Bioeconomics of Spatial Exploitation in a Patchy Environment*

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This paper presents a model of renewable resource exploitation that incorporates both intertemporal dynamics and spatial movement. The model combines the H. S. Gordon–Vernon Smith hypothesis of a rent dissipation process with Ricardian notions that resources are exploited across space in a pattern dependent upon relative profitabilities. The population structure is characterized in a manner consistent with modern biological ideas that stress patchiness, heterogeneity, and interconnections among and between patches. Generally, we find the equilibrium patterns of biomass and effort across the system to be dependent upon bioeconomic conditions within each patch and the nature of the biological dispersal mechanism between patches. We use simple examples to illustrate how the distribution of effort throughout the system reflects the heterogeneity and the spatial biological linkages.

I. INTRODUCTION

Economists' models of renewable resource exploitation have utilized various abstractions for both analytical tractability and to focus attention on variables of particular interest in the policy process. The most prominent and widely cited examples of bioeconomic analysis begin, for example, with the assumption that the exploitable biomass is enumerable in terms of either total weight or numbers, and that the principal birth–death–growth processes can be adequately described by a small number of parameters. These "lumped parameter" models include, for example, the widely used Shaefer [32] model in which biomass dynamics are characterized by the intrinsic growth rate and the carrying capacity of the environ-

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ment. The logistic–Shaefer model is the foundation for the bulk of fisheries economics literature.

While economists have been content to stick to these simple models as descriptions of biological processes, there has been a subtle paradigm shift in biology away from these simplifications. There is, in fact, a well-developed literature that incorporates many more realistic features of populations than those embedded in the simple lumped parameter abstractions. Biologists are well versed, for example, in the intricacies introduced by considering age- and size-structured populations and no serious modeler would ignore these aspects in slow-growing, broad age distribution populations where exploitation targets particular sizes, ages, or sexes either for market reasons or because of regulations. In addition, biologists have begun to focus much more seriously than economists on the implications of space in their models of populations. The newest paradigms in biology, from the genetic to the population level, recognize that real populations are heterogeneously distributed across space and that the spatial dimension adds some new insights to our understanding of biological processes.

Aside from keeping up with these new developments in biology, there are several other reasons why resource economists might want to devote some attention to the spatial dimensions of bioeconomic activities. First, in systems in which the resource is distributed heterogeneously in space, we are most likely missing a considerable amount of interesting behavior by aggregating out the spatial aspects of economic activity. To take a simple example, suppose vessels are moving back and forth between several patches in response to changes in relative profit opportunities. It is easy to conceive of circumstances where much of the between patch movement cancels out when aggregated, suggesting very little behavioral responsiveness when in fact there is a considerable amount of response. If we are interested in estimating behavioral elasticities, we would uncover little with aggregated data but we would uncover much more with data disaggregated over space in this example. In order to structure empirical analysis, however, we need a theory which deduces testable hypotheses about how decision makers behave over space. A second reason for incorporating space into models of exploitation is that there is a considerable amount of new interest in spatial management options, particularly among biologists and fisheries and wildlife managers. For example, biologists have promoted natural refuges as management tools, under the expectation that permanent closures of certain areas might enhance overall biological productivity of an exploited system. Similarly, others have proposed rotating harvest zones, under which areas are closed for a period and then reopened for exploitation after they have been allowed to recover back to a natural state. In order to analyze these

1See, Skellam [33]; Levin [23, 24]; Allen [2]; Hastings [17, 18]; Holt [19]; Possingham and Roughgarden [26]; Huffaker, Bhat, and Lenhart [21].

2Among the few examples of work by economists incorporating space are the paper by Brown and Roughgarden [10] examining larval pools in a metapopulation model, papers by Huffaker, Bhat, and Lenhart [5, 6, 21] examining spatial–intertemporal control of a pest population, and papers by Schulz and Skonhoft [31], Skonhoft and Solstad [34] analyzing exploitation of transboundary terrestrial species. In addition, there has been some work linking landscape ecology features to economic behavior. See, for example, a paper by Albers [1] examining tropical forest management and Bockstael [7] and Geoghegan, Wainger, and Bockstael [15] reporting interesting new empirical relationships in a rural–suburban setting.

3See, Holt [19]; Levin [23]; Man, Law, and Polunin [25].

4See, Bohnsack [8]; Botsford et al. [9]; Davis [13]; Dugan and Davis [14]; Roberts and Polunin [28].
kinds of new options, we need a conceptual model that explicitly considers spatial characteristics of the resource base as well as spatial dimensions of the exploiting industry. In this paper, we present a model of renewable resource exploitation that incorporates both intertemporal dynamics and spatial movement. The model combines both the H. S. Gordon 16–Vernon Smith 35 hypothesis of a rent dissipation process with Ricardian notions that resources are exploited across space in a pattern depending upon relative profitability. We characterize the population structure in a manner consistent with modern biological ideas that stress patchiness, heterogeneity, and interconnections among and between patches. For the purpose of this paper we assume a “patch” is a location in space that contains or has the potential to contain an aggregation of biomass. We also assume that patches are located a fixed and discrete distance from one another. The biological interconnections between patches may be of many varieties and we develop a general model which nests several cases and then we explore the implications of several of the most common from the biological literature.

In the next section we begin by describing a biological model of a spatially interconnected population system. For simplicity, we first ignore the possibility of harvesting in order to focus attention on the natural biological forces inducing population movement across space and time. We also elaborate on the biological side of the system by showing how various descriptions of biological systems in the ecological literature can be reduced to special cases of a general model through specifications of restrictions on the dispersal parameters. In Section III, we sketch out a simple open access harvesting model which captures essential features of the Gordon rent dissipation model in a patchy environment. Then in Section IV we pull together the biological and economic components and we solve an example of a spatially explicit bioeconomic model. We discuss equilibrium properties and we show how they reflect the specific nature of the biological and economic system. Section V discusses some of the important insights that emerge when we add the spatial dimension to bioeconomic models of exploitation.

II. A SPATIAL MODEL OF POPULATION BIOLOGY

Biologists have explored a range of population models that incorporate spatial features, starting with the paper by Skellam 33. These models are sometimes referred to as metapopulation models, where a metapopulation is defined as a group of linked subpopulations distributed across a set of spatially discrete habitats or patches. The number of organisms in each patch is assumed to depend upon

5A referee raised a question about whether institutional configurations other than open access ought to be considered, because most fisheries are essentially limited (or restricted) access. This is a good point, and one that had been made persuasively by Homans and Wilen [20]. Our response is twofold. First, as a matter of modeling philosophy, developing more realistic models often benefits by starting with simple models and adding structure, once the simpler model is understood. In this case, adding spatial structure complicates the model considerably and hence starting from the simple polar extreme is a sensible first step along the way to developing more encompassing models. Second, and more to the point of the referee’s concerns, unless real world regulatory structures establish property rights (i.e., ITQs), there are still open-access incentives operating which affect decisions across many margins, including location choice in a spatial system. Hence our approach would apply, even in more general circumstances with some forms of regulations and limited entry.
"own" density-dependent growth processes as well as dispersal from and to other patches in the system. The dispersal process is important because it allows for the possibility of temporary local extinction without driving the whole population to extinction. This could occur, for example, if the population in one patch is temporarily driven to zero and subsequently recolonized via dispersal from other patches.

Following Levin [23, 24], Hastings [17, 18], and others [19, 38], most analytical spatial population models are structured as follows,

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

where \( \dot{x}_i \) is the instantaneous rate of change of biomass in patch \( i \), \( x_i \) is the biomass in patch \( i \) in time \( t \), \( f_i(x_i) \) is the per capita growth rate in patch \( i \), \( d_{ii} \) is the rate of emigration from patch \( i \) \( (d_{ii} \leq 0) \), and \( d_{ij} \) is the dispersal rate between patches \( i \) and \( j \) \( (d_{ij} \geq 0) \). In this system there are \( n \) patches, each of which has own population dynamics described by the per capita growth function \( f_i(x_i) \). In addition to density-dependent own growth processes, each patch also contributes and receives organisms via dispersal to and from other patches. In the previous formulation, dispersal is written as separable from own growth processes and linear in population levels. At any point in time a given patch may be a net contributor to, or a net receptor from, the rest of the system. The net dispersal associated with patch \( i \) is \( ND_i = d_{ii}x_i + \sum_{j \neq i}^{n} d_{ij}x_j \) in the preceding model.

The dispersal representation in (1) is capable of depicting a range of qualitatively different dispersal processes via appropriate choice of the coefficients \( d_{ij} \). There are various assumptions that have been made in the biological literature regarding the nature of the dispersal process, depending upon the assumed behavior of the organism and the nature of the habitat the population inhabits. A common assumption is that population biomass flows in directions over space that depend upon relative densities. Perhaps the simplest representation of this type of density-dependent dispersal is with dispersal out of patch 1 as \( d_{12}x_1 + d_{22}x_2 = b(x_2/k_2 - x_1/k_1) \) and dispersal into patch 2 as \( d_{21}x_2 + d_{21}x_1 = -b(x_2/k_2 - x_1/k_1) \) in a two patch model. In this simple case, there is a common marginal dispersal rate \( b \), and population disperses in a manner dependent upon the population densities relative to their natural carrying capacities. Hence if the population in patch 2 is 90% of its carrying capacity and the population in patch 1 is at 85% of carrying capacity, dispersal flows from patch 2 to patch 1 regardless of absolute population levels. Dispersal is thus an equilibrating force here that augments natural growth processes; when populations are low relative to their carrying capacities, both own growth and dispersal from other patches operate in a complementary fashion to bring populations in each patch to their carrying capacities. It is also the case that the directional gradient of the dispersal process is endogenous at any point in time, and the system responds in a gravity flow manner over space to bring the whole...
system into equilibrium. This type of system approaches what we call a *homogeneous equilibrium* in which each population reaches its carrying capacity, at which point system dispersal goes to zero. It is homogeneous in the sense that the system is in a space–time steady-state; population levels are unchanging over time, and there is no dispersal or movement over space in equilibrium.\(^8\)

While most spatial ecology literature focuses on relative density-dependent dispersal mechanisms, there have been some formulations based on *unidirectional* processes.\(^9\) This special subclass of models, often referred to as sink-source models, depicts populations flowing from a source to a sink regardless of the population or density level in the sink. For example, a two patch sink-source model might have growth in the source area equal to \(\dot{x}_i = r_i x_i (1 - x_i/k_i) + d_{ij} x_j\) and might have growth in the sink area equal to \(\dot{x}_j = r_j x_j (1 - x_j/k_j) + d_{ji} x_i\) (recall \(d_{ii} < 0\)). This type of model exhibits qualitatively different behavior compared with the general density dependent formulation in its unexploited equilibrium. In a sink-source model, the equilibrium may be a *nonhomogeneous* (or flux) *equilibrium*, in the sense that while population levels in each patch are unchanging over time, there is actually movement over space between patches in equilibrium. With this type of dispersal process, biomass continues to flow into the sink even after both populations reach their equilibria, at which point, the source patch has births exactly offset by deaths and migration and the sink patch has deaths exactly offset by births and immigration.\(^10\)

The general model in Eq. (1) is thus capable of depicting a broad spectrum of biological conditions in a system distributed over space. If we are content to characterize the dispersal mechanism as linear and separable from the own growth process, we can stack Eq. (1) for all \(n\) patches and we can express the whole system in matrix fashion as

\[
\dot{x} = F(x)x + Dx. \tag{2}
\]

The biological system in (2) is comprised of \(n\) dynamic equations where \(x\) is a \(n \times 1\) vector whose components \((\dot{x}_i)\) are the instantaneous rate of change of biomass in patch \(i\) in time \(t\), \(x\) is a \(n \times 1\) vector whose components \((x_i)\) are the level of biomass in patch \(i\) in time \(t\), \(F(x)\) is a \(n \times n\) diagonal growth matrix where the diagonal components \(f(x_i)\) are the average growth rates in patch \(i\), and \(D\) is a \(n \times n\) matrix of dispersal rates \((D_{ij} = d_{ji}\) for all \(i, j\)). The biological model in (2) depicts the dispersal of elements of the population differentiated by location through \(D\), and heterogeneous own-patch-specific biological conditions such as intrinsic growth rates and carrying capacities through \(F(x)\). This system behaves over time and space in a manner reflecting the dual effects of own-patch-specific growth processes and dispersal processes, the former captured in the first component of (2) whereas the latter captured by the matrix \(D\). While biologists have characterized various natural systems in many ways, most can be thought of as

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\(^8\)Note that homogeneity in this case stems from two assumptions. First, dispersal is assumed to depend upon differences in relative densities \((x_i/k_i - x_j/k_j)\). Second, we are considering an unexploited equilibrium where population in each patch approaches carrying capacity. For both reasons, in this system spatial movement goes to zero in equilibrium.

\(^9\)See, for example, Pulliam [27]; Tuck and Possingham [37]; Sanchirico and Wilen [30]; Sanchirico [29].

\(^10\)This may lead to an unexploited equilibrium population in the source patch that is less than \(k_i\), and similarly, an equilibrium population in the sink greater than \(k_j\).
special cases of the general system in (2), depicted with restrictions on the $D$ matrix.\textsuperscript{11}

In Figure 1, we illustrate five general types of biological systems nested in (2) (discussed separately in Carr and Reed \cite{11}). See Table I. The five types of biological systems are: fully integrated, closed, sink-source, multiple source, and spatially linear. A \textit{fully integrated} system allows for the biomass to disperse directly from any patch to any other patch throughout the system. The dispersal matrix for this system would have nonzero elements in each column–row position. A \textit{closed} system is the opposite case where maintenance of biomass density within each patch is only determined by own production and there is no dispersal out of or into the system ($D$ is the null matrix). A \textit{sink-source} system occurs when one or multiple patches provide unreciprocated biomass replenishment to other patches. A sink-source system with one patch feeding all others would have

\textsuperscript{11}Ecologists generally impose some structure on the dispersal process, either to ensure sensible interpretation or for analytical convenience. In this paper we will impose the following restrictions on the $D$ matrix: (i) $d_{ii} \leq 0$, (ii) $d_{ij} \geq 0$, and (iii) $\sum_{k=1}^{n} d_{ki} = 0$ for $i = 1, 2, \ldots, n$ (column sums to zero). Assumptions (i) and (ii) are essentially accounting restrictions that allow us to separate population fractions that are leaving one area from those that are arriving. Assumption (iii) is an “adding up” restriction which ensures that whatever leaves a patch during dispersal from a group of patches also shows up in the receptor patches. A stronger version of this adding up restriction that is sometimes imposed is the symmetry condition $d_{ij} = d_{ji}$, which ensures that whatever leaves patch $i$ specifically for patch $j$ also arrives in patch $j$ specifically from patch $i$. However, this symmetry condition excludes sink-source dispersal processes and hence we impose the weaker condition (iii).
TABLE I
Restrictions on the Dispersal Parameters

<table>
<thead>
<tr>
<th>Spatial configuration</th>
<th>Restrictions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fully integrated</td>
<td>$d_{ij} &lt; 0, d_{ij} &gt; 0$ for all $i, j = 1, \ldots, n$</td>
</tr>
<tr>
<td>Closed</td>
<td>$d_{ij} = 0$ for all $i, j = 1, \ldots, n$</td>
</tr>
<tr>
<td>Sink-source</td>
<td>source (patch $k$): $d_{ik} &lt; 0, d_{ik} = 0$</td>
</tr>
<tr>
<td></td>
<td>sink: $d_{ik} &gt; 0, d_{ij} = 0$ for $(i, j) \neq k$ where $i, j = 1, \ldots, n$</td>
</tr>
<tr>
<td>Multiple-source</td>
<td>source (patch $k$): $d_{ik} &lt; 0, d_{ik} &gt; 0$</td>
</tr>
<tr>
<td></td>
<td>sink: $d_{ik} &gt; 0, d_{ij} = 0$ for $(i, j) \neq k$, $i, j = 1, \ldots, n$</td>
</tr>
<tr>
<td>Spatially linear</td>
<td>$d_{ii} &lt; 0, d_{ij} &gt; 0, d_{ik} = 0$ where $(i, j)$ are neighbors for $i = 1$ and $n$</td>
</tr>
<tr>
<td></td>
<td>$d_{ii} &lt; 0, d_{ij} &gt; 0, d_{ik} &gt; 0, d_{ik+1} = 0$ where $(i, j, k)$ are neighbors for $1 &lt; i &lt; n$</td>
</tr>
</tbody>
</table>

nonzero elements only in the column corresponding to the source. The multiple source case occurs when many patches contribute biomass to one common pool which then is redistributed among the patches, as, for example, with a breeding ground or a juvenile nursery area. The system would have nonzero elements in the common pool patch column, and the system would have zeros in every row element that was not linked (either as contributor or receptor) to the source patch. Lastly, the spatially linear case nests various spatial configurations (e.g., linear, circular, or square) and assumptions regarding the edge effects of neighboring patches. For example, if patches are arrayed in a line, patch dispersal may only occur in a pairwise manner between adjacent patches and this can be denoted by a dispersal matrix which is band diagonal.

Note that each of these cases involves dispersal structure between patches which reflects inherent behavioral characteristics of the population and/or oceanographic features of the spatial system. For example, a pelagic species with high mobility inhabiting a relatively homogeneous marine environment might be depicted with a fully integrated metapopulation system with relatively high dispersal rates. This system would equilibrate faster than a corresponding system with slow dispersal rates and/or blocked dispersal paths caused by currents, prevailing winds, or geographic and oceanographic barriers. A relatively sedentary species inhabiting a substrate with a high degree of variability might be characterized by blocked dispersal paths between certain groups of patches and low dispersal rates. Similarly, we might have a species characterized by a lifecycle involving larval dispersal into a juvenile area, which subsequently disperses to various patches in a manner dependent upon currents and prevailing winds. This could be depicted with a sink-source structure involving unidirectional and unreciprocated biomass replenishment from one or several source patches. The important point is that even in its linear and separable formulation, (2) is relatively general and capable of capturing a broad range of ecological circumstances.

III. OPEN ACCESS EXPLOITATION IN A SPATIAL SETTING

In this section we develop a model of an industry exploiting a patchy resource, under conditions of open access. While the model is basically an economic model reflecting economic behavior, it is also qualitatively symmetric with the population
model discussed in the foregoing text. In the spatial population model, the key state variables are patch-specific population levels, which may adjust across space and time in response to relative densities, both within the patch and across patches. In the economic model, the key state variables (effort) adjust in response to rent differentials across space and time, both within each patch and between patches.

The model we develop here is a generalization of two important papers characterizing open access resource exploitation. The first is the paper by H. S. Gordon, published in 1954 [16]. Gordon hypothesized that under open access, any rents that would normally accrue to a resource owner would instead accrue to entrants. This additional incentive, over and above entrants' normal opportunity costs, would attract excess effort until average (and not marginal) returns were driven down to opportunity costs. Hence open access conditions would attract excess effort and rents would be dissipated.12 Gordon’s model was extended in 1968 by Vernon Smith [35], who hypothesized an explicit dynamic entry–exit process in addition to a biological growth mechanism.

Both the Gordon and Smith models begin by assuming that a composite effort variable \( E \) (which we refer to as vessels, for simplicity) exists so that total industry harvest can be written \( H(E, X) \) where \( X \) is the population biomass. Assume output price \( p \) is given, industry level operating costs are \( C(E, X) \), and industry level opportunity costs associated with other uses of the composite input outside this particular fishery are \( \pi E \). We can thus write average net rents generated per vessel as \( NR(E, X) = [pH(E, X) - C(E, X) - \pi E]/E \). In Gordon’s story, under open access effort continues to enter until average gross operating profits equal opportunity costs, thereby dissipating all potential rents. Smith used the same structure, but in addition, hypothesized a dynamic process describing entry–exit behavior.13 Smith’s model depicted the interaction between the harvesting industry and the population as

\[
\dot{E} = \Phi(NR), \\
\dot{X} = F(X) - H(E, X).
\]

(3)

In this generalized model, the rate of change of effort is assumed increasing in average net rents per vessel such that when average net rents are positive entry

12 Interestingly, Gordon [16] also briefly addressed the issue of how effort might distribute itself across space, with an analysis of different fishing grounds. In his (static) model, effort would distribute itself over different grounds until average rent in each patch was equalized at some common opportunity cost. As he suggested, this allocation would be inefficient, because it would be desirable to allocate effort over space to equalize marginal and not average rents.

13 Smith’s model is more complete than Gordon’s in several ways. First, it replaces Gordon’s awkward representation of yield–population relationships with an explicit density-dependent biological growth function. Second, it introduces variable factors and distinguishes them from vessel capital, which is assumed to enter sluggishly in response to rents. Finally, it brings the entry–exit and biological dynamics to the forefront of attention, showing how open-access exploitation dynamics can generate oscillatory overshoot. This possibility provoked several subsequent papers that examined whether an open-access industry might drive a fishery to extinction during the initial phase of oscillatory overshoot (Berck [3], and Leung and Wang [22]).
occurs and when negative exit occurs. Smith’s dynamic model nests Gordon’s static model because, in equilibrium, average net rents are driven to zero by entry. In addition, however, the model generates predictions about the approach paths, which may be asymptotic or oscillatory, depending upon (among other things) the relative speed of industry response to rent opportunities.

In both the Gordon and Smith models of a single patch, the number of vessels operating in the patch changes over time in a manner dependent upon bioeconomic conditions in the patch relative to outside opportunities. In generalizing to a multiple patch environment, it seems desirable to incorporate this same assumption that each vessel has opportunities outside the fishery in question, particularly in an open-access setting. In addition, however, in a multiple patch setting there is an opportunity cost to participating in any given patch, namely, the rents that could be earned in any other patch. Hence a fully specified model of behavior in a patchy environment needs to account for both external and internal profit opportunities. In this setting, movement to and from any particular patch ought to be related to relative profit opportunities both vis-à-vis opportunities outside the whole fishery as well as opportunities in other patches within the fishery.

These ideas can be operationalized as follows. Consider the system discussed in Section II in which there are \( n \) distinct biological patches represented by an integer valued index \( i \). Let \( E_i(t) \) be the effort level in patch \( i \), let \( x_i(t) \) be the biomass level in patch \( i \) in period \( t \), and let \( NR_i(E_i, x_i) \) be the instantaneous average net rents per vessel associated with harvesting in patch \( i \). As in the single patch model in (3), net rents are assumed to be average gross operating profits per vessel, less an opportunity cost \( p \) per vessel. Gross operating profits are assumed to be a function of \( E_i(t) \) and \( x_i(t) \) via a harvesting function \( H_i(E_i, x_i) \), a cost function \( C_i(E_i, x_i) \), and a parametric output price \( p \). Opportunity costs per vessel \( p \) are assumed to reflect alternative income earning opportunities outside of the fishery, which we assume to be constant per unit of vessel capacity and common across all patches.

In this \( n \)-patch system, we can model the forces operating to change the distribution of effort over space as

\[
\dot{E}_i = \Phi_i(NR_i) + \sum_{j=1, j \neq i}^{n} \Delta_{ij}(NR_j, NR_i), \quad i = 1, 2, \ldots, n. \quad (4)
\]

This behavioral equation is a spatial generalization of the entry–exit part of equation system (3). Entry into and exit from a particular patch \( i \) is again hypothesized to depend upon own-patch rents vis-à-vis outside opportunities, depicted by the \( \Phi_i(NR_i) \) function; when \( \Phi_i \) is positive effort is entering the fishery into patch \( i \) from outside the fishery and when negative vessels are exiting to an outside pool. We continue to assume that \( \Phi_i \) is increasing in \( NR_i \) so that patches with the highest net rents in a system are experiencing the highest rates of entry, other things equal. In addition, vessels move into and out of any given patch \( i \) to other patches depending upon relative opportunities within the fishery. The second component of (4) depicts this dispersal of effort to and from various other patches in the system. Total dispersal to and from other patches is designated by a summation of \( j - 1 \) pairwise dispersal functions. We choose the convention of
adding dispersal relationships so that when $\Delta_{ij}$ is positive, vessels are assumed to be moving to patch $i$ from $j$ and vice versa when negative.\textsuperscript{14,15}

The simplest explicit representation of the previous system, and one which we use in the remainder of this paper, is a linear specification where $\Phi_i(NR_i) = s_i NR_i$ and $\Delta_{ij} = s_{ij}(NR_i - NR_j)$ so that

$$
\dot{E}_i = s_i NR_i + \sum_{j=1}^{n} s_{ij}(NR_i - NR_j), \quad i = 1, 2, \ldots, n.
$$

In this specification (qualitatively similar to the biological dispersal model discussed in Section I), the rate of change of effort in a particular patch is proportional to the level of rents in that patch relative to both outside opportunities ($\pi$), where the own-patch responsiveness rate is $s_i$, and is proportional to rents in different patches in the system. In this system, when rents are higher in patch $i$ than $j$, there is dispersal from $j$ into $i$ by an amount proportional to rent arbitrage opportunities ($NR_j - NR_i$), where the cross patch responsiveness rate is $s_{ij}$. The larger the difference in rents between patches $i$ and $j$, the higher the rate of movement of vessels between the two patches, other things equal. Whether a given patch is a net receptor or net contributor to the rest of the system depends upon its interrelationships with all other patches under the summation. At any given point in time, patch $i$ may be attracting vessels from patch $j$ and contributing vessels to patch $k$ in a manner that depends upon relative rents across the whole system. Other things equal, these spatial forces tend to redistribute effort in a manner that, in the long run, equalizes average net rents across all patches at the common opportunity cost. Note that this is not the optimum way to distribute vessels because this is an open-access system; there are too many vessels in the whole system and they are allocated across the fishing grounds to equalize average rather than marginal rents.

As we did with the spatially explicit biological model, we can stack Eq. (5) for all $n$ patches and we can express the system as

$$
\dot{E} = Sr(x,E) + \Delta r(x,E).
$$

The economic system in (6) is comprised of $n$ patch-specific dynamic equations where $E$ is a $n \times 1$ vector whose components are the instantaneous rate of change of effort in each patch ($\dot{E}_i$), $S$ is a $n \times n$ diagonal matrix of entry–exit response rates ($S_{ii} = s_i$),\textsuperscript{16} $\Delta$ is an $n \times n$ matrix of dispersal response rates between patches $i$ and $j$ ($\Delta_{ii} = \sum_{j=1}^{n} s_{ij}$ and $\Delta_{ij} = -s_{ij}$), and $r(x,E)$ is a $n \times 1$ vector of net rents in patch $i$ where net rents in patch $i$ are a function of the biomass in patch $i$ and the

\textsuperscript{14}In order to avoid certain implausible results, we need to impose a symmetry condition on the dispersal functions such that $\Delta_{ij} = -\Delta_{ji}$ for all $i, j = 1, \ldots, n$. This condition states that whenever there is a gain recorded in patch $i$ by the vessels attracted from patch $j$, there must be a corresponding loss associated with an exact symmetrical movement elsewhere in the system, namely, the number of vessels lost from patch $j$ that are moving into patch $i$. This ensures that vessels are not lost during the process of dispersal.

\textsuperscript{15}It is important to point out that the total effort operating in the fishery ($E_{\text{total}}(t) = \sum_{i=1}^{n} E_i(t)$) changes from one period to the next as a function of a weighted sum of net rents throughout the system ($E_{\text{total}} = \sum_{i=1}^{n} E_i = \sum_{i=1}^{n} \Phi_i(NR_i)$).

\textsuperscript{16}If $s_i = s$ for all $i = 1, \ldots, n$, then $S = sI$ where $I$ is an $n \times n$ identity matrix.
level of effort in patch $i$. The characteristics of the matrices $S$ and $\Delta$ and the functional form of net rents will determine the steady-state levels and the stability of the system.

Equation system (6) is a simple representation of the process of effort distributing itself across different fishing grounds as first discussed by Gordon and it also generalizes Smith’s ad hoc depiction of bioeconomic dynamics by adding spatial dispersal. The model is still ad hoc in the same ways that the Smith–Gordon models are. In particular, there is no explicit microtheory of behavior here; aggregate entry–exit behavior is simply assumed to depend in a myopic and proportional way on current rents. Several points can be made in defense of this structure however. First, with respect to the assumption that behavior is myopic, it should be expected that, under real world open access conditions, behavior is relatively myopic. This is because under open access it does not pay to be too foresighted since sacrifices made today for tomorrow are likely to be eroded away by open access competitive behavior. Second, even if we wished to include less myopic expectations behavior (see Berck and Perloff [4]), there really is no well developed microdynamic theory of open access behavior. Third, as it turns out, the simple model has been found to predict effort dynamics quite accurately. For example, Wilen [39] and Conrad and Bjorndal [12] and others have found that simple entry–exit functions fit the empirical data in open access settings quite well. Finally, from a modeling perspective, it makes sense to appeal to Occam’s razor and to start with the simplest model which still captures fundamental forces. In this setting, we rely on only two premises: that individuals seek to arbitrage profit opportunities over time and space and that they do so sluggishly due to various intertemporal and spatial adjustment costs (the most important of which may be that it simply takes time to move across space).

IV. EQUILIBRIUM IN A SPATIAL BIOECONOMIC MODEL

In this section we bring together the two components discussed in Sections I and II and we discuss the implications of the spatially integrated bioeconomic model. First we discuss some general characteristics of the intertemporal–spatial dynamics and the nature of equilibrium in this system. Then, we solve for a closed form solution for a particular specification of the model and we illustrate how various biological systems give rise to corresponding bioeconomic equilibria. The spatial bioeconomic model developed here depicts a mobile metapopulation system and a mobile harvesting system operating over that population. The integrated system can be represented by

$$\dot{x} = F(x)x + Dx - h(x,E),$$
$$\dot{E} = Sr(x,E) + \Delta r(x,E).$$

(7)

Biomass levels in each patch change over time according to three additively separable forces: own-patch birth–death ($F(x)x$), between-patch dispersal ($Dx$), and harvest $h(x,E)$. Effort levels in each patch respond to own-patch rents relative to outside the fishery opportunities ($Sr(x,E)$), and between-patch rents which generate fleet dispersal ($\Delta r(x,E)$). With this integrated model, we can explore various features of bioeconomic heterogeneity associated with individual patches in the
system, including possibilities of different biological productivity and differences in costs, prices, and/or catchability in each patch. In addition, the model is capable of depicting a range of potential linkages between patches that reflect biological and oceanographic features associated with the landscape ecology inhabited by the population. For example, a biological system along a narrow coastal upwelling environment might be best depicted as a system of patches located in a line, with each one linked mainly to those adjacent to it. In contrast, a system located in a large continental shelf area might best be viewed as a fully (or at least highly) integrated system, with each patch linked to most of the others via larval mixing and circulation. These two systems would be characterized by suitably specified restrictions on the biological dispersal matrix.17

In disequilibrium, both biological and economic forces are operating to influence convergence to the bioeconomic equilibrium. For example, in a relative density-dependent system, patches that are closer to their natural carrying capacities “feed” other patches via dispersal, thus speeding the process of system convergence to long run equilibrium. In addition, other things equal, patches with higher biomass levels attract vessels from other patches with lower levels, also reinforcing the ability of low biomass patches to catch up with higher biomass counterparts. Biological and economic dispersal thus both act as system averaging forces, smoothing out the influence of bioeconomic heterogeneity, and linking the inherently dynamic process of convergence across space. In the long run, the system equilibrium can be characterized by

\[
\dot{x} = F(x)x + Dx - h(x, E) = 0 \Rightarrow h(x, E) = [F(x) + D]x, \\
\dot{E} = (S + \Delta)r(x, E) = 0 \Rightarrow r(x, E) = 0.
\] (8)

From inspection, several properties of the spatial equilibrium can be inferred. First, in an open access spatial equilibrium, net rents in each patch are zero as we would expect.18 Second, the matrix of response parameters in the entry–exit–dispersal system does not affect the equilibrium levels of either effort or biomass but rather (as in Smith’s model) affects the speed of adjustment and qualitative characteristics of the approach paths in each patch. High response rates generate oscillatory overshoot and undershoot in dampened convergence and slow response rates correspondingly generate approach paths that are asymptotic. Third, the biological equilibrium is maintained where harvest equals yield in each patch, but patch yield is composed of both intrinsic growth and dispersal from and to other patches.

17 With respect to economic dispersal, generally we would expect that the fleet would be relatively free to move from any patch to any other patch and hence the fleet dispersal matrix would be fully integrated. However, ecological landscape features or management policy might prevent vessel dispersal between some linkages and this would be modeled with restrictions on the fleet dispersal matrix. For example, a fishery operating over a system of peninsulas and fjords might find it possible to move from patch 1 to patch 2 to patch 3 and back, but not directly between patch 1 to patch 3, and this would be modeled with restrictions on the fleet dispersal matrix. It can easily be shown that the industry’s equilibrium equation in (8) can be simplified to the following: \(Ar = 0\) where \(A = (S + \Delta)\). Furthermore, it can be shown that \(A\) is symmetric, quasi-dominant diagonal, and nonsingular. From the properties of \(A\), a basic result from linear algebra is that the only solution to \(Ar = 0\) is \(r = 0\) (result (8)).
As discussed earlier, this bioeconomic system is capable of depicting a very broad range of ecological and economic circumstances. Many of the most interesting implications of this integrated model emerge out of various assumptions about linkages and dispersal summarized in the $D$ matrix. The $D$ matrix not only identifies exactly which patches are biologically linked to one another, but it also defines the mechanisms by which patches are linked and equilibrium is achieved. For example, biological dispersal might be driven by a density-dependent or unidirectional process but in either case, when the exploited biological system is in equilibrium, own-patch growth is balanced by harvesting and net migration. In contrast, the economic system is in equilibrium when net rents are equalized across space and entry–exit stops when these rents are zero. In general, the combined bioeconomic equilibrium is a nonhomogeneous or flux equilibrium in the sense that there is some movement across space in equilibrium, even though the population size and the fleet size in each patch is constant. The flux in the system arises out of the biological system and not the economic system, however, because each patch’s population size is maintained by the balance between own-patch natural growth and harvesting, and system wide immigration or emigration to and from the other patches.

The kinds of issues that this type of system can address are several. For example, what does the equilibrium distribution of effort and population look like over space? In which patches are population levels (or harvest or effort levels) large or small? How is the spatial distribution affected by various configurations of patch-specific parameters? What role is played in this system by biological dispersal? Because the avenues for dispersal are captured in the properties of the $D$ matrix, how do alternative configurations of these linkages affect the spatial distribution of the population and fleet? How are aggregate variables such as total effort or total population size affected by the types of linkages and dispersal rates? What types of biological systems equilibrate with higher or lower spatial variability in effort and populations? Do dispersal processes amplify or mute the inherent sources of heterogeneity in a patchy system?

In order to get a feel for the answers to some of these questions, we consider next a special case of the preceding general model which allows us to solve for a closed form solution to an $n$-patch system. As it turns out, it is easy to derive a closed form solution for the model in which net rents per patch are multiplicatively separable with respect to effort $(NR_i(x_i, E_i) = NR(x_i)E_i)$. Here we consider the common functional representation where rents are linear in $x$ and proportional to $E_i$, namely, $NR_i = pqx_iE_i - (c_i + \pi)E_i$. If we set this equation equal to zero and if we solve for $x_i$, we get a rent dissipating equilibrium biomass level for each patch which depends upon own-patch economic parameters only and which we designate $w_i$.19 In this special case, the proportionality of net rents to effort generates a recursive solution because the equilibrium biomass levels can be solved independently from the equilibrium effort levels. The biomass levels can then be substituted into the effort equilibrium equations. The results are closed form solutions for biomass levels $(x_i^{\ast})$ which are functions of the economic parameters and

19 Thus for this rent specification $x_i = w_i = (c_i + \pi)/pq$, Note we do not need to impose the assumption that net rents are linear in $x_i$ to be able to isolate a solution for $x_i$. For example, if net rents in patch $i$ are $NR_i = pqx_iE_i - (c_i/x_i)E_i - \pi E_i$ then the steady-state biomass level is $x_i^{\ast} = (\pi + \sqrt{\pi^2 + 4pqc_i})(q/pq)$. 
TABLE II
Steady-State Levels for the Different Types of Spatial Biological Links

<table>
<thead>
<tr>
<th>Spatial configuration</th>
<th>Biomass levels</th>
<th>Effort levels</th>
<th>Patches</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fully integrated</td>
<td>( x_i^{ss} = \frac{c_i + \pi}{pq_i} = w_i )</td>
<td>( E_i^{ss} = \frac{1}{q_i} \left[ r_i \left( 1 - \frac{w_j}{k_j} \right) + d_{ii} + \sum_{j=1}^{n} d_{ij} \frac{w_j}{w_i} \right] )</td>
<td>( \forall i )</td>
</tr>
<tr>
<td>Closed</td>
<td>( x_i^{ss} = \frac{c_i + \pi}{pq_i} = w_i )</td>
<td>( E_i^{ss} = \frac{1}{q_i} \left[ r_i \left( 1 - \frac{w_j}{k_j} \right) \right] )</td>
<td>( \forall i )</td>
</tr>
<tr>
<td>Sink-source</td>
<td>( x_i^{ss} = \frac{c_i + \pi}{pq_i} = w_i )</td>
<td>( E_i^{ss} = \frac{1}{q_i} \left[ r_i \left( 1 - \frac{w_j}{k_j} \right) + d_{ii} \right] )</td>
<td>( i = \text{source} )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( E_j^{ss} = \frac{1}{q_j} \left[ r_j \left( 1 - \frac{w_j}{k_j} \right) + d_{jj} \frac{w_j}{w_i} \right] )</td>
<td>( j = \text{sink} )</td>
</tr>
<tr>
<td>Multiple-source</td>
<td>( x_i^{ss} = \frac{c_i + \pi}{pq_i} = w_i )</td>
<td>( E_i^{ss} = \frac{1}{q_i} \left[ r_i \left( 1 - \frac{w_j}{k_j} \right) + d_{ii} + \sum_{j=1}^{n} d_{ij} \frac{w_j}{w_i} \right] )</td>
<td>( i = \text{source area} )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( E_j^{ss} = \frac{1}{q_j} \left[ r_j \left( 1 - \frac{w_j}{k_j} \right) + d_{jj} + d_{kj} \frac{w_j}{w_i} \right] )</td>
<td>( j = \text{sink} )</td>
</tr>
<tr>
<td>Spatially linear</td>
<td>( x_i^{ss} = \frac{c_i + \pi}{pq_i} = w_i )</td>
<td>( E_i^{ss} = \frac{1}{q_i} \left[ r_i \left( 1 - \frac{w_j}{k_j} \right) + d_{ii} + d_{ij} \frac{w_j}{w_i} + d_{ki} \frac{w_k}{w_i} \right] )</td>
<td>( j, k = \text{neighbors} )</td>
</tr>
</tbody>
</table>

solutions for the effort levels \( E_i^{ss} \) which are functions of both the biological and economic parameters. The solutions for this system under different biological dispersal conditions are given in Table II.

The implications of various configurations of biological dispersal and linkages in this particular system are relatively straightforward because they are essentially isolated in the equilibrium levels of effort in each patch. As can be seen in Table II, the equilibrium biomass levels for each patch in this system are only functions of that particular patch’s own economic parameters. In contrast, the equilibrium levels of effort in each patch depend upon the spatial structure of the entire system’s biology; specifically, the dispersal links embodied in the \( D \) matrix, as well as own-patch growth rates and carrying capacities. For example, the closed system, which is essentially \( n \) biologically independent patches, generates a bioeconomic equilibrium in which the equilibrium level of effort in each patch is inversely proportional to the equilibrium biomass level, which is itself dependent upon economic parameters only for the patch in question. In contrast, the equilibrium levels of effort in each patch in the fully integrated system depend upon not only own biomass but on the equilibrium biomass levels of all other patches (each dependent, in turn, on own-patch-specific economic parameters).\(^{20}\)

To better visualize some of the implications of different ecological structures and biological dispersal mechanisms, consider a simple three patch example. The first

\(^{20}\)Note that the presence of economic and/or biological heterogeneity is necessary to generate interesting conclusions; if the economic and biological parameters are equal across all patches in a fully integrated system, the bioeconomic equilibrium is identical to the closed system.
question of interest is: how does the spatial equilibrium pattern of effort depend upon the type of biological system the industry is exploiting? We choose parameters as follows: first, prices, catchability coefficients, intrinsic growth rates, and opportunity costs are assumed equal across all patches at values $p$, $q$, $r$, and $\pi$, respectively. Second, we normalize so that population is measured in density terms $x$. Third, costs are arbitrarily assumed greater in patch 3 than in patches 1 and 2, perhaps due to strong currents, or other oceanographic conditions. In particular, we assume $(c_3 + \pi) = \lambda(c_2 + \pi) = \lambda(c_1 + \pi)$, where $\lambda > 1$. Let $\bar{\xi}$ be the population density satisfying the rent dissipation equation for the parameters associated with patches 1 and 2.\textsuperscript{21} By our assumption regarding cost differences in patch 3, we know that the equilibrium density in patch 3 is $\lambda\bar{\xi}$ with $\lambda > 1$. Thus the equilibrium density of biomass will be higher in the high cost patch compared with the two lower cost patches.

Now we are in a position to examine how different types of biological dispersal–linkage mechanisms influence the spatial equilibrium determination of effort. Note first that the closed system is simply three separate and unconnected patches and hence it is a good benchmark with which to compare all of the other cases. Table III shows the equilibrium population and effort levels in each patch

\textsuperscript{21}Thus, for example, if $pq_1x_1(c_1 + \pi)E_i = 0$, we have $x_1 = (c_1 + \pi)/pq_1 = \pi = x_2$ and $x_3 = \lambda(c_1 + \pi)/pq_1 = \lambda\pi$. 

### Table III

<table>
<thead>
<tr>
<th>Spatial configuration</th>
<th>Patch effort levels</th>
<th>Total effort level ($\Sigma_{i=1}^3 E_i$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Closed</td>
<td>$E_{i_1}^* = E_{i_2}^* = \frac{r}{q}(1 - \bar{\xi})$</td>
<td>$\frac{r}{q}[2(1 - \bar{\xi}) + (1 - \lambda\bar{\xi})]$</td>
</tr>
<tr>
<td></td>
<td>$E_{i_3}^* = \frac{r}{q}(1 - \lambda\bar{\xi})$</td>
<td></td>
</tr>
<tr>
<td>Fully integrated</td>
<td>$E_{i_1}^* = E_{i_2}^* = \frac{r}{q}\left[\frac{1}{1 - \lambda} - \frac{b}{r}(1 - \lambda)\right]$</td>
<td>$\frac{r}{q}[2(1 - \bar{\xi}) + (1 - \lambda\bar{\xi})] - \frac{2b}{q}\left[2 - \lambda - \frac{1}{\lambda}\right]$</td>
</tr>
<tr>
<td></td>
<td>$E_{i_3}^* = \frac{r}{q}\left[\frac{1}{1 - \lambda} - \frac{2b}{r}(1 - \lambda)\right]$</td>
<td></td>
</tr>
<tr>
<td>Spatially linear</td>
<td>$E_{i_1}^* = \frac{r}{q}(1 - \bar{\xi})$</td>
<td>$\frac{r}{q}[2(1 - \bar{\xi}) + (1 - \lambda\bar{\xi})] - \frac{b}{q}\left[2 - \lambda - \frac{1}{\lambda}\right]$</td>
</tr>
<tr>
<td>(two = center)</td>
<td>$E_{i_2}^* = \frac{r}{q}\left[\frac{1}{1 - \lambda} - \frac{b}{r}(1 - \lambda)\right]$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$E_{i_3}^* = \frac{r}{q}\left[\frac{1}{1 - \lambda} - \frac{b}{r}(1 - \lambda)\right]$</td>
<td></td>
</tr>
<tr>
<td>Sink-source</td>
<td>$E_{i_1}^* = \frac{r}{q}\left[\frac{1}{1 - \lambda} - \frac{2b}{r}(1 - \lambda)\right]$</td>
<td>$\frac{r}{q}[2(1 - \bar{\xi}) + (1 - \lambda\bar{\xi})] - \frac{b}{q}\left[1 - \frac{1}{\lambda}\right]$</td>
</tr>
<tr>
<td>(one = source)</td>
<td>$E_{i_2}^* = \frac{r}{q}\left[\frac{1}{1 - \lambda} + \frac{b}{r}\right]$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$E_{i_3}^* = \frac{r}{q}\left[\frac{1}{1 - \lambda} + \frac{b}{r}\right]$</td>
<td></td>
</tr>
</tbody>
</table>
for several types of biological systems. Note next that the biomass levels do not change across system types with different linkages; this is because we are using a special case of the rent function which allows each patch’s population density to be determined only by its own-patch economic variables. Note also that equilibrium biomass levels reflect the inherent heterogeneity of the economic conditions; in particular, where costs are relatively high, biomass levels are correspondingly high.

Now, what happens as the closed system is opened up via biological dispersal linkages? Consider first the fully integrated system, with density-dependent dispersal flowing between all patches. From Table III, we can see that the spatial distribution of effort in equilibrium in the integrated system involves more effort in patches 1 and 2, and less effort in patch 3, relative to the closed case. Why does this happen? Because with biological dispersal, biomass flows out of the high density patch (patch 3), to the lower density patches, dispersing effort as a result. Interestingly, the total effort drawn into the integrated system is also greater than in the closed system. This occurs because the biological dispersal gradient operates in the direction of intrinsically more profitable areas. Thus, in this case at least, biological dispersal and linkages increase overall potential rents and skew the relative distribution of effort more than would be the case in a closed system.

Consider next the spatially linear case in which, for example, patches are located along a line. Suppose that there are three patches so that the center patch is connected to both outside patches whereas each outside patch is only connected to the center patch. This differs from the fully integrated case in an important way, because the two outside patches are not directly connected to each other. Thus this case illustrates the importance of so-called “edge effects” in a spatial system.

Consider first a case where the economic parameters for each outside patch are identical and at levels to generate higher equilibrium population densities than the center patch. Then biomass would flow from the edges to the center, skewing both effort and harvest toward the center. Now consider, in contrast, the case considered here where patch 3 is high cost relative to patches 1 and 2. As we would expect, the higher population density in patch 3 generates dispersal from 3 to 2, but because patches 1 and 2 have identical population densities, there is no dispersal from patch 2 to patch 1. Table III shows equilibrium effort levels for patches 1–3, and we find levels equal to, greater than, and less than corresponding levels in the closed case, respectively. As we might expect, total effort is greater than the level in the closed case for reasons discussed earlier, but not as great as in the fully integrated case. This is a sort of spatial Le Chatelier effect in operation; the

22 Note in this paper we only consider interior solutions. In an n-patch setting, the conditions for interior solutions are rather complex, but Table III shows the restrictions on the parameters that are required to guarantee them. For example, in the closed system, for effort to be positive in patches 1 and 2 we require that \( \pi < 1 \) for \( i = 1, 2 \). For effort to be positive in patch 3, we require \( \lambda \pi < 1 \). Thus, to ensure interior solutions, costs cannot be too high relative to price in any of the patches, but in the high cost patch in particular. In other linked systems, the conditions ensuring interior solutions are more complicated because they generally depend upon combinations of parameters in all (or subsets of) the patches. For example, in a two-patch sink-source system (with patch 1 the source) we would need \( 1 - w_1 - b/r_1 > 0 \) and \( 1 - w_2 + b/r_2 > 0 \) for interior solutions with \( E_1 \) and \( E_2 \) positive.

23 This system is equivalent, in Smith’s single patch model 35, 36, to one with a phase diagram in \((E, X)\) space characterized by a horizontal \( E \) nullcline. A more general model, with rents nonlinear in effort, would integrate our decoupled special case, and would make it necessary to solve for the equilibrium values of \( E \) and \( x \), simultaneously (for example, if \( C(E, x) \) is twice-differentiable and concave in \( E \)).
spatially linear system is more constrained by fewer between-patch linkages than the fully integrated case and as a result, potential rents are not as high.

Now consider the three patch sink-source case where we (arbitrarily) designate patch 1 as the source patch. Recall that with sink-source linkages, biomass is hypothesized to depend upon absolute population levels (or densities) in the source and not to depend upon relative densities between patches. Assume the total biomass outflow from patch 1 to be $2b_1$, distributed equally between patches 2 and 3. Again, the intuition behind what should happen here relative to the closed case is clear; biomass flows from patch 1 to patches 2 and 3, attracting effort into both receptor patches from patch 1. What happens to total system effort in this case? Interestingly, it falls relative to the closed system and a bit of reflection suggests why. In this case, the biological dispersal gradient is working against the spatial distribution of profitability and hence overall rent potential falls as dispersal occurs. Basically vessels are being repelled out of low cost area 1 into higher cost area 3, so that every unit of harvest associated with dispersal is caught with higher average costs. Note also that dispersal in this case acts to homogenize the inherent heterogeneity generated by the differences in fundamental cost–price ratios, averaging out these differences over space.

Figure 2 illustrates and compares these and an additional multiple source case. For comparison purposes, we compare each case with the reference closed system of biologically independent patches. Thus the shaded areas represent effort differences in each patch, relative to the closed system, induced by various structural biological linkages among patches. Each biological dispersal system generates a different spatial equilibrium distribution of effort. As Figure 2 shows, the qualitative variety of spatial equilibria possible is large and reflective of the dispersal characteristics in the biological system. In some cases biological integration exacerbates the skewness of effort relative to the closed system case. For example, when patches 1 and 2 are fully integrated to patch 3, biomass flows from patch 3 to the other patches, enhancing their attractiveness and drawing effort. On the other hand, in a simple sink–source system in which patch 1 is the source patch linked unilaterally to patches 2 and 3, the effect is to enhance the biomass levels in both sinks, causing effort flows out of one and into the other two receptors. This qualitative pattern is dramatically reversed in the multiple source case, where the addition of density-dependent flows results in effort dispersal from patch 3 into patch 1 and no change in patch 2.

This simple example hints at some of the richness that emerges when we explicitly consider spatial factors in a model of bioeconomic exploitation. While there are numerous other aspects of both the dynamics and equilibria we could consider, we have focused primarily on how effort and the population distribute over space in response to various bioeconomic phenomena and the nature of biological linkages. As we have shown here, the spatial pattern of effort is driven fundamentally by patch-specific cost–price ratios. In areas where the ratio $(c_i + \pi)/\delta_i p_i$ is high, effort is low and vice versa. Because effort governs exploitation, patches with low effort have relatively high biomass levels. These observations are illustrated by the closed structure, which effectively maps the heterogeneity in the economic parameters into corresponding heterogeneity in the spatial distribution of effort and biomass.

What role do linkages play in determining the spatial equilibrium? Basically biological and economic linkages serve either to smooth out or to exacerbate any
bioeconomic imbalances via dispersal of both the population and effort. For example, suppose we begin with the closed system and then we imagine it transformed into one with a relative density based dispersal process. Then the initial (closed system) conditions, which involve a higher biomass level in the relatively low profit patch, generate biological dispersal from the high biomass patch to the other two lower biomass patches. This, in turn, generates higher rents there, attracting more effort until the exit from the low profit patch is matched by dispersal to the higher profit patches. In this case, dispersal in both the biological and economic components of the system exacerbates the initial heterogeneity due to fundamental differences in patch-specific profitability. In equilibrium, the integrated system has a more spatially skewed distribution of effort because dispersal acts to complement fundamental relative profit forces.
As we have seen with the sink-source case, however, linkages can also work against fundamental heterogeneities induced by cost–price differences across patches. In our sink-source case, biomass is (arbitrarily) assumed to flow unidirectionally from patch 1 to patches 2 and 3, with a flow based on patch 1’s density. This enhances biomass levels in each of the receptor patches, making each relatively more attractive, compared with the closed system case. In equilibrium, the source ends up losing biomass and effort, and patches 2 and 3 gain biomass and effort. This works contrary to the fundamental incentives to move away from patch 3 toward patch 1 (and patch 2) based on economic parameters.

V. DISCUSSION

This paper generalizes the basic open access models of Gordon and Smith in the spatial dimension. The biological model embeds spatial features in a manner consistent with developments in biology focusing on patchiness, heterogeneity, and linkages between patches. The economic model of harvester behavior is simple, positing myopic open-access behavior responding sluggishly to potential arbitrage opportunities both outside the fishery and within the fishery across space. While the combined bioeconomic system is relatively simple, it captures the fundamental forces that we would expect to be operating in an open-access system exploited by a spatially mobile and economically responsive fleet.

As we have demonstrated, space matters in interesting and complicated ways, and there are predictable patterns that emerge in a spatially explicit bioeconomic system. These spatial patterns reflect both within-patch bioeconomic forces and between-patch biological and economic linkages. The range of possibilities of both patch-specific heterogeneity and types of dispersal linkages is large in the real world, of course. Our model is general and capable of depicting many of these scenarios. At the same time, the model suggests some important generalizations about how various within- and between-patch forces interact. For example, because harvesters are assumed to respond to relative as well as to absolute rents, there is a fundamental and endogenous “economic gradient” operating at each point in time, depicting incentives to reallocate effort over space toward patches that exhibit higher relative rents. At the same time, there is a “biological gradient” operating to reallocate biomass over space via migration to areas of lower density or that are otherwise natural sinks. The manner in which these two forces operate together determines the process of bioeconomic convergence over space and time. In some systems they operate in a complementary fashion and in other systems they work against each other.

Although it is reasonably straightforward to characterize the dynamics of convergence, we focus in this paper on the equilibrium properties of this system. As we have shown with a simple example, it is possible to predict how equilibrium spatial patterns of the two important state variables (effort and biomass) are affected by different configurations of patch-specific parameters and between-patch linkages. In our example, the pattern of biomass levels is determined by bioeconomic ratios specific to each patch. In patches where costs are high or catchability or prices are low, effort is driven away by lower rents toward high rent patches in a manner determined by the economic gradient. But as effort reallocates, it also affects biological dispersal, which is reacting according to the biological gradient. In a
density dependent dispersal system, patches with relatively higher biomass levels will also generate biomass dispersal, driving away even more effort in second and subsequent rounds of adjustment. Hence in some cases, the ability of the fleet to respond to rent differentials across space reinforces any initial forces due to heterogeneity in cost–price ratios, skewing effort even more dramatically than would be the case in an unlinked system. Of course, it is also possible with other biological linkages to homogenize the fundamental heterogeneity driven by bioeconomic ratios. For example, in a sink-source system in which the source is a lower cost area relative to the sink, the fleet would skew toward the source without any biological dispersal. But with sink–source dispersal, in this example biomass will flow toward the sink, supporting more effort there. Thus in this case, spatial dispersal by the fleet smoothes the initial spatial distribution associated with patch-specific fundamentals.

An important implication of these results is that, in an exploited system, whether a particular patch is a source or sink in equilibrium (and in transition) may depend as much on economic parameters as on biological parameters. This seems to be an important point missed by biologists who have begun to promote closed zones and natural refugia as spatial management measures. A typical argument made to justify setting a particular area aside and protected from harvesting involves pointing to high productivity as a source area for juveniles, larvae, etc. In instances where evidence is used to support the case for a particular area, biologists typically attempt to measure indicators of dispersal by tagging juveniles or doing genetic analysis of adults at various locations. In an integrated bioeconomic system, however, whether a particular patch acts as a de facto source depends not only upon biological but also on economic factors as well. Any tagging or measurement of movement in this type of system might conclude that observed net dispersal is due to special biological characteristics, when in fact, it is due to special economic circumstances.

A question that might naturally be asked is: is adding the spatial dimension really worth all of the effort? This is a legitimate question because, even though the model discussed here is relatively simple, it requires some effort before patterns emerge from among the richness of all the cases that can be examined. Our answer to the fundamental question is an unequivocal yes. In the first place, we may simply be missing a great deal of important information by aggregating over space. A n important part of what economists do is to try and understand economic behavior. Renewable natural resource exploitation is a somewhat unique activity because the “firm” often moves to the resource. This opens up the possibility of adding degrees of freedom in empirical work by taking advantage of the behavioral reaction to changes in incentives over space as well as time. Of course adding spatial complexity adds parameters to be estimated too, but as our model suggests, there are sensible specifications that might be utilized to increase estimation efficiency over the system as a whole. In addition, by ignoring spatial decisions and simply estimating aggregate time series models, we may be grossly biasing estimates of behavioral relationships by washing out all of the true responsiveness in the system. At the very least, then, this modeling system seems useful for framing empirical analysis that can take advantage of richer data sets incorporating both spatial and intertemporal features of behavior.

A second important reason why spatial analysis may be worth the effort is more normative than predictive. As discussed at the beginning of the paper, there is a
virtual groundswell of interest among biologists in using spatially differentiated management techniques. The suggestions seem to be emerging from new ecological paradigms that move away from presumed obsolete views which treat populations as homogeneous and spatially uniform units. In the new biological models, populations are comprised of many spatially distinct patches, some of which may be linked by dispersal processes. This suggests a new suite of options involving managing the population by managing the patches. For example, one popular suggestion is to set aside specific areas from harvesting, so that they might act as sources to the other areas. Another related suggestion is to close an area for a period, and then open it while closing another, etc. This “rotating harvest zones” suggestion (or the permanent closed zone or refugia idea) is thought by proponents to give the system a chance to rejuvenate from commercial exploitation, to develop a richer and more diverse species portfolio, and to provide other often unspecified but implied beneficial effects.

Unfortunately, most of the analysis of these proposals focuses exclusively on biological implications of spatial management, paying virtually no attention to the harvesting sector. There are no analyses of the costs of establishing refugia or rotating harvest zones and there is no analysis of how the fleet might react to these policies. What happens to those parts of the fleet that are removed from an area? How will changes in fleet distribution affect the remaining open access part of the system? Under what circumstances will total system biomass increase? When will total harvest rise or fall? These are questions that must be answered before these new proposals are given any chance in a political system in which harvesters are stakeholders with a legitimate position at the table. In order to answer these kinds of questions, we must begin with conceptual structures of the sort developed here, which account for economic motivations and behavior over space and time, just as they account for biological growth and dispersal processes.

REFERENCES

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