Designing a Cost-Effective Marine Reserve Network: A Bioeconomic Metapopulation Analysis

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Abstract

Marine reserves are gaining attention around the world as a tool to both conserve ocean resources and improve the productivity of fisheries. Using simulation analysis, we investigate in a limited-entry fishery comprising nine subpopulations the inherent bioeconomic trade-offs associated with cost-effective designs of marine reserve networks—that is, the trade-offs between the degree of connectedness of a site and the biological and economic heterogeneity. We find in many cases that closing two low-value patches can result in larger biological gains and lower costs than closing one high-value patch. We also simulate biological productivity effects after creation of a reserve and find that under special conditions, aggregate sustainable rents are maximized with the closing of a portion of the fishable habitat. Finally, we find that the biological gains of implementing a more rationalized management system can outweigh the gains from closing multiple subpopulations under open access.

Key Words: limited-entry; marine reserve networks; spatial management.

JEL Classification Numbers: Q22

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James N. Sanchirico*

1. Introduction

The notable declines in New England groundfish and California rockfish stocks, along with charges that societies are mining the oceans in an unsustainable fashion, have prompted debate over how to restore or maintain healthy fisheries and ocean ecosystems. The marine conservation, fishery biology, and ecology communities are calling for increasing the scale and scope of closed areas in the management of marine ecosystems. The list of potential benefits from closing areas to all extractive uses includes conservation of biodiversity, additional sources of larvae and biomass, increased levels of biomass throughout the fishery, increased catches, and a hedge against management failures (Polacheck 1990; Dugan and Davis 1993; Roberts and Polunin 1991; Carr and Reed 1993; Roberts 1998; Lauck et al. 1998; Murray et al. 1999; Scientific Consensus Statement 2001). All of these benefits are thought to lead to and enhance the long-run functioning of marine ecosystems (Palumbi 2003).[1]

Regardless of whether regulators are contemplating single or multiple closures (a reserve network), current users of the grounds that may be closed fear the immediate effects and the lost access to particular fishing grounds in the future. Those concerns have legitimacy, and given the

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[1] The biological and economic literature on marine reserves is expanding rapidly, and an in-depth literature review is beyond the scope of this paper. Some examples of review articles are Carr and Reed (1993); Farrow (1996); Thomson (1998); Allison et al. (1998); Guenette et al. (1998); Sanchirico (2000); National Research Council (2001); Botsford et al. (2003).

diverse set of stakeholders in fishery policy, compromises over the location, size, and number of marine reserves are inevitable. Therefore, it is important to develop models that can illuminate the intricacies involved in designing cost-effective reserve networks. Such a model could help fishery managers reduce the set of feasible sites and thus reduce transaction costs in the negotiation process.

In the United States, the current precedent for site selection, as developed in the creation of reserves in the Channel Islands off southern California and in the Tortugas off the Florida Keys, is that biologists propose a list of areas, and then the fishing industry and other groups propose areas more suitable to their needs. This iterative process has been successful in reaching agreements in these two settings, but no one would describe it as the path of least resistance (Schmidt 1997). But what if regulators could predict *ex ante* which sites would encounter the least resistance from the fishing industry and at the same time satisfy the stated biological goals—that is, identify which sites and which fisheries would provide society the greatest return on its investment?

The marine reserve literature has shown theoretically and empirically that reserves can improve considerably the biological conditions in the reserve (Halpern 2003; Palumbi 2003). But whether the fishing industry directly benefits depends on whether the dispersal benefits ("spillover") from the reserves are greater than the opportunity cost of closing the area to fishing. The principal components of the dispersal benefits[2] and opportunity costs[3] have for the most part

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[2] In general, dispersal benefits are a function of the connectivity of the system, population levels in the reserve, and dispersal mechanisms and rates—all of which depend on the species the reserve is set up to protect (Botsford et al. 2001). For sedentary adults that are broadcast spawners, for example, the dispersal benefit is increased production of eggs and larvae. For species with mobile adult populations, the benefits depend on whether the adults disperse randomly or follow seasonal migration patterns.

been derived using models that consider two patches in an open-access setting (e.g., Hannesson 1998; Pezzey et al. 2000; Sanchirico and Wilen 2001). Some exceptions are papers by Polacheck (1990) and Holland and Brazee (1996), which treat total fishing effort as constant and fishing mortality in the closed area is simply transferred into the open area after reserve establishment. Sanchirico and Wilen (2002) consider the impact of reserve creation on limited-entry fisheries in a three-patch simulation with fishing effort responding endogenously.

Although those analyses are sufficient to develop intuition regarding the potential impacts of marine reserves, policymakers are operating in settings involving numerous potential sites (e.g., Leeworthy and Wiley 2000, 2002). These settings present questions that cannot necessarily be investigated in a two- or three-patch analysis. For example, do site selection rules based solely on a patch's biological and/or economic characteristics go astray by not considering the bioeconomic conditions of the remaining fishable habitat, especially the patches that are connected to the reserve? Because the location of the patch relative to biogeographic, oceanographic, and anthropogenic factors is a critical determinant of its role in the system, the benefits and costs of eliminating fishing effort from any one patch will likely depend on its location and on the relative—not just absolute—characteristics.

To address and understand these issues, we extend the current literature on the bioeconomic analysis of marine reserves in a number of ways. First, we develop a nine-patch, spatially explicit bioeconomic model that is used to design cost-effective options for a single closure in a system with multiple patches and for multiple-patch closures or reserve networks.

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[3] Opportunity costs are a function of whether fishermen contract or expand their effort, and where they focus their effort after the area is set aside. These responses depend on the bioeconomic conditions in the area prior to its closure. The appropriate metric depends on the institutional setting in which reserves are being contemplated, the time frame over which reserves are to be evaluated, and the set of stakeholders. Under open-access conditions, researchers have focused on the equilibrium level of aggregate catch; rents are not a good metric because they are dissipated both before and after reserve creation in equilibrium. There is, however, the potential for transitional quasi-rents (Holland and Brazee 1996; Sanchirico 1998; Hannesson 1998; Pezzey et al. 2000). In this case, the present value of these quasi-rents might be a suitable measure of the opportunity costs of closing an area to fishing. When the fishery is characterized by more rationalized management—for example, licensed limited entry or individual quotas—there is the possibility that reserves could increase the overall rents (Sanchirico and Wilen 2002).

The multiple-patch simulation-based framework enables us to investigate many more designs in the presence of complex connectivity structures and habitat heterogeneity than can be done empirically.[4] Because policymakers are required to predict the biological and economic benefits and costs of setting aside areas before in-depth empirical analysis can be completed, analysis that can simulate fishery characteristics can play an important role in the debate on the potential design of reserve networks.

Second, we analyze the optimal design of reserve networks in a licensed, limited-entry fishery where we measure the effects of reserves on returns to fishing. In particular, we depict a regulator who maximizes the present value of fishery-wide rents by choosing the optimal level of aggregate effort and by deciding whether to prohibit fishing in any given patch. Our model, therefore, is consistent with the traditional scope of fishery management, where regulations on fishing effort are applied over large areas.

Third, we compare limited-entry with open-access reserve network designs, everything else being equal. Considering both open-access and limited-entry fisheries under the same set of parameters illustrates rather strikingly how the “value” of a patch depends not just on its structural characteristics but also on the institutional setting under which the fishery is regulated. Finally, we consider whether improvements in biological productivity after creation of the reserve will affect the design of marine reserves, including whether reserves are an integral part of the optimal solution.

With all the usual caveats associated with stylized bioeconomic models, our model provides insights into how the biological and economic location of the patch in the system can play an important role in determining the net effects of reserves. For example, for almost all the cases we analyzed, we find that the optimal solution for the regulator is to keep all patches open

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[4] Of course, a detailed empirical bioeconomic case study is needed to quantify the benefits and costs for any particular fishery (e.g., Holland 2000; Smith and Wilen 2003).

to fishing. This implies that any management system that includes patch closures would likely need to be coupled with a license retirement program (e.g., vessel buybacks). We also illustrate that the biological gains (measured as increases in equilibrium biomass) from moving the system from open-access to a more rationalized system can be greater than maintaining the fishery under open-access conditions, even with a significant fraction of the open-access fishery closed to fishing. In addition, we show that models that ignore the endogenous response of fishing effort to reserves will predict larger increases in biomass than models that take these responses into account. Finally, in fisheries with relatively substantial rates of mixing across subpopulations, we find that if biological productivity and not simply biomass densities increase post reserve creation, then multiple closures might be part of the optimal solution. Overall, our analysis illustrates rather clearly the relevant margins where trade-offs associated with a particular design exist—factors that can sometimes be difficult to disentangle in more complex empirical settings.

The paper is organized as follows. In Section 2, we develop a spatially explicit bioeconomic model of a commercial fishing fleet operating under a limited-entry regime that exploits different subpopulations of a metapopulation. The model depicts a limited-entry fishery because most important fisheries in developed countries worldwide are either subject to some kind of limited-entry regulation or likely to have such programs in the near future. In Section 3, we analyze the effects of reserves on aggregate biomass and rents in a nine-patch setting. Section 4 concludes with a discussion of the findings of the paper and the need to couple effort-reduction policies, such as vessel buybacks, with the establishment of marine reserves.

2. Bioeconomic Metapopulation Model

Most of the economics literature investigating marine reserves is built on the traditional view that a fishery comprises one large homogeneous habitat with a population that is perfectly mixed throughout.[5] But fisheries consist of multiple patches of stocks that are interconnected and can have different roles in the sustainability of the population and returns to fishing effort. The importance of habitat quality and heterogeneity on persistence of populations has recently gained support among ecologists (Levin 1992), especially in the assessment of marine reserves (Garcia-Charton and Perez-Ruzafa 1999; Crowder et al. 2000). This has led, for example, to the recent work on mapping marine habitats and biogeographic representations, and in particular, the use of these maps in reserve selection algorithms with goals of setting aside areas to maximize habitat and biogeographic coverage (Sala et al. 2002). The traditional bioeconomic view, however, does not provide any dimensions over which the benefit and costs of these strategies can be assessed.

The bioeconomic metapopulation model utilized here treats space explicitly in the form of discrete patches, where each patch can sustain a local population through self-replenishment; this is a critical trait that ensures that the populations within the reserves are sustainable (Sanchirico 1998; Sanchirico and Wilen 1999). Unlike most previous literature, we focus on reserve creation in a regulated-access fishery and investigate the effects of habitat heterogeneity and connectivity in a multiple-patch system.[6] We assume that the regulator has two controls on fishing effort: the ability to issue licenses to limit the aggregate amount of fishing effort, and the power to close an area to fishing altogether. Each control is set such that the present value of sustainable fishery-wide rents is maximized. For simplicity, we also assume that there are no opportunities for capital stuffing in this limited-entry program (only one composite input is considered), even though it is widely recognized that this is a serious problem in fisheries. The

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[5] These models investigate how different sizes of marine reserves affect such measures as spawning stock biomass, yield per recruit, catch levels, and stock and catch variability (Polacheck 1990; Holland and Brazee 1996; Hannesson 1998; Pezzey et al. 2000). By assuming that reserves are a fraction of the fishery, these models are discrete spatial approximations to a continuous space-time formulation. A typical assumption in these formulations is that the scale of the open and closed area is separable from the underlying biological and economic production functions—an assumption that is likely not to hold as the reserve size approaches zero and one.

[6] Although marine ecosystems are very complex and many processes are poorly understood, improvements in genetic analysis, mark and recapture methods, otolith geochemistry, and oceanographic models of currents, gyres, and coastal upwelling processes are leading to a better understanding of larval and adult (juvenile) dispersal processes.

licenses are tradable, and we assume that the market is efficient, implying that the license price reflects the discounted stream of expected fishery-wide rents (Stefanou and Wilen 1992).

At the optimal equilibrium, the license price will eliminate profit margins between the limited-entry fishery and alternative fisheries, and between any patch i and j in the fishery. With respect to the former margin the license price will rise to the point that owners of vessel capital will be indifferent between (a) participating in an alternative fishery and earning a market return on their capital, and (b) participating in the limited-entry fishery by paying the price and earning a marginal profit per vessel. In equilibrium, the license price will be determined by the biological and economic characteristics and stringency of the effort limits. If, for example, the total level of effort is set at the open-access levels, then the license price is equal to zero, as anticipated production rents are zero.

The second (spatial) margin exists between any patch i and another alternative patch j. For example, if patch i has higher profits per unit of effort than patch j, it pays for fishermen to move from j to i, everything else being equal. The result will be lower per unit profits in i and higher profits in j. This process will continue until the marginal rate of return to fishing effort in each patch is equalized at the common license price. That is, at the equilibrium, a vessel owner facing a common license price will be indifferent between fishing in patch j and in patch i.

Given our focus on the sustainable optimal equilibrium, the regulator's problem is subject to the equilibrating conditions associated with the license price, the biological equilibrium in each patch, and the constraint that the sum of effort in each patch is equal to the number of licenses. In particular, the mixed-integer programming problem the regulator solves is

$$\max_{E^{Tot},\gamma_i} \quad \Psi = \frac{1}{\delta}\sum_{i=1}^{N}\gamma_i R_i(E_i, x_i) \tag{1}$$

subject to $$\gamma_i h_i(x_i, E_i) = f_i(x_i)x_i + d_{ii}x_i + \sum_{\substack{j=1 \\ j\neq i}}^{n_i} d_{ij}x_j \tag{2}$$

$$\gamma_i(R_i(E_i, x_i) - \delta L E_i) = 0 \tag{3}$$

$$\gamma_i\left(\frac{\partial R_i(E_i, x_i)}{\partial E_i} - \delta L\right) = 0 \tag{4}$$

$$E^{Tot} = \sum_{i=1}^{N} \gamma_i E_i \tag{5}$$

where γ_i is a 0/1 variable that is equal to 1 if the patch is open to fishing and 0 if the patch is closed to fishing, E^{Tot} is the aggregate level of effort chosen by the regulator, L is the common license price per unit of effort, δ is the discount rate, E_i is the patch level of effort in patch i, and x_i is the biomass level in patch i. The aggregate amount of effort (number of licenses) is modeled as a continuous variable.

Equation (2) is the sustained biological equilibrium defined at the point where catch directly offsets biological growth and dispersal. The components of equation (2) are defined as follows: $f_i(x_i)$ is the per capita growth rate in patch i , h_i is the catch rate in patch i, d_{ii} is the rate of emigration from patch i ($d_{ii}<0$), and d_{ij} is the dispersal rate between patches i and j. The open/closed variable occurs in the constraint to indicate that when a patch is closed, it equilibrates at an unexploited biological equilibrium. The biological system depicted here is a deviant of the standard linear metapopulation model in which there are N discrete patches in space, each of which is characterized by "own" patch dynamics as well as linkages to other patches. In this formulation, own growth is separable from dispersal, and the dispersal process can be flexibly modeled via appropriate choice of the coefficient d_{ij}, which can be interpreted as the dispersal of the fish population subject to fishing pressure. The set of patches biologically connected to any given patch is defined by n_i.

Equation (3) is the long-run entry-exit condition present in a licensed, limited-entry fishery, where $R_i(E_i,x_i)$ is equal to the total profits in the fishery net the opportunity costs per unit effort, E_i is the patch i level of effort, and δ is the discount rate. We can substitute (3) into the objective function to simplify the problem. The new objective function of the regulator is

$$\max_{E^{Tot},\gamma_i} \quad \Psi = L \bullet \sum_{i=1}^{N} \gamma_i E_i = L \bullet E^{Tot} \tag{1'}$$

Equation (1') clearly illustrates the role that the aggregate level of effort plays in determining the aggregate rents in the fishery in the long run. With this substitution, the regulator's problem consists of equations (1'), (2), (4), and (5).

Although the regulator sets the total level of effort, the equilibrium distribution of effort throughout the patches is determined by equation (4), where each vessel contributes the amount of effort such that the marginal return from another unit of effort is equal to the license price. The effect of a common license price is that the marginal return per unit of effort is equalized across the system. Under the current assumptions, this is the same equilibrium condition that would arise under an individual transferable quota (ITQ) system with an aggregate total allowable catch, where quotas are tradable across the patches with a trading ratio of one. The equilibrium license price is the equilibrium permit price of such a system. It is important to point out that these are not first-best solutions because the regulator is not determining the optimal spatial distribution of effort, only the total effort for the system.[7]

In this model, the regulator can affect the spatial distribution of effort by implementing closures alongside the aggregate effort. Although this is a rather blunt instrument as opposed to a spatially explicit licensing or ITQ system, there is no *ex ante* reason to expect that under the current assumptions, reserves will have efficiency costs. For example, the use of an aggregate instrument (e.g., cap and trade) is susceptible to the hotspot effect, where the spatial distribution of effort is inefficient. The closure of one patch may under certain circumstances bring the biological gradient in line with the economic gradient, thereby mitigating all or part of the hotspot effect. Finally, equation (5) depicts a fishery that is regulated by a limited-entry licensing system with licenses placed on vessels; it ensures that the amount of effort operating in the fishery is equal to the number of licenses.

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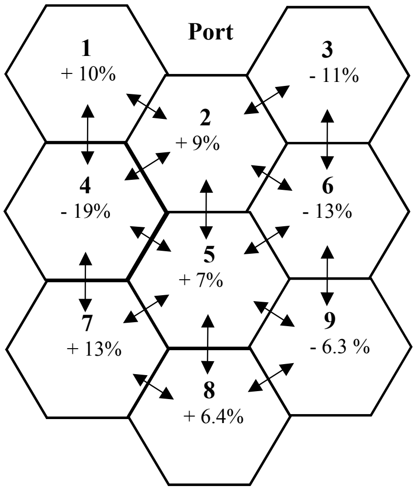
[7] Depending on the specification of the rent function with respect to catch rates and fishing effort, the number of policy instruments the regulator will need to apply in each patch to arrive at the optimal first-best equilibrium will vary (Smith 1969, Brown 1974).

There are several reasons we choose to model a licensed, limited-entry setting. First, it is not clear what is the appropriate benchmark for assessing marine reserves. Is it more correct to use the preexisting regulatory framework, with its overcapacity and overfishing? Or is it more appropriate to measure the effects of closures in a more rationalized system that has the ability to sustain some of the potential economic benefits? We choose the later, since we believe that based on the current trends, most fisheries throughout the world will be characterized by rationalized management, such as individual fishing quotas, limited-entry programs, and cooperatives. Second, the use of aggregate catches as an appropriate measure for determining bioeconomic win-win conditions is troubling. It is, of course, a defensible short-run measure when the baseline is open-access conditions. But from an efficiency perspective, changes in rents are a more appropriate measure. Also, measuring changes in terms of aggregate rents provides a simple and straightforward way to calculate the cost-effectiveness associated with closing a particular patch or patches. It is simply the difference between the rents when all patches are open to fishing and the rents when some patches are closed. This difference could, of course, be positive.

Overall, the bioeconomic metapopulation system outlined here is particularly useful for examining the impacts of reserve formation in a heterogeneous fishery. It also allows us to conduct many more investigations into the role of various ecological and economic structures than can be currently done empirically. In addition, in ongoing research we are using the model to analyze other spatial instruments, such as gear restrictions and individual transferable quotas, and to compare these instruments with reserves.

Biological Dispersal and Connectivity

We follow the long tradition in the ecology literature of depicting dispersal processes as dependent on relative densities.[8] That is, biomass flows from patches with high density to patches with lower density, everything else being equal. To ensure that the amount of biomass that leaves one patch for another is equal to or less than the amount that enters the patch, we impose restrictions on the dispersal parameters. In particular, we impose the symmetry condition that $d_{ij}=d_{ji}$. The symmetry condition, along with $\sum_{k=1}^{n_i} d_{ki} = 0$ i=1,2,...,n_i, ensures that whatever leaves patch i for j also arrives in j specifically from i. This is equivalent to assuming that there is no mortality in the dispersal process.



Patch	Number of linkages
1	2
2	5
3	2
4	4
5	6
6	4
7	3
8	3
9	3

Figure 1: Nine-Patch Metapopulation System

Note: The arrows represent the linkages. Port location will be used in the calculation of hypothetical travel costs to each of the patches in the simulation analysis. The percentages refer to the percentage deviation from the mean intrinsic growth rate; for example, patch 7 has the highest growth rate and patch 4 has the lowest.

In Figure 1, we illustrate the integrated nine-patch biological system that is characterized

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[8] The literature on reserves also discusses other formulations that depict unidirectional flow, generally assumed to be the result of oceanographic processes, such as currents, winds, and temperature. These models are often referred to as sink-source models (Pulliam 1988; Tuck and Possingham 2000), and they characterize dispersal flow as a process that is independent of population densities in the sinks.

by varying degrees of connectedness, where the arrows represent linkages between the patches. The shape of the patches was chosen to maximize the heterogeneity in the number of linkages. For example, patch 3 is linked to two other patches, whereas patch 2 is linked to 5, and patch 5 is linked to 6. We consider nine patches because this is the smallest number that captures the broadest set of connections. More patches would just duplicate the general pattern illustrated. Figure 1 also illustrates the elements of the sets n_i and a hypothetical location for a fishing port. In patch 1, for example, n_i consists of {2, 4}.

This metapopulation framework may be used to depict a wide variety of circumstances regarding both the behavioral characteristics of dispersal processes and the oceanographic features of a spatial setting. For example, the model can be used to describe a broadly homogeneous continental shelf area with many local microhabitats containing resources, where dispersal distances in some patches might be limited by currents, gyres, or geological features (e.g., a spit). Some patches may have higher biological productivity than others, and some, like larval pools that receive and disperse larvae from other patches, may have no inherent productivity. The framework therefore enables us to investigate in many settings how the selection of sites for reserves can affect dispersal benefits and opportunity costs.

3. Design of Marine Reserve Networks

In this section, we illustrate using numerical examples the trade-offs between biological and economic heterogeneity and connectedness that are inherent in designing a cost-effective marine reserve network. This is accomplished by solving for the optimal level of aggregate effort to maximize fishery rents subject to constraints (1), (2), and (4) for all possible configurations of reserves, including multiple-patch closures. In total, there are 2^9 (512) possible reserve configurations, each with a different optimal aggregate effort level. Then the solutions from all the 512 runs are ranked by aggregate rents to find the optimum. In more complicated systems or with more patches, the computational burden of such an approach would be too great and require the use of either branch-and-bound or heuristic algorithms.[9]

We measure the cost-effectiveness of a reserve or reserve network by comparing the aggregate rent when all patches are open to fishing with the case when patches are closed. If the case when all patches are open has the highest aggregate rents, then our measure is equal to one. Deviations below one represent cases where aggregate rents are lower, and when greater than one, rents are higher with closures than without. Of course, there are benefits of marine reserves beyond the fishing industry; for example, regulators might be interested in closing approximately 10% of the habitat for conservation of biodiversity. However, exercises such as this that find the site or sites where the effects on the fishing industry are minimized will likely reduce opposition to creating a reserve for biodiversity conservation.

The following functional specifications are employed. The per capita growth function is logistic $f(X_i)=r_i(1- X_i/ K_i)$ where r_i is the patch specific intrinsic growth rate, and K_i is the carrying capacity in patch i.[10] We follow tradition and model a Schafer production function where catch in each patch i, h_i, is proportional to the patch stock and effort level, $h_i= q_i E_i X_i$ where q_i is the catchability coefficient in patch i. We consider quadratic total costs, $C(E_i)=c_i E_i + c E_i^2$ where the slopes of the marginal cost functions in each patch are equal, but the marginal costs vary because of different intercepts c_i. The intercepts are assumed to vary with transportation costs from a hypothetical port and also include a constant opportunity cost of

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[9] The operational research and conservation biology literatures have studied extensively the terrestrial reserve site selection problem, paying particular attention to developing optimization and heuristic algorithms to solve these problems (e.g., see Polasky et al. 2000 and Haight et al. 2000).

[10] Each example was also solved with a per capita exponential (gompertz) growth function where $f(X_i)=r_i ln(K_i/ X_i)$. The exponential growth function is asymmetric with a maximum sustainable yield to the left of the corresponding level in a logistic curve. Not surprisingly, we find that the effects on reserve design are negligible between the logistic and exponential growth. Therefore, we do not present the exponential results. In addition, we ran the model using a growth function with a minimum viable population size $f(X_i) X_i = r_i(K_i - X_i)(X_i- k_i)$, where $0< k_i < K_i$ and k_i is the threshold below which the population goes extinct. Obviously, if the equilibrium population level that is determined by the economic and biological characteristics falls below k_i, then closing that particular patch will likely increase the bioeconomic benefits to the system.

effort. Total rents net the license price in patch i are equal to $R(E_i, x_i)=p\ h_i - C(E_i) - L\ E_i =(p\ q_i\ E_i\ X_i - (c_i\ E_i + c\ E_i^2) - L\ E_i)$ where p is a common ex-vessel price.

We improve the convergence of the model and reduce the dimensions of the parameter space by rescaling the system to measure biomass density $(x_i = X_i / K_i)$, which requires a scale adjustment on the intrinsic growth rates and catchability coefficients. We also set the price and catchability coefficients to one. With this scaling, patch-specific heterogeneity is expressed via growth rates and transportation costs. The patch-specific growth rates were chosen from a uniform distribution, $r_i \sim$ U(.5*r, 1.5*r), where r represents the mean level across the system and is set equal to .37. Transportation costs are assumed to vary with a patch's location relative to the port, as illustrated in Figure 1. In particular, there is one cost for the "inshore" patches (1, 2, and 3) and one for the "offshore" patches (7, 8, and 9). The patches in the middle (4, 5, and 6) have transportation costs equal to average of the inshore and offshore patches. Allowing for more variation across patches does not alter the qualitative predictions illustrated, but it does make disentangling what is attributable to what more difficult. We also assume that there is a common fish dispersal rate (d_{ij}=b for all i,j) across the patches in the system.

Because there are too many model perturbations to illustrate in this paper, we focus on cases at the extremes to illustrate potential differences.[11] In particular, we investigate an example involving low and high transportation costs. In both cases, the pattern of costs is identical but the levels differ by 30%. The cost parameter levels were chosen such that the low-cost example corresponds to the case when the fishery under open-access conditions is severely overexploited, based on the classification system of the UN Food and Agriculture Organization. The high-cost example describes a fishery where the inshore patches are severely overexploited, but the offshore areas have populations above maximum sustainable yield. The high-cost example is not

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[11] In each scenario, we did extensive sensitivity analysis on parameter levels, including linear cost functions, but for expositional purposes, we present only some of the results. We discuss additional findings throughout the text. Further details on the other simulations, along with the Matlab code, are available upon request from the author.

unlike many fisheries in the early stages of development, and the low-cost example describes a fishery that is most likely considering a moratorium or creating a reserve network.

We also report results for the case when all patches are biological integrated with the structure illustrated in Figure 1 and when the biological system is closed (b=0). We present the closed case because the results map one-to-one each patch's contribution to overall fishery-wide rents. For example, if patch 2 is the highest-cost patch in which to operate, then closing it will result in the smallest reduction in aggregate rents, and patch 2 would be the top-ranked design. Furthermore, the comparison between closed and integrated systems, where the differences are due to the spatial linkages, illustrates the role that linkages play in determining the relative contribution of each patch to overall fishery-wide rents. We also consider an example of high and low dispersal rates, which provide insights into different degrees of connectedness within one ecological structure.[12]

In addition, we compare cost-effective reserve design in an open-access fishery with the solutions found in the limited-entry system described above. Because rents are dissipated in the long run with and without reserves, we measure the cost-effectiveness in terms of aggregate catches. The comparison across the two management systems illustrates rather clearly the importance of institutional features on the design of a reserve network. It also shows that the gains from rationalizing the fishery in terms of increases in aggregate biomass levels far exceed the gains from closing areas under open access. Furthermore, the open-access simulations provide insights when total effort is unconstrained or constrained at levels near open-access levels.

Finally, we simulate a situation where the biological system undergoes a structural change when a patch is closed to fishing. This example qualitatively captures the situation where

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[12] Based on Sanchirico and Wilen (2001), we measure the dispersal rate off the intrinsic growth rate. In particular, the low dispersal rate is equal to 20% percent of the mean growth rate, and the high dispersal case is equal to 55% of the mean growth rate.

exploitation changes the fundamental properties of the marine ecosystem, and the only way to restore a patch is by closing off the area entirely. The documented effects of bottom trawling on the sea floor are an example of possible structural changes due to harvesting operations (Morgan and Chuenpagdee 2003). We measure the change by assuming that once a patch is closed, the intrinsic growth in that patch increases by 25%. That is, not only will the total population change, but also the rate at which it will grow could increase. These changes could be due to improvements in habitat quality, reduction of by-catch, and increases in the age or size structure of the population in the reserve.

Of course, the findings illustrated here depend on parameter levels, functional forms, and ecosystem structure. The results are therefore best viewed as illustrative of general processes rather than as indicators of the expected magnitude of the impacts from marine reserves. In general, the research on marine reserves has investigated their implications given a set of functional representations, and this analysis is no different. This raises questions regarding the generality of the conclusions. A general analysis is unlikely to yield definite conclusions, since there is not likely one model that summarizes the vast biological and economic heterogeneity found in commercial fisheries. We address these questions by considering various representations of the biological system and the cost function along with undertaking sensitivity analysis on major rate parameters.

Numerical Examples

We first discuss the case where both the biological and the economic habitats are homogeneous, but heterogeneity exists because of the varying degrees of linkages across the patches, as illustrated by the arrows in Figure 1. When the system is homogeneous and the biological system is closed (no dispersal), there is no difference in aggregate rents, effort, or biomass when each of the nine patches is closed to fishing. Linkages and dispersal do create differences even in the homogeneous setting, however, and play an important role in determining the magnitude of the differences across the cases. Not surprisingly, we find in the integrated homogeneous system that closing patch 5 leads to the smallest reduction in rents. Patch 2 is not far behind. This result confirms the hypothesis of Allison et al. (1998), who propose that the greater the number of patches a patch is connected to, the greater the dispersal benefits. Patches with greater linkages will increase the dispersal benefits and provide the greatest opportunities for limiting the impacts on the fishing industry. However, at the same time, the increase in the aggregate biomass is smallest when patch 5 is closed. With more avenues for dispersal, the biomass level is lower because growth is offset by net dispersal in equilibrium. Even though there is no biological and economic heterogeneity, we still find a bioeconomic trade-off between aggregate biomass increases and returns to fishing effort in this simple example.

Next, we consider examples where cost and biological heterogeneity exist: the cost heterogeneity follows the transportation cost gradient, and the biological heterogeneity is captured by differences in growth rates. The relative levels across the system are illustrated in Figure 1 by the percentage deviation from the mean growth rate. For example, patch 4 has the lowest growth rate in the system, and patch 7 has the highest.[13] Therefore, reserve site selection algorithms that choose the most biologically productive areas to close first would close patch 7, followed by patch 1, patch 2, and patch 8.

In general, there is nothing special about the current configuration of biological heterogeneity, and of course, there are many other possible situations we could have analyzed. This one was chosen because it provided a nice balance between potential combinations of high- and low-cost areas and areas of high and low biological productivity. In terms of aggregate rents, areas that are low in cost with high intrinsic growth rates are bioeconomic hotspots, and high cost and low productivity combine to create bioeconomic underperformers. The current configuration includes at least one hotspot and one underperformer within each of the three regions (inshore, midshore, and offshore), depicted in Figure 1. This allows us to investigate

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[13] Higher biological productivity in this setting occurs because some areas consistently have greater marginal productivity for all population levels. This disparity could be due, for example, to unique oceanographic and geological conditions or to the presence of greater amounts of prey in one area than another. It does not capture spawning sites that hold large concentrations of fish only during certain times of the year.

whether under certain conditions it might be more cost-effective to close two underperformers (e.g., patches 4 and 9) than to close one hotspot (e.g., patch 1 or 2), even though the hotspot is more biologically productive.

Table 1: Reserve Site Selection Rankings

	Low-Cost Example				*High-Cost Example*			
	Limited Entry			*Open Access*	*Limited Entry*			*Open Access*
Rank	*b=0*	*Low b*	*High b*	*Low b*	*b=0*	*Low b*	*High b*	*Low b*
1	None	None	None	2,4,5	None	None	None	2
2	4	4	4	2,5,6	9	9	9	None
3	9	6	6	2,4,6	8	7	7,9	4
4	6	5	9	2,6,7	7	4	7	2,4
5	8	9	5	2,6,8	4	8	8	6
6	3	2	7	2,4,9	6	6	4	4,6
7	7	8	8	1,5,6	8,9	7,9	4,9	3
8	5	7	2	2,5,9	5	4,9	8,9	2,6
9	2	3	4,9	2,4,8	7,9	8,9	6	5
10	1	4,6	4,6	4,5,6	7,8	5	7,8	3,4
11	4,9	4,9	3	2,5,8	3	4,8	7,8,9	2,5
12	4,6	4,5	6,7	3,4,5	4,9	6,7	6,7	2,9
13	4,8	4,8	4,8	2,5,7	4,8	7,8	6,9	3,5
14	6,9	1	7,9	1,3,5	4,7	6,9	4,7,9	7
15	8,9	6,8	6,8	2,3,5	6,9	4,7	4,7	4,5

Note: The numbers correspond to the patches in Figure 1. In the limited-entry setting, the patches are ranked according to aggregate rents, but in the open-access setting, we calculate the smallest (largest) change in equilibrium harvests from the case where all patches are open. In some designs, more than one patch is closed. All results are derived using a quadratic cost function as described in Section 2.

In Table 1, we present the top 15 configurations based on equation (6) for each case. This includes cases where multiple patches are closed, thereby providing information on potential optimal combinations of patch closures. Such information is important, for example, if the effects of marine reserve networks need to be analyzed, and if marine scientists recommend that 20% of the habitat (two patches) be closed to maintain a certain level of biodiversity. In addition, the top 15 cases are sufficient to illustrate that the economic and biological value associated with each patch in the fishery depends not just on its characteristics but also on its biological and economic location in the system. It is important to point out that the solutions in the table correspond to the optimal solutions for a given set of closures.

Below, we consider a low- and high-cost example, and within each case, we report the closed case (b=0) and low and high dispersal rates. In addition, we illustrate an example where closures have the effect of improving the biological productivity in the patch post reserve creation.

Low-Cost Example

Under the current assumptions, we find that keeping all the patches open to fishing is the optimal solution to equations (1), (2), (3), (4), and (5). Again, there are other reasons to close areas, and in this case, patch 4 is the cost-effective closure over the range of dispersal rates. Recall that patch 4 has the lowest growth rate and intermediate transportation costs. The presence of linkages and higher rates of dispersal does not change the fact that removing patch 4 from the system has the smallest effect on aggregate rents, as illustrated by the closed-case findings. Consistent with Sanchirico and Wilen (2002), we find that regulators should close the least-productive biological areas when the fishery is rationalized, subject to the condition that the patches are biologically self-sustaining. That is, closing the most biologically productive patches increases the opportunity costs because patches with greater intrinsic growth rates are more economically productive, everything else being equal.

Closing patch 4 will, of course, also affect the distribution of effort and biomass across the system. The postreserve spatial distributions of fishing effort and biomass are illustrated in Figure 2.[14] We find that effort increases in all patches, but the greatest increases occur in patches that are linked to patch 4. In these patches, spillover creates the greatest per unit increase in rents, and therefore the patches end up drawing greater levels of effort, everything else being equal. This effect, commonly referred to as “fishing the line,” has been observed around marine

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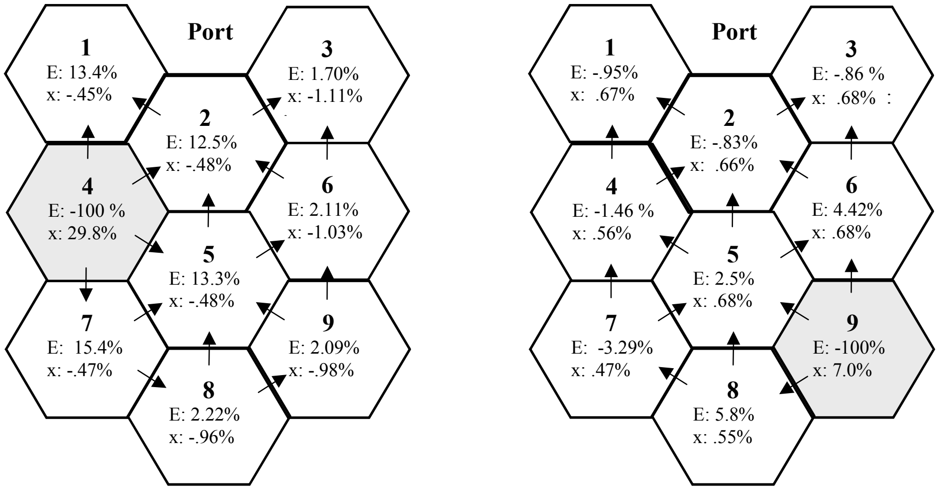
[14] The patterns of changes in the spatial distribution of effort and biomass in the top case did not change when the dispersal rate increased, and therefore we do not present the high dispersal results in Figure 2.

reserves in California, Florida, New England, and New Zealand (PISCO 2002).[15]



Low cost / low dispersal High cost / low dispersal

Figure 2: Impacts of Closures on Spatial Distribution of Effort and Biomass

Note: Shown are the percentage changes in effort and biomass in each patch from two cases: when all patches are open and when the top-ranked patch is closed. The reserve patch is shaded. The unidirectional arrows connecting the patches illustrate the equilibrium flow of biomass.

Although all patches experience increases in effort, aggregate effort is still lower with patch 4 closed than when all patches are open, because the increases do not outweigh the optimal reduction in effort required to maximize rents once an area is closed. In this example, the optimal reduction in effort is approximately 1%, implying that closing patch 4 will need to be accompanied by only a small reduction in the number of fishing licenses. The cost to society of closing patch 4, which is the reduction in fishery-wide rents, is slightly greater than 3% of aggregate fishery rents. If a reserve is sited to conserve biodiversity, the reduction in fishery

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[15] Although not addressed here, the fact that effort increases along the borders implies that searching costs, which some argue are considerable in most fisheries, could be lower once a reserve created—a benefit that comes into the model via stock-dependent cost functions. In fact, it is very likely that any spatial management policy based on the ecological system will reduce searching costs, since one would expect that fishermen have at least the same quality of information as the regulators.

rents represents a threshold for the amount the public is willing to pay to conserve marine biodiversity, if the benefits of the setaside are greater than the costs. The estimate for this threshold is readily available in this setting because the licensed, limited-entry system provides a price that captures the social value of the sustained exploitation of the fish population.

We also find that closing patch 4 results in an approximate 30% increase in biomass in the reserve. Although models that ignore the endogenous response of fishing effort to reserves might predict a 30% increase in aggregate biomass, when these responses are incorporated, the aggregate increase is only 3%.[16] Figure 2 illustrates that the optimal biomass levels in the other patches decrease in response to the increase in effort levels once patch 4 is closed. We find that the largest decreases occur in patches that are not directly connected to the reserve (patches 3, 6, 8, and 9). The decreases are smaller for the patches directly connected to patch 4, because patch 4 acts as a source of biomass that mitigates some of the effects of the increased effort. The arrows in Figure 2 depict the flow of biomass in the equilibrium. We also find that the inshore (low-cost) patches 1 and 3 are sinks in this system, and that other patches act as both sources and sinks in equilibrium depending on the relative density levels of the linked patches (e.g., patches 2 and 5).

Table 1 also illustrates the ranking of closing other patches in the system. Although patch 9 is ranked second when there is no dispersal, the presence of biological dispersal makes patch 6 second in both the low- and high-dispersal cases. This is a somewhat unexpected result, since patch 6 has lower costs and a lower growth rate than patch 9. The switch occurs because the characteristics of the neighboring patches enhance the dispersal benefits (magnitude of the

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[16] In this analysis, we find small percentage increases in aggregate biomass once a reserve is created because we are comparing reserve creation with an optimal second-best solution. Typically, researchers find much larger increases in aggregate biomass after a reserve is created because reserves are compared with open-access cases in which patches are overexploited (e.g., Hannesson 1998; Pezzey et al. 2000; Sanchirico and Wilen 2001). In addition, we find that the redistribution of effort after a reserve is created can reduce the levels of biomass in other patches (see Figure 2). Therefore, the gains in the reserve can in some circumstances be offset by decreases in population levels in other patches.

spillover) from patch 6. The size of the dispersal benefits depends on the neighboring patch characteristics for two reasons. First, the greater the differences between patch characteristics, the greater the likelihood of a difference in density levels in the two areas, implying higher levels of movements. Second, if the reserve provides biomass to areas that have lower costs per unit of effort, then the value of dispersal is larger than if the reserve is providing biomass to areas with higher per unit costs. In other words, dispersal benefits are greater when the biological dispersal gradient is in accordance with the economic gradient.

Table 1 also illustrates that the rate of dispersal has an effect on the rankings, everything else being equal. For example, with low dispersal, patch 5 is ranked fourth, and with high dispersal, patch 9 is ranked fourth. Moreover, patch 2 is ranked sixth with low dispersal and eighth with high dispersal. The differences arise because with higher dispersal rates, the potential reserve population is smaller, everything else being equal.[17]

Finally, we find that in some cases it is more cost-effective to close two patches than it is to close a single patch. For example, with low dispersal rates, it is preferable to close patches 4 and 6 rather than patch 1. This phenomenon occurs when there exists bioeconomic hotspots and underperformers. With multiple closures, however, the top combinations do not necessarily reflect the combinations of the top individual patches, as in the closed system. For example, in the high-dispersal case, closing patches 6 and 7 results in a lower reduction in rents than closing patches 4 and 5. This is because patches 4 and 5 are linked but patches 6 and 7 are not, implying that the spillover benefits are potentially higher when 6 and 7 are closed than when 4 and 5 are closed. Because patches 6 and 7 are not directly connected, there is less redundancy in the

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[17] We also did sensitivity analysis on the intrinsic growth rates. For example, we reran the cases presented in Table 1 with the intrinsic growth rates 30% lower (we maintained the pattern illustrated in Figure 1). Qualitatively, there was no significant difference in the patterns; for example, patches 4 and 9 were still the optimal closure in the low- and high-cost cases, respectively. There were some differences in the rest of the top 15 (patches changed by one or two places) because of the interdependencies of the dispersal rates and growth rates. We also ran the model with different patterns of growth rates and levels, but again the results in Table 1 are illustrative of the general patterns that we found in these other analysis.

biological system (i.e., two reserve patches are directly connected and supply each other with biomass directly). In designing reserve networks, many researchers contend that the reserves should be connected, but as these results illustrate, that might not be the best strategy if a regulator is concerned with the effects on the industry.[18]

Our multiple-patch closure results are consistent with the terrestrial reserve design literature, which typically considers reserves as a means to protect biodiversity or ecosystem services. This literature finds, as we do, that the cost-effective pair of patches to close is not necessarily the combination of the two highest-ranking single-patch closures, because of the interdependencies due to the underlying spatial bioeconomic processes. In reserve selection problems, these effects pose problems for heuristic algorithms, such as the greedy algorithm, that simply choose the highest-ranking patches without taking into account these interdependencies (e.g., see Newbold 2002).

The two left panels in Figure 3 present the aggregate rent-biomass trade-offs for the low-cost example when closing multiple patches. The graph illustrates the percentage reduction in rents for a percentage increase in biomass for every combination of one-, two-, three-, and four-patch closures, where each mark represents a different closure permutation. The optimal solution is the base case from which the percentages are calculated, and in this case, the no-closure case is optimal. Not surprisingly, the more patches that are closed, the more likely that rents are lower and biomass levels are higher. What is surprising, however, is the degree to which the results are not monotonic with respect to the number of closures. In the high-dispersal case, for example, the lowest-performing two-patch closure has increases of biomass around 5% but at a cost of 10%. However, for the same cost, the regulator could have closed three patches and had approximately an 8% increase in biomass. As evident by the range of the axes, higher dispersal

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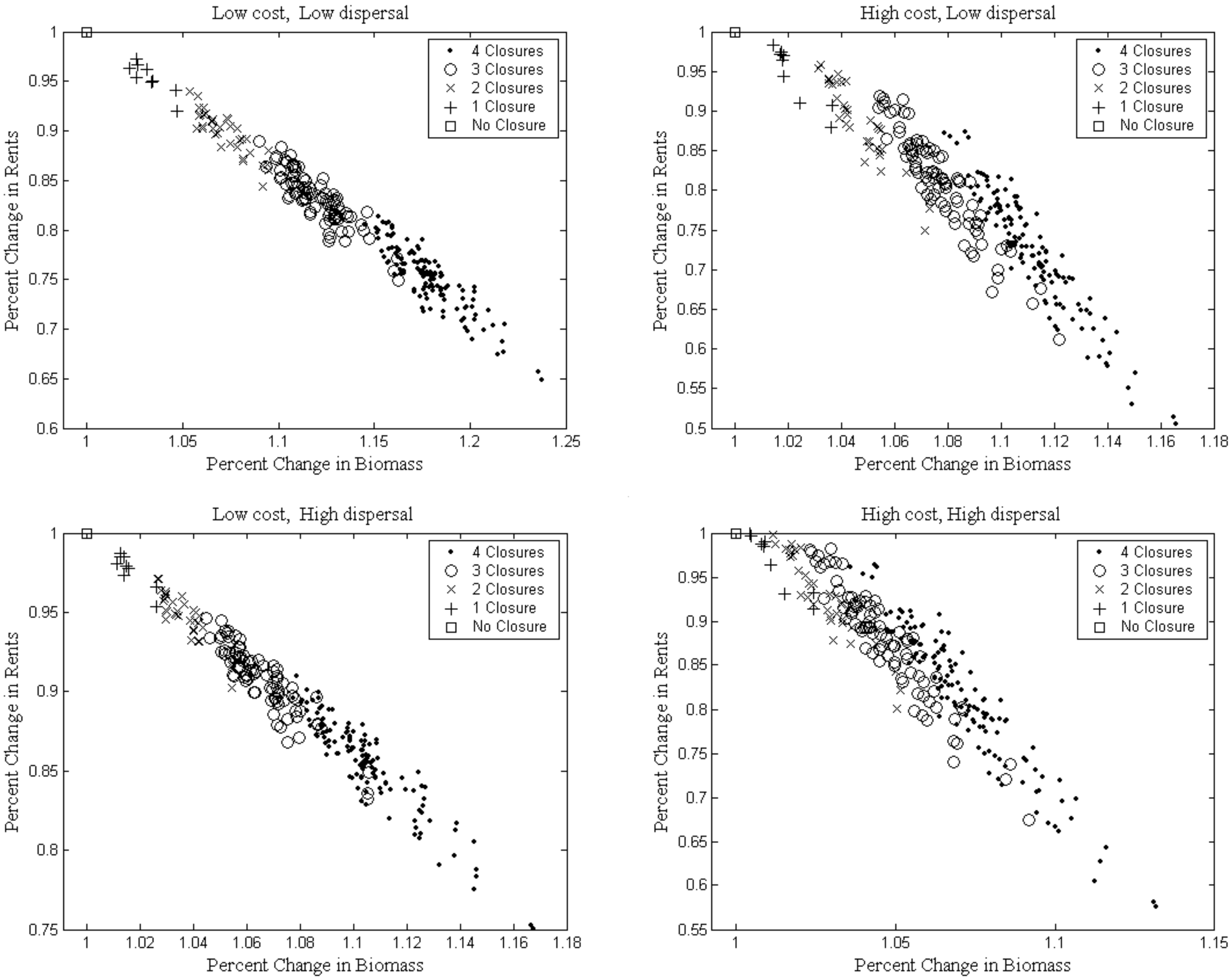
[18] A justification for linking reserves is that without the link, neither patch's population levels will persist, since neither population is self-sustaining. All patches are self-sustaining, however, in this example. Another reason for including redundancy as a design criterion for a marine reserve network is to hedge against the collapse of any one reserve population.



Low cost, Low dispersal

High cost, Low dispersal

Low cost, High dispersal

High cost, High dispersal

Figure 3: Trade-Off Between Aggregate Rent and Biomass

Note: The marks in each panel illustrate for each permutation of 1, 2, 3 and 4 closures the percentage change in aggregate rents and biomass from the optimal case, which in these examples is the case with no closures. The high-cost example has costs that are 30% higher than the low cost, and difference between the low and high dispersal is on the same order. The pattern of costs and growth rates does not vary across these examples.

rates also decrease the magnitude of the effects, everything else being equal. Overall, these results further illustrate the spatial effects in cost-effective reserve selection due to patch connectedness and heterogeneity and the importance of using the best available (natural and social) science in designing reserve networks.

Using the results from the simulations, we fit a line where the slope measures the average percentage reduction in aggregate rents to a percentage increase in aggregate biomass and is equal to –1.3. Therefore, under the current assumptions and across one, two, three, and four closures, we find that for every percentage increase in aggregate biomass, there is on average a 3% reduction in rents. Surprisingly, the magnitude of the dispersal rate has virtually no effect on this estimate, since the estimate with high dispersal is also –1.3. One could imagine comparing such a measure across different fisheries, enabling regulators to determine *ex ante* which fisheries may involve less opposition to reserves by the fishing industry.

High-Cost Example

The high-cost example captures a fishery where the optimal biomass levels in the inshore patches are below maximum sustained yield, and the middle and offshore biomass levels are greater than maximum sustained yield. Effort levels in the offshore patches are low because of the high costs, and for all practical purposes, the patches are relatively unexploited. A fishery with these characteristics is not likely to be considered for a marine reserve network. However, we illustrate the case because the differences between the results with high and low costs are helpful in understanding the fundamental processes. Recall that the only difference between the low- and the high-cost cases are that the costs are 30% higher in each patch.

Given that the offshore patches see very little fishing effort at the optimal, it is not surprising that the offshore patches are the three top-ranked closures in the closed case, where the ordering is from least to most biologically productive (patches 9, 8, and 7). We also see in Table 1 that even in the closed case, it is least costly to close both patches 8 and 9 rather than patches 1, 2, 3, or 5. The rankings with dispersal again differ from the closed case.

In Table 1, it is evident that closing the area of high biological productivity (patch 7) is not as costly as in the low-cost example. Why is this case if only the absolute levels have changed? In this case, patch 7 is simply too expensive to fish in, even with the higher productivity per unit of effort. Therefore, its economic value to the system is much lower than before, reducing the economic effects of its closure and hence making it less costly to close. This illustrates a rather obvious rule of thumb in reserve design in rationalized fisheries: close highly productive areas that are high in cost. Unfortunately, the advocates of marine reserves have not paid attention to the latter part of that statement and instead argue for closing areas based solely on the ecology of the patch. In addition, we find that the hypothesis of Allison et al. (1998) does not hold when the system is biologically and economically heterogeneous. In fact, closing multiple patches ranks above closing patches 5 and 2, and with high dispersal rates, neither patch 5 nor patch 2 is in the top 15 combinations.

Another difference between these two examples is the spatial distribution of effort and biomass (see Figure 2). Unlike in the low-cost example, effort levels decrease in the patches not directly connected to the reserve. Because patch 9 saw little fishing effort prior to closure, the difference in aggregate effort levels is small between closing patch 9 and keeping all patches open. In addition, the increase in optimal biomass is small (7% increase) and not enough to have significant ripple effects beyond the patches directly connected to it. With effort moving toward the border of the reserve, we find that there is a slight increase in patch biomass levels in the nonbordering patches. This is the opposite result from the low-cost example, where patch biomass levels decrease outside the reserve.

Figure 3 also illustrates strong spatial interdependencies where closing four patches can be achieved at the same cost as closing two, but with a doubling of the increases in aggregate biomass. In general, the results plotted in the two right panels of Figure 3 are more bunched relative to the low-cost cases, but the magnitude of the changes is larger. The high-cost, high-dispersal case is also surprising in that for certain combinations of four patches, there is very little change in rents. Overall, the estimated slope is –3.2, which means that on average there is 3.2% reduction in rents for each 1% increase in biomass. This is higher than in the low-cost case, but just as before, a 30% increase in the dispersal rate had virtually no effect on the estimate.

Open-Access Designs

We also report the top designs when the fishery is operating under open access. In this case, we solve equations (2) and (3) with L set equal to zero for all possible configurations of closures and rank the cases according to total catch. The results for the case of low cost and low dispersal are reported in Table 1 alongside the limited-entry results. Given the current assumptions on the cost levels, the open-access population levels without a reserve are severely exploited. Based on the previous literature (Holland and Brazee 1996; Hanneson 1998; Pezzey et al. 2000; Sanchirico and Wilen 2001), we would expect reserves to increase catches under the current cost assumptions. This is indeed what we find, except now we find that the optimal design is a reserve network where patches 2, 4, and 5 are closed. In fact, the top 15 results consist of closing some collection of three patches or 33% of the fishable habitat.

Under open-access conditions, the opportunity cost of closures is the lost catch, implying that closing the patches that are overexploited is likely to have the smallest impact on the industry. Overexploited patches typically have lower cost, which is the case with patch 2. In a multiple-patch system with complex dispersal patterns and heterogeneous growth rates, however, the rule of thumb that has emerged from simple two-patch analysis does not necessarily hold (Holland and Brazee 1996; Hannesson 1998; Sanchirico and Wilen 2001). The top design involves closing patch 2 but also patches 4 and 5, both of which that have higher costs than patches 1 and 3. The combination of habitat and connectivity heterogeneity along with cost heterogeneity—all likely characteristics of fisheries—leads to more complex design considerations. The low-cost rule-of-thumb solution falls within the top 15, however. An important question for future empirical work on reserve designs, therefore, is quantifying the empirical magnitude of the potential reduction in catches from applying the rule of thumb.

In Table 1, we also report the open access case with high costs and low dispersal, everything else being equal.[19] The top-ranked design is the closure of patch 2; the second is leaving all patches open to fishing. Recall that costs in this case are such that the inshore patches are overfished, and the offshore patches have populations above maximum sustained yield even under open-access conditions. Compared with the low-cost example, we find that the top 15 results consist of closing single and two patches. This difference is due to the fact that the gains from closures are not as high, since the equilibrium population levels are not as depleted as in the low-cost case.

Considering both open-access and limited-entry fisheries under the same set of parameter levels illustrates rather strikingly how the value of a patch depends not just on its structural characteristics but also on the institutional setting by which the fishery is regulated. As Table 1 shows, the top design is different even under identical assumptions on parameter levels. We also find that the aggregate biomass levels with all patches open to fishing under the more rationalized system are, on average, three times larger than the levels under open access with three patches closed to fishing. These results imply that the gains from moving the system from open access to a more rationalized system will result in larger increases in the aggregate biomass than keeping the fishery operating under open-access conditions, even with 30% of the fishery closed to fishing. Although the 30% result is dependent on the current set of assumptions, we believe that the qualitative result holds in more general settings.

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[19] The open-access designs were also run using a depensatory growth function with a minimum viable population level around 10% of the carrying capacity. Although we did not find any qualitative effect on the limited-entry results because in our examples the equilibrium levels exceed the threshold, the same is not true for the open-access cases. There, we find that the equilibrium population levels are close to the threshold level under logistic growth (in the model with depensatory growth they would be zero). For example, in the case of low costs and low dispersal, we find that under open-access conditions, aggregate catches are maximized when all the inshore (low-cost) patches are closed. This result differs from the logistic analysis. Upon reflection this result is not surprising, since with each patch open, the catch levels in the inshore patches are very small when the equilibrium level is close to the threshold level. The importance of the result is somewhat muted, since we find that the potential increases in aggregate biomass levels from moving to a more rationalized management system far exceed those from using marine reserves under open access.

Biological Productivity Effects of Marine Reserves

Whereas traditional closures were designed to protect the spawning area of a single species, many researchers consider marine reserves the only *ecosystem* tool available for fishery management (Palumbi 2002). In addition to being able to protect a system from future fishing effort, reserves can help the system recover from years of exploitation. There is empirical evidence of increased biomass, density, size, and diversity in reserves in both temperate and tropical environments (Halpern 2003). Improvements in age and size distribution are important because there is evidence that egg production exhibits increasing returns to scale with respect to size (PISCO 2002). To fully capture these effects, an age-size cohort model is needed, but in a lumped parameter model, we can proxy for these effects by assuming that the intrinsic growth rate in a patch will increase after it is closed. That is, not only will the total population increase, but also the rate at which it will grow.

We investigate the implications of structural changes in biological productivity post reserve creation by considering the optimal designs when the intrinsic growth rate of patches increase by 25% once they are closed, everything else being equal. The patches that remain open to fishing experience neither an increase nor a decrease in the intrinsic growth rate; a decrease could occur if fishing effort increased in these areas post reserve creation. In our formulation, the reserve patch experiences the direct effect, but the effect ripples throughout the system based on the connectivity patterns. Admittedly, this is an ad hoc representation of what biologists are considering. Having said that, we expect that the qualitative results from this exercise are illustrative of the potential biological productivity effects from closures. It is important to point out that we are modeling these as discrete effects that are assumed to hold only when there is no fishing pressure in the patch. There are, of course, other possible formulations, such as including discrete jumps in ecosystem productivity in the range of positive fishing effort (threshold effects) or modeling these effects as a continuous function of fishing effort. In many ways, this specification provides the most optimistic scenario for reserves to be optimal in our setting.

Therefore, if we do not find that reserves are optimal in this setting, they are unlikely to be optimal in the other possible specifications.

Table 2: Reserve Site Selection Rankings with Biological Productivity Effects

	Low-Cost Example		*High-Cost Example*	
	Limited Entry		*Limited Entry*	
Rank	*Low b*	*High b*	*Low b*	*High b*
1	None	4,6,8	None	4,6,7,9
2	4	4,6	9	6,7,9
3	5	2,7,9	4	4,6,7,8,9
4	6	4,6,9	7	4,7,9
5	4,6	6,7	4,9	6,7,8,9
6	2	4,9	6	4,7,8,9
7	9	6,7,9	7,9	4,6,8,9
8	4,9	4,6,7	8	4,6,9
9	7	5,6	4,6	4,6,7
10	8	7,9	6,7	4,6,7,8
11	4,5	7,8	4,8	7,8,9
12	5,6	5,6	6,9	7,9
13	4,8	2,9	6,8	4,8,9
14	2,9	4,7,9	8,9	6,7,8
15	6,7	2,4,9	4,7	4,6,8

Note: The numbers correspond to the patches in Figure 1. The patches are ranked according to aggregate rents. In some designs, more than one patch is closed. All results are derived using a quadratic cost function and the assumption that the intrinsic growth rate in the closed patch(es) increases by 25% relative to the case when the patch is open to fishing.

Table 2 reports the results of these simulations for the four cases (low versus high cost and low versus high dispersal).[20] Across the cost examples, we find that leaving all patches open to fishing is the optimal solution in the low-dispersal cases. On the other hand, when we consider these effects in fisheries with higher rates of dispersal, reserves are part of the optimal second-best solution. We did not find this result when these biological productivity effects were not present. In the high-cost example, leaving all patches open to fishing results in a approximately

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[20] The open-access designs are not presented because they are qualitatively similar to those presented in Table 1.

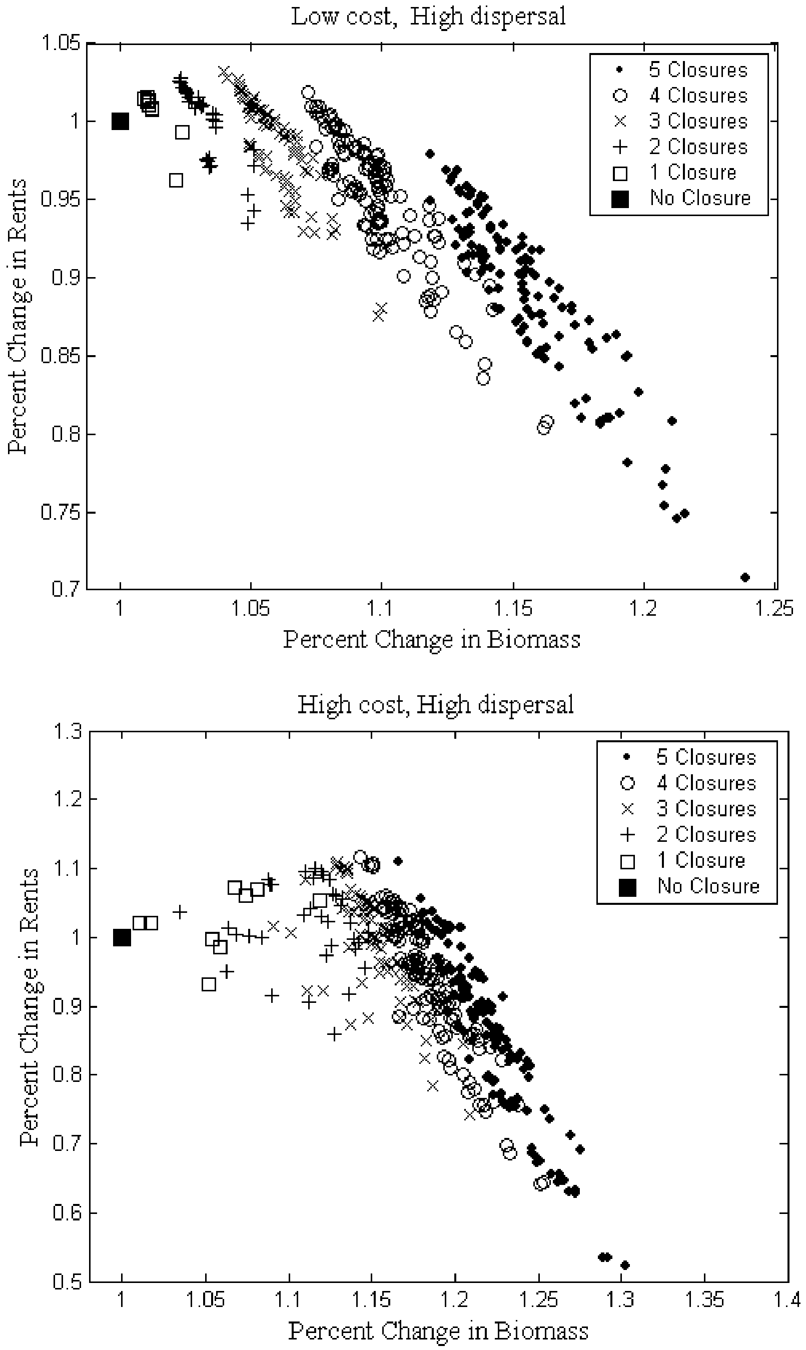

Figure 4: Biological Productivity Effects of Marine Reserves

Note: The marks in each panel represent each permutation of 1, 2, 3, 4 and 5 closures. All parameter levels and functions are equal to those used to derive the results for these particular cases in Figure 3, except that reserve patches experience a 25% increase in the intrinsic growth rates.

10% reduction in rents and a 13% reduction in aggregate biomass compared with the optimal design, which is the closure of patches 4, 6, 7, and 9. In the optimal design, the lower-cost patches (1, 2, and 3) and patch 5, which has the highest biologically productivity of the next lowest-cost patches (4, 5, and 6), are receiving biomass directly from a closed patch. Therefore, reserve biomass is flowing directly into patches that have the highest bioeconomic value to the fishery. We see in Table 2 that the top 15 designs consist of different combinations of closing patches 4, 6, 7, 8, and 9, where patches 7 and 9 appear in 11 of the top 15. These same patches constitute the 15 top-ranked designs in the low-dispersal setting, although the combinations and ordering differ.

The results for the low- and high-cost example in the high-dispersal case are illustrated in Figure 4, where we plot the percentage deviation in aggregate rents and biomass from the optimal design (illustrated at the point (1,1)). We do not illustrate the low-dispersal cases because the results are qualitatively similar to those presented in Figure 3. In both cases illustrated in Figure 4, the present value of sustainable aggregate rents when all patches are open to fishing is lower than a large fraction of the designs involving single and multiple closures. In the top panel, three closures or 33% of the habitat is the optimal design; in the lower panel, four closures is optimal. It is clear from Figure 4 that some designs outperform others, implying that randomly selecting areas to close, as advocated by Roberts (1994), can result in lower biological gains and larger reductions to the value of the fishery as opposed to employing the best available natural and social science.

4. Conclusions

Unlike most of the researchers on marine reserves, we analyze the optimal (second-best) design of reserve networks in a limited-entry fishery where the regulator is choosing the level of optimal aggregate fishing effort and deciding which patches to close to maximize the present value of sustainable rents. The first-best optimal is when the regulator can control the level of effort in each location. By assumption, this is not attainable in this paper; instead we model the situation where the regulator can use a combination of closures, which is an extreme control of fishing effort in any location, and controls on the aggregate total effort. The model is, therefore, consistent with the traditional regulatory scale of fishery management, where regulations are applied across large areas that in many circumstances include multiple subpopulations. The only difference with traditional management is our regulator knows the spatial structure but is unable to design policies at such a fine scale because of political constraints.

The multiple-patch analysis highlights the relative role that linkages and patch heterogeneity play in determining the net effects of reserve creation—a point that is missed in a two-patch analysis. This includes not just the primary linkages between the reserve and its nearest neighbors but also the secondary linkages between the patches connected to the reserve and the other patches in the system. The biological literature has focused on the biological effects of connectivity, which are illustrated here, but we find that linkages are also important for predicting the response of fishing effort. Choosing patches that have the greatest potential to provide spillover to other patches is not the best bioeconomic strategy unless the bioeconomic system is homogeneous. As the degree of bioeconomic heterogeneity increases in the system, however, it is the bioeconomic habitat conditions combined with the nature of the linkages that are the critical drivers.

In general, we find that the optimal second-best solution is to permit fishing in each patch. When there are biological productivity effects post reserve creation, however, we find that multiple closures can be an integral part of an efficient solution, depending on the dispersal rate. The former result is consistent with the previous literature, but to our knowledge, the latter result has not been previously highlighted. Not surprisingly, we find that patches that are low in productivity and/or high in cost are more likely to lower the opportunity costs associated with closing a particular patch, and therefore these patches are more likely to be acceptable to the fishing industry, everything else being equal. We also show that a significant determinant of the magnitude of the benefits from a reserve is the bioeconomic characteristics of the neighboring patches. This implies that simple site selection rules based solely on a patch's bioeconomic characteristics might go astray unless the conditions of the remaining fishable habitat, especially the patches that are connected to the reserve, are considered.

In some cases, we find that closing two patches lowers aggregate rents less than closing one patch—a discovery that necessitates the analysis of reserve creation in a multiple-patch setting. The result is due to the combination of bioeconomic hotspots—low-cost patches of high biological productivity—with high-cost and low-productivity areas, where the opportunity cost of closing a hotspot is greater than that of closing two of the least-productive patches. Our findings also show that in order to realize the greatest economic gain, reserves need to be accompanied by effort-reduction policies. In general, the larger the habitat closed, the greater the number of licenses that need to be purchased, everything else being equal.

Given the current political economy of reserve creation and based on our findings, regulators might want to combine effort-reduction policies with closures because the industry might object less if it sees potential compensation for the lost fishing habitat. Compensation is provided to the exiting fishermen when their licenses are purchased (or through vessel buyback programs). The remaining fishing effort is also indirectly compensated, since the returns per unit of fishing effort could be higher once the optimal number of licenses is retired. Without coupling reserve creation with policies that rationalize a fishery, any economic gains from a reserve will be dissipated as fishermen continue to operate under rule-of-capture incentives—the very circumstances that have created momentum for increasing the scale and scope of marine reserves.

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