Dynamics of Spatial Exploitation:
A Metapopulation Approach

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Abstract

We present a bioeconomic model of a harvesting industry operating over a heterogeneous environment comprised of discrete biological populations interconnected by dispersal processes. The model generalizes the H. S. Gordon [1954]/V. Smith [1968] model of open-access rent dissipation by accounting for intertemporal and spatial "Ricardian" patterns of exploitation. This model yields a simple, but insightful, framework from which one can investigate factors that contribute to the evolution of resource exploitation patterns over space and time. For example, we find that exploitation patterns are driven by biological and fleet dispersal and biological and economic heterogeneity. We conclude that one cannot really understand the biological processes operating in an exploited system without knowing as much about the harvesting system as about the biological system.

This paper is forthcoming in *Natural Resource Modeling*.

Contents

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James N. Sanchirico and James E. Wilen*

Introduction

In this paper we present a bioeconomic model of a harvesting industry operating over a patchy environment comprised of discrete biological populations interconnected by dispersal processes.   The model generalizes the H. S. Gordon [1954] and V. Smith [1968] models of open-access rent dissipation by accounting for intertemporal and spatial patterns of exploitation. The spatial patterns exhibit the fundamental process underlying Ricardo's theory of resource scarcity, whereby lands of higher fertility are brought into cultivation first, followed by the cultivation of successively less profitable land (Barnett and Morse [1963]). The model of harvester behavior is combined with a metapopulation model that incorporates modern biological concepts depicting resource patchiness, heterogeneity, and interconnections among and between patches. This approach yields a simple, but insightful, bioeconomic model from which one can investigate factors that contribute to the evolution of resource exploitation patterns over space and time.

Traditional lumped parameter bioeconomic models of fisheries typically begin by assuming a homogeneous distribution of fish. A biological model is then coupled to a model of a harvesting industry characterized as operating either as a sole owner without monopoly power or as open access (see, for example, Clark [1990]). The models of a sole owner illustrate optimal harvest policies and are often compared to the case of open access to illustrate the inefficiencies associated with lack of ownership first discussed by H. S. Gordon [1954]. Gordon showed that with the absence of resource ownership, rents in the fishery would be captured by entrants, and excess returns would attract effort until they were dissipated.   Although Gordon focused on the equilibrium, he acknowledged that the issues affecting fishery management are inherently a dynamic bioeconomic phenomenon. Vernon Smith, in 1968, generalized the Gordon model to account for the stock and industry dynamics in a formulation symmetric to the Lotka-Volterra predator-prey model.

Although the predictions of the Gordon and Smith models are prevalent throughout the resource economics literature, there is only a small body of empirical literature testing the implications of Gordon's

equilibrium results or the dynamic approach paths highlighted in the V. Smith paper. A paper by Hilborn and Kennedy [1992] and a paper by Gillis et al. [1993] test and find support for a version of Gordon's rent equalization hypothesis in the Tasmanian rock lobster fishery and bottom trawl fishery in the Hecate Strait, respectively. With respect to the transitional dynamics, there are two studies, one of the North Pacific fur seal industry between 1880 and 1911 (Wilen [1976]) and another of the Northwest Atlantic harp seal industry (Conrad and Bjorndal [1991]), that showed convergent oscillations of the type predicted by the Gordon/Smith model.

To illustrate the implications of combining the Gordon/Smith and Ricardian hypotheses within a bioeconomic model of a metapopulation, we consider the evolution of a fishery from a relatively unexploited state to an open-access equilibrium. Initially, following Gordon/Smith, one might expect vessels to enter the fishery when the rents become greater than the opportunity costs of harvest capital. In addition, following Ricardo, the initial effort level would be concentrated in the most profitable grounds (or patches), only diffusing into the less profitable areas after the most profitable areas are exploited. However, unlike the irreversible process imagined by Ricardo, where a land's fertility is depleted and the farmer moves on to another parcel, renewable resources can rebound from periods of overexploitation in a metapopulation. Thus the equilibration process might involve both spatial and intertemporal cycles of over- and undershoot as harvesting effort, harvests, and biomass respond to variations in the patterns of economic opportunities.

There are many reasons why resource economists might want to investigate the implications of incorporating the spatial dimension in bioeconomic models.[1] First, conservation biologists have long since abandoned the assumptions of homogeneous environments and distributions of stocks for a new paradigm that focuses on patchy heterogeneous environments and linkages between the patches. Second, if a resource is truly distributed heterogeneously in space, then resource economists are most likely missing a considerable amount of interesting behavior and information by ignoring the spatial dimension. For example, spatial patterns of vessel and biomass movements across the system could reveal information about the structural composition of the fishery that could be used to improve resource stewardship. In addition to these potential modeling gains, spatial models of populations, bioregions, and ecosystems are being used within the conservation biology literature to promote new marine resource stewardship concepts referred to as spatial management. For example, biologists have recently promoted

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[1] In general, ecologists have paid more attention to spatial exploitation patterns than economists have. Hilborn and Walters [1987] generalized a model used by Caddy [1975] to describe scallop harvesting in a discrete formulation. Allen and McGlade [1987] developed a multispecies model with a more elaborate depiction of information, and Klieber and Edwards [1988] developed a simulation model of a spatially mobile tuna/dolphin fishery. See also McGlade and Allen [1984]; Hilborn and Ledbetter [1979]; MacCall [1990]; Tuck and Possingham [1994]; Supriatna and Possingham [1999]; Martel, Walters, and Wallace [2000], and Walters [2000]. Only recently have economists begun to focus on the spatial implications of resources exploitation. For example, see a recent paper by Brown and Roughgarden [1997] examining larval pools in a metapopulation model, papers by Huffaker, Bhat and Lenhart[1992] and Bhat, Huffaker and Lenhart [1993, 1996] examining spatial/intertemporal control of a pest population, papers by Skonhoft and Solstad [1996] and Schulz and Skonhoft [1996] analyzing exploitation of transboundary terrestrial species. See also Bockstael [1996], Albers [1996], Sanchirico [1998], Bulte and Cornelis [1999], Wilson et al. [1999], and Sanchirico and Wilen [1999].

natural refuges as management tools, under the expectation that permanent closures of certain areas might enhance overall biological productivity of an exploited system (Roberts and Polunin [1991]). 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 to a natural state (Botsford, et al. [1993]). To analyze the bioeconomic implication of these 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 the next section, we begin by outlining a biological model of a spatially interconnected population system and then combine it with a simple open-access harvesting model that captures essential features of the Gordon/Smith rent dissipation model in a patchy environment. We then solve for the rent-dissipating equilibrium of the spatially explicit bioeconomic model and present an example to highlight the implications of spatial heterogeneity on the equilibrium distribution and the adjustment paths of effort and biomass. We conclude with a discussion of some of the important insights that emerge when we add the spatial dimension to bioeconomic models of exploitation.

Metapopulation Model

Dating back to the work of Skellam in 1951, biologists and ecologists have been developing comprehensive and rigorous new theories on the implications of space in models of populations. This research and modeling effort has culminated in a new class of population models often referred to as metapopulation models. Metapopulation models are composed of a group of linked subpopulations distributed across a set of spatially delineated habitats or patches. For the purpose of this paper we assume that "patches" are locations in space that contain or have the potential to contain an aggregation of biomass and are located a fixed and discrete distance from one another. The number of organisms in each patch can be assumed to depend either upon both density-dependent growth processes and dispersal from and to other patches in the system or only upon growth processes or dispersal. The dispersal process 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 extinguished and subsequently recolonized via dispersal from the other patches.

We consider here a general N patch discrete metapopulation model. Following Levin [1974; 1976], Hastings [1982; 1983], and Vance [1984], let the rate of change of biomass equations across the system be given by:

$$\dot{\bar{X}} = \mathbf{F(X)}\bar{X} + \mathbf{D}\bar{X} \tag{1}$$

where $\dot{\bar{X}}$ is an $n \times 1$ vector of patch growth rates $\dot{X}_i$ and $\bar{X}$ is an $n \times 1$ vector of patch biomass levels X_i. $\mathbf{F(X)}$ is a $n \times n$ diagonal matrix of own-patch per capita growth functions ($F_{ii}=f_i(X_i)$ for all $i=1,\dots n$), which in the case of logistic growth are $f_i(X_i)=r_i(1-X_i/k_i)$. $\mathbf{D}$ is an $n \times n$ matrix of dispersal coefficients, where 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.[2]

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[2]Most models impose some structure on the dispersal process. In this paper we will impose the following restrictions on the **D** matrix: (i) $d_{ii}\leq 0$, (ii) $d_{ij}\geq 0$, which allow us to identify population fractions that leave from and arrive to one

The dispersal mechanism in the system could either be density dependent (biomass moves from areas of higher to lower concentrations) or independent (typically unidirectional flow from a source to a sink patch(es)).[3]

This model is capable of depicting a variety of behavioral characteristics of a population and also oceanographic features of a spatial setting. Different circumstances are best viewed as alternative parameter restrictions on the dispersal matrix. For example, a <u>closed system</u> is a set of "island" patches, depicted by **D** being a null matrix. At the other extreme, a <u>fully integrated system</u> allows for dispersal in a density-dependent manner from any patch to any other throughout the system and is characterized by a dispersal matrix with full rank. Other cases would be variants, including <u>linear cascade systems</u> with linkages only between neighboring patches (**D** band diagonal), <u>sink-source systems</u> in which one patch provides unreciprocated biomass replenishment to other patches (Pulliam [1988]; Tuck and Possingham [1994]) (**D** a column matrix), or <u>multiple-source cases</u> in which many patches contribute biomass to one common pool that then is redistributed among the patches.

A discrete model of this type can also depict a range of productivity assumptions in a system of individual patches (Carr and Reed [1993], Allison et al. [1998], Sanchirico [1998], and Sanchirico and Wilen [1999]). Some patches may have high biological productivity compared with others, whereas some may have no inherent productivity, as would be the case with a larval pool that receives and disperses larvae from a number of other patches. Thus, even in its linear and separable formulation, equation (1) is relatively general and capable of capturing a broad range of ecological circumstances.

A Model of Spatial Exploitation

In a patchy environment, we might observe an exploiting industry non-uniformly distributed over a finite number of patches, and the distribution would change over time. Although there is little explicit micro-theory of how and why vessels might choose to participate and locate in a particular area, there has been some empirical work investigating the behavioral motivations for vessel movement patterns across fishing grounds (patches). Hilborn and Ledbetter [1979] tested whether boats move in traditional patterns, to maximize weekly catch, or to optimize economic gain subject to the cost of the areas in the British Columbia salmon purse seine fleet and found strong evidence that vessels moved in an attempt to optimize economic gain. Eales and Wilen [1986] also found in the California pink shrimp fishery that patch economic rents were a significant predictor of vessel locational choice decisions. More recently, Evans [1995] found significant evidence that vessels move to optimize economic gain in the California

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area for another. In addition, we assume (iii) $\sum_{k=1}^{n} d_{ki} = 0$ i=1,2,...,n (column sums to zero), 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 is the symmetry condition $d_{ij}=d_{ji}$, which ensures that whatever leaves patch i specifically for j also arrives in j specifically from i. Because this symmetry condition excludes sink-source dispersal processes, we impose the weaker condition (iii).

[3] Density-dependent dispersal processes are employed in papers by Huffaker et al. [1992] and Bhat et al. [1993 and 1996] examining spatial/intertemporal control of a pest population, in papers by Skonhoft and Solstad[1996] and Schulz and Skonhoft[1996] analyzing exploitation of transboundary terrestrial species and in papers by Sanchirico and Wilen [forthcoming] examining the implications of marine reserve creation.

salmon fleet. Thus a sensible hypothesis is that the industry responds to relative and absolute rents across time and space where the differences in rents may be due to economic, biological, and geographical heterogeneity.

How could such behavior be formally represented? As it turns out, it is relatively straightforward to add a spatial dispersal component to the Gordon/ 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 aggregate effort and biomass, respectively, in each patch i, and let $NR_i(E_i,X_i)$ be the corresponding net rents in patch i. Net rents are assumed to be average gross operating profits per vessel, less an opportunity cost π 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 π are assumed to reflect alternative income earning opportunities outside of the fishery, which we will assume to be constant per unit of vessel capacity and common across all patches. Thus we can write net rents in patch i as: $NR_i=[pH(E_i,X_i)-C(E_i,X_i)-\pi(E_i)]/E_i$.

We then hypothesize that the level of effort, E_i in patch i, will change according to:

$$\dot{E}_i = s_i NR_i(E_i,X_i) + \sum_{\substack{j=1 \\ j \neq i}}^{N} s_{ij}[NR_i(E_i,X_i) - NR_j(E_j,X_j)] \quad \text{for all } i=1,...,N \qquad (2)$$

In this specification, effort in patch i changes in response to two forces. The first is the patch-specific level of rents vis-à-vis outside opportunities, captured in the first term. When net revenues in patch i exceed the opportunity cost of vessels, entry occurs from the outside pool of potential effort, and "own-patch" responsiveness is determined by the rate parameter s_i. The second force operating on each patch may be called Ricardian dispersal, depicted by the second term consisting of a sum of pair-wise spatial dispersal rates, each proportional to rent differentials across space. 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 drive the redistribution of effort over space in a manner that equalizes net rents across all patches in the long run. Because this model assumes that participants are myopic rather than forward-looking optimizers, an assumption appropriate to the open-access nature of the exploitation depicted, the level and spatial distribution of the effort operating in the system is not optimal.

Spatial Bioeconomic System

The bioeconomic system depicted here characterizes a harvesting industry behaviorally responsive to rents within the system vis-à-vis outside opportunities and across opportunities over space.   It nests the Gordon/Smith model when the number of patches is 1 ($d_{ij}=0$ and $s_{ij}=0$). In a manner similar to the biological system, we can stack equation (2) for all N patches and combine that with the biological system to get:

$$\dot{\vec{E}} = \mathbf{S}\vec{R}(E,X)$$
$$\dot{\vec{X}} = \mathbf{F(X)}\vec{X} + \mathbf{D}\vec{X} - \vec{H}(E,X) \qquad (3)$$

Here $\vec{E}$ and $\vec{R}(E,X)$ are $n \times 1$ vectors, **S** is an $n \times n$ matrix ($S_{ii} = s_i + \sum_{j=1, i \neq j}^{n} s_{ij}$, and S_{ij}=-s_{ij} for

i,j=1,…,n with i $\neq$ j), and $\vec{H}$ is an $n \times 1$ vector of harvest rates dependent upon both biomass and effort. In disequilibrium, biological and economic forces are acting in accordance with and against one another to influence convergence to the bioeconomic equilibrium. For example, in a density-dependent dispersal process, the high-profit areas will attract larger amounts of effort from the outside pool and from other patches in the system. As a result of the higher levels of exploitation, high-profit patch biomass levels drop faster than those in low-profit areas. At the same time, areas with relatively low fishing pressure initially act as de facto sources for the high-profit patches via dispersal, and this will, other things equal, speed the convergence of the system to the long-run equilibrium as biomass levels are averaged throughout the system. In the long run, the system equilibrium can be characterized by:

$$\vec{\dot{X}} \overset{set}{=} 0 \Rightarrow [\mathbf{F(X)}+\mathbf{D}]\vec{X}-\vec{H}(E,X)=0$$

$$\vec{\dot{E}} \overset{set}{=} 0 \Rightarrow \vec{R}(E,X)=0$$

(4)

Note that the matrix of biological dispersal coefficients (**D**) affects the equilibrium vector of biomass ($\bar{X}$) and effort levels ($\bar{E}$) in each patch, but the matrix of economic response parameters (**S**) only affects the rate of convergence to equilibrium. This occurs because the zero-rent conditions are independent of the response rates, as in the Vernon Smith model of a single patch. In equilibrium, although the biomass levels in each patch are constant, the levels in each patch will be maintained in part by biological dispersal, and hence there will be some biomass movement across space matching outflows to inflows. Note also that the equilibrium is, in general, fully integrated and simultaneous so that the equilibrium levels of biomass and effort in each patch depend upon biological and economic parameters (except response rates) in all other patches. In addition, the character of the equilibrium depends importantly on the structure of the biological dispersal matrix **D**.

A Spatial and Intertemporal Example

In this section, we illustrate with an example how dispersal linkages affect both the equilibrium and intertemporal distribution of effort and biomass throughout the system. As is obvious from the above description of the biology and economics, there are numerous types of spatial configurations that we might observe in nature, each with its own implications for the equilibrium and approach paths in a bioeconomic system. To isolate the implications of the different ecological structures and biological dispersal mechanisms, we focus on a system in which the fleet dynamics are fully integrated and represented by the general dispersal system in equations (3) and (4) above. For the biological system, we consider and compare here i) a closed system, ii) a fully integrated system, and iii) a cascade system. As it turns out, the closed case is a good benchmark from which to analyze how linkages and density-dependent dispersal affect the distributions over time and space. Note that the three cases can be thought of as a continuum representing the degree of linkage present in a system, with the closed and fully integrated systems denoting none and complete linkage, respectively, and the linear or cascade system falling in between.

For simplicity, we employ a standard set of functional assumptions and a set of rather simple assumptions regarding the degree of heterogeneity in the fishery. Both sets of assumptions are summarized in Table 1. With respect to the degree of heterogeneity in the system, we assume that the system is essentially

homogeneous except for (arbitrarily) assumed differences in costs perhaps due to strong currents or other oceanographic conditions. In addition, we normalize and rescale the parameters (q_i, r_i) so that population is measured in biomass density ($x_i = X_i/k$). Note that by assuming carrying capacities are equal, the biomass density level is equivalent to the level of biomass in the patches.

Table 1: Function and parameter assumptions.

	Functions	*Parameter*	*Restrictions*
Economic			
Harvest	$H_i(E_i,x_i)= q_iE_ix_i$	Catchability coefficient	$q_i=q \ \forall i$
Costs	$C_i(E_i,x_i)=(c_i+\pi_i) \ E_i$	Cost per unit of effort	$c_1=c_2=c, \ c_3=\lambda c, \ \lambda>1$
		Opportunity cost	$\pi_i=\pi \ \forall i$
Net rents	$NR_i(E_i,x_i)=[p_iq_ix_i-(c_i+\pi_i)]E_i$	Prices	$p_i=p \ \forall i$
		Entry/exit response rates	$s_i=s \ \forall i$
		Spatial response rates	$s_{ij}=s_{ji} \ \forall i,j$
Biological			
Own patch Production	$F(x_i) = r_i \ x_i \ (1-x_i/k_i)$	Intrinsic growth rates	$r_i=r \ \forall i$
		Carrying capacities	$k_i=k \ \forall i$
Density-dependent dispersal	$d_{11}x_1+d_{12}x_2+d_{13}x_3=$ $\quad b(x_2/k_2-x_1/k_1)+$ $\quad b(x_3/k_3-x_1/k_1)$	Dispersal rates	$d_{ii}=-N_i*b$ and $d_{ij}=b$ $N_i = $ # of patches connected to patch i

Under these functional assumptions, it is possible to derive a closed-form steady-state solution for the model. As a first step, we set net rents in patch i equal to zero ($NR_i = pq_ix_iE_i-(c_i+\pi)E_i=0$) and solve for x_i, yielding a rent-dissipating equilibrium biomass level for each patch that depends only upon own-patch economic parameters ($x^{ss}_i \equiv (c_i+\pi_i)/pq_i$). As a second step, the biomass levels can then be substituted back into the biomass equilibrium equations, and the results are closed-form solutions for both biomass and effort levels. Because net rents are multiplicatively separable with respect to effort, with each patch's biomass level dependent only on its own bioeconomic parameters, the biomass levels do not change across the three cases. A more general model, with rents nonlinear in effort, would integrate our decoupled special case and make it necessary to solve for the equilibrium values of E_i and x_i simultaneously (Sanchirico [1998]).

Under Table 1 assumptions, we can express the equilibrium biomass levels in terms of the assumed cost-to-price ratio differences. For example, if $\bar{x}$ is the population density satisfying rent dissipation in patches one and two, the density in patch three will be $\lambda\bar{x}$ with $\lambda>1$, reflecting the fact that patch three is the high-cost patch

Comparisons of the Equilibrium Distributions

We first investigate how the spatial *equilibrium* pattern of effort depends upon the type of biological system the industry is exploiting. The equilibrium levels of effort and aggregate effort levels across the three cases appear in Table 2. Note first that the closed system is simply three separate and unconnected patches and that the equilibrium biomass and effort levels reflect the inherent heterogeneity of the economic conditions in the system; in particular, where costs are relatively high, the biomass level is correspondingly high, and effort level is low. Thus the equilibrium density of biomass will be higher in patch three compared with the two lower-cost patches one and two because fewer vessels are attracted there because of the higher costs.

**Table 2: Steady-state biomass density and effort levels for the
different types of spatial structures.**

| SPATIAL STRUCTURE	PATCH EFFORT LEVELS	TOTAL EFFORT LEVEL ($\sum_{i=1}^{3} E_i$)
Closed	$E_1^{ss} = E_2^{ss} = \dfrac{r}{q}(1-\bar{x})$ $E_3^{ss} = \dfrac{r}{q}(1-\lambda\bar{x})$	$\dfrac{r}{q}[2(1-\bar{x})+(1-\lambda\bar{x})]$
Fully-integrated	$E_1^{ss} = E_2^{ss} = \dfrac{r}{q}[(1-\bar{x}) - \dfrac{b}{r}(1-\lambda)]$ $E_3^{ss} = \dfrac{r}{q}[(1-\lambda\bar{x}) - \dfrac{2b}{r}(1-\frac{1}{\lambda})]$	$\dfrac{r}{q}[2(1-\bar{x})+(1-\lambda\bar{x})] - \dfrac{2b}{q}[2-\lambda-\frac{1}{\lambda}]$
Linear cascade system (2 is center)	$E_1^{ss} = \dfrac{r}{q}(1-\bar{x})$ $E_2^{ss} = \dfrac{r}{q}[(1-\bar{x}) - \dfrac{b}{r}(1-\lambda)]$ $E_3^{ss} = \dfrac{r}{q}[(1-\lambda\bar{x}) - \dfrac{b}{r}(1-\frac{1}{\lambda})]$	$\dfrac{r}{q}[2(1-\bar{x})+(1-\lambda\bar{x})] - \dfrac{b}{q}[2-\lambda-\frac{1}{\lambda}]$

Now what happens to the distribution of effort and biomass as the closed system is "opened up" via biological linkages? In the fully integrated case with density-dependent dispersal, we find that the spatial distribution of effort in equilibrium involves more effort in patches one and two and less in patch three relative to the closed case. This happens because with density-dependent dispersal, the equilibrium cost-induced differential in density levels between the patches creates biological dispersal from patch three to patches two and one. This inflow of biomass from patch three into patches one and two supports larger amounts of effort in these patches compared with patch three, which can only support lower levels of

equilibrium effort.   Thus, in this case at least, we find that the equilibrium distribution of effort is more spatially skewed than in the closed case (as is illustrated in Figure 1, Panel A).

Can we say anything about the level of aggregate effort? As it turns out, under these assumptions, the fully integrated system can support higher levels of effort than the closed case. This occurs because biomass flows from areas of low profitability (patch three) to areas of high profitability (patches one and two). Thus the biological dispersal gradient reinforces the economic gradient, creating more potential rents than in the decoupled system and, as a result, drawing and supporting higher levels of aggregate effort.

Consider next the linear cascade case, where the patches are located along a line and the center patch is connected to both outside patches whereas each outside patch is only connected to the center patch. This case differs from the fully integrated case because the two outside patches are not directly connected to each other, and hence it illustrates the importance of "edge effects" in a spatial system. In this case, again the higher population density in patch three generates dispersal from patch three, which can only flow into patch two. Because patches one and two have identical cost-price ratios, they also have identical population densities, and hence there is no dispersal from patch two to patch one in equilibrium. Table 2 shows aggregate equilibrium effort levels for patches one, two, and three for these three biological systems. As can be seen, aggregate equilibrium levels of effort may be equal to, greater than, and less than corresponding levels in the closed case, respectively. Total effort in the cascade system is greater than the level in the closed case, for reasons discussed above, but not as great as in the fully integrated case. This is a spatial Le Chaterlier effect, because the cascade system is more "constrained" by fewer between-patch linkages than the fully integrated case.[4] This implies that potential rents are not as high for the cascade system, and hence a lower amount of aggregate effort is attracted.

Figure 1: Impact of biological linkages on the spatial distribution of effort

Panel A: Fully-Integrated   Panel B: Linear Cascade

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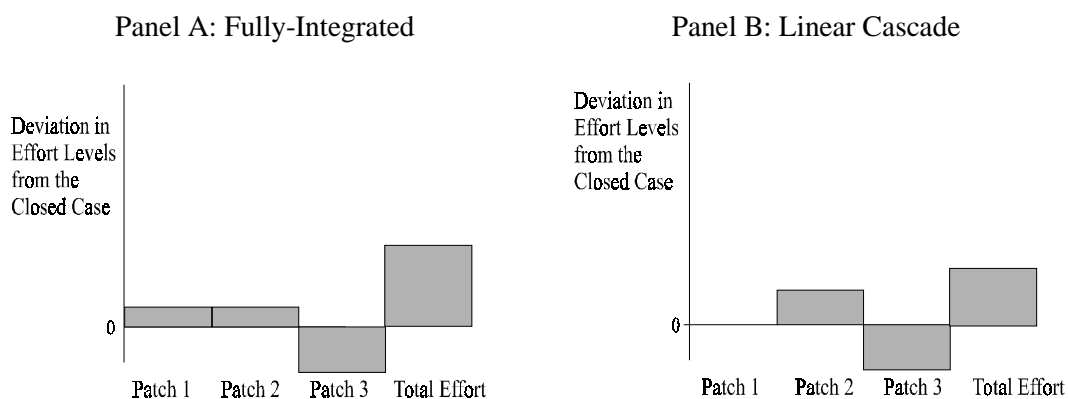
[4] The Le Chaterlier Effect was first introduced into economics by Paul Samuelson (1947). The idea was borrowed from thermodynamics, and the essential point is that the responsiveness of constrained systems to perturbations will

This simple example hints at some of the richness that emerges when we explicitly consider spatial factors in a model of bioeconomic exploitation. In this example, the spatial pattern of effort is driven fundamentally by patch-specific cost-price ratios, but biological spatial linkages and the mechanisms also influence the equilibrium pattern. We summarize the main results on the equilibrium distribution of biomass and effort as follows:

- With a closed structure, the spatial equilibrium of both biomass and effort will reflect the essential heterogeneity in the biological and economic parameters. For example, if all patches have the same biological parameters but different economic parameters, high cost/price patches will have higher biomass densities and lower amounts of effort, other things equal.

- When biological linkages connect patches in a system, dispersal of biomass and effort acts to either homogenize or amplify the density differentials that would exist under a closed system.

- In a linked system, the degree to which the ultimate spatial equilibrium reflects the heterogeneity of the fundamental bioeconomic parameters depends upon the biological and economic gradients. Spatial biological forces can operate in concert with, or against, spatial economic forces and the equilibrium depends upon the respective strengths and spatial directions of the two forces.

Comparisons of Spatial and Intertemporal Dynamics

In this section, we investigate the implications of the biological and economic spatial factors on the transitional dynamics. To do this, we numerically calculate the trajectories for the three-patch system using solvers specifically designed for nonlinear large-scale stiff ordinary differential equations (Shampine and Reichelt [1996]). We continue to use the closed case as a benchmark to which to compare the adjustment paths of the fully integrated and cascade systems. To analyze the effects of the dispersal/linkages on the dynamics of adjustment, we must specify numerical parameter values. On the biological side, we continue to assume that the patches are homogeneous with equal intrinsic growth rates ($r=0.8$) and carrying capacities ($k=10$), and a common dispersal rate proportional to the intrinsic growth rate ($b=0.25r$). We also assume identical catchability coefficients ($q=0.5$), prices ($p=25$), and opportunity costs ($\pi=3$), with patch three harvest costs assumed to be higher than those for patches one and two ($c=3$, $c_3=6$ ($\lambda=2$)). Finally, we assume that the fleet's marginal adjustment rates to spatial rents are equal across the system ($s_{ij}=s^*=0.0004$ for all i,j where i$\neq$j) and that the entry response parameters are also equal across the patches ($s_i=s=0.0055$).

In the examples to follow, we illustrate the transitional paths of effort and biomass in each patch, the net movements of effort between patches, and the net biomass dispersal functions for each patch from a relatively "unexploited" state ($x_i(0)=.5k_i$ and $E_i(0)=.10*[(r_i/q_i)*(1-w_i/k_i)]$ for i=1,2,3) to an open-access equilibrium (see Table 2 for equilibrium levels). The net movement of effort for patch i in any period is defined as: $NM_i(t)=s_{ij}(NR_i(t)-NR_j(t))+s_{ik}(NR_i(t)-NR_k(t))$, where $NM_i(t)>0$ implies movement into patch i and $NM_i(t)<0$ implies movement out of patch i. Similarly, the general net biomass dispersal function is:

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be smaller than the responsiveness of unconstrained systems. In the modeling presented here, the fully integrated system is less constrained than (for example) the linear cascade system.
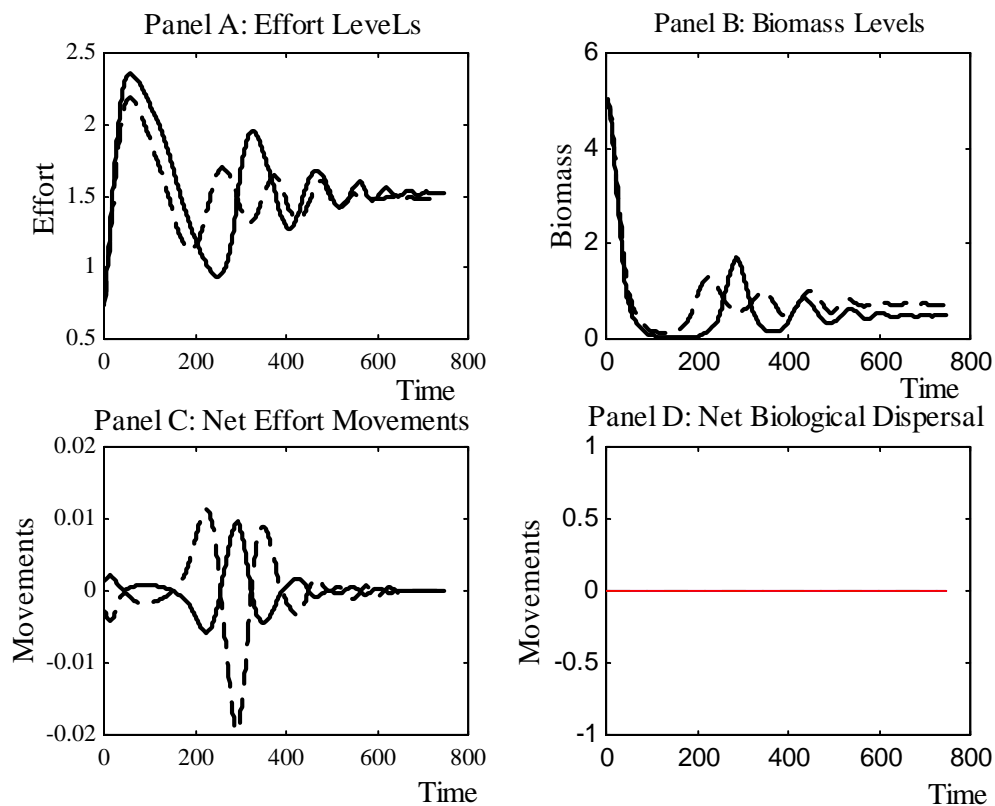
$ND_i(t)=d_{ii}x_i(t)+d_{ij}x_j(t)+d_{ik}x_k(t)$. If the net biomass dispersal function is positive, then biomass is entering patch i from the rest of the system, and if negative, then patch i is acting as a source for the system in that period. Recall that, in equilibrium, net rents are dissipated, implying that the movement of effort both in and out of the fishery and among the patches goes to zero.

The simulations illustrated here are not policy simulations for a particular fishery, nor are the parameters calibrated or estimated using fisheries data. Instead, the simulations are intended to illustrate the possible qualitative effects of economic and biological linkages as determinants of the adjustment to equilibrium. Although this system is reasonably complex and flexible, patterns do emerge that reveal how vessels and populations might co-evolve in a heterogeneous spatial environment (Sanchirico [1998]).

The spatial dynamics of the adjustment period for the *closed* biological system are presented in a series of panels labeled Figure 2. Panels A and B show individual effort/biomass dynamics in each patch. When the fishing pressure begins to increase, effort is drawn into all three patches from an outside pool. Then as biomass is driven down, profits turn negative and system-wide exit occurs. This in turn reduces harvest rates until biomass begins to recover and the second cycle of the convergent oscillatory process begins. In the first phase, effort levels in patches one and two are larger than those in patch three because of higher initial profits. The greater effort levels drive patches one and two to lower stock levels than in patch three. As a consequence, patch three has higher relative net rents and ends up attracting some of the vessels exiting patches one and two (see Figure 3). These cycles of overshoot and undershoot repeat and dampen as the system approaches equilibrium, in which patch three ends up with higher biomass and lower effort than patches one and two because of the assumed differences in costs.

From a whole-system perspective, the patchy model reproduces the results that Vernon Smith [1968; 1969] deduced in his simple single-patch model. However, there are important patch-specific differences in behavior that result in oscillations in the spatial distribution of effort that are not synchronized. For example, although each patch exhibits over- and undershoot, this occurs as a result of the fleet's movement among patches as well as from inflow and outflow to the outside pool. Figure 2 panel C plots the vessels' movements between patches in response to relative rents. The different qualitative spatial cycles illustrated in Figure 2 panel C are decomposed and summarized in Figure 3.[5] In the first cycle of overshoot, patches one and two are relatively more profitable to operate in, due to the variable operating cost assumptions, than patch three, thereby attracting effort from patch three. The combination of attracting effort from patch three simultaneously with the entry from an outside pool of effort compound one another, and, consequently, the level of effort operating in patches one and two increases at faster rate than in patch three. The increase in effort levels is transmitted through the harvest production function into biomass levels, and, consequently, the level of biomass in patch three

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[5] In any period the amount of effort leaving patch i for patch j is: $s_{ij}(NR_i-NR_j)$, where $NR_j>NR_i$. For illustrative purposes, the adjustment period is broken into different phases of vessel movement patterns in which the phases are distinguished by qualitatively different spatial movement. For example, suppose a patch is attracting vessels over one period and then the patch begins to repel vessels over another. In this case, we would characterize the movement pattern with two phases. This means that the phases in one example do not coincide with those in other examples, although the graphs of the levels over time can be used to compare the differences in timing between the phases.

Figure 2: Adjustment paths in a closed biological system

Panel A: Effort LeveLs

Panel B: Biomass Levels

Panel C: Net Effort Movements

Panel D: Net Biological Dispersal

*The solid line represents patches one and two and the dashed line represents patch three.

falls at a slower rate than in patches one and two. In the second phase, patch three, which has remained relatively free from harvest, begins to attract effort from patches one and two. Overall, the spatial movements of effort follow a rotating harvest pattern where vessels fish down a patch and then move on to other areas. This provides an opportunity (albeit temporary) for biomass levels to recover from periods of heavy exploitation.   In the end, however, these phases dampen in the approach to equilibrium, at which point rents are equalized and dissipated and movements both in and out and across the (closed) system are zero.
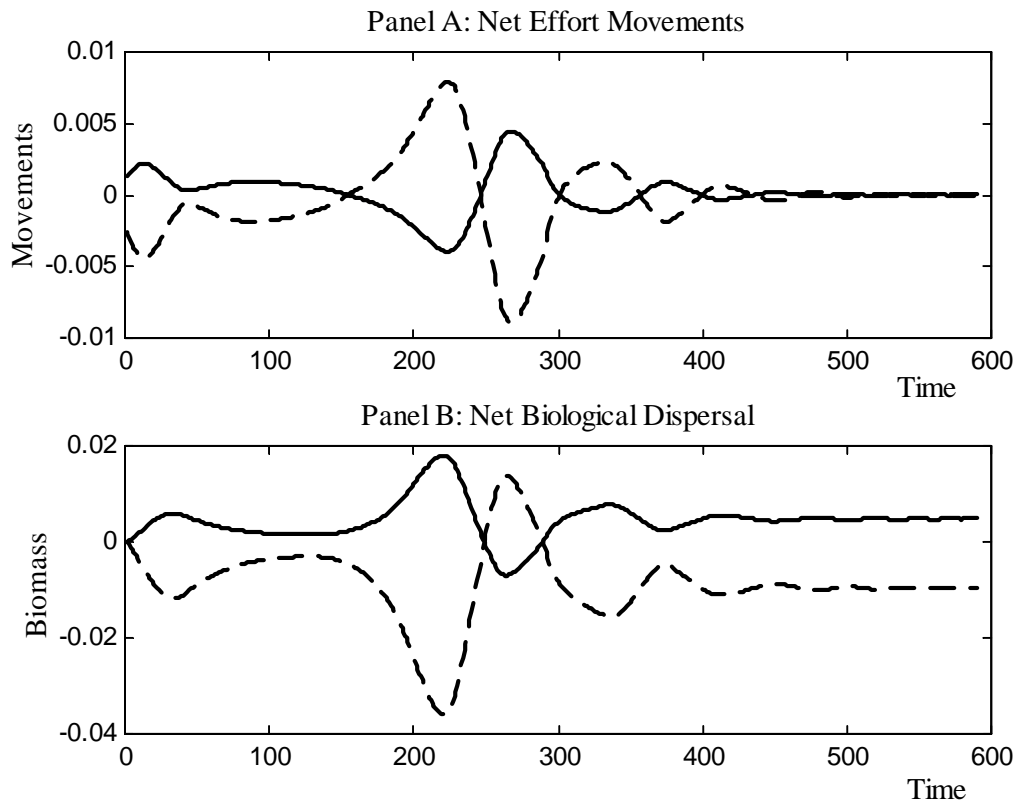
Figure 3: Between-patch fleet dynamics during over- and undershoot phases.
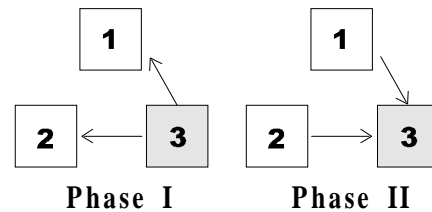
We investigate next, as we did in the previous section, the effects of biological linkages. In general, in the *fully integrated* case, the within-patch cyclical patterns of effort, biomass, and harvest levels are qualitatively similar to those in the closed case. Because of these similarities, we focus here only on the points of departure between the two cases. The first and rather obvious point is that in the fully integrated case there exists biological dispersal between the patches during the approach to equilibrium. Figure 4, panel B, illustrates the manner in which a patch is a net receptor or contributor of biomass in any period, and Figure 5 decomposes this into the individual patch interactions throughout the adjustment period. For example, in the first phase, we find that patch three acts as a temporary de facto source of biomass for both patches one and two because of the lower initial rents from the higher costs per unit of effort. However, as vessels move to patch three, the biomass levels in patches one and two begin to recover. As the biomass recovers in patches one and two, the level in patch three is dropping because of higher effort levels. Consequently, in the second phase patches one and two reverse roles and begin to act as de facto source patches for patch three. As can be seen in Figure 4, panel B, this reversal is short lived, and in the remainder of the adjustment period patch three returns to acting as the de facto source for the system (phase A in Figure 5).

Aside from the obvious effects of biomass dispersal, there are two rather subtle yet fundamental differences between the closed and fully integrated case. First, the magnitudes of the effort movements differ, with lower peaks and troughs witnessed at turning points in the integrated system. Second, the amount of "time" until the system converges to the equilibrium is shorter in the fully integrated than in the closed case.[6] What mechanisms drive these differences? Essentially, the density-dependent movements of the biomass out of patch three into patches one and two reduce the initial differential caused by price-cost ratio differences. This, in turn, reduces the magnitude of the effort dispersal needed to bring net rents into equilibrium. Thus, whereas in the closed case only the fleet can move between areas to bring the economic system into equilibrium, in the fully integrated system, both biomass and effort dispersal are acting and operating in ways that reinforce each other in equalizing biomass densities and rents across the system. This can be seen in Figure 4, panels A and B, where the two processes are essentially smoothing out differences across the system and bringing the whole system closer to the neighborhood of equilibrium earlier than would be the case without biological (density-dependent) dispersal linkages.

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[6] In this example, the ratio of the length of the adjustment period between the cases (fully integrated/closed) is 0.80. Also, note that the length of time until rents are dissipated is a function of the industry's entry/exit response rates (s_i), intrinsic growth rates (r_i), economic and biological dispersal rates (s_{ij} and d_{ij}), and initial conditions.

Figure 4: Movement patterns in the fully integrated case.*

Panel A: Net Effort Movements

Panel B: Net Biological Dispersal

*The solid line represents patches one and two and the dashed line represents patch three.
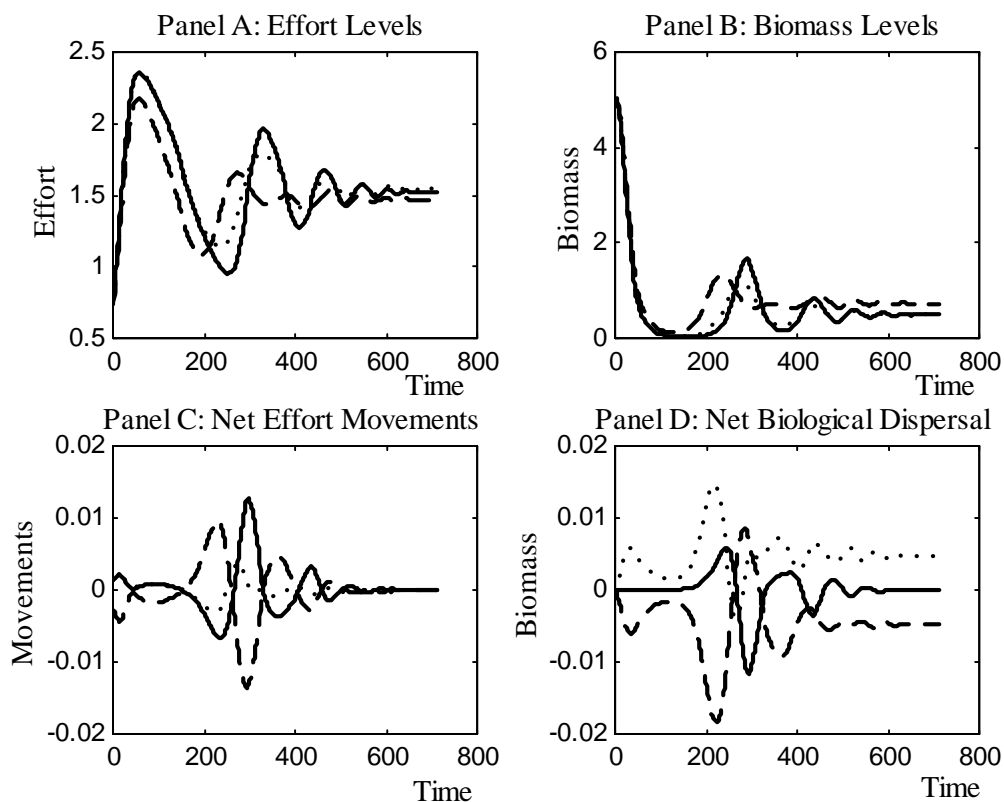
Figure 5: Between-patch biomass dynamics during over- and undershoot phases
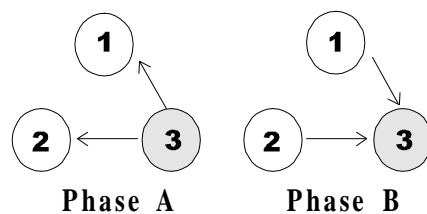
What are the intertemporal implications of the spatial Le Chaterlier effect? In other words, how does the approach path pattern in a system that is more constrained (with fewer linkages) compare to the two extreme cases? The adjustment of the effort and biomass in the *linear cascade* case is illustrated in

Figure 6. The patterns of effort entering the fishery are very similar to the previous cases. After the initial entry phase, however, a divergence between patches one and two emerges that is a result of the biological "edges" in this system.   This is illustrated in Figure 6, panels C and D, and summarized in Figures 7 and 8. It can be seen that the effort and biomass levels in patch two begin to deviate from those in patch one because of the higher profits in patch two resulting from the dispersal of biomass from the adjacent (and high cost) patch three.   In the fully integrated case, biomass leaving patch three is shared equally between patches one and two because the system is fully integrated, resulting in identical industry adjustments between the two patches.

Figure 6: Adjustment paths in the linear cascade system.*

Panel A: Effort Levels

Panel B: Biomass Levels

Panel C: Net Effort Movements

Panel D: Net Biological Dispersal

* The solid line represents patch one, the dotted line represents patch two, and the dashed line represents patch three.

Another interesting feature of this system has to do with the spatial characteristics of the fleet's approach to equilibrium. In this case, there exist five phases in the adjustment process, as illustrated in Figure 6 and detailed in Figure 8.   We find that because of the lack of inflow of biomass via dispersal (Figure 7, phase A), rents in patch one decrease faster than in patch two while at the same time the fishing pressure in patch three is relatively low. As a result, vessels begin to leave patch one for patch two and three. In addition, as a result of the relative lack of exploitation in patch three in phase I, rents are temporarily

higher than in patches one and two, creating incentives for vessels to move back into patch three. As with the closed and fully integrated systems, these cycles of overshoot and undershoot repeat (see Figure 6, panel C) and dampen as the system approaches equilibrium. Unlike the closed and fully integrated systems, however, the existence of a structural asymmetry results in a more complex pattern of biomass and effort over time.

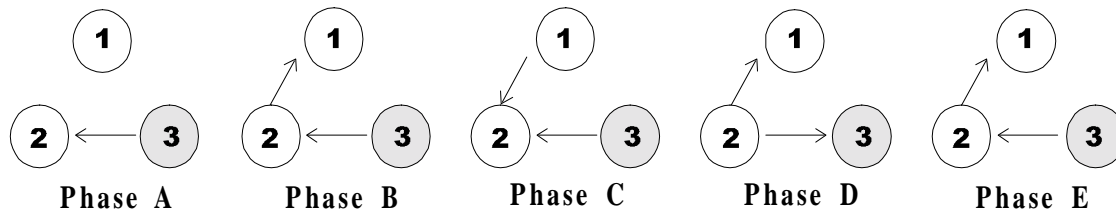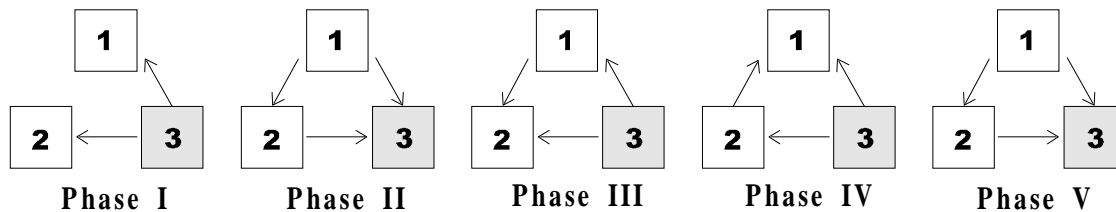**Figure 7: Spatial patterns of biomass movements in the linear cascade system**

Phase A   Phase B   Phase C   Phase D   Phase E

Figure 8: Spatial patterns of fleet movements in the linear cascade system

Phase I   Phase II   Phase III   Phase IV   Phase V

Although the exact nature of the overshoot-undershoot cycles within and across patches and the speeds of adjustments are particular to the set of parameter values and functional forms, the qualitative results from the numerical analysis highlight the effects of linkages on spatial and intertemporal resource exploitation. The various cases discussed above illustrate and highlight different characteristics of biological and economic systems that can be attributed to observed patterns of exploitation. These characteristics are summarized by the following points:

- In the closed case, vessel movement is the only endogenously driven mechanism smoothing out the initial effects of the cost/price heterogeneity and biomass distribution.

- The fully integrated system illustrates how economic and biological dispersal homogenize rent and biomass density differences when both the biological and economic gradients act together to dissipate the dissimilarities across the patches in the system.

- The spatially linear or cascade case illustrates the effects of biological "edges," which can act in complement with or in opposition to the dynamics driven by cost/price and biological heterogeneities. As a result of the asymmetries introduced by edges, this system exhibits more complex spatial and intertemporal behavior than the other systems.

The magnitude and length of the adjustment period depends upon the number and type of the economic and biological linkages in the system. Ceteris paribus, more linkages speed the adjustment process. In

addition, having a system in which the biological gradient operates in tandem with the economic gradient speeds adjustment.[7]

Discussion

The model developed here generalizes traditional bioeconomic models based on assumptions of homogeneous distributions of biomass across space. The biological model is linked to a spatial model of harvester behavior that is economically motivated and endogenous to the spatial distribution of the resource. In this model, rent dissipation is occurring across more than one margin. That is, not only are rents being dissipated by attracting effort from the outside pool, they are also being dissipated by vessels moving back and forth across the system.

While the structure of the model is very flexible and easily adaptable to more complex depictions of the biological and economic systems, we choose to illustrate the model with a very stylized example in order to highlight the effects of incorporating the spatial dimension into traditional bioeconomic models. In previous work, we have investigated the implications of more general net rent functions and done extensive sensitivity analysis on the parameters, and all of the qualitative results still hold (Sanchirico [1998]). Of course, the rates of convergence and the specific movement patterns of the numerical analysis are conditional on our functional form, parameter assumptions, and initial conditions. Even though the qualitative results are in line with the empirical findings, it is unclear if the convergence properties of this model will be reinforced when tested in more complex biological (e.g., discrete space and time logistic model, age/size structure, migration patterns) and economic systems (e.g., transportation costs, informational lags). Whether the functional relationships and relative parameter values used here are reflective of the marine environment, however, is an empirical question and left for further research.

In general, the incorporation of space into the analysis of resource management leads to important insights into how and why patterns of resource exploitation might develop across space and time. For instance, on a fundamental level, biological and economic heterogeneity across space plays a large role in determining spatial distributions of effort and biomass. However, at the same time, linkages via dispersal (both fleet and biomass) can either exacerbate or dampen the influences of heterogeneity depending upon the bioeconomic dispersal mechanisms assumed. In the example presented here, we found that the distribution is more spatially skewed in the presence of linkages with an endogenous density-dependent dispersal process than when the system is biologically closed.

The spatial and intertemporal patterns of exploitation generally depict a Ricardian process in which areas of higher profitability are exploited more intensively earlier. For instance, as the fishery is opened to exploitation, effort flows into each of the patches at a rate proportional to the net rents in the patch and the differences in rents across the systems. As the fishery develops, the most profitable patches have vessels

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[7] For example, we have also analyzed a three-patch sink-source system in which patch three is the source and the high-cost patch and found that the system converges to an equilibrium relatively fast (Sanchirico [1998]). This is because biomass dispersal would flow in the same direction as effort needed to flow to bring both biomass and effort into equilibrium. The same biological system with patch one as the high-cost patch would reach equilibrium more slowly, because the economic gradient would be "pushing" effort in the direction opposite to that driven by the biological gradient.

entering not only from outside the fishery but also from the other, less-profitable areas within the fishery. As a result of the initial periods of high effort and relative overharvesting, the biomass levels in high-profit areas drop faster than in the other patches, and ultimately it becomes more profitable to move to other areas. After some time, the biomass in the area that was initially overharvested begins to recover and vessels return to capture the spatial rents. This process continues in a dampening set of over- and undershoot cycles until, in equilibrium, rents are dissipated and vessels are no longer moving between areas.[8]

An important point highlighted in this paper is that whether or not a patch is acting as a de facto source or sink depends not only on the biological factors but also on the economic conditions *and* the particular phase of the adjustment process. In essence, "sources" and "sinks" in a density-dependent system are intertemporal *bioeconomic* phenomenon. We find, for example, that cost differences in a biologically homogeneous system generate biological dispersal between patches. In this case, conventional mark-recapture tagging might conclude that the high-cost patch is a source and could attribute this to unique biological characteristics when, in fact, biomass movement is fundamentally due to economic factors. In addition, as our example illustrated, a patch can change from a source to a sink in a system because of relative biological and economic gradients, an observation that has implications for spatial management. For example, in choosing a location for a marine reserve, it is possible that what might appear over one period of time to be an unusually biologically productive patch might actually turn out to be a relatively unproductive patch after the patch is closed.

Finally, there are number of implications that can be drawn from this modeling exercise regarding the viability of various spatial management options. First of all, the model suggests that understanding more about the role space plays in a patchy system of resource exploitation is vital to any policy analysis. Of particular importance is the conclusion that we cannot really understand the biological processes operating in an exploited system without knowing as much about the harvesting system as we do about the biological system. This generally calls for much more emphasis on joint bioeconomic modeling and investigations of both economic processes operating over space and time and biological processes. With a better understanding of the implications of space in an exploited system, we can begin to sensibly address the policy questions concerning how spatial management might affect the overall "health" of the fishery, how choices based upon biological and economic heterogeneity might be made, and how biological and economic linkages affect whether or not these policies might prove beneficial.

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[8] We focused here on cases where vessels are free to move between all the patches under various ecological structures from the most restricted (closed) to the least restricted (fully integrated). As a result, the structural asymmetries are only present in the biological system. However, another question to ask is, how do structural asymmetries in the fishing sector affect the spatial and intertemporal bioeconomic patterns? These structural asymmetries in the fishing sector could be the product of the 200-mile exclusive economic zone or institutional rigidities within a state or nation. For instance, if vessel mobility is restricted to a subset of the biological system of patches, then it is possible that this structural asymmetry could result in maintaining the effects of spatial heterogeneity for longer periods of time. These results might be analogous to the closed case above where, instead of the fleet moving about to equalize net rents, the dispersal of biomass would equalize the patch densities.

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