A Bioeconomic Model of Marine Reserve Creation*

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This paper employs a dynamic and spatial model of renewable resource exploitation to investigate the effects of marine reserve creation. The model combines a metapopulation model incorporating resource patch heterogeneity and dispersal with a behaviorally based spatially explicit harvesting model that assumes that fishermen choose location in a manner that eliminates spatial arbitrage opportunities. The combined spatial bioeconomic model is used to simulate the effects of reserve creation under various ecological structures. We identify parameter configurations and ecological dispersal processes that give rise to a double-payoff in which both aggregate biomass and harvest increase after an area of the fishery is set aside and protected from exploitation. © 2001 Academic Press

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I. INTRODUCTION

For the past decade there has been growing support among biologists for an expansion of the use of marine reserves, or areas protected from fisheries exploitation and other consumptive uses.1 Many proponents of reserves see them as a natural extension of the terrestrial park system, designed to protect unique examples of marine habitat from particular types of degradation and to provide laboratories within which to study relatively undisturbed marine ecosystems. This notion of protected areas for study and observation is not a new one, and there are many examples of areas of special interest identified in various coastal zones around the world. What is new is the momentum gathering behind proposals by an

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1See, for example, Davis [5]; Polacheck [19]; Dugan and Davis [6]; Botsford et al. [2]; Quinn et al. [21]; Roberts and Polunin [23]; Man et al. [16]; Carr and Reed [4]; Allison et al. [1]; Lauck et al. [13].
alliance of environmental groups, nongovernmental organizations (NGOs), and conservation biologists, to significantly increase the scale of protected marine habitat. This is evident, for example, in the proclamation endorsed by 400 prominent marine scientists at the First Symposium on Marine Conservation Biology to “increase the number and effectiveness of marine protected areas so that 20% of Exclusive Economic Zones and High Seas are protected from threats by the year 2020.” It is also evident in several similar endorsements by the World Conservation Union and the parties to the Convention on Biological Diversity, as well as in the new role afforded “critical habitat” in the recently revised Magnuson–Stevens Fishery Conservation and Management Act to manage U.S. fisheries. In response to this groundswell of scientific support, President Clinton recently announced on May 26, 2000, a directive to establish a system of marine protected areas in the coastal waters of the United States.

Most would agree that protected areas are likely to generate new consumptive and nonconsumptive benefits, as well as research and education benefits and perhaps some existence values. Much of the empirical case study research on the ecological impacts of reserves supports this likelihood, showing that within the boundaries of reserves, populations grow to larger sizes, attain broader age and size distributions, and achieve more diverse assemblages. In addition, there is evidence in some cases that the productive quality of the habitat increases, particularly where bottom trawling and dredging were destructive of the substrate.

Some of these benefits from closed areas are likely to be captured in enhanced value of certain on-site activities such as diving, whereas others may be existence or heritage values associated with particular unique marine ecosystems. A major challenge exists to evaluate and quantify the net benefits from these beneficial ecosystem changes within newly established and potential reserves.

Not everyone supports a major expansion of marine reserves, of course, and fishermen have been among the most vocal skeptics. At issue to fishermen is whether there will be significant costs to them in the form of lost access to areas of traditional use. Whether reserves are likely to be costly to fishermen is a complicated issue. We know, for example, that closing all coastal habitat would essentially cost fishermen all of their current income and we also know that doing nothing leaves us with the status quo in fisheries management. But what about closing some fraction of coastal habitat, on the order of the 20–30% levels suggested by conservation biologists? Several different kinds of arguments have been put forth suggesting that reserves at this level would actually benefit fishermen. One argument is that status quo management methods are not safe enough and are destined to fail over the long run. Those who believe this conclude that reserves are the only way to ensure protection of marine populations from the management process itself. More interesting arguments have been put forth

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2See Carr and Raimondi [3].
3See, for example, the recent special issue of Conservation Biology, January 1999.
4This is the position taken by Ludwig et al. [15] and implicitly endorsed by many proponents of reserves as “insurance” against management failure.
5For example, “compared to the benefits, reserves have few costs. Over the short-term, reducing the area of fishing grounds is a cost, since catches may fall. However, a reduction in the area of fishing grounds of 10–20% will probably hardly even be noticed in terms of yield, since catches normally vary considerably from year to year. Even if catches are reduced, it is a cost which few fishers can afford not to pay!” (Roberts [22]).
suggesting that closing some areas may actually enhance fisheries productivity. This argument is based on the possibility that larger protected populations of more fecund individuals within reserve boundaries may actually increase the flow of larvae outside the boundaries, thus enhancing the fishery in the remaining open areas. The mechanisms that might lead to this possibility are complicated, and they depend most importantly on life cycle and oceanographic transport mechanisms, about which little is known empirically.6

From the standpoint of skeptical fishermen, the question is not just will a reserve increase available abundance outside of its boundaries, but rather will this increased abundance generate a sustainable increase in harvest sufficient to offset the losses associated with foreclosed harvest opportunities in the reserve? This is the question we focus on in this paper. We undertake a predictive analysis with a political economy perspective, and it begins by recognizing the potential legitimacy of the claims of displaced fishermen as stakeholders. Some proponents of reserves would argue that fishermen have no prior rights to traditional fishing grounds and that their implicit “takings” suggestions are therefore invalid. We take a more pragmatic stance, recognizing that while this may be true from a strictly legal sense, prior use of open access resources has historically been respected and indeed, generally used as a basis for subsequent alienation and privatization of rights. Furthermore, regardless of the legal basis for claiming permanent rights, the political reality is that it will be much more difficult to establish reserves in areas in which displaced fishermen suffer large losses. Hence we seek to identify circumstances in which the opposition to reserves by potentially displaced fishermen will be minimized, namely situations in which fishermen might actually gain from reserve creation. In the next section we lay out a simple bioeconomic model involving exploitation over space. In the third section, we use the model to analyze the implications of closing areas and establishing reserves. The final section discusses the results and summarizes.

II. A BIOECONOMIC MODEL OF SPATIAL EXPLOITATION

A serious exploration of reserve design issues should incorporate key ecological concepts dealing with the role of space in biological systems and the manner in which space affects fundamental processes. Of particular importance are notions of resource patchiness and heterogeneity, biophysical linkages, and dispersal mechanisms connecting patches.7 These concepts are currently being used to address issues in terrestrial reserve design such as whether it is best to have a single large or several small reserves, how corridors, edges, and patch configurations affect species viability and diversity, and how viable population sizes are maintained via spatial dispersal.

Since establishing marine reserves is generally most contentious in an exploited system, a robust model also ought to incorporate a reasonable representation of a harvesting system with sensible behavioral assumptions as well as realistic depictions of the institutional setting within which harvesting typically takes place. In most discussions of marine reserves, the harvesting sector has been treated

6See Carr and Reed [4], and Carr and Raimondi [3].
7Not coincidentally, these are core intellectual concepts from the new field of conservation biology, a field that has emerged out of trying to understand issues raised by reserve creation in terrestrial settings.
superficially. For example, some biological models of marine reserves assume that fishing mortality is constant before and after reserves, an assumption clearly unlikely if reserve creation alters economic incentives (Man et al. [16]; Carr and Reed [4]). Others assume that total fishing effort is constant but fishing mortality in the closed area is simply transferred into the open area after reserve establishment (Polacheck [19]; Holland and Brazee [12]). This is a step better than ignoring behavioral responses, but it only makes sense in particular circumstances, such as under limited entry programs with rents high enough to support the new higher effort level in the open area.

The model employed in this paper embeds two critical features that seem necessary to address the more important reserve design issues. First, while it is continuous in time, it is discrete over space. This discreteness is an important feature in our mind. Most other models developed to explore reserves consider the problem of carving out a fraction of space in an otherwise homogeneous system in which mixing is perfect, uniform, and (generally) instantaneous. While this is convenient analytically, it makes it difficult to explore the implications of recent work in ecology that stresses patchiness and heterogeneity across space. Ideally, if the policy issue were one of choosing patches to select, then it would be important to know the characteristics to focus on from the spectrum of choices. Would it be better to pick areas with high intrinsic growth rates? High dispersal rates? Large numbers of linkages? Or, would it be wise to focus on high cost areas? Or low catchability areas? These issues cannot be readily addressed in analytical models that homogenize away important bioeconomic differences between patches. Second, our approach incorporates a richer depiction of the harvesting sector by embedding behavioral assumptions that motivate choice over space as well as over time. In particular, we assume that fishermen respond to profit opportunities by entering and exiting the fishery and by moving over space in response to spatial arbitrage opportunities. Consequently, the bioeconomic system is fully integrated over time and space, a feature that leads to the conclusion that reserve design is a joint economic and biological problem.

A. The Biological Model

We begin with a 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. Following typical metapopulation formulations, let the own rate of change of biomass in patch \( i \) be given by:

\[
\dot{x}_i = f_i(x_i) x_i + d_{ii} x_i + \sum_{j=1}^{n} d_{ij} x_j, \quad i = 1, \ldots, n
\]

where \( x_i \) is the biomass level in patch \( i \), \( f_i(x_i) \) is the per capita growth 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 \( j \). In this formulation, own growth is separable from dispersal and the dispersal process can be flexibly modeled via appropriate choice of the coefficients \( d_{ij} \).\(^{11}\) The ecological literature typically depicts dispersal processes as either density dependent or uni-directional. Density dependent dispersal processes have biomass flowing between patches in a manner dependent upon relative densities. The simplest type of representation of a density dependent dispersal process would be one in which the dispersal mechanism between patch one and two is

\[
d_{11}x_1 + d_{12}x_2 = b(x_2/k_2 - x_1/k_1)\]

and between patch two and one is

\[
d_{22}x_2 + d_{21}x_1 = b(x_1/k_1 - x_2/k_2)\].

In this simplest of cases, there is a single common dispersal parameter \( b \), and population biomass flows between patches in a manner dependent upon patch densities relative to natural carrying capacities. In this system, own growth is augmented by dispersal flows from areas of high relative densities to areas of low relative densities.

Although some of the analytical ecology literature focuses on density dependent dispersal processes, there have been other formulations that depict uni-directional 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 [20]; Tuck and Possingham [28]), and they characterize dispersal flow as a process that is independent of population densities in the sinks. For example, a two patch sink-source model might have growth in the source patch equal to

\[
r_1x_1(1 - x_1/k_1) - b(x_1/k_1)
\]

and growth in the sink patch equal to

\[
r_2x_2(1 - x_2/k_2) + b(x_1/k_1).
\]

With this type of dispersal process, biomass continues to flow between patches even after each population has reached its natural equilibrium. This general metapopulation model may be used to depict a wide variety of circumstances regarding both behavioral characteristics of a population and oceanographic features of a spatial setting.

B. A Model of Spatial Exploitation

To complete the bioeconomic model, we need to add a model of an exploiting industry. The model we use here depicts fishermen operating under open access conditions, responding to profits by entering until net rents are driven to zero, as depicted in the important papers by H. S. Gordon [7] and Vernon Smith [27]. It is relatively straightforward to generalize the Gordon/Smith open access models to consider movement over space as well as entry/exit from an outside pool. This can be done by adding a spatial dispersal component to the Smith model, in a manner similar to the metapopulation depiction of biological dispersal. Let \( E_i \) and \( x_i \) denote the patch specific levels of effort and biomass, respectively, in each patch \( i \) and let \( R(E_i, x_i) \) be corresponding rents in patch \( i \). Then we can hypothesize that the level of effort, \( E_i \) in patch \( i \), will change according to:

\[
\dot{E}_i = s_iR_i(E_i, x_i) + \sum_{j=1}^{n} s_{ij}[ R_i(E_i, x_i) - R_j(E_j, x_j)] , \quad i = 1, 2, \ldots, n
\]

\(^{11}\)This lumped parameter representation is itself very stylized since it ignores important aspects of real population growth and dispersal dynamics including age- and size-specific mechanisms, selectivity issues, and more complicated spawner/recruit processes. However, it is analytically tractable whereas richer models must be analyzed using simulation methods.
In this specification, effort in patch $i$ changes in response to the level of rents vis-à-vis outside opportunities (captured in the first term), and net dispersal, depicted by the second term. The second term consists of a sum of pairwise spatial dispersal rates, each proportional to rent differentials across space between the patch in question and alternative patches. Hence there will be dispersal from patch $j$ into patch $i$ if rents in $i$ exceed those in $j$, and dispersal to $j$ from $i$ if the net difference is negative. At any point in time, patch $i$ may be contributing to a subset of patches experiencing higher relative rents and drawing from another subset experiencing relatively lower rents. For the system as a whole, these spatial forces tend to redistribute effort over space in a manner that, in the long run, equalizes net rents across all patches.\footnote{To be consistent with the ecology literature, we impose the following restrictions on the dispersal matrix: (i) $d_{ij} < 0$ emigration out of $i$, (ii) $d_{ij} > 0$ immigration into $i$ from $j$, and (iii) $\sum_{k=1}^{n} d_{ik} = 0$, $i = 1, 2, \ldots, n$ implying no births or deaths during dispersal. For example, if the matrix has full rank, the implication is that each patch is connected to every other patch via dispersal, as might be the case in a broadly homogeneous continental shelf area with many local microhabitats containing resources. On the other hand, one might wish to depict a coastal upwelling system within a narrow band of substrate in which the patches are adjacent with each linked via dispersal to neighboring patches only. In this case the $D$ matrix would be band diagonal. A sink-source system with a single source and multiple sinks would be represented with entries only in the column representing the source. Note too that it is possible to capture a range of heterogeneous circumstances with respect to the system of individual patches. Some patches may have inherently high productivity whereas others may have no inherent productivity, as would be the case with a larval pool that receives and disperses larvae from other source patches. See, for more detailed descriptions, Carr and Reed [4], Allison \textit{et al.} [1], Sanchirico [24], and Sanchirico and Wilen [25].}

We can stack Eqs. (1) and (2) for all $n$ patches, and combine with the biological system to get:

$$\dot{E} = SR(E, x) + \Delta R(E, x)$$

$$\dot{x} = F(x)x + Dx - H(E, x)$$

where $\dot{x}$ and $x$ are $n \times 1$ vectors, $F(x)$ is a $n \times n$ diagonal matrix ($F_{ii} = f_i(x_i)$ for all $i = 1, \ldots, n$), and $D$ is an $n \times n$ matrix.\footnote{The elements of $S$ and $\Delta$ are: $S_{ii} = s_i$, $S_{ij} = 0$, $\Delta_{ii} = \sum_{k=1}^{n} s_{ki}$, and $\Delta_{ij} = -s_{ij}$ for $i, j = 1, \ldots, n$ with $i \neq j$.} The dispersal matrix $D$ captures the kind of dispersal process (density dependent or sink-source) as well as the spatial configuration of patches.\footnote{In Sanchirico and Wilen [25], we use the model to show how various systems of biological linkages result in different spatial equilibrium configurations of effort, harvest, biomass and dispersal. In addition, we have examined alternative institutional assumptions, including systems governed by limited entry, by seasonal length restrictions, and by first-best instruments such as taxes and individual transferable quotas.} Here $E$ and $R(E, x)$ are $n \times 1$ vectors, $S$ and $\Delta$ are an $n \times n$ matrix\footnote{We can stack Eqs. (1) and (2) for all $i, j, \ldots, n$.} and $H(E, x)$ is a vector of harvest rates dependent upon both biomass and effort. This depicts a spatially explicit biological system that is exploited by a harvesting industry responsive to rents within the system vis-à-vis both outside opportunities and opportunities across space. While the above spatial and intertemporal bioeconomic system is capable of addressing a range of questions in a variety of economic and biological circumstances,\footnote{For example, if the matrix has full rank, the implication is that each patch is connected to every other patch via dispersal, as might be the case in a broadly homogeneous continental shelf area with many local microhabitats containing resources. On the other hand, one might wish to depict a coastal upwelling system within a narrow band of substrate in which the patches are adjacent with each linked via dispersal to neighboring patches only. In this case the $D$ matrix would be band diagonal. A sink-source system with a single source and multiple sinks would be represented with entries only in the column representing the source. Note too that it is possible to capture a range of heterogeneous circumstances with respect to the system of individual patches. Some patches may have inherently high productivity whereas others may have no inherent productivity, as would be the case with a larval pool that receives and disperses larvae from other source patches. See, for more detailed descriptions, Carr and Reed [4], Allison \textit{et al.} [1], Sanchirico [24], and Sanchirico and Wilen [25].} it is particularly...
useful for examining the formation of reserves. If we begin, for example, with a system in which harvesters freely move across all patches in a biological system, we can characterize the nature of the exploited equilibrium that would emerge, as well as the nature of the adjustment process to that exploited equilibrium. In this (pre-reserve) equilibrium, the level of own biological growth in each patch will be exactly offset by total net dispersal between the patch and other linked patches, and the harvest in the patch in question. In addition, net rents will be identically equal to zero in each patch, leading to an economic equilibrium over time and space. The pre-reserve bioeconomic steady state can be formally written as:

\[ \dot{x} = 0 \Rightarrow [F(x) + D]x - H(E, x) = 0 \]

\[ \dot{E} = 0 \Rightarrow (S + \Delta)R(E, x) = 0 \]  

Note that while the matrix of biological dispersal coefficients affects the equilibrium vector of biomass and effort levels in each patch, the matrix of economic response parameters only affects the speed of response to equilibrium. This occurs because the economic system equilibrates when net rents in each patch are zero, and the conditions that generate zero rents are independent of the response rates, as in the Vernon Smith model of a single patch.

III. EVALUATION OF THE IMPACTS OF RESERVE CREATION

In this section, we use the model outlined above as a point of departure for examining the implications of reserve creation. In principle, examining the predictive implications of reserve creation with this model is straightforward; once the base case of an exploited equilibrium has been examined and characterized, we can then simulate the implementation of a reserve system and compare. With the establishment of a reserve system, areas that were previously exploited will be closed to harvesting, with the initial effect that biomass in the reserves will grow. As biomass in the closed areas grows, density differentials between patches will be generated, potentially causing new patterns of biomass dispersal into the open areas. But dispersal of biomass will, in turn, generate new patterns of relative rents over space, leading to a realignment of effort. In the long run, a new equilibrium distribution of biomass, effort, and harvest will emerge, and one could directly compare pre-reserve and post-reserve equilibria.

While it is reasonably straightforward to see how we might trace through the predictive implications of reserve creation, it is less clear how we should evaluate the normative implications. For example, since this is an open access model, aggregate rents will be dissipated both before and after reserve creation and hence the conventional welfare implications are blurred.\(^{17}\) At the same time, issues arise about how to evaluate the biological implications. What is gained, after all, by

\(^{17}\)This is also a result of assuming fleet homogeneity and a simple output market for the commodity. If, for example, we relaxed the assumption of fleet homogeneity we could calculate inframarginal welfare effects from the resulting restructuring of the participants after reserves are created. In addition, we could also calculate the welfare implications of a more complex market structure for the harvesting sector. For example, if harvests go down and prices rise, then reserve creation causes changes in consumer surplus.
setting aside no-harvesting zones? What kinds of nonconsumptive benefits are
generated within the reserve, and how should these be evaluated? And, is it better
to have more aggregate biomass, or should we pay attention to its spatial distribu-
tion as well?

We take a simple political economy approach here by focusing on two questions.
First, will reserves increase aggregate sustainable system-wide biomass? Second,
can reserves increase aggregate sustainable harvests? Our interest in the aggregate
biomass criterion stems from the belief that most biologists, managers, and
regulators are mostly concerned about stock safety. If managers are interested in
system “safety,” then it is sensible to judge any increase in aggregate biomass due
to reserve formation as a good policy. Our reading of the management science
literature suggests that this is the most important fishery-related motivation behind
recent support of marine reserves as a management instrument. Aggregate
(rather than patch-specific) biomass is a reasonable criterion in a metapopulation
system, because individual patches may be driven to low levels and the system will
maintain itself as long as other patches can disperse biomass into the low-density
patches.

How might an open access industry view reserve creation? We again adopt a
political economy perspective and assume that the industry is interested in aggre-
gate sustainable harvest. This seems sensible since we are beginning with an
exploited system. Under these initial conditions, any patch closures that reduce
aggregate sustainable harvests would likely be regarded unfavorably. But how
likely is it that reserve formation might ever increase aggregate harvests? As we
show below, there are circumstances when both biomass and harvests can increase
with reserve formation. In these circumstances, setting aside areas from harvest
creates a “win-win” bioeconomic fisheries payoff in the sense that aggregate
system biomass levels (a proxy for stock safety) increase, and total harvest increases
after closing one or a group of areas.

In what follows we use a simple example with two patches to show how closing
one patch affects the two important aggregate variables of potential interest.
Fortunately, a two-patch system is sufficient to characterize the qualitative implica-
tions of reserve formation under most settings. We begin by assuming that both

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18 This is illustrated by the recent special issue of Ecological Applications devoted to sustainable
management of fisheries (Feb. 1998) and in particular the articles by Lauck et al. and Allison et al. [1].
19 It is even possible, in fact, to temporarily extinguish the population in a given patch in a
metapopulation system, because other linked patches will replenish the patch via dispersal. In what
follows we will assume that the main biological goal is one of maintaining a high system level of
biomass.
20 While economists will certainly question whether a reserve that increases aggregate harvests ought
to be judged as welfare improving (especially since rents are zero before and after reserves), we must
emphasize that we are not evaluating reserves from a welfare theoretic perspective. Instead we are
asking the question: When is it likely, in a political arena, that both proponents of reserves (mainly
biologists and managers) and natural opponents of reserves (fishermen) might find themselves in
agreement that reserve formation is desirable?
21 All of the analysis in this paper assumes a comparative static perspective for analytical tractability.
A more complete analysis could be conducted using comparative dynamics in order to trace transitory
effects. In earlier work (Sanchirico [24] and Sanchirico and Wilen [25]), we showed that the transitory
effects involve a period of negative system rents followed by a period of positive rents that are
eventually dissipated to zero. This implies that if one is interested in (transitory) rents as a criterion with
which to analyze reserves, whether their net present value is positive or not depends upon the discount
rate relative to the own growth rates, dispersal rates, and harvest sector response rates.
patches can be characterized by logistic own biological growth processes, \( f(x_i) = r_i(1 - x_i/k_i) \) with possibly different intrinsic growth rates \( r_i \) and carrying capacities \( k_i \) (with \( i = 1, 2 \)). Now normalize by defining \( X_i = x_i/k_i \) so that instead of measuring biomass abundance, we measure biomass density in each patch.\(^{22}\) We leave the dispersal process unspecified for the moment, since we will examine a range of processes including density dependent and uni-directional. Although we could assume a variety of forms for the production function and cost function, it is analytically convenient to assume that the production function is a Schaefer function so that \( h_i = q_i E_i X_i \) and the cost function is linear in effort so that \( C(E_i) = c_i E_i \). These assumptions are convenient because they allow the system to be solved recursively. To see this, note that with these specifications, the rent equations are separable so that \( R(E_i, X_i) = R(X_i)E_i \), where \( R(X_i) = p_i q_i X_i - (c_i + \pi) \). With separability, rents are dissipated in each patch when the equilibrium levels of biomass densities are \( X_i^{eq} = w_i = [(c_i + \pi)/p_i q_i] \). The equilibrium biomass densities are functions of the production function and cost function parameters as well as the (assumed common) opportunity cost \( \pi \).\(^{23}\) Once the \( X_i^{eq} \)'s are determined, they can be plugged into the respective equations (Eqs. 4) describing biological equilibria in each patch to determine the corresponding equilibrium effort level, as shown in Table I.

Table I shows equilibrium levels of biomass density, effort, and harvest in each of two patches in several different types of two-patch systems before a reserve is established. In each case, the rent dissipation density levels of biomass are first determined as described above, so that biomass equilibrates with harvesting at a rent dissipating level that depends upon relative cost/price parameters. In high cost patches, the equilibrium density will be high, and it will be low in low cost patches. Once equilibrium biomass densities are determined for each patch, these

\(^{22}\)Expressing the system in density terms requires changing the dimensions of both the growth rates \( r_i \) and the catchability coefficients \( q_i \). In the exposition that follows, we use the original notation for these parameters, with the understanding that they are rescaled. We thank a reviewer and Lee Anderson for highlighting this.

\(^{23}\)This clarifies why we characterize costs as having both a patch-specific component and a fishery-wide component. Other things being equal, patch-specific costs will have differential impacts on equilibrium biomass levels across space whereas the common opportunity cost will affect the overall level of effort in the fishery.

### Table I
Pre-reserve Bioeconomic Equilibria

<table>
<thead>
<tr>
<th>Dispersal system</th>
<th>Biomass density</th>
<th>Effort levels</th>
<th>Harvest levels</th>
</tr>
</thead>
<tbody>
<tr>
<td>Closed Patch i</td>
<td>( w_i )</td>
<td>( E_i = \frac{r_i}{q_i} (1 - w_i) )</td>
<td>( H_i = r_i w_i (1 - w_i) )</td>
</tr>
<tr>
<td>Sink-source (i)</td>
<td>( w_i )</td>
<td>( E_i = r_i (1 - w_i) - \frac{b}{q_i} )</td>
<td>( H_i = r_i w_i (1 - w_i) - bw_i )</td>
</tr>
<tr>
<td>Sink (j)</td>
<td>( w_j )</td>
<td>( E_j = \frac{r_j}{q_j} (1 - w_j) + \frac{b}{q_j} )</td>
<td>( H_j = r_j w_j (1 - w_j) + bw_j )</td>
</tr>
<tr>
<td>Density-dependent Patch i</td>
<td>( w_i )</td>
<td>( E_i = r_i (1 - w_i) + \frac{b}{q_i} \left( \frac{w_j}{w_i} - 1 \right) )</td>
<td>( H_i = r_i w_i (1 - w_i) + b(w_j - w_i) )</td>
</tr>
</tbody>
</table>
can be used to compute equilibrium effort and harvest levels. Note that the type of biological dispersal system determines the characteristics of each of the equilibria. Table I also indirectly reveals conditions necessary for interior pre-reserve equilibria. For example, in the closed case, positive effort levels require that the equilibrium biomass densities be profitable, which in turn requires that $w_i = [(c_i + \pi)/p_i q_i]$ be less than one. This is intuitive, since it is equivalent to the condition that the marginal (and average) product of effort be positive at the equilibrium biomass density. The necessary conditions for interior solutions for the linked cases are more complicated and generally involve joint conditions associated with the parameters of both patches. For example, an interior solution in the density dependent case in which both patches attract positive pre-reserve effort in patch $i$ calls for $r_i(1 - w_i) + b(w_i/w_i) - 1 > 0$. Figure 1 graphs the implied parameter combinations that lead to an interior equilibrium in the density dependent case. Note that in a density dependent system, there are regions of cost/price ratios that would be sustainable in a closed system but that will not sustain an interior

24 While it is not uncommon to characterize marine systems as sink-source systems, there is some debate about whether the notion applies directly. The notion of a sink was originally developed (see Pulliam [20]) to depict more closed terrestrial systems in which local reproduction needed augmentation from outside sources to offset mortality. Marine systems are typically more open so that local populations are almost always replenished via transport mechanisms from parent populations located elsewhere. For many populations of marine organisms, the offspring of parental populations located at a particular place replenish other locations, and the extent to which they do so relative to recruitment supplied to their own parental population determines the relative role of the location as a sink. This is why larval transport mechanisms and understanding of the fate of larvae are critical to making sensible policy decisions about reserve location in marine systems. We include analysis of a simplified sink-source system for three reasons. First, it is a reasonable depiction of some marine systems, such as those inhabiting coral reefs. Second, it provides some analytical insights that can form the basis for understanding reserve formation in more complex ecosystems. And third, our simplified sink-source system is a limiting case of the more general density dependent system in the sense that it depicts the upper bound on dispersal. For example, in the density dependent case, if patch one's biomass is approximately zero then the dispersal flow is $-bX_1$ out of patch two and $+bX_1$ into patch one, which is precisely the dispersal process modeled in the sink-source case.
equilibrium in a linked system. In addition, the feasible interior solution region depends upon cost/price ratios and other biological parameters in both patches; this reflects the fact that the harvest in any one patch is dependent upon the dispersal between the patches, which in turn depends upon relative densities and hence cost/price ratios in both patches. We will also assume for consistency across the cases that the dispersal rate not be too high; in particular not higher than the intrinsic growth rate. This makes sense since if dispersal exceeds intrinsic growth, one would not expect to be able to sustain a biological equilibrium with positive biomass. In all of what follows, we will assume that the pre-reserve equilibrium is an interior equilibrium in which each patch is profitable to harvest before the reserve is established.

Now suppose that we wish to model the implications of creating a reserve in one of the patches, say patch one, by setting effort to zero in that patch and allowing entry/exit to proceed in the open patch until, in equilibrium, rents are zero. The impacts of reserve creation in the entire system depend most importantly upon two factors. First, the type of biological dispersal system (closed, sink-source, density dependent) is important, since biological linkages influence the manner in which biomass disperses over space after reserve creation. Second, the biological and economic parameters are important, since they both determine the pre-reserve (status quo) equilibrium as well as the nature of the system after reserve creation.

A. The Closed System

A few of the possibilities are obvious without much analysis. For example, suppose that we have a patchy but closed system, with no biological dispersal between patches. Suppose further that the pre-reserve equilibrium is an interior equilibrium in the sense that each patch is profitable to harvest. In this limiting case, creating a reserve eliminates harvest in the no-harvest patch, causing biomass to increase to its carrying capacity. Since the remaining patch is already at its bioeconomic equilibrium, and since there is no biological dispersal to disturb conditions in the open patch, there will be no change in the open part of the system as a result of the closure. Hence we have the following result:

**Proposition 1.** In a closed system with no biological linkages, creating a reserve by closing a patch will increase aggregate biomass and decrease aggregate harvest.

Reserves in this type of system thus contribute to the public conservation and biodiversity objectives, but at the expense of the industry. This could potentially set up circumstances for public conflict over reserve creation.

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25 For example, it can be seen that as \( b \) approaches zero (the closed system) all bioeconomic ratios in the interval \([0, 1]\) allow interior solutions, which is not the case when \( b > 0 \).

26 While this assumption is not a necessary (only sufficient) condition for an interior open-access equilibrium in the density dependent case, it is a necessary condition for the sink-source case and as a result we maintain the assumption throughout the analysis for symmetry and comparability across cases. It can also be shown that as \( b \) approaches \( r \) (with \( r_i = r \) for all \( i \)), the feasible region collapses to a lens with intersections at zero and \([1, 1]\). Thus as the dispersal rate increases, the interior region gets smaller.
B. Sink-Source Systems

Consider another case with a biologically linked system. Suppose that we have a sink-source system with biomass flowing from patch one to patch two. Assume, as above, that the uni-directional flow is proportional to biomass density in patch one so that:

\[
\begin{align*}
\dot{X}_1 &= r_1 X_1 (1 - X_1) - b X_1 - q_1 E_1 X_1 \\
\dot{X}_2 &= r_2 X_2 (1 - X_2) + b X_1 - q_2 E_2 X_2
\end{align*}
\]  

Before the reserve is put into place, biomass in patch one will be below carrying capacity and growth will be just matched by harvest and emigration. In patch two (the sink), biomass will equilibrate at a level where harvest just equals growth plus immigration. Now suppose that the sink is closed and designated a reserve. Then we can determine that:

**Proposition 2.** In a sink-source system with uni-directional density dependent flow, closing the sink will increase aggregate biomass and decrease aggregate harvest.

This can be seen as follows. The sink biomass will equilibrate where \( \dot{X}_2 = 0 \Rightarrow r_2 X_2 (1 - X_2) + b X_1 - q_2 E_2 X_2 = 0 \), which will be at a higher biomass level than the pre-reserve level. At the same time, biomass in the source will be unchanged, since biomass flows uni-directionally from the source, and hence closing the sink will not affect dispersal or biomass in the source. In addition, since biomass is unaffected in the source and since it is already in a bioeconomic equilibrium, there will be no impact on those harvesting from the source. The net system effect will be a loss in harvest from the sink unmatched by any gain in the source and a gain in biomass in the sink when harvesting is eliminated. Again there will be an increase in system biomass at the expense of the industry’s aggregate harvest, generating a potential conflict between those supporting reserves and the industry.

The other sink-source case, in which the source is designated a reserve, is more interesting because it sets up the possibility for increases in both aggregate biomass and harvest after the reserve is established. Whether a reserve will produce this double payoff or not depends upon system parameters, and as will be seen, certain configurations of both economic and biological circumstances are consistent with an increase in both biomass and harvest after reserve creation. As above, we assume that the pre-reserve equilibrium is where \( \dot{X}_1 = 0 \Rightarrow r_1 X_1 (1 - X_1) - b X_1 - q_1 E_1 X_1 = 0 \) and \( \dot{X}_2 = 0 \Rightarrow r_2 X_2 (1 - X_2) + b X_1 - q_2 E_2 X_2 = 0 \) so that biomass flows in a uni-directional manner from patch one to two. In this case, closing the source will allow biomass to increase to a new unharvested equilibrium such that \( \dot{X}_1 = 0 \Rightarrow r_1 X_1 (1 - X_1) - b X_1 = 0 \), or \( X_1^R = 1 - (b/r_1) \). In the sink patch a bioeconomic equilibrium will be established such that \( X_2^R = w_2 \equiv (c_2 + \pi)/p_2 q_2 \). Hence the pre-reserve system-wide biomass will be \( w_1 k_1 + w_2 k_2 \), whereas the post-reserve biomass will be \( X_2^R k_1 + w_2 k_2 \), with \( X_2^R = 1 - (b/r_1) \). Therefore, system-wide biomass increases when \( X_1^R \) is greater than \( w_1 \). Note from Table I, however, that the condition that ensures a pre-reserve interior equilibrium for the source patch requires that \( w_1 \) be less than \( (1 - b/r_1) \). Hence the post reserve biomass density \( X_2^R \) will always be larger than the pre-reserve level \( w_1 \), and thus establishing a reserve in the source of a sink-source system increases overall
biomass. These findings for biomass in the sink-source case are not surprising; closing a patch that was previously exploited will generally increase overall system biomass as the reserve seeks its new unexploited equilibrium.

As discussed above, the more interesting question is when does aggregate harvest also increase when a reserve is created? Recall that we found that when the sink is closed, aggregate harvest will fall. When the source is closed, in contrast, there is a chance that aggregate harvest can increase. This can be seen as follows. First note (from Table I) that aggregate system-wide harvest without the reserve is simply \( H_0 = r_1 w_1(1 - w_1) + r_2 w_2(1 - w_2) \) or the sum of own growth in the pre-reserve equilibrium in each patch.\(^{27}\) After the source reserve is established, the source will equilibrate at \( X_1^R = 1 - (b/r_1) \) and the sink will equilibrate where \( X_2 = 0 \Rightarrow r_2 w_2(1 - w_2) + bX_1^R - qEw_2 = 0 \). But this suggests that the total harvest after the reserve is established is:

\[
H_{\text{reserve}} = r_2 w_2(1 - w_2) + b[(1 - b/r_1)]
\]  

And we have:

**Proposition 3.** In a sink-source system with uni-directional flow, closing the source will unequivocally increase aggregate biomass. Aggregate harvests will also increase if:

\[
\{b[(1 - b/r_1)] - bw_1\} - \{r_1 w_1(1 - w_1) - bw_1\} > 0
\]  

Note that the first part of the inequality is the benefit from reserve creation, namely the increase in dispersal from the source due to a larger source biomass. The second term is the cost, namely the loss in pre-reserve harvest from the closed (source) area. The condition thus states the intuitively sensible result that system harvest will rise after closing the source patch if the gain in dispersal exceeds the harvest loss from the old pre-reserve source patch.

This condition can be met in a number of ways. Dropping the common \( bw_1 \) terms, the condition becomes one in economic and biological parameters \( w_1 = (c_1 + \pi/p,q_4) \) and \( b/r_1 \). Figure 2 graphs some combinations of parameters for which aggregate harvest increases when a source patch in a sink-source system is closed. The shaded area represents combinations of parameters that simultaneously satisfy the conditions for a pre-reserve interior equilibrium \((E_1, E_2) \geq (0,0)\) and also (7) above. The condition allowing aggregate harvests to increase is plotted on Fig. 2 as follows. First, consider condition (7) as an equality \((b/r_1)[1 - (b/r_1)] - w_1(1 - w_1) = 0\). This function is labeled \( \phi(w_1) \) and is quadratic in \( w_1 \) with a value of zero at the two real values of \( w_1 \) symmetric around \((1/2)\), namely, \( w_1 = b/r_1 \) and \( w_1 = 1 - (b/r_1) \).\(^{28}\) The function also is equal to \((b/r_1)[1 - (b/r_1)]\) when \( w_1 \) is

\(^{27}\)Note that this equation appears not to contain any contribution of dispersal to aggregate harvest. This is because while the equilibrium harvest in each patch equals the sum of own growth and dispersal, the extra harvest due to dispersal in the sink is precisely cancelled out by a corresponding subtraction of dispersal from the source.

\(^{28}\)Figure 2 is drawn with \( b/r_1 \) less than \( 1/2 \). If \( b/r_1 \) is greater than \( 1/2 \), the function will look the same except that the two values where \( w_1 \) intersects zero will be transposed on the axis.
zero and it falls until \( w_1 = 1/2 \) and then rises. For circumstances that lead to aggregate harvest increasing after reserve formation, we need to look for values of \( w_1 \) which make the inequality in (7) positive, generally small and large values. But the large values can be eliminated from consideration because these will not satisfy the pre-reserve interior equilibrium requirements and hence we are left with the shaded area.

What does this tell us intuitively about the economic circumstances that lead to a double payoff in which both aggregate biomass and harvest increase in the sink-source case? First, for any pre-reserve conditions in the sink, a double payoff will be more likely to arise if source patch cost/price ratios are very low. A bit of reflection suggests why. When source patch costs are low (or prices high), the pre-reserve biomass density will be driven to a low level through open access rent dissipation. Under these situations, there are two factors boosting the possibility of aggregate harvest gains. First, with a low biomass, the harvest in the source will also be low and hence the opportunity costs in foregone harvests will be low. Second, with a low initial biomass, when the source is closed the corresponding increase in biomass in the closed patch will be large. Since the increase in dispersal into the open patch depends upon the patch density differential before and after the reserve, the gain in dispersal into the sink will also be large under these conditions.

What biological conditions favor an increase in harvest after reserve creation? Note that the above condition in (7) depends not only upon economic factors embedded in \( w_1 \), but also on biological factors embedded in the ratio \( b/r_1 \). First, hold \( r_1 \) fixed, and vary the dispersal rate \( b \). If the dispersal rate is very low, then the range of circumstances giving rise to the double payoff is restricted. This is the case because with low dispersal rates, closing the source does not yield a comparatively high payoff in the sink. Alternatively, if \( b \) is very high to begin with, then the equilibrium biomass density in the source patch after reserve formation will be low, and there will not be a large change in dispersal after reserve formation. One can see, in fact, that dispersal rates that are not too high or too low relative to \( r_1 \) are most likely to lead to conditions favoring an aggregate harvest increase after
reserve formation. Similar reasoning applies to the intrinsic growth rate in the source patch; if \( r_1 \) is low, relative to the dispersal rate, the source patch equilibrium level will be low and it will be less likely for the reserve to generate increases in harvests.

C. Density Dependent Systems

Consider next the density dependent case in which:

\[
\begin{align*}
\dot{X}_1 &= r_1X_1(1 - X_1) + b(X_2 - X_1) - q_1E_1X_1 \\
\dot{X}_2 &= r_2X_2(1 - X_2) + b(X_1 - X_2) - q_2E_2X_2
\end{align*}
\]  

(8)

In this system, before the reserve is established, entry will occur in each patch until net rents are driven to zero at some equilibrium population densities \((w_1, w_2)\) determined by economic parameters. These equilibrium densities can then be used to solve for the corresponding equilibrium levels of effort and harvest as depicted in Table I. We assume that the conditions are satisfied for a pre-reserve interior equilibrium as illustrated in Fig. 1. Now assume that patch one is closed, creating a reserve. Under the assumptions made here, the biomass density level in patch two will remain \(w_2\), but patch one density will grow until the first Eq. in (8) is satisfied with zero harvest at:

\[
X_1^R = \frac{1}{2} \left( \frac{r_1 - b}{r_1} \right) + \frac{1}{2} \sqrt{\left( \frac{r_1 - b}{r_1} \right)^2 + \frac{4b}{r_1 w_2}}
\]  

(9)

Since the sum of biomass in the system before the reserve is \(w_1k_1 + w_2k_2\) and the sum after the reserve is established is \(X_1^Rk_1 + w_2k_2\), there will be an increase in aggregate biomass after the reserve is formed in a density dependent system when (9) is greater than \(w_1\). It is easy to show that if the pre-reserve equilibrium is an interior equilibrium, then \(X_1^R\) is greater than \(w_1\) always. In other words, if there is some effort and harvesting taking place in a patch before that patch is designated a reserve, that patch will always equilibrate at a higher biomass density than its pre-reserve equilibrium. Thus reserve creation in a density dependent system will always increase aggregate system biomass.

What happens to aggregate harvests when a reserve is created in a density dependent system? Returning to Table I, note that aggregate harvests before the reserve are \(r_1w_1(1 - w_1) + r_2w_2(1 - w_2)\). After a reserve is created in patch 1, aggregate harvest will be \(r_2w_2(1 - w_2) + r_1X_1^R(1 - X_1^R)\). Hence aggregate harvests increase after reserve formation if \(r_1X_1^R(1 - X_1^R) > r_1w_1(1 - w_1)\) with \(X_1^R\) given in (9). But this expression can be rearranged to get:

\[
(X_1^R - w_1) > \left[ (X_1^R)^2 - (w_1)^2 \right] = (X_1^R - w_1)(X_1^R + w_1)
\]  

(10)

\(29\) In fact, when \(b/r_1 = 1/2\) the range of \(w_1\) satisfying (6) is largest.

\(30\) This can be seen as follows. First begin with the inequality condition that guarantees \(E_1\) to be positive. Then add \((1/2)[(1 - (b/r_1))^2\) to both sides and rearrange. Take the square root of both sides and rearrange again to show \(X_1^R\) greater than \(w_1\).
Since \((X_1^R - w_1)\) is positive, we can divide through to get the condition:

\[
X_1^R + w_1 < 1
\]  

as defining the circumstances that lead to a double payoff in the density dependent case. After substituting Eq. (11) for \(X_1^R\) and rearranging, we get the condition, expressed in terms of economic and biological parameters, that:

**PROPOSITION 4.** In a density-dependent system, creating a reserve by closing a patch will increase aggregate biomass. Aggregate harvest will also increase if

\[
\left\{(r_1/b)(w_1) - w_1[1 + (r_1/b)] + 1\right\} > w_2
\]

The function on the left of the inequality has a value of one when \(w_1 = 0\), and it has zero points at \(w_1 = (b/r_1)\), symmetrically located around the minimum at \(w_1 = (1/2)[1 + (b/r_1)]\). Figure 3 plots the left-hand side of the inequality as a function of \(w_1\), labeled \(\gamma(w_1)\). Figure 3 also plots all feasible points that satisfy the conditions for an interior equilibrium by showing regions of parameters for which \(E_1\) and \(E_2\) are positive. The intersection of these with the conditions generating a double payoff is shown in the shaded region.

In a manner similar to the sink-source case, the density dependent case allows for the possibility that closing one patch may actually increase aggregate harvest in addition to increasing aggregate biomass.\(^3\) As was the case with the sink-source system, a double payoff is more likely to emerge when the patch to be closed is at a low level before the reserve is established. If this is the case, it is more likely that reserve formation will cost less (in foregone harvests) and benefit the industry more (in large reserve biomass levels and high dispersal to the open area). A

\(^3\)An interesting additional possibility is that creating a reserve (closing a patch) may actually make another previously unharvested patch become economically viable. To see this, assume that \(E_2 = 0\) prior to the establishment of a reserve in patch one. From Table I this implies that \(E_2w_2 = r_2w_2(1 - w_2) + b(w_1 - w_2) = 0\). After the reserve is created, the cost/price ratio \(w_2\) will be unchanged, but the biomass in patch one will increase to \(X_1^R > w_1\). Replacing \(w_1\) with \(X_1^R\) makes the second term larger than in the pre-reserve expression, implying that \(E_2 > 0\).

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**FIG. 3.** Double payoff conditions. Density dependent case.
difference between the density dependent case and the uni-directional sink-source case is that economic conditions in the open area also matter. For given economic parameters associated with the reserve patch, a double payoff is more likely when the open patch is not too dissimilar. For example, if the cost/price ratio is low in the reserve patch, a double payoff will be more likely if the cost/price ratio also is low in the open patch. This result occurs because the dispersal between the two patches is dependent upon relative densities. If cost/price ratios in the open patch are high relative to the reserve patch, its pre-reserve density will also be high. But this will lead to pre-reserve dispersal from the open patch to the patch designated as the reserve. When the reserve is actually created, biomass density in the reserve will have to increase substantially to reverse the dispersal flow and begin to create any positive benefits in the open patch.

The biological parameters interact in a more complicated way with density dependence compared with the sink-source system. In a similar manner, as the dispersal rate \( b \) is small, the parameter space likely to lead to double payoffs shrinks, and for similar reasons. As the dispersal rate gets large (relative to \( r_1 \)), there are two offsetting effects. First, the potential double payoff region of combinations of \((w_1, w_2)\) gets larger. But as \( b \) gets larger, the region in which a feasible interior pre-reserve equilibrium can be established shrinks. The combination of these effects determines the size of the region yielding a double payoff after reserve formation. Note also that other things being equal, as \( r_1 \) rises, the feasible region for a possible double payoff shrinks. The intuition behind this conclusion is straightforward; since the equilibrium level of the pre-reserve harvest in the patch to be closed is positively related to its own growth rate, the opportunity cost of closing a patch is higher when \( r_1 \) is large. Looked at in an alternative way, the losses from closure will be large when \( r_1 \) is large and hence it is less likely that they can be overcome by increased dispersal. Correspondingly, as the growth rate in the open area \( r_2 \) gets larger, the region of \( w_2 \) over which double payoffs are possible also rises. Higher levels of own growth in the receptor patch (relative to the dispersal rate) will support harvests under higher cost conditions than lower growth levels.

IV. DISCUSSION

As discussed in the introduction, while there are many arguments made to support the use of marine reserves for conservation and biodiversity benefits, the most vocal objections to reserves have come from fishermen presently exploiting areas under consideration as set-asides.\(^3\) From their perspective, marine reserve proposals are akin to asking them to give up harvesting rights. In most marine settings, of course, fishermen do not have legal “rights” to harvest and hence part

\(^3\)This objection seems to be related to both the scale of recent proposals and to the fact that the mechanisms necessary to generate benefits to fishermen are unclear. Closed areas are not new to fishermen; many fisheries management policies already protect fish during critical phases of the life cycle. In fact, one of the first fishery management interventions ever used was the prohibition of fur sealing around the rookeries of the Pribilows in the 1890s (Wilen [29]). Area closures have also been used to protect areas with abundant immature fish in the Pacific halibut and the Icelandic cod fisheries and commercial fishing is often prohibited in bays and estuaries and juvenile nursery grounds. In addition, area closures have been used to isolate diseased populations, reduce gear conflicts, and enhance market value by altering selectivity (OECD [17]).
of this public/private conflict may have to be settled in the courts and legislative process. At the same time, it seems sensible from a political perspective to look for circumstances that might appear attractive to both conservationists and fishermen. We have termed these *double payoff* circumstances, in which it might be possible to both increase aggregate biomass and aggregate harvest in a spatially linked system by closing one or more areas to exploitation.

Our analytical investigation shows that, indeed, it is possible to increase both aggregate biomass and harvests under some circumstances. This exercise is nontrivial because we are comparing various second-best equilibria, and whether it is possible to “improve” the status quo depends upon the nature of that initial position as well as the incentives that influence the change. We demonstrate that the double payoff issue is both a biological and an economic problem. This bears emphasis because much of the literature on reserves either treats the problem as if it is a purely biological problem (e.g., close patches that are most biologically productive) or with naive assumptions about harvesters’ behavior (e.g., effort in closed areas simply disappears). As our analysis shows, closing an area in an exploited open access system always increases aggregate system biomass. Closing an area also increases aggregate harvests whenever the system dispersal benefits to the remaining open areas are large relative to foregone harvest. This means that dispersal mechanisms matter. For example, reserves in closed systems will not generate any harvest benefits although they will increase aggregate biomass. With biologically linked systems, the types and relative strength of biological linkages are important. In a sink-source system, for example, since dispersal is dependent upon the source it is important to close the source rather than the sink, and whether harvesting gains are possible depends upon initial conditions in the source. If the source is relatively unprofitable, there will be little advantage to closing it because the pre-reserve biomass will already be relatively high. Similarly (and perhaps paradoxically) if the dispersal rate for a source is too high, it may not pay to close the patch. This is because with a high dispersal rate, there will already be a high “leakage” out of the source and creating a marine reserve will have relatively small impacts on the remaining open system. If the dispersal rate is too low, it also may not pay to create a reserve. With low dispersal, less is gained by closing an area because only a small amount of biomass leaks out to the open area. In the limiting case of the closed system one essentially gives up all the reserve harvest for no gain.

In the more general density dependent case, aggregate harvests again may be increased under certain specific conditions. When cost/price ratios in the reserve-designate are low, the initial open access equilibrium position will be characterized by overharvesting, a low biomass, and low sustained harvests. In this case, closing the area is achieved at little cost in foregone harvests and it generates the largest benefits since dispersal to the remaining open areas is proportional to the new higher biomass density. In extreme cases, closure may even cause pre-reserve

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33 It also may seem counterintuitive that a constrained system can yield more harvest than an unconstrained system. It must be remembered that we are examining an open access system and not an optimized system, however. Given that an open access system is already distorted, we may view reserve creation as using spatial instruments (closures) to alter the system of distortions. While a system with spatial closures may seem more constrained, the overall effect of closures on system-wide distortions may be beneficial in the sense of enabling higher sustained harvests than in the unfettered open access system.
dispersal to reverse direction. This points to another feature of general density dependent systems and that is that whether a patch is a de facto sink or source depends upon both biological and economic factors. A low cost area may be driven to low biomass levels and hence become a sink in a general density dependent system vis à vis other higher cost patches. But closing low cost areas may reverse the biomass density gradient, causing the closed area to become a source for the remaining system. We also showed that a high intrinsic growth rate could work against the double payoff because high own growth rates increase the opportunity cost of closing an area. These types of conclusions seem to run counter to simple biological analyses which have treated the reserve selection issue as if it were one of simply finding and closing inherently high productivity areas.

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