

ECONOMICALLY OPTIMAL MARINE RESERVES WITHOUT SPATIAL
HETEROGENEITY IN A SIMPLE TWO-PATCH MODEL

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ABSTRACT

Bioeconomic analyses of spatial fishery models have established that marine reserves can
2 be economically optimal (i.e., maximize sustainable profit) when there is some type of spatial
heterogeneity in the system. Analyses of spatially continuous models and models with more
4 than two discrete patches have also demonstrated that marine reserves can be economically
optimal even when the system is spatially homogeneous. In this note we analyze a spatially
6 homogeneous two-patch model and show that marine reserves can be economically optimal
in this case as well. The model we study includes the possibility that fishing can damage
8 habitat. In this model, marine reserves are necessary to maximize sustainable profit when
dispersal between the patches is sufficiently high and habitat is especially vulnerable to
10 damage.

Introduction

12 Marine reserves are zones where extractive fishing is prohibited (Lubchenco et al., 2003).
13 While there is growing scientific consensus that marine reserves are useful for biological
14 conservation, their economic costs and benefits are debated (Hart, 2006; Hart and Sissenwine,
15 2008), with consequences for their political feasibility as a fisheries management tool. To
16 help understand the biological and economic circumstances under which marine reserves may
17 be economically beneficial, theoreticians have turned to studying bioeconomic models that
18 include a spatial dimension (Herrera and Lenhart, 2010). The analysis and interpretation of
19 these models can be difficult, so to keep matters simple models often divide the habitat into
20 two patches, one of which is designated as an unfished reserve. Analyses of two-patch models
21 have found that reserves can be economically beneficial (i. e., increase yield or profit) when
22 there is an asymmetry in either the biological or economic characteristics between the reserve
23 and fished patches. In particular, closures may support elevated catch levels if they export
24 larvae or adult fish into fished areas (Pezzey et al., 2000; Costello and Polasky, 2008), if they
25 are sited in areas that are more expensive to fish than open areas (Sanchirico and Wilen,
26 2001; Sanchirico et al., 2006), or if they stabilize catch levels in the face of environmental
stochasticity (Hannesson, 2002).

28 What is more surprising is that reserves can be economically optimal even when space is
29 completely homogeneous. Using a partial differential equation model that treats space as a
30 one-dimensional continuum, we have shown that marine reserves can be profit maximizing
31 even when the biological and economic parameters are the same at every location (Moeller
32 and Neubert, 2013). Similarly, White et al. (2008) found economically optimal reserves in
33 a model that approximates a continuous habitat with a system of many identical patches
34 arranged in a ring; however, they did not find any case where reserves were required to
35 maximize profit when there were only two patches. Their study followed on from a paper by
36 White and Kendall (2007) who found that fishing *yield* could be improved when one patch
was closed to fishing and the other was completely harvested. They did not investigate the

38 effect of closed areas on profit.

These results leave open the possibility that reserves might only be profit maximizing in a
40 spatially homogeneous model if there are more than two patches. The purpose of our present
paper is to present a counterexample to that idea. We show here that marine reserves may
42 emerge as part of the economically optimal (i. e., profit maximizing) management strategy
even in completely homogeneous two-patch settings.

44 What distinguishes our model from previous two-patch models (aside from spatial ho-
mogeneity) is that we account for the possibility that fishing may negatively impact habitat
46 quality. Destructive fishing practices like bottom trawling reduce the complexity of benthic
habitats, affecting survivorship of fish populations (Collie et al., 1997; Watling and Norse,
48 1998; Hiddink et al., 2006). Here, we assume that fishing directly reduces the habitat’s car-
rying capacity, with the severity of the habitat damage scaling with fishing effort intensity
50 (Auster, 1998; Fogarty, 2005). This habitat-quality feedback, coupled with the dispersal of
fish between patches, drives an asymmetrical distribution of fishing effort, in which habitat
52 quality is preserved in one half of the habitat to sustain elevated fish stocks and profits.
Although habitat damage as a result of fishing is often neglected in the bioeconomic litera-
54 ture, some theoretical work has attempted to incorporate these feedbacks into marine reserve
models (see Armstrong and Falk-Petersen (2008) for a review). These treatments generally
56 take a retroactive perspective, focusing on the recovery of the habitat fraction in reserve
(Rodwell et al., 2003; Armstrong, 2007), or are limited in their economic analysis of reserve
58 viability (Lindholm et al., 2001; Upton and Sutinen, 2005) (but see Moeller and Neubert
(2013) for an exception).

60 We begin with a brief examination of the optimal harvest of a single population. This
will allow us to address the effects of harvest-related habitat impacts in isolation from spatial
62 considerations. It will also provide context for the results of our analysis of the two-patch
model. As it turns out, dispersal changes the relationship between optimal fishing effort and
64 the degree to which fishing impacts habitat quality.

Analysis and Results

66 One-Patch Model

Imagine a stock whose density $N(t)$, in the absence of harvesting, is governed by the logistic
68 differential equation:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right). \quad (1)$$

In most bioeconomic models, the effect of harvesting is included in model (1) by subtracting
70 a fishing mortality term from the right hand side. Thus

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) - qEN, \quad (2)$$

where E is a measure of the fishing effort (Clark, 1990). The positive proportionality constant
72 q is the so-called “catchability coefficient;” it depends upon characteristics of the habitat and
on the harvesting technology. Variables, parameters, and their typical units are summarized
74 in Table 1.

In our model, we follow Fogarty (2005) and imagine that in addition to increasing fish
76 mortality directly, fishing also damages habitat such that it reduces the environmental car-
rying capacity K . In particular, we will replace the constant K in (2) with

$$K(E) = \frac{K_0}{1 + gE}. \quad (3)$$

78 The larger the value of the parameter g , the more carrying capacity is suppressed by effort.

In this sense, g represents the sensitivity of the habitat to fishing. Substituting our effort-
80 dependent carrying capacity (3) into the stock equation (2) gives

$$\frac{dN}{dt} = rN \left[1 - \frac{(1 + gE)N}{K_0}\right] - qEN. \quad (4)$$

For a fixed level of effort, the equilibrium stock density is found by setting $dN/dt = 0$

82 in equation (4) and solving for N . There are two solutions: 0 and another equilibrium that
 we will call \hat{N} . Whenever \hat{N} is positive, it is the only stable equilibrium. When it is not
 84 positive, 0 is stable.

Now imagine that the effort level is under the control of a sole-owner who can sell the
 86 harvest at a price p per unit biomass and faces a fixed cost per unit effort c . Then, at
 equilibrium, the owner will generate profit at the rate Π :

$$\Pi = pqE\hat{N} - cE. \quad (5)$$

88 A reasonable objective for the owner would be to maximize the equilibrium profit (5) by
 prudently choosing the effort level E .

90 Our model (4)-(5) has six parameters (r , K_0 , g , q , p , and c ; see Table 1). By introducing
 dimensionless versions of the variables

$$n = \left(\frac{1}{K_0}\right) N, \quad \tau = rt, \quad h = \left(\frac{q}{r}\right) E, \quad \pi = \left(\frac{1}{rpK_0}\right) \Pi, \quad (6)$$

92 we find that equations (4) and (5) are transformed to

$$\frac{dn}{d\tau} = n[1 - (1 + \gamma h)n] - hn \quad (7)$$

and

$$\pi = h(n - w). \quad (8)$$

94 These two equations depend on only two parameters: the dimensionless habitat sensitivity

$$\gamma = \left(\frac{r}{q}\right) g, \quad (9)$$

and the dimensionless cost

$$w = \left(\frac{1}{qpK_0}\right) c. \quad (10)$$

96 In this rescaled version of our model the sole owner's problem is to maximize the dimension-
less profit π by choosing the dimensionless effort h .

98 For model (7) the stable equilibrium stock size, found by setting $dn/d\tau = 0$, is given by

$$n = \begin{cases} (1 - h)/(1 + \gamma h), & \text{if } 0 \leq h \leq 1 \\ 0, & \text{if } h > 1. \end{cases} \quad (11)$$

As we see in Fig. 1, the equilibrium stock declines with effort and declines more quickly if
100 habitat is vulnerable to fishing damage (i. e., when $\gamma > 0$). By substituting the equilibrium
size (11) into (8) and differentiating with respect to h , one can find the profit maximizing
102 effort level

$$h^* = \begin{cases} (1 - w)/2, & \text{if } \gamma = 0 \text{ and } w \leq 1, \\ \gamma^{-1} \left[-1 + \sqrt{(1 + \gamma)/(1 + \gamma w)} \right], & \text{if } \gamma > 0 \text{ and } w \leq 1, \\ 0, & \text{if } w > 1, \end{cases} \quad (12)$$

as well as the resulting optimal stock size

$$n^* = \begin{cases} (1 + w)/2, & \text{if } \gamma = 0 \text{ and } w \leq 1, \\ \gamma^{-1} \left[-1 + \sqrt{(1 + \gamma)(1 + \gamma w)} \right], & \text{if } \gamma > 0 \text{ and } w \leq 1, \\ 1 & \text{if } w > 1. \end{cases} \quad (13)$$

104 The maximum sustainable profit, π^* , is then given (using equation (8)) by $h^*(n^* - w)$.

By plotting h^* , n^* and π^* as functions of γ (Fig. 2), we see that as habitat sensitivity
106 increases, equilibrium profit decreases, and less effort is required to maximize profit. De-
spite this decrease in effort, the equilibrium stock size also decreases as habitat sensitivity
108 increases. These results are consistent with those of Fogarty (2005) who studied yield (as

opposed to profit) using a similar model.

110 Two-Patch Model

Let us now expand our view slightly and consider two stocks, N_1 and N_2 , coupled by in-
 112 dividuals who disperse between them with constant per capita emigration rate D . Assume
 that these two stocks live in completely identical habitats. That is, each habitat “patch”
 114 has exactly the same population growth rate and responds to harvesting in exactly the same
 way. The population dynamic portion of our model then becomes

$$\frac{dN_i}{dt} = rN_i \left(1 - \frac{N_i}{K(E_i)} \right) - qE_i N_i + D(N_j - N_i), \quad \text{for } i = 1, 2, \quad j \neq i, \quad (14)$$

116 where $K(E)$ is again given by formula (3). If we also assume that the costs, prices, and
 catchability coefficients are identical in both patches then the sole owner’s objective is to
 118 maximize

$$\tilde{\Pi} = \sum_{i=1}^2 pqE_i N_i - cE_i \quad (15)$$

over nonnegative values of E_1 and E_2 .

120 Before analyzing model (14)-(15), we again rescale the variables and parameters (listed
 in Table 1) via

$$n_i = \left(\frac{1}{K_0} \right) N_i, \quad \tau = rt, \quad h_i = \left(\frac{q}{r} \right) E_i, \quad \delta = \frac{D}{r}, \quad \text{and,} \quad \tilde{\pi} = \left(\frac{1}{rpK_0} \right) \tilde{\Pi} \quad (16)$$

122 to arrive at the dimensionless version of the two-patch population dynamic model

$$\frac{dn_i}{d\tau} = n_i [1 - (1 + \gamma h_i)n_i] - h_i n_i + \delta(n_j - n_i), \quad (17)$$

(for i and j equal to 1 or 2, and with $j \neq i$) and the economic model

$$\tilde{\pi} = \sum_{i=1}^2 h_i(n_i - w). \quad (18)$$

124 This dimensionless form (17)-(18) reemphasizes the fact that the two patches in the model
are completely identical: harvesting effort costs the same (w) in each patch, each patch is
126 equally sensitive to harvest (γ), and individuals in both patches have the same emigration
rate (δ).

128 Given all this spatial homogeneity, it would be reasonable for a sole owner to think that
applying effort equally, at the rate h^* , in each patch would maximize profit. It turns out
130 that this is not always true (Fig. 3). In the absence of dispersal ($\delta = 0$) or when habitat
is invulnerable ($\gamma = 0$), it is indeed optimal to apply the same fishing effort in each patch.
132 However, when both δ and γ are positive, it can be optimal to focus all of one's effort in one
patch and treat the other patch as an unfished reserve.¹ The more sensitive the habitat, the
134 lower the emigration rate at which reserves become optimal (Fig. 4). In the limit of extreme
habitat sensitivity (γ very large), fishing in both patches would generate infinitesimal profit
136 due to habitat degradation. Thus, so long as $\delta > 0$, it becomes more profitable to close one
of the patches and catch emigrating fish in the other. The threshold values of δ and γ above
138 which reserves become optimal depend upon the cost of fishing w . The larger w , the more
sensitive the habitat or the higher the emigration rate must be for reserve optimality.

140 In addition to allowing for the possibility of spatially asymmetric harvesting, the two-
patch model behaves differently than the single-patch model with regard to the relationship
142 between optimal effort and habitat sensitivity (compare Fig. 2, Fig. 5). Optimal aggregate
effort in the two-patch model ($h_1^* + h_2^*$) does not monotonically decline with habitat sensitivity.
144 Rather, it declines until the point at which it becomes optimal to stop harvesting in one of
the patches. Aggregate effort then increases until the habitat becomes extremely sensitive,

¹Because the patches are identical, it does not matter which patch is fished and which is placed in reserve.

146 when it decreases again. Aggregate optimal stock size ($n_1^* + n_2^*$) and aggregate optimal profit
147 ($\tilde{\pi}^*$) decrease with habitat sensitivity, just as they do in the one-patch model.

148 **Discussion**

149 Three points emerge from our brief analysis. The first is that we have found a counter
150 example to the idea that marine reserves would not be optimal in a homogeneous two-patch
151 model. In the (admittedly stylized) system we analyzed here the two patches are intrinsically
152 identical, both biologically and economically. Nevertheless, we have shown that it can be
153 most profitable to harvest in one patch and establish a reserve in the other. This result,
154 along with our previous analysis of a continuous-space model (Moeller and Neubert, 2013)
155 and the results of White and Kendall (2007) and White et al. (2008), lead us to a warning:
156 Though it may be tempting to manage spatially homogeneous systems in a homogeneous
157 manner, one should resist this temptation absent a careful analysis.

158 The second point is that ignoring feedbacks between fishing and habitat quality can lead
159 to qualitative errors in the design of spatial management strategies. In our model, marine
160 reserve creation is only economically optimal when fishing damages habitat. Thus, from a
161 purely economic perspective, reserve benefits may be limited by the context of the affected
162 fishery. However, in the many cases where fishing damages habitat, our results establish
163 that the economic benefits of marine reserves should not be dismissed out of hand. The
164 dependence of these results on habitat sensitivity and dispersal rates serves to highlight the
165 importance of tailoring management strategies to particular fisheries and their biological
166 effects.

167 The third point is that, if habitat is sensitive to damage from fishing, there may be
168 substantial value to be gained by implementing technologies that reduce the impact of fishing
169 gear. For example, in the one-patch system, altering gear to reduce γ from 10 to 0 would
170 result in a quintupling of profit (Figure 2). Optimal effort levels also depend upon habitat

sensitivity, with potential implications for fishery employment (Neubert and Herrera, 2008).

172 Our results come from intentionally simple models, in which we have assumed environ-
mental homogeneity and analyzed equilibrium outcomes. While these models served our
174 purpose of illustrating the optimality of marine reserves even in homogeneous two-patch
systems, we note some important caveats. First, by focusing on model equilibria, we have
176 ignored time-dependent processes such as discounting, or the potentially dynamic response
of habitat quality to fishing pressure. Thus, our results do not account for the potential
178 costs of management transitions to the profit-maximizing steady state, which may impact
the economic optimality of marine reserves depending on the timescale of analysis. Second,
180 we have not considered the many ways that environmental heterogeneity can influence profit-
maximizing fishing distributions. Other authors have considered these effects, and shown
182 that reserves are more likely to be optimal in places where costs (either implicit, as where
fishing is more deleterious to fish stocks, or explicit, as where costs per unit of fishing effort
184 are greater) are high relative to other locations (Pezzey et al., 2000; Costello and Polasky,
2008; Sanchirico and Wilen, 2001; Sanchirico et al., 2006).

186 Over the past decade, increasing attention has been paid to the economic benefits of
both terrestrial and marine reserves (e.g., Grafton et al., 2005; Naidoo and Adamowicz,
188 2005). These benefits include activities that take place within reserves (e.g., ecotourism), and
spillover of benefits into adjacent areas (e.g., pollination and pest control services). Reserves
190 can also act as a population refuge for harvested stocks, and have long been implemented
for their conservation benefits in this regard. Our model highlights a special intersection
192 of conservation and economic interests by focusing on a case in which the act of harvesting
a stock (fishing) reduces the carrying capacity (damages the habitat) of that stock. Thus,
194 the establishment of reserves protects both a source stock population and intact habitat,
enhancing the economic value of the fishery.

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204 **References**

- Armstrong, C. W. (2007). A note on the ecological-economic modelling of marine reserves
206 in fisheries. *Ecological Economics*, 62:242–250.
- Armstrong, C. W. and Falk-Petersen, J. (2008). Habitat–fisheries interactions: a missing
208 link? *ICES Journal of Marine Science*, 65:817–821.
- Auster, P. J. (1998). A conceptual model of the impacts of fishing gear on the integrity of
210 fish habitats. *Conservation Biology*, 12(6):1198–1203.
- Clark, C. W. (1990). *Mathematical Bioeconomics: The Optimal Management of Renewable*
212 *Resources*. John Wiley & Sons, 2nd edition.
- Collie, J. S., Escanero, G. A., and Valentine, P. C. (1997). Effects of bottom fishing on the
214 benthic megafauna of georges bank. *Marine Ecology Progress Series*, 155:159–172.
- Costello, C. and Polasky, S. (2008). Optimal harvesting of stochastic spatial resources.
216 *Journal of Environmental Economics and Management*, 56:1–18.
- Fogarty, M. J. (2005). Impacts of fishing activities on benthic habitat and carrying capac-
218 ity: approaches to assessing and managing risk. *American Fisheries Society Symposium*,
41:769–784.
- 220 Grafton, R., Kompas, T., and Schneider, V. (2005). The bioeconomics of marine reserves: a
selected review with policy implications. *Journal of Bioeconomics*.
- 222 Hannesson, R. (2002). The economics of marine reserves. *Natural Resource Modeling*,
15(3):273–290.
- 224 Hart, D. R. (2006). When do marine reserves increase fishery yield? *Canadian Journal of*
Fisheries and Aquatic Science, 63:1445–1449.

- 226 Hart, D. R. and Sissenwine, M. P. (2008). Marine reserve effects on fishery profits: a comment
on white et al. (2008). *Ecology Letters*, 11.
- 228 Herrera, G. E. and Lenhart, S. (2010). Spatial optimal control of renewable resource stocks.
In Cantrell, S., Cosner, C., and Ruan, S., editors, *Spatial Ecology*, pages 343–358. Chapman
230 & Hall, Boca Raton.
- Hiddink, J., Jennings, S., Kaiser, M. J., Queirós, A., Duplisea, D. E., and Piet, G. J.
232 (2006). Cumulative impacts of seabed trawl disturbance on benthic biomass, production,
and species richness in different habitats. *Canadian Journal of Fisheries and Aquatic
234 Sciences*, 63:721–736.
- Lindholm, J. B., Auster, P. J., Ruth, M., and Kaufman, L. (2001). Modeling the effects of
236 fishing and implications for the design of marine protected areas: juvenile fish responses
to variations in seafloor habitat. *Conservation Biology*, 15(2):424–437.
- 238 Lubchenco, J., Palumbi, S. R., Gaines, S. D., and Andelman, S. (2003). Plugging a hole in
the ocean: the emerging science of marine reserves. *Ecological Applications*, 13(1):S3–S7.
- 240 Moeller, H. V. and Neubert, M. G. (2013). Habitat damage, marine reserves, and the value
of spatial management. *Ecological Applications*, 23:959–971.
- 242 Naidoo, R. and Adamowicz, W. L. (2005). Economic benefits of biodiversity exceed costs
of conservation at an African rainforest reserve. *Proceedings of the National Academy of
244 Sciences of the United States of America*, 102(46):16712–16716.
- Neubert, M. G. and Herrera, G. E. (2008). Triple benefits from spatial resource management.
246 *Theoretical Ecology*, 1:5–12.
- Pezzey, J. C. V., Roberts, C. M., and Urdal, B. T. (2000). A simple bioeconomic model of
248 a marine reserve. *Ecological Economics*, 33:77–91.

- 250 Rodwell, L. D., Barbier, E. B., Roberts, C. M., and McClanahan, T. R. (2003). The impor-
tance of habitat quality for marine reserve–fishery linkages. *Canadian Journal of Fisheries
and Aquatic Science*, 60:171–181.
- 252 Sanchirico, J. N., Malvadkar, U., Hastings, A., and Wilen, J. E. (2006). When are no-take
zones an economically optimal fishery management strategy? *Ecological Applications*,
254 16(5):1643–1659.
- Sanchirico, J. N. and Wilen, J. E. (2001). A bioeconomic model of marine reserve creation.
256 *Journal of Environmental Economics and Management*, 42:257–276.
- Upton, H. F. and Sutinen, J. G. (2005). When do marine protected areas pay? an analysis
258 of stylized fisheries. *American Fisheries Society Symposium*, 41:745–757.
- Watling, L. and Norse, E. A. (1998). Disturbance of the seabed by mobile fishing gear: a
260 comparison to forest clearcutting. *Conservation Biology*, 12(6):1180–1197.
- White, C. and Kendall, B. E. (2007). A reassessment of equivalence in yield from marine
262 reserves and traditional fisheries management. *Oikos*, 116:2039–2043.
- White, C., Kendall, B. E., Gaines, S., Siegel, D. A., and Costello, C. (2008). Marine reserve
264 effects on fisher profit. *Ecology Letters*, 11:370–379.

Table 1: Variables and parameters used in the models, together with their typical units.

Symbol	Description	Typical Units	Dimensionless Version
Variables:			
N, N_i	stock, in patch i	<i>tonnes</i>	n, n_i
E, E_i	fishing effort, in patch i	<i>vessels</i>	h, h_i
$\Pi, \tilde{\Pi}$	profit	<i>dollars</i> · <i>day</i> ⁻¹	$\pi, \tilde{\pi}$
t	time	<i>days</i>	τ
Parameters:			
r	per capita population growth rate	<i>day</i> ⁻¹	
K_0	carrying capacity without harvest	<i>tonnes</i>	
g	habitat sensitivity	<i>vessel</i> ⁻¹	γ
q	catchability coefficient	<i>vessel</i> ⁻¹ · <i>day</i> ⁻¹	
D	per capita emigration rate	<i>day</i> ⁻¹	δ
p	market price of stock	<i>dollars</i> · <i>tonne</i> ⁻¹	
c	cost of fishing effort	<i>dollars</i> · <i>vessel</i> ⁻¹ · <i>day</i> ⁻¹	w

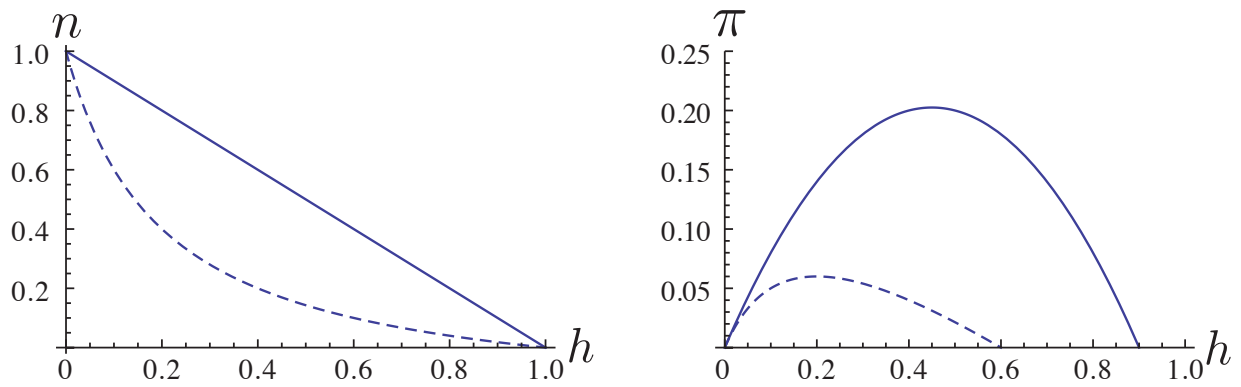


Figure 1: Equilibrium of the dimensionless “one-patch” model (7)-(8). Stock size (n) and profit (π) are shown as functions of effort (h). For the solid curves $\gamma = 0$; for the dashed curves $\gamma = 5$. For this figure the dimensionless cost of effort w was set to 0.1.

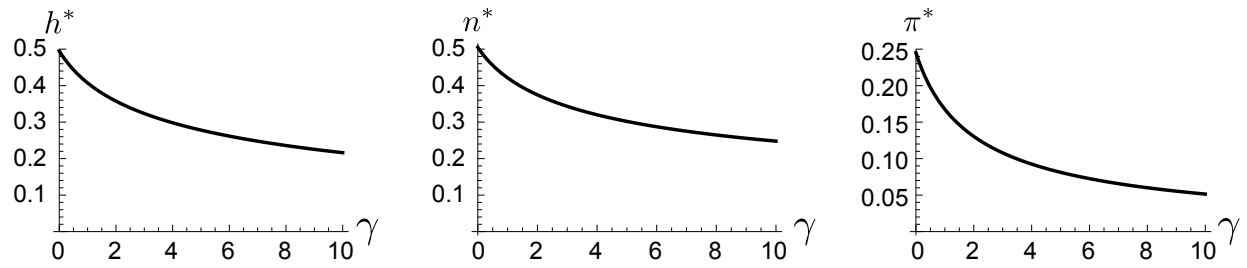


Figure 2: Optimal equilibrium management of the one-patch model (7)-(8). Profit-maximizing effort (h^*), stock size (n^*) and maximum profit (π^*) are shown as functions of the dimensionless habitat sensitivity (γ). For this figure the dimensionless cost of effort w was set to 0.01.

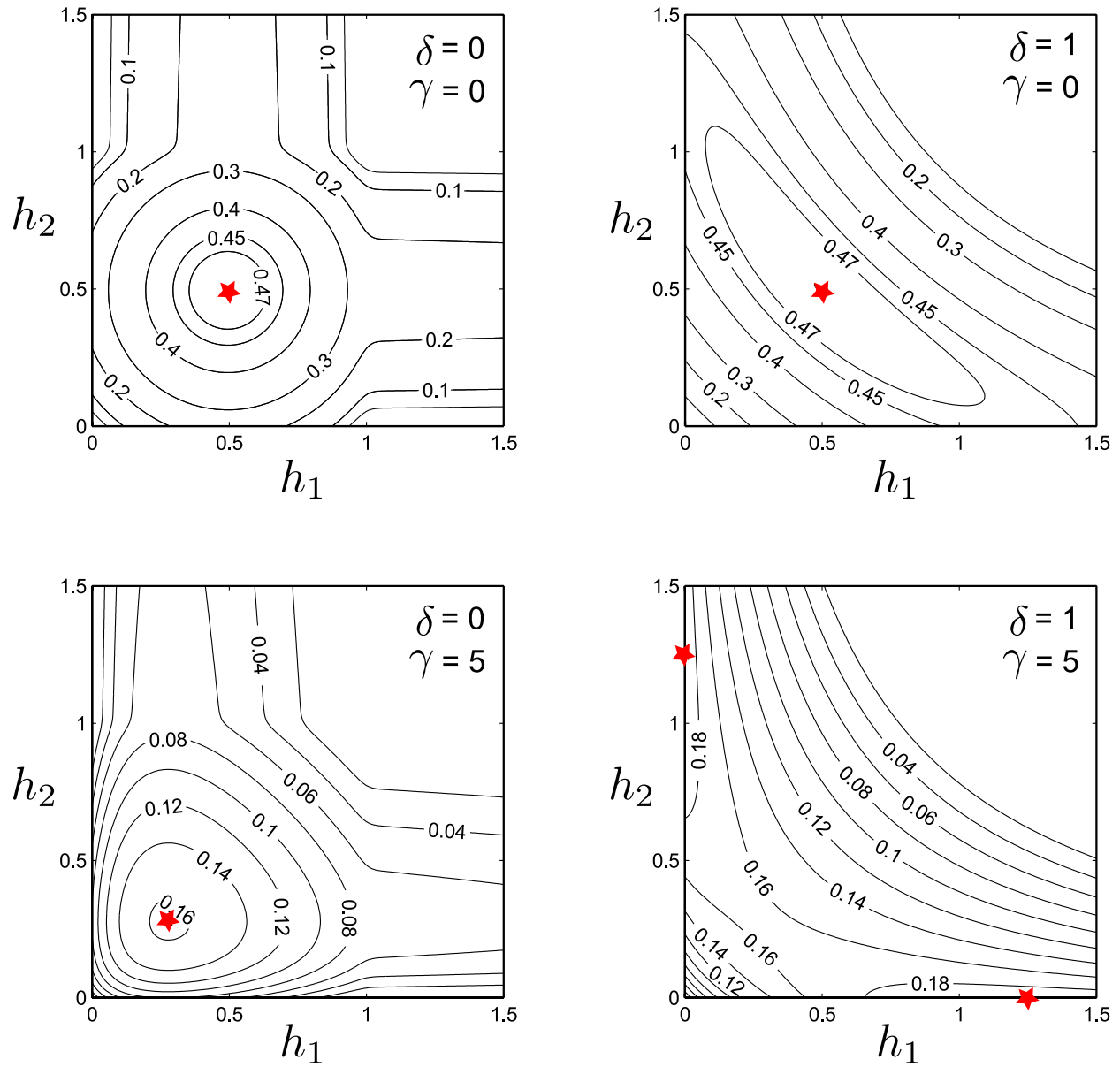


Figure 3: Total equilibrium profit for the two-patch model (17). Contours of total equilibrium profit ($\tilde{\pi}$, equation (18)) are shown as functions of effort in each patch. Profit maximizing combinations of effort are marked with an red star. For this figure the dimensionless cost of effort w was set to 0.01.

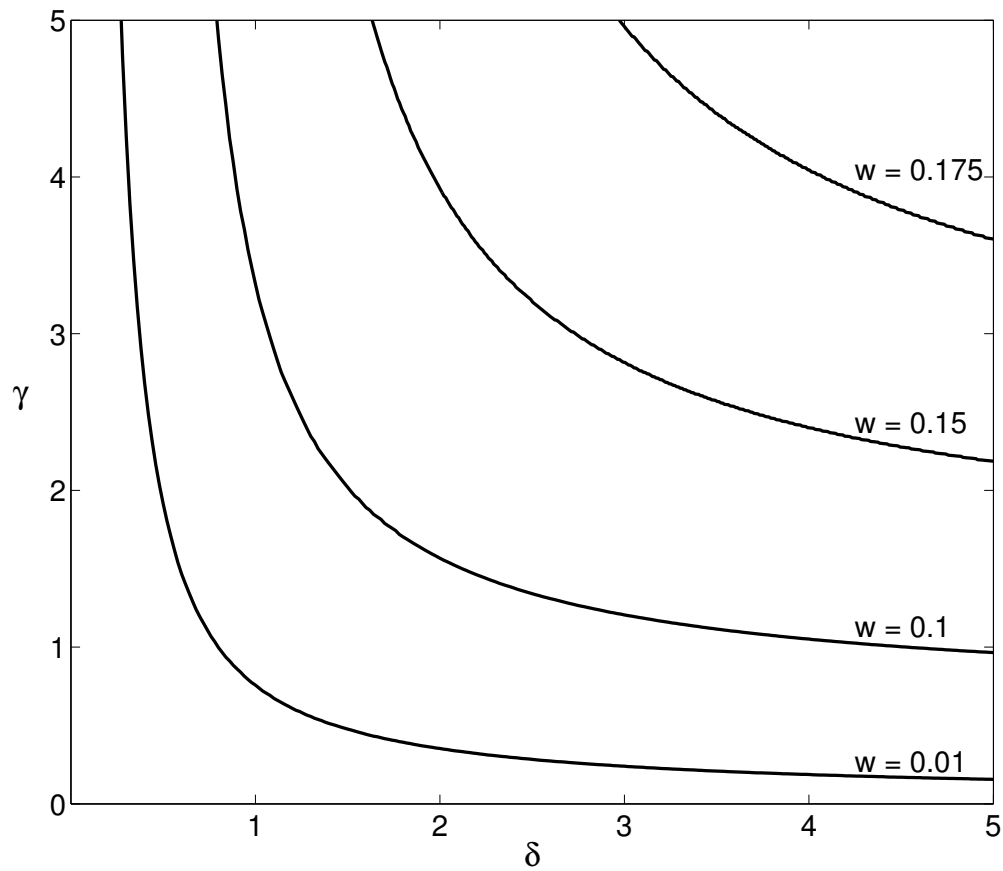


Figure 4: Reserve implementation thresholds for the two-patch model (17). Contours show where management strategies transition from fishing both patches (below the contour), to where one patch is fished and the other is treated as an unfished reserve (above the contour), as a function of habitat sensitivity γ and emigration rate δ . Each contour represents a value of w .

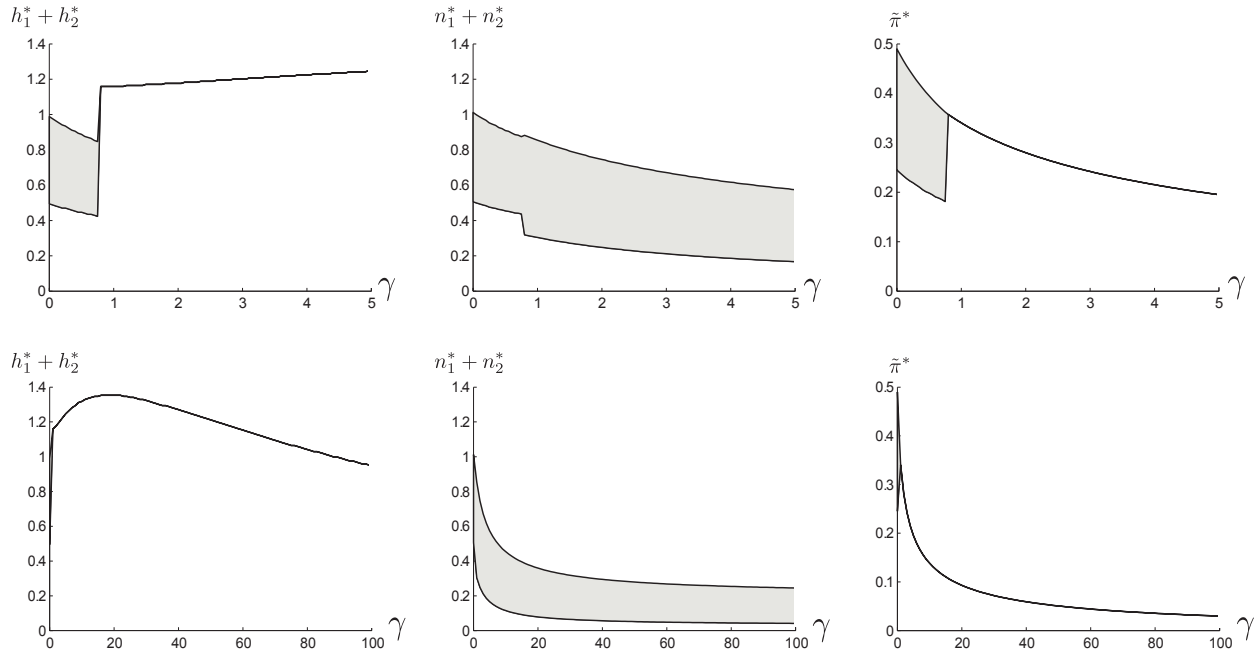


Figure 5: Optimal equilibrium management of the two-patch model (17)-(18). In each plot, the top curve represents the total of the quantity (either effort, stock size, or profit) in both patches as functions of habitat sensitivity γ . The distance between the top and bottom curves (shaded) gives the contribution to the plotted quantity from one of the two patches. Because these quantities vary rapidly for small γ , the top row shows results for $0 \leq \gamma \leq 5$. The bottom row shows the same quantities over a wider range, $0 \leq \gamma \leq 100$. For this figure the dimensionless cost of effort w was set to 0.01 and the dimensionless per capita emigration rate δ was set to 1.