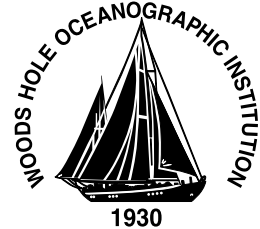# Massachusetts Institute of Technology
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MASTER OF SCIENCE THESIS

On the Economic Optimality of Marine Reserves
When Fishing Damages Habitat

by

Holly Villacorta Moeller

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Holly Villacorta Moeller

B.A., Rutgers, The State University of New Jersey (2008)

Submitted in partial fulfillment of the requirements for the degree of

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Author . . . .
Department of Biology
May 21, 2010

Certified by. . . . .
Michael G. Neubert
Associate Scientist, Woods Hole Oceanographic Institution
Thesis Supervisor

Accepted by . . . .
Simon Thorrold
Chair, Joint Committee for Biological Oceanography
Woods Hole Oceanographic Institution

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Abstract

In this thesis, I expand a spatially-explicit bioeconomic fishery model to include the negative effects of fishing effort on habitat quality. I consider two forms of effort-driven habitat damage: First, fishing effort may directly increase individual mortality rates. Second, fishing effort may increase competition between individuals, thereby increasing density-dependent mortality rates. I then optimize effort distribution and fish stock density according to three management cases:

(1) a sole owner, with jurisdiction over the entire fishery, who seeks to maximize profit by optimizing effort distribution;

(2) a manager with limited control of effort and stock distributions, who seeks to maximize tax revenue by setting the length of a single, central reserve and a uniform tax per unit effort outside it; and

(3) a manager with even more limited enforcement power, who can only set a tax per unit effort everywhere in the habitat space.

I demonstrate that the economic efficiency of reserves depends upon model parameterization. In particular, reserves are most likely to increase profit (or tax revenue) when density-dependent fish mortality rates are affected. Interestingly, for large habitats that are sufficiently sensitive to density-dependent fish mortality effects, reserve networks (alternating fished and unfished areas of fixed periodicity) emerge. These results suggest that spatial forms of management which include marine reserves may enable significant economic gains over nonspatial management strategies, in addition to the well-established conservation benefits provided by closed areas.

Thesis Supervisor: Michael G. Neubert
Title: Associate Scientist, Woods Hole Oceanographic Institution

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Chapter 1

Introduction

Recent reports of fishery collapse and overexploitation have driven natural resource managers and conservationists to call for the implementation of 'no take' marine reserves to protect habitat and harvested stocks. Where reserves have been successfully established, they have rapidly become sanctuaries for elevated stock biomass and population density, shown elevated levels of biodiversity, and protected intact habitat relative to adjacent fished areas (reviewed in Halpern and Warner 2002, and Lester et al. 2009). However, reserves may face steep opposition when closures are perceived as economically costly. Prohibiting fishing in a reserve removes any enclosed stock biomass from potential harvest, and forces fishermen to either reduce effort overall, or intensify fishing effort elsewhere (Smith and Wilen 2003).

Many bioeconomic modeling studies have evaluated the economic costs of marine reserves. Frequently, the models used rely on a priori reserve designation, in which a fixed fraction of the habitat is closed to fishing, and stock biomass and fishing intensity are subsequently calculated to maximize yield or profit (Gerber et al. 2003; see Armstrong and Skonhoft 2006, Gårdmark et al. 2006, and White and Kendall 2007 for examples).

The economic costs-benefit analysis of reserves in such models, then, depends upon the cost of fishing and species life history. In particular, closures are more likely

to be economically efficient when reserves are net exporters of larvae or harvestable biomass (Gerber et al. 2005, Sanchirico et al. 2006, White and Kendall 2007, Costello and Polasky 2008, but see Gårdmark et al. 2006 for an exception), when closures encompass areas that would be costly to fish in their absence (Smith and Wilen 2003, Sanchirico et al. 2006), or when fish stocks are already overexploited (Gerber et al. 2003, Costello and Polasky 2008).

An alternative modeling strategy begins with a spatially explicit habitat space on which a fish stock is supported. The spatial distribution of effort is then calculated according to economic assumptions about fishery ownership and fisherman behavior. Reseves (i.e. zones of zero fishing effort) may emerge from this analysis when fished species are mobile (Neubert 2003), and when habitat is heterogeneous (Costello and Polasky 2008).

Here, I expand on such analyses by considering the effects of fishing on habitat quality. Modeling and empirical evidence suggest that habitat may display a wide range of sensitivities to damage from fishing gear (Fogarty 2005, Hiddink et al. 2006a, Hiddink et al. 2006b), and reserves may be more economically effective when protecting the most vulnerable habitat (NRC 2001, Hiddink et al. 2007). Fishing effort may damage habitat through biomass removal and reduction in habitat complexity (Fogarty 2005, Hiddink et al. 2006b), reducing the habitat's ability to support fish biomass.

I consider two mechanisms by which habitat quality feeds back on stock populations. First, habitat effects may be density independent. That is, an individual fish may experience increased mortality or reduced fecundity because food supply is diminished or habitat cover is eliminated (Mangel 2000). Second, habitat effects may be density-dependent: Habitat damage may intensify competition for a reduced number of spatial resources, increasing density-dependent reductions in birth rate and increases in mortality rate (Lindholm et al. 2001). In this study, I consider a range of density-independent and density-dependent habitat sensitivities to fishing.

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This effort-driven feedback on habitat means that, even if habitat is initially of homogeneous quality, any localized high-effort patches will reduce the quality of habitat in that location relative to the surroundings. I also allow adult, harvestable members of the fish population to move (through diffusion), and assume that fish that exit the habitat are lost to the system. Therefore, motility provides a second driver of spatial heterogeneity in the model.

In the analysis that follows, I consider sustainable harvest (i.e. equilibrium solutions to the model) from three economic perspectives. First, I take the viewpoint of a single owner, and calculate effort and stock distributions that maximize profit from the entire fishery. I show that the inclusion of habitat damage in our models increases the likelihood that reserves emerge in the economically optimal (profit-maximizing) case. However, this result is sensitive to changes in the model's parameters – especially habitat size and fish mobility – and the mechanism through which habitat damage affects vital rates.

I then consider an alternative scenario, in which a manager may designate a reserve in the center of the habitat which is closed to fishing. Previous modeling studies have shown that, when fishing effort is redistributed around the reserve, closures alone may reduce fishery yield because the new effort distribution severely degrades fish biomass (Hanneson 1998). Therefore, I also allow the manager to set a tax on effort outside the reserve area. Areas outside the reserve are considered "open access": individual fishermen continue to add effort until profits are completely dissipated (Homans and Wilen 1997). The manager seeks to maximize tax revenue, so increasing the tax rate or expanding the central reserve represent tradeoffs between reducing taxable effort and increasing stock size and, potentially, revenue.

This "limited" management scheme allows analysis of reserve optimality in a more realistic context. Again, the inclusion of reserves in an optimally managed fishery depends sensitively upon habitat size and the parameterization of habitat damage.

Finally, I consider a third "tax only" scenario, in which the manager may only

set tax per unit effort, which is constant over the entire habitat. This third-best case represents the most basic form of fishery management, and results in approximately uniform distributions of effort wherever fish stocks are sufficiently high that effort is economically viable.

Chapter 2

The Model

Consider a stock living in a linear habitat. Imagine that its biomass density (N) at location X and time T changes as a result of local population growth, diffusion, and harvesting. Such a stock evolves in time according to the partial differential equation

$$\frac{\partial N(X,T)}{\partial T} = g(N, E(X)) + D\frac{\partial^2 N}{\partial X^2} - qE(X)N, \tag{2.1}$$

where g is the rate of population growth due to births and deaths and D is the diffusion coefficient. Let us assume that harvesting occurs at a rate that is proportional to both the stock density and the effort density, $E(X)$. The "catchability coefficient", q, is the proportionality constant.

At equilibrium $\partial N/\partial T = 0$, so we may write $N(X,T) = N(X)$, and equation (2.1) becomes

$$D\frac{\partial^2 N}{\partial X^2} = qE(X)N - g(N, E(x)). \tag{2.2}$$

Finally, assume that individuals cannot survive outside of a stretch of habitat of length L. Therefore we impose the Dirichlet boundary conditions

$$N(-L/2) = N(L/2) = 0. \tag{2.3}$$

The profit generated by this fishery is calculated by subtracting the total cost of harvesting (TC) from the total revenue (TR). For a fixed price per unit catch p, the total revenue is given by

$$\text{TR} = \int_{-L/2}^{L/2} pqE(X)N(X)\,dX \tag{2.4}$$

(where it is understood that $N(X)$ is the unique positive solution of (2.2) if it exists). Let us assume that the marginal cost of effort at a given location increases linearly with effort, reflecting the increasing costs that harvesters impose upon one another when more of them try to fish in the same location. Thus

$$\text{TC} = \int_{-L/2}^{L/2} [w_0 + w_1 E(X)]\,E(X)\,dX \tag{2.5}$$

where w_0 and w_1 are the cost per unit effort and the marginal cost per unit effort when $E = 0$. The equilibrium profit (a. k. a. "rent"), $P[E(X), N(X)]$, is given by the integral $\text{TR} - \text{TC}$, whose integrand

$$R(X) = pqE(X)N(X) - [w_0 + w_1 E(X)]\,E(X) \tag{2.6}$$

is the "rent density."

Neubert and Herrera (2008) analyzed model (2.1)-(2.6) to find the effort distribution that maximized P at equilibrium. In their treatment, the growth function g was logistic, and fishing had no impact on habitat quality. Here, we will assume that fishing does have an effect on habitat quality and that this effect is manifest in the model as a change in the birth and death rates of individuals. Since the logistic equation does not contain these vital rates we must first construct a growth function that does. The simplest such model is

$$g(N) = (b - d)N, \tag{2.7}$$

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where b is the per capita birth rate and d is the per capita death rate. So that the population will not grow without bound, we posit that the birth rate declines with population density while the mortality rate grows with population density (Sinclair 1989), i. e.,

$$b = b_0 - b_1 N \text{ and } d = d_0 + d_1 N. \tag{2.8}$$

To complete the growth model we assume that fishing increases either the intrinsic mortality rate d_0 or the rate at which mortality increases with population density d_1. Taken together, these assumptions bring us to the growth model

$$g(N, E) = \left\{ (b_0 - b_1 N) - [d_0 + h_0 E + (d_1 + h_1 E) N] \right\} N \tag{2.9}$$

or, upon rearranging terms,

$$g(N, E) = [b_0 - (d_0 + h_0 E) - (b_1 + d_1 + h_1 E) N] N. \tag{2.10}$$

Chapter 3

Analysis

Our analysis of this model will proceed in three stages. First, we will analyze a non-spatial version of the model. We will find the effort level that maximizes P and determine how this effort level depends on the destructiveness of fishing (via the parameters h_0 and h_1). Next we will reinstate the spatial dimension, and find the spatial distribution of effort that maximizes P. In some cases this distribution contains no-take reserves, and we will determine how the size and number of reserves changes with h_0 and h_1. Finally we will compute so called "limited management" solutions that result from imposing a single no-take reserve along with a tax on effort.

Before we begin, note that the model has 12 parameters. However, using the following change of variables

$$u = \frac{b_1 + d_1}{b_0 - d_0} N, \quad t = (b_0 - d_0)T, \qquad x = \sqrt{\frac{b_0 - d_0}{D}} \, X,$$

$$(3.1)$$

$$f = \frac{q}{b_0 - d_0} E, \qquad \text{and} \qquad \pi = \frac{(b_1 + d_1)}{p\sqrt{(b_0 - d_0)^3 D}} \, P,$$

we can obtain rescaled versions of the state equation,

$$\frac{\partial^2 u}{\partial x^2} = uf - [(1 - \gamma_0 f) - (1 + \gamma_1 f)u]u \quad \text{for} \quad -\ell/2 < x < \ell/2, \qquad (3.2)$$

the boundary conditions,

$$u(-\ell/2) = u(\ell/2) = 0, \tag{3.3}$$

and the profit integral,

$$\pi(f, u) = \int_{-\ell/2}^{\ell/2} uf - (\omega_0 + \omega_1 f) f \, dx. \tag{3.4}$$

In the process, we have reduced the number of parameters from twelve to five, where

$$\ell = \sqrt{\frac{b_0 - d_0}{D}} L, \quad \gamma_0 = \frac{h_0}{q}, \quad \gamma_1 = \frac{h_1(b_0 - d_0)}{q(b_1 + d_1)}, \tag{3.5}$$

$$\omega_0 = \frac{w_0(b_1 + d_1)}{pq(b_0 - d_0)}, \quad \text{and} \quad \omega_1 = \frac{w_1(b_1 + d_1)}{pq^2}. \tag{3.6}$$

3.1   The Non-Spatial Model

A "non-spatial" version of model (3.2)-(3.4) is one in which there is no flux of biomass anywhere (i. e. $\partial u/\partial x = 0$ everywhere) and the variables f and u become constants. In this case the state equation (3.2) reduces from an ordinary differential equation to the algebraic equation

$$[(1 - \gamma_0 f) - (1 + \gamma_1 f)u]u - fu = 0, \tag{3.7}$$

and the objective functional (3.4) becomes

$$\pi(f, u) = [uf - (\omega_0 + \omega_1 f)f] \, \ell. \tag{3.8}$$

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The sole-owner's objective is to maximize π by choosing a nonnegative harvest rate $f = f^*$ and nonnegative stock size $u = u^*$ that satisfy (3.7). From (3.7) we have

$$
u^* = \begin{cases} \frac{1-(1+\gamma_0)f^*}{1+\gamma_1 f^*}, & \text{if } f^* < 1/(1+\gamma_0) \\ \\ 0, & \text{otherwise.} \end{cases}
\tag{3.9}
$$

Substituting u^* into (3.8) gives the profit as a function of effort.

In Figs. 3.1 and 3.2 I have plotted the equilibrium stock size and the profit as functions of effort. In general, the equilibrium stock size is lower when fishing damages habitat. When fishing increases the density-independent mortality rate γ_0, the reduction in equilibrium stock size is greater at higher effort levels. In contrast, when fishing increases the density-dependent mortality rate γ_1 the reduction in equilibrium stock size is greatest at intermediate effort levels. Profit is also reduced at all effort levels when fishing damages habitat, and follows the same patterns as the equilibrium stock size. That is, profit is reduced dramatically at high effort levels when $\gamma_0 > 0$, and at intermediate levels when $\gamma_1 > 0$.

Figs. 3.3 and 3.4 present the profit-maximizing effort level, profit, and stock size as functions of γ_0 and γ_1. Not surprisingly all of these quantities decrease as either γ_0 or γ_1 increase. Optimal profit and effort decline more rapidly with γ_0 than with γ_1, but the optimal stock size is relatively insensitive to γ_0 compared to γ_1.
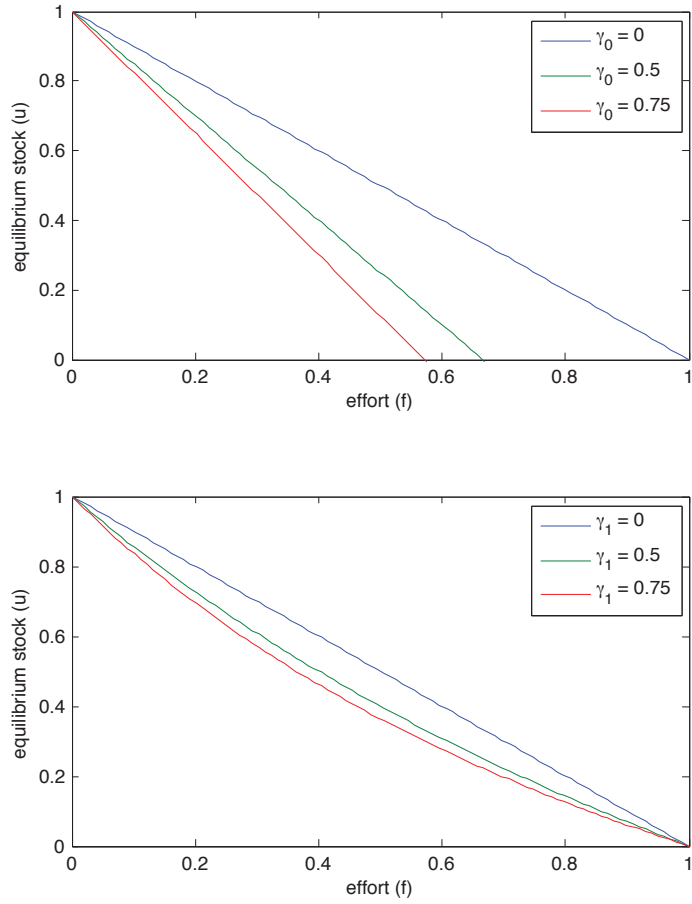
Figure 3.1: The effect of habitat-damaging fishing on equilibrium stock size. Except as specified in the figure legends, parameter values are: $\gamma_0 = \gamma_1 = 0$, and $\ell = 1$.
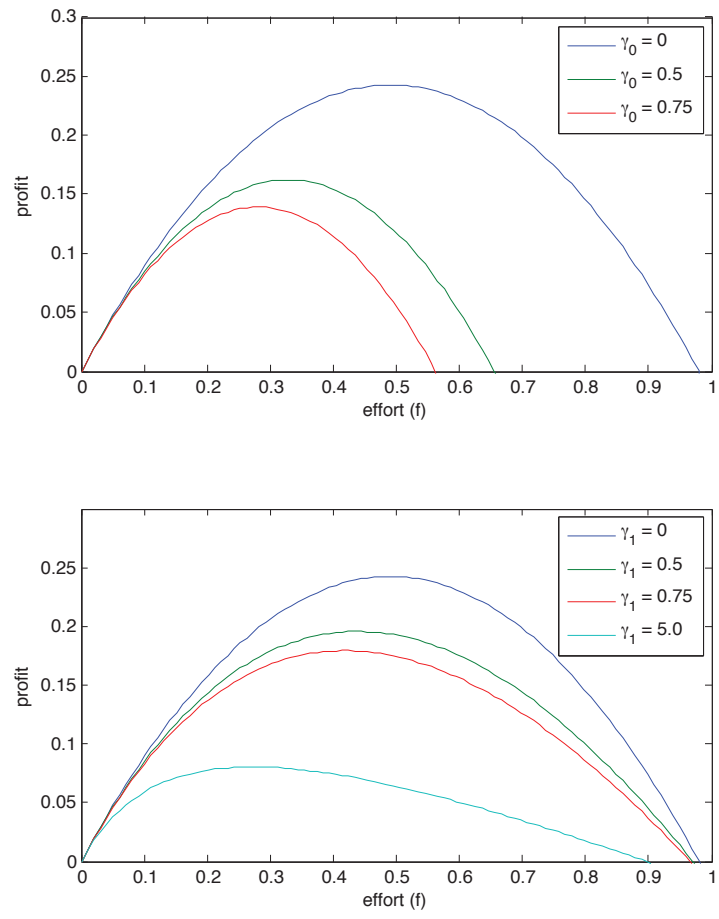
Figure 3.2: The effect of habitat-damaging fishing on profit. Except as specified in the figure legends, parameter values are: $\omega_0 = 0.01$, $\omega_1 = 0.001$, $\gamma_0 = \gamma_1 = 0$, and $\ell = 1$.
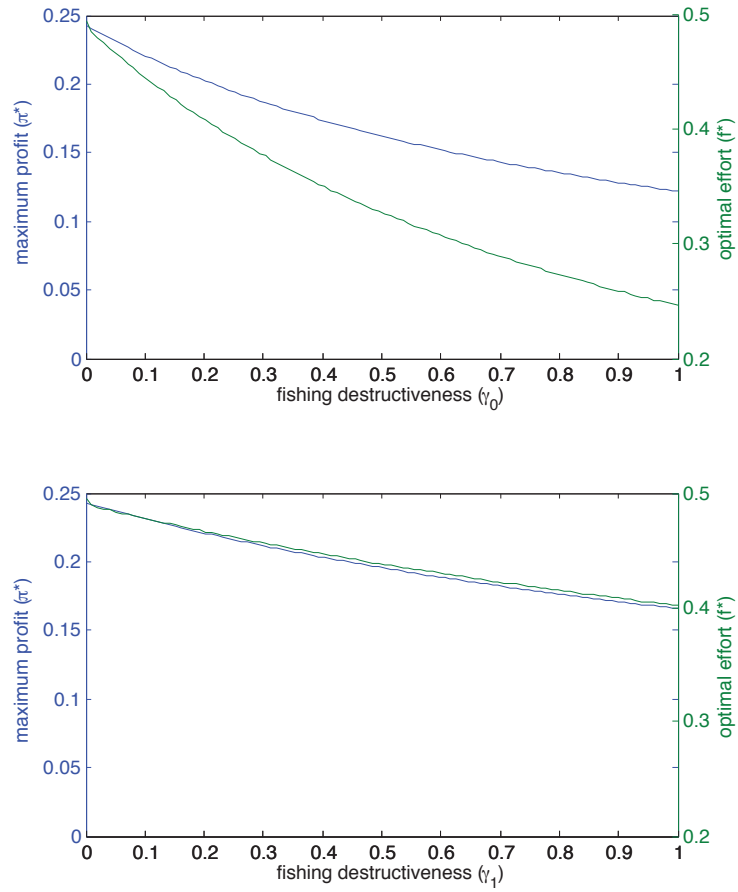
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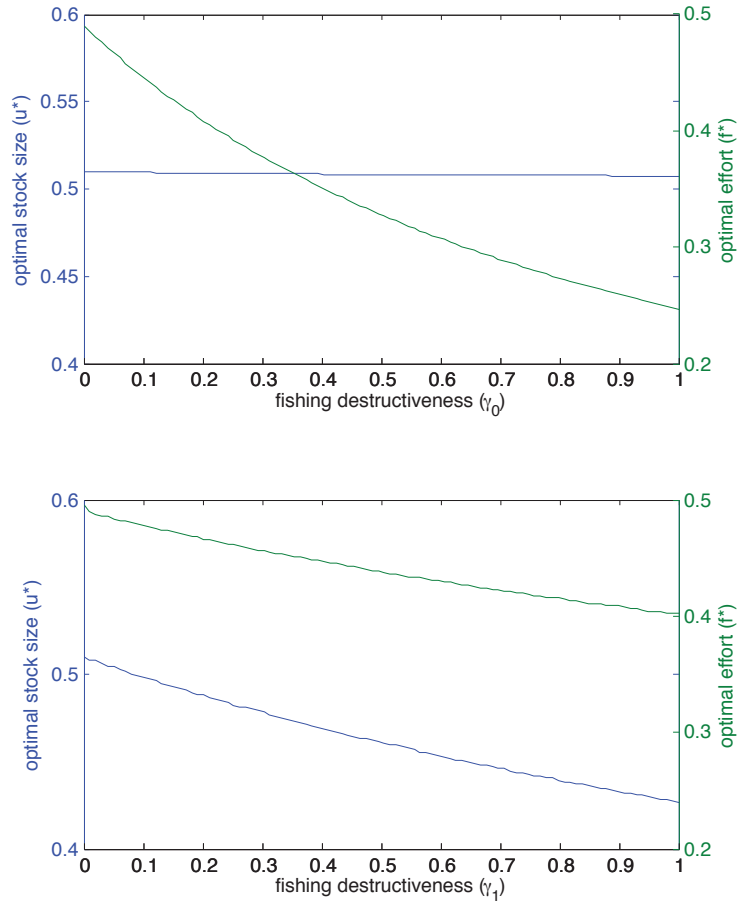
Figure 3.4: The effect of habitat-damaging fishing on optimal stock size and effort. Except as specified in the figure legends, parameter values are: $\omega_0 = 0.01$, $\omega_1 = 0.001$, $\gamma_0 = \gamma_1 = 0$, and $\ell = 1$.

3.2   The Spatial Model

We now return to the spatial model (3.2)-(3.4), and compare three management scenarios. The first scenario we examine is the first-best, or Sole Owner case in which the regulator can control the level of effort at every point in space and does so to maximize equilibrium rent. We then examine a second-best case in which the regulator can impose a combination of a centrally-located reserve and a tax on effort outside of the reserve. We assume regulated open access outside of the reserve. In this case the objective is to maximize the collected tax. Finally, we examine a third-best case in which the regulator is only able to impose a tax on effort and does so to maximize the collected tax.

3.2.1   First-Best Management Strategy: Sole Owner

In this case, the analysis is simplified by treating state equation (3.2) as a system of two first-order differential equations, one for the stock and one for its flux:

$$\frac{du}{dx} = -v \tag{3.10}$$

$$\frac{dv}{dx} = [1 - \gamma_0 f - (1 + \gamma_1 f)u]u - uf. \tag{3.11}$$

Pontryagin's Maximum Principle tells us that the effort distribution f that maximizes the profit integral (3.4) also maximizes the Hamiltonian

$$H = [pu - \omega_0 - \omega_1 f]f - \lambda_1 v + \lambda_2\{[1 - \gamma_0 f - (1 + \gamma_1 f)u]\,u - fu\} \tag{3.12}$$

at each point in space. In addition, the stock density, the optimal effort distribution, and the shadow prices—λ_1, the shadow price of flux, and λ_2, the shadow price of stock—satisfy the state equations (3.10) and (3.11) as well as the adjoint equations

$$\frac{\partial \lambda_1}{\partial x} = -\frac{\partial H}{\partial u} = -\{pf + \lambda_2\,[(1 - \gamma_0 f) - 2u(1 + \gamma_1 f) - f]\} \tag{3.13}$$

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$$\frac{\partial \lambda_2}{\partial x} = -\frac{\partial H}{\partial v} = \lambda_1, \tag{3.14}$$

and the boundary conditions

$$u(-\ell/2) = u(\ell/2) = 0 \tag{3.15}$$

$$\lambda_2(-\ell/2) = \lambda_2(\ell/2) = 0. \tag{3.16}$$

Setting $\partial H/\partial f = 0$ we find that the optimal harvest distribution is given by

$$f^*(x) = \max\left\{0, \frac{pu - \omega_0 - \lambda_2(\gamma_0 u + \gamma_1 u^2 + u)}{2\omega_1}\right\} \tag{3.17}$$

I solved system (3.10)-(3.17) numerically (see Appendix 2: Matlab Codes) for multiple habitat lengths (ℓ) and habitat sensitivity coefficients (γ_0 and γ_1). In Fig. 3.5, I show the sole-owner's effort distribution and the resulting stock density when fishing does not affect habitat quality ($\gamma_0 = \gamma_1 = 0$). At the habitat edges, where biomass density is low, the cost per unit catch is high; these areas are unprofitable and unfished. Just inside of these low-biomass regions, however, fishing intensity is highest, as the owner attempts to capture fish before they swim out of the habitat and perish.

The role of habitat length. When the habitat size is small, the central portion of the habitat remains unfished. This area is an *enforced reserve*—a zone where biomass density is high enough to be profitably, but not optimally, fished. Such a reserve would require active monitoring to prevent poaching. At the edges of the fish habitat, *edge reserves* are always present. These small unfished zones represent locations where fishing is not prohibited by management, but does not occur because stock populations are too low to overcome the costs of fishing effort (that is, marginal costs exceed marginal revenues).

For larger habitats, fishing again occurs in the middle of the habitat, at a low and
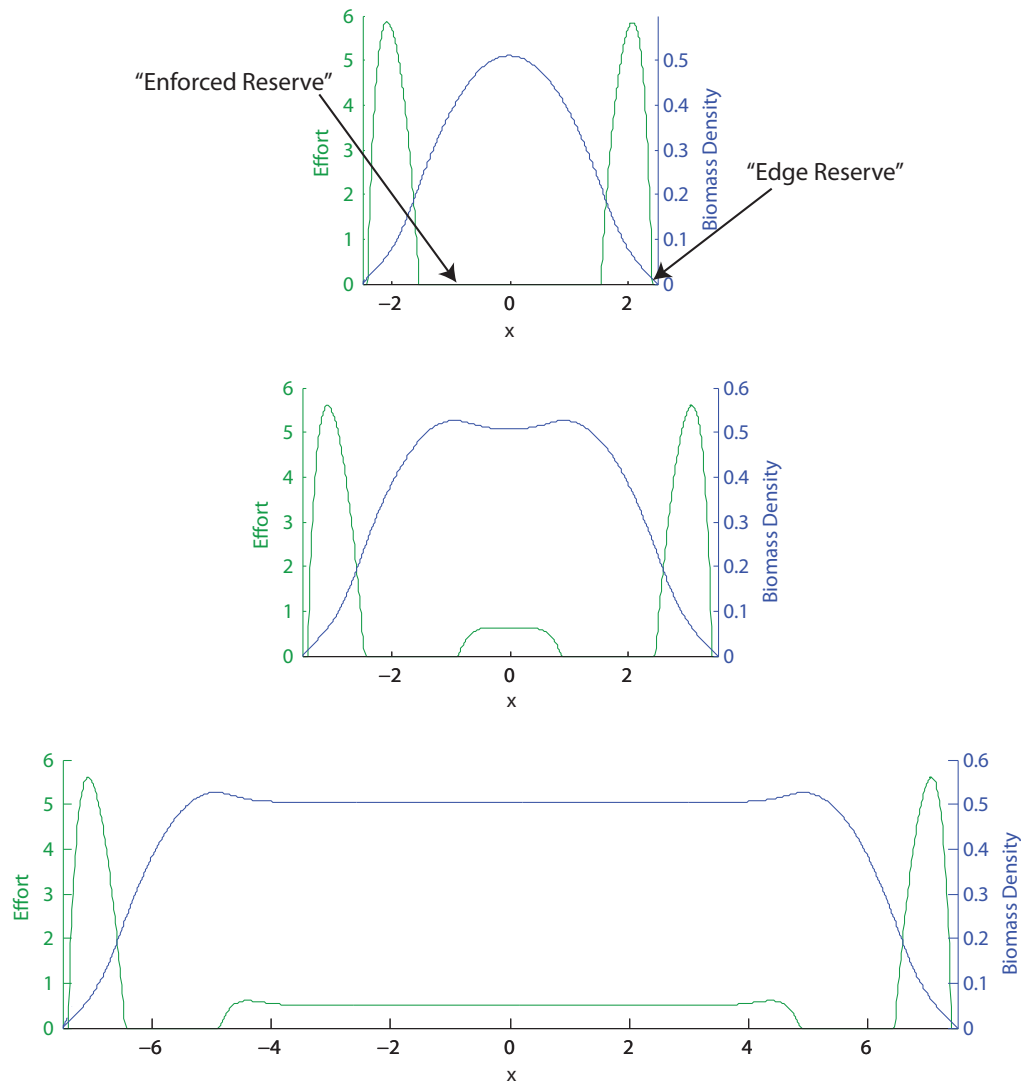
Figure 3.5: Optimal effort and population biomass distributions in the absence of habitat effects under Sole Owner management. The parameter values in each case are $\omega_0 = 0.01$, $\omega_1 = 0.001$, and $\gamma_0 = \gamma_1 = 0$. The habitat lengths are different in each graph. At the top, $\ell = 5$; in the middle, $\ell = 7$; at the bottom, $\ell = 15$.

constant level, similar to the nonspatial case. Enforced reserves remain just inside of high-effort edge peaks. When the cost of effort is higher, enforced reserves are no longer optimal.

Impacts of habitat damage. In Figs. 3.6–3.8 we show how the sole owner's distribution of effort changes if fishing damages habitat such that density independent mortality rates are increased (i.e. $\gamma_0 > 0$). In general, the results are as might be predicted from our analysis of the nonspatial model. The more damaging fishing is, the more effort is reduced at every location. Changes in γ_0 have hardly any effect on the number, size and location of enforced reserves or on the optimal distribution of the stock. The total fraction of habitat optimally placed in reserve is relatively insensitive to changes in γ_0 (Fig. 3.13).

These results stand in contrast to those we obtained when we allowed habitat damage to increase the density dependent component of mortality (by setting $\gamma_1 > 0$; see Figs. 3.9–3.11). In this case, the number, size and location of enforced reserves can change dramatically with changes in habitat sensitivity. In particular, the fraction of habitat optimally placed in reserve increases dramatically when $\gamma_1 > 0$ (Fig. 3.13). In addition, some areas experience much higher levels of fishing effort than they do in the absence of habitat effects.

For a side-by-side comparison of each habitat length, for the full suite of habitat sensitivities, see Fig. 3.12.

When ℓ and γ_1 are large, a network of reserves interwoven with intensely fished areas emerges as the optimal effort distribution (Fig. 3.14). The reserve network becomes periodic, with alternating intensely-fished areas and reserves of uniform length.

Profit and biomass. Fishery profit declines with increasing habitat sensitivity, as in the nonspatial model (Fig. 3.15). Total population biomass is again relatively insensitive to increasing γ_0. Density-dependent effects on fish biomass are complicated by effort distribution: when effort distribution shifts to reserves alternated with intense

fishing, equilibrium biomass may increase slightly because of the increased reserve area (Fig. 3.15). In general, total population biomass is less sensitive to increasing γ_1 than would be predicted by the non-spatial analysis.
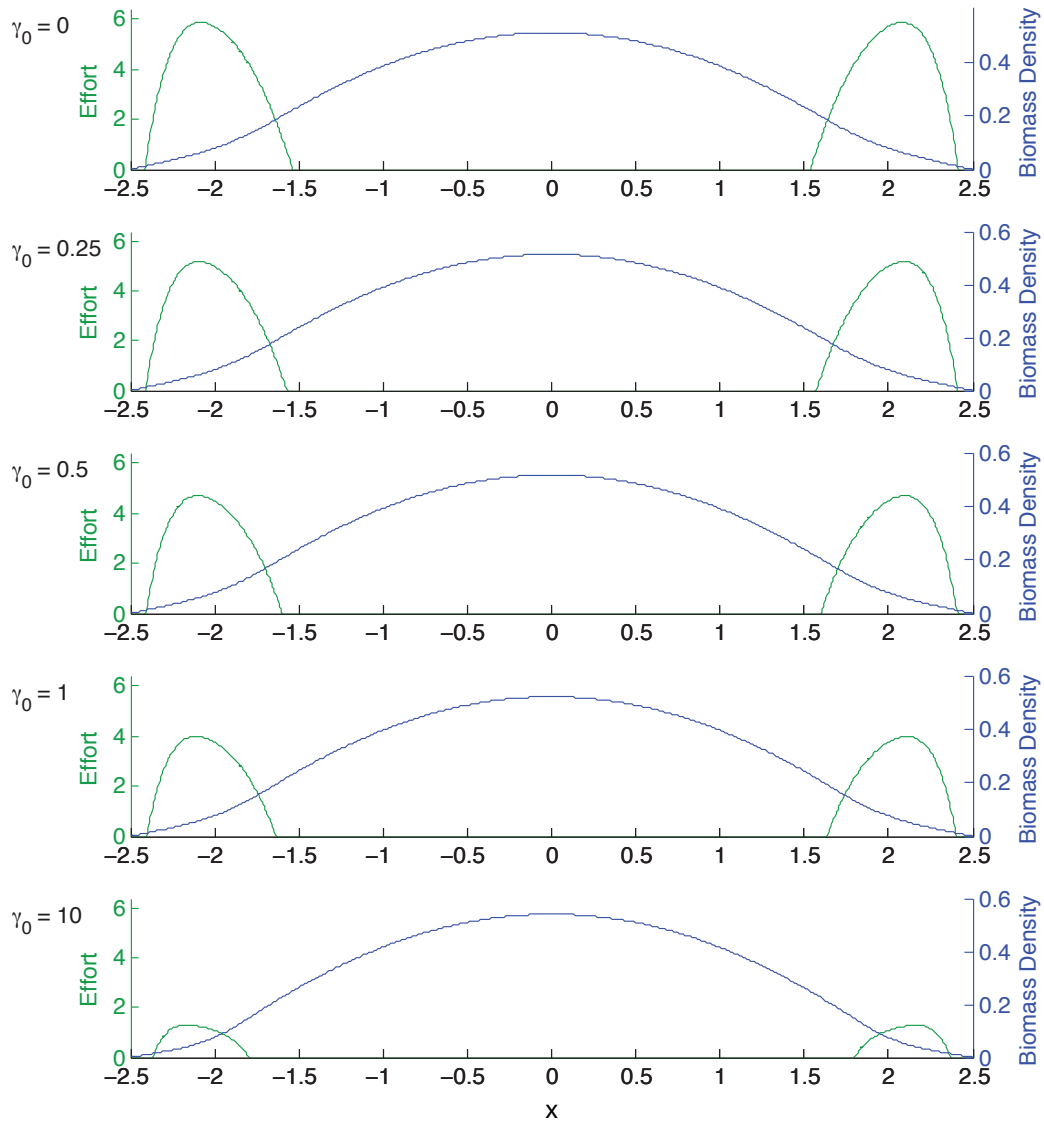
Figure 3.6: Optimal effort and population biomass distributions under Sole Owner management in the face of density-independent habitat effects. The parameter values in each case are $\omega_0 = 0.01$, $\omega_1 = 0.001$, $\gamma_1 = 0$, and $\ell = 5$.
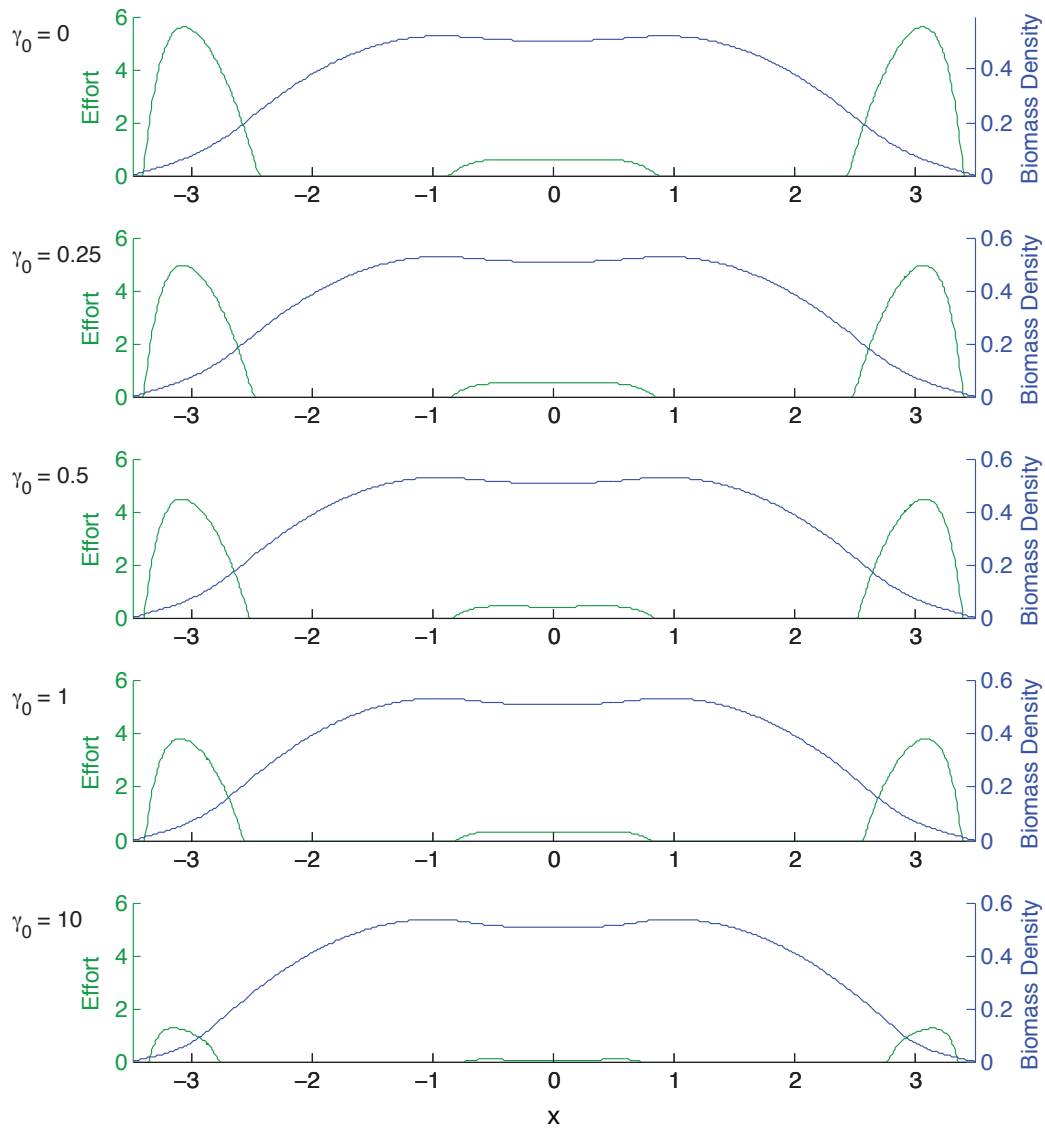
Figure 3.7: Optimal effort and population biomass distributions under Sole Owner management in the face of density-independent habitat effects. The parameter values in each case are $\omega_0 = 0.01$, $\omega_1 = 0.001$, $\gamma_1 = 0$, and $\ell = 7$.
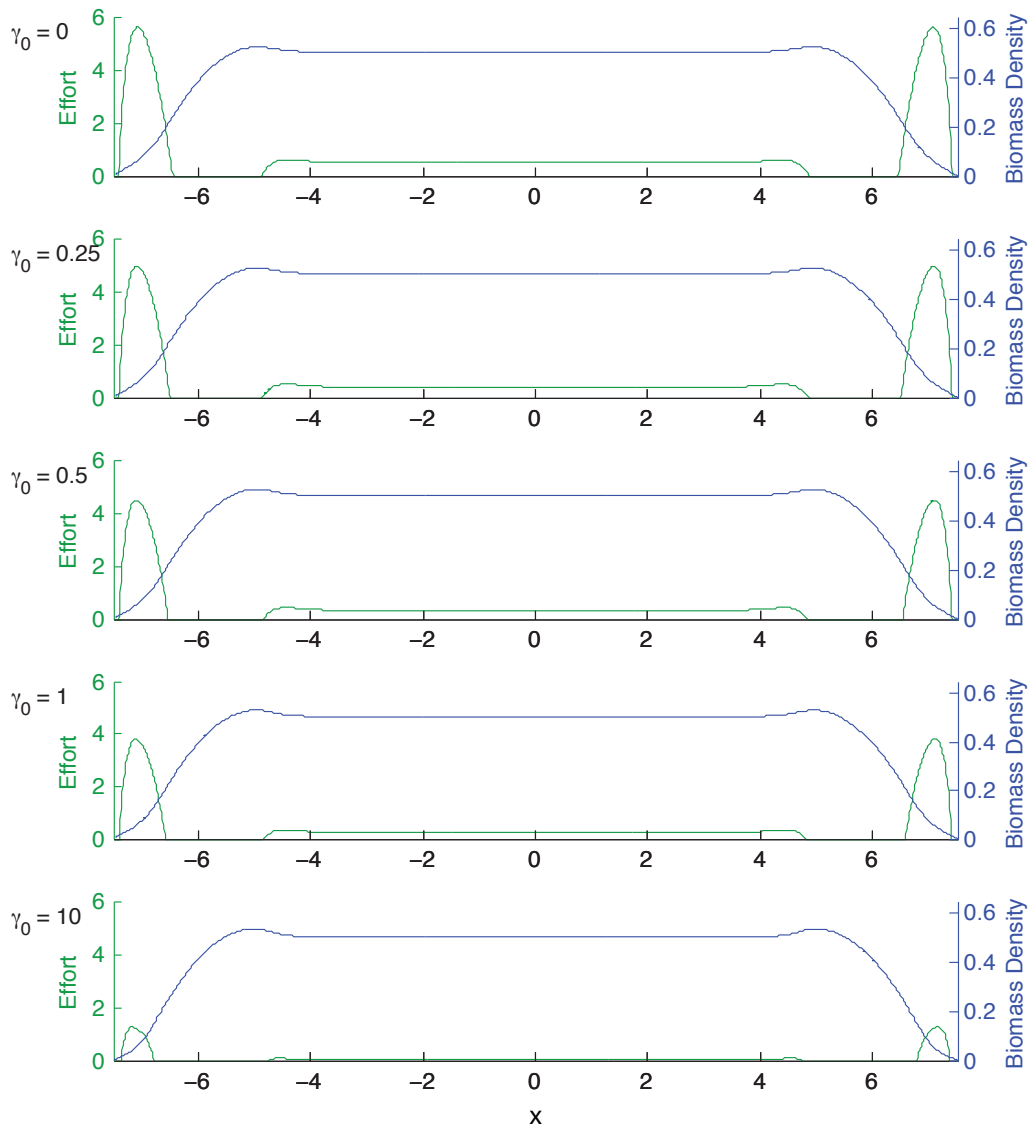
Figure 3.8: Optimal effort and population biomass distributions under Sole Owner management in the face of density-independent habitat effects. The parameter values in each case are $\omega_0 = 0.01$, $\omega_1 = 0.001$, $\gamma_1 = 0$, and $\ell = 15$.
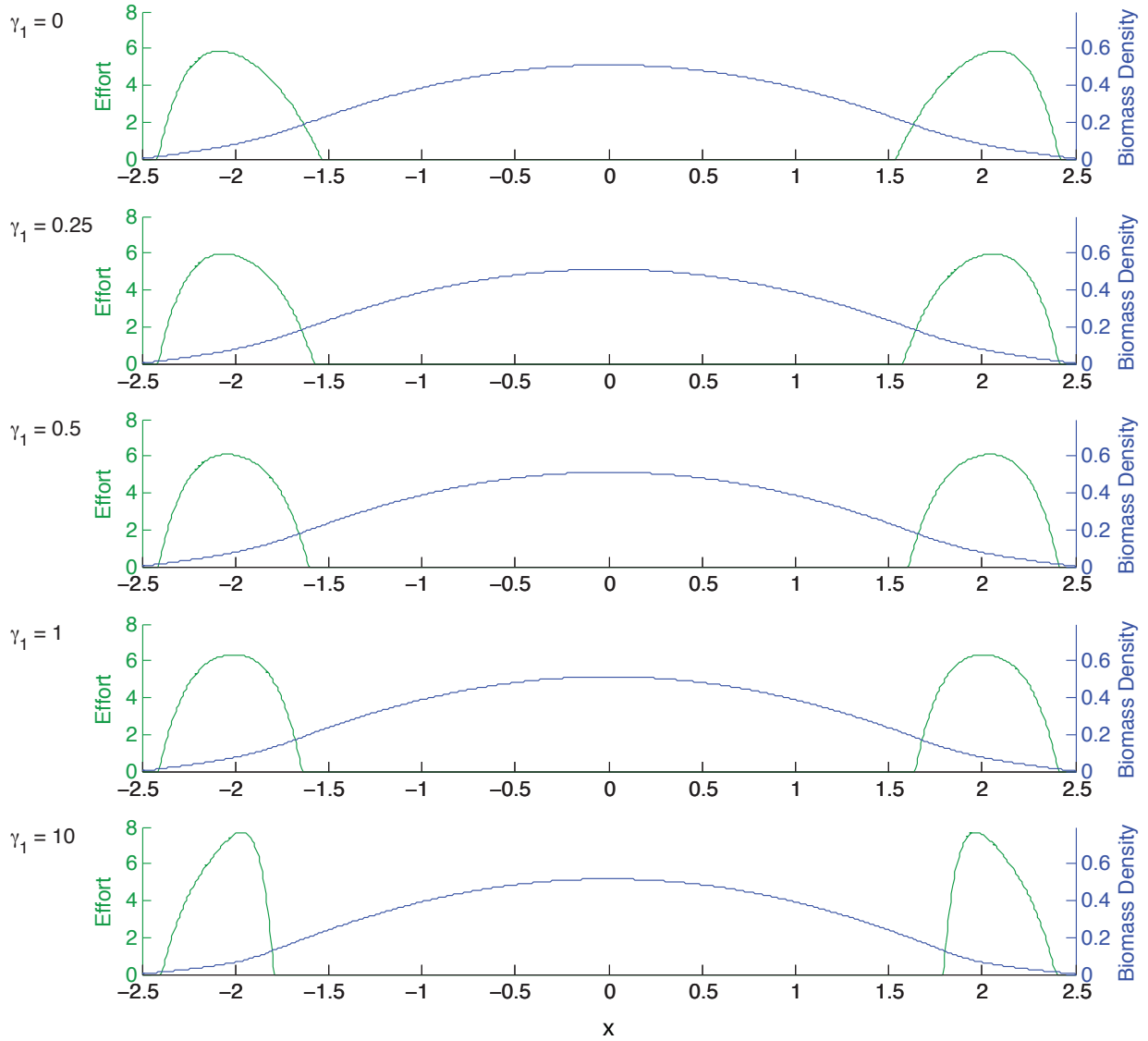
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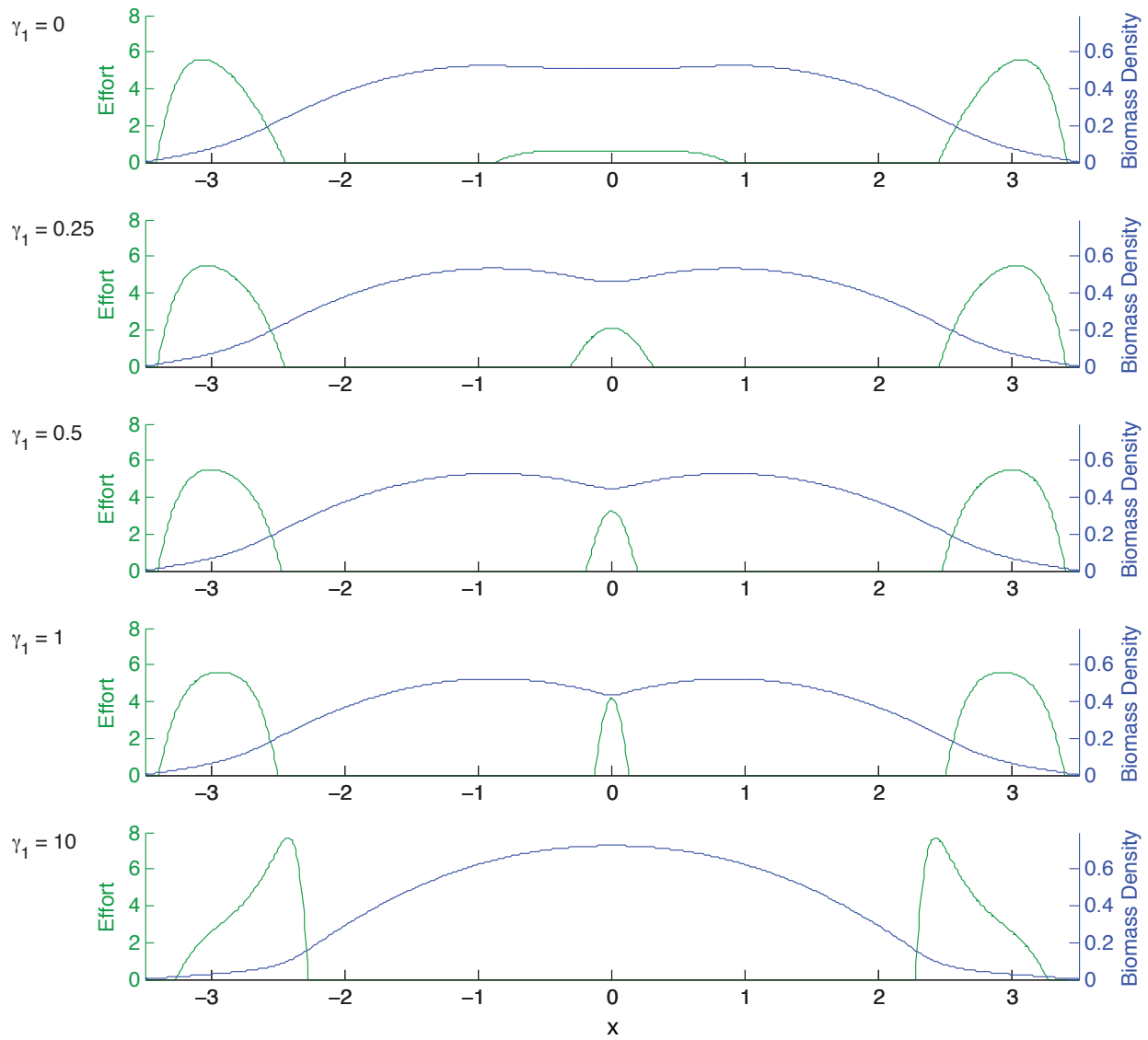
Figure 3.10: Optimal effort and population biomass distributions under Sole Owner management in the face of density-dependent habitat effects. The parameter values in each case are $\omega_0 = 0.01$, $\omega_1 = 0.001$, $\gamma_0 = 0$, and $\ell = 7$.
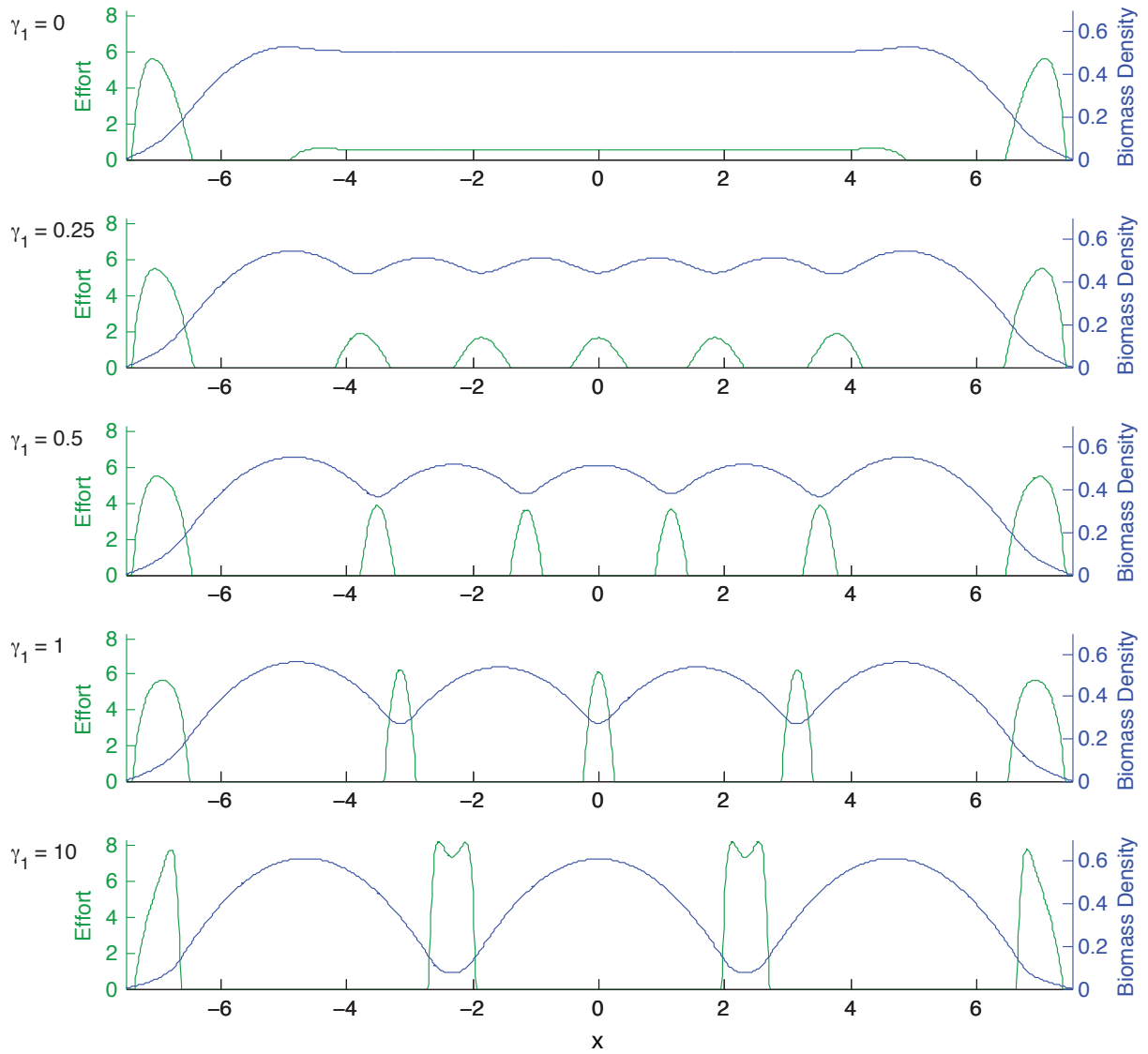
Figure 3.11: Optimal effort and population biomass distributions under Sole Owner in the face of density-dependent habitat effects. The parameter values in each case are $\omega_0 = 0.01$, $\omega_1 = 0.001$, $\gamma_0 = 0$, and $\ell = 15$.
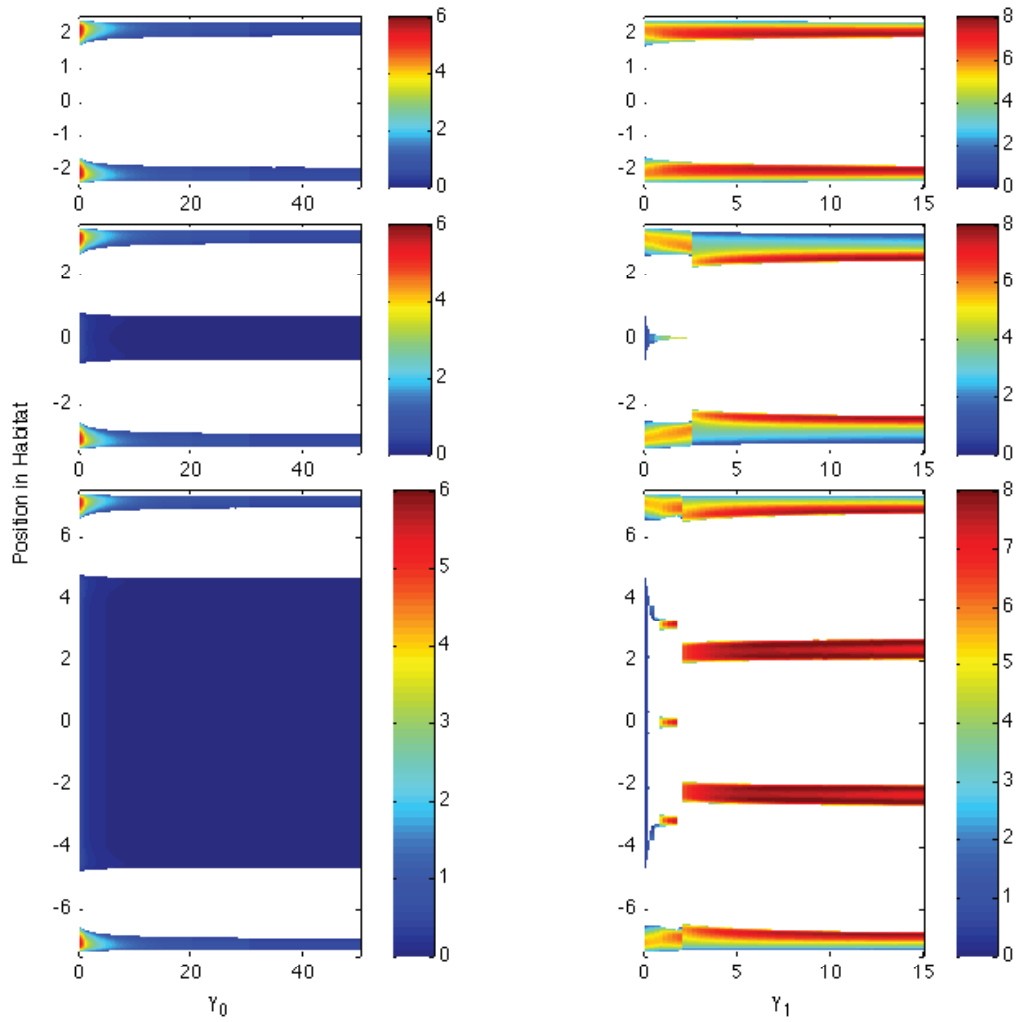
Figure 3.12: Optimal effort distributions (color) as functions for various habitat lengths (top: $\ell = 5$; middle: $\ell = 7$; bottom: $\ell = 15$) and habitat sensitivities under Sole Owner management. Unless otherwise specified in the graph, the parameter values in each case are $\omega_0 = 0.01$, $\omega_1 = 0.001$, and $\gamma_0 = \gamma_1 = 0$.
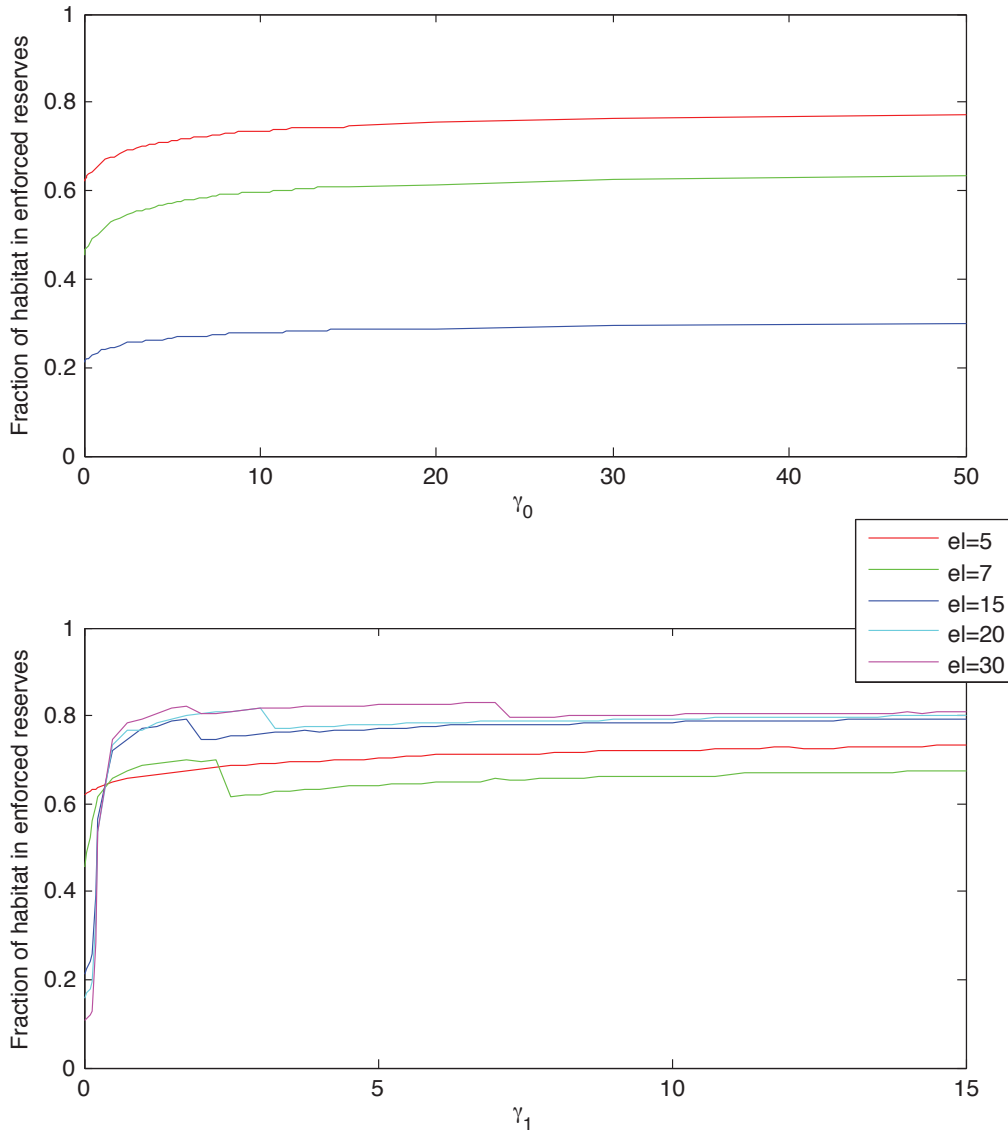
Figure 3.13: Fraction of habitat placed in enforced reserves for varying habitat sensitivities under sole-owner management The cost parameters in each case are $\omega_0 = 0.01$, $\omega_1 = 0.001$. Habitat lengths and sensitivities to damage are varied.
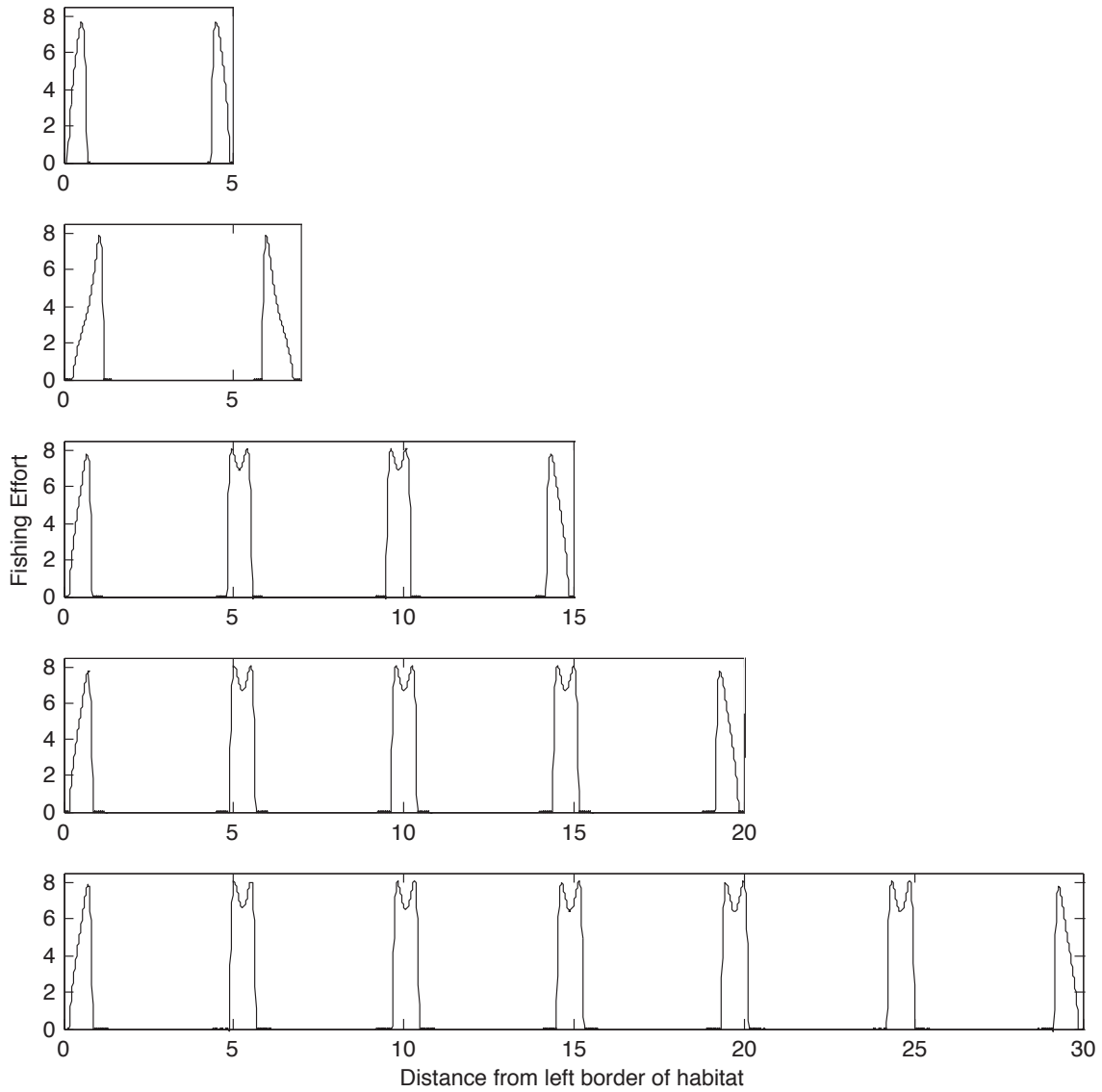
Figure 3.14: Optimal effort distribution for various habitat lengths under Sole Owner management. Parameter values are $\omega_0 = 0.01$, $\omega_1 = 0.001$, $\gamma_0 = 0$, and $\gamma_1 = 15$. Note the emergence of "reserve networks" with evenly spaced reserves and effort peaks.
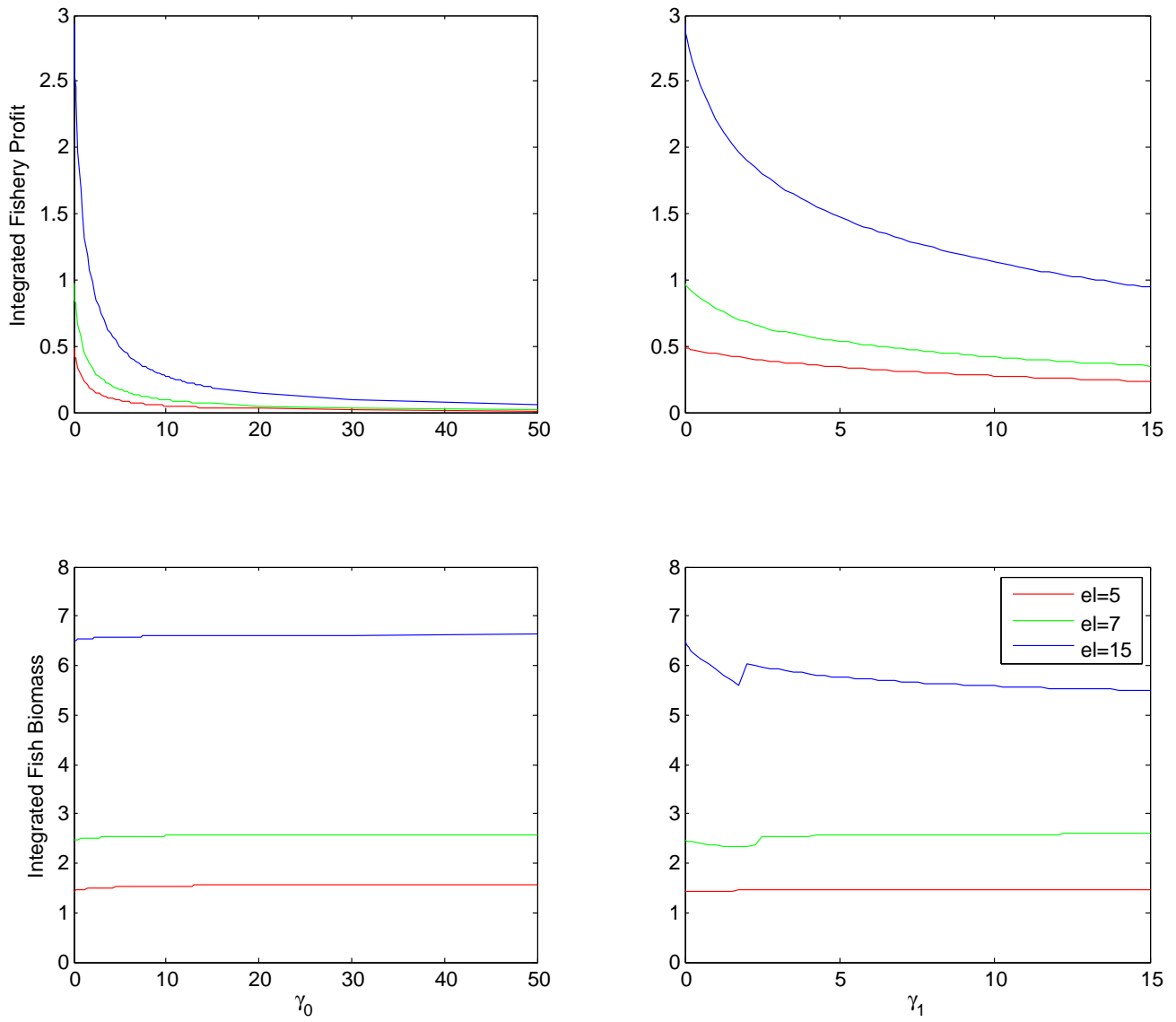
Figure 3.15: The effects of habitat damage on profit and stock biomass under Sole Owner management. Increases in habitat sensitivity drive profits and stock sizes down. However, in the case of density-dependent effects, standing stock may increase if effort distribution shifts to a reserve network distribution.

3.2.2 Second-Best Management Strategy: Tax and Defend

In this scenario, we take the view of a fisheries manager whose goal is to maximize rent using a combination strategy of setting aside a no-take reserve and taxing fishing effort at a rate τ outside of the reserve. The fishery is then considered to be "regulated open access" (Homans and Wilen 1997): that is, effort expands until the total revenue (from biomass caught) equals the total costs (the sum of the cost of effort and the effort tax) in all locations where fishing is permitted.[1,2]

Mathematically, we may represent this case by setting the rent density function (which now includes tax) equal to zero for all x.

$$R(x) = p(x)u(x)f(x) - (\omega_0 + \omega_1 f(x))f(x) - \tau f(x) = 0 \tag{3.18}$$

We also re-introduce price, $p(x)$, to allow reserve designation (inside the reserve, $p(x) = 0$; outside, $p(x) = 1$):

$$p(x) = \begin{cases} 1, & \text{if } |x| > \ell_r/2, \\ 0, & \text{otherwise.} \end{cases} \tag{3.19}$$

The regulator's objective is to choose the reserve size ℓ_r and the tax rate τ so as to maximize tax revenue (π):

$$\pi(\ell_r, \tau) = \tau \int_{-\ell/2}^{\ell/2} f(x)\, dx \tag{3.20}$$

---

[1] However, because the tax revenue may be returned to the fishermen or to society directly, or indirectly in the form of government services, the maximization of tax revenue is still a reasonable goal.

[2] This implies that we could also have described the "first-best" Sole Owner management strategy as a case of spatially variable tax. The results would have been identical, except that we would have maximized 'tax revenue' instead of 'rent'. See Appendix 1 for more details.

At equilibrium, we have from (3.18)

$$f(x) = \tilde{f}(x) \equiv \max\left\{0, \frac{p(x)u(x) - \tau - \omega_0}{\omega_1}\right\} \tag{3.21}$$

We can then solve the two-point boundary-value-problem

$$\left[(1 - \gamma_0\tilde{f}) - (1 + \gamma_1\tilde{f})u\right] - \tilde{f}u + \frac{\partial^2 u}{\partial x^2} = 0 \tag{3.22}$$

with

$$u(-\ell/2) = u(\ell/2) = 0 \tag{3.23}$$

numerically (see Appendix 2: Matlab Codes) to find the stock distribution $\tilde{u}(x)$ for fixed ℓ_r and τ. The manager selects the combination $\ell_r = \ell_r^*$ and $\tau = \tau^*$ that produces the second-best (Tax and Defend) stock and effort distributions $\tilde{u}^*$ and $\tilde{f}^*$.

Effort and biomass in the absence of habitat effects.   In the open-access case, fishermen act as competitors with one another, rather than cooperating to produce maximum profits over the entire system. In the absence of a designated reserve, fishing occurs at a constant level throughout the habitat space, except at the very edges, where the effects of diffusion drive fish biomass density so low that no fishing can be profitable. The constant level of fishing effort is determined by habitat length and habitat effects: as habitat length increases, the area can support a heavier fishing load; however, the more fishing damages habitat, the lower fish biomass density falls, and the lower the sustainable effort level drops.

In Figs. 3.16–3.18, I illustrate the effects of varying management regimes on fisheries of three different habitat lengths in the absence of habitat effects. Imposing a tax per unit effort effectively increases ω_0, the cost per unit effort, for a fisherman. This enlarges the edge areas where fishing is not economical, and reduces fishing effort over the entire habitat length. When a reserve is also included, fishing effort intensifies at the reserve's edges. This is the phenomenon of "fishing the line" (Kellner et. al

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2007), in which fishermen seek to capture spillover from the reserve by fishing along its borders.

The optimal control regime in the absence of habitat effects depends upon habitat length (Fig. 3.19). For larger habitats, centrally located reserves are not optimal. Both the total tax revenue collected and the optimal tax per unit effort increase with habitat length (Fig. 3.20). As reserve length increases, the optimal tax per unit effort falls until reserves cover almost all of the habitat, and total tax revenue falls to zero while stock density increases to the habitat's length-specific carrying capacity.

Including habitat effects. As in earlier analyses, including effort-driven habitat damage that increases γ_0 reduces fishery tax revenues for any habitat length (Fig. 3.21). Similarly to the nonspatial case, when the habitat effects are density-independent, equilibrium population biomass is relatively insensitive to their inclusion.

As designated reserve length increases, the optimal tax rate decreases. Optimal tax is relatively insensitive to increasing γ_0, suggesting that, when habitat damage directly affects density-independent vital rates, a single choice of management strategy is optimal, regardless of habitat sensitivity.

The qualitative distribution of optimal effort is also relatively insensitive to γ_0. However, effort intensity decreases with increasing habitat sensitivity, while stock biomass density remains relatively unchanged (Fig. 3.22–3.24). A reserve is present only when habitat length is small, and its size increases only slightly with increasing γ_0.

In contrast, when habitat effects are density-dependent ($\gamma_1 > 0$), their inclusion drives decreases in population biomass and optimal tax level for a given reserve length (Fig. 3.25). Including density-dependent habitat effects also affects the optimality of designated reserves. For large habitats ($\ell > 5$), increasing γ_1 results in the emergence of a reserve when reserves were not previously part of the optimal Tax and Defend

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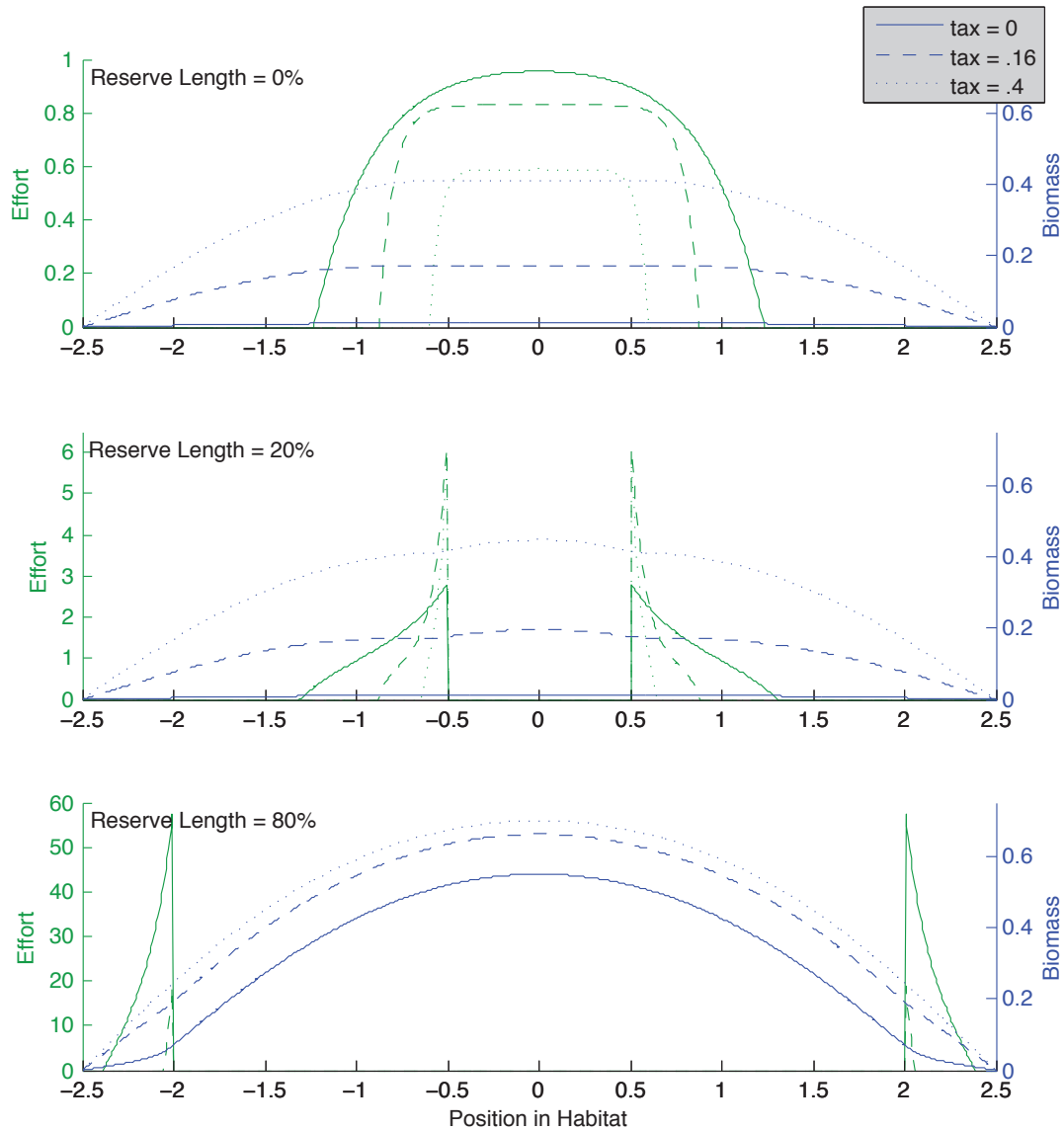
Figure 3.16: Effort and population biomass distributions in the absence of habitat effects. While increasing reserve fractions increases standing stock within the reserve, it also shifts effort to the reserve edges where it intensifies (note changes in effort scale). Increasing tax decreases effort and increases stock biomass. Parameter values were: $\ell = 5$, $\omega_0 = 0.01$, $\omega_1 = 0.001$, and $\gamma_0 = \gamma_1 = 0$.
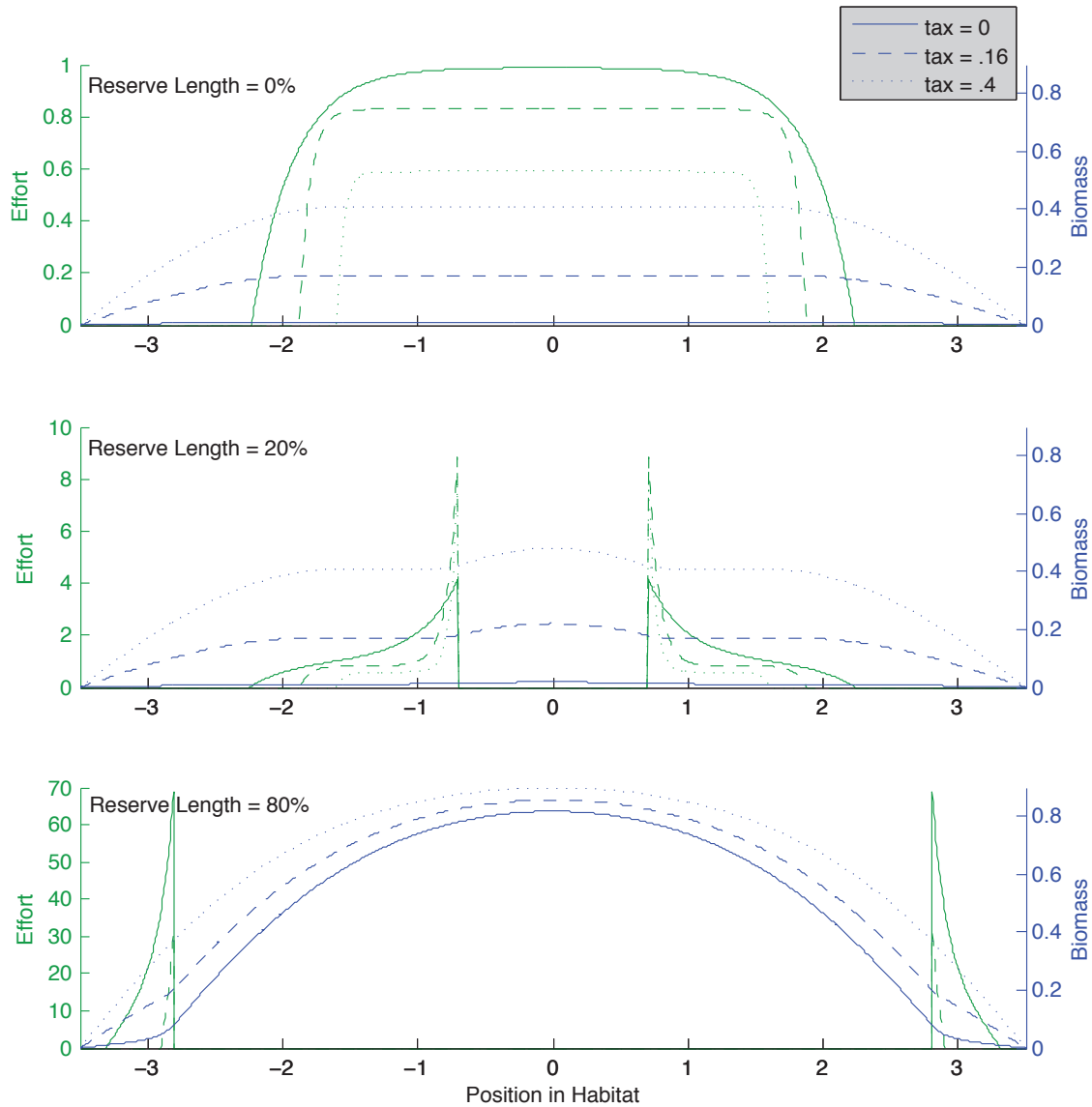
Figure 3.17: Effort and population biomass distributions in the absence of habitat effects. While increasing reserve fractions increases standing stock within the reserve, it also shifts effort to the reserve edges where it intensifies (note changes in effort scale). Increasing tax decreases effort and increases stock biomass. Parameter values were: $\ell = 7$, $\omega_0 = 0.01$, $\omega_1 = 0.001$, and $\gamma_0 = \gamma_1 = 0$.
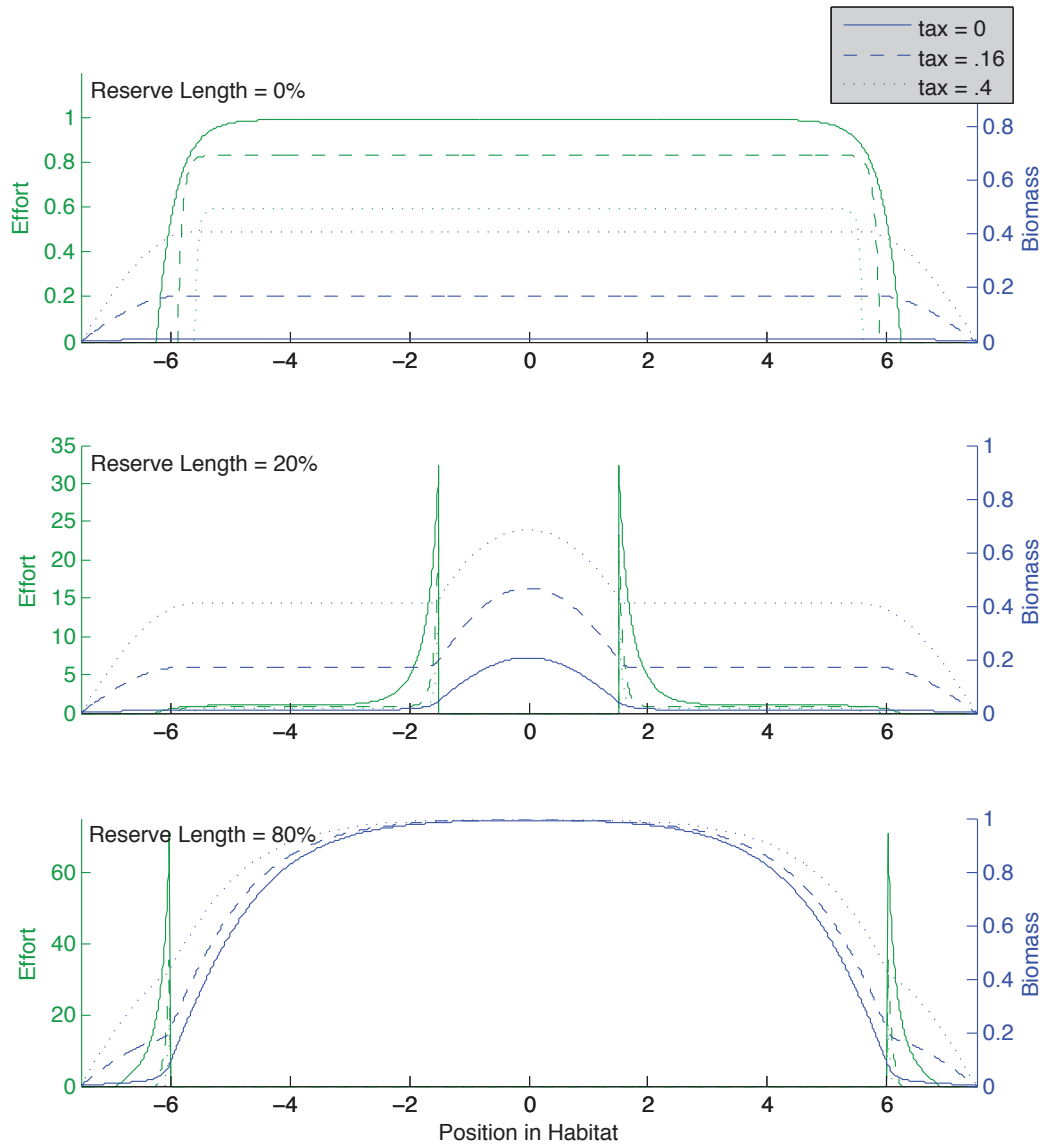
Figure 3.18: Effort and population biomass distributions in the absence of habitat effects. While increasing reserve fractions increases standing stock within the reserve, it also shifts effort to the reserve edges where it intensifies (note changes in effort scale). Increasing tax decreases effort and increases stock biomass. Parameter values were: $\ell = 15$, $\omega_0 = 0.01$, $\omega_1 = 0.001$, and $\gamma_0 = \gamma_1 = 0$.

Figure 3.19: Optimal effort and population biomass distributions in the absence of habitat effects. The parameter values in each case are $\omega_0 = 0.01$, $\omega_1 = 0.001$, $\gamma_1 = 0$, and $\ell = 5$, 7, and 15.

Figure 3.20: Optimal tax revenue and tax level for varied reserve fractions. Results from three habitat lengths $\ell = 5$, 7, and 15) shown.
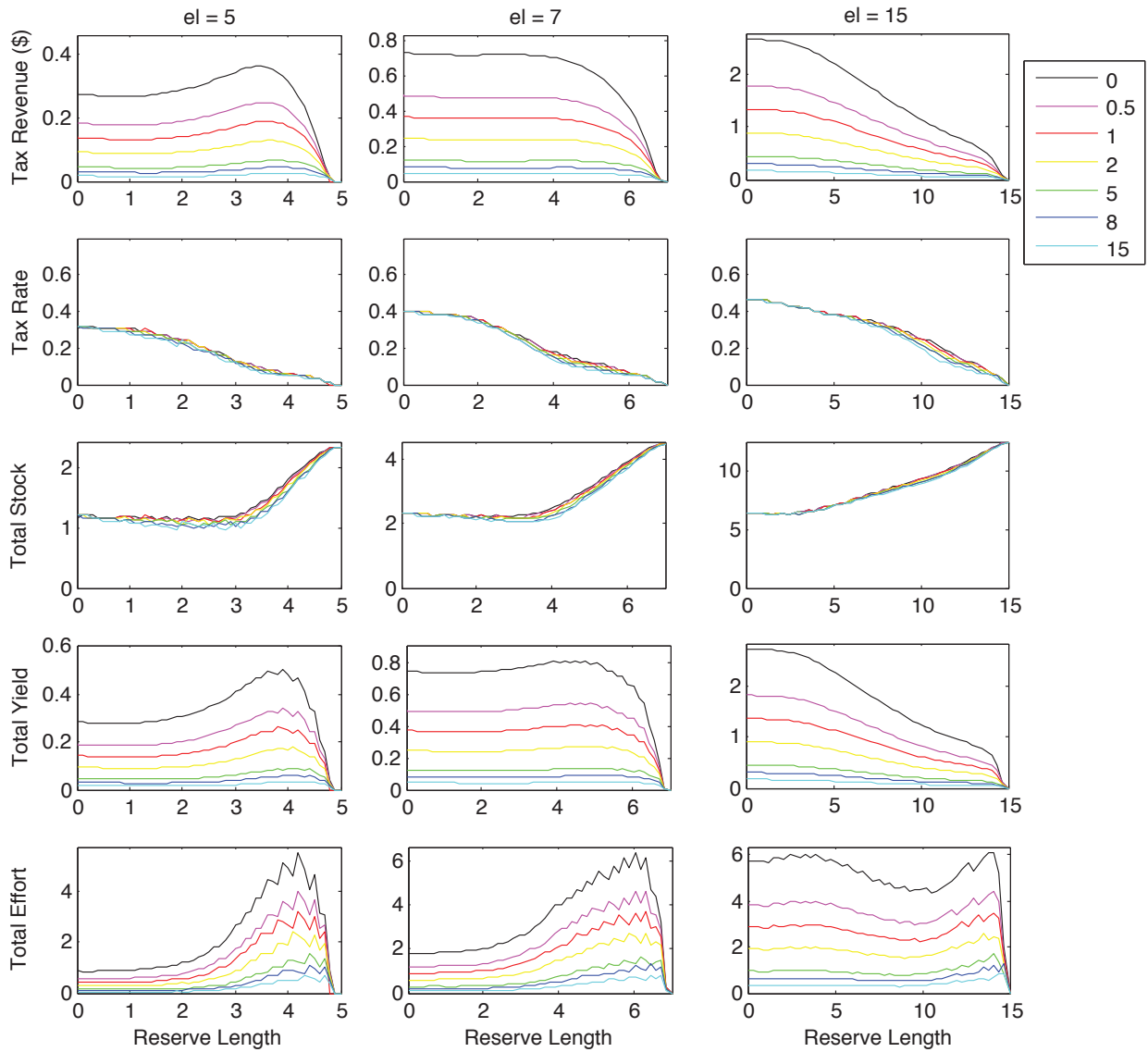
Figure 3.21: Effects of density-independent habitat damage on tax revenue, biomass, tax, and yield .
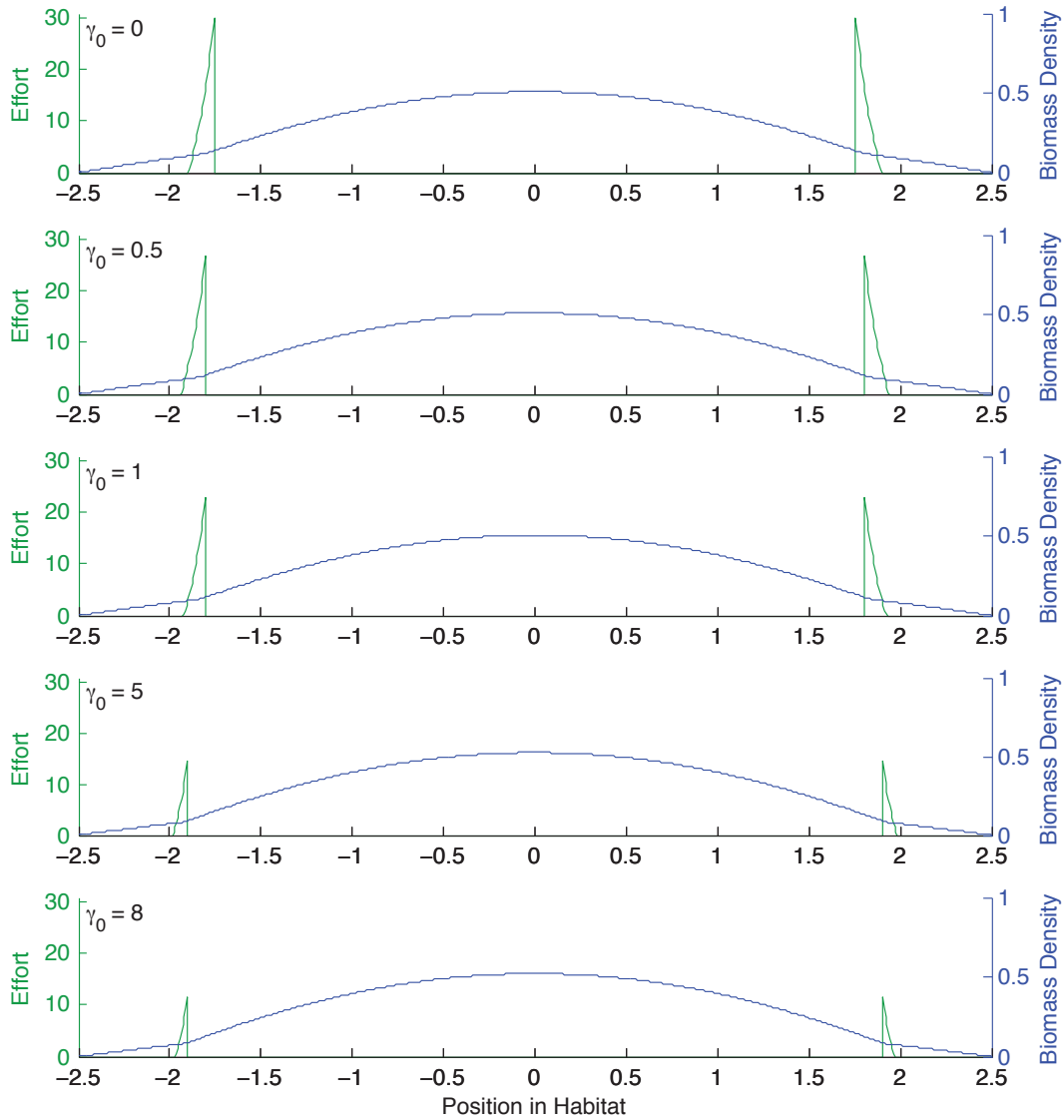
Figure 3.22: "Second-best" effort and stock densities for various levels of the density-independent habitat sensitivity coefficient γ_0. These densities result from choosing a combination of a centrally-located reserve and a spatially independent tax on effort so as to maximize the total tax collected.
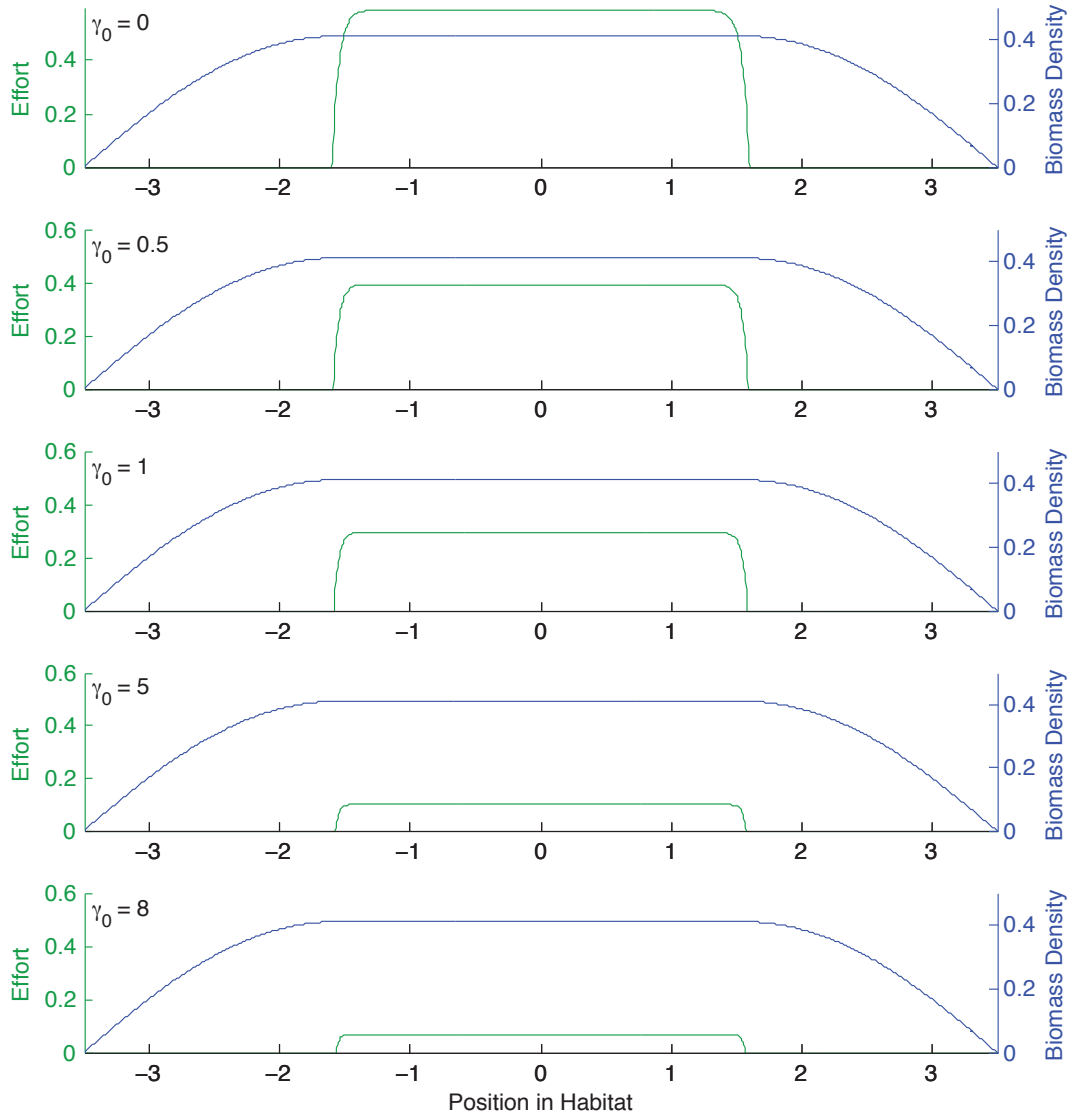
Figure 3.23: "Second-best" effort and stock densities for various levels of the density-independent habitat sensitivity coefficient γ_0. These densities result from choosing a combination of a centrally-located reserve and a spatially independent tax on effort so as to maximize the total tax collected.
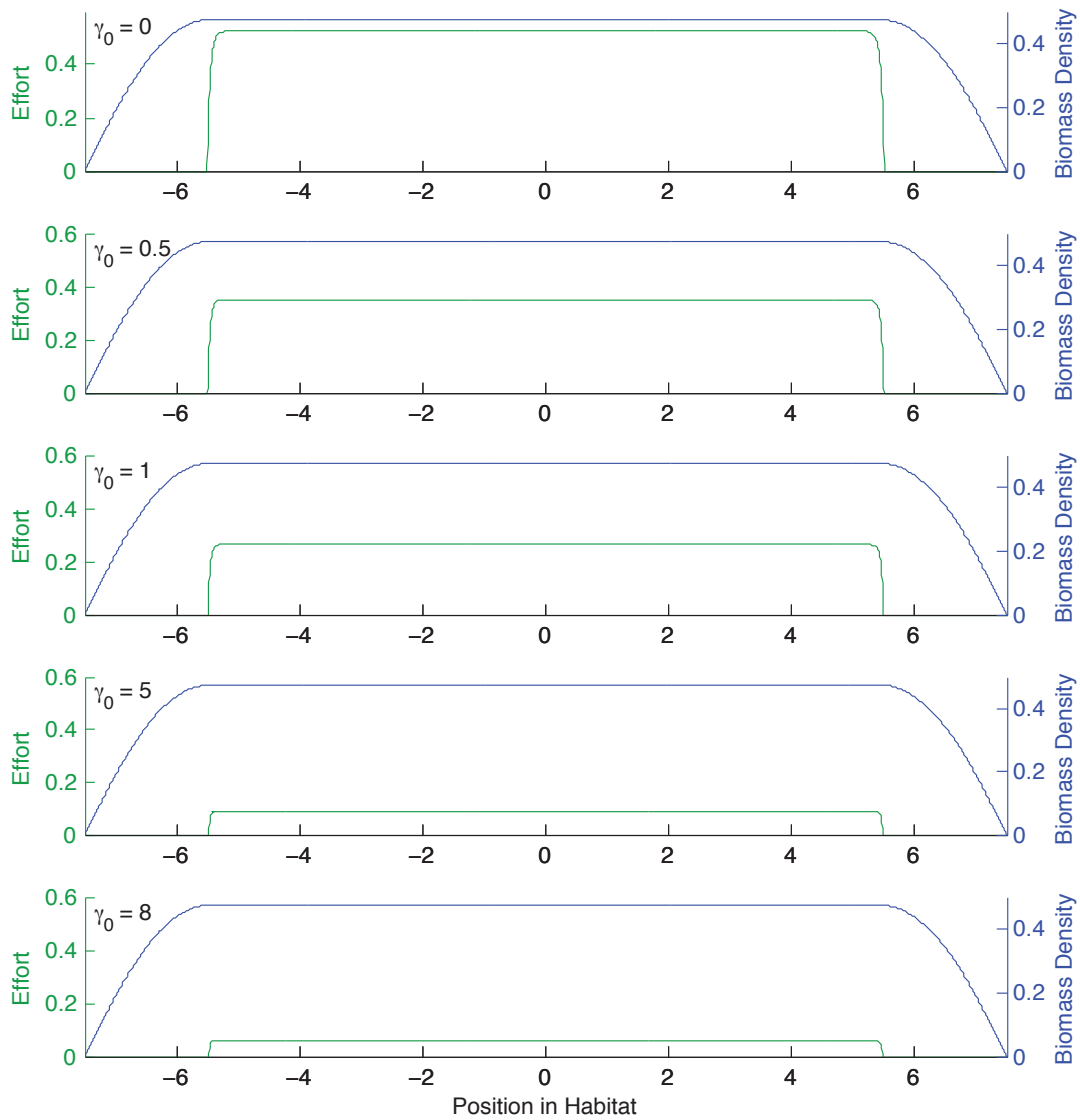
Figure 3.24: "Second-best" effort and stock densities for various levels of the density-independent habitat sensitivity coefficient γ_0. These densities result from choosing a combination of a centrally-located reserve and a spatially independent tax on effort so as to maximize the total tax collected.

management strategy (See Fig. 3.26 to 3.28).

The more sensitive the habitat is to effort-driven damage, the more likely a reserve is to be optimal. For fixed γ_1, the larger the habitat, the smaller the fraction of the habitat should be set in reserve when managing for maximum tax revenue (Fig. 3.29). Optimal tax is inversely related to fraction of habitat in reserve (Fig. 3.30), resulting in a complex relationship between habitat size, habitat sensitivity, and total effort (Fig. 3.31). However, setting aside habitat in a reserve cannot prevent habitat-damage driven declines in standing stock biomass (Fig. 3.32) and tax revenues (Fig. 3.33).
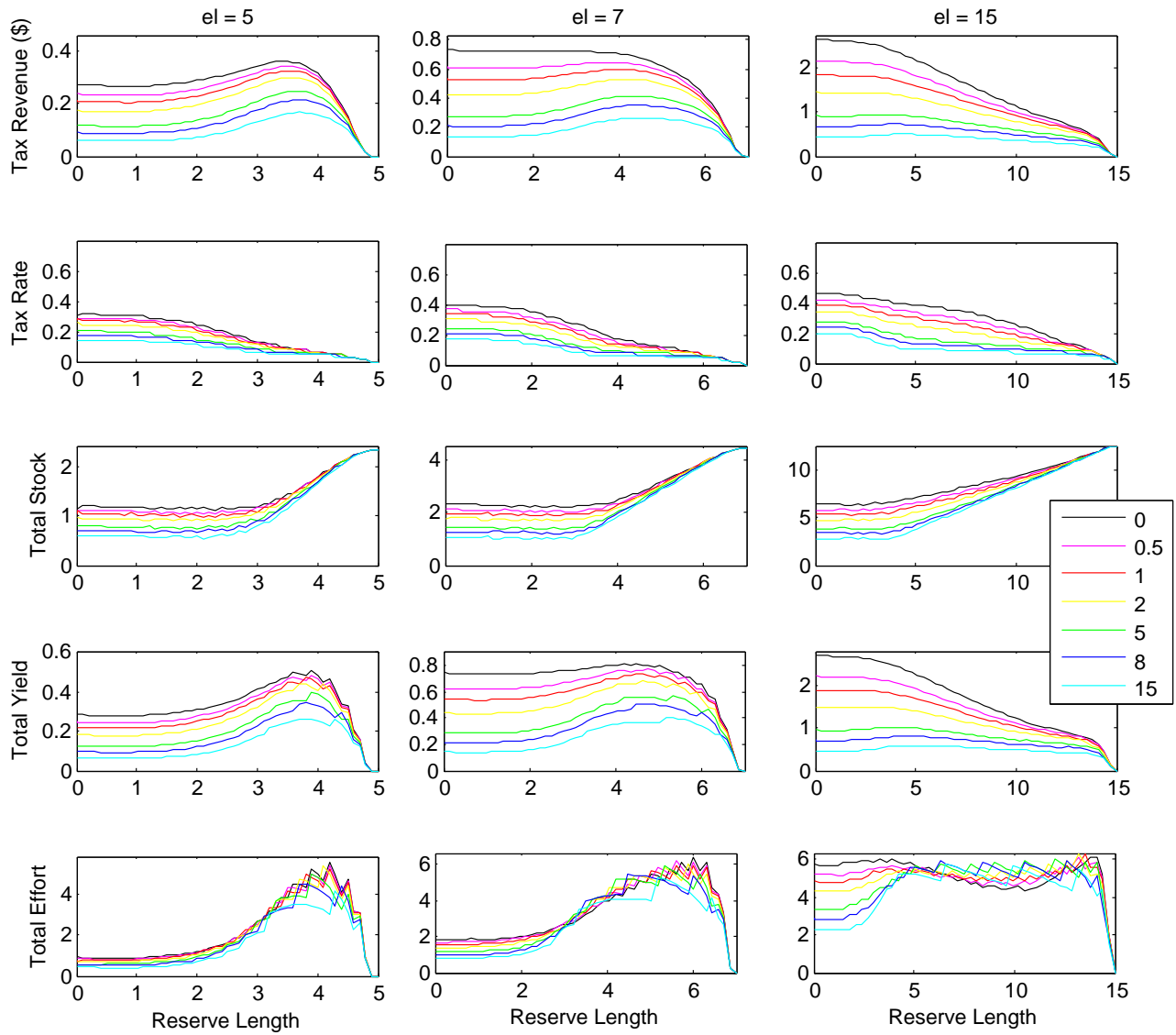
Figure 3.25: Effects of density-dependent habitat damage on tax revenue, biomass, tax, and yield .

Figure 3.26: Second-best effort and stock densities for various levels of the density-dependent habitat sensitivity coefficient γ_1. These densities result from choosing a combination of a centrally-located reserve and a spatially independent tax on effort so as to maximize the total tax collected.

Figure 3.27: Second-best effort and stock densities for various levels of the density-dependent habitat sensitivity coefficient γ_1. These densities result from choosing a combination of a centrally-located reserve and a spatially independent tax on effort so as to maximize the total tax collected.

Figure 3.28: Second-best effort and stock densities for various levels of the density-dependent habitat sensitivity coefficient γ_1. These densities result from choosing a combination of a centrally-located reserve and a spatially independent tax on effort so as to maximize the total tax collected.
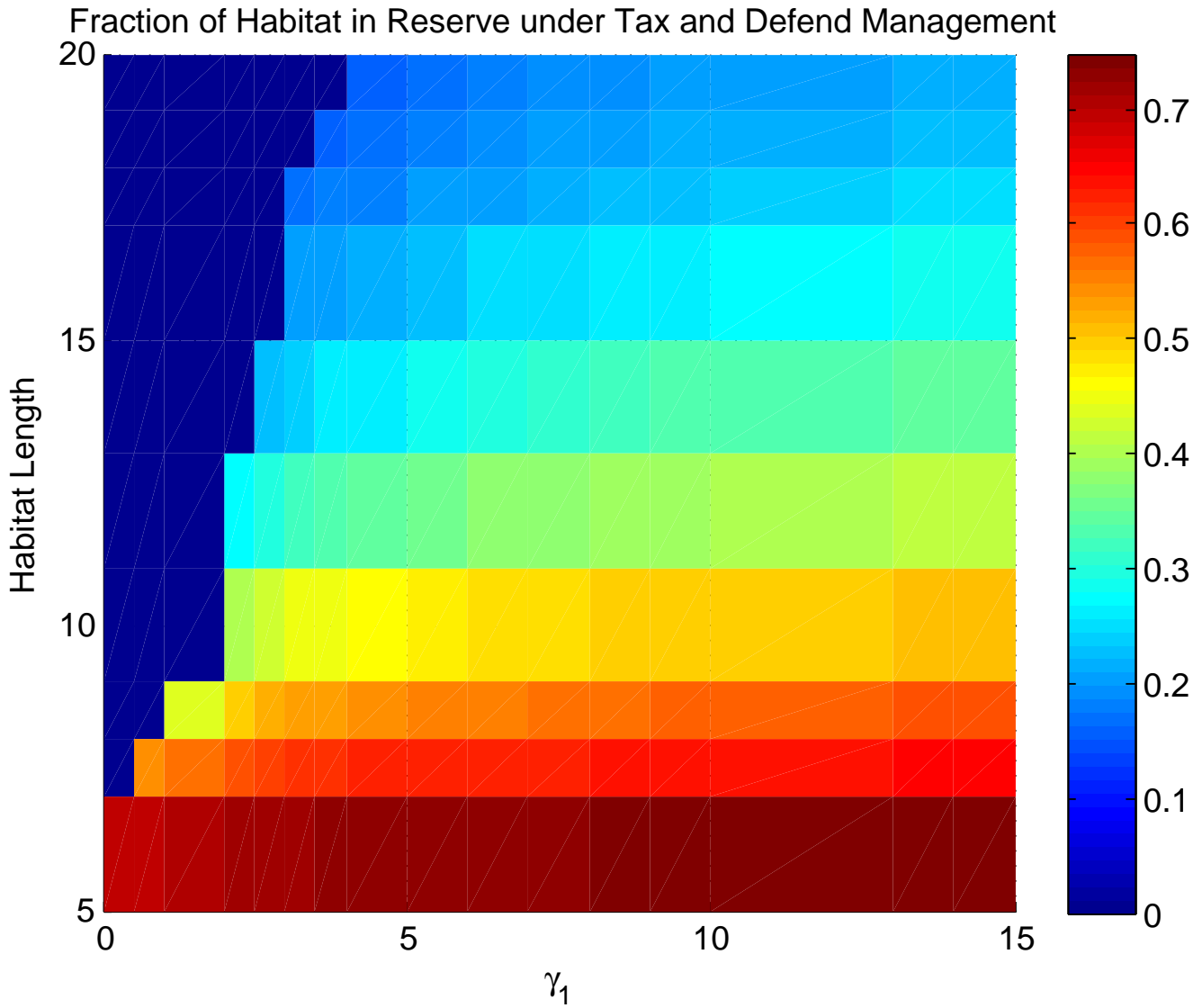
Figure 3.29: Optimal reserve fraction when habitat damage produces density-mediated mortality effects. As habitat length increases, the threshold habitat sensitivity for reserve institution increases. Once reserves are part of the optimal solution, they expand with increasing habitat sensitivity.
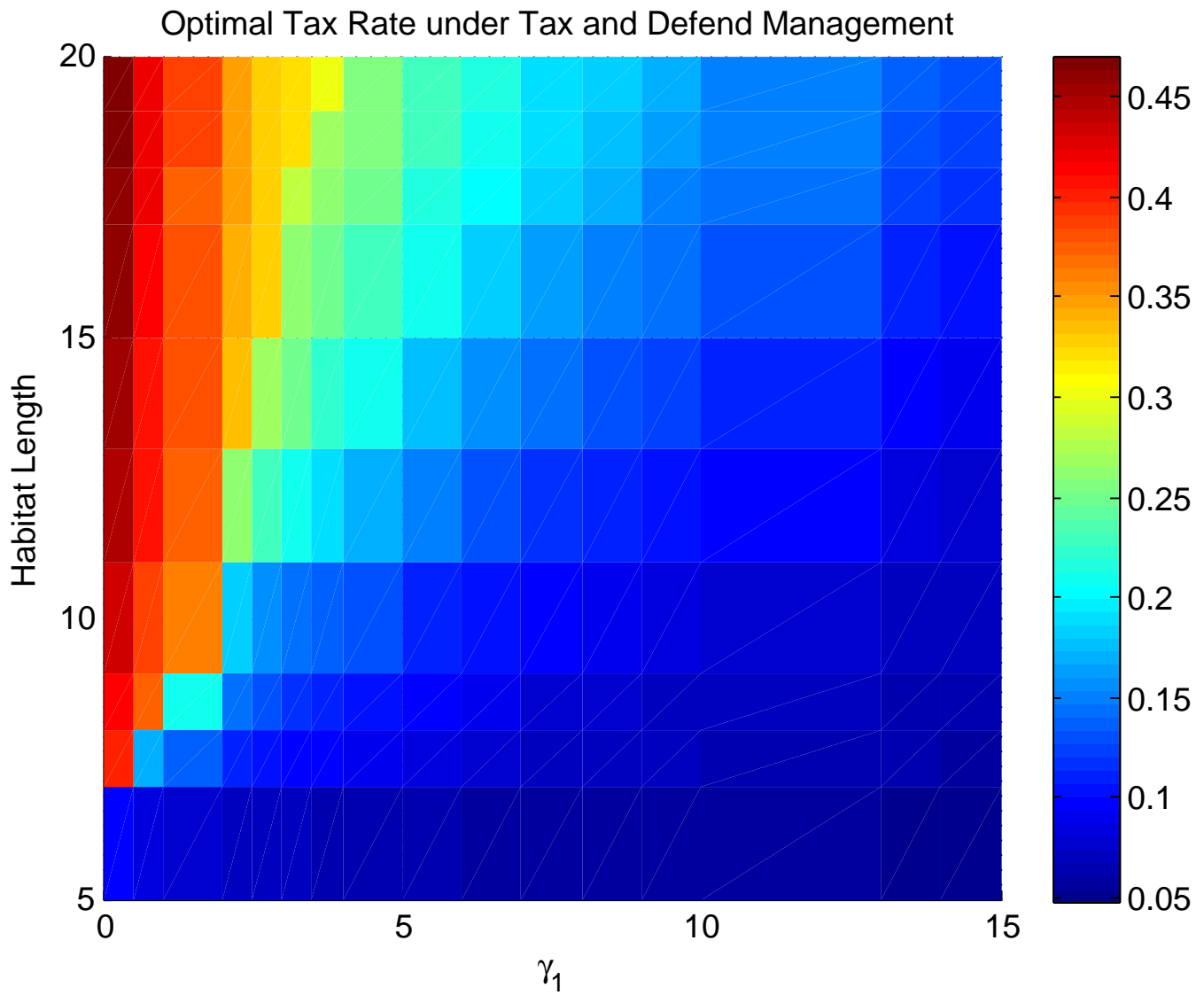
Figure 3.30: Optimal tax per unit effort when habitat damage produces density-mediated mortality effects. As habitat sensitivity increases, the optimal tax per unit effort decreases. However, for a given sensitivity, increasing habitat size results in an increase in optimal tax rate.
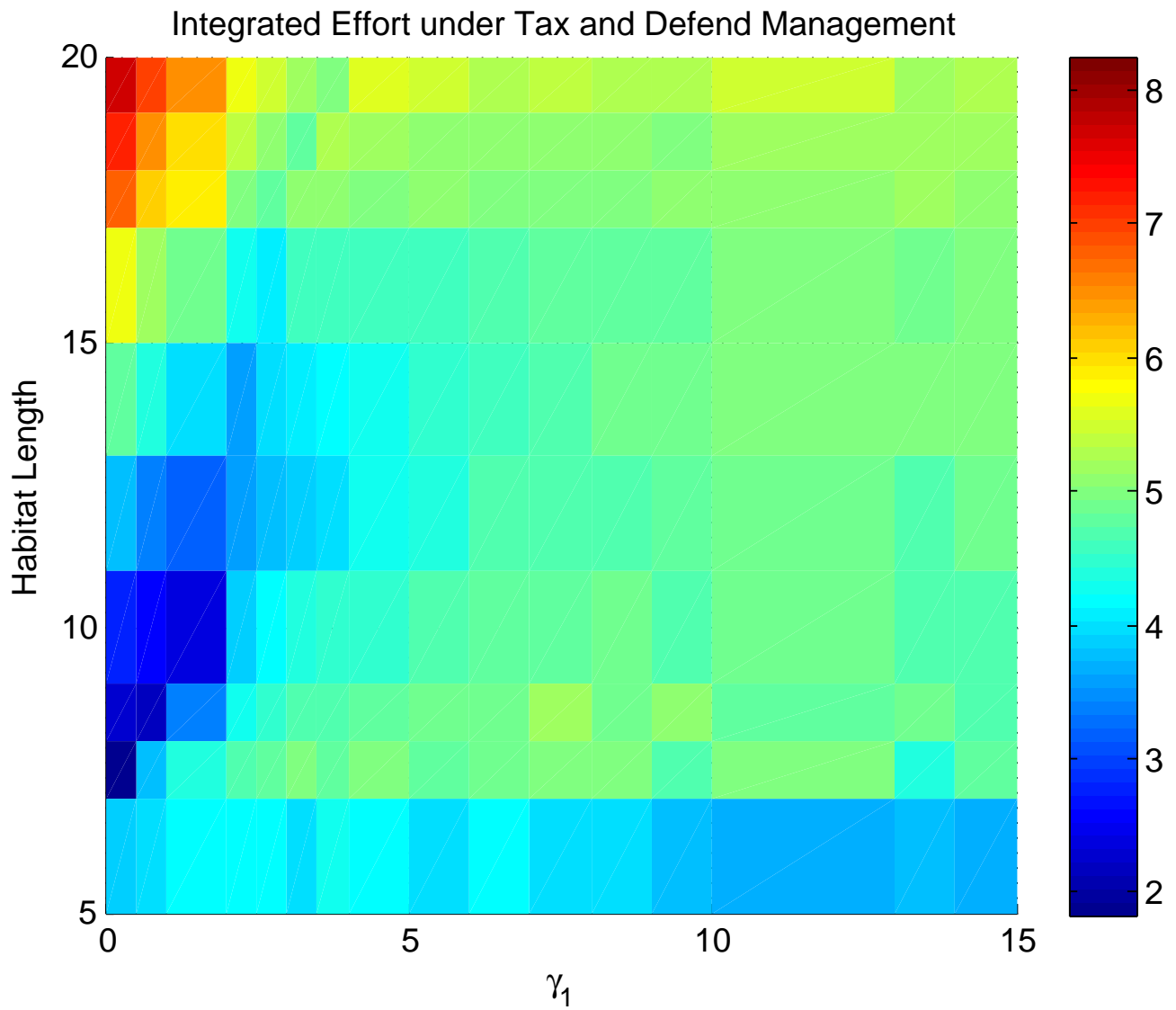
Figure 3.31: Optimal total effort when habitat damage produces density-mediated mortality effects. Although the relationship between habitat sensitivity, habitat length, and cumulative effort is complex, total effort generally increases with increasing habitat size.
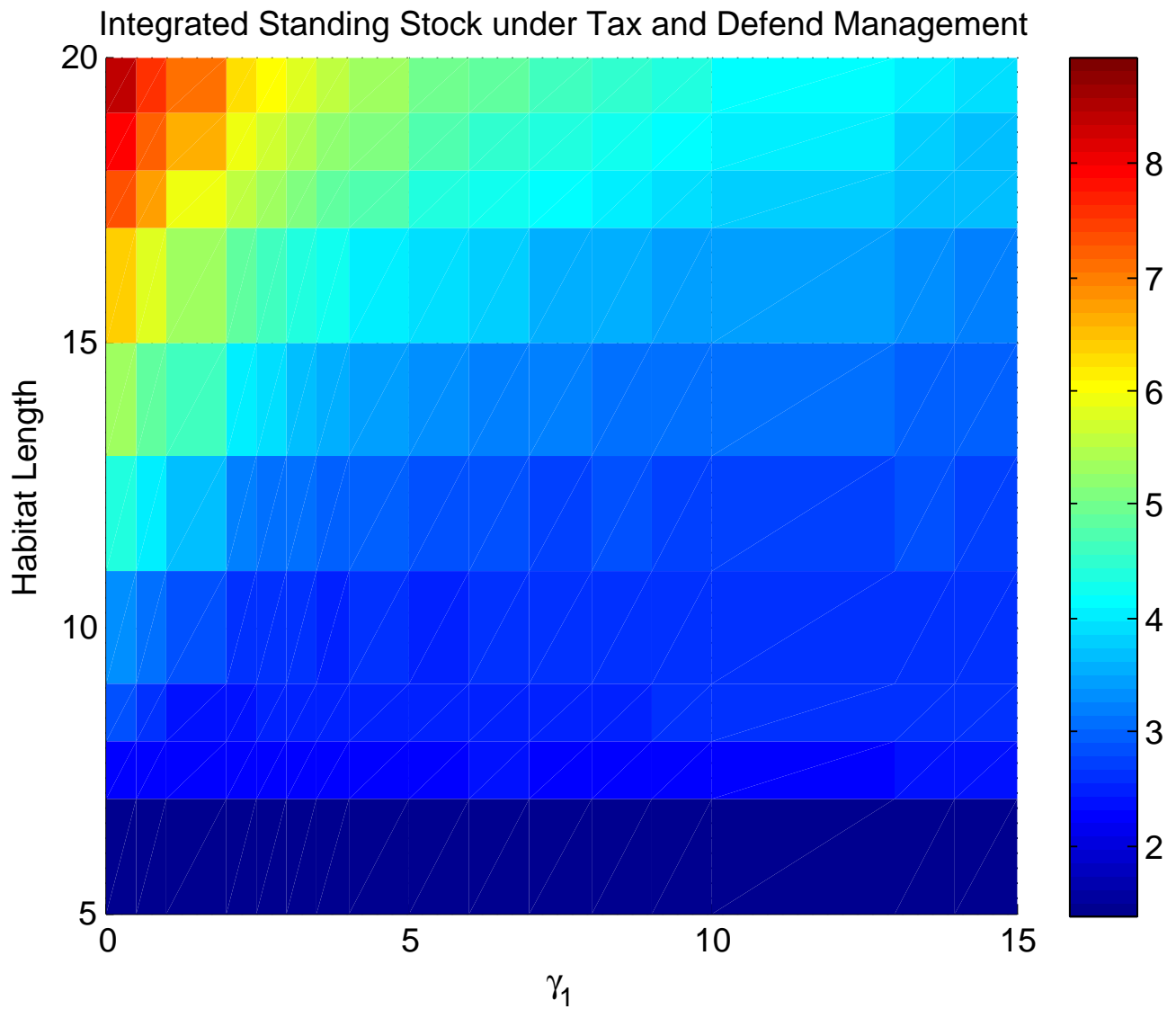
Figure 3.32: Total stock biomass under optimal Tax and Defend management when habitat damage produces density-mediated mortality effects. Stock size is proportional to habitat length and declines with increasing habitat sensitivity.
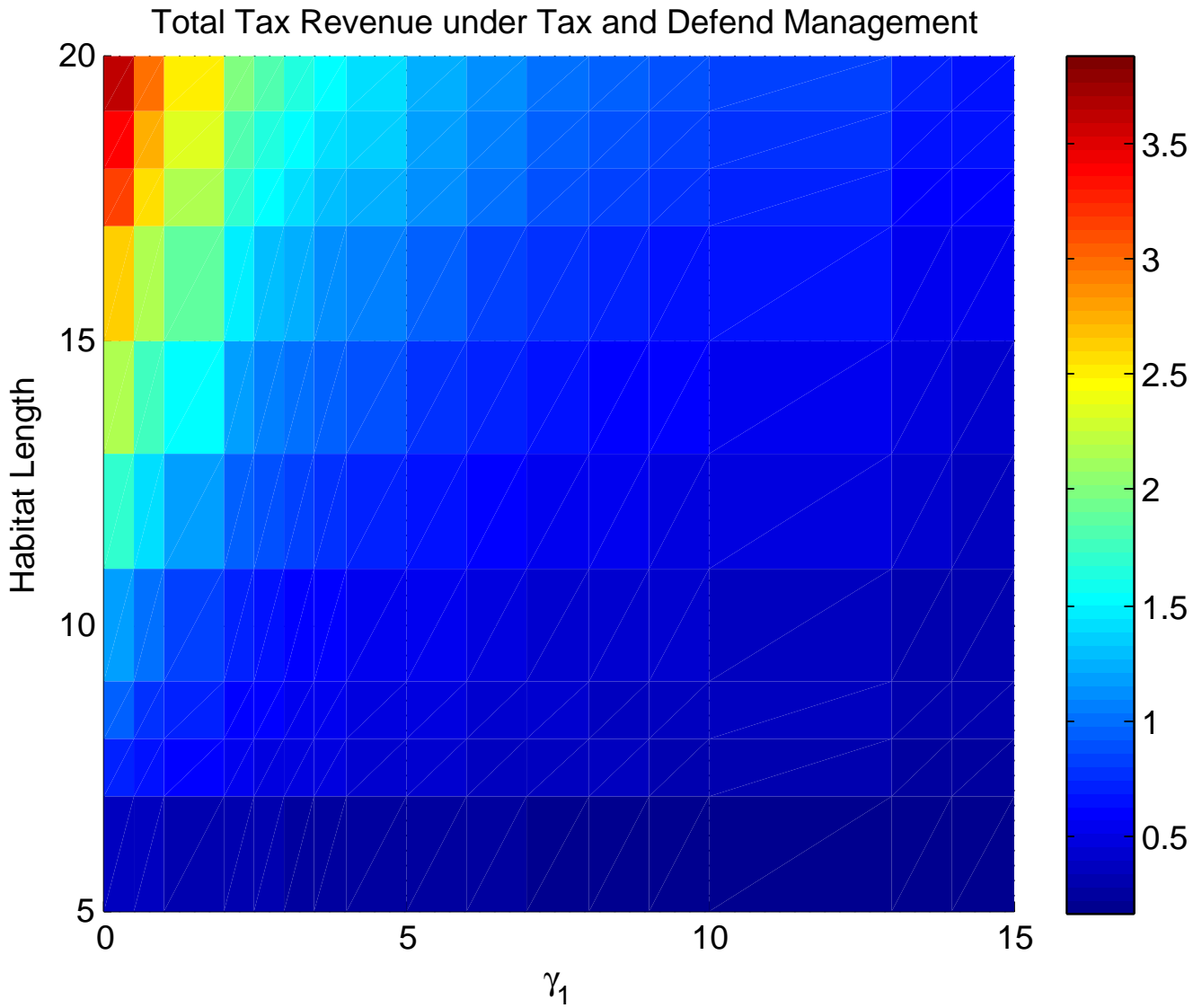
Figure 3.33: Total tax revenue under optimal Tax and Defend management when habitat damage produces density-mediated mortality effects. Trends in revenue mirror those of stock biomass.

3.2.3   Third-Best Management Strategy: Tax Only

The final scenario we examine is the strategy of assessing a non-spatial tax on effort. This amounts to a special case of the second-best problem in which the reserve length is held at zero.

Except for the case $\ell = 5$, where reserves were once optimal, this additional management limitation does not affect the optimal management strategy in the absence of habitat effects (Fig. 3.34). A low level of effort is concentrated in the center of the habitat, where biomass density is highest and approximately constant. Near the habitat edges, biomass density falls and it becomes uneconomical to fish, so effort drops to zero.

When habitat damage affects fish mortality through density-independent mechanisms (i.e. when $\gamma_0 > 0$), results are similar to previous analyses in that effort decreases everywhere. Biomass density is, again, relatively independent of habitat sensitivity (Fig. 3.35–3.37).

Because reserves can no longer be enforced, including density-dependent mortality drivers (i.e. when $\gamma_1 > 0$) does not change the qualitative distribution of effort. In general, as γ_1 increases, effort in the center of the habitat becomes more diffuse: that is, where effort is present, its intensity is reduced, but the area over which the effort is distributed increases slightly. In addition, biomass density is reduced relative to the undamaged habitat case (Fig. 3.38–3.40).

A comparison of third-best management results for a variety of habitat sensitivities reveals the sensitivity of tax revenue to habitat damage (Fig. 3.41).

When habitat damage increases density-independent mortality rates, the optimal choice of tax per unit effort is fixed for a given habitat length. However, when habitat damage increases density-dependent mortality rates, the manager should lower the tax rate with increasing habitat sensitivity for optimal results. This reduction in tax rate "opens" a larger fraction of habitat to fishing because the cost per unit effort experienced by fishermen is lowered and, therefore, the threshold biomass density at

which fishing occurs is also reduced. Therefore, the relationship between total effort and γ_1 is complex: for increasing habitat sensitivity, total effort may actually increase.
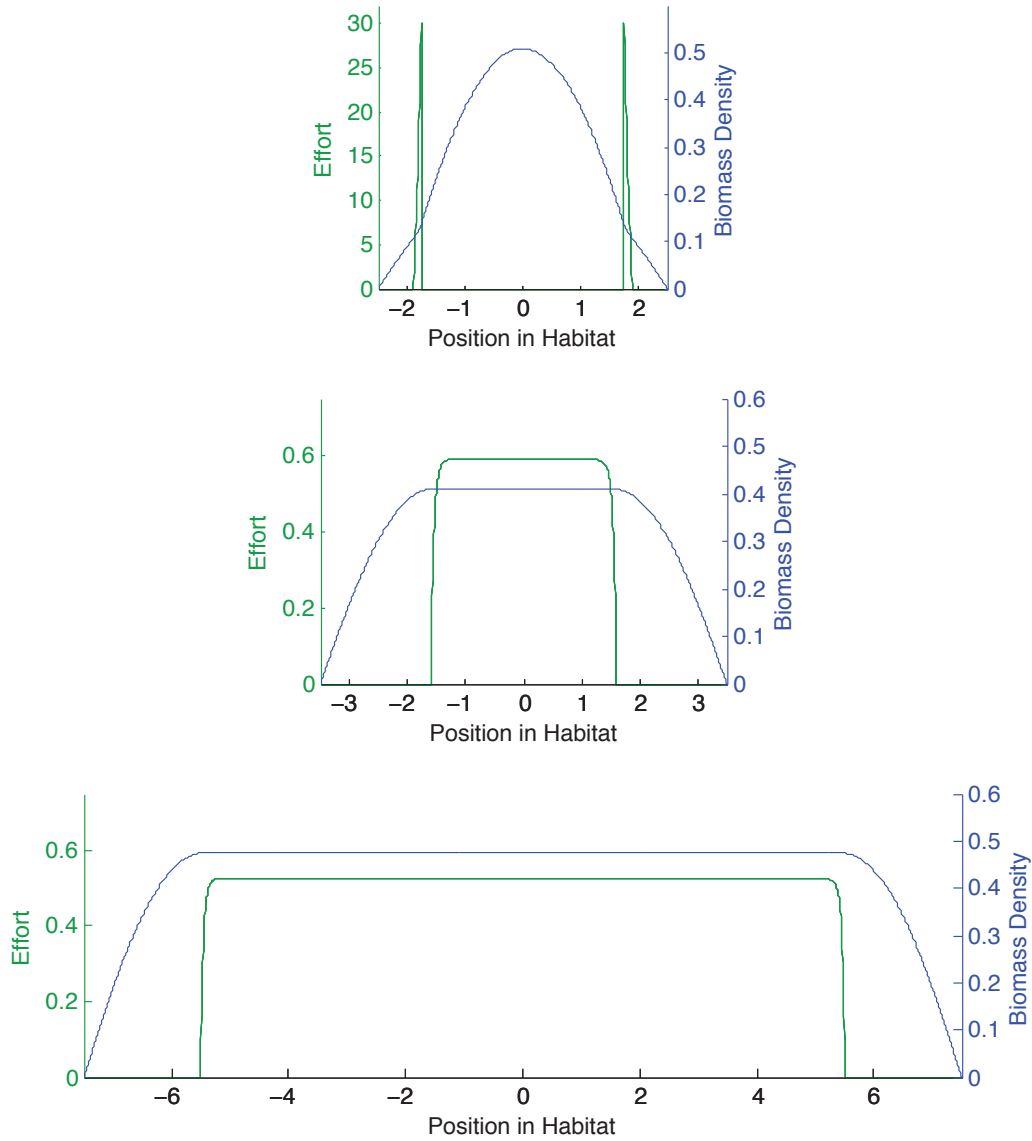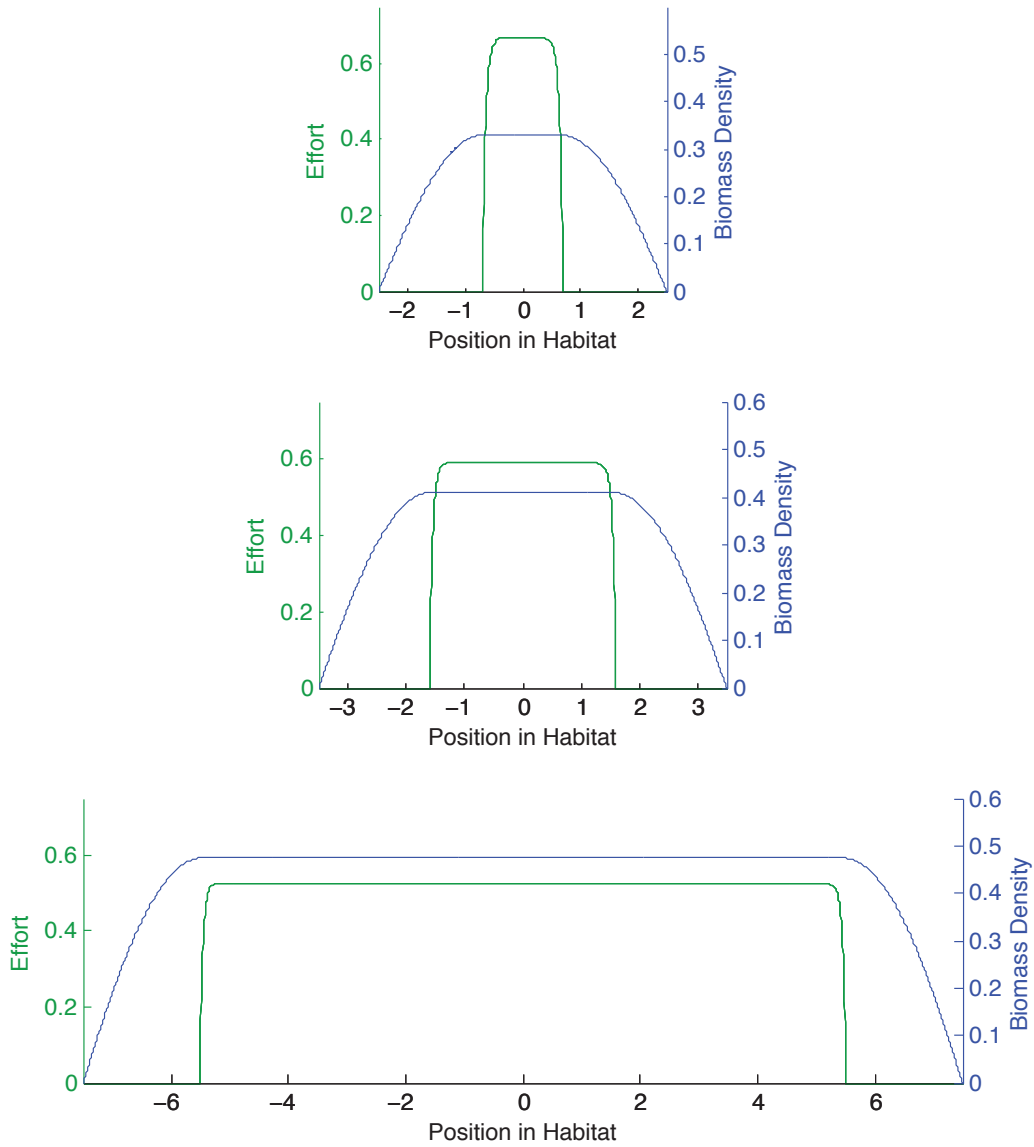
Figure 3.34: Optimal effort and population biomass distributions in the absence of habitat effects. The parameter values in each case are $\omega_0 = 0.01$, $\omega_1 = 0.001$, $\gamma_1 = 0$, and $\ell = 5$, 7, and 15.
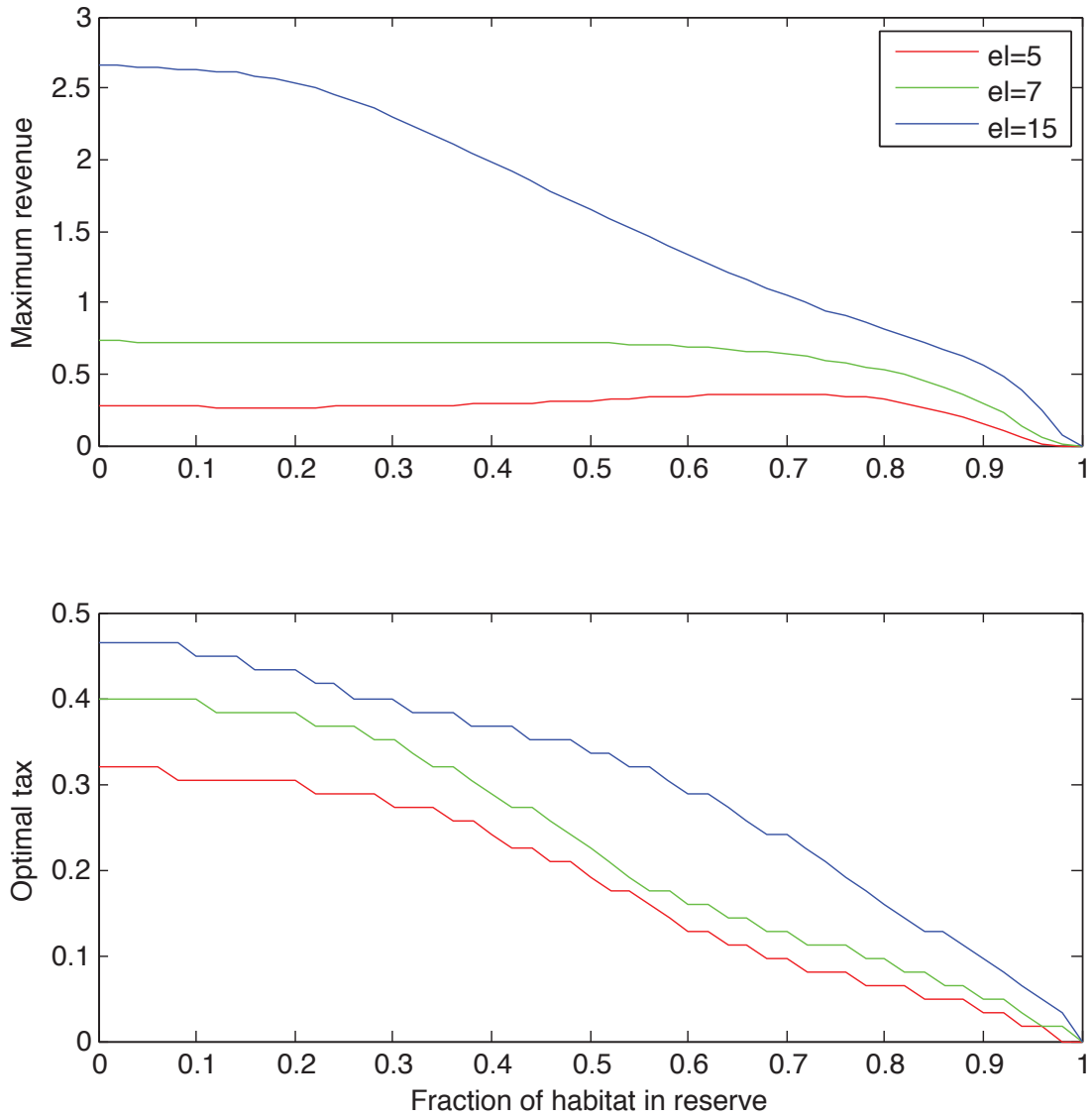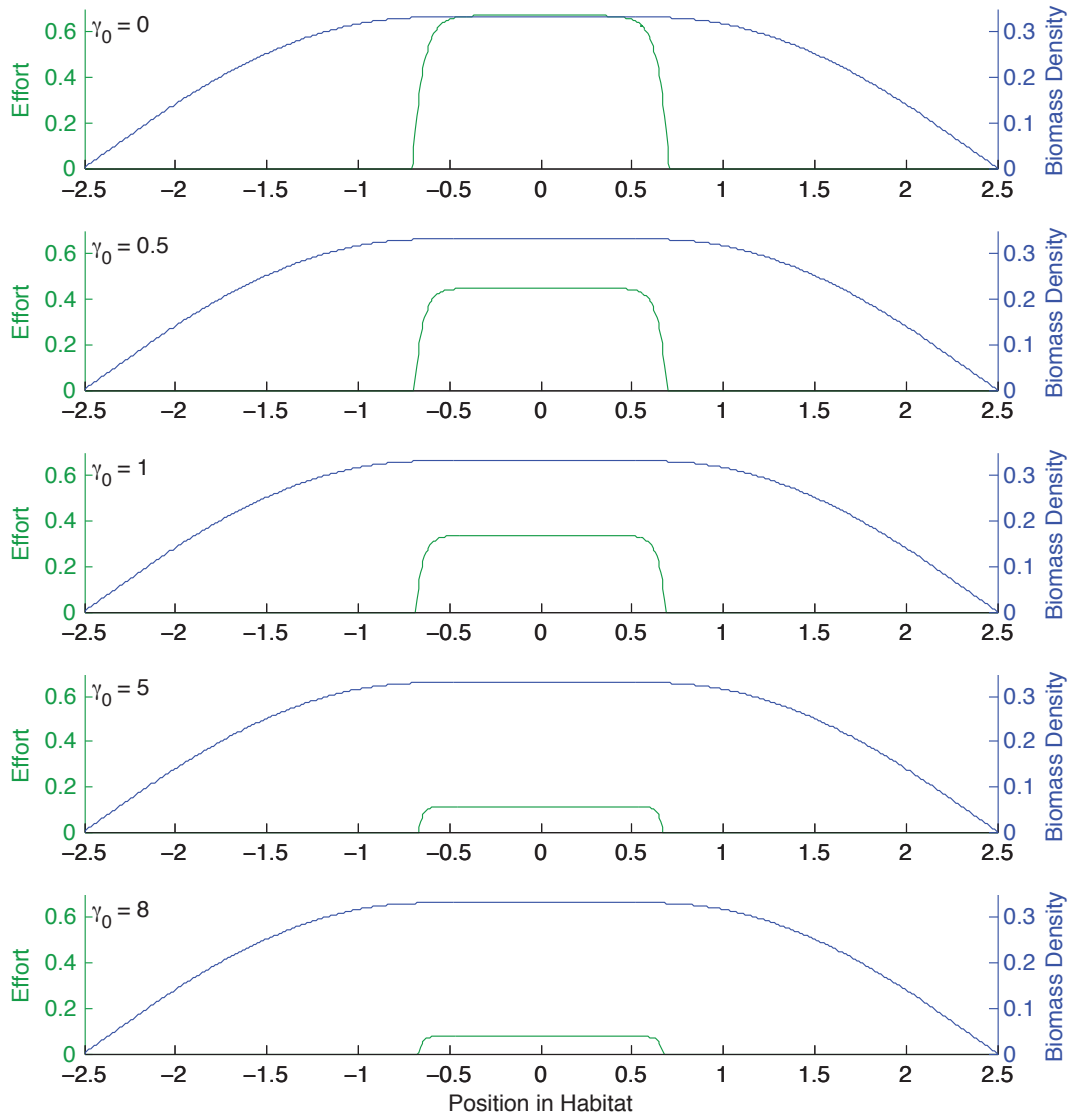
Figure 3.35: Third-best effort and stock densities for various levels of the density-independent habitat sensitivity coefficient γ_0. These densities result from choosing a spatially independent tax on effort so as to maximize the total tax collected.
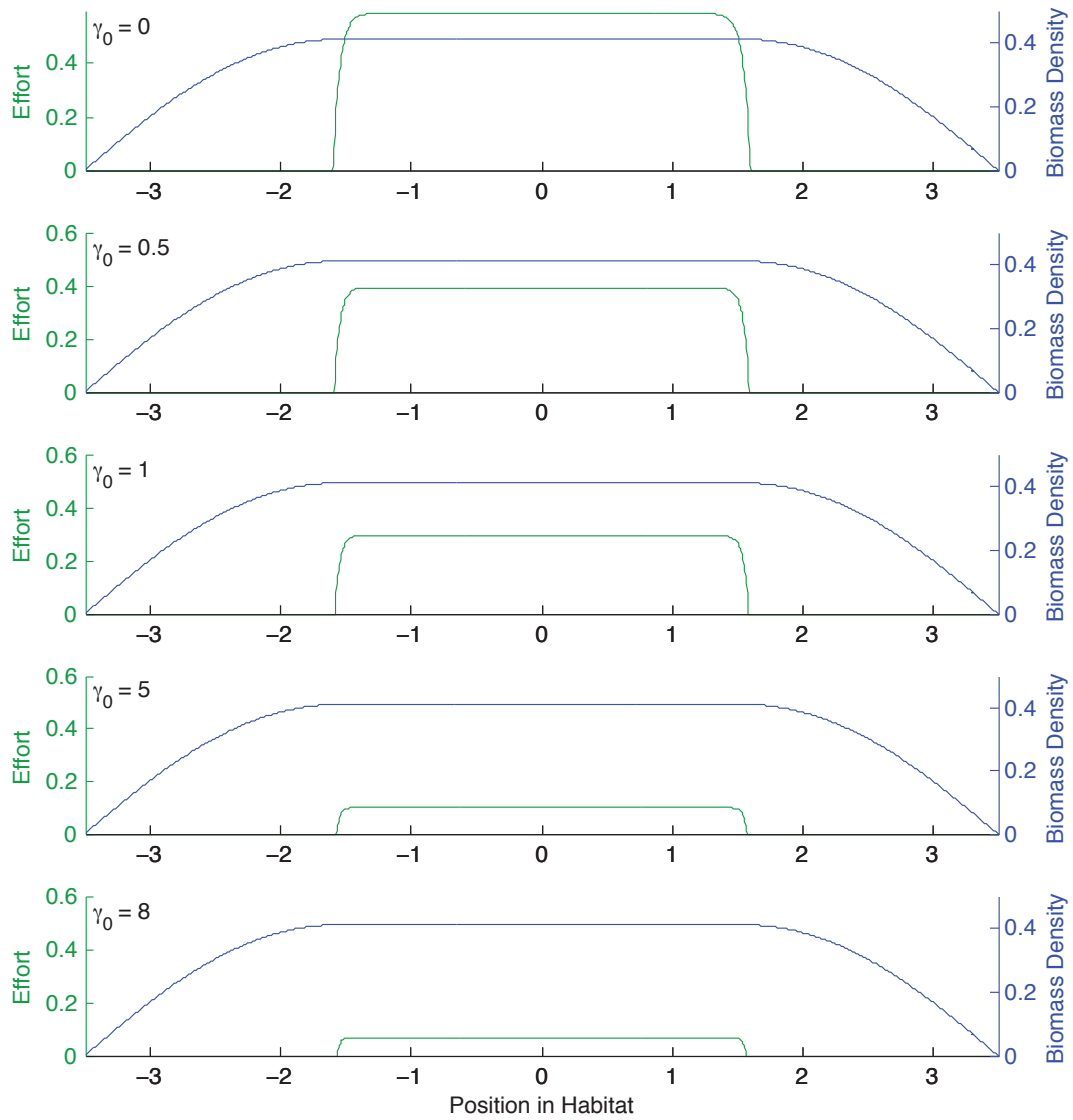
Figure 3.36: Third-best effort and stock densities for various levels of the density-independent habitat sensitivity coefficient γ_0. These densities result from choosing a spatially independent tax on effort so as to maximize the total tax collected.
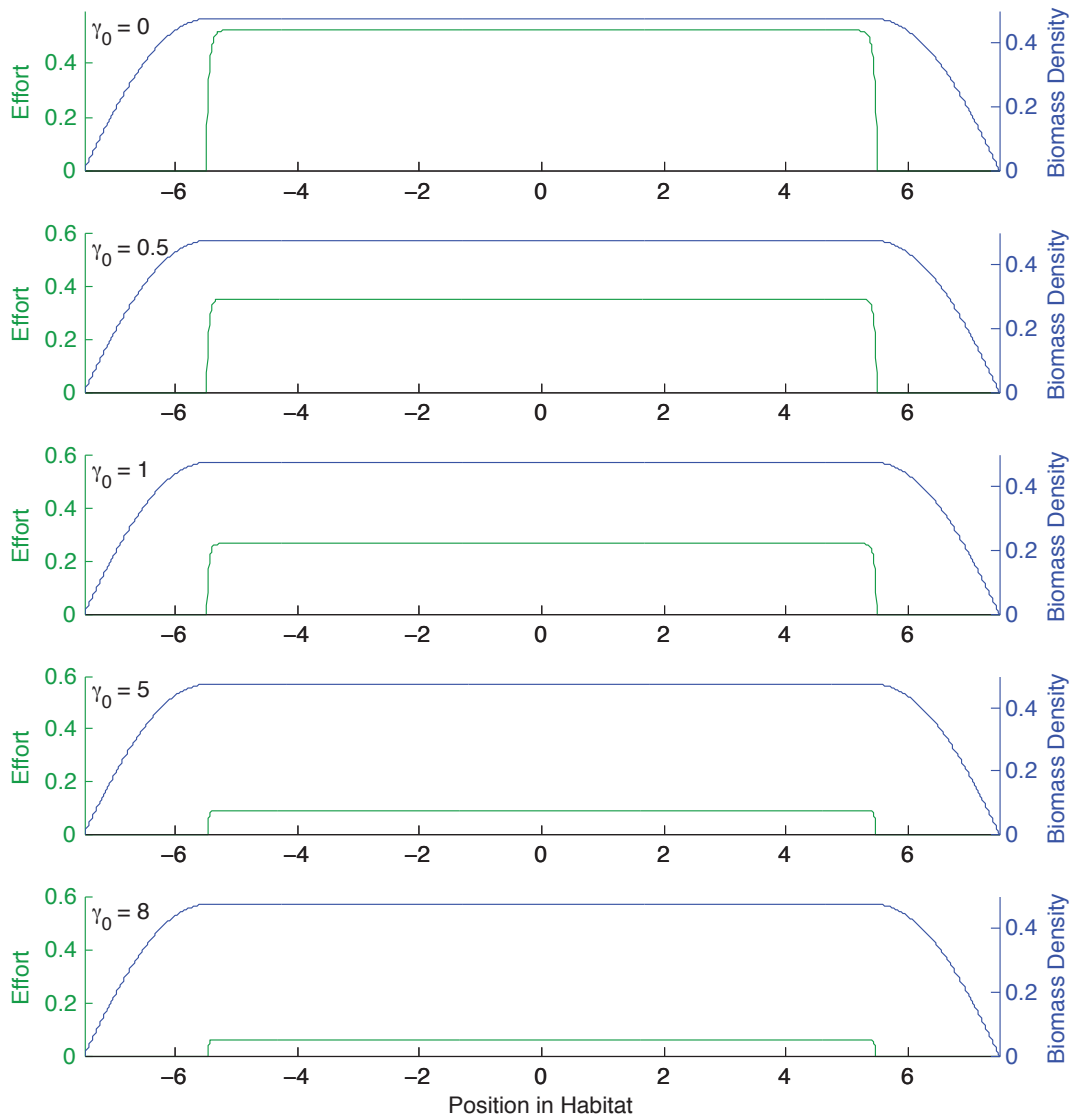
Figure 3.37: Third-best effort and stock densities for various levels of the density-independent habitat sensitivity coefficient γ_0. These densities result from choosing a spatially independent tax on effort so as to maximize the total tax collected.
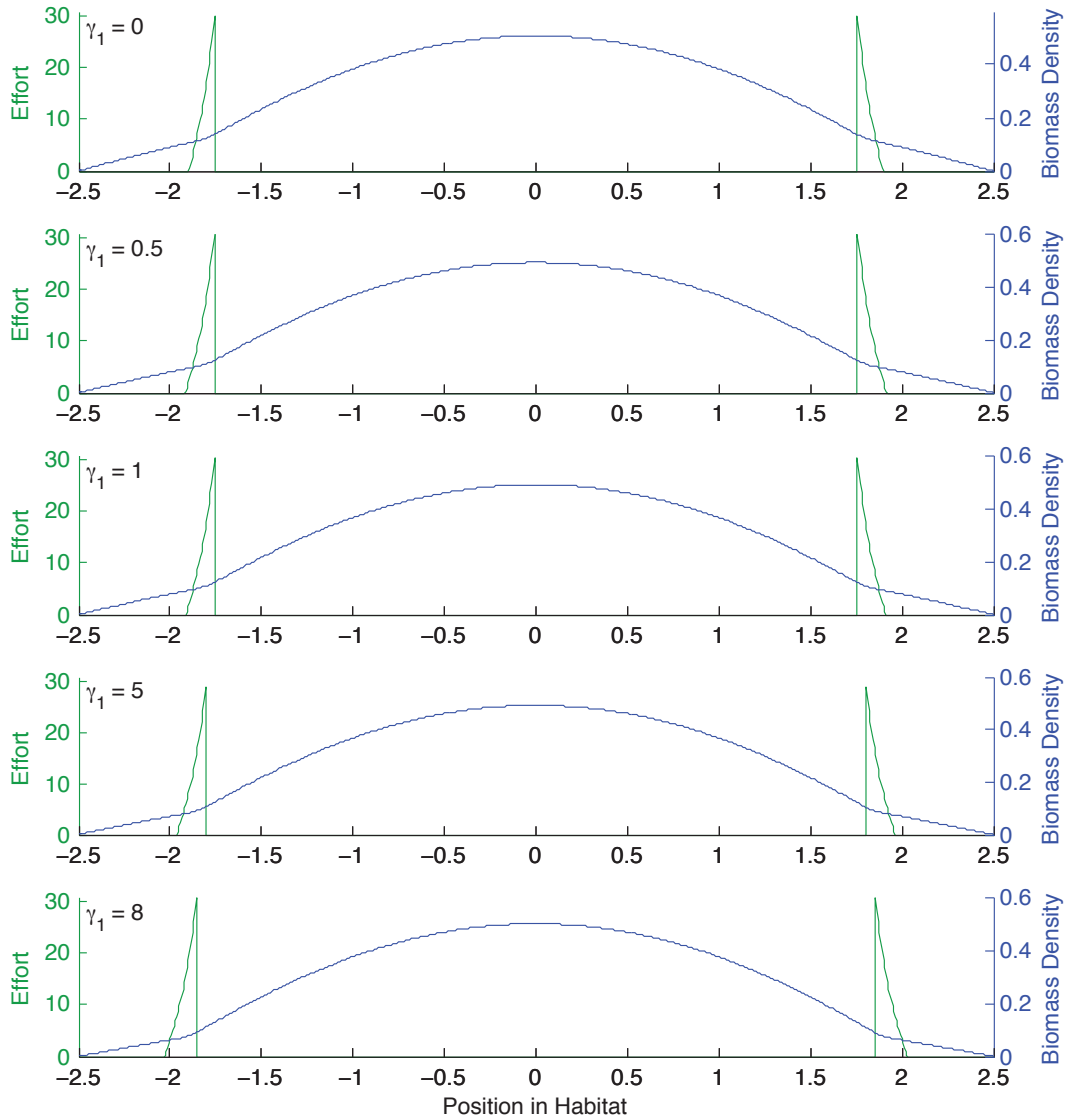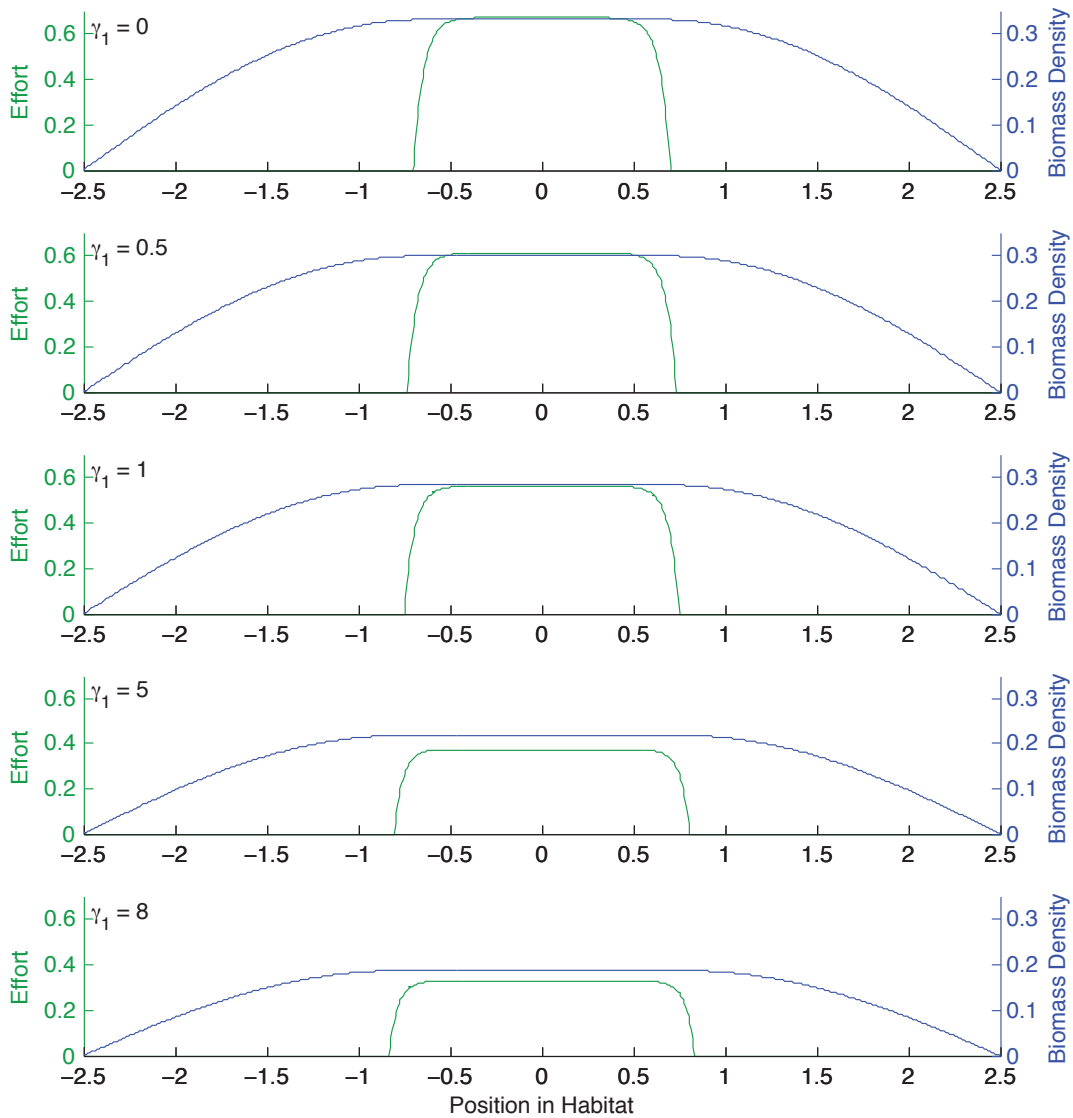
Figure 3.38: Third-best effort and stock densities for various levels of the density-dependent habitat sensitivity coefficient γ_1. These densities result from choosing a spatially independent tax on effort so as to maximize the total tax collected.
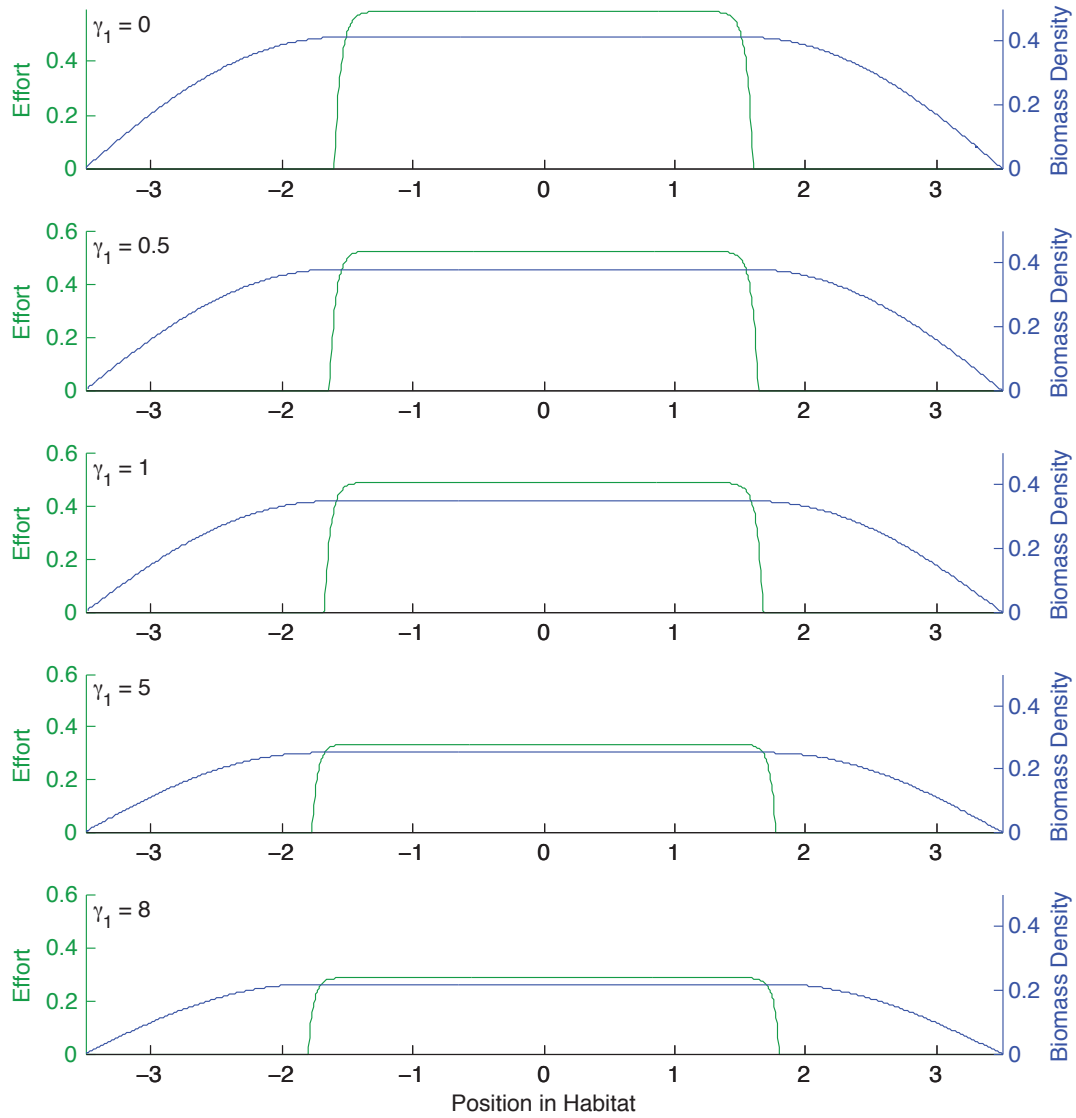
Figure 3.39: Third-best effort and stock densities for various levels of the density-dependent habitat sensitivity coefficient γ_1. These densities result from choosing a spatially independent tax on effort so as to maximize the total tax collected.
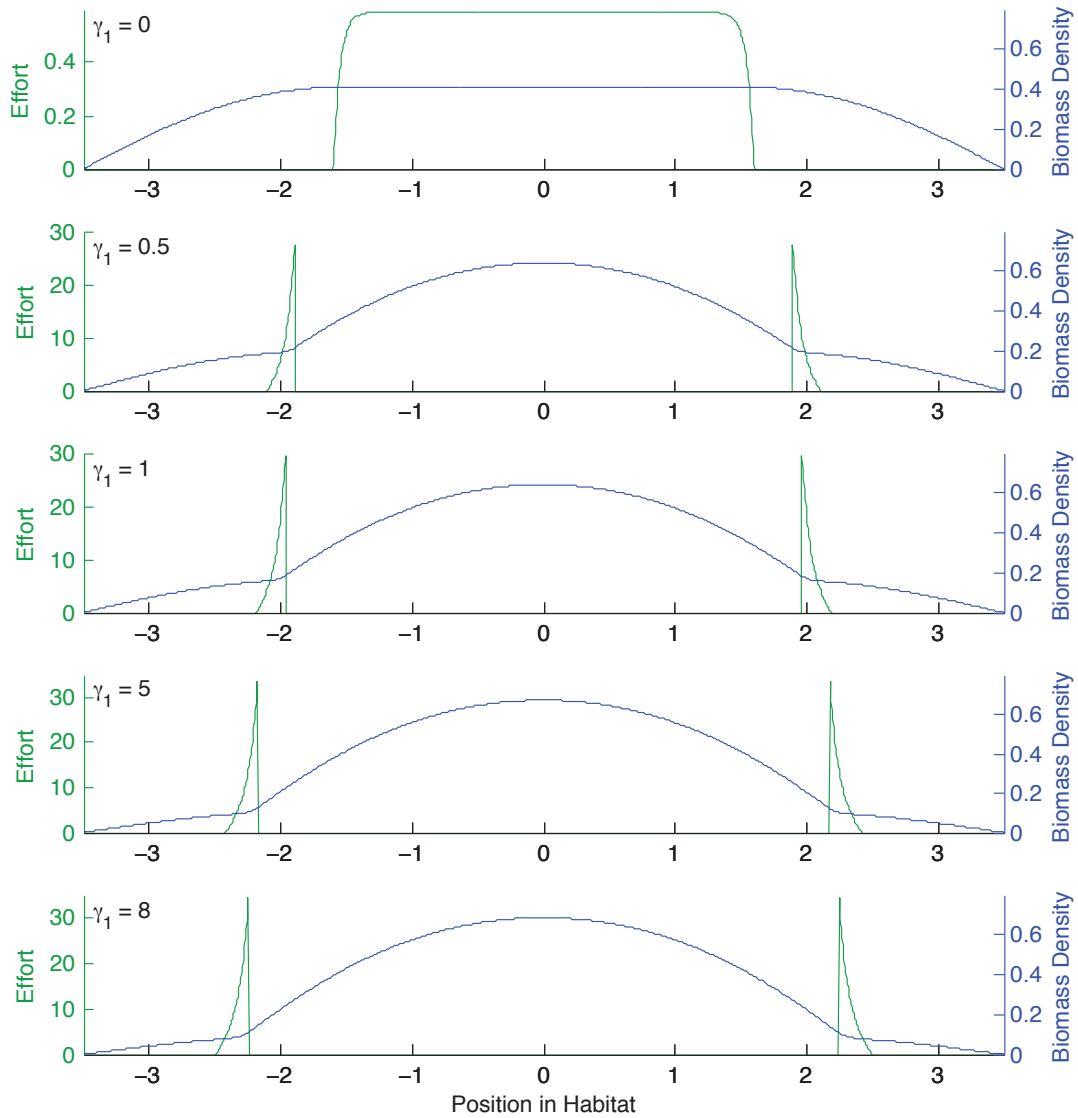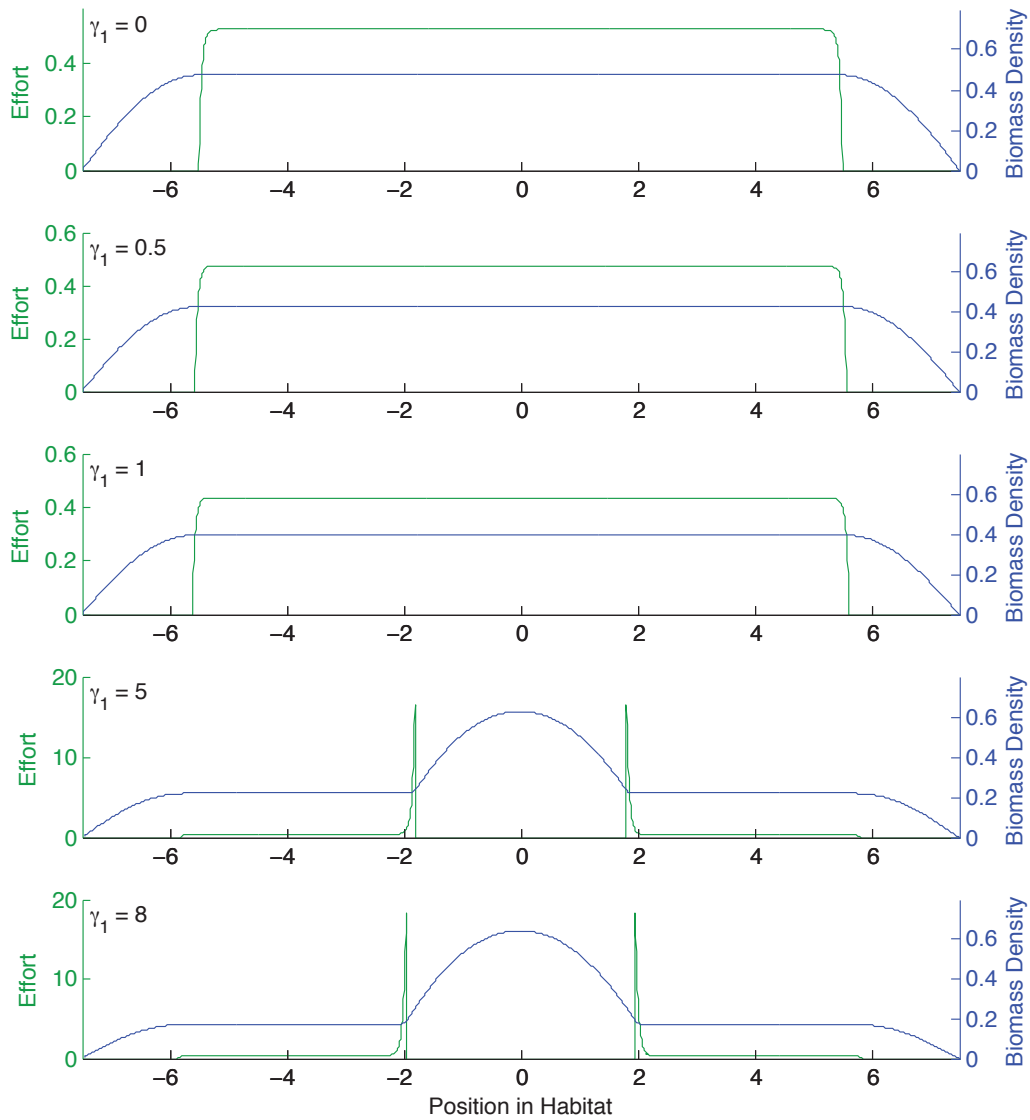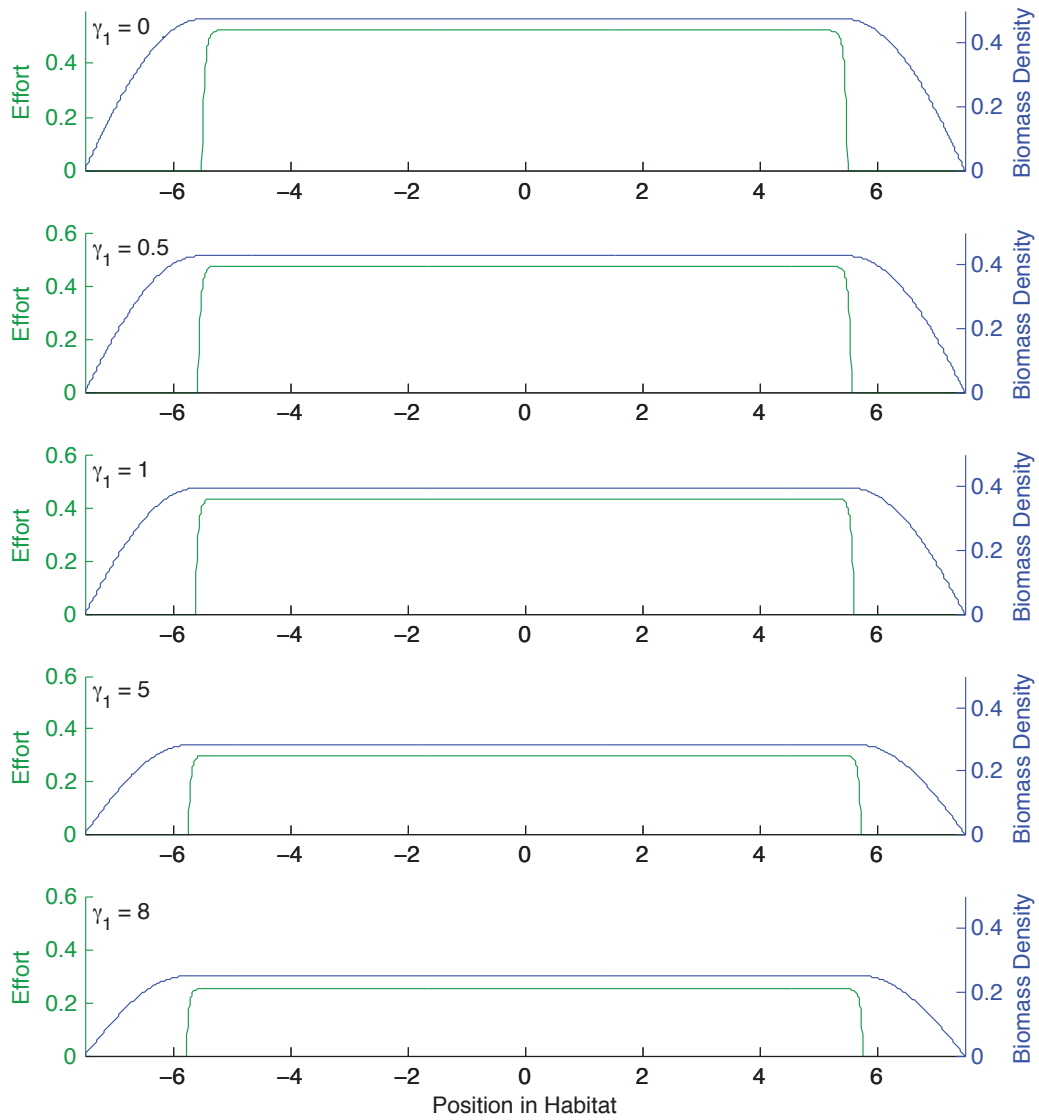
Figure 3.40: Third-best effort and stock densities for various levels of the density-dependent habitat sensitivity coefficient γ_1. These densities result from choosing a spatially independent tax on effort so as to maximize the total tax collected.
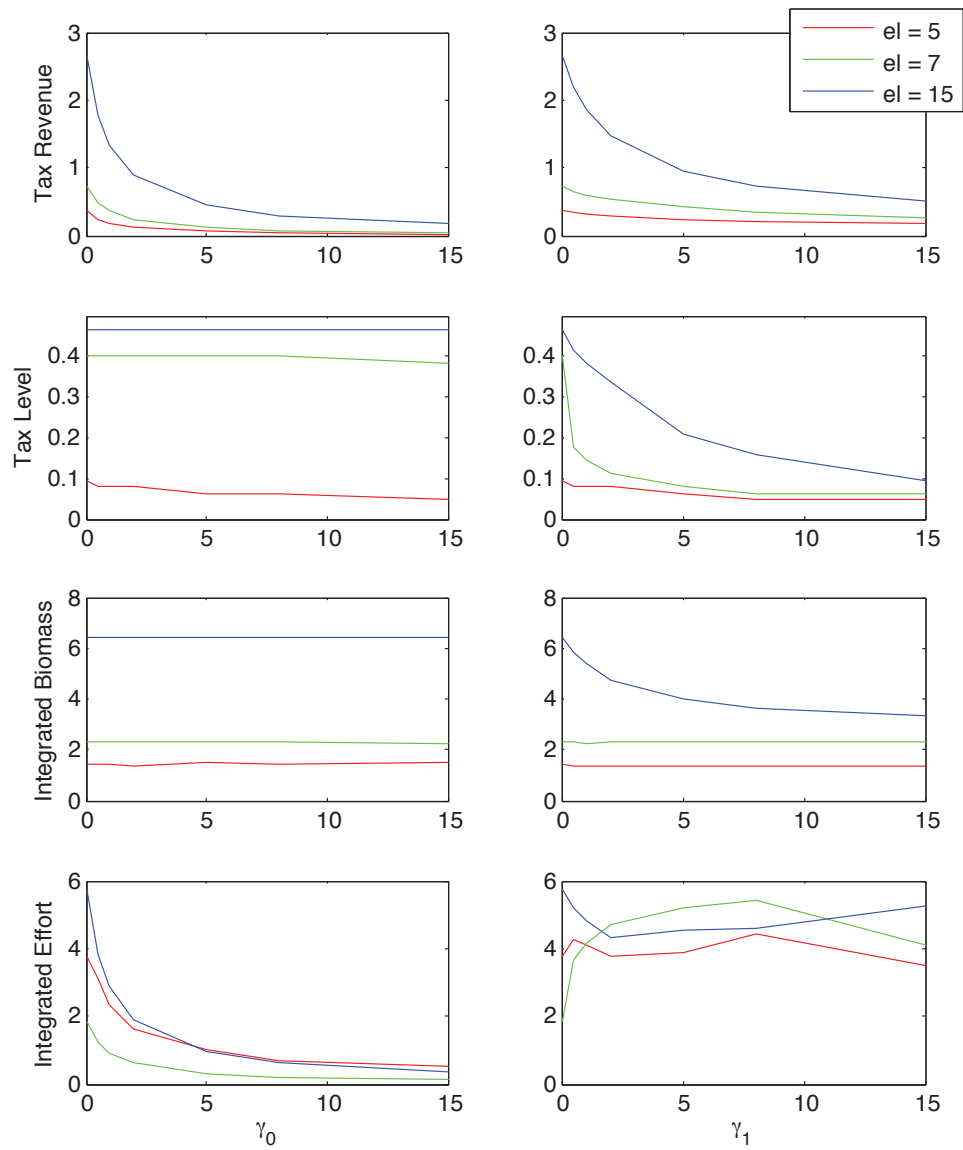
Figure 3.41: Integrated revenue, biomass, and effort for the Tax Only model. Also, optimal tax level at which these results occur.

Chapter 4

Comparison of Management Strategies

Distributions of effort and stock biomass differ across management strategies, as do integrated profits (whether acquired directly, through fish sales, or indirectly, through tax collection), stock biomass, and total effort. Here, I compare the management strategies to each other, and to the nonspatial baseline case, to determine their relative economic and conservation costs. Note that I have scaled integrated profit, stock biomass, and total effort for the nonspatial case by multiplying by habitat length. This produces a significant overestimate for all three parameters because it does not account for the effects of diffusion. In the spatial model, diffusion causes a reduction in biomass density at the habitat edges, which drives reductions in stock, profit, and effort.

4.1   Relative Distributions of Effort and Biomass

When habitat damage affects density-independent fish mortality rates, the qualitative distributions of stock biomass and fishing effort do not change with increasing habitat sensitivity. While stock biomass is relatively insensitive to changes in habi-

tat sensitivity for all management schemes, effort decreases across the habitat (note changing effort axis scales in Figs. 4.1, 4.3, and 4.5).

As habitat size increases, the expanding central low-effort moderate-biomass region of the Sole Owner management solution mirrors the stock biomass and effort intensity of the nonspatial optimum. By comparison, under Tax Only management, where effort is present, its intensity exceeds both Sole Owner and nonspatial optima, resulting in depressed stock densities. In addition, the Tax Only case is the most spatially homogeneous, displaying a constant level of effort in the center of the habitat, where fish biomass is high enough to support fishing.

In general, sole owner effort distributions are the most heterogeneous, with diffusion-driven peaks at habitat edges and central peaks when reserve networks are optimal. However, effort density is highest when reserves are part of the optimal solution under Tax and Defend management. Tax and Defend reserves tend to emerge with increasing habitat sensitivity to damage that affects density-dependent fish mortality rates (i.e. increasing γ_1). (When reserves are not present, the Tax and Defend case is the same as the Tax Only case and is thus overlaid by Tax Only data in Figures 4.1 - 4.9.) The adjacent Tax and Defend high effort actually intensifies with increasing γ_1; by contrast, effort intensity for other management strategies remains constant or decreases.

Interestingly, when reserves are present in both Sole Owner and Tax and Defend management scenarios, their boundaries may be closely aligned. In these cases, although edge effort is more intense for the Tax and Defend case, within the reserve, stock biomass mirrors Sole Owner density levels. When Tax and Defend reserves are larger than Sole Owner ones, their internal stock density may actually exceed Sole Owner within-reserve stocks, though generally, Sole Owner reserve biomass densities are the highest of all management strategies.

4.2 Integrated Management Impacts on Profits, Biomass, and Effort

When habitat damage affects density-independent mortality, the effects on total profit, biomass, and effort are qualitatively similar for all three management strategies. That is, total profits and integrated effort decline with increasing habitat sensitivity, while total stock biomass is relatively insensitive. However, the degree of separation between each management strategy is sensitive to habitat length: the larger the habitat, the more results resemble the nonspatial case because a smaller fraction of the habitat experiences edge effects.

Again, we emphasize that comparisons to the nonspatial case are limited by the absence of these edge effects when the nonspatial case is rescaled to the appropriate habitat length. However, the nonspatial result provides a useful upper bound for profit and biomass. Sole Owner management produces the most total profit and stock biomass of any spatial management strategy, and requires two to four times the amount of effort to do so as the Tax Only management strategy. In fact, the optimal effort level for the Tax Only strategy may be even less than that of the nonspatial result, because managers cannot control effort distribution except by using a tax to increase the size of edge reserves.

When habitat damage affects density-dependent mortality, heterogeneous spatial management may produce profits that exceed even the nonspatial reference point. This occurs when the use of reserves allows managers to set aside patches of high stock density, which grow – and export fish biomass – in the absence of deleterious habitat effects. Therefore, in the spatial case, total stock biomass also tends to exceed the nonspatial baseline. This is true even for the Tax Only case, because management sets tax levels to protect stock biomass and thereby increases the size of the unfished zones at the habitat edges. Again, applying the spatially explicit Sole Owner management strategy produces substantial increases in total effort.

When reserves are part of the Tax and Defend management strategy, their inclusion reduces the profit differential between Sole Owner and Limited Management cases. However, the relationship between the reserves and cumulative biomass is less clear. In some cases, especially when the Tax and Defend reserve mirrors the Sole Owner reserve, cumulative biomass can mirror that of the Sole Owner case. More generally, though, Tax and Defend and Tax Only cases show similar standing stocks. Indeed, central reserves may even be deleterious to stock because they create zones of intense fishing effort at their boundaries.
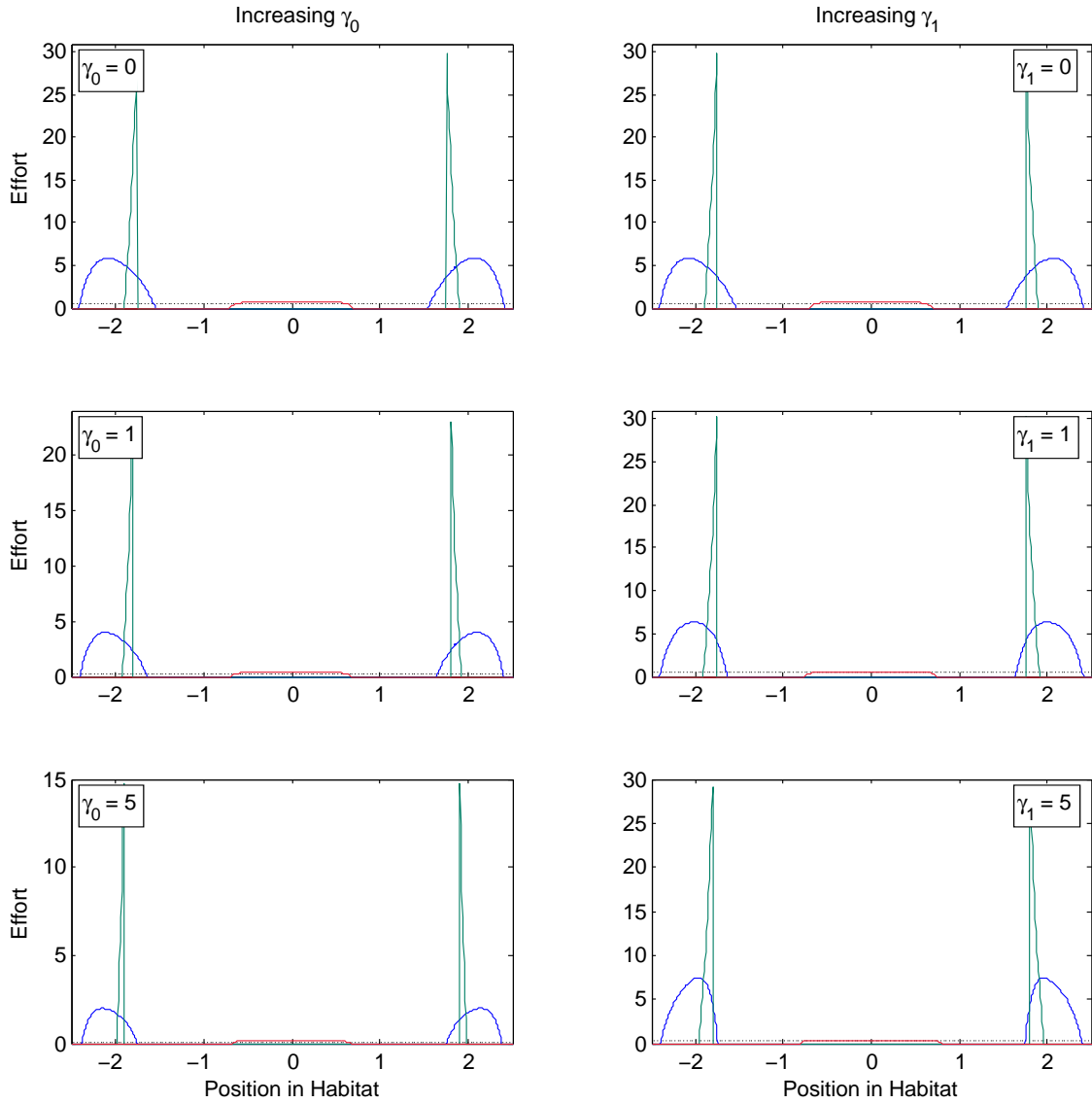
Figure 4.1: The spatial distribution of effort under three different spatial management schemes for $\ell = 5$. Results for three sets of habitat sensitivities are shown. The nonspatial effort level is projected across the habitat for comparison (dashed line). Except as specified in the figure legends, parameter values are: $\omega_0 = 0.01$, $\omega_1 = 0.001$, and $\gamma_0 = \gamma_1 = 0$.
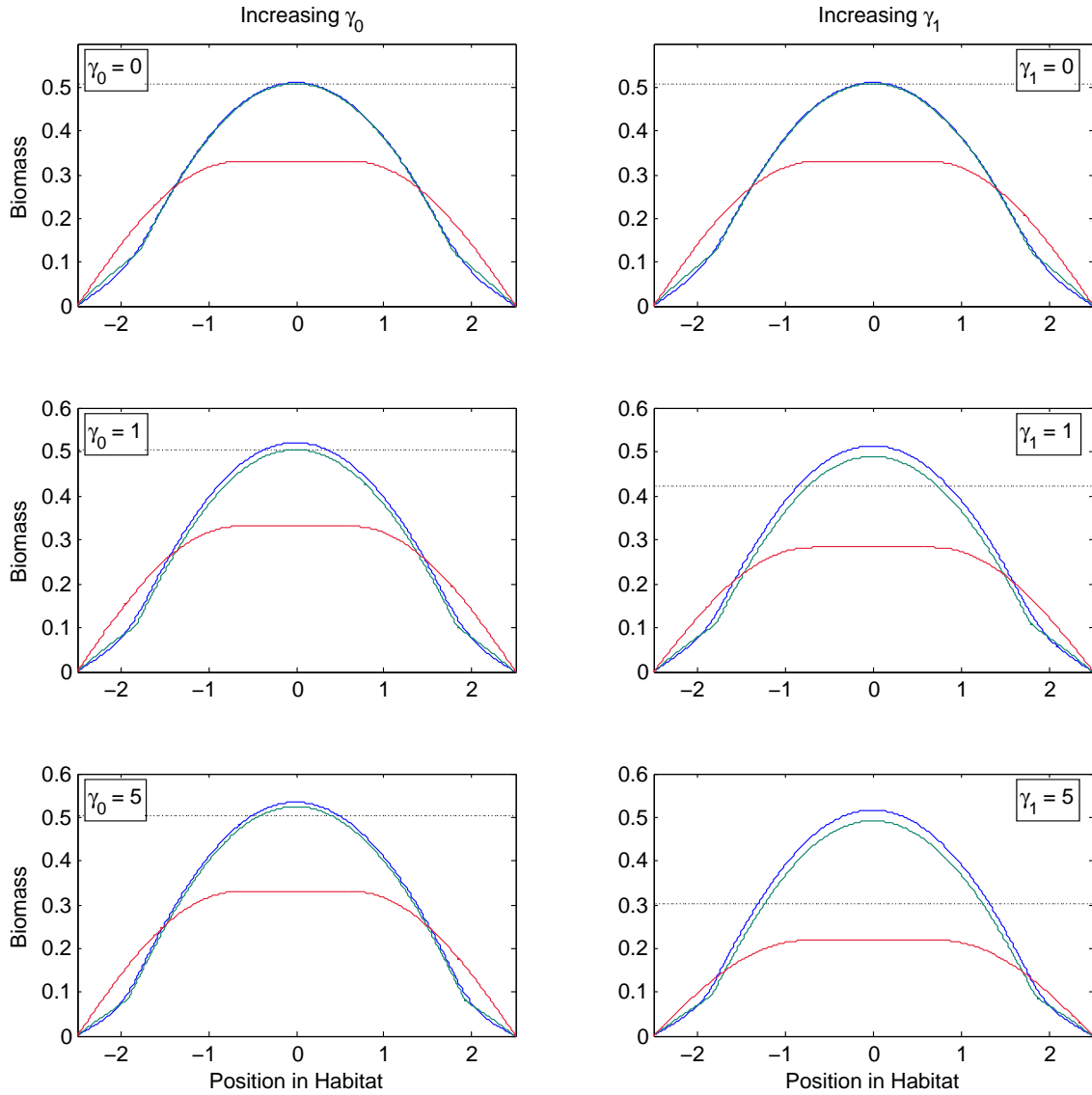
Figure 4.2: The spatial distribution of stock biomass under three different spatial management schemes for $\ell = 5$. Results for three sets of habitat sensitivities are shown. The nonspatial stock density is projected across the habitat for comparison (dashed line). Except as specified in the figure legends, parameter values are: $\omega_0 = 0.01$, $\omega_1 = 0.001$, and $\gamma_0 = \gamma_1 = 0$.
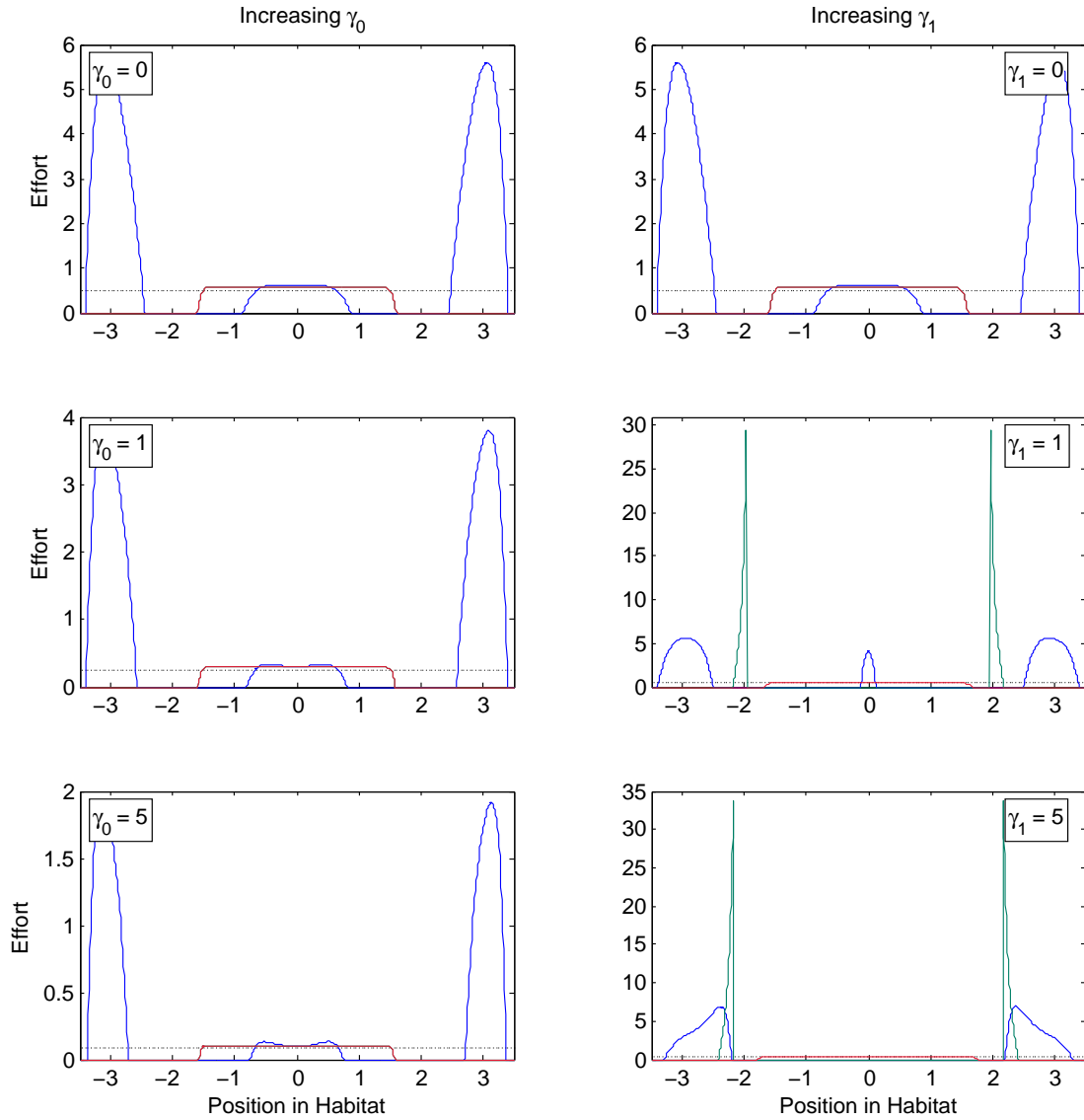
Figure 4.3: The spatial distribution of effort under three different spatial management schemes for $\ell = 7$. Results for three sets of habitat sensitivities are shown. The nonspatial effort level is projected across the habitat for comparison (dashed line). Except as specified in the figure legends, parameter values are: $\omega_0 = 0.01$, $\omega_1 = 0.001$, and $\gamma_0 = \gamma_1 = 0$.
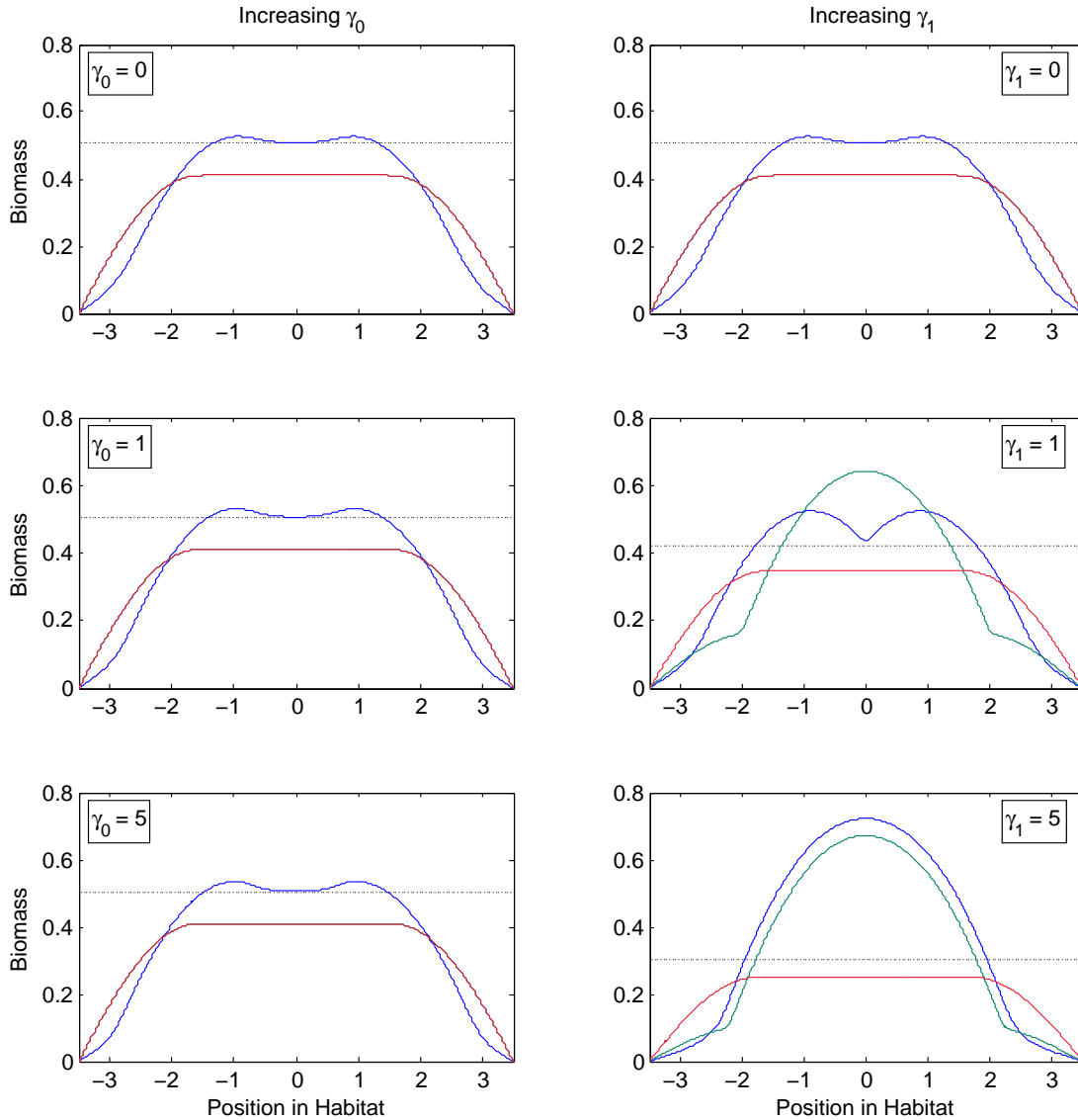
Figure 4.4: The spatial distribution of stock biomass under three different spatial management schemes for $\ell = 7$. Results for three sets of habitat sensitivities are shown. The nonspatial stock density is projected across the habitat for comparison (dashed line). Except as specified in the figure legends, parameter values are: $\omega_0 = 0.01$, $\omega_1 = 0.001$, and $\gamma_0 = \gamma_1 = 0$.
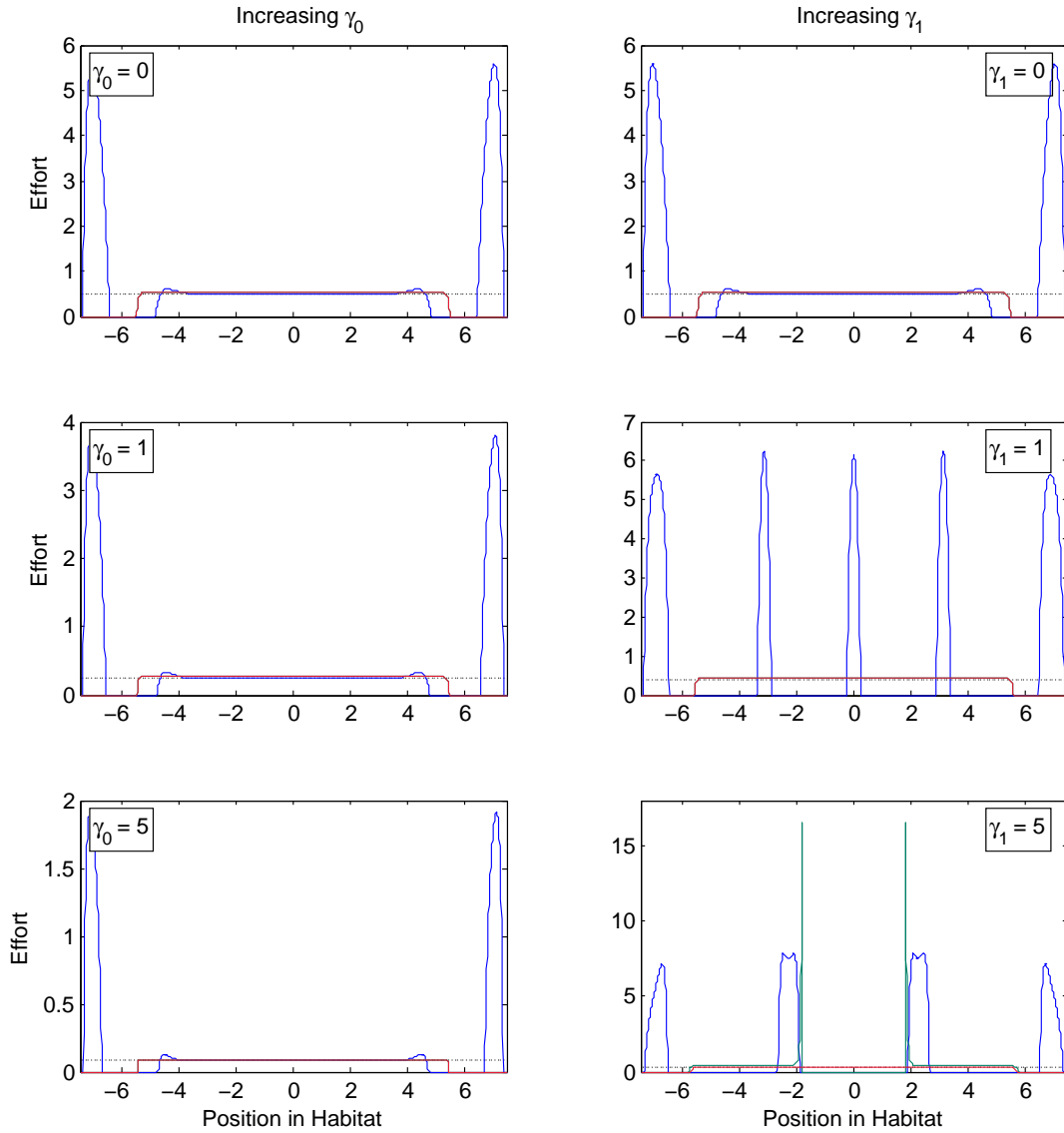
Figure 4.5: The spatial distribution of effort under three different spatial management schemes for $\ell = 15$. Results for three sets of habitat sensitivities are shown. The nonspatial effort level is projected across the habitat for comparison (dashed line). Except as specified in the figure legends, parameter values are: $\omega_0 = 0.01$, $\omega_1 = 0.001$, and $\gamma_0 = \gamma_1 = 0$.
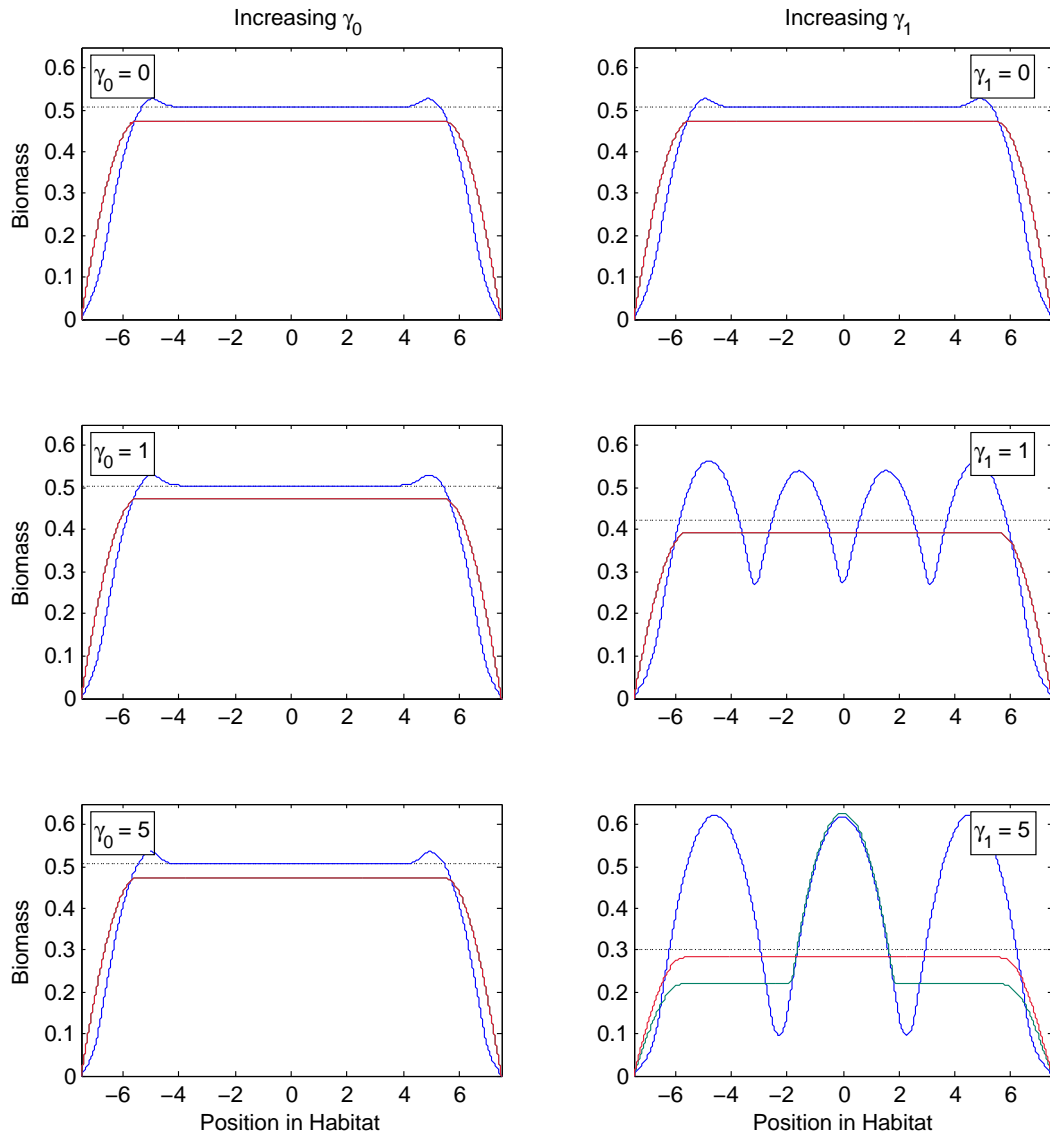
Figure 4.6: The spatial distribution of stock biomass under three different spatial management schemes for $\ell = 15$. Results for three sets of habitat sensitivities are shown. The nonspatial stock density is projected across the habitat for comparison (dashed line). Except as specified in the figure legends, parameter values are: $\omega_0 = 0.01$, $\omega_1 = 0.001$, and $\gamma_0 = \gamma_1 = 0$.
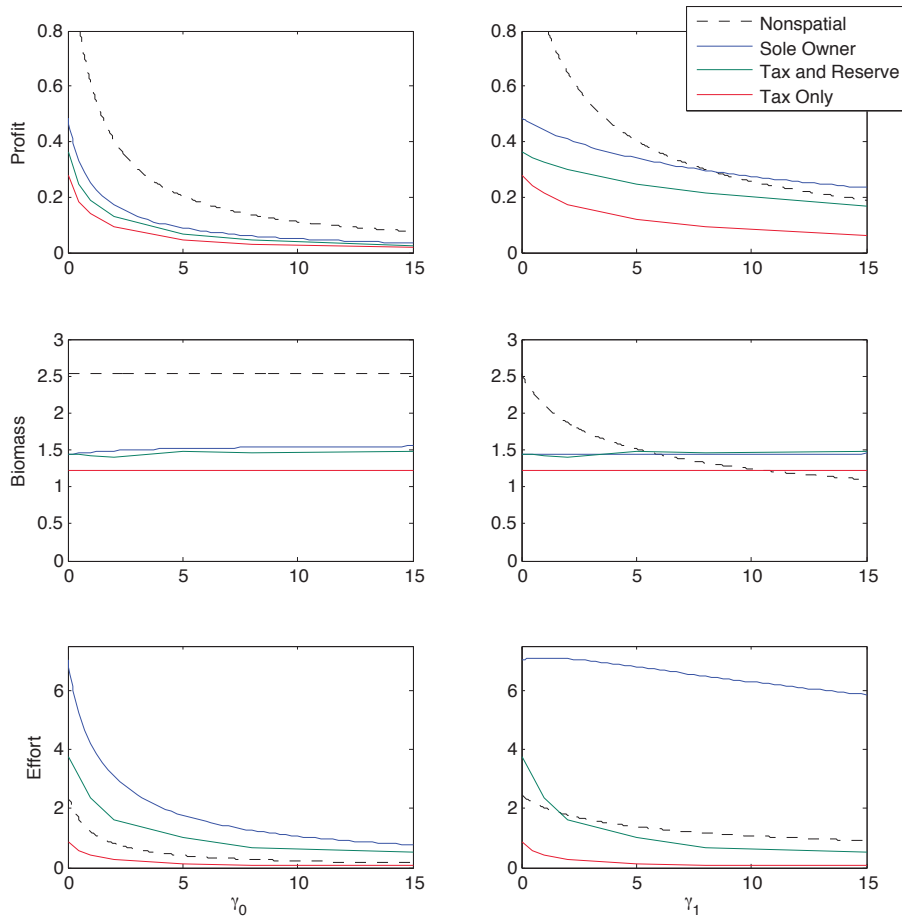
Figure 4.7: Integrated profit, stock biomass, and effort as a function of habitat sensitivity under three different spatial management schemes for $\ell = 5$. Again, nonspatial results are presented for reference (dashed line). Note that nonspatial biomass numbers are elevated relative to spatial results because, in the spatial case, diffusion leads to a decrease in biomass at the habitat edges. Except as specified in the figure legends, parameter values are: $\omega_0 = 0.01$, $\omega_1 = 0.001$, and $\gamma_0 = \gamma_1 = 0$.
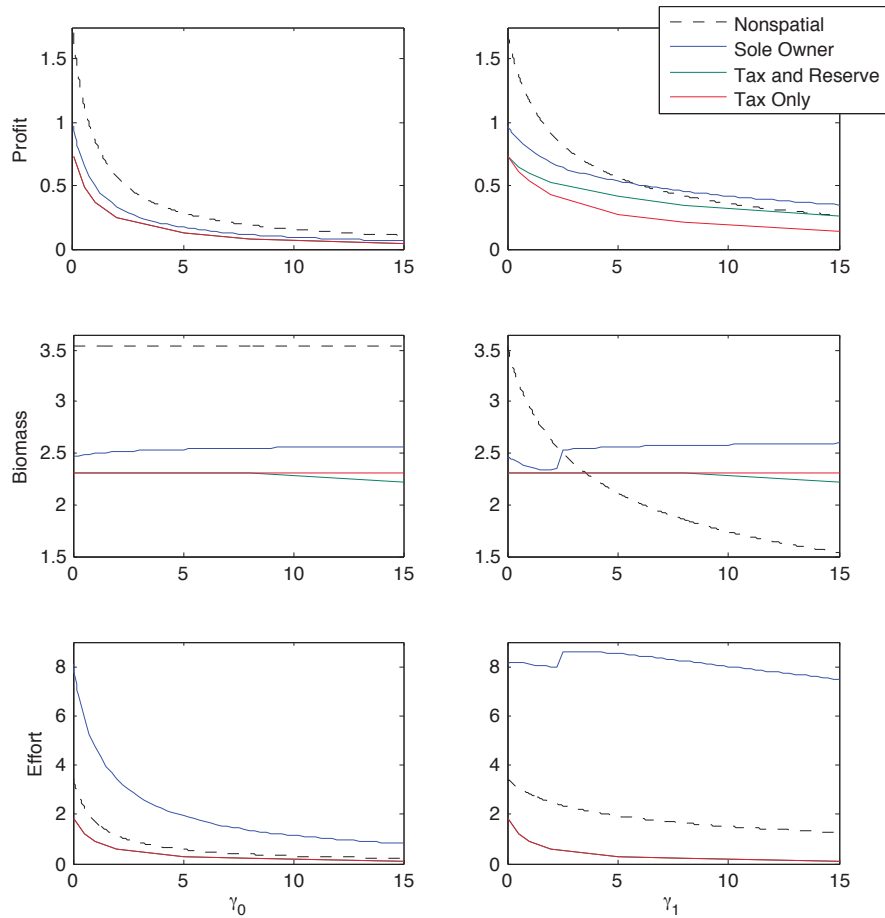
Figure 4.8: Integrated profit, stock biomass, and effort as a function of habitat sensitivity under three different spatial management schemes for $\ell = 7$. Again, nonspatial results are presented for reference (dashed line). Note that nonspatial biomass numbers are elevated relative to spatial results because, in the spatial case, diffusion leads to a decrease in biomass at the habitat edges. Except as specified in the figure legends, parameter values are: $\omega_0 = 0.01$, $\omega_1 = 0.001$, and $\gamma_0 = \gamma_1 = 0$.
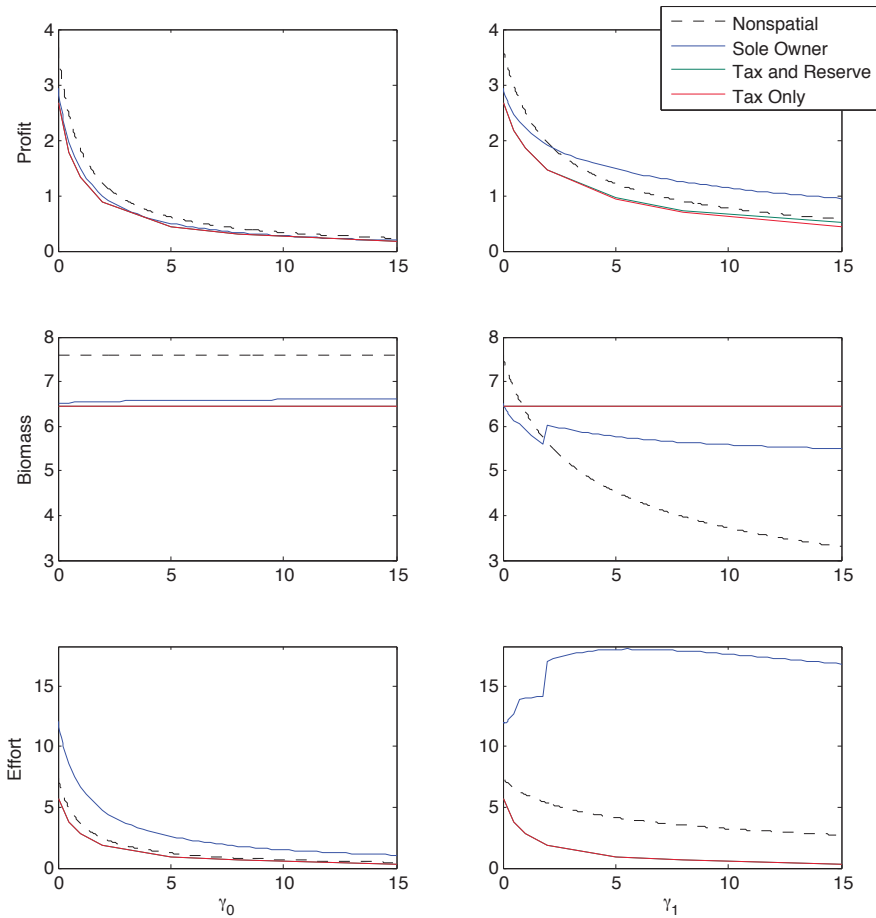
Figure 4.9: Integrated profit, stock biomass, and effort as a function of habitat sensitivity under three different spatial management schemes for $\ell = 15$. Again, nonspatial results are presented for reference (dashed line). Note that nonspatial biomass numbers are elevated relative to spatial results because, in the spatial case, diffusion leads to a decrease in biomass at the habitat edges. Except as specified in the figure legends, parameter values are: $\omega_0 = 0.01$, $\omega_1 = 0.001$, and $\gamma_0 = \gamma_1 = 0$.

Chapter 5

Discussion

5.1 Overview

My results demonstrate that closing portions of habitat to fishing may be not just economically viable, but also economically beneficial, when fishing damages habitat. By considering the case when fish vital rates are negatively impacted by fishing, I introduce habitat heterogeneity driven by differences in fishing intensity. Fish mortality may be directly increased by habitat damage, or may be elevated through density-dependent mechanisms (represented by γ_0 and γ_1, respectively, in our models).

Including habitat damage by using positive and increasing values of γ_0 does little to affect the economic optimality of marine reserves, though habitat damage does dramatically decrease fishery profits and total fishing effort under all management schemes. However, stock biomass is relatively unaffected by habitat sensitivity.

These results likely stem from the fact that, mathematically, increases in γ_0 effectively increase the catchability coefficient, q, meaning that more fish are lost to the population for every unit of effort than when no habitat effects are modeled. However, these fish are not collected as part of the fishery harvest, so their deaths do not increase the fishery's profit. This feedback necessarily results in a decrease in effort to sustain stock biomass at optimal levels; as a consequence, catch and profits are

reduced.

By contrast, varying γ_1, which controls habitat sensitivity to density-dependent mortality effects, may dramatically affect effort and biomass distributions. Under first-best management conditions, sufficiently high habitat sensitivity may result in reserve networks: unfished areas interspersed with shorter regions of high-intensity fishing effort. As expected, this highly spatially variable effort distribution produces significant economic gains. The Sole Owner management strategy also generally results in increased standing stock biomass compared to other management schemes.

The network pattern which emerges from the Sole Owner analysis suggests that even limited management may be made more effective by designating more numerous, smaller reserves, rather than a single, central one. However, our study of second-best management strategies shows that even single, central reserves may be optimal, depending upon habitat size and sensitivity.

Tax and reserve combinations are optimal because they work together to protect a segment of fish habitat from damage and reduce effort outside of the reserve. Previous studies have found that constraints on fishing capacity are critical to maintaining optimal stock density and ensuring effectiveness of reserves (Hanneson 1998, Hiddink et al. 2006a). Under the Tax and Defend management scenario studied above, we have seen how the optimal tax rate declines with increasing reserve fractions to balance the reduction in effort necessary from closing additional habitat to fishing.

Again, I emphasize the important role of model parameterization in determining the optimal effort distribution. When habitat damage is parameterized as a driver of density-independent fish mortality, effort distribution changes little, except for slight expansions of any existing reserves. In contrast, when habitat damage is a density-dependent driver of increased fish mortality, reserves emerge as an increasing function of habitat sensitivity.

Perhaps most importantly, we have seen that a spatial approach to fisheries management may produce significant gains in profit over nonspatial approaches, especially

in the first-best case of Sole Owner management. However, the relative significance in differences between management strategies depends upon habitat length: as habitat length increases, the fraction of the habitat that experiences edge effects shrinks. Thus, for increasing ℓ, the benefits of spatial management become apparent only for higher and higher levels of habitat sensitivity γ_1.

Still, when γ_1 is sufficiently high, the emergence of periodic reserve networks is noteworthy. These networks persist even as habitat size increases, suggesting that a spatial variation of "pulse fishing" may be optimal in the presence of habitat effects.

5.2 Comparison to Previous Studies

This analysis is not the first attempt at including habitat damage in fisheries models, but rather represents a unique, spatially-explicit approach to effort feedbacks not previously considered in the literature. Earlier studies have relied on two-patch models, with patch size determined by *a priori* designation of reserves (Mangel 2000, Upton and Sutinen 2005, Armstrong 2007).

In an early attempt at including habitat in marine reserve bioeconomics models, Mangel (2000) considered the economic impacts of reserve designation in two habitat types – spawning and fishing grounds – when the manager's goal is to maintain habitat and stock size. By simulating fish populations and catch levels forward over a finite time horizon, he found that no-take reserves can act as a source of biomass replenishment for fishing grounds, and provide insurance against fishery collapse in a stochastic environment. However, although his model allowed for habitat loss over time, this loss was not linked to fishing effort. Therefore, while his results use a connection between habitat loss and additional fish mortality to justify marine reserves, they do not relate to controls on fishing effort.

By contrast, Upton and Sutinen (2005) linked effort to habitat directly by making habitat damage depend upon effort intensity. In their model, habitat damage reduced

habitat quality, which subsequently reduced the population parameters of growth rate and carrying capacity. Their use of logistic models for habitat and population differs from our approach, in which effort directly affects the vital rates of individual members of the population. In their subsequent analysis of a two-patch system (with one patch designated as a reserve) under "open access", they show that the inclusion of habitat effects increases the economic optimality of marine reserves. (Note that their "open access" economic parameterization is actually more similar to our "sole owner" management scenario.)

Armstrong (2007) modeled fishery yield for true "open access" management when reserve carrying capacity is elevated relative to fished areas. She finds that, when habitat effects are considered, placing 75% of habitat in reserves can maximize yield outside the reserve, and that this maximum yield may exceed that obtained under the spatially homogeneous management of a sole owner. While her approach to habitat effects is fundamentally different from the one we have taken above (in which habitat damage is mediated through effort intensity), her results support the conclusion that considering habitat effects may increase the economic optimality of marine reserves.

While the modeling efforts described above generally support the conclusion that including habitat effects increases the optimality of marine reserves, none allow for the emergence of reserves in the way that we have under sole owner management conditions. By avoiding a priori reserve designation in the sole owner case, we have sidestepped any assumptions about optimal effort location and intensity. We have also allowed effort to feed back directly on fish vital rates, so that habitat quality at equilibrium depends upon local effort intensity, rather than developing complex relationships between effort and habitat dynamics, or making blanket assumptions about the effects of reserves on carrying capacity.

Perhaps the most significant improvement of this model over previous studies, however, is its use of continuous, explicit space. Because we consider the unique dynamics of all positions on a linear habitat space, we avoid the necessity of dividing

fish habitat into discrete patches. This allows for significant heterogeneity in effort and biomass density across short distances, and, ultimately, enables the emergence of not only reserves, but also reserve networks, which alternate unfished closed areas with regions of intense fishing.

5.3 Future Directions

Periodic reserve networks. In the Sole Owner scenario above, reserve networks of fixed period emerge for sufficiently large habitat lengths and density-dependent sensitivities. This merits further analysis by expanding the set of reserve lengths and habitat sensitivities examined.

Multi-stage fish populations. Fishing effort and habitat damage affect members of the fish population differentially based on stage (e.g. larvae, juveniles, and adults) and size (i.e. gear mesh size restrictions). Including stage structure allows a more mechanistic approach to modeling these differences (Gerber et al. 2005). Previous studies have divided fish populations into age classes to differentiate between mobile and sessile stages (e.g. Lindholm et al. 2001, White and Kendall 2007, White 2009) and restrict catch effort to certain segments of the fish population (e.g. White and Kendall 2007). However, few - if any - of these studies have considered the additional consequences of effort-driven habitat damage from an economic perspective. Therefore, the next step in our research will be to investigate differences between unstructured and stage-structured fish population models.

Multi-use habitat. Complexity can also be added to the economic side of the model. Under real-world circumstances, fisheries frequently overlap with other fish habitat uses, such as recreation. A sole manager may, therefore, collect rents from both an extractive fishery (modeled here) and nonextractive tourism. Considering such nonextractive uses may enhance the optimality of reserves, particularly if tourists

do not want to encounter industrial fishing gear while exploring fish habitat.

Multi-species fisheries. Fish populations never exist in isolation, and our inclusion of habitat effects in a fishery model is only a first effort at including biotic and abiotic factors in fisheries models. Removal of species biomass affects the adjacent trophic levels directly, by removing a predatory species or prey item. The ecological consequences are inevitably of conservation interest, but may also affect fisheries management when other species are of commercial value. Multi-species fisheries models consider such interactions and the role of bycatch in fisheries economics.

Appendix A

Spatially Variable Tax

Mathematically, we represent the open access case by setting the profit function (which now includes tax) equal to zero for all x:

$$\Pi(x) = pu(x)f(x) - (\omega_0 + \omega_1 f(x))f(x) - \tau(x)f(x) = 0 \tag{A.1}$$

Thus, at equilibrium, f is a function of τ:

$$f(\tau) = max\left[0, \frac{pu - \tau - \omega_0}{\omega_1}\right] \tag{A.2}$$

The manager seeks to maximize tax revenue (R), given by:

$$R = \int_{-\ell/2}^{\ell/2} \tau(x)f(x)dx \tag{A.3}$$

As before, I apply Pontryagin's Maximum Principle to obtain the Hamiltonian:

$$H = \tau f + \lambda_1(-v) + \lambda_2\left[(1 - \gamma_0 f)u - (1 + \gamma_1 f)u^2 - fu\right] \tag{A.4}$$

Substituting for non-zero effort using (A.2), I obtain the Hamiltonian as a function of τ, and its derivatives:

$$
\begin{aligned}
H &= \frac{pu\tau - \tau^2 - \omega_0\tau}{\omega_1} - \lambda_1 v + \lambda_2 u \left[(1 - \frac{\gamma_0 pu - \gamma_0\tau - \gamma_0\omega_0}{\omega_1}) \right] \\
&\quad - \lambda_2 u \left[(1 + \frac{\gamma_1 pu - \gamma_1\tau - \gamma_1\omega_0}{\omega_1})u + \frac{pu - \tau - \omega_0}{\omega_1} \right] \quad\quad\quad\quad \text{(A.5)} \\
\frac{\partial\lambda_1}{\partial x} &= -\frac{\partial H}{\partial u} = \lambda_2 \left[(\frac{2\gamma_0 pu - \gamma_0\tau - \gamma_0\omega_0}{\omega_1} - 1) + u(1 + \frac{3\gamma_1 pu - 2\gamma_1\tau - 2\gamma_1\omega_0}{\omega_1}) \right] \\
&\quad + \lambda_2 \left[\frac{2pu - \tau - \omega_0}{\omega_1} \right] - \frac{p\tau}{\omega_1} \\
\frac{\partial\lambda_2}{\partial x} &= -\frac{\partial H}{\partial v} = \lambda_1 \\
\frac{\partial H}{\partial \tau} &= \frac{pu - 2\tau - \omega_0}{\omega_1} + \lambda_2 u \left[\frac{\gamma_0 + \gamma_1 u + 1}{\omega_1} \right] \quad\quad\quad\quad\quad\quad\quad\quad \text{(A.6)}
\end{aligned}
$$

This final partial derivative is set equal to zero to maximize the Hamiltonian and, therefore, tax revenue. This gives:

$$
\tau^* = \frac{1}{2} \left[pu - \omega_0 + \lambda_2 u(\gamma_0 + \gamma_1 u + 1) \right]. \quad\quad\quad\quad \text{(A.7)}
$$

Note that, in the optimal sole owner case, the owner maximizes the revenue, or the difference between total profit ($\int_{-\ell/2}^{\ell/2} puf dx$) and total cost ($\int_{\ell/2}^{\ell/2} (\omega_0 + \omega_1 f)f dx$). In this optimal management case, tax takes the place of this profit differential. Therefore, the optimal management results recapitulate the sole-owner results for spatial distribution of effort and fish biomass. The only difference is that profit is returned through the manager as collected tax, rather than as profits to the fishermen directly.

Appendix B

Matlab Code

B.1 Code for the Non-Spatial Model

```matlab
%Nonspatial Sole Owner model:
%Original Matlab code written April 21, 2010 by Holly V. Moeller

%This code solves numerically for the optimal effort level (and
%resulting biomass density) to maximize profit from the management
%perspective of a %single owner.

%Habitat damage affects density dependent or density independent fish
%life history rates through a range of habitat sensitivity parameters
%(gamma_0 and gamma_1). Here we calculate the effects of this habitat
%damage on effort and stock, and, subsequently, on profit.


%Defining the parameter space:
gamma_0_set = [0 (1:15*100)/100];    %Density-independent coefficients
```

```matlab
gamma_1_set = gamma_0_set;              %Density-dependent coefficients

w_0_set = 0.01;                         %Cost per unit effort

w_1 = 0.001;                            %Marginal cost per unit effort

p = 1;                                  %Price per unit catch


%The effort level that will drive the fish population to extinction,
%for a %given habitat sensitivity, gamma_0:
fR_set = 1./(1+gamma_0_set);


%Data-holding matrices when fishing increases density-independent
%mortality
profStore_0vary = zeros(size(gamma_0_set,2),size(percentspace,2)); %Profit
tr_0vary = zeros(size(profStore_0vary));    %Revenue
tc_0vary = zeros(size(profStore_0vary));    %Cost


%Data-holding matrices when fishing increases density-dependent
%mortality
profStore_1vary = zeros(size(gamma_1_set,2),size(percentspace,2));
tr_1vary = zeros(size(profStore_1vary));
tc_1vary = zeros(size(profStore_1vary));


%The first column of this matrix holds values for gamma_0 varied;
%The second column holds values for gamma_1 varied.
equilfStore = zeros(max(size(gamma_0_set,2),size(gamma_1_set,2)),2);
equiluStore = zeros(size(equilfStore));
equilprofStore = zeros(size(equilfStore));
equiltcStore = zeros(size(equilfStore));
equiltpStore = zeros(size(equilfStore));


%Check that cost per unit effort is not so high that it prohibits
%fishing:
if p - w_0 <= 0
    disp('Alert: No profitable fishing possible!')
    break
```

```matlab
    end

%Iterate the calculation for each value of gamma_0
for i = 1:size(gamma_0_set,2)
    gamma_1 = 0;
    gamma_0 = gamma_0_set(i);
    proffcn = @(f)p.*(1-gamma_0.*f-f)./(1+gamma_1.*f).*f - w_0.*f...
        - w_1.*f.*f;
    tpfcn = @(f)p.*(1-gamma_0.*f-f)./(1+gamma_1.*f).*f;
    tcfcn = @(f)f.*(w_0+w_1.*f);
    fL = 0; %Left bound for effort distribution
    fR = fR_set(i); %Right bound for effort distribution

    %Calculate the profit, revenue, and cost for a variety of effort
    %levels
    f = fR*[0:100]/100;
    for j = 1:size(f,2)  % Calculate economic parameter distribution
        profStore_0vary(i,j) = proffcn(f(j));
        tr_0vary(i,j) = tpfcn(f(j));
        tc_0vary(i,j) = tcfcn(f(j));
    end

    %Calculate the overall best choice of effort, and resultant profit
    %and stock size:
    dpidf = @(E)E^3*(-2*w_1*gamma_1*gamma_1)+E^2*(-p*gamma_0*gamma_1...
        -p*gamma_1-w_0*gamma_1*gamma_1-4*w_1*gamma_1)...
        +E*(-2*p*gamma_0-2*p-2*w_0*gamma_1-2*w_1)+p-w_0;
    fstar = fzero(dpidf, [fL fR]);
    ustar = (1-gamma_0*fstar-fstar)/(1+gamma_1*fstar);
    equilprofStore(i,1+(k-1)*size(w_0_set,2)) = p*ustar*fstar...
        - fstar*(w_0+w_1*fstar);
    equiluStore(i,1+(k-1)*size(w_0_set,2)) = ustar;
    equilfStore(i,1+(k-1)*size(w_0_set,2)) = fstar;
    equiltpStore(i,1+(k-1)*size(w_0_set,2)) = p*ustar*fstar;
```

```matlab
        equiltcStore(i,1+(k—1)*size(w_0_set,2)) = w_0*fstar+w_1*fstar*fstar;
end


%Iterate the same calculation for each value of gamma_1
for i = 1:size(gamma_1_set,2)
    gamma_1 = gamma_1_set(i);
    gamma_0 = 0;
    proffcn = @(f)p.*(1—gamma_0.*f—f)./(1+gamma_1.*f).*f — w_0.*f...
        — w_1.*f.*f;
    tpfcn = @(f)p.*(1—gamma_0.*f—f)./(1+gamma_1.*f).*f;
    tcfcn = @(f)f.*(w_0+w_1.*f);
    fL = 0;
    fR = 1;
    f = fR*[0:100]/100;
    for j = 1:size(f,2)  %%%% Calculate economic parameter distribution
        profStore_1vary(i,j,k) = proffcn(f(j));
        tr_1vary(i,j,k) = tpfcn(f(j));
        tc_1vary(i,j,k) = tcfcn(f(j));
    end
    dpidf = @(E)E^3*(—2*w_1*gamma_1*gamma_1)+E^2*(—p*gamma_0*gamma_1...
        —p*gamma_1—w_0*gamma_1*gamma_1—4*w_1*gamma_1)...
        +E*(—2*p*gamma_0—2*p—2*w_0*gamma_1—2*w_1)+p—w_0;
    fstar = fzero(dpidf, [fL fR]);
    ustar = (1—gamma_0*fstar—fstar)/(1+gamma_1*fstar);
    equilprofStore(i,2+(k—1)*size(w_0_set,2)) = p*ustar*fstar...
        — fstar*(w_0+w_1*fstar);
    equiluStore(i,2+(k—1)*size(w_0_set,2)) = ustar;
    equilfStore(i,2+(k—1)*size(w_0_set,2)) = fstar;
    equiltpStore(i,2+(k—1)*size(w_0_set,2)) = p*ustar*fstar;
    equiltcStore(i,2+(k—1)*size(w_0_set,2)) = w_0*fstar+w_1*fstar*fstar;

end
```

B.2   Code for the Spatial Model

B.2.1   Sole Owner Model: Calling the Sole Owner scripts

```matlab
%Code to iterate SoleOwner spatial model
%Written by H. Moeller on February 26, 2010

%The sole-owner spatial model solves for profit-maximizing distributions
%of biomass and effort for a given combination of parameters:
%   el = habitat length,
%   x = vector of habitat locations at which to save data
%   gamma_0 = habitat sensitivity to density-independent mortality effects
%   gamma_1 = habitat sensitivity to density-dependent mortality effects
%   w_0 = cost per unit effort
%   w_1 = marginal cost per unit effort
%   p = price per unit catch
%   t_end = length of time to simulate analysis forward

%Set up parameter space:
%Enter choice for which gamma to vary:
%   0 = vary gamma_0
%   1 = vary gamma_1
gammavary = 0;
if gammavary == 0;
    gamma_1 = 0;
elseif gammavary == 0;
    gamma_0 = 0;
else
    disp('Error: ineligible choice for gamma to vary.')
end
%The values taken by the varied sensitivity coefficient:
variedgamma = [0, .05, .1, .15, .2, (1:60)/4];
```

```matlab
gammasize = size(variedgamma,2);


w_0=0.01;    %Cost per unit of fishing effort
w_1=0.001;   %Marginal cost per unit effort
t_end = 1000000;    %Length of time to run model forward
p=1;        %Price per unit of catch
el=7;       %Length of habitat
xstep=100*(el+5)+1;  %Number of points in the x-vector describing
                     %habitat length


%FILENAME:
if gammavary == 0
    filenamer = (['SoleOwner_el-' num2str(el) '_varyg0']);
elseif gammavary == 1
    filenamer = (['SoleOwner_el-' num2str(el) '_varyg1']);
end


t = linspace(0,t_end);
x = linspace(-el/2,el/2,xstep);


%Create storage variables for final spatial distributions
% .. one row for each gamma value
% .. one column for each spatial gridpoint
% .. one matrix for each set of initial conditions
fStore = zeros(gammasize,size(x,2),gammasize+1);
uStore = zeros(size(fStore));
l2Store = zeros(size(fStore));
hab1Store = zeros(size(fStore));
hab2Store = zeros(size(fStore));
solchecku = zeros(size(fStore));


%Create storage variables for initial spatial distributions
fStore_i = zeros(gammasize,size(x,2),gammasize+1);
uStore_i = zeros(size(fStore));
```

```matlab
l2Store_i = zeros(size(fStore));

%Create storage variables for integrated fishery data
% .. one row for each gamma value
% .. one column for each set of initial conditions
IntProfStore = zeros(gammasize,gammasize+1);
lrfracStore = zeros(size(IntProfStore));
regfracStore = zeros(size(IntProfStore));
solcheckmax = zeros(size(IntProfStore));
solcheckmin = zeros(size(IntProfStore));
runtimekeeper = zeros(size(IntProfStore));

%First run: use random initial conditions
disp('Beginning run set.  Initial conditions randomized.')
for i = 1:gammasize
    if gammavary == 0
        gamma_0 = variedgamma(i);
        atlargegamma = variedgamma(i);
    elseif gammavary == 1
        gamma_1 = variedgamma(i);
        atlargegamma = variedgamma(i);
    end
    [sol,u,lambda2,Effort,Profit,IntProfit,lrlength,lrfrac,reglength,...
     regfrac,RunTime]=SoleOwner_randIC(gamma_0,gamma_1,w_0,w_1,p,x,el,t);
    %Store run results
    fStore(i,:,1) = Effort(end,:);
    fStore_i(i,:,1) = Effort(1,:);
    uStore(i,:,1) = u(end,:);
    uStore_i(i,:,1) = u(1,:);
    l2Store(i,:,1) = lambda2(end,:);
    l2Store_i(i,:,1) =lambda2(1,:);
    hab1Store(i,:,1) = sol(end,:,3);
    hab2Store(i,:,1) = sol(end,:,4);
    IntProfStore(i,1) = IntProfit;
```

```matlab
        lrfracStore(i,1) = lrfrac;
        regfracStore(i,1) = regfrac;
        runtimekeeper(i,1) = RunTime;
        %Perform equilibrium check
        solchecku(i,:,1) = sol(end,:,1) - sol(end-1,:,1);
        checkmax = max(solchecku(i,:,1));
        checkmin = min(solchecku(i,:,1));
        solcheckmax(i,1) = checkmax;
        solcheckmin(i,1) = checkmin;
        %Print commentary on the run
        disp(['  gamma: ' num2str(atlargegamma) ', Running Time: '...
            num2str(RunTime) ', Solution errors: ' num2str(checkmax) ...
            ' to ' num2str(checkmin)])
        save(filenamer)
end


%This variable holds the initial conditions for non-random runs
starter = zeros(1,size(x,2),4);


%Subsequent runs: initial conditions from previous results
for i = 1:gammasize    %this is the 3rd matrix dimension, i.e.
                        %starting conditions
    disp(['Beginning run set with initial conditions from gamma_1 = '...
        num2str(variedgamma(i))])
    %Read in the initial conditions from the randomized result
    starter(1,:,1) = uStore(i,:,1);
    starter(1,:,2) = l2Store(i,:,1);
    starter(1,:,3) = hab1Store(i,:,1);
    starter(1,:,4) = hab2Store(i,:,1);


    for j = 1:size(gamma_1_set,2)   %this is the 1st matrix dimension,
                                     %i.e. gamma_1 value

        if gammavary == 0
            gamma_0 = variedgamma(i);
```

```
            atlargegamma = variedgamma(i);
        elseif gammavary == 1
            gamma_1 = variedgamma(i);
            atlargegamma = variedgamma(i);
        end
        [sol,u,lambda2,Effort,Profit,IntProfit,lrlength,lrfrac,...
        reglength,regfrac,RunTime]=SoleOwner_altIC(starter,gamma_0,...
        gamma_1,w_0,w_1,p,x,el,t);
        %Store run results
        fStore(j,:,i+1) = Effort(end,:);
        fStore_i(j,:,i+1) = Effort(1,:);
        uStore(j,:,i+1) = u(end,:);
        uStore_i(j,:,i+1) = u(1,:);
        l2Store(j,:,i+1) = lambda2(end,:);
        l2Store_i(j,:,i+1) =lambda2(1,:);
        hab1Store(j,:,i+1) = sol(end,:,3);
        hab2Store(j,:,i+1) = sol(end,:,4);
        IntProfStore(j,i+1) = IntProfit;
        lrfracStore(j,i+1) = lrfrac;
        regfracStore(j,i+1) = regfrac;
        runtimekeeper(j,i+1) = RunTime;
        %Perform equilibrium check
        solchecku(j,:,i+1) = sol(end,:,1) - sol(end-1,:,1);
        checkmax = max(solchecku(j,:,i+1));
        checkmin = min(solchecku(j,:,i+1));
        solcheckmax(j,i+1) = checkmax;
        solcheckmin(j,i+1) = checkmin;
        %Print commentary on the run
        disp(['  gamma: ' num2str(atlargegamma) ', Run Time: '...
            num2str(RunTime) ', Solu. errors: ' num2str(checkmax)...
            ' to ' num2str(checkmin)])
        save(filenamer)
    end
end
```

B.2.2 Sole Owner Model with Random Initial Conditions

```
%Population—Scale Fishery Model of Habitat Effects
%Code written February 25, 2010 by Holly V Moeller

%This model describes a fished population in which fishing intensity
%modifies fish reproductive rate and mortality rate both directly and
%mediated through density dependence.  It takes the perspective of a
%sole owner, who has jurisdiction over a habitat of fixed length and
%optimizes effort distribution to maximize profit.

%This model is called by "Run_SoleOwner", in which the parameters are
%named and described.

%This code was written on February 25, 2010, based on work by H. Moeller
%and M. Neubert.
%Subsequent Modifications:

function [sol,u,lambda2,Effort,Profit,IntProfit,lrlength,lrfrac,...
    reglength,regfrac,RunTime]=SoleOwner_randIC(gamma_0,gamma_1,w_0,...
    w_1,p,x,el,t)
tic;    %Record total run time

%Find solution by simulating model forward with PDE solver:
sol = pdepe(0,@pdefcn,@pdeic,@pdebc,x,t);
%Each row of sol represents a timepoint; each column a value of x
%Sol's third dimension follows assigment in the pdepe function.

%Extract solution components:
u = sol(:,:,1);             %Fish population biomass
lambda2 = sol(:,:,2);       %Shadow cost of leaving stock
Effort = zeros(size(u));    %Backcalculates effort based on shadow price
for j = 1:size(Effort,1)    %and biomass density
```

```matlab
    for k = 1:size(Effort,2)
        Effort(j,k)=fso([u(j,k),lambda2(j,k)]);
    end
end
Eff = Effort(end,:);
Profit = p.*u.*Effort - Effort.*(w_0+w_1*Effort);
IntProfit = trapz(x,Profit(end,:));


%Calculate fraction of habitat in reserve
crop = zeros(size(x));
crop2 = zeros(size(x));
for ressize = 1:size(x,2)
    if Eff(ressize) == 0
        crop(ressize) = 1;   %Notes location as part of reserve
        eval3 = p*u(end,ressize)-w_0; %eval3 Checks to see if reserve
                                      %would be fished in open-access case.
        if eval3 > 0
            crop2(ressize)=1; %Notes location must be regulated/managed
        else
            crop2(ressize)=0; %Notes location has too few fish to be fished
                              %profitably in sole owner or open access case.
        end
    else
        crop(ressize) = 0;
        crop2(ressize) = 0;
    end
end
lrlength = trapz(x,crop);   %Measures length of all areas with no effort.
lrfrac = lrlength/el;       %Calculates frac. of total habitat in reserve.
reglength = trapz(x,crop2); %Measures length of "managed" reserve
regfrac = reglength/el;     %Calculates frac. of habitat in managed res.


%System of PDEs describing fishery dynamics
    function [c,g,s] = pdefcn(x,t,y,DyDx)
```

```matlab
        c = [1,1,1,1];
        g = [DyDx(1),DyDx(2),0,0];
        f_so = fso(y);
        s1 = (y(3)-y(4).*y(1)).*y(1)-f_so.*y(1);     %Biomass density
        s2 = p*f_so+y(2).*(y(3)-2*y(1)*y(4)-f_so);   %Shadow price of stock
        s3 = .5*(1-gamma_0*f_so-y(3));   %Density-independent sensitivity
        s4 = .5*(1+gamma_1*f_so-y(4));   %Density-dependent sensitivity
        s = [s1,s2,s3,s4];
    end
%Initial conditions: randomized
    function [y0] = pdeic(xi)
        y0 = [0.5*(1+(2*rand-1)),0.5*(1+(2*rand-1)),.01,.01];
    end
%Dirichlet boundary conditions: biomass density goes to zero at the habitat
%edges; flux across the boundaries is allowed.
    function [pl,ql,pr,qr] = pdebc(xl,yl,xr,yr,t)
        pl = [yl(1),yl(2),0,0];
        ql = [0,0,1,1];
        pr = [yr(1),yr(2),0,0];
        qr = [0,0,1,1];
    end
%Sole owner maximization of effort, from Hamiltonian analysis
    function z = fso(y)
        fstar = (p*y(1)-w_0-y(2)*(gamma_0*y(1)+gamma_1*y(1)*y(1)+y(1)))/2/w_1;
        z = max(0,fstar);
    end


%Biomass density and the shadow price of stock should be positive for all
%timepoints and locations. However, when random initial conditions are
%used, the first few timepoints can contain transient negative values.
%Therefore, to verify that all u's and lambada 2's are greater than zero,
%we look only over the last 97 timepoints:
if any(any(u<0)) > 0
    disp('Alert!  Negative u.')
```

```matlab
        disp(['w_0 =' num2str(w_0) ', \gamma_0 =' num2str(gamma_0) ...
            ', \gamma_1 =' num2str(gamma_1)])
end
if any(any(lambda2<0)) > 0
    disp('Alert! Negative \lambda_2.')
    disp(['w_0 =' num2str(w_0) ', \gamma_0 =' num2str(gamma_0) ...
        ', \gamma_1 =' num2str(gamma_1)])
end

RunTime = toc;
end
```

B.2.3   Sole Owner Model with Alternate Initial Conditions

```matlab
%Population—Scale Fishery Model of Habitat Effects
%Code written February 25, 2010

%This model describes a fished population in which fishing intensity
%modifies fish reproductive rate and mortality rate both directly and
%mediated through density dependence.  It takes the perspective of a
%sole owner, who has jurisdiction over a habitat of fixed length and
%optimizes effort distribution to maximize total profit.

%This model is called by "Run_SoleOwner", in which the parameters are
%named and described.

%This code was written on February 25, 2010, based on work by H. Moeller
%and M. Neubert.

function [sol,u,lambda2,Effort,Profit,IntProfit,lrlength,lrfrac,...
    reglength,regfrac,RunTime]=SoleOwner_altIC(starter,gamma_0,gamma_1,...
    w_0,w_1,p,x,el,t)
tic;    %Track run time

%Find solution by simulating model forward with PDE solver:
sol = pdepe(0,@pdefcn,@pdeic,@pdebc,x,t);
%Each row of sol represents a timepoint; each column a value of x
%Sol's third dimension follows assigment in the pdepe function.

%Extract solution components:
u = sol(:,:,1);              %Fish population biomass
lambda2 = sol(:,:,2);        %Shadow cost of leaving stock
Effort = zeros(size(u));     %Effort is back—calculated using fso function
for j = 1:size(Effort,1)
    for k = 1:size(Effort,2)
```

```matlab
            Effort(j,k)=fso([u(j,k),lambda2(j,k)]);
    end
end
Eff = Effort(end,:);
Profit = p.*u.*Effort - Effort.*(w_0+w_1*Effort);
IntProfit = trapz(x,Profit(end,:));


%Calculate fraction of habitat in reserve:
crop = zeros(size(x));
crop2 = zeros(size(x));
for ressize = 1:size(x,2)
    if Eff(ressize) == 0
        crop(ressize) = 1;          %Notes location as part of reserve
        eval3 = p*u(end,ressize)-w_0; %eval3 Checks to see if reserve
                                    %would be fished in open-access case.
        if eval3 > 0
            crop2(ressize)=1; %Notes location must be regulated/managed
        else
            crop2(ressize)=0; %Notes location has too few fish to be fished
                                %profitably in sole owner or open access case.
        end
    else
        crop(ressize) = 0;
        crop2(ressize) = 0;
    end
end
lrlength = trapz(x,crop);   %Measures length of all areas with zero effort.
lrfrac = lrlength/el;       %Calculates frac. of total habitat in reserve.
reglength = trapz(x,crop2); %Measures length of "managed" reserve
regfrac = reglength/el;     %Calculates frac. of total hab. in managed res.


%System of Partial Differential Equations describing fishery dynamics
    function [c,g,s] = pdefcn(x,t,y,DyDx)
        c = [1,1,1,1];
```

```matlab
        g = [DyDx(1),DyDx(2),0,0];
        f_so = fso(y);
        s1 = (y(3)-y(4).*y(1)).*y(1)-f_so.*y(1);      %Stock biomass
        s2 = p*f_so+y(2).*(y(3)-2*y(1)*y(4)-f_so);  %Shadow price of stock
        s3 = .5*(1-gamma_0*f_so-y(3));   %Density-independent sensitivity
        s4 = .5*(1+gamma_1*f_so-y(4));   %Density-dependent sensitivity
        s = [s1,s2,s3,s4];
    end
%Initial conditions: taken from previous run data
    function [y0] = pdeic(xi)
        if exist('starter','var')   %If previous run's data is present
            y0 = [pdeval(0,x,starter(1,:,1),xi); ...
                 pdeval(0,x,starter(1,:,2),xi); ...
                 pdeval(0,x,starter(1,:,3),xi); ...
                 pdeval(0,x,starter(1,:,4),xi)];
        else    %Otherwise, use random initial conditions
            y0 = [0.5*(1+(2*rand-1)),0.5*(1+(2*rand-1)),.01,.01];
        end
    end
%Dirichlet boundary conditions: biomass density goes to zero at habitat
%boundaries, but flux across the habitat edge is allowed. Fish that exit
%the habitat are considered lost to the system.
    function [pl,ql,pr,qr] = pdebc(xl,yl,xr,yr,t)
        pl = [yl(1),yl(2),0,0];
        ql = [0,0,1,1];
        pr = [yr(1),yr(2),0,0];
        qr = [0,0,1,1];
    end
%Sole owner maximization of effort, from Hamiltonian analysis.
    function z = fso(y)
        fstar = (p*y(1)-w_0-y(2)*(gamma_0*y(1)+gamma_1*y(1)*y(1)...
            +y(1)))/2/w_1;
        z = max(0,fstar);
    end
```

```matlab
%Biomass density and the shadow price of stock should be positive for all
%timepoints and locations. However, when random initial conditions are
%used, the first few timepoints can contain transient negative values.
%Therefore, to verify that all u's and lambada 2's are greater than zero,
%we look only over the last 97 timepoints:
if any(any(u(3:end,:)<0)) > 0
    disp('Alert!  Negative u.')
    disp(['w_0 =' num2str(w_0) ', \gamma_0 =' num2str(gamma_0)...
        ', \gamma_1 =' num2str(gamma_1)])
end
if any(any(lambda2(3:end,:)<0)) > 0
    disp('Alert! Negative \lambda_2.')
    disp(['w_0 =' num2str(w_0) ', \gamma_0 =' num2str(gamma_0)...
        ', \gamma_1 =' num2str(gamma_1)])
end


RunTime = toc;
end
```

B.2.4 Limited Management: Calling the Tax/Reserve script

```
%Tax and Defend or Tax Only Management Model
%Code written by Holly V. Moeller on April 7 2010
%Subsequent Modifications:  4/11/2010 -- HVM added code to choose range
%                                       of tax levels based on results of previous lr
%                                       4/15/2010 -- HVM converted lr_set to a
%                                       calculation based on the number of intervals
%                                       in x, to hopefully smooth out the data points

%When tax is not spatially explicit, a manager must choose a fixed tax
%per unit effort to apply over the entire habitat.  The manager may also
%choose to distribute reserves throughout the habitat (i.e. designate
%"no take" areas; in the model, we do this by setting price = 0).

%Outside the reserve, we have the "open access" case, where total
%revenue is equal to total costs.

%The manager's goal is to set the tax level to maximize revenue. Because
%it is not possible to write differential equations describing this
%maximization, we discretize a range of tax levels and reserve lengths,
%and solve reserve/tax combinations analytically. We then choose the tax
%revenue-maximizing combination.

%Note that this run script works for either Second-Best (Tax and Defend)
%or Third-Best (Tax Only) management strategies because Tax Only is a
%special case of Tax and Defend management, in which reserve length = 0.

%FILENAME:
filenamer = 'OptTax_el-5_g0-0_g1-0_w0-pt01_xstep';

%Choose parameter space:
gamma_0 = 0;    %Habitat sensitivity to density-independent mort. effects
```

```matlab
gamma_1 = 0;      %Habitat sensitivity to density—dependent mortality effects
w_0 = .01;        %Cost per unit effort
w_1 = .001;       %Marginal cost per unit effort
el = 5;           %Habitat length
xstep = 100*(el+5);%Number of habitat locations at which to store results
t_end = 10000;    %Length of time to run simulation forward to equilibrium
p = 1;            %Price per unit catch
taxmax = 0.8;     %Upper bound for tax per unit effort


x = linspace(-el/2, el/2, xstep);    %Vector of locations to record data
t = linspace(0,t_end);                %Vector of timepoints to record data


%Determine the set of reserve lengths: because we record data only for
%the spatial locations of the vector x, we must choose the reserve length
%carefully so that the boundaries of the reserve fall just outside the
%nearest recorded x—coordinate. Generally, we choose fifty—one possible
%reserve lengths: lr = 0 (e.g., Tax Only), and lr = 2%,4%,...,100% of
%habitat.
xstep_inc = round((xstep - 1)/100);
lrstep_set = [0, (1:50)*2*xstep_inc+1];
lr_set = el*lrstep_set/xstep;


%Create the set of tax levels, again stepping up by 2%:
tax_set = [0, (1:50)*taxmax/50];



% %Create holding matrices for results for final spatial distributions of
% effort and population.  Each row holds results for a particular tax
% level. Each column holds results for a particular spatial coordinate.
% There is one matrix for each reserve length.
fStore = zeros(size(tax_set,2),size(x,2),size(lr_set,2));    %Store effort
uStore = zeros(size(fStore));                                %Store pop'n
yStore = zeros(size(fStore));                                %Store yield
solchecku = zeros(size(fStore));                             %Store errors
```

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```matlab
% ... storing point results
% ... rows = each tax level
% ... columns = each reserve length
runtimekeeper = zeros(size(tax_set,2),size(lr_set,2)); %Store runtime
maxprofkeeper = zeros(size(runtimekeeper));            %Store prof error
IntTaxStore = zeros(size(runtimekeeper));              %Total tax revenue
IntPopStore = zeros(size(runtimekeeper));              %Total pop'n size
IntYieldStore = zeros(size(runtimekeeper));            %Total yield
IntEffStore = zeros(size(runtimekeeper));              %Total effort
solcheckmax = zeros(size(runtimekeeper));
solcheckmin = zeros(size(runtimekeeper));


% ... storing optimal result for a particular reserve length
optf_lr = zeros(size(lr_set,2),size(x,2));             %Effort distrib.
optu_lr = zeros(size(optf_lr));                        %Stock distrib.
optYield_lr = zeros(size(optf_lr));                    %TOtal yield
optRev_lr = zeros(size(lr_set));                       %Tax revenue
optEff_lr = zeros(size(lr_set));                       %Total effort
optPop_lr = zeros(size(lr_set));                       %Total stock
opttax_lr = zeros(size(lr_set));                       %Tax per unit effort
optctr_lr = zeros(size(lr_set));                       %Holding variable


%Run through, finding maximum revenue for each reserve length.
%Note that this code works on the assumption that the plot of total
%revenue on tax level is concave down for any given reserve length ——
%that is, there is only one choice of tax that maximizes revenue. Thus,
%after the first calculation (for reserve length = 0, or the "Tax Only"
%management strategy), we calculate solutions only for a range of 7 tax
%levels adjacent to the tax level that produced the most recent optimum.
%This reduces run time considerably.
newstart = 1;
for j = 1:size(lr_set,2)   %Iterate for each reserve length...
    lr = lr_set(j);
```

```matlab
disp(['Beginning run set: reserve case; lr = ' num2str(lr) '; el = '...
    num2str(el) ])
if newstart == 1
    %If a run is just beginning, or a previous run yielded multiple
    %results
    disp('Fresh start!')
    for i = 1:size(tax_set,2)    %Iterate for all tax levels...
        taxlevel = tax_set(i);
        %Run the model:
        [u,Effort,Profit,RunTime]=TaxModel_randIC(gamma_0,...
            gamma_1,w_0,w_1,x,el,lr,t,taxlevel,p);
        %Store run results:
        fStore(i,:,j) = Effort(end,:);
        uStore(i,:,j) = u(end,:);
        %Check to see that the model has reached equilibrium:
        solchecku(i,:,j) = u(end-1,:) - u(end,:);
        solcheckmax(i,j) = max(solchecku(i,:,j));
        solcheckmin(i,j) = min(solchecku(i,:,j));
        %Check to see that managed open access criterion is met:
        maxprofkeeper(i,j) = max(max(abs(Profit)));
        %Record running time:
        runtimekeeper(i,j) = RunTime;
        %Calculate additional results:
        for k = 1:size(x,2)
            yStore(i,k,j) = fStore(i,k,j)*uStore(i,k,j);
        end
        IntTaxStore(i,j) = taxlevel*trapz(x,Effort(end,:));
        IntPopStore(i,j) = trapz(x,u(end,:));
        IntYieldStore(i,j) = trapz(x,yStore(i,:,j));
        IntEffStore(i,j) = trapz(x,Effort(end,:));
        disp(['Revenue: ' num2str(IntTaxStore(i,j)) '  tax: '...
            num2str(taxlevel) ', lr: ' num2str(lr) ', time: '...
            num2str(RunTime) ', Err: ' num2str(solcheckmax(i,j))...
            '-' num2str(solcheckmin(i,j)) ', Prof Err: ' ...
```

```
            num2str(maxprofkeeper(i,j)) ', Res Err: ' ...
            num2str(reglengthCheck(i,j)) ])
    end

    %Determine optimal results for the given reserve length
    optRev_lr(j) = max(IntTaxStore(:,j));    %The maximum tax revenue
    counter = 0;      %Tracks the number of revenue maxima
    itrack = [0, 0];
    for i = 1:size(tax_set,2)
        if abs(IntTaxStore(i,j) - optRev_lr(j)) < 0.00001
            counter = counter + 1;
            opttax_lr(j) = tax_set(i);
            optctr_lr(j) = i;
            for k = 1:size(x,2)
                optf_lr(j,k) = fStore(i,k,j);
                optu_lr(j,k) = uStore(i,k,j);
            end
            if counter == 1
                itrack(1) = i;
            elseif counter == 2
                itrack(2) = i;
            end
        end
    end

    if counter == 1
        newstart = 2;    %For next run, use bounded tax values
        %Set range of tax values to test for next value of lr
        lowbound = optctr_lr(j) - 3;
        highbound = optctr_lr(j) + 3;
        if lowbound < 1                      %Makes sure tax > 0
            lowbound = 1;
        end
        if highbound > size(tax_set,2)    %Makes sure tax < max tax
```

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```matlab
                    highbound = size(tax_set,2);
            end
        elseif counter == 2
            Δ = itrack(2) - itrack(1);
            if Δ < 2    %i.e., if maxima are adjacent
                lowbound = itrack(1) - 3;
                highbound = itrack(2) + 3;
                if lowbound < 1
                    lowbound = 1;
                end
                if highbound > size(tax_set,2)
                    highbound = size(tax_set,2);
                end
                disp(['ALERT: two closeby rev maxima. Δ: '...
                    num2str(Δ) ])
            else
                disp(['ALERT: two widely spread rev maxima. Δ: '...
                    num2str(Δ) ])
                newstart = 1;    %start fresh!
            end
        else
            disp(['ALERT: multiple revenue maxima. lr: ' num2str(lr)...
                'counter: ' num2str(counter) ])
            newstart = 1;        %start fresh!
        end
        save(filenamer) %Save frequently!
    else    %When a maximum has been found for the previous lr
        disp('Using bounded tax values!')
        for i = lowbound : highbound    %Iterate for nearby tax levels
            taxlevel = tax_set(i);
            %Run the model:
            [u,Effort,Profit,RunTime]=TaxModel_randIC(gamma_0,...
                gamma_1,w_0,w_1,x,el,lr,t,taxlevel,p);
            %Store run results:
```

```matlab
        fStore(i,:,j) = Effort(end,:);
        uStore(i,:,j) = u(end,:);
        %Check to see that the model has reached equilibrium:
        solchecku(i,:,j) = u(end-1,:) - u(end,:);
        solcheckmax(i,j) = max(solchecku(i,:,j));
        solcheckmin(i,j) = min(solchecku(i,:,j));
        %Check to see that managed open access criterion is met:
        maxprofkeeper(i,j) = max(max(abs(Profit)));
        %Record running time:
        runtimekeeper(i,j) = RunTime;
        %Calculate additional results:
        for k = 1:size(x,2)
            yStore(i,k,j) = fStore(i,k,j)*uStore(i,k,j);
        end
        IntTaxStore(i,j) = taxlevel*trapz(x,Effort(end,:));
        IntPopStore(i,j) = trapz(x,u(end,:));
        IntYieldStore(i,j) = trapz(x,yStore(i,:,j));
        IntEffStore(i,j) = trapz(x,Effort(end,:));
        disp(['Revenue: ' num2str(IntTaxStore(i,j)) '  tax: '...
            num2str(taxlevel) ', lr: ' num2str(lr) ', time: '...
            num2str(RunTime) ', Err: ' num2str(solcheckmax(i,j))...
            '-' num2str(solcheckmin(i,j)) ', Prof Err: '...
            num2str(maxprofkeeper(i,j)) ', Res Err: ' ...
            num2str(reglengthCheck(i,j)) ])
    end

    %Determine optimal results for the given reserve length
    optRev_lr(j) = max(IntTaxStore(:,j));   %The maximum tax revenue
    counter = 0;     %Tracks the number of revenue maxima
    itrack = [0, 0];
    for i = 1:size(tax_set,2)
        if abs(IntTaxStore(i,j) - optRev_lr(j)) < 0.00001
            counter = counter + 1;
            opttax_lr(j) = tax_set(i);
```

```
            optctr_lr(j) = i;
            for k = 1:size(x,2)
                optf_lr(j,k) = fStore(i,k,j);
                optu_lr(j,k) = uStore(i,k,j);
            end
            if counter == 1
                itrack(1) = i;
            elseif counter == 2
                itrack(2) = i;
            end
        end
end


if counter == 1
    newstart = 2;    %For next run, use bounded tax values
    %Set range of tax values to test for next value of lr
    lowbound = optctr_lr(j) - 3;
    highbound = optctr_lr(j) + 3;
    if lowbound < 1                      %Makes sure tax > 0
        lowbound = 1;
    end
    if highbound > size(tax_set,2)    %Makes sure tax < max tax
        highbound = size(tax_set,2);
    end
elseif counter == 2
    Δ = itrack(2) - itrack(1);
    if Δ < 2    %i.e., if maxima are adjacent
        lowbound = itrack(1) - 3;
        highbound = itrack(2) + 3;
        if lowbound < 1
            lowbound = 1;
        end
        if highbound > size(tax_set,2)
            highbound = size(tax_set,2);
```

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```matlab
            end
            disp(['ALERT: two closeby rev maxima. Δ: '...
                num2str(Δ) ])
        else
            disp(['ALERT: two widely spread rev maxima. Δ: '...
                num2str(Δ) ])
            newstart = 1;   %start fresh!
        end
    else
        disp(['ALERT: multiple revenue maxima. lr: ' num2str(lr)...
            'counter: ' num2str(counter) ])
        newstart = 1;      %start fresh!
    end
    save(filenamer) %Save frequently!
    end
end
```

B.2.5   Tax and Defend (or Tax Only) Model

```
%Tax and Defend Fishery Management Strategy
%Code written on April 7, 2010 by H. Moeller


%This code should be called by "Run_TaxDefend" or "Run_TaxOnly" scripts.


%Subsequent Modifications:
%    April 10, 2010 —— Random starting conditions


%Here, we numerically solve a partial differential equation for fish
%stock biomass density under tax and defend management for a variety of
%biological and economic parameter values.


%Under Tax and Defend management, a single manager sets the size of a
%central reserve (lr), and a tax per unit effort (taxlevel) which is
%enforced on all fishing effort outside of the reserve. Outside the
%reserve, fishing effort enters until direct profits (from the sale of
%fish) are completely dissapated (e.g. "managed open access"):
%    price per unit catch * effort * stock density = cost per unit effort
%    for every location outside the reserve.


%The single manager's goal is to maximize tax revenue:
%    Tax Revenue = tax per unit effort * total effort


%This code takes input model parameters for:
%    habitat length (el),
%    a vector of x—coordinates for which to record data (x),
%    habitat %sensitivity (gamma_1 and gamma_0),
%    fishing costs (w_0 and w_1),
%    tax per %unit effort (taxlevel),
%    price per unit catch (p),
%    reserve length (lr), and
```

```matlab
%     the length of time to run the simulation forward (t)
%It outputs the tax revenue—maximizing distribution of effort (Effort)
%and stock biomass density (u).


function [u,Effort,Profit,RunTime]=TaxModel_randIC(gamma_0,gamma_1,...
    w_0,w_1,x,el,lr,t,taxlevel,p)
tic; %Track computational time


%Find a solution by simulating the model forward with a PDE solver
sol = pdepe(0,@pdefun,@icfun,@bcfun,x,t);


%Extract solution components
u = sol(:,:,1); %Biomass density at every location in the habitat
                %specified by the vector, x. "u" is a matrix with a row
                %for every timepoint, t, and a column for every
                %location, x.
%Compute effort and profit at every timepoint and location
Effort = zeros(size(u));
Profit = zeros(size(u));
for j = 1:size(Effort,1)
    for k = 1:size(Effort,2)
        Effort(j,k)=foa(u(j,k),x(k));    %Refer to effort function below
        Profit(j,k)= pricer(x(k))*u(j,k)*Effort(j,k)...
            —Effort(j,k)*(taxlevel+w_0+w_1*Effort(j,k));
    end
end


%Check that the managed open access criterion is met
IntProfit = trapz(x,Profit(end,:));
if IntProfit > .0005
    disp('Managed open access criterion failed: profit too high!')
end


%In our model, reserves are enforced by setting price = 0 inside the
```

```matlab
%reserve, and price = 1 outside the reserve.
    function price = pricer(xi)
        if lr == 0
            price = p*1;
        else
            price = p*(abs(xi) > (lr/2));
        end
    end


%Tax revenue is maximized subject to a PDE describing stock biomass:
    function [c,g,s] = pdefun(xi,t,u,dudx)
        c = 1;
        g = dudx;
        fu = foa(u,xi);
        s = ((1-gamma_0.*fu) - (1+gamma_1.*fu).*u(1)).*u(1) - fu.*u(1);
    end


%At t = 0, we initialize the simulation with random starting conditions
    function u_0 = icfun(xi)
        u_0 = 0.5*(1+(2*rand-1));
    end


%We use Dirichlet boundary conditions: at the habitat's edge, stock
%density goes to zero, but movement by diffusion is permitted. Fish may
%swim out of the habitat, but then they are considered "lost" to the
%system.
    function [pl,ql,pr,qr] = bcfun(xl,ul,xr,ur,t)
        pl = ul(1);
        pr = ur(1);
        ql = 0;
        qr = 0;
    end


%Optimal effort is a function of stock density and economic parameters. We
```

```matlab
%constrain effort to be greater than or equal to zero.
    function z = foa(u,xi)
        a = (pricer(xi).*u(1)-taxlevel - w_0)/w_1;
        z = max(a,0);
    end


%We expect biomass density to be nonnegative for all locations at all
%times. However, because we use random initial conditions, sometimes
%transient negative values occur in the early timesteps. So, we check
%for negative biomass densities at any position in the habitat, at any
%timepoint after the first two recorded.
if any(any(u(3:end,:)<0)) > 0
    disp(['Alert!  Negative u.  ***  w_0 =' num2str(w_0)...
        ', \gamma_0 =' num2str(gamma_0) ', \gamma_1 =' num2str(gamma_1)])
end


RunTime = toc;  %It's always handy to track the runtime of these scripts.
end
```

Bibliography

[1] Armstrong, C.W. 2007. A note on the ecological-economic modelling of marine reserves in fisheries. *Ecol. Econ* 62: 242-250.

[2] Armstrong, C.W. and A. Skonhoft. 2006. Marine reserves: a bio-economic model with asymmetric density dependent migration. *Ecol. Econ.* 57: 466-476.

[3] Costello, C. and S. Polasky. 2008. Optimal harvesting of stochastic spatial resources. *J. Environ. Econ. Mgmt.* 56: 1-18.

[4] Fogarty, M.J. 2005. Impacts of fishing activities on benthic habitat and carrying capacity: Approaches to assessing and managing risk. *Am. Fisheries Society Symposium* 41: 769-784.

[5] Gårdmark, A., N. Jonzén, and M. Mangel. 2006. Density-dependent body growth reduces the potential of marine reserves to enhance yields. *J. Appl. Ecol.* 43: 61-69.

[6] Gerber, L.R. et al. 2003. Population models for marine reserve design: a retrospective and prospective synthesis. *Ecol. Appl.* 13: 847-864.

[7] Gerber, L.R. et al. 2005. The role of dispersal and demography in determining the net efficacy of marine reserves. *Can. J. Fish. Aquat. Sci* 62: 863-871.

[8] Halpern, B.S. and R.R. Warner. 2002. Marine reserves have rapid and lasting effects. *Ecol. Lett.* 5: 361-366.

[9] Hannesson, R. 1998. Marine reserves: What would they accomplish? *Marine Resource Economics* 13: 159-170.

[10] Hiddink, J.G. et al. 2006a. Predicting the effects of area closures and fishing effort restrictions on the production, biomass, and species richness of benthic invertebrate communities. *ICES J. Marine Sci.* 63: 822-830.

[11] Hiddink, J.G. et al. 2006b. Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. *Can. J. Fish. Aquat. Sci.* 63: 721-736.

[12] Hiddink, J.G., S. Jennings, and M.J. Kaiser. 2007. Assessing and predicting the relative ecological impacts of disturbance on habitats with different sensitivities. *J. Appl. Ecol.* 44: 405-413.

[13] Homans, F.R. and J.E. Wilen. 1997. A model of regulated open access resource use. *J. Environ. Econ. Mgmt.* 32: 1-21.

[14] Kellner, J.B., et al. 2007. Fishing the line near marine reserves in single and multispecies fisheries. *Ecol. Appl.* 17: 1039-1054.

[15] Lester, S.E. et al. 2009. Biological effects within no-take marine reserves: a global synthesis. *MEPS* 384: 33-46.

[16] Lindholm, J.B. et al. 2001. Modeling the effects of fishing and implications for the design of marine protected areas: Juvenile fish responses to variations in seafloor habitat. *Conserv. Biol* 15: 424-437.

[17] Mangel, M. 2000. Trade-offs between fish habitat and fishing mortality and the role of reserves. *Bull. Mar. Sci.* 66: 663-674.

[18] Neubert, M.G. 2003. Marine reserves and optimal harvesting. *Ecology Letters* 6: 843-849.

[19] Neubert, M.G. and G.E. Herrera. 2008. Triple benefits from spatial resource management. Theor. Ecol. 1: 5-12.

[20] NRC (National Research Council) Committee on the Evaluation, Design, and Monitoring of Marine Reserves and Protected Areas in the United States, Ocean Studies Board. 2001. Marine Protected Areas: Tools for sustaining ocean ecosystems. National Academy Press, Washington, D.C., 288p.

[21] Sanchirico, J.N. et al. 2006. When are no-take zones an economically optimal fishery management strategy? *Ecol. Appl.* 16: 1643-1659.

[22] Sinclair, A.R.E. 1989. Population Regulation in Animals. In Ecological Concepts. The contribution of ecology to an understanding of the natural world. pp. 197-241.

[23] Smith, M.D. and J.E. Wilen. 2003. Economic impacts of marine reserves: the importance of spatial behavior. *J. Environ. Econ. Mgmt.* 46: 183-206.

[24] Upton, H.F. and J.G. Sutinen. 2005. When do marine protected areas pay? An analysis of stylized fisheries. *Am. Fish. Soc. Symp.* 41: 745-757.

[25] White, C. and B.E. Kendall. 2007. A reassessment of equivalence in yield from marine reserves and traditional fisheries mangement. *Oikos* 116: 2039-2043.