experience an instantaneous

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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 $a_{ij} = \exp(-\delta_{ij}) = \exp\left[-\left(\hat{\delta}_{ij} + \frac{c_{ij}}{\kappa_{ij}}\right)\right]$. Using the cost function

(9) and expression (7) for $\lambda(\mathbf{A})$, the joint first-order condition (8) becomes

$$\frac{f\kappa_a}{a\kappa_f} = \frac{a + \left(a^2 + 4fj\right)^{1/2}}{2j}.$$
(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 onward, 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 spreading rapidly ($\lambda = 1.2$). 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 in which 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.

Cost-effective control of oyster drills

Oyster drills (*Ocinebrellus 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 per 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 $\lambda = 1.06$, 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 eggs 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 (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 in which we recorded all drills and egg cases that we observed, which reflects the ease of reducing of each stage. The relative ease of finding egg capsules versus snails varied through the year because of seasonal reproduction, with a peak in the ratio of eggs to drills in midsummer at 10 (Nemah) or 25 (Peterson Station) (Fig. 2). At other sites, where we do not have repeated measurements over the year, we have observed egg:drill ratios as high as 60:300. The right eigenvector of the population matrix (11) is the stable stage distribution (0.9934, 0.0066). This stable stage distribution indicates that the actual egg:drill ratio is 150. In most cases, then, we find fewer eggs than would be expected from the intrinsic dynamics of Ocinebrellus: eggs are more difficult to find than adult snails. 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) for κ_a and κ_f .

RESULTS

Population elasticities of invaders

With life-cycles characteristic of invasive species, population elasticities are highly dependent on both population growth (λ) and the demographic values. 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 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 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 twostage 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.

Ocinebrellus 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 (11) in equation (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.

Minimizing costs of controlling invaders

We consider next the implications of the above population elasticity features for the mix of life-stage interventions that will minimize the cost of ensuring that an invasive population does grow. As the population elasticity analysis suggests, rapidly invading species ($\lambda = 1.2$) that are 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. For longlived, low-fecundity invaders it was optimal to reduce adult survival alone unless $\kappa_a/\kappa_f \ge 1.25$ (Fig. 4). At still higher cost ratios ($\kappa_a/\kappa_f \ge 10$), a strategy targeting only fecundity became optimal. In contrast, mixed strategies were favored for short-lived, highly fecund species only at the lowest relative cost ratios examined (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 equal (Fig. 4c). These differences across life histories reflect changes in the MBR—that is, the marginal contributions of survival and fecundity to λ —and are thus qualitatively consistent with population elasticity analyses.

Cost-effective control of oyster drills

We used the estimated population matrix for *Ocinebrellus inornatus* (11) to calculate the MBR as functions 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 (9) with cost parameter ratios $K \equiv \kappa_a/\kappa_f$ of 1 and 1.5. In the case where K = 1.5, the optimal policy includes effort expended against fecundity (Fig. 5). This is visible in that the intersection of marginal cost (MC) and the MBR is around a = 0.25, a level at which the population is still growing. To halt population growth, some further action is needed, and the equality of MC and MBR means that it is now efficient to combine attacks on both life stages. In the case where K = 1, 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(MBR) 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 Figure 5, because the curves are drawn with fecundity fixed.

The discussion of control strategies above, however, makes it fairly clear that in this case, targeting only adults is cost-effective. With an actual ratio in the field of \sim 150 eggs per adult,

and worker collection ratios of 10 to 25 eggs per adult, we have K in the range of 1:15 to 1:6, well below the value (\sim 1.2) at which targeting fecundity begins to be cost effective.

DISCUSSION

Based on population elasticity analysis, the most effective method for reducing the growth rate of an 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 ($\lambda > 1$), control by removing adults would likely be effective only if adult survival was naturally high. Control by removing juveniles would be particularly effective when prereproductive 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 stop the invasion. The relative costs of control substantially influenced solutions to the Lagrangian minimization problem. Changes in cost can switch the stage that should be the target of control efforts by requiring more expensive interventions to 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 Figure 4, when costs to reduce each life stage were equal ($\kappa_a/\kappa_f = 1$), 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 transitions simultaneously, were best over a range of moderate survival and fecundity values. This mixed strategy was never predicted by population elasticities, which reflected only small proportional changes in each transition.

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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, the Lagrangian was minimized by reducing adult survival over a range of realistic MCR based on how easily we found egg capsules versus adults in field surveys (Fig. 6). Currently, control efforts target adults, the phase that is easiest to remove, despite its lower population elasticity. 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 overrule 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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Figure 1. Life cycle diagram for (a) two-stage life history with a one-year nonreproductive juvenile period and (b) three-stage life history with a juvenile period of two or more years. Transitions among stages of the life cycle are shown as arrows where f = per capita fecundity, j = juvenile survival, and a = adult survival.



Figure 2. Ratio of eggs to adult oyster drills, *Ocinebrellus 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; on average 10 juveniles emerge from each capsule.

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.



Figure 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) one year (j=0.5), (d–f) two years (j1=j3=0.71), (g–i) three 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.



Figure 4. Adult survival and fecundity values that minimize the costs of invasion control $(\lambda = 1)$, found by Lagrangian optimization (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) $\hat{a} = 0.6$, $\hat{f} = 1.44$; and (c) $\hat{a} = 0.9$, $\hat{f} = 0.72$. With no intervention $\lambda = 1.2$ in all cases.



Figure 5. Costs and benefits of reducing adult survival of oyster drills, *Ocinebrellus inornatus*.