

No-take Zones as Optimal Fishery Management

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Abstract

Discussions on the use of marine reserves (no-take zones) for fishery management are, for the most part, devoid of analyses that consider the ecological and economic effects simultaneously. To fill this gap, we develop a two patch ecological-economic model to investigate the effects of no-take zones on fishery profits. Because the fishery effects of reserves depend critically on the nature of the ecological connectivity, our model includes both juvenile and adult movement, with density dependence in settlement differentiating

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between the two types of dispersal. Rather than imposing a reserve on our system and measuring its effect on profits, we ask when does maximizing profits *imply* that a reserve should be created. Spatial fishery closures as an optimal solution are more likely to occur when the closed area is a net source of biomass and has higher costs of fishing or lower biological productivity, and are more likely for fish populations with density independent settlement ("adult movement") than with density dependent settlement ("larval dispersal").

keywords: marine reserve, bioeconomic model, dispersal, density dependence

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Introduction

Notable declines in marine resource stocks, along with a growing marine conservation movement, have prompted debate over how to restore or maintain healthy ocean ecosystems. Many marine conservationists and scientists are calling for increasing the scale and scope of fishery closures or no-take marine reserves. Some of the potential benefits include conservation of biodiversity, protecting sources of larvae and biomass, increased levels of biomass, increased catches, and providing a hedge against management failures (Carr and Reed 1993; Allison, Lubchenco, and Carr 1998; National Research Council 2001; Botsford, Micheli, and Hastings 2003; Gerber et al. 2003, Roberts et al. 2003). To date, the strongest empirical evidence exists for the effects within the reserves, such as increased levels of fish populations, larger individuals, and improvements in species richness (Halpern 2003).

Commercial and recreational fishermen, on the other hand, fear the immediate effects on their livelihoods and the lost access to particular fishing grounds in the future. As the recent deliberations around siting marine reserves off of California (Channel Islands) and Florida (Tortugas) illustrate, these concerns have legitimacy, and compromises over the location, size, and number of marine reserves are inevitable (Berstein et al. 2004). Developing models that can illuminate the economic and ecological trade-offs involved in siting marine reserves are, therefore, important as they can be used to reduce the set of contentious sites, transaction costs, and feelings of disenchantment in the negotiation process.

For the most part, the theoretical research on the fishery management effects of marine reserves has focused on measuring changes to aggregate catch levels (e.g., Holland and Brazee 1996; Hannesson 1998; Hastings and Botsford 1999; Sanchirico and Wilen 2001;

and Sanchirico 2004). For example, Sanchirico and Wilen (2001) find that when dispersal benefits (spillover) due to adult movements are greater than the opportunity cost of closing the area, which is the lost catch, then aggregate catch totals might increase post-reserve creation.

Catch levels, however, are not necessarily synonymous with the economic profitability of a fishery, because fishing costs often depend on spatial factors, such as local abundance and steam time to and from the fishing grounds. And even though catch levels are a measure of interest, there still remain important questions about the effects of a closure on the economics and ecology of the system. For example, under what biological and economic conditions would closing off areas to fishing lead to greater fishing profits than when all areas are open to fishing? How does the relative timing of dispersal and density dependent effects affect the likelihood of closures as an optimal solution? Gerber et. al (2003) raised similar questions when discussing the efficacy of marine reserves.

To address these questions, we develop a spatially-explicit bioeconomic optimal control model of two patches, and investigate conditions under which marine reserves are boundary solutions that maximize the system-wide present discounted value from the stream of fishery profits. In a closely related paper, Neubert (2003) also does not impose a reserve but rather allows one to emerge as an optimal solution. Unlike most of the previous research on marine reserves (e.g., Hastings and Botsford 1999, and the cases reviewed in Gerber et al., 2003), we allow for spatial heterogeneity due to economic and ecological habitat conditions, such as closeness to port and/or coral reefs versus offshore sandy shoals. Under various spatial heterogeneity assumptions, we analyze cases where the patches are linked by both density dependent (here thought of as juvenile or larvae) and density independent (adult) dispersal processes.

We highlight the effects of ecological connectivity by comparing with the benchmark

case where it is optimal to have fishing in both patches when the system consists of independent (not connected) patches. Given our encompassing structure, this is accomplished by setting the dispersal parameters to zero. Then we introduce different types of connectivity via assumptions on the dispersal parameters, such as source-sink directional movement, random movements based on relative densities, and perfect and imperfect mixing of juvenile populations. Across these different systems, we investigate conditions under which the optimal policy switches from fishing in both patches to closing one of the patches to fishing.

In addition to finding conditions for profit maximizing fishery closures, our model highlights the biological and economic values associated with ecological connectivity, density independent and dependent dispersal mechanisms, and spatial heterogeneity. As such, our model can be used to investigate other types of spatial management, such as employing different levels and types of uses in a zonal system.

The paper is organized as follows. We introduce the ecological and economic components of the model in the next two sections. We then discuss the value associated with ecological connectivity at the optimal solution. An analysis of the conditions under which a reserve is optimal follows. We conclude with a discussion of our findings.

Ecological Model

Our bioeconomic model treats space explicitly in the form of two discrete patches (Levin 1992); fish populations may disperse between the patches via various mechanisms at a variety of rates. Focusing on two discrete patches with connectivity may seem restrictive, but, as in Hastings and Botsford (2003) one can argue that such an approach can approximate models with space treated continuously. In models that treat space homogeneously, the distance between reserves is the only relevant aspect of the location of the reserve in

space. In a patchy environment, however, it is easy to imagine that reserve location, and not just relative position, is critical, if the reserve is to be biologically and economically optimal. This framework is especially suited to investigate how patch or habitat heterogeneity interacts with dispersal and connectivity to affect the potential benefits from closures. Because we allow for population dynamics in both patches, we do not impose the "scorched earth" assumption, which says that all fish that leave the reserve are harvested (see, for example, Hastings and Botsford 1999). Our model, therefore, better mimics actual systems, such as the recent system of reserves established in the Channel Islands or the closed areas on the Grand Banks.

We begin with two habitats or patches with population sizes x_1 and x_2 . The populations are assumed to grow at rates $F_1(x_1, x_2)$ and $F_2(x_1, x_2)$, which depend on the population sizes in both areas. In particular, the population dynamics within each patch are:

$$\frac{dx_1}{dt} = F_1(x_1, x_2) - h_1 = (A_1x_1 + B_1x_2)(1 - x_1) + d_{12}x_2 - d_{11}x_1 - h_1 \quad (1)$$

$$\frac{dx_2}{dt} = F_2(x_1, x_2) - h_2 = (A_2x_2 + B_2x_1)(1 - x_2) + d_{21}x_1 - d_{22}x_2 - h_2 \quad (2)$$

where h_i is the catch level in patch i .

For a single isolated patch, (for example, let $x_2 = 0$) the population x_1 increases logistically with a growth rate A_1 but loses individuals at a density-independent rate d_{11} . When a second patch is included in the dynamics, we consider two possibilities for fish from the second patch settling into the first patch. First, the settlement rate maybe a function of the density in the first patch (which is denoted by the term $B_1x_2(1-x_1)$) and second, the settlement rate maybe independent of the density in the first patch (denoted by the term $d_{12}x_2$). These two types can be thought of as juvenile and adult settlement, respectively, where adult survivorship is assumed unaffected by density dependent mechanisms.

While this model is very general, there are some constraints on the dispersal parameters that should be imposed to ensure that what leaves one area is greater than or equal to what arrives in another. (This restriction does not allow for the possibility of biomass entering the system from patches other than the two we consider.) With respect to adult dispersal, we assume that there is no mortality and that what leaves patch i for patch j arrives in patch j . This is equivalent to assuming that $d_{ii} = d_{ji}$. We do allow d_{ii} and d_{jj} to vary, which allows us, for example, to investigate source-sink systems.

Because juvenile dispersal is more likely to be subjected to mortality during the settlement process (equivalent to settling in neither of the two habitats), we allow for the possibility of mortality by imposing the restriction that $A_i + \frac{B_j}{m_j} \leq a_i^0$ where m_j is the probability of juvenile survival during the dispersal process, and a_i^0 is the per capita recruits produced by patch i when there is no connectivity (all juveniles settle in the local patch). This condition states that the juveniles produced in patch i will either settle in patch i , settle in patch j or settle in neither patch. When B_j is equal to zero and all juveniles are retained locally, the restriction just says that the per-capita arrival density of larvae is equal to the level when there is no connection.

We can rescale the growth rates A_i and B_i to reflect the adding up constraint, where $a_i = \frac{A_i}{a_i^0}$ and $b_j = \frac{B_j}{a_i^0}$. The new constraint is $a_i + \frac{b_j}{m_j} = 1$, where b_j can now be interpreted as the share of larvae produced in patch i that contributes to population growth in patch j . Unless otherwise noted, we will assume that both m_j are equal to one and that the above constraint holds with an equality.

While much of the current theory explaining the potential utility of reserves (e.g., Botsford and Hastings, 1999; Botsford, Hastings, and Gaines 2001) has considered situations where adults are stationary and the larval stage is the dispersing one, such as with broadcast spawners, it is not immediately clear how the conclusions carry over to the

important case where adults are mobile. An advantage of equations 1 and 2, therefore, is that we nest within a single formulation (albeit ad hoc) various dispersal mechanisms and rates. The model also highlights the role and timing of density dependent effects relative to dispersal (Gerber et al. 2003). For example, it can be shown that the juveniles from patch x_2 have the largest influence on patch x_1 's growth when the population in x_1 is small, everything else being equal ($\frac{\partial F_1(x_1, x_2)}{\partial x_2} = b_1(1 - x_1) + d_{12}$) (Sanchirico 2005).

Without fishing ($h_i = 0$), the system will approach an unexploited biological equilibrium. For biological realism, we assume that the parameters are such that a stable, positive equilibrium exists. Formally, we define the biological equilibrium as follows:

Definition. A population size (x_1^b, x_2^b) is said to be at its biological equilibrium if $F_1(x_1^b, x_2^b) = F_2(x_1^b, x_2^b) = 0$.

It is easy to see that if the patches are disconnected from each other (closed biological system), that the biological equilibrium is equal to one in each patch (since we have scaled population size). This is also true with only juvenile settlement.

Economic Model

Following Clark (1990), we focus on a fishery where a regulator (sole-owner) has direct and complete control of harvest levels and whose objective is to maximize the present discounted value of fishery profits (as opposed to maximizing sustainable yield) by choosing the harvest levels in each patch $\mathbf{h}(t) = (h_1(t), h_2(t))$. To solve this problem, harvest in each habitat is a measurable function of time and is constrained between 0 and $h_{i,max}$: $0 \leq h_i(t) \leq h_{i,max}$. If, under some conditions $h_i(t) = 0$ for all t for one of the patches, then a reserve in that patch would be the optimal harvest strategy. The objective function of the regulator to be maximized is formally written as:

$$J(\mathbf{h}) = \int_0^{\infty} \exp(-\delta t) \left\{ \left[p_1 - \frac{c_1}{x_1} \right] h_1(t) + \left[p_2 - \frac{c_2}{x_2} \right] h_2(t) \right\} dt$$

where p_i is the price received at the dock from fish in patch i , c_i is a fishing cost parameter in patch i , and δ is the social discount rate (Clark 1990). We allow prices to vary across space due to differences in product quality, but for simplicity assume prices remain constant over time. We also assume that prices are not responsive to changes in harvest levels, for example, when the fishery in question makes only a small contribution to a global fish market.

The unit costs of catching fish in patch i is $\frac{c_i}{x_i}$ and is a function of two components; the (density) level of the fish population in the patch and a patch dependent cost parameter. Unit fishing costs are assumed to be stock dependent: where the greater the population density, costs are lower, everything else being equal. The constants c_i represent factors (unrelated to population size) involved in fishing a particular area, such as distance from fishing grounds (patches) to port. Operating costs could also differ across patches due to oceanographic conditions and sea floor topography. Whether unit costs of fishing in period t are low or high in an area depends, therefore, on the fish stock size and the cost of operating in the area. For example, patches that are further offshore (greater c_i than inshore areas) may have lower unit costs than inshore patches if offshore density effects outweigh fundamental cost factor effects.

Similar bioeconomic models have been developed in other settings to address different questions. For example, Tuck and Possingham (1994) investigate optimal management in a two-patch sink-source system with no economic heterogeneity and Brown and Roughgarden (1999) use an optimal control model with larval dispersal to illustrate the value of larval pools to system wide fishery profits. Other studies are by Huffaker et. al. (1992), Skonhøft and Solstad (1996), Jannmatt (2004), and Sanchirico and Wilen (In press).

We assume, as do the aforementioned studies, that the regulator is knowledgeable, understanding population dynamics and dispersal mechanics of the biology, with perfect foresight.

Our assumptions are obviously simplistic and likely bias the results against finding closures as an optimal solution. For instance, the case for reserves will most likely strengthen, when one includes factors, such as uncertainty in the biology or economics, inability to control harvest levels directly (bycatch issues), difficulties in enforcement, indirect economic benefits from tourism, ecological benefits or the many institutional issues that plague current day fishery management. Biasing the result against finding closures, however, is useful as a first step as it highlights very clearly and intuitively the underlying (primitive) conditions under which reserves might be optimal.

Optimal Solution

Our model is a two-state, two control optimal control problem that is linear in the controls (harvest rates) and whose dynamics are bang-bang-singular in nature. Because the solution techniques are well-documented in Clark(1990) and Kamien and Schwartz (1991) and due to space limitations, we present them in an appendix. Some points are worth mentioning, however. First, the optimal harvest in each period is determined from maximizing the objective function subject to the population growth equations (1 and 2) and a set of initial conditions. A reasonable initial condition would place the two populations (x_1, x_2) at their open-access equilibrium, which reflects unregulated conditions. This equilibrium is defined as follows:

Definition. A population is said to be at its open access equilibrium if $(x_1^{oa}, x_2^{oa}) = (\frac{c_1}{p_1}, \frac{c_2}{p_2})$.

At the open-access equilibrium, the net unit profit in each patch, as defined by $p_i - \frac{c_i}{x_i}$,

equals zero. The higher the cost or lower the price of fish, the greater the open-access equilibrium level of biomass in each patch. If the patches are economically profitable to operate in, then the open access equilibrium is less than the biological equilibrium in each patch, i.e. $(x_1^{oa}, x_2^{oa}) \leq (x_1^b, x_2^b)$. (For more discussion on this assumption, see the appendix.)

Second, while singular control problems consist of periods where the harvest would be zero or its maximum value at any t , the complexity of even this simple model prohibits us from analyzing all of the possible permutations. Instead we assume that both of the controls (harvest rates) are at their singular value. This is known as the doubly-singular solution (Clark 1990). For this optimization problem, the doubly-singular solution is a steady state (state and adjoint (costate) equations are at rest). Once the system reaches these values, the population size and optimal harvest in both patches remain constant.

The appendix describes how to calculate the values of the population size and the harvest when the system is at the doubly-singular solution. Given the structure of our problem, we arrive at two equations that implicitly define the optimal (steady-state) equilibrium (x_1^*, x_2^*) for the doubly-singular solution, which depends on biological growth and dispersal parameters as well as the economic parameters,

$$\begin{aligned}
(\delta - a_1 + 2a_1x_1)[p_1 - \frac{c_1}{x_1}] - \frac{c_1}{x_1^2}a_1x_1(1 - x_1) = \\
- d_{11}[p_1 - \frac{c_1}{x_1}] + d_{21}[p_2 - \frac{c_2}{x_2}] + \frac{c_1}{x_1^2}[d_{12}x_2 - d_{11}x_1] - \\
b_1x_2[p_1 - \frac{c_1}{x_1}] + b_2[p_2 - \frac{c_2}{x_2}](1 - x_2) + \frac{c_1}{x_1^2}b_1x_2(1 - x_1) \quad (3)
\end{aligned}$$

$$\begin{aligned}
(\delta - a_2 + 2a_2x_2)[p_2 - \frac{c_2}{x_2}] - \frac{c_2}{x_2^2}a_2x_2(1 - x_2) = \\
- d_{22}[p_2 - \frac{c_2}{x_2}] + d_{12}[p_1 - \frac{c_1}{x_1}] + \frac{c_2}{x_2^2}[d_{21}x_1 - d_{22}x_2] - \\
b_2x_1[p_2 - \frac{c_2}{x_2}] + b_1[p_1 - \frac{c_1}{x_1}](1 - x_1) + \frac{c_2}{x_2^2}b_2x_1(1 - x_2) \quad (4)
\end{aligned}$$

The terms on the left hand side of equation 3 and 4 are the conditions that define the optimal biomass levels in a closed ecological system, where all connectivity parameters are zero (b_i and d_{ij}). In a non-spatial system without connectivity, Clark(1990) has shown that the optimal doubly singular biomass is the level that just makes the "liquidation" value of an instantaneous reduction in biomass from catching one more unit of fish today (profit from selling the fish) equal to the present discounted value of the loss from the long term reduction in the steady state biomass from that additional catch taken today.

When each patch is independent, analytical solutions to equations 3 and 4 are possible. (See appendix for derivation and details). Clark(1990) has shown that the higher the operating cost, c_i , the higher the optimal biomass level, and the higher the price of fish, the lower the optimal biomass level, all things equal. Optimal biomass levels are also inversely related to the discount rate, which is the social rate of time preference for consumption (Goulder and Stavins 2002).

Equations 3 and 4 illustrate, however, that there are other benefits and costs, resulting from the ecological connectivity of the system, that influence the determination of the optimal biomass level. For example, liquidating one unit of steady-state biomass in patch one affects spillover of adults and juveniles into patch two, as well as density dependent survival of juveniles migrating into patch one from patch two.

While the optimal biomass levels will depend on the simultaneous solution of these equations, we describe patch-specific economic effects as a way to provide intuition about the value of ecological connectivity at the sustainable solution. Generally speaking, a unit of biomass that leaves a patch for another could have been caught in its origin. This represents a loss in potential net profits in the patch of origin. However, all is not lost, because the biomass can be caught at their destination instead. Whether a unit of biomass is more "valuable" in terms of profit in one or the other patch depends on the relative

prices and costs in the two patches. In addition, movement of biomass across space affects the standing population levels in the patches, and as such, the costs of fishing, which are stock dependent. Density dependent or independent dispersal will modify the form of these three effects, but the intuition remains the same.

Consider these effects, one term at a time in equation 3, beginning with the effect of adult dispersal on the optimal biomass level (also discussed in Sanchirico and Wilen, In Press). Assuming no juvenile dispersal, only the first three terms on the right hand side of equation 3 apply. The first term $-d_{11}(p_1 - \frac{c_1}{x_1})$ is the (instantaneous) loss in marginal profits from a one unit sustained reduction in biomass patch 1, where $[p_1 - \frac{c_1}{x_1}]$ is the sustainable (per unit) profit from catching fish in patch 1. A fish that leaves patch 1 and enters patch 2, however, can be caught in patch 2. The second term, $d_{21}[p_2 - \frac{c_2}{x_2}]$, measures the sustained returns from catching the fish that migrates from patch 1 into patch 2. The marginal change in biomass in patch 1 (holding biomass in patch 2 constant) due to dispersal will also affect the costs of fishing, because of the assumption that fishing costs are stock dependent. The third term reflects the cost effect, $\frac{c_1}{x_1}(d_{12}x_2 - d_{11}x_1)$, where the second component is the net dispersal in patch 1. Positive net dispersal implies fish are on net entering patch 1. The cost effect is the change in the total cost of fishing in patch 1 that results from an increase in an infinitesimal unit of fish in patch 1.

How does optimal management trade off density dependent dispersal or juvenile settlement? We again examine equation 3, but this time we assume that the d_{ij} are equal to zero. The first term $b_1x_2[p_1 - \frac{c_1}{x_1}]$ is the (marginal) loss in sustainable profit in patch 1 due to the competition between juveniles arriving from patch 2 and those already present in patch 1.

The second term, $b_2[p_2 - \frac{c_2}{x_2}](1 - x_2)$ represents the change in net sustained profits in patch 2 associated with juveniles that leave patch 1 and are caught in patch 2. Everything

else being equal, this is smaller, the greater the density of fish in patch 2, reflecting the density dependent survival there. Because juveniles that arrive in a patch are instantaneously subject to the growth process in the patch, the growth/settlement rate scales this effect. Although immigrant juveniles from patch 2 lower the potential investment returns in patch 1 via their effect on the biological growth process (a reduction of the growth rate), they also affect the standing population size in the patch. With stock dependent costs, higher population sizes imply lower costs, all else equal.

The third term, $\frac{c_1}{x_1}[b_1x_2(1-x_1)]$ represents the change in patch one's sustained fishing costs due to the shuffling of biomass (juveniles) across the patches. The term out front is the change in the unit cost of fishing in patch 1. The term in brackets is the share of sustainable harvest in patch 1 due to the influx of juveniles from patch 2. This can be seen by noting that the steady-state harvest in patch 1 is equal to $h_1 = a_1x_1(1-x_1) + b_1x_2(1-x_1)$. Therefore, the term reflects the change in total (sustainable) costs of catching fish in patch 1 that are attributable to the juveniles arriving from patch 2. Unlike the case for density-independent dispersal, the magnitude of this effect depends directly on the density of the resident fish population.

With both adult and juvenile settlement occurring, the regulator needs to trade-off not just biomass in the local patch, but also the value associated with "nature's" reallocation. Because the regulator is setting the optimal harvest in each patch, she will need to trade-off catching more fish in patch 1, which implies lower population levels and therefore fewer adults and juveniles dispersing to patch 2, against catching less fish in patch 1 and maybe more in patch 2. This trade-off is determined by the relative profitability associated with harvesting that is itself a function of both the ecological conditions of the patches as well as with the nature of the connectivity.

When are no-take zones optimal?

We now turn to the question: under what economic and biological conditions are reserves, or permanent fishery closures, optimal? We are interested in how the different types of connectivity increase or decrease the feasible region over which reserves are optimal relative to the case with no connectivity. For example, are systems with adult dispersal more favorable from an economic perspective than systems with juvenile dispersal for marine reserves?

In this system, a reserve would be the optimal long term management strategy whenever the optimal harvest level $h_i = 0$ at the steady-state solution. In what follows, we analyze separately how fishing cost c_i and biological growth a_i parameters lead to a boundary solution. We choose to look at costs, because many of the natural science articles on marine reserves that focus on yields often neglect fishery costs (e.g., Hastings and Botsford 2000, Tuck and Possingham 2000, and Nuebert 2003), although the effects of differential costs on site selection when catch is the objective have been considered in some places (e.g., NRC 2001, Sanchirico and Wilen 2001, Sanchirico 2004). Investigating growth rates sheds light on whether highly (biological) productive patches are more likely to lead to optimal fishery closures than lower productivity patches, everything else being equal.

In both cases, we rely on numerical solutions to provide insight into these questions. Unless otherwise stated, we assume that prices are the same across the patches and equal to one and a discount rate of 7%. We also perform sensitivity analysis on the discount rate and on the assumptions regarding parameter homogeneity.

Operating Cost of Fishing

With respect to the impact of costs of fishing, we investigate with no loss of generality altering the cost only in patch 1, c_1 , while holding all other parameters constant. We find the *critical value of cost*, denoted c_1^{crit} , which is the level of c_1 that generates $h_1 = 0$, i.e.

closure as an optimal solution, for the doubly-singular steady-state solution, given a set of biological parameters and cost in the second patch.

We can determine the steady-state harvest rates in patch 2 for the doubly-singular solution from the equations 1 and 2 set equal to zero ($\frac{dx_1}{dt} = 0$). We solve for the set $(c_1^{crit}, x_1^*, x_2^*)$ by simultaneously solving equations 3 and 4, and $F_1(x_1, x_2) = 0$. The resulting solution, therefore, satisfies the conditions for the doubly singular control and that the harvest in patch x_1 is 0. The harvest in patch x_2 is then determined at its equilibrium value by $F_2(x^*, y^*) = h_2^*$.

With certain sufficiently simple systems, we can solve for the critical values analytically. For example, assume that the ecological system is closed. Then a reserve in patch one implies that the population is at the natural equilibrium of one. The minimum level of costs in patch x_1 that generates this is also equal to one. Recall that the open-access equilibrium provides a lower bound for the optimally regulated fishery and when costs in patch x_1 are one; the open-access equilibrium biomass level is one (recall we are assuming that prices are equal to one also). It can also be shown that that when the reserve is a pure sink patch $d_{ij} = 0$ and $b_2 = 0$, a reserve is optimal under the same conditions as when the system is closed. Tuck and Possingham (2000) find a similar result.

Using a contour plot, Figure 1 illustrates the levels of c_1^{crit} as a function of the adult dispersal rates d_{ij} , here measured as a percentage of the intrinsic growth rates in each patch. While we allow that the adult per capita movement rates d_{ij} could differ from one patch to the other, we will assume conditions that imply no loss during settlement. That is, the density of fish leaving one patch is assumed the same as the density entering the other patch. To focus on the effects of adult dispersal, the juvenile connectivity parameters b_i are set to zero.

We use as a reference the closed ecological system, which is illustrated at the point

where dispersal into each area is zero. Confirming our earlier result, for the closed system (at the point $(0,0)$), the critical cost level is equal to one. Holding dispersal into the fished area at zero (moving along the y -axis in Figure 1), the critical cost parameter increases as the dispersal rate into the reserve increases. As discussed earlier, when the adult dispersal rate increases and there is a net flow into the patch, the marginal cost of fishing will be lower, everything else being equal. The increase in the "standing stock" of biomass reduces the costs of fishing (makes the patch more profitable to operate in), which implies that for a reserve to be optimal the unit operating cost of fishing must increase. The corollary is that even with a cost coefficient greater than one (all points to the left of the "dispersal cost threshold" line in Figure 1) but less than the critical cost level, it is possible that fishing would occur in patch 1 when it would not occur in the case with no connectivity. Thus, dispersal can make fishing profitable in places that would otherwise be unexploited.

We now discuss what happens when the reserve is a source patch. In this case, we hold dispersal into the reserve at zero and consider the case where the only dispersal flow is into the fished area (move along the x -axis). As we increase the dispersal entering the fished area, the critical cost parameter decreases. That is, the economic gains from fish swimming from the high cost (reserve) to the low cost patch (fished area) more than compensate for the lost returns from closing patch 1. As the dispersal rate increases, this effect increases and for high enough levels, we find that the critical cost parameter may actually be below the operating cost level in patch 2, where $c_2 = 0.25$. This occurs for all points to the right of the "cost in open patch" line in Figure 1. We thus have a somewhat surprising case whereby it is economically efficient to close the patch with the lower operating cost. In fact, as is illustrated in Figure 1, it maybe profitable to close a patch with very low costs, depending on the dispersal rate, because the closed patch is

more valuable as a source for the other patch.

As we move off either axis, the degree of net dispersal (mixing) depends on the relative optimal density levels and dispersal rates. For all the points to the left of the "net dispersal equal to zero" line the reserve acts as a net sink and to the right a net source. Figure 2 further illustrates the net dispersal flows (measured as a percentage of the aggregate biomass) into the reserve at the critical point, where a positive (negative) number implies that the reserve is on net receiving (providing) biomass from (into) the fished area. Because we allow for different dispersal rates d_{ij} , net adult dispersal is a function of these differences and the patch optimal population levels at the critical cost levels. In particular, net adult dispersal into the reserve patch is defined as, $-d_{11}x_1 + d_{12}x_2$. Comparing Figure 1 and 2, it is easy to see that as the population dispersing into the reserve increases, the magnitude of the critical cost decreases. This implies that as the dispersal flow increases the value of the reserve to the system outweighs the local returns from fishing in the patch, because without the connectivity, it would be optimal to fish in the patch.

While a unidirectional source-sink network with the reserve located in the source is the most likely scenario leading to closure as the economically efficient solution, our results imply that even more general settings can be candidates for optimal closures. We denote these more general class of systems as net sources. It is not enough, however, for measured flows to be leaving the closed area for closure to be economically optimal. The cost of fishing must be such that given the ecological network, it is more profitable to allow fish to grow in the reserve and disperse to the fished area than to fish in both areas.

We illustrate in Figure 3 and Figure 4 the case with juvenile dispersal only or with the d_{ij} set to zero. Again, the closed ecological equilibrium is represented at the point $(0, 0)$ or zero mixing of juveniles. Unlike the above analysis, dispersal in this setting is

measured as the share of juveniles produced in patch i settling in patch j . Therefore, as we move away from the origin along the x -axis for example, we increase the share of the juveniles from the reserve settling in the fished b_2 , but this increase implies that local retention a_1 decreases (recall, we are imposing the constraint that $a_1 + b_2 = 1$).

Regardless of the contribution of juveniles from outside the reserve, when the reserve is a pure sink (along y -axis), the critical cost parameter for a closure is equal to one. This is the same level as the closed case. Why is the cost effect that prevailed with adult dispersal not present in this case? For the simple reason that with the reserve population equal to one, any potential positive effects are eliminated due to density-dependence. When the fished area is a sink for juveniles, the feasible region of the critical cost parameter increases with increasing dispersal from the reserve, everything else being equal. That is, the critical cost parameter that would lead to setting aside the source area is lower for higher dispersal rates.

For juvenile dispersal, the critical cost coefficient levels, however, are always greater than the corresponding coefficients in the fished area. Therefore, unlike the adult dispersal case illustrated in Figure 1, closures are only optimal for the high cost patch. The range of costs where a reserve is optimal is also smaller for juvenile dispersal than for adult dispersal, everything else being equal.

Similar to Figure 1, when moving off either axis, it is still the case that the more dependent the fished area is on juveniles from the reserve, the lower the critical cost coefficient. Figure 4 plots the net dispersal in this system, which is equal to $b_1x_1 - b_2x_2$, and is measured as a percentage of the aggregate optimal biomass at the critical cost levels. Relative to the adult dispersal case (Figure 2), the dispersal flows are greater in this system, but the critical cost parameter range is smaller, everything else equal (compare the ranges of the colorbar across Figure 1 and Figure 3). Again, this is due to

the density-dependence in juvenile dispersal.

Biological Growth Rates

Many advocates for reserves argue for finding and closing more biologically productive areas, which in our model can be represented with higher a_i parameters. To investigate this conjecture, we solve for the critical growth rate in patch 1 such that a closure would be optimal and compare it to the level in the open patch. If the critical rate is above the level in the open patch, then we can conclude that closing the more biologically productive patch is optimal.

To investigate this case, we solve for the set $(a_1^{crit}, x_1^*, x_2^*)$ by simultaneously solving equations 3 and 4, and $F_1(x_1, x_2) = 0$. We solve for the set with different rates of dispersal across the two systems. Unlike the cost case, however, there are likely to be combinations of dispersal rates that lead to infeasible critical levels with negative growth rates. These are infeasible because there are conditions on the growth and dispersal parameters that need to hold to ensure a positive equilibrium biomass level. For example, when a patch is a pure source (d_{12} and d_{22} are equal to zero), it must be the case that $a_1 > d_{11}$. If $a_1 \leq d_{11}$, then the net intrinsic growth rate is negative (or zero) leading to zero population levels.

We illustrate in Figure 5 and Figure 6 the cases with adult dispersal only and adult and juvenile dispersal, respectively. The axes are now simply the dispersal rate or share of juveniles contributing to the other patch's growth. To compare relative magnitudes of the dispersal rates divide by the critical growth parameters, where the levels are represented by the contour lines. In both figures, the region with negative growth rates is labeled infeasible and the growth rate in the fished area is also labeled.

Figure 5 illustrates that the optimal reserve has higher critical growth rates (a_i) than the fished area when the reserve is a net source area with high dispersal rates. This

case is most likely to occur when the reserve is a pure source (along the x-axis). The intuition for this result can be seen with the single patch case with logistic growth, where higher growth rates lead to higher yields, everything else being equal. In a patchy system, higher growth rates are areas that are more profitable and therefore, the foregone profits (or opportunity costs) from closing these areas are higher. However, when the dispersal from the reserve is sufficient to outweigh these higher returns, it becomes optimal to close the patch with higher growth rates. Sanchirico and Wilen(2002) found a similar result.

Unlike the previous analysis where we assumed adult and juvenile dispersal separately, we consider both processes simultaneously when mapping out the critical intrinsic growth rate in the presence of juvenile dispersal. The critical intrinsic growth rate we solve for is a_1^o , which is the growth rate when all juveniles are retained locally. Because of the adding up restriction (recall, the unscaled version is $A_i + \frac{B_j}{m_j} = a_i^0$ with $m_j = 1$), when we vary the share of juveniles dispersing B_i or B_j , we need to ensure that this constraint is met at each point. In general, solving for this triplet is a highly non-linear problem and when adult dispersal rates are set to zero, the numerical results are unstable. On the other hand, when adult dispersal is included, the solutions are more easily found. Therefore, we hold the adult dispersal rates fixed and equal across the patches at $d_{ij} = d = .3$. The remaining parameters are the same as the adult dispersal analysis in Figure 5.

Not surprisingly, the pattern is very similar between Figure 5 and Figure 6 with some differences. First, the region where the growth rate in the reserve is greater than in the fished patch is smaller, everything else being equal. Second, the infeasible region is larger and it now encompasses the origin. It is important to note that in this case the reserve is a pure source of juveniles along the x-axis, but it is only a net source with respect to adult dispersal.

Across the two cases when the objective is to maximize the present discounted value

from fishing, closing patches with high intrinsic growth rates is the optimal policy when the patch is also a net source with high spillover. In an ecosystem context, these appear to be necessary conditions for a patch to be considered a bioeconomic hotspot. Therefore, while we find that closing the high intrinsic growth patch does not always lead to optimal fishery closures, the corollary to our result is that closing low biological productivity areas might be optimal.

Sensitivity Analysis

In most marine systems, the assumption that there is no mortality in the juvenile dispersal process is very optimistic. We investigate this by setting the mortality rates equal and less than one and generate figures similar to those presented. We find that the level of the critical cost parameter is higher and growth rate is lower, everything else being equal. The value associated with the ecological network decreases with increased dispersal mortality. As the mortality increases, it pays even with higher operating costs to catch the fish before they are subject to the higher mortality, which implies keeping the area open to fishing.

We also investigated the effect of lower discount rates across all cases. Because the lower the discount rate, the higher the optimal population, as illustrated in the closed analytical solution in the appendix, it is possible that lower discount rates could favor closures. We find increases in the feasible regions for critical costs and growth rates when we the analysis is done with a 2% discount rate.

Finally, in the cost analysis, we explore the effects of asymmetries in the biological growth rates and in the growth rate analysis, asymmetries in the operating costs. With respect to the case of asymmetries in biological growth rates, we focus on the case of higher growth rates in the fished area when solving for the critical cost parameters. Due to the opportunity costs associated with higher growth rates, this case is more likely to

lead to significant changes in the feasible cost region. The results, however, did not vary significantly from those presented in the Figures 1 and 3. We also considered the case of lower costs in the fished area when solving for the critical growth rates, which again is likely to favor optimal closures. Relative to Figure 5 and Figure 6, we find a larger feasible region (smaller infeasible region).

Conclusions

We identify situations where long-term fishery profits are maximized and where reserves emerge as part of the optimal solution. In reality, most fisheries are not optimally managed, since it is difficult to precisely determine population sizes or accurately regulate harvest. However, our model does shed light on general conditions where reserves are more likely to be politically acceptable, regardless of whether the goal of the reserve is increased catches, biodiversity, or profits.

Intuitively, optimal management of patchy biological systems trades off at the margin the loss in profits from a fish leaving, the gain profit from the fish being caught in another area, and the change in fishing costs due to the reallocation of the stock. The evaluation of the trade-off is based on relative profitability, which depends on both economic and ecological conditions, and the nature of the dispersal mechanisms. We showed, for example, that dispersal processes can make patches more profitable to fish than if there is no biological connection between the patches.

With respect to optimal no-take zones, we find, not surprisingly, that the conditions for this to exist depend on the spatial heterogeneity of the system and dispersal mechanisms. For example, in most situations the significantly higher cost patch is likely to be closed optimally. Closing lower cost patches, however, can be optimal when the dispersal rate into the fished area is very high and there is little, if any, out migration of biomass from

the area. This is due to the ecological network effect. We also found optimal closures to be more likely when the growth rate is lower than in the fished area and this runs contrary to the popular notion of finding and closing the high biological productive patches.

The specific form of ecological connectivity is another driver. The optimal harvest regime depends on the endogenous source-sink dynamics, which are determined by differences in population levels across space, as well as on the biological mechanisms acting on dispersal. Relative to density-dependent settlement, the density independent system increased the range of parameters where a complete closure is the optimal solution. This is somewhat surprising, but can be explained by the fact that as the reserve population increases, density-dependent effects become more pronounced and begin to dominate the connectivity factors. Regardless of the mechanism, the range of parameters leading to complete closure increases with increases in the dispersal rate, provided that the reserve is acting as a net source.

Our results echo the theme (e.g., Gerber et al., 2003; Guichard et al. 2004) that the key to understanding the optimal management of marine species is knowledge of dispersal. Unfortunately, dispersal is notoriously difficult to estimate for many marine species (e.g., Shanks et al., 2003). It is for this reason that we emphasize the qualitative nature of our result rather than the quantitative nature. Our work should also reinforce the idea that efforts made to improve estimates of connectivity in marine systems may have potentially large payoffs in efficient management.

We emphasize that our assumptions are conservative in the sense that they are more likely to bias the results against finding optimal solutions that include reserves. An important area for future research is to understand which of the many dimensions of fishery management, such as bycatch, multispecies interactions, economic and biological uncertainties, could also provide circumstances where marine reserves are optimal. Because

ocean management is broader than just fisheries management, it seems prudent to also investigate effects when there exists *in situ* values to the fish stock, such as when there are non-consumptive uses. All of these analyses would need to consider the spatial ecology and economics together and would need a foundation from which to compare the results. Our integrated ecological-economic model provides one such a framework.

As information on the nature and strength of ecological connectivity and patchy environments in marine systems increases, the ability to tailor policies to account for these interactions will increase. In fact, we are likely to move toward a zonal approach (Pew Commission 2003; Sanchirico 2004), with varying types of uses permitted across zones, with no-take zones one possible use. A key component in the planning of a zonal system will likely involve the identification of bioeconomic hotspots that might or might not be closed to all extractive uses. In a spatial system, some of the characteristics of a hotspot, as identified in our analysis, would be a patch that is a net source with high dispersal flows out of it, relatively higher cost and with lower biological productivity, everything else being equal. Further clarification on how to define and empirically identify these hotspots is an important area for future (interdisciplinary) research. Importantly, as our analysis shows, hotspots are more properly viewed as determined by both biological and economic factors, rather than biological factors alone.

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Appendix

To solve for the optimal harvest levels, the regulator maximizes the objective function subject to the population growth functions (equation 1 and 2), and a set of initial conditions. This optimal harvest level can be determined by maximizing the Hamiltonian, which is defined as:

$$H = \exp(-\delta t) \left\{ \left[p_1 - \frac{c_1}{x_1} \right] h_1(t) + \left[p_2 - \frac{c_2}{x_2} \right] h_2(t) \right\} + \lambda_1 (F_1 - h_1) + \lambda_2 (F_2 - h_2)$$

where λ_i are the shadow prices or adjoint variables that represent the marginal value of an additional unit of patch x_1 or x_2 biomass on the present discounted fishery profits (Kamien and Schwartz 1991).

Since the problem is linear in the controls, we can first rearrange the Hamiltonian to isolate the control variables. Once this is done, we observe that there are switching functions in the Hamiltonian that we designate as:

$$\sigma_i(t) = \exp(-\delta t) \left(p_i - \frac{c_i}{x_i} \right) - \lambda_i$$

These switching functions are the time-varying coefficients that multiply each of the controls in the rearranged Hamiltonian. By the Pontryagin necessary conditions, each control must be chosen to maximize the Hamiltonian at each instant. Since controls enter the Hamiltonian linearly, the optimal levels of the control instruments must satisfy:

$$h_i^* = \begin{cases} h_{i,max} & \text{when } \frac{\partial H}{\partial h_i} > 0, \\ \text{singular} & \text{when } \frac{\partial H}{\partial h_i} = 0 \\ 0 & \text{when } \frac{\partial H}{\partial h_i} < 0. \end{cases}$$

When a switching function is positive, the optimal control for that patch is set at its maximum and when the switching function is negative the control must be set at its

minimum allowable value. If the switching function is zero, the control must be set at its "singular value", which is to be determined as discussed below. In addition to the switching functions, the necessary conditions include the biomass state equations along with the adjoint equations. With respect to the latter, Pontryagin's Principle states that for an optimal solution $(x_1^*, x_2^*, h_1^*, h_2^*)$ there exist adjoints λ_1 and λ_2 such that

$$\frac{d\lambda_i}{dt} = -\frac{\partial H}{\partial x_i} \quad (5)$$

Double Singular Solutions

For this optimization system, the doubly-singular solution is a steady state. Once the system reaches these values, the population size and optimal harvest in both patches remain constant. However, we do not prove the stability properties of the equilibrium, as it is not possible analytically; thus, it remains unclear whether the system will ever reach this equilibrium under the optimal control. The true optimal solution may consist of a complex harvesting regime; however, implementation of these solutions is not realistic. We focus our analysis on the doubly-singular solution, which is clearly the optimal constant solution. We next determine the doubly-singular solution using Pontryagin's equations. Since H is linear in h_i , the doubly-singular solution yields

$$\lambda_i = \exp(-\delta t) \left[p_i - \frac{c_i}{x_i} \right] \quad (6)$$

Differentiating 6 yields:

$$\frac{d\lambda_i}{dt} = -\delta \exp(-\delta t) \left[p_i - \frac{c_i}{x_i} \right] + \exp(-\delta t) \frac{c_i}{x_i^2} \frac{dx}{dt}$$

and from Pontryagin's Principle in equation 5 we find:

$$\frac{d\lambda_i}{dt} = -\exp(-\delta t) \frac{c_i}{x_i} h_i(t) - \lambda_i (a_i(1 - 2x_i) - b_2 x_j - d_i i) - \lambda_j (b_j(1 - x_j) + d_i j)$$

Substituting 6 into 5 and simplifying we have for each patch $i = 1, 2$ with $i \neq j$:

$$\begin{aligned} [p_i - \frac{c_i}{x_i}][a_i(1 - 2x_i) - b_ix_j - d_{ii} - \delta] + [p_j - \frac{c_j}{x_j}](b_j(1 - x_j) + d_{ji}) + \\ \frac{c_i}{x_i^2}((a_ix_i + b_ix_j)(1 - x_i) + d_{ij}x_j - d_{ii}x_i) = 0 \end{aligned} \quad (7)$$

These two equations specify the equilibrium (x_1^*, x_2^*) for the doubly-singular control problem, which depends on biological growth and dispersal parameters as well as the economic parameters.

Open-access Solutions

For fisheries that are economically profitable to operate in, the following condition must hold $(x_1^{oa}, x_2^{oa}) \leq (x_1^b, x_2^b)$. We can rewrite this condition as $\frac{c_i}{p_i} \leq x_i^b$. If $\frac{c_i}{p_i} \geq x_i^b$ then fishers would operate at a net loss in that patch at the biological (unexploited) equilibrium, which by assumption is largest feasible population level. Therefore, by requiring this condition to hold, we limit our consideration to systems where the open-access equilibrium is less than the biological one. This also implies that the optimally managed biomass levels will reside somewhere between the case of no management (open-access) and the biological equilibrium.

Optimal stock size in closed-ecological system

In particular, we find that the optimal solution involves moving to a steady-state in which the biomass in each patch satisfies:

$$x_i^* = \frac{1}{4a_ip_i} [(a_i - \delta)p_i + a_ic_i + \sqrt{(a_i - \delta)p_i + a_ic_i)^2 + 8a_ip_ic_i\delta}]$$

In this case, the optimal equilibrium biomass densities are functions only of own-patch specific economic and biological parameters. We also know that the optimal biomass levels could be above or below the maximum sustainable yield ($MSY_i = 1/2$) in our closed

biological system) depending upon the degree of stock dependence in harvesting costs. For example, with no stock dependent costs, it can be shown that the optimal population level must satisfy the condition that $\frac{\partial F_1(x_1)}{\partial x_1} = \delta$, which implies that optimal population level is below MSY. With stock dependent costs, this condition is more complex but Clark (1990) has shown that it can, with high costs lead to an equilibrium above MSY.

Figures

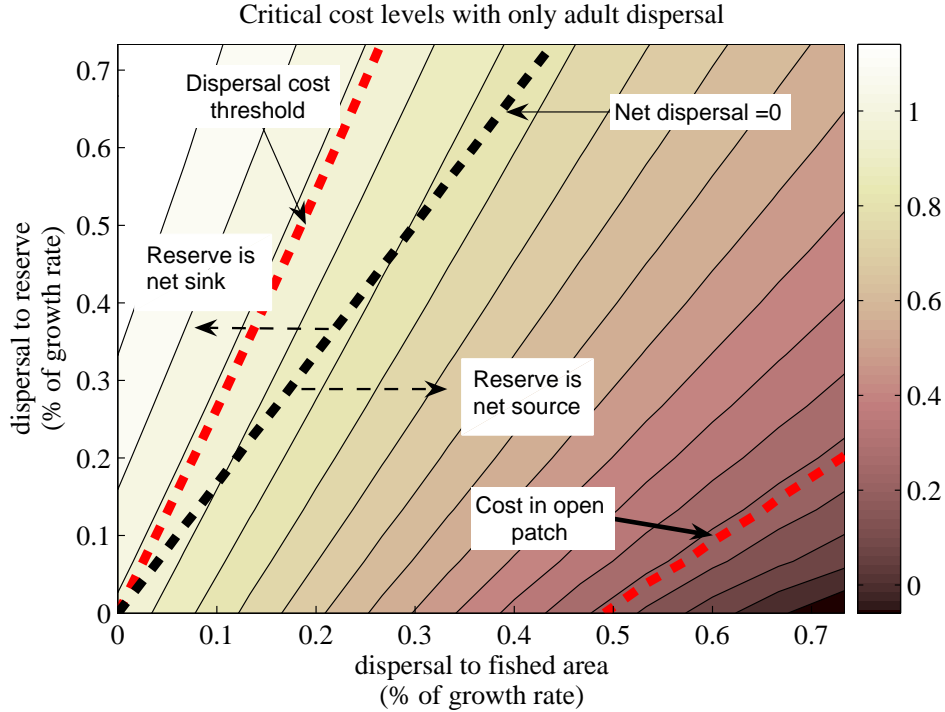


Figure 1: Density-independent dispersal, critical cost levels and optimal closures Note: We measure the dispersal rate as a percentage of the patch intrinsic growth rates. The y-axis corresponds to cases where the reserve patch is a pure sink and the x-axis corresponds to the case where the reserve patch is a pure source. The contour lines correspond to critical cost levels where closing patch one to fishing is part of the optimal solution. To the left of the "Dispersal cost threshold" line, cost levels are such that in the absence of dispersal into the reserve, operating in the patch is not economically feasible, but because dispersal into the patch reduces the operating costs (stock dependent costs), we find that the patch is open to fishing for costs greater than one but less than the critical value. To the right of the line identifying the fishing cost in the open patch is the area where the critical cost levels fall below the level of costs in the open patch to fishing ($c_2 = .25$). The region between the two dashed lines represents the area where the critical cost level is less than one (so fishing would occur if the patches were not biologically connected), but due to dispersal the optimal solution consists of closing the patch to fishing. We also illustrate the point at which net dispersal in the system at the critical cost levels is zero, where areas to the right of this line the reserve is a net source and to the left the reserve is a net sink in the system.

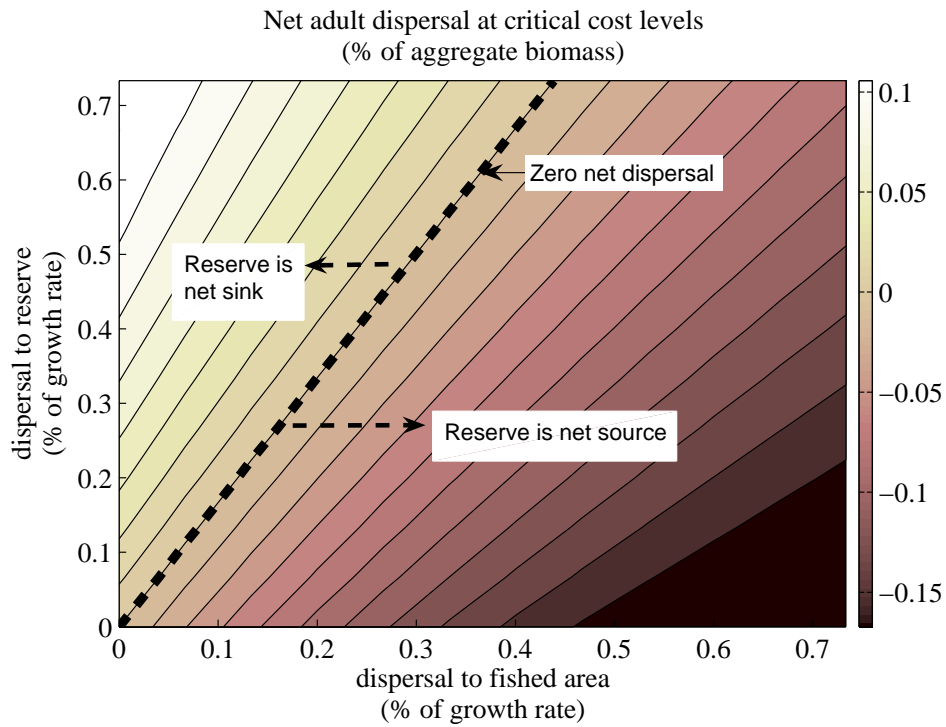


Figure 2: Net adult dispersal at the critical cost level Note: On both axes, we measure the dispersal rate as a percentage of the patch intrinsic growth rates. The y-axis corresponds to cases where the reserve patch is a pure sink and the x-axis corresponds to the case where the reserve patch is a pure source. The contour lines correspond to net dispersal levels measured as a percentage of the aggregate biomass at the critical cost levels illustrated in Figure 1. The zero net dispersal line bifurcates the graph, where areas to the right of this line the reserve is a net source and to the left the reserve is a net sink in the system.

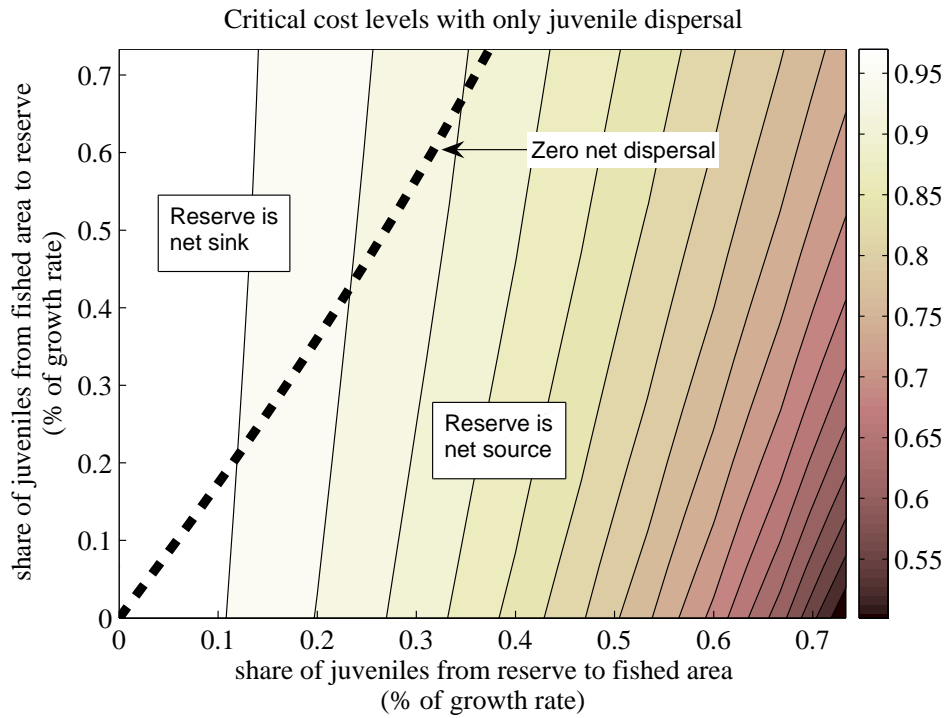


Figure 3: Density-dependent dispersal, critical cost levels and optimal closures Note: On both axes, we measure the share of juveniles that move from one patch to the other as a percentage of the patch intrinsic growth rates (recall we impose the adding up restriction on the juvenile dispersal process). The y-axis corresponds to cases where the reserve patch is a pure sink and the x-axis corresponds to the case where the reserve patch is a pure source. The contour lines correspond to critical cost levels where closing patch 1 to fishing is part of the optimal solution. The zero net dispersal line at the critical cost levels bifurcates the space where areas to the right, the reserve is a net source and to the left, the reserve is a net sink. Unlike in Figure 1, we do not find cases where the critical cost parameter is lower in the reserve patch than in the fished area.

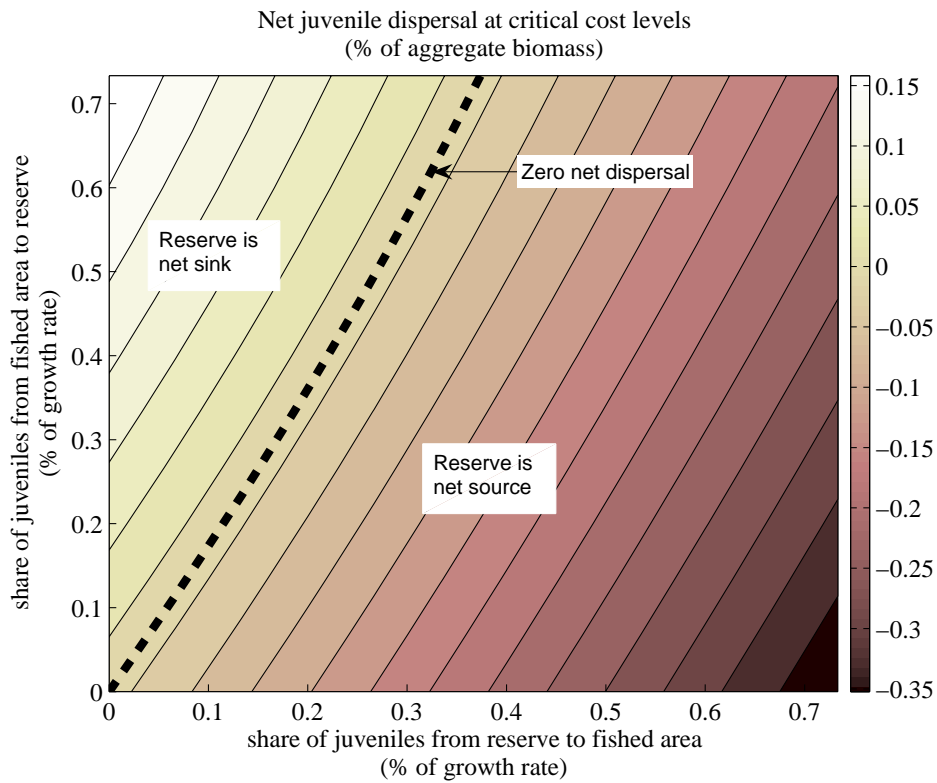


Figure 4: Net juvenile dispersal at the critical cost level Note: On both axes, we measure the share of juveniles that move from one patch to the other as a percentage of the patch intrinsic growth rates (recall we impose the adding up restriction on juvenile dispersal process). The contour lines correspond to net dispersal levels measured as a percentage of the aggregate biomass at the critical cost levels illustrated in Figure 3. The zero net dispersal line bifurcates the graph, where areas to the right of this line the reserve is a net source and to the left the reserve is a net sink in the system. Relative to Figure 2, the dispersal flows as a percentage of growth rates are larger.

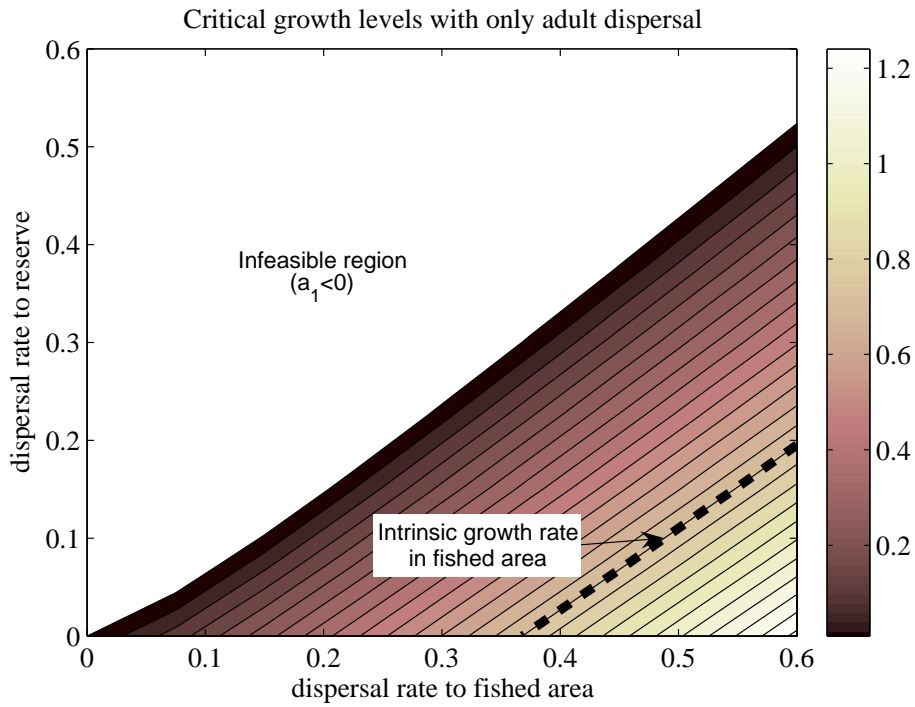


Figure 5: Density-independent dispersal, critical growth rates, and optimal closures Note: The axes are the dispersal rates d_{ij} . The contour lines correspond to the critical growth rates that would lead to optimal closures when the costs in both patches are equal (.25). Except for the bottom right area, which is delineated by the dashed line, the low growth patch is closed to fishing. Only for high dispersal rates in systems where the reserve is acting close to a pure source do we find that the growth rate is higher in the reserve than in the fished patch.

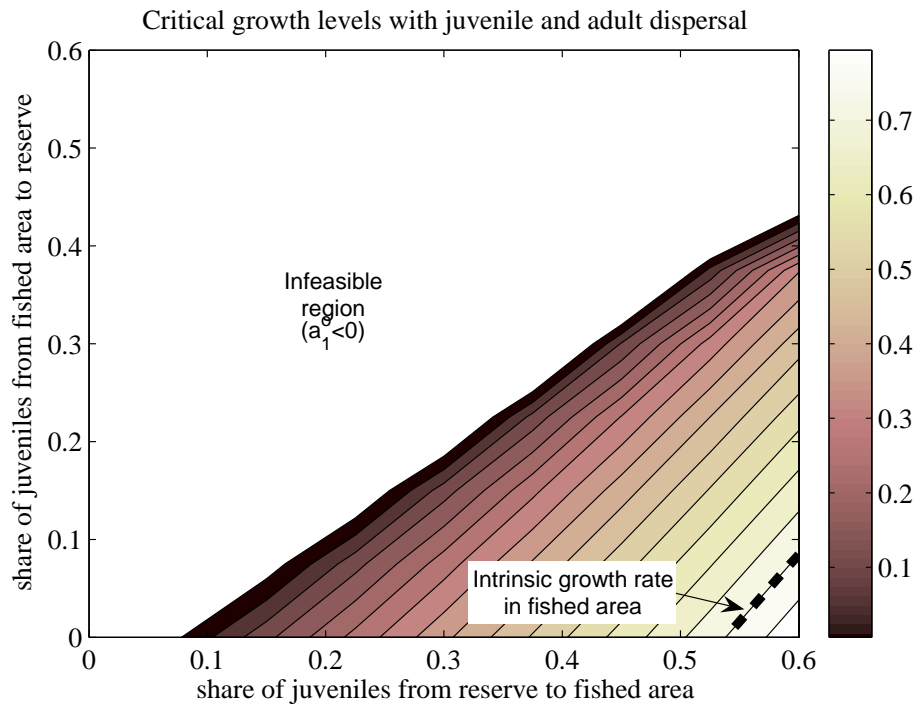


Figure 6: Density-independent and dependent dispersal, critical growth rates, and optimal closures Note: The axes are the share of the juveniles that go from one patch to the other. The contour lines correspond to the critical growth rates a_1^o that would lead to optimal closures when the costs in both patches are equal (.25) and adult dispersal rates are equal (.3). Except for the bottom right area, which is delineated by the dashed line, the low growth patch is closed to fishing.