

ON THE BIOECONOMICS OF MARINE RESERVES WHEN DISPERSAL EVOLVES

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Abstract

1
2 Marine reserves are an increasingly used and potentially contentious tool in fisheries manage-
3 ment. Depending upon the way that individuals move, no-take marine reserves can be necessary for
4 maximizing equilibrium rent in some simple mathematical models. The implementation of no-take
5 marine reserves often generates a redistribution of fishing effort in space. This redistribution of
6 effort, in turn, produces sharp spatial gradients in mortality rates for the targeted stock. Using
7 a two-patch model, we show that the existence of such gradients is a sufficient condition for the
8 evolution of an evolutionarily stable conditional dispersal strategy. Thus, the dispersal strategy
9 of the fish depends upon the harvesting strategy of the manager and vice versa. We find that an
10 evolutionarily stable optimal harvesting strategy (ESOHS)—one which maximizes equilibrium rent
11 given that fish disperse in an evolutionarily stable manner—never includes a no-take marine re-
12 serve. This strategy is economically unstable in the short run because a manager can generate more
13 rent by disregarding the possibility of dispersal evolution. Simulations of a stochastic evolutionary
14 process suggest that such a short-run, myopic strategy performs poorly compared to the ESOHS
15 over the long run, however, as it generates rent that is lower on average and higher in variability.

16 Keywords: *evolution of dispersal, evolutionarily stable strategy, fisheries management, marine pro-*
17 *tected areas, optimal harvesting.*

1 Introduction

No-take marine reserves are a type of “marine protected area” in which fishing is prohibited. Closed areas like marine reserves have been used to manage artisanal fisheries on small spatial scales for many years (Fogarty et al., 2000). The advent of geographical positioning systems (which make the possibility of enforcing closures more feasible (Pala, 2014)) combined with the decline of fish stocks, an increased demand for marine fish protein (FAO Fisheries Department, 2014), and a call for ecosystem-based management, have led not only to increased study of the efficacy of marine reserves but also to an increase in their implementation. Marine protected area coverage worldwide has increased by over 150% since 2003 (Toropova et al., 2010).

A number of studies have shown that marine reserves can contribute to the conservation of stocks and to the ecosystems that support them (e.g., Halpern and Warner, 2002; Halpern, 2003; Lester et al., 2009). Increases in individual size, biomass, population density and species diversity have been shown to increase subsequent to reserve establishment (see examples in, for example, Lester and Halpern, 2008).

The potential economic costs or benefits of reserves are less clear (Kaiser, 2005; White et al., 2008; Hart and Sissenwine, 2009; Fletcher et al., 2015, in press). Some modeling studies (e.g., Neubert, 2003; Sanchirico and Wilen, 2005; Sanchirico et al., 2006; Armstrong, 2007; Neubert and Herrera, 2008; Joshi et al., 2009; Moeller and Neubert, 2013) have shown that the establishment of marine reserves for conservation purposes does not necessarily require a reduction in economic productivity. Indeed, in some models reserves are necessary to maximize yield or sustainable rent. Others (including Polacheck, 1990; Quinn et al., 1993; Man et al., 1995; Holland and Brazee, 1996; Nowlis and Roberts, 1999; Guenette and Pitcher, 1999; Hastings and Botsford, 1999; Li, 2000; Pezzey et al., 2000; Sanchirico and Wilen, 2001; Apostolaki et al., 2002) have shown that reserves may be yield-neutral or produce minor improvements when compared with non spatial effort-control policies. In some cases, the establishment of a reserve decreases yield (Tuck and Possingham, 1994).

The optimality of reserves, then, would seem to depend both on the objective as well as the ecological and economic circumstances. One phenomena, however, emerges from all of these modeling studies, as well as from real-world observations (Fig. 1): the imposition of marine reserves can produce a radical redistribution of fishing effort in space. Effort is displaced from reserve areas

47 and frequently concentrates near their borders as harvesters attempt to catch the “spillover” from
48 the reserves. As a consequence, the establishment of marine reserves can produce sharp spatial
49 gradients in mortality (Neubert, 2003; Kellner et al., 2007; Joshi et al., 2009; Abbott and Haynie,
50 2012; Moeller and Neubert, 2013).

51 It is easy to imagine, that as a result of these gradients, there would be strong selective pressure
52 to evolve context-dependent dispersal (McPeck and Holt, 1992)—that is, low dispersal rates within
53 the reserve and high dispersal rates outside—or, equivalently, the ability for dispersing individuals
54 to detect and preferentially settle in better patches. Since the potential economic benefits of reserves
55 rely on dispersal of individuals from reserves into fished areas, evolution of dispersal might work
56 against the generation of sustainable rent.

57 In this paper we explore that possibility with the aid of a simple, “two-patch” model (Holt, 1985).
58 We begin by briefly demonstrating that, in the absence of evolution, reserves can be economically
59 optimal when the two patches are sufficiently different in either their biological or economic prop-
60 erties (Sanchirico et al., 2006). We then ask whether reserves are ever optimal (in the sense of
61 maximizing equilibrium rent) when dispersal evolves.

62 Our analysis of this second problem builds on the work of Law and Grey (1989) and Grey
63 (1993) who were perhaps the first to seriously investigate the interplay between harvest and evo-
64 lution, i. e., the inclusion of evolutionary change in the constrained optimization problem of the
65 resource manager. They developed the concept of an *evolutionarily stable optimal harvest strat-*
66 *egy (ESOHS)*¹—a harvesting strategy “which gives the greatest sustainable yield, after evolution
67 caused by cropping has taken place.” Law and Grey (1989) were particularly concerned with the
68 problem of how age-specific harvesting selects for changes in the age at maturity, so they developed
69 the ESOHS concept in the context of life-history theory (which generally ignores dispersal). We
70 extend their idea here to the evolution of dispersal in a spatially managed fishery and find that
71 evolution qualitatively changes the nature of the optimal distribution of fishing effort.

¹We prefer the pronunciation *ess-oh-ess* for this acronym.

72 **2 Model**

73 The model we use is similar to those of Clark (1990, pg. 337) and Sanchirico et al. (2006), both
 74 of which derive from the classic model of Gordon (1954). The model describes the dynamics of a
 75 stock distributed across two spatial locations, or “patches,” connected by dispersal. Each patch is
 76 characterized by an intrinsic rate of growth r_i and a carrying capacity k_i . Individuals leave a patch
 77 at a constant per capita rate m and enter a common pool of dispersers. From this pool a fraction
 78 ε (instantaneously) choose to settle into patch 1; the remaining fraction, $1 - \varepsilon$, settle in patch 2.
 79 In this sense, ε can be thought of as a disperser’s preference for patch 1. Patches are harvested at
 80 nonnegative patch-dependent effort rates E_i . If the population size of the stock in patch i is x_i ,
 81 this fishing effort generates yield at the rate $q_i E_i x_i$. The proportionality constants q_i are called the
 82 “catchability coefficients.”

83 Under this model, the dynamics of the stock in the two patches are given by the ordinary
 84 differential equations

$$\frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{k_1}\right) - m(1 - \varepsilon)x_1 + m\varepsilon x_2 - q_1 E_1 x_1, \quad (1)$$

$$\frac{dx_2}{dt} = r_2 x_2 \left(1 - \frac{x_2}{k_2}\right) + m(1 - \varepsilon)x_1 - m\varepsilon x_2 - q_2 E_2 x_2. \quad (2)$$

85 If the price of fish is p , and the cost per unit of effort in patch i is c_i , then the rent generated
 86 by harvesting is

$$\pi[E_1, E_2; \varepsilon] = \sum_{i=1}^2 (pq_i x_i - c_i) E_i. \quad (3)$$

87 At first, we concern ourselves with the case in which a manager is able to control the levels of effort
 88 in each of the patches (for example by limiting the number of boat-days available for fishing or by
 89 taxing effort) and does so with the objective of maximizing the rent, π , at equilibrium.

90 It is a simple matter to numerically calculate the equilibrium stock sizes from equations (1) and
 91 (2) for any combination of E_1 and E_2 . These can be substituted into formula (3) to determine the
 92 equilibrium rent. We call the effort levels that maximize the equilibrium rent E_i^* , the corresponding
 93 stock sizes x_i^* , and the maximum equilibrium rent π^* .

94 The optimal solution in patch i will fall into one of three categories depending upon the signs

95 of E_i^* and the marginal rent in patch i , $pq_i x_i^* - c_i$. If

- 96 1. $E_i^* > 0$, we say the patch is *fished*; if
- 97 2. $E_i^* = 0$ and $pq_i x_i^* - c_i \leq 0$, we say the patch is *unfished*; and if
- 98 3. $E_i^* = 0$ and $pq_i x_i^* - c_i > 0$, we say the patch is in *reserve*.

99 We distinguish between unfished and reserve patches because the latter would require enforcement
100 by the regulator—an individual harvester would have incentive to fish in that patch, but doing so
101 would reduce the total rent at equilibrium. In unfished patches the marginal rent is negative, and
102 rational harvesters (which we assume) avoid it of their own accord.

103 The optimal equilibrium effort levels in each patch are determined by the model parameters
104 (Fig. 2). When the patches are economically and ecologically identical, and dispersers settle indif-
105 ferently (i. e., $\varepsilon = 0.5$), the optimal strategy is to ensure that both patches are harvested at the
106 same rate (or not fished at all if $pq_i k_i - c_i \leq 0$). Asymmetric settlement, or differences in intrinsic
107 growth rates, carrying capacities, or harvest costs can result in the optimal closing of one patch
108 (blue and red regions of Fig. 2). For the rest of the paper, we will explore cases in which patch
109 1 is in one way (and only one way) better (for the harvesters) than patch 2; that is, all of the
110 inequalities

$$r_1 \geq r_2, \quad k_1 \geq k_2, \quad c_1 \leq c_2, \quad q_1 \geq q_2, \quad (4)$$

111 are satisfied and only one is satisfied as a strict inequality. This is the case for all of the parameter
112 combinations encompassed by Fig. 2 and subsequent figures.

113 3 Evolution of dispersal and the ESS

114 In general, the optimal harvesting effort, and thus the per capita mortality rate, in each patch
115 will differ. The dispersal strategy may evolve in response to this mortality gradient. Evolution,
116 in turn, affects optimal fishing strategies, including the optimality of reserves, through changes in
117 dispersal. Here, we consider the evolution of ε , the proportion of dispersers that settle into patch
118 1. We derive the evolutionarily stable strategy (ESS), $\hat{\varepsilon}$, the dispersal phenotype against which no
119 alternative phenotype can increase under selection. In this section, we find an expression for $\hat{\varepsilon}$ and

120 show that it is a “weak form ESS.” This ESS is also convergence-stable, making it an evolutionary
 121 attractor to which the population will converge in the long run.

122 3.1 Calculating the ESS

To determine $\hat{\varepsilon}$, we begin by considering a population composed of a single “resident” phenotype with dispersal preference ε . The equilibrium stock sizes, \bar{x}_1 and \bar{x}_2 , satisfy

$$\left[r_1 \left(1 - \frac{\bar{x}_1}{k_1} \right) - q_1 E_1 \right] \bar{x}_1 - m(1 - \varepsilon)\bar{x}_1 + m\varepsilon\bar{x}_2 = 0, \quad (5)$$

$$\left[r_2 \left(1 - \frac{\bar{x}_2}{k_2} \right) - q_2 E_2 \right] \bar{x}_2 + m(1 - \varepsilon)\bar{x}_1 - m\varepsilon\bar{x}_2 = 0. \quad (6)$$

123 We will find it useful to define α_i as the per capita growth rate, including fishing mortality, in patch
 124 i if it were isolated (i. e., if $m = 0$). That is,

$$\alpha_i = \left[r_i \left(1 - \frac{\bar{x}_i}{k_i} \right) - q_i E_i \right]. \quad (7)$$

125 α_i can be thought of as the fitness of an individual in patch i at equilibrium.

126 The phenotype that characterizes the resident population evolves through invasions (and se-
 127 quential replacement) by rare mutants—alternative phenotypes that appear at low frequencies.
 128 Mutants are identical to residents, save for their dispersal preference, which we will denote as ε' .
 129 A mutant’s fate depends on its *invasion fitness*—its initial growth rate in the resident population.
 130 When it first appears, the mutant is rare, and its effect on the resident’s population dynamics is
 131 negligible (Metz, 2008). Thus if x'_1 and x'_2 are the mutant populations in the two patches, their
 132 dynamics are initially given by the linear system

$$\frac{d}{dt} \begin{pmatrix} x'_1 \\ x'_2 \end{pmatrix} = \mathbf{A}' \begin{pmatrix} x'_1 \\ x'_2 \end{pmatrix} \quad (8)$$

133 where

$$\mathbf{A}' = \begin{pmatrix} \alpha_1 - m(1 - \varepsilon') & m\varepsilon' \\ m(1 - \varepsilon') & \alpha_2 - m\varepsilon' \end{pmatrix}. \quad (9)$$

134 The invasion fitness is then given by the dominant eigenvalue of \mathbf{A}' (which is always real):

$$\lambda' = \frac{1}{2} \left(\alpha_1 + \alpha_2 - m + \sqrt{(\alpha_1 - \alpha_2)^2 + 2(\alpha_1 - \alpha_2)(2\varepsilon' - 1)m + m^2} \right). \quad (10)$$

135 Note that the invasion fitness is a function of both the mutant phenotype and the resident phenotype
 136 (because the α 's depend upon the equilibrium population sizes of the resident, which, in turn depend
 137 on ε).

138 If the invasion fitness (10) is positive, the mutant can replace the resident, inducing evolutionary
 139 change; if negative, the mutant will be extirpated. An ESS, $\hat{\varepsilon}$, is a resident phenotype that cannot
 140 be replaced by any ε' , making it resistant to further evolution (Geritz et al., 1998). A condition
 141 that must be satisfied by any ESS is that the selection gradient $d\lambda'/d\varepsilon'$ vanishes when $\varepsilon' = \varepsilon = \hat{\varepsilon}$.
 142 Differentiating the invasion fitness (10) with respect to ε' and evaluating at $\varepsilon' = \varepsilon = \hat{\varepsilon}$ gives

$$\left. \frac{\partial \lambda'}{\partial \varepsilon'} \right|_{\varepsilon' = \varepsilon = \hat{\varepsilon}} = \frac{(\alpha_1 - \alpha_2)m}{\sqrt{(\alpha_1 - \alpha_2)^2 + 2(\alpha_1 - \alpha_2)(2\hat{\varepsilon} - 1)m + m^2}} = 0. \quad (11)$$

143 Since we have assumed that m is positive, a vanishing selection gradient (11) implies that
 144 $\alpha_1 = \alpha_2$; but, adding (5) and (6) we find that

$$\alpha_1 \bar{x}_1 + \alpha_2 \bar{x}_2 = \alpha_1 (\bar{x}_1 + \bar{x}_2) = 0. \quad (12)$$

145 Thus, when the resident population sizes are positive, $\alpha_1 = \alpha_2 = 0$. That is, when the patch
 146 preference is at its ESS value, $\hat{\varepsilon}$, the per capita growth rates in the two patches (including fishing
 147 mortality) are identical and zero.

148 By setting $\alpha_1 = \alpha_2 = 0$ in equilibrium equations (5) and (6), we see that the only potential
 149 ESS is

$$\hat{\varepsilon} = \frac{\hat{x}_1}{\hat{x}_1 + \hat{x}_2}, \quad (13)$$

150 where

$$\hat{x}_i = k_i \left(1 - \frac{q_i E_i}{r_i} \right) \quad (14)$$

151 are the corresponding population sizes.

152 Substituting the condition $\alpha_1 = \alpha_2 = 0$ into (10), we see that the invasion fitness of any mutant

153 is 0 whenever the resident phenotype is given by (13). Because the invasion fitness is never positive,
 154 no mutant phenotype can increase under selection, confirming that (13) is a local ESS. Because
 155 the invasion fitness is always 0, however, every mutant will have the same fitness as the resident,
 156 making (13) a ‘weak form ESS’ (*sensu* Uyenoyama and Bengtsson, 1982).

157 3.2 Convergence stability of the ESS

158 As we show next, the evolutionarily stable dispersal strategy (13) is also convergence stable—an
 159 evolutionary attractor to which a monomorphic population will converge through small, successive
 160 mutations (Geritz et al., 1998). We thus expect the settlement preference to evolve to, and remain
 161 at, $\hat{\varepsilon}$.

162 We demonstrate the convergence stability of $\hat{\varepsilon}$ using the second derivatives of the invasion fitness
 163 (10). Convergence stability requires that

$$\left(\frac{\partial^2 \lambda'}{\partial \varepsilon \partial \varepsilon'} + \frac{\partial^2 \lambda'}{\partial \varepsilon'^2} \right) \Big|_{\varepsilon' = \varepsilon = \hat{\varepsilon}} < 0. \quad (15)$$

164 That is, the sum of these second derivatives, taken with respect to the resident and mutant pheno-
 165 types, must be negative at the ESS $\hat{\varepsilon}$ (Eshel, 1983; Geritz et al., 1998).

166 Because α_1 and α_2 do not depend on the mutant strategy ε' , it follows that $\partial^2 \lambda' / \partial \varepsilon'^2 = 0$ when
 167 $\alpha_1 = \alpha_2$. Thus, (13) will be a convergence-stable ESS if $\partial^2 \lambda' / \partial \varepsilon \partial \varepsilon' < 0$ at $\varepsilon' = \varepsilon = \hat{\varepsilon}$.

168 To calculate $\partial^2 \lambda' / \partial \varepsilon \partial \varepsilon'$, first differentiate the invasion fitness (10) with respect to ε' :

$$\frac{\partial \lambda'}{\partial \varepsilon'} = \frac{(\alpha_1 - \alpha_2)m}{\sqrt{(\alpha_1 - \alpha_2)^2 + 2(\alpha_1 - \alpha_2)(2\varepsilon' - 1)m + m^2}}. \quad (16)$$

Next, recall that α_1 and α_2 depend on the resident trait ε , and rewrite the equilibrium conditions
 (5) and (6) as

$$\alpha_1 = m \left[1 - \frac{\varepsilon(\bar{x}_1 + \bar{x}_2)}{\bar{x}_1} \right], \quad (17)$$

$$\alpha_2 = m \left[\varepsilon - \frac{(1 - \varepsilon)\bar{x}_1}{\bar{x}_2} \right]. \quad (18)$$

169 Note that the equilibrium stock sizes \bar{x}_1 and \bar{x}_2 are both functions of ε .

170 We can substitute (17) and (18) into (16), and then differentiate with respect to ε to obtain
 171 $\partial^2 \lambda' / \partial \varepsilon \partial \varepsilon'$. After evaluating the resulting expression at $\varepsilon' = \varepsilon = \hat{\varepsilon}$, as given by (13), we find that

$$\left. \frac{\partial^2 \lambda'}{\partial \varepsilon \partial \varepsilon'} \right|_{\varepsilon' = \varepsilon = \hat{\varepsilon}} = \frac{m}{\hat{x}_1 \hat{x}_2} \left[\hat{x}_2 \frac{d\bar{x}_1}{d\varepsilon} - \hat{x}_1 \frac{d\bar{x}_2}{d\varepsilon} - (\hat{x}_1 + \hat{x}_2)^2 \right]. \quad (19)$$

The derivatives $d\bar{x}_1/d\varepsilon$ and $d\bar{x}_2/d\varepsilon$ can be found by differentiating the equilibrium equations (5) and (6) with respect to ε . When evaluated at $\varepsilon' = \varepsilon = \hat{\varepsilon}$ and $\bar{x}_i = \hat{x}_i$, as given by (14), these derivatives are

$$\left. \frac{d\bar{x}_1}{d\varepsilon} \right|_{\varepsilon' = \varepsilon = \hat{\varepsilon}} = \frac{mk_1 r_2 \hat{x}_2 (\hat{x}_1 + \hat{x}_2)^2}{mk_2 r_1 \hat{x}_1^2 + r_2 \hat{x}_2 [mk_1 \hat{x}_2 + r_1 \hat{x}_1 (\hat{x}_1 + \hat{x}_2)]}, \quad (20)$$

$$\left. \frac{d\bar{x}_2}{d\varepsilon} \right|_{\varepsilon' = \varepsilon = \hat{\varepsilon}} = -\frac{mk_2 r_1 \hat{x}_1 (\hat{x}_1 + \hat{x}_2)^2}{mk_2 r_1 \hat{x}_1^2 + r_2 \hat{x}_2 [mk_1 \hat{x}_2 + r_1 \hat{x}_1 (\hat{x}_1 + \hat{x}_2)]}. \quad (21)$$

172 After substituting (20) and (21) into (19), we find that

$$\left. \frac{\partial^2 \lambda'}{\partial \varepsilon \partial \varepsilon'} \right|_{\varepsilon' = \varepsilon = \hat{\varepsilon}} = -\frac{m}{\hat{x}_1 \hat{x}_2} \left(\frac{r_1 r_2 \hat{x}_1 \hat{x}_2 (\hat{x}_1 + \hat{x}_2)^3}{mk_2 r_1 \hat{x}_1^2 + r_2 \hat{x}_2 [mk_1 \hat{x}_2 + r_1 \hat{x}_1 (\hat{x}_1 + \hat{x}_2)]} \right) < 0. \quad (22)$$

173 It follows that inequality (15) is satisfied and the ESS settlement preference (13) is a convergence-
 174 stable strategy.

175 4 The ESOHS and effects of evolution on optimal management

176 In general, the rent that is generated in each patch depends upon the fishing effort in both patches.
 177 This is not the case when the patch preference ε is at its ESS value $\hat{\varepsilon}$, which becomes clear upon
 178 substituting the equilibrium stock sizes (14) into the rent (3):

$$\pi[E_1, E_2; \hat{\varepsilon}] = \hat{\pi} = \sum_{i=1}^2 \left(pq_i k_i \left(1 - \frac{q_i E_i}{r_i} \right) - c_i \right) E_i. \quad (23)$$

179 This means that when we maximize rent over E_1 and E_2 , we are maximizing the rent in the patches
 180 independently of each other. Thus, a reserve cannot be part of an ESOHS; a patch should never
 181 be closed unless it is unprofitable to harvest (i. e., falls in the ‘unfished’ category). Specifically, the

182 ESOHS is

$$\hat{E}_i^* = \begin{cases} \frac{r_i(pq_i k_i - c_i)}{2pq_i^2 k_i} & \text{if } pq_i k_i - c_i > 0, \\ 0 & \text{otherwise.} \end{cases} \quad (24)$$

183 The resulting stock sizes in each patch at the ESOHS are

$$\hat{x}_i^* = \begin{cases} \frac{1}{2} \left(k_i + \frac{c_i}{pq_i} \right) & \text{if } pq_i k_i - c_i > 0, \\ k_i & \text{otherwise.} \end{cases} \quad (25)$$

184 The evolutionarily stable settlement preference at optimal harvest, $\hat{\varepsilon}^*$, can be calculated using (13)
 185 with stock sizes $\hat{x}_i = \hat{x}_i^*$.

186 Spatial heterogeneity in biological or economic parameters is reflected in the ESOHS (Fig. 3).
 187 When the patches differ in their biological parameters (r or k), the ESOHS effort level in the
 188 worse patch is smaller than it would be if the patches were identical and the parameter values
 189 were equal to their values in the good patch (Fig. 3, first two columns). If the only difference
 190 between the patches is due to a difference in intrinsic growth rate (i. e., if $r_2 < r_1$), the ESOHS
 191 settlement preference, $\hat{\varepsilon}^*$, remains $1/2$, and the stock sizes are equal to one half of the (identical)
 192 carrying capacity in each patch. In contrast, when the carrying capacities of the two patches differ
 193 (i. e., $k_2 < k_1$), $\hat{\varepsilon} > 1/2$, and settlement in patch 1 is more frequent than settlement in patch
 194 2. In combination with the lower carrying capacity, this dispersal asymmetry results in a smaller
 195 equilibrium stock size in patch 2.

196 When the patches differ in one of their economic parameters (either c or q ; Fig. 3, last two
 197 columns), $\hat{\varepsilon}^* < 1/2$; that is, settlement is more frequent in the economically poorer patch. If the
 198 patches only differ in the cost of fishing (i. e., $c_2 > c_1$), then the ESOHS effort in the more expensive
 199 patch, as expected, is lower than in the less expensive patch. Combined with the settlement
 200 asymmetry, this results in a larger standing stock in the poorer patch. Similarly, there is a larger
 201 standing stock in patch 2 when fish are harder to catch there (i. e., $q_2 < q_1$). In contrast with
 202 differences in cost, however, the ESOHS effort level in the patch with lower catchability (\hat{E}_2^*) is
 203 higher than it is in the patch where fish are easier to catch (at least until fish become so difficult
 204 to catch that it is no longer worth harvesting in patch 2 at all).

205 4.1 Management with reserves

206 Marine reserves may be part of an economically optimal, equilibrium management strategy when
207 dispersal does not evolve; however, as (24) shows, this is not the case when dispersal does evolve.
208 While marine reserves are not part of the ESOHS, they may be desirable for other purposes. It is
209 therefore interesting to know how the establishment of a reserve would impact profits. The impact
210 of a reserve is contingent upon whether the organisms evolve in response to differences in growth
211 or mortality conditions.

212 We placed either patch 1 or patch 2 in reserve and calculated the unconstrained rent-maximizing
213 level of effort in the other patch. We also calculated the effort level when the resulting settlement
214 preference was constrained to be evolutionarily stable. We found that using reserves when the
215 settlement preference ε evolves can produce dramatically lower profits (Fig. 4). When a patch is
216 placed in reserve, ε evolves to increase the tendency of fish to disperse to that patch (i.e., when
217 patch 1 is in reserve, ε increases relative to its value when both efforts are optimized to the ESS
218 settlement preference). At least for the parameter values we studied, ε varies most with variation
219 in k_2 and varies least with r_2 (Fig. 4, top row).

220 4.2 Is the ESOHS economically stable?

221 The ESOHS represents the best equilibrium harvesting strategy under the constraint that the
222 strategy will not produce further evolutionary change. At the ESOHS no mutant phenotypes can
223 invade and displace the resident phenotype. We have assumed that those mutants are rare, so that
224 there will generally be a long time between mutation events. In between such events, however, the
225 ESOHS is suboptimal. More rent could be extracted from the resource if the manager were to set
226 the effort levels at their *unconstrained* levels (i. e., $\pi[\hat{E}_1^*, \hat{E}_2^*; \hat{\varepsilon}^*] \leq \pi[E_1^*, E_2^*; \varepsilon^*]$), and the manager
227 will be sorely tempted to do so. As a result, we should not expect the ESOHS to be economically
228 stable.

229 As a consequence of fishing at (short-term) optimal levels, rather than according to the ESOHS,
230 the resident phenotype would no longer be an ESS and would be vulnerable to an invasion by a more
231 fit mutant. Of course the manager could simply change his or her harvesting strategy to optimize
232 the rent given this new phenotype. Because of the way it disperses, the potential profitability of

233 a new phenotype would likely be different than that of the resident. Imagine that this iterative
234 process—harvesting at rent-maximizing rates, invasion of a new phenotype, adjustment of the
235 harvesting rates, etc.—continued for a long time. At some times the instantaneous rent would be
236 larger than that that could be generated by the ESOHS; in some instances, it would be less.

237 We simulated this “reactionary” policy by introducing a mutant phenotype according to a
238 Poisson process with rate constant μ . We drew the mutant phenotype ε' from a normal distribution
239 with mean equal to the resident phenotype ε , and standard deviation σ , truncated so that $0 < \varepsilon' <$
240 1. Whenever a mutant appeared, we computed the invasion fitness (10). If the invasion fitness
241 was positive, we replaced the resident by the mutant phenotype and calculated a new harvesting
242 policy that would maximize equilibrium rent for the new phenotype. (In doing so, we implicitly
243 assume that invasion implies displacement. For sufficiently small mutations, Geritz et al. (2002)
244 have proved that this substitution does occur.)

245 We show a single realization of such a reactionary harvesting policy in Fig. 5. When the mutant
246 invades, the efforts in each patch, the population levels, and the profits also fluctuate. In the case
247 illustrated, ε tends to be less than the ESOHS ε value, while the effort and population levels tend
248 to be higher than the ESOHS level in patch 1 (blue lines) and lower in patch 2 (orange lines). The
249 rent derived from the reactionary policy tends to be less than the ESOHS rent for this realization.

250 We simulated this stochastic process for a variety of parameter values to assess the average
251 performance of a reactionary versus ESOHS harvesting policy; we found that the rent generated
252 by the ESOHS always exceeded the average rent generated by reactionary harvesting (Fig. 6, top
253 row). It appears that, on average, harvesting at rates that maximize short-term profits selects for
254 new phenotypes that are inimical to expected long-term sustainable rent. In addition to boosting
255 average rent, using the ESOHS has the additional advantage of reducing (to zero) the variability in
256 profits that would accompany reactionary harvesting (Fig. 6, bottom row). Our simulations suggest
257 that the more different the two patches are, the lower and the more variable are the reactionary
258 rents.

259 5 Discussion

260 In a simple two-patch model, we have shown that almost every optimal harvesting strategy is
261 unstable in the face of dispersal evolution. The exception is a unique evolutionarily stable optimal
262 harvesting strategy, or ESOHS, where dispersal, as described by the settlement preference, is a
263 convergence-stable, weak-form ESS. The ESOHS, however, is potentially economically unstable: in
264 the short term, a manager could always generate more rent using a different distribution of effort
265 (sometimes using a reserve), at least until a new phenotype invades. A manager who employs a
266 myopic, reactionary strategy of constantly maximizing equilibrium rent, assuming that the current
267 phenotype will not change, suffers reduced average rent, and higher variation in rent, over long
268 timescales. In the real world, there would be economic and social benefits of a consistent harvest
269 strategy, compared to one that changed unpredictably in response to evolutionary changes.

270 Marine reserves do not play a role in the ESOHS for the two-patch model. This is because
271 evolution of dispersal acts to equalize fitness between the two patches and push population densities
272 to levels that result in no net movement between them. Without this net movement of individuals,
273 or “spillover,” from the reserve patch into the fished patch, reserves only reduce economic benefits.
274 The equilibration of fitness across habitats is the sine qua non of the so-called *ideal free distribution*
275 (Fretwell and Lucas, 1969). Based on our results with the two-patch model, we conjecture that,
276 more generally, marine reserves will never be economically optimal when the dispersal behavior of
277 individuals leads to the ideal free distribution of the population. The evolution of dispersal, however,
278 does not inevitably lead to the ideal free distribution. In particular, the ideal free distribution does
279 not emerge as the result of an evolutionary stable dispersal strategy when the environment has a
280 source-sink structure and is characterized by temporal variability in fitness (Holt and Barfield, 2001;
281 Schreiber, 2012). Describing the ESOHS in such circumstances, if one exists, would be challenging.

282 Our results, when combined with the results from Baskett et al. (2007), who found that in-
283 creased fragmentation of a reserve network tended to reduce dispersal distance (i. e., increase local
284 retention), suggests that evolution of dispersal may be an important consideration for spatially
285 managed fisheries. However, our understanding of the likely effects of dispersal evolution on opti-
286 mal management is still nascent. For example, dispersal may encompass a host of traits, including
287 larval duration, the proportion of offspring which disperse or migrate (à la Baskett et al., 2007;

288 Dunlop et al., 2009), or adaptive movements of mature individuals (à la Abrams et al., 2012). How
289 reserves impact population sizes and selection pressures will depend on the particular dispersal
290 trait.

291 Of course, settlement preference is not the only life history trait that may evolve in response
292 to harvesting (Borisov, 1978; Jørgensen et al., 2007; Allendorf et al., 2008; Heino and Dieckmann,
293 2009). Most other studies have focused on size-selective harvest, evolution of age or size at maturity
294 (Kuparinen and Merilä, 2007) and the consequences (both negative and positive) that such fisheries
295 induced evolution can have on sustainable yield or rent (Law and Grey, 1989; Heino, 1998; Law,
296 2000; Ratner and Lande, 2001; Eikeset et al., 2013). Intriguingly, it has been suggested that
297 marine reserves might ameliorate the consequences of fisheries induced evolution of such traits
298 (Baskett et al., 2005; Mielke et al., 2010). The ramifications of marine reserves in real evolving
299 systems are likely to be complicated by the simultaneous evolution of multiple traits which may
300 have countervailing effects.

301 While our study suggests that evolution of dispersal may reduce the efficacy of reserves as a rent-
302 maximizing strategy, our analysis focused on equilibrium management on very long timescales. As
303 Sanchirico et al. (2006) highlighted, solving for the optimal harvest trajectory between two patches
304 through time is much more difficult; different results regarding marine reserve optimality may
305 emerge in this case.

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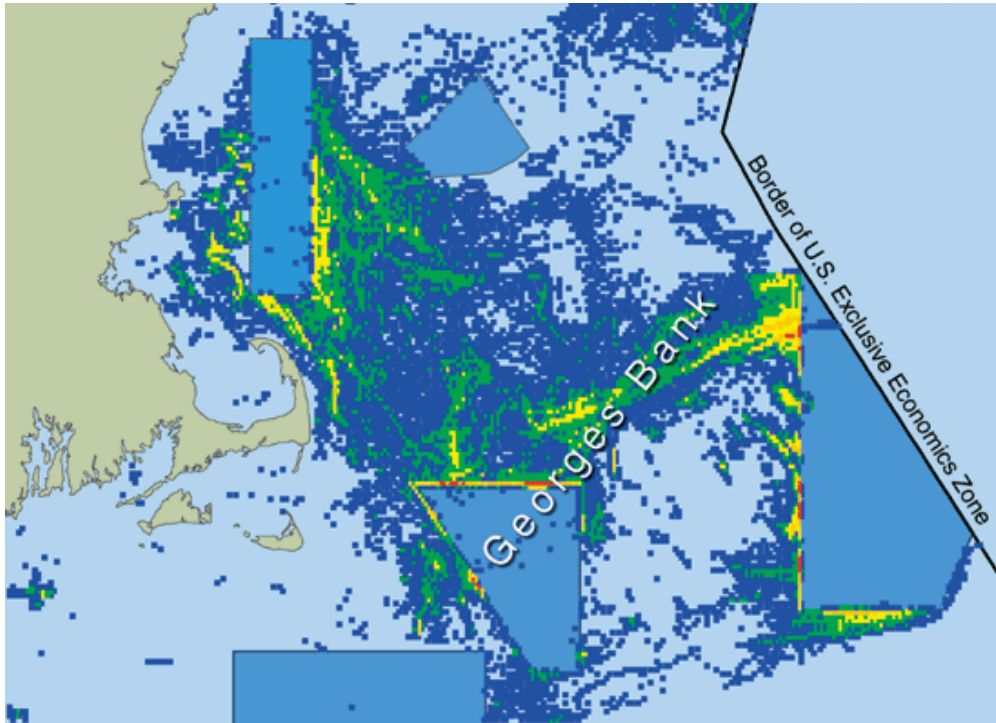


Figure 1: Marine reserves (blue polygons) designed to manage scallop harvest off the New England Coast. Dots indicate estimates of fishing effort in 2003, based on satellite tracking of vessels. Warmer colors (green to red) denote more intense activity. The highest intensity of fishing occurred right at MPA borders. Graphic from Fogarty and Murawski (2004).

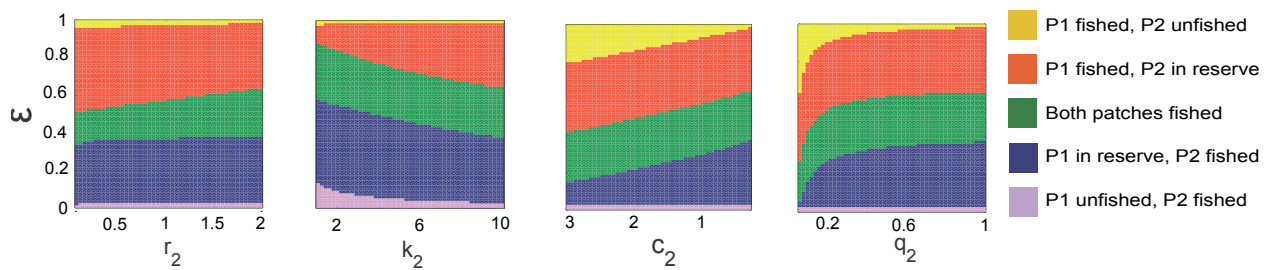


Figure 2: Optimal fishing effort, in the absence of evolution, in each patch as patch 2 quality varies. Patch 2 is the ‘poorer’ patch in every case, with variations in patch 2 parameters noted on the abscissae. All other parameters are equal between patches, with $k_i = 10, r_i = 2, q_i = 1, c_i = 0.25, m = 4, p = 1$. Note that the axis for c_2 is flipped, because patch 2 becomes ‘better’ (less costly to fish) as c_2 decreases.

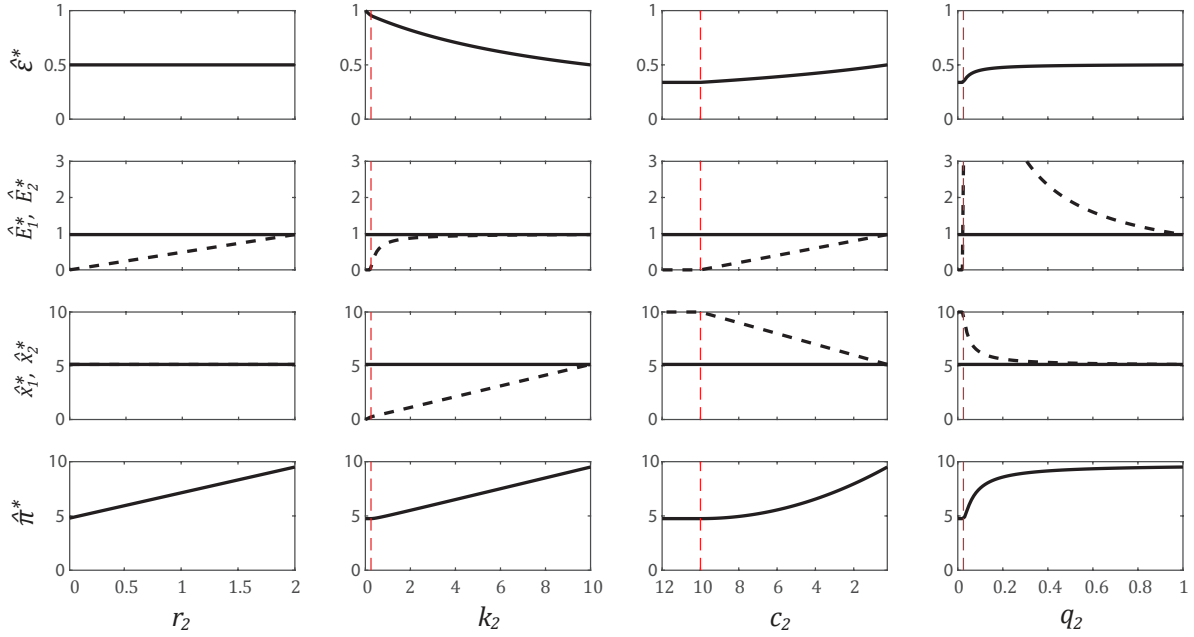


Figure 3: ESOHS settlement preference ($\hat{\varepsilon}^*$), fishing efforts (\hat{E}_i^*), stock sizes (\hat{x}_i^*) and sustainable rent ($\hat{\pi}^*$). Parameters not plotted are the same as in Fig. 2. In the middle two rows, the solid curves indicate effort or stock size in patch 1; the dashed curves depict the same quantities in patch 2. Note that the abscissa is reversed when it denotes the value of c_2 . This makes those figures consistent with the rest in that patch 2 becomes either biologically or economically “worse” as one moves from right to left along the abscissa. Patch 2 is unfished for parameter values to the left of the vertical, red, dashed line in each plot.

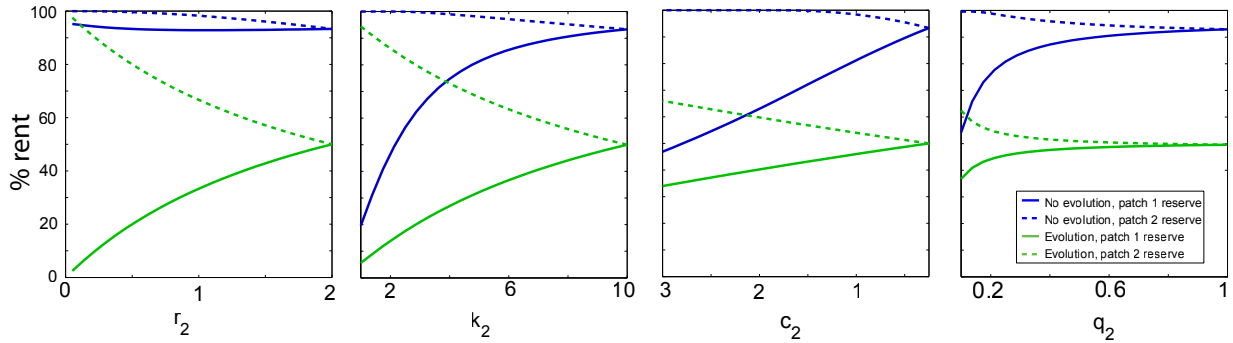


Figure 4: Percent of equilibrium rent lost, relative to an optimally managed system with no evolution (in blue) or with evolution (in green). Either patch 1 is in reserve (solid line) or patch 2 is in reserve (dashed line), and effort in the other patch is managed so as to maximize equilibrium rent. Note that when there is no evolution, closing patch 2 may be part of the optimal management strategy (when the dashed blue line is at 100%). Parameters are the same as in Fig. 2.

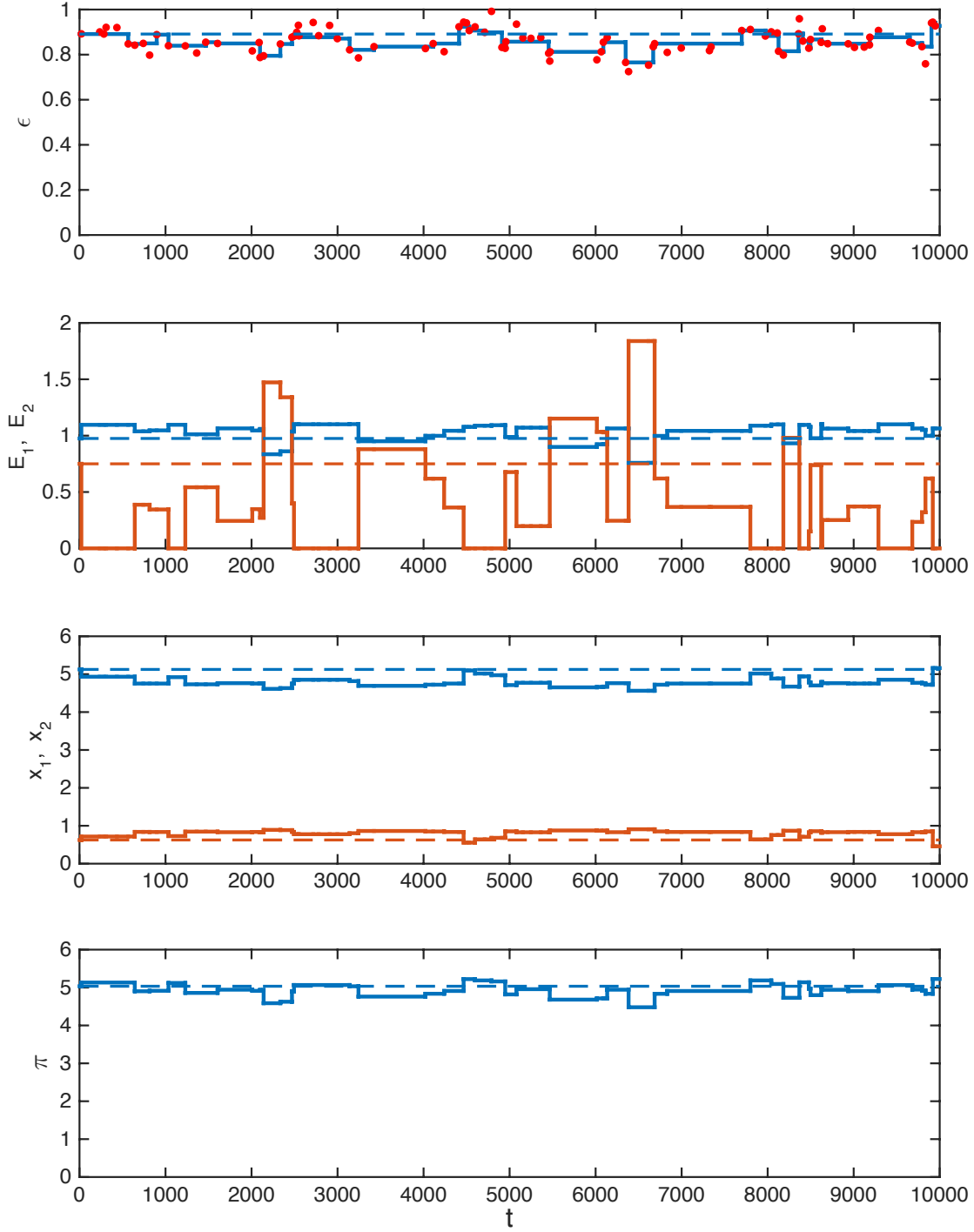


Figure 5: ESOHS harvesting (dotted lines) versus “reactionary” harvesting (solid lines) in which the manager sets effort so as to maximize rent at the current settlement preference (ε) without regard to evolutionary stability. Effort and stock size in patch 1 are shown in blue; in patch 2, orange. Mutants (red dots) appear according to a Poisson process with rate $\mu = 0.01$. Each mutant phenotype ε' is drawn from a normal distribution with mean given by the resident phenotype ε , and standard deviation $\sigma = 0.05$, truncated so that $0 < \varepsilon' < 1$. Parameters are the same as in Fig. 2, except $k_2 = 1$.

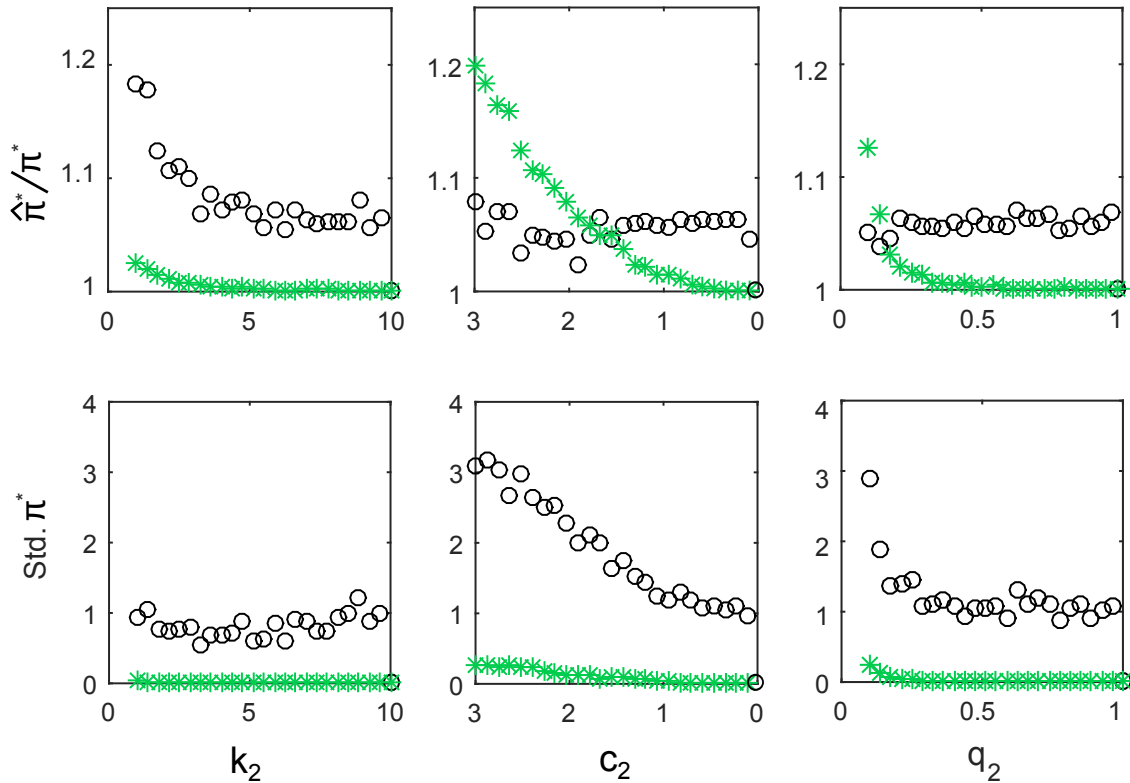


Figure 6: Ratio of average rent (top row) and standard deviation in rent (bottom row) of the ESOHS strategy ($\hat{\pi}^*$) compared to “reactionary” harvesting (π^*) in which the manager sets effort so as to maximize rent at the current settlement preference (ε) without regard to evolutionary stability (cf. Fig. 5). As in earlier figures, all parameters are equal between patches, except for that which is noted on the abscissa. Mutants appear according to a Poisson process at the rate $\mu = 0.01$; their phenotype is drawn from a normal distribution with mean given by the resident phenotype, and standard deviation $\sigma = 0.05$ (green stars) or $\sigma = 0.5$ (black circles), truncated so that $0 < \varepsilon' < 1$. Averages were calculated over the time interval $[0, 100,000]$.